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Forest overstory composition and seedling height influence defoliation of understory regeneration by spruce budworm

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ABSTRACT

Higher hardwood content in stands results in lower defoliation of overstory balsam fir (*Abies balsamea* (L.) Mill.) caused by spruce budworm (*Choristoneura fumiferana* Clem.). To determine whether higher overstory hardwood content also reduced defoliation and mortality of balsam fir regeneration of varying height classes during a spruce budworm outbreak, we sampled 36 plots representing three classes of hardwood content (0–25%, 40–65%, and 75–95%) across a gradient of fir-hardwood stands. Twenty-seven plots were sampled in nine stands near Amqui, Quebec in an early stage spruce budworm outbreak (3 years of defoliation), and nine plots were sampled in three stands in the North Shore of Quebec in a later stage budworm outbreak (7 years of defoliation). Linear mixed-effects models with repeated measures (years) were used to analyze differences in defoliation of fir regeneration as a function of hardwood content, six height classes, and three years (2013, 2014, 2015). In the Amqui plots, defoliation of fir regeneration was significantly related to all factors and interaction terms except for hardwood content, while in the North Shore plots, defoliation was significantly related to all factors and the hardwood content x height class and hardwood content x year interaction terms. Defoliation of balsam fir regeneration was 85% higher in softwood than in hardwood stands in 2013 and 2014 in the North Shore plots, when the budworm outbreak was severe. Defoliation was at least 10% higher on regeneration taller than 30 cm than on smaller regeneration in the Amqui plots in 2015 and over 15% higher in the North Shore plots. In general, balsam fir regeneration in softwood stands had higher levels of defoliation than in hardwood stands when defoliation was severe, and regeneration taller than 30 cm had higher defoliation than smaller regeneration.

1. Introduction

Eastern spruce budworm (*Choristoneura fumiferana* (Clemens)) outbreaks are a major natural disturbance affecting millions of hectares of forest across eastern North America (MacLean, 2004) and recurring every 30–40 years (Royama, 1984; Boulanger and Arseneault, 2004; Royama et al., 2005). Spruce budworm outbreaks play an important role in the landscape dynamics of balsam fir (*Abies balsamea* (L.) Mill.) dominated forests (MacLean, 2004). Budworm larvae feed repeatedly on current-year shoots of balsam fir and spruce (*Picea* sp.), leading to wide-spread growth reduction and mortality (e.g., MacLean and Ostaff, 1989). Following outbreaks, forests are often reoccupied by balsam fir (i.e., cyclic succession) as advanced regeneration in the understory recruits into gap openings created by defoliation and mortality (Baskerville, 1975; Bouchard et al., 2006; Spence and MacLean, 2012; Virgin and MacLean, 2017). However, as overstory foliage becomes sparse with cumulative defoliation during the later stages of an outbreak, larger and heavier budworm larvae, especially in the fifth and sixth instars, may disperse downwards into the understory (Ghent, 1958; Batzer, 1968). In such cases, budworm larvae may feed on advance balsam fir seedlings, potentially altering the direction of succession towards dominance by other tree species (Bouchard et al., 2006; Sainte-Marie et al., 2014).

Although factors that control vulnerability of overstory trees to spruce budworm defoliation are well studied (e.g., MacLean, 1980; Bergeron et al., 1995; Su et al., 1996; Hennigar et al., 2008), less is known about the susceptibility and vulnerability of understory vegetation to budworm attack. This hinders our ability to project stand dynamics and succession following outbreaks.

Factors hypothesized to affect susceptibility and vulnerability of balsam fir regeneration to defoliation and mortality during a spruce budworm outbreak include: (1) intensity of the outbreak, which is influenced by forest overstory composition (e.g., monospecific balsam fir forests versus mixed-species forests); and (2) height of balsam fir

