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ORIGINAL ARTICLE

Needle longevity of balsam fir is increased by defoliation by spruce budworm

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Abstract

Key message **Retention of 10–16-year-old balsam fir needles increased significantly with cumulative spruce budworm defoliation. Mean needle longevity on defoliated 50-year-old fir was almost double that for undefoliated 25-year-old fir.**

Abstract Conifers experiencing environmental change affecting photosynthetic capacity have been observed to compensate by adjusting foliage longevity and increasing retention of old foliage. Defoliation by spruce budworm [*Choristoneura fumiferana* (Clem.)] is one such change, therefore, it was hypothesized that conifers, such as balsam fir [*Abies balsamea* (L.) Mill.] may increase foliage life spans to compensate for losses of photosynthetic capacity to defoliation. Understanding foliage longevity is a key component of predicting foliage complement, which is the main driver of effects of defoliation on forest growth and productivity. Defoliation and needle loss were assessed on 16 age classes of foliage on mid-crown branches sampled from 134 mature balsam fir trees near Amqui and Causapscal, Quebec, and related to needle age and cumulative defoliation (summed annual defoliation from 2012 to 2016). A general linear mixed model fitted to the needle survivorship data accounted for 68% of the total deviance. The model interaction term of cumulative defoliation with foliage age indicated that for foliage ages less than about 9 years, increased cumulative defoliation resulted in lower needle survival, possibly because of backfeeding of spruce budworm on 5+-year-old foliage, while in the older age classes, needle survival increased with increasing cumulative defoliation. For the oldest, 11–16-year-old foliage age classes, 10–16% more foliage per age class was retained under severe defoliation than under light defoliation. As a result, median needle age increased from 9.5 to 10.4 years as cumulative defoliation increased from 0 to 500%. Mean needle longevity of 9.5 years for 50-year-old balsam fir with low defoliation observed in this study was considerably higher than the mean of 5.5 years previously observed for 22- to 27-year-old fir in Cape Breton, Nova Scotia. Such differences in needle longevity and retention would cause considerable differences in predictions of tree growth using foliage-based stand growth models.

Keywords *Abies balsamea* · *Choristoneura fumiferana* · Needle retention · Foliage life span · Foliage longevity

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Introduction

Conifers experiencing environmental changes affecting photosynthetic capacity, either positively or negatively, may respond by adjusting their foliage life spans to increase needle retention. For example, shade grown white pine (*Pinus strobus* L.) have twice as long mean foliage life expectancy as those grown in the open (Whitney 1982), and stand spacing, or decreased stand density, increases mean needle life spans of balsam fir by ~1 year (Piene and Fleming 1996). Senescence is a series of complex events, where cells undergo changes to their structure, metabolism, and gene expression over time (Gan and Amasino 1997). There is debate on the topic; however, the main consensus of the primary driving force behind foliage senescence is reallocation of nutrients (Leopold 1978; Chabot and Hicks 1982; Weaver et al. 1998; Woo et al. 2013). Senescence is initiated when the photosynthetic rate of a leaf drops below a certain threshold proposed to be at the point when the costs of the leaf no longer outweigh the benefits, i.e., the leaf does not produce enough carbon (Gan and Amasino 1997).

Spruce budworm (*Choristoneura fumiferana*) defoliation is an environmental change that strongly affects photosynthetic capacity of host trees (Clark 1961), so it would be logical to assume that foliage life spans may vary in response. Repeated annual defoliation results in growth reduction and eventually tree mortality, both of which can exceed 90% in mature balsam fir [*Abies balsamea* (L.) Mill.] stands (e.g., MacLean 1980, 2016). In spaced stands with low defoliation, the mean needle life span of balsam fir was 5.5 years (Fleming and Piene 1992b), and in unspaced, low-defoliated stands, the mean needle life span was 4.7 years (Piene and Fleming 1996). Significant variation in mean needle longevity occurred over 6 years of study, with a range of 4.1–6.1 years, most likely due to weather or long-term cycles in needlefall (Fleming and Piene 1992a). Long-term cycles in needlefall include variation with tree age (Maillette 1982). Species descriptions of balsam fir typically indicate maximum needle longevity of 8 years (Clark 1961; Collingwood and Brush 1984) or 8–10 years (Keeler 1908). Cumulative needlefall of young ($\sim$25 years old) undefoliated balsam fir were divided into three phases: early life (0–1 years old) with $<$10% needlefall per year; mid-life (2–4 years old), characterized by cumulative needlefall of $\sim$10, 15, and 20% in years 2 through 4; and old age ($>$4 years old) with cumulative needlefall of $\sim$35, 45, 50, 55, 65, and 70% in years 5 through 10 (Fleming and Piene 1992a, b). Crown level explained little variation in the rates of age-specific needlefall of balsam fir (Fleming and Piene 1992a, b).

Foliage senescence is relatively constant and predictable under constant environmental conditions (Weaver et al. 1998); however, environmental changes, hormones, and nutrient demands from other plant parts termed “correlative control” can alter its progression (Chabot and Hicks 1982; Gan and Amasino 1997; Weaver et al. 1998; Woo et al. 2013). Adjustments of foliage life spans are possible through changes in gene expression to regulate senescence-associated genes (Weaver et al. 1998; Woo et al. 2013). Changes in senescence-associated gene expressions have been stimulated through the direct addition of hormones (e.g., cytokinin, abscisic acid) and exposure to external stresses (e.g., drought, darkness; Weaver et al. 1998). Under correlative control of senescence, high nutrient demands, especially nitrogen, from other plants parts such as reproductive tissues, can result in the removal of nutrients from older foliage to supply the demanding plant parts, which in turn results in premature senescence of older foliage (Gan and Amasino 1997).

Environmental change encompasses many factors from weather patterns to pathogens, and evergreen trees can compensate for environmental changes through adaptation of foliage life cycles (Chabot and Hicks 1982). Fertilization of Douglas fir [*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco] decreased needle longevity by almost 30% compared to unfertilized trees (Balster and Marshall 2000) because fertilization allowed for increased and efficient growth of new foliage, which resulted in the premature senescence of less productive, older foliage. In contrast, as elevation of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) increased from 2800 to 3200 m, needle longevity increased by 38%, due to a greater need for carbon gain to compensate for lower photosynthetic rates of newer foliage in response to high elevations (Schoettle 1990). Low temperatures, low nutrients, and short growing seasons related to elevation increased needle longevity in Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L.) (Reich et al. 1996).

Spruce budworm is the most damaging insect in North American forests, with a summed area of over 450 million hectares of moderate–severe (30–100%) defoliation of current-year foliage in Canada from 1975 to 2000 (MacLean 2016). Piene (1980) demonstrated that foliar nutrient concentrations (nitrogen, phosphorous, potassium, calcium, and magnesium) of young balsam fir defoliated by spruce budworm were higher, with nearly twice the dry weight than undefoliated trees, and fewer needles on defoliated trees reduces the distribution of nutrients between needles, so that remaining needles may accumulate a larger proportion of available nutrients (Piene 1980). The increase of foliar nutrients in older age classes of needles could extend the life spans of conifer needles during defoliation events. As well, defoliation of recent foliage creates gaps in the canopy, providing greater light penetration to older age classes of foliage, and this has been suggested to increase the photosynthetic capacity of older foliage that would have naturally been shaded out and senesced, ultimately allowing increased life spans of the older foliage (Clark 1961; Baskerville and Kleinschmidt 1981).

Understanding effects of insect defoliation on needle longevity is important in modeling foliage accretion and retention as a component of defoliation-based stand growth models (e.g., Baskerville and Kleinschmidt 1981). No data exist on effects of spruce budworm defoliation on needle retention although there is considerable information about age-specific rates of needlefall and effects of some environmental factors on needlefall. We hypothesized that under increasing cumulative defoliation by spruce budworm, balsam fir would increase foliage life spans of remaining foliage to compensate for losses to their photosynthetic capacity. To test this hypothesis, we measured needle longevity on balsam fir trees selected to have a wide range of defoliation levels near Amqui and Causapscal in the Bas-Saint-Laurent region of Quebec, where defoliation has occurred since 2012 (QMRNF 2011, 2012, 2016). Objectives were to determine: (1) the relationship between needle survival and cumulative spruce budworm defoliation level; and (2) the proportion of cumulative needle loss per foliage age class at a range of cumulative defoliation levels.

Methods

Study area and spruce budworm outbreak

The study area was located near Amqui and Causapscal within the Bas-Saint-Laurent region of Quebec, Canada (47°N and 68°W). The area has an average elevation of 152 m, mean temperature of 4 °C, annual precipitation of 99 cm, May–September rainfall of 48 cm, and annual growing season of ~160 days (Rowe 1972). The study area is in the Great Lakes-Saint Lawrence region (Rowe 1972), Temiscouata-Restigouche area. Forests are characterized by sugar maple [*Acer saccharum* (Marshall)], beech [*Fagus grandifolia* (Ehrh.)], and yellow birch [*Betula alleghaniensis* (Britt)] in the highlands, and balsam fir and white spruce in the valleys (Rowe 1972). Mature conifers (~50 years old), mainly black spruce, white spruce, and balsam fir, dominate the study area.

Annual aerial surveys conducted in the area by Quebec Ministère Ressources Naturelles et de la Faune (QMRNF) from 2011 to 2016 indicated that the initial year of spruce budworm defoliation in the region was 2012, when low (0–30% of current-year foliage removed) and moderate (31–70% of current-year foliage) defoliation levels were first observed; in 2011, no defoliation had been observed. Spruce budworm aerial surveys correlate reddish coloration from insect feeding with percentage foliage consumed (MacLean and MacKinnon 1996). In 2013, defoliation generally remained low to moderate, with some severe (71–100% of current-year foliage) defoliation. In 2014, there was widespread moderate and increased severe defoliation, while in 2015 and 2016, defoliation was moderate to severe in most areas, but subsided to low defoliation in 2016 in some areas.

Plot selection and sampling

In 2014, a network of 75 circular 400 m^2 plots were established in spruce or balsam fir stands, and selected to provide a wide range of defoliation levels (attempting to locate ten plots in each 10% defoliation class for 2014 foliage). In 2016, a subset of 44 of these plots were selected based on balsam fir content and three classes of cumulative defoliation: 22 plots with low (0–150% summed annual defoliation from 2012 to 2016), 11 plots with moderate (151–350%), and 11 plots with severe (351–500%) defoliation were sampled. Plots numbers were selected to achieve required sample sizes of 30 branches with low, 50 branches with moderate, and 41 branches with severe defoliation (sample size calculations discussed below).

Following completion of defoliation, in early August 2016, mid-crown branches were sampled from randomly selected codominant balsam fir trees using pole pruners with the capability to reach >18 m. One mid-crown branch per tree accurately represents current defoliation (±7.6%) and previous defoliation (±6.7%) (MacLean and Lidstone 1982), so one mid-crown branch was sampled from usually three trees per plot until the required branch sample sizes were obtained per defoliation class.

Determination of needlefall and defoliation was performed using the period approach, which uses the age structure of the needle population at a specific point in time to identify rates of needlefall or defoliation (Fleming and Piene 1992a). Spruce budworm feeds strongly preferentially on current-year foliage and will only feed on older foliage if no current foliage remains (Miller 1963). Needlefall and defoliation were measured using the shoot-count method, which is commonly used for estimating spruce budworm defoliation that provides accuracy at ±7% (MacLean and Lidstone 1982). We sampled 25 shoots per age class per branch, if present; average number of shoots sampled was 25 for current to 8-year-old foliage, 20 for 9–10-year-old, 10 for 11-year-old, 5 for 12–15-year-old, and 3 for 16-year-old foliage. Overall sample size was 134 branches and over 32,400 shoots measured.

The percent of needles missing per shoot can be caused by defoliation on shoots where little natural needlefall is expected and defoliation is known to have occurred, or by natural needlefall on shoots where little defoliation has occurred, or by a combination. We estimated defoliation or needlefall per shoot using seven classes (Piene et al. 1981; MacLean and Lidstone 1982: 0, 1–20, 21–40, 41–60, 61–80, 81–99, or 100% needles missing per shoot). Before estimating defoliation, foliage age classes on each branch were identified and labeled, always by the same person, who initially practiced assessing foliage age on a test sample of >40 branches previous to this study. Shoot-count defoliation and needlefall estimates were made on each age class back to year 2000 (16 years old), as no needles were ever found past this age.

Using the measured defoliation per age class, each branch was categorized into low (0–150%), moderate (151–350%), or severe (351–500%) cumulative defoliation, calculated as the sum for all defoliated years, 2012–2016. Evidence that 2012 was the first year of significant defoliation in the plots included: (1) aerial spruce budworm surveys that reported no defoliation in 2011, but light and moderate defoliation beginning in 2012 (QMRNF 2011, 2012); and (2) data collected in the plots during 2014 that showed mean needle loss of 21% on the 2012 (2 years old) and 11% on 2011 (3 years old) foliage age classes, which compared to cumulative proportion of needles fallen on undefoliated trees of 15% for 2-year-old and 25% for 3-year-old needles (Fleming and Piene 1992a). Because our measured defoliation or needlefall exceeded that from undefoliated trees in 2012 and was less than for undefoliated trees in 2011, we believe that needle loss in 2011 was mainly a function of natural needlefall and only minor defoliation, and needlefall in 2012 was primarily due to defoliation. Therefore, throughout this paper, we use the terms 'defoliation' and 'needlefall' to differentiate spruce budworm feeding caused removal of needles on the 0–4-year-old (2012–2016) age classes versus senescence-caused removal of needles on 5–16-year-old age classes.

Within each cumulative defoliation category (low, moderate, and severe), sample sizes of number of shoots per branch were calculated (MacLean and MacKinnon 1998):

$$n = s^2 t^2_{\alpha(2)(n-1)} F_{\beta(1),(n-1,v)} / d^2, \qquad (1)$$

where n is the required sample size; s^2 is the sample variance; $t_{\alpha(2)(n-1)}$ is the two-tailed critical value of Student's t distribution; $F_{\beta(1),(n-1,v)}$ is the one-tailed critical value of the F distribution; and d is the half-width of the confidence interval. The midpoints of each shoot-count defoliation class (0, 10, 30, 50, 70, 90, and 100%) were used in calculations. For each foliage age class (ages 0–16 years, for foliage produced in years 2016–2000) and each cumulative defoliation category (low, moderate, and severe), Eq. 1 was used to calculate the number of shoots required to estimate needle loss (by defoliation or needlefall). Calculations were made at 90% confidence that the 95% confidence interval was ±10%. Sample size calculations were done iteratively, as additional data were accumulated, and produced required sample sizes ranging from 1 to 452 shoots, depending on age class and defoliation level. These were converted into number of branches required based on mean number of shoots per age class. For example, 452 shoots required to determine mean defoliation for 1-year-old foliage divided by 25 shoots sampled per branch = 18 branches required. The maximum number of branches required per age class per defoliation class was used: 30, 50, and 41 branches required for low, moderate, and severe cumulative defoliation classes, respectively.

Data analyses

Mean defoliation (in years 2012–2016) or needlefall (in years 2000–2011) per foliage age class per branch was calculated. Cumulative defoliation was calculated as the sum for the 2012–2016 age classes, but we also tried an alternative calculation weighted by foliage age class (MacLean et al. 2001; MacLean 2016). Generally, R^2 values between needlefall per foliage age class and cumulative defoliation were higher for the summed annual defoliation, so we used that in subsequent analyses. Summed annual defoliation is intuitive as it can be interpreted as each 100% in the sum is equivalent to one age class of foliage removed, i.e., 500% = defoliation of all current foliage from 2012 to 2016.

Foliage survival was calculated as 1 − percent needlefall and analyzed using a generalized linear model with mixed effects in R (R Development Core Team 2016). Hierarchical random effects accounting for Site, Plots within Site, and Trees within Plots were estimated using the glmmPQL() function in R. Survival was modeled as a binomially distributed variable using a logit link (McCullagh and Nelder 1989). The influence of cumulative defoliation on median foliage lifespan was determined by solving the resulting general linear mixed model for foliage age, holding survivor probability at 0.5 across the range of cumulative defoliation of 0–500%. Because the random effects were constrained to have a mean of 0, only the fixed effects were used in solving for median age.

Results

Temporal defoliation patterns per cumulative defoliation class

Temporal annual defoliation patterns of plots in the three cumulative defoliation classes (low 0–150%, moderate 151–350%, and severe 351–500%; equivalent to removal of 0–1.5, 1.5–3.5, or 3.5–5 age classes of foliage) were most variable in the moderate class (Fig. 1). Observed defoliation resulted from a combination of spruce budworm population level and operational aerial biological insecticide (*Bacillus thuringiensis* var. Kurstaki) spraying applied in some plots from 2014 to 2016: in 2014, 38, 23, and 0% of the low, moderate, and severe category plots were sprayed; and in 2015 and 2016, 100, 41, and 0% of low, moderate, and severe category plots were sprayed. We specifically targeted the 134 branches sampled from 44 plots to include insecticide-sprayed areas, as this was the only way to acquire a low defoliation sample in 2015–2016. Plots in the low cumulative defoliation

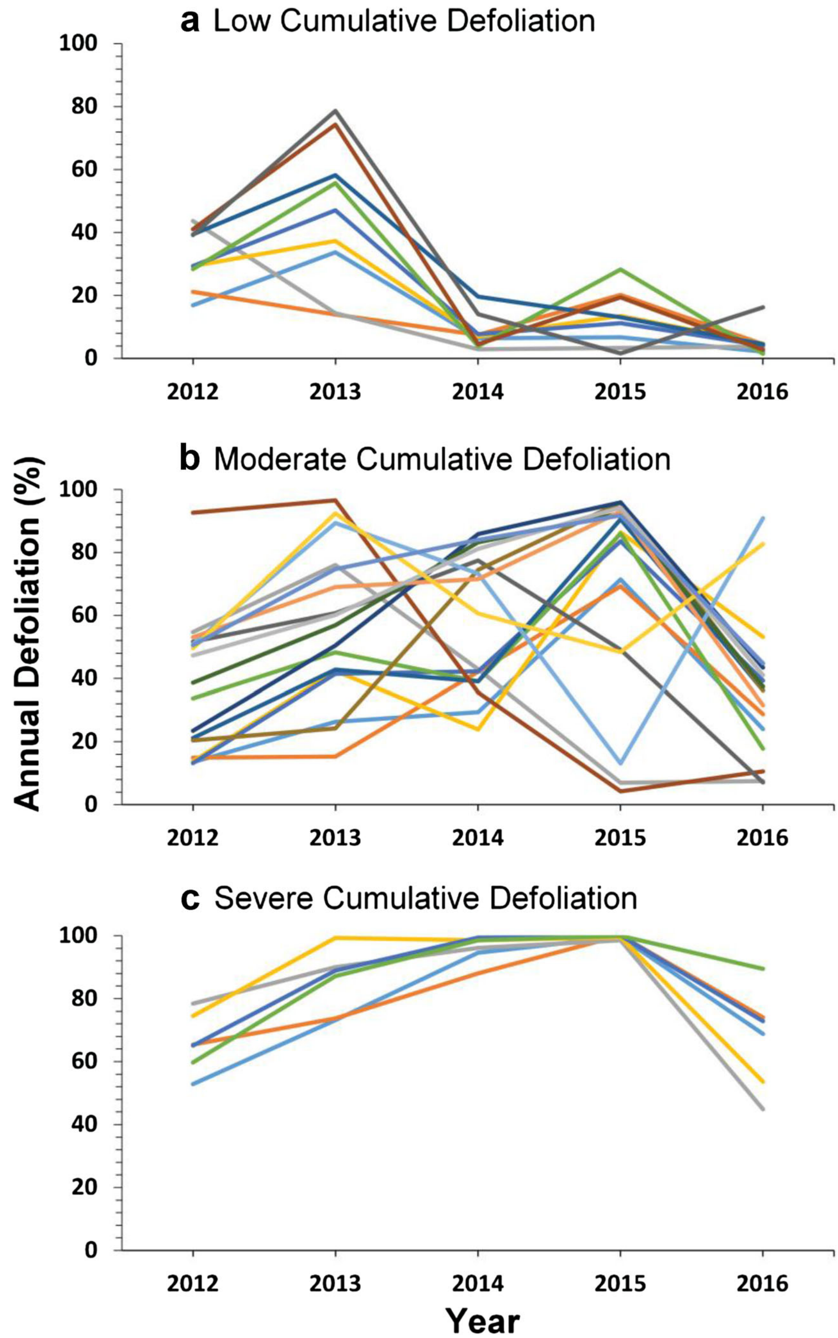
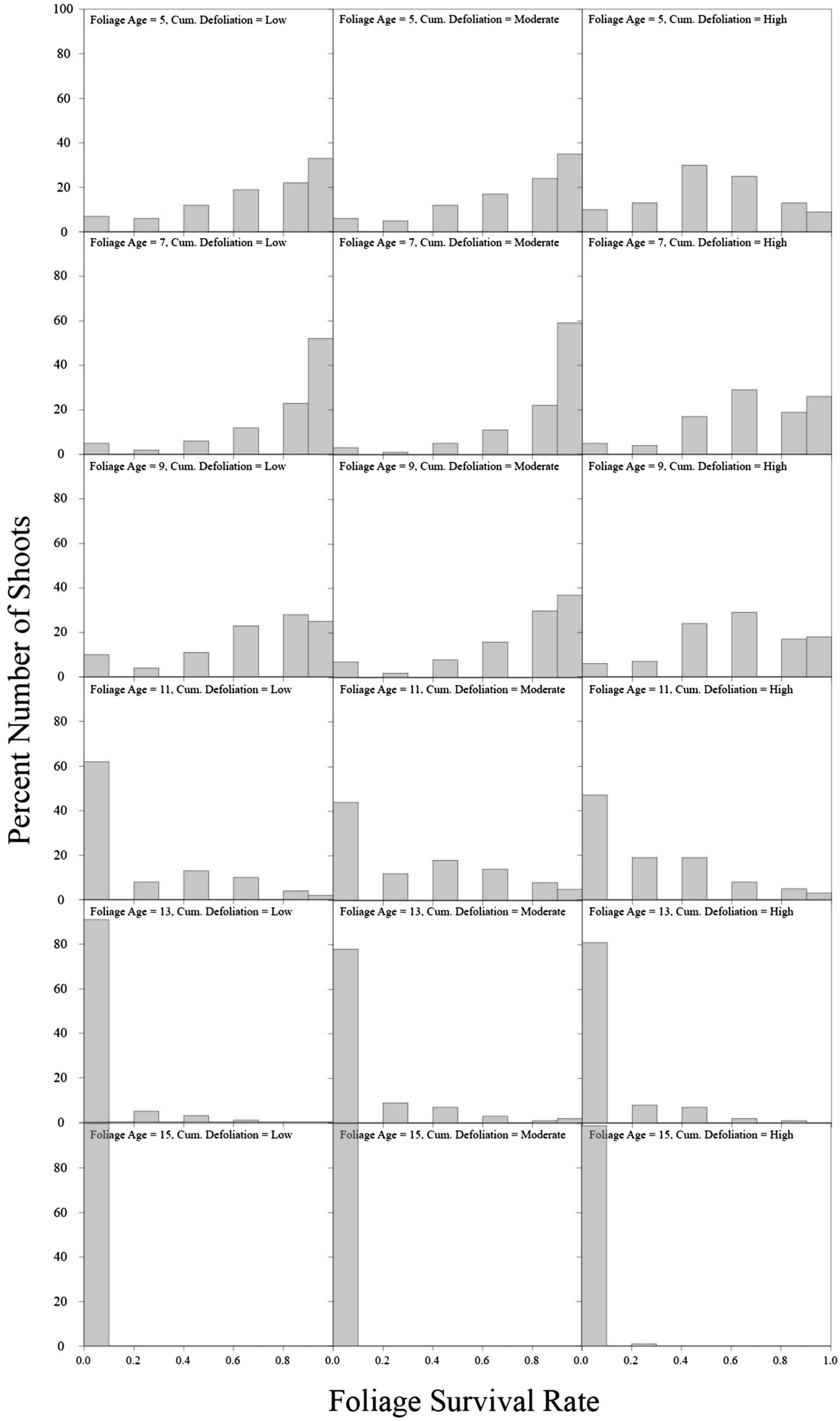


Fig. 1 Current annual defoliation of individual sample plots (each line) from 2012 to 2016, **a** low ($n = 9$), **b** moderate ($n = 17$), and **c** severely ($n = 6$) defoliated plots, representing 0–150, 151–350, and 351–500% cumulative (summed current annual) defoliation, respectively

category generally had increasing current annual defoliation from 2012 to 2013, with 30–80% current defoliation in most plots in 2013, and then low (<30%) annual defoliation from 2014 to 2016 (Fig. 1a). Plots in the moderate cumulative defoliation category had highly variable temporal patterns of spruce budworm defoliation, generally with annual defoliation exceeding 70% in 2015, and reflecting insecticide spraying of 23–41% of plots from 2014 to 2016 (Fig. 1b). Plots in the severe cumulative defoliation category, none of which were sprayed with insecticide, had near complete defoliation of current foliage from 2013 to 2015, and then lower defoliation in 2016 (Fig. 1c). Figure 1 clearly shows that a given cumulative defoliation class can result from alternative temporal patterns over 5 years.

Effect of cumulative defoliation on needlefall

The foliage survival rate of sampled shoots varied widely for foliage age classes 5–11 years, and low, moderate, and high cumulative defoliation classes, but survival was consistently low for 13–15-year-old foliage (Fig. 2). Foliage


Foliage Age = 5, Cum. Defoliation = Low
Foliage Age = 5, Cum. Defoliation = Moderate
Foliage Age = 5, Cum. Defoliation = High
Foliage Age = 7, Cum. Defoliation = Low
Foliage Age = 7, Cum. Defoliation = Moderate
Foliage Age = 7, Cum. Defoliation = High
Foliage Age = 9, Cum. Defoliation = Low
Foliage Age = 9, Cum. Defoliation = Moderate
Foliage Age = 9, Cum. Defoliation = High
Foliage Age = 11, Cum. Defoliation = Low
Foliage Age = 11, Cum. Defoliation = Moderate
Foliage Age = 11, Cum. Defoliation = High
Foliage Age = 13, Cum. Defoliation = Low
Foliage Age = 13, Cum. Defoliation = Moderate
Foliage Age = 13, Cum. Defoliation = High
Foliage Age = 15, Cum. Defoliation = Low
Foliage Age = 15, Cum. Defoliation = Moderate
Foliage Age = 15, Cum. Defoliation = High
Percent Number of Shoots
Foliage Survival Rate
0
20
40
60
80
100
0.0
0.2
0.4
0.6
0.8
1.0

◀**Fig. 2** Relative frequency histogram of needle survival by foliage age class and cumulative defoliation level. Low defoliation was less than 150%, moderate was 150–350%, and high was >350%

age classes 0–4 years were excluded from Fig. 2 because they were directly influenced by defoliation. In the younger foliage age classes (<10 years), needle survivorship decreased slightly with increasing cumulative defoliation (Fig. 2). In the older foliage age classes, survivorship increased slightly as cumulative defoliation increased. By age 11, 45–60% of foliage had died, in comparison with 80–90% of 13-year-old foliage and 100% of 15-year-old foliage (Fig. 2).

The general linear mixed model fitted to the survivor data was:

$$\mathrm{logit(survival)} = \beta_0 + b_{0j} + \beta_1 \mathrm{age} + \beta_2 \mathrm{defoliation} + \beta_3 \mathrm{age} \times \mathrm{defoliation}, \quad (2)$$

where logit() is the logistical transformation ($\ln[p/(1-p)]$), survival = foliage survival probability; age = foliage age class (years); defoliation = cumulative defoliation 2012–2016 (%); β_i's are the fixed effects parameter estimates; and b_{0j}'s are the $N(0, \sigma^2)$ random effects (j denotes the hierarchical nesting—Site, Plot within Site, and Tree within Plot within Site). A summary of the model fit is shown in Table 1. Overall, the model including random effects accounted for approximately 68% of the total deviance with the fixed effects accounting for 37% alone. Site and Tree within Plot within Site both accounted for significant amounts of deviance ($p < 0.05$ based on log-likelihood ratio tests), while Plot within Site did not ($p = 0.69$).

While the main effect for cumulative defoliation (β_2) indicates that needle survival decreases with increasing defoliation, the interaction term with foliage age (β_3) indicates that this trend reverses as foliage age increases (Fig. 3). For foliage ages classes less than about 9 years, increased cumulative defoliation resulted in lower needle

Table 1 Parameter estimates and associated standard errors (in parentheses), standard deviations for hierarchical random effects, and residual standard deviation for the general linear mixed model (Eq. 2) fitted to the needle survival data

Parameter	Estimate
β_0	6.340 (0.1873)
β_1	−0.6506 (0.009904)
β_2	−0.007213 (0.0003533)
β_3	0.0007570 (0.00003180)
$s\ (b_{0,\ \mathrm{Site}})$	0.4921
$s\ (b_{0,\ \mathrm{Plot/Site}})$	0.001706
$s\ (b_{0,\ \mathrm{Tree/Plot/Site}})$	0.6558
s (residual)	0.6361

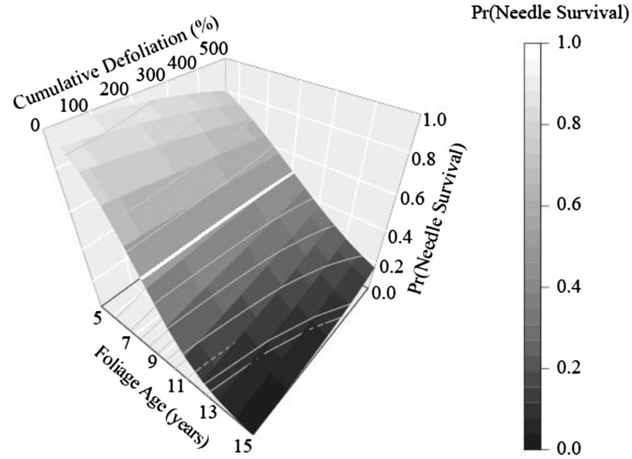


Fig. 3 Surface plot of needle survival based on the fixed effects parameters from Eq. 2. The *thick white line* indicates median foliage age across the range of cumulative defoliation

survival, while in the older age classes, survival increased (Fig. 3). As a result, median needle age increased from 9.5 to 10.4 years as cumulative defoliation increased from 0 to 500%.

Scatter diagrams of needle loss for 5–12-year-old foliage age classes plotted against cumulative defoliation showed wide variability, but consistent and significant trends of reduced needle loss (i.e., increased survival) at intermediate (200–300%) defoliation of 5–12-year-old foliage (Fig. 4). Percentage of variability explained by cubic regressions fit to each age class explained 22–34% of the variability for foliage ages 5–8 years, and 7–15% of the variability for 9–12 years (Fig. 4). Similar relationships fit to the oldest 13–16-year-old foliage age classes (not shown) were not significant.

Proportion of needles fallen as a function of cumulative defoliation

There were large differences in needlefall for a given age class between 50, 300, and 450% cumulative defoliation levels for 10 years and older age classes (Table 2). For these age classes, the cumulative proportion of needles fallen at 450% cumulative defoliation was always lower than that of 50% cumulative defoliation, with differences ranging from 4% at age 10 to 16% at age 13 (Table 2). The most prominent differences were for age classes 11–15 years, with needle retention on average 14% higher for these age classes at 450% cumulative defoliation than at 50%. When comparing 50 and 300% cumulative defoliation levels, the largest differences occurred between ages 11–16, with needle retention 7% lower, on average, at 450% cumulative defoliation than at 50%. Finally, comparing 300 and 450% cumulative defoliation, differences were greatest between ages 12–16 with needle retention on

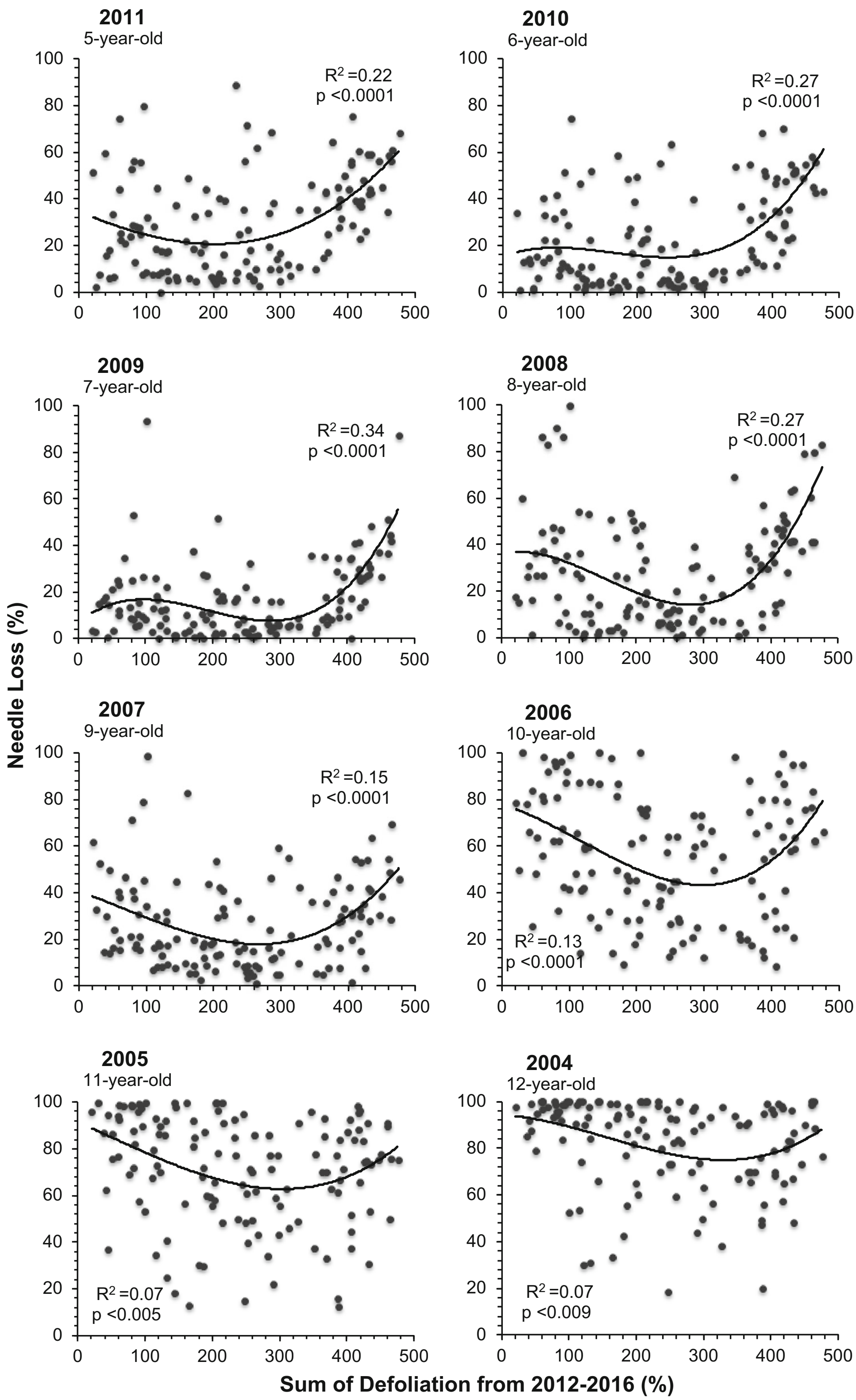


Fig. 4 Variation in mean needle loss of 5- to 12-year-old foliage age classes per branch versus sum of defoliation from 2012 to 2016; 0–4-year-old foliage). The *curves* show cubic relationships fit to each foliage age class

Table 2 Predicted cumulative proportion of needles fallen by age class calculated for six levels of cumulative defoliation, using the generalized linear mixed model shown in Table 1

Age class	Needle loss (%)						Differences between cumulative defoliation levels		
	Cumulative defoliation (%)								
	50	150	250	300	350	450	50/300	50/450	300/450
5	0.05	0.07	0.10	0.11	0.13	0.18	0.06	0.12	0.06
6	0.09	0.12	0.15	0.16	0.18	0.23	0.07	0.13	0.06
7	0.16	0.18	0.21	0.23	0.25	0.28	0.07	0.13	0.05
8	0.25	0.28	0.30	0.31	0.33	0.35	0.06	0.10	0.04
9	0.39	0.40	0.41	0.41	0.41	0.42	0.02	0.04	0.01
10	0.54	0.53	0.52	0.51	0.51	0.50	**−0.02**	**−0.04**	**−0.01**
11	0.68	0.66	0.63	0.62	0.61	0.58	**−0.06**	**−0.10**	**−0.04**
12	0.80	0.77	0.73	0.71	0.69	0.65	**−0.09**	**−0.15**	**−0.06**
13	0.88	0.85	0.81	0.79	0.77	0.72	**−0.09**	**−0.16**	**−0.07**
14	0.93	0.91	0.87	0.85	0.83	0.78	**−0.08**	**−0.15**	**−0.08**
15	0.96	0.94	0.92	0.90	0.88	0.83	**−0.06**	**−0.14**	**−0.07**
16	0.98	0.97	0.95	0.93	0.91	0.87	**−0.05**	**−0.11**	**−0.06**

Differences between the cumulative proportions of needles fallen at 50 and 300, 50 and 450, and 300 and 450% cumulative defoliation levels are shown, where 50, 300, and 450% are equivalent to 0.5, 3, and 4.5 age classes of foliage defoliated over 5 years. Bold values indicate reduced needlefall (or increased needle retention) as a function of defoliation. Needlefall proportion was calculated as 1 − needle survival

average of 7% lower at 450% cumulative defoliation than at 300%. The lack of effect on reduced needle loss on the 5–9-year-old age classes may reflect backfeeding that occurred during the highest defoliation years, 2013–2015 (Fig. 1).

Discussion

Effect of cumulative defoliation on needlefall

The relationship between needlefall or retention and defoliation is complex and influenced by factors including temperature, stand density, water, light, and nutrient availability (Chabot and Hicks 1982). Our results showed significant effects of cumulative defoliation on needlefall, with the model (Eq. 2) including random effects accounting for 68% of the total deviance. Although the main effect for cumulative defoliation (β_2) indicated that needle survival decreased with increasing defoliation, the interaction term with foliage age (β_3) indicated that this trend was reversed as foliage age increased. For foliage ages classes less than about 9 years, increased cumulative defoliation resulted in lower needle survival, while in the older age classes, survival increased. As a result, median needle age increased from 9.5 to 10.4 years as cumulative defoliation increased from 0 to 500%. In contrast, previous results for younger balsam fir trees showed mean needle longevity ranging from only 4.1 to 6.1 years (Fleming and Piene 1992a).

Our results therefore support the hypothesis that increasing cumulative defoliation had a significant effect on needlefall per age class, where needlefall decreased with increased cumulative defoliation for foliage 10 years and older. The surface plot of needle survival based on the fixed effects parameters from Eq. 2 (Fig. 3) showed that the curves of needle survival declined with cumulative defoliation for foliage aged 5–9 years. This was probably because of backfeeding, which occurs during severe defoliation when current shoot presence is low or completely depleted (Miller 1963). When several years of new shoots are completely removed from a tree, spruce budworm must feed on older foliage, which results in defoliation and high needle loss of the older age classes of foliage. However, the surface plot for foliage aged 10–15 years showed that curves of needle survival increased with cumulative defoliation.

Distributions of number of shoots by foliage survival rate indicated lower proportions of shoots with 0–10% survival with high cumulative defoliation than for low cumulative defoliation. At the highest, 400–500% cumulative defoliation of the five most recent age classes, balsam fir is observed to begin to die (MacLean 1980). Therefore, it is highly likely that after ~300% cumulative defoliation, trees enter a "survival mode", allocating scarce nutrients to only crucial tissues and processes which may not be the survival of older age classes of needles, but rather the production of new shoots. New shoot production is critical for tree survival during severe defoliation periods, and epicormic shoot production can more than double (Batzer 1973).

Several site and stand factors have been previously shown to alter the retention of conifer foliage, including elevation (Schoettle 1990), light availability (Whitney 1982), and stand density (Piene and Fleming 1996). Our results suggest that insect defoliation also affects the retention of conifer foliage.

Cumulative proportion of needles fallen by foliage age

Natural needlefall occurs within every age class of needles on a tree, and on young balsam fir, up to 35% of needles on a 4-year-old balsam fir shoot can be lost due to natural needlefall (Fleming and Piene 1992a). Therefore, although we calculated mean defoliation for the 2012–2016 foliage age classes (ages 0–4 years; Fig. 1), this measured defoliation is actually a combination of both defoliation and natural needle loss, especially for the 2012 (4 years old) foliage. According to Fleming and Piene (1992a), 5-year-old needles can have up to 60% cumulative needlefall; however, measured combined defoliation and needlefall for 5-year-old (2011) foliage in our plots was variable, ranging from 5 to 60% among plots, and in many cases was considerably lower than observed by Fleming and Piene (1992a) for young undefoliated fir trees.

Fleming and Piene (1992a) found that cumulative proportion of needlefall on undefoliated young balsam fir was 0.05, 0.15, 0.38, 0.80, 0.95, 0.99, and 1.0 for ages 0, 2, 4, 6, 8, 10, and 12, respectively. In comparison, for older balsam fir our results based on Eq. 2 showed that with low (50%) cumulative defoliation and foliage ages 6, 8, 10, 12, 14, and 16 years, cumulative proportion of needles fallen was 0.09, 0.25, 0.54, and 0.80, 0.93, and 0.98, respectively; for moderate (300%) defoliation, 0.15, 0.30, 0.52, 0.73, 0.87, and 0.95; and for severe (450%) defoliation 0.23, 0.35, 0.50, 0.65, 0.78, and 0.87 (Table 2). Summing differences in needlefall between 50 and 450% cumulative defoliation for the 10–16-year-old age classes amounts to 0.84, equivalent to a total of nearly one additional age class of older foliage retained with severe cumulative defoliation. Fleming and Piene (1992a, b) found that foliage was virtually non-existent past age 9, whereas we had up to 55% of 10-year-old and 22% of 12-year-old foliage remaining with moderate defoliation. Mean needle longevity was 5.5 years for Fleming and Piene (1992a), whereas we found needles generally present up to 14 years of age, and mean needle longevity at 50% cumulative defoliation of 9 years. Median needle age increased from 9.5 years to 10.4 years as cumulative defoliation increased from 0% to 500% in our results. The main difference between the two studies was stand age, $\sim$25 years old for Fleming and Piene (1992a) versus $\sim$50 years old in our study. Older conifers have longer needle longevity (Maillette 1982), and genetic variability between populations (Reich et al. 1995) also could have effects.

Significance of results

Spruce budworm outbreaks have serious consequences on forest productivity. Defoliation reduces the photosynthetic capacity of trees, which reduces growth and causes tree mortality (MacLean 1980). Understanding the dynamics of photosynthetic capacity of trees and stands during spruce budworm outbreaks can improve predictions of future stand growth and survival (Fleming and Piene 1992a) and permit calibration of foliage-based stand growth models. This study aimed to better understand the dynamics of needle longevity at varying levels of spruce budworm defoliation. Understanding how trees adjust foliage lifespans in response to insect defoliation provides information about the foliage remaining and photosynthetic capacity during defoliation periods. This would allow forest managers to better predict stand development and volume growth during outbreak periods, using foliage-based stand growth models designed to predict growth during spruce budworm outbreaks (e.g., Baskerville and Kleinschmidt 1981). Needle biomass per age class is the primary contributor to stand growth in this model, which mimics survival of eight age classes of foliage, as survivorship after 8 years was thought to be negligible (Baskerville and Kleinschmidt 1981). However, our results suggest that needle retention persists much longer than 8 years and is influenced by defoliation and tree age. At foliage ages 8, 10, 12, and 14 years, there was 75, 46, 20, and 7% of foliage remaining on trees with low defoliation, respectively; 69, 49, 29, and 15% remaining on moderately defoliated trees; and 65, 50, 35, and 22% remaining of severely defoliated trees. These results are much different than the 0% remaining foliage after 8 years reported by Baskerville and Kleinschmidt (1981) and indicate that adjustments are needed in growth models dependent on foliage survivorship, depending on tree age and cumulative defoliation level. Even the oldest, 16-year-old age class in our severely defoliated plots retained 13% of the foliage, versus 2% in lightly defoliated plots.

Conclusion

As hypothesized, retention of balsam fir needles increased with increasing cumulative defoliation. A general linear mixed model fitted to the needle survivorship data accounted for 68% of the total deviance. The model interaction term of cumulative defoliation with foliage age indicated that for foliage ages classes less than about 9 years, increased cumulative defoliation resulted in lower needle survival, probably because of backfeeding of spruce budworm on 5–9-year-old foliage. However, for older age classes, needle survival increased with increasing cumulative defoliation by 10–16% per age class for 11–16-year-old foliage. As a result, median needle age increased from 9.5 to 10.4 years as cumulative defoliation increased from 0 to 500%. Mean needle longevity estimates from this study on 50-year-old defoliated balsam fir were almost double those for 25-year-old balsam fir from Fleming and Piene (1992a). Further work could explore causes for these dramatic differences in needle longevity by tree age, and examine relationship to tree, stand, or site characteristics. The results of this study improve our understanding of the role of older balsam fir foliage retention during spruce budworm defoliation, and indicate that foliage-based stand growth models underestimate both foliage longevity and foliage retention increases caused by defoliation.

Author contribution statement DAM did study design and provided plot data, OD did data collection and analyses, JAK did statistical analyses, and all authors contributed to writing.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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