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regeneration in the understory. During an outbreak, defoliation of balsam fir is significantly lower in mixed-species forests that contain a higher relative abundance of non-host overstory species (MacLean, 1980; Bergeron et al., 1995; Su et al., 1996; Campbell et al., 2008). For example, in forests where overstory broadleaf or hardwood species (e.g., *Acer* spp., *Betula* spp., *Populus* spp.) were < 40%, defoliation of overstory balsam fir ranged from 58 to 71%; however, where hardwood content was > 80%, fir defoliation was < 15% (Su et al., 1996). This is thought to result from more abundant or diverse parasitoid populations in mixed stands and/or greater small-larval dispersal losses in stands with nonhost species (Campbell et al., 2008). Also, taller balsam fir regeneration may be more apt to intercept spruce budworm larvae dispersing from the overstory and have higher numbers of larvae feeding on them, thus height of fir regeneration may influence level of budworm defoliation and mortality (Spencer, 1985; Ruel, 1991). For instance, small fir regeneration (< 30 cm in height) had 60% less defoliation than larger ones, with most mortality only occurring in fir taller than 30 cm (Vincent, 1956). Spencer (1985) also noted that 90% of severe defoliation occurred on fir regeneration taller than 30 cm, and fir regeneration taller than 50 cm had approximately 15% more damage than shorter ones (Ruel and Huot, 1993).

Early reports observed that when conifer regeneration was completely overtopped by hardwood tree species, it appeared to protect the regeneration from defoliation (Craighead, 1924; 1925). However, most research on the effect of budworm outbreaks on fir regeneration has been conducted in fir forests (e.g., Vincent, 1956; Spencer, 1985; Ruel and Huot, 1993) and has not determined regeneration response under different overstory compositions. Moreover, although size of overstory balsam fir has been correlated to rates of defoliation and mortality (e.g., Bergeron et al., 1995), most studies have not considered trees < 5 cm DBH.

In this study, we investigated the influence of forest overstory composition and regeneration height on defoliation and mortality from spruce budworm attack. Defoliation of regeneration may differ with timing during a budworm outbreak, as a function of cumulative defoliation of overstory trees, therefore we sampled plots representing both a gradient in balsam fir and hardwood overstory composition and early and late stages of a budworm epidemic. Our objectives were to determine whether (i) overstory hardwood content influenced defoliation and mortality of balsam fir regeneration during a spruce budworm outbreak; and (ii) height of balsam fir regeneration influenced its defoliation and mortality. We hypothesized that (i) balsam fir regeneration will experience lower rates of defoliation and mortality as overstory hardwood content increases, due to reduced budworm population density and the facilitative effects of higher overstory tree diversity; and (ii) taller regeneration will have higher defoliation than shorter regeneration, because their higher, wider crowns are more likely to intercept budworm larvae moving downward from the upper canopy.

2. Methods

2.1. Plot establishment

We established 36 plots representing a wide gradient in overstory hardwood-balsam fir content, with 12 plots selected in each of 0–25%, 40–65%, and 75–95% hardwood, with the remainder balsam fir, representing softwood, mixedwood, and hardwood overstory types, respectively. Plots were sampled in July-August 2015, as clusters of three randomly located 0.05-ha (radius = 12.6 m) plots at least 50 m apart in 12 different stands (Fig. 1). Nine stands (27 plots) were located near Amqui, Quebec, representing an early stage spruce budworm outbreak (3 years of defoliation), and three stands (nine plots) were on the Quebec North Shore, north of Baie Comeau, representing a late stage outbreak (7 years of defoliation) (QMRNF, 2016).

2.2. Regeneration sampling

In each plot, four transects were sampled radiating out from the plot center along northwest, northeast, southeast, and southwest directions. Three 2 m × 2 m quadrats were randomly selected along each transect. In each quadrat, all living and dead regeneration were tallied by species. Balsam fir regeneration were recorded in six height classes: 0–4.9 cm, 5–14.9 cm, 15–29.9 cm, 30–44.9 cm, 45–59.9 cm, > 60 cm and DBH < 4 cm (similar classes used by Spence and MacLean, 2011), in order to address our hypothesis that taller regeneration will have higher defoliation than smaller regeneration).

Ten balsam fir regeneration were randomly selected per height class and plot, and measured for defoliation. One balsam fir per height class was selected per quadrat (if present), and if required, additional trees were selected outside quadrats but inside the plot. After defoliation was complete in 2015, percentage defoliation on each of the 2013, 2014, and 2015 foliage age classes was visually estimated on each of 25 annual shoots per age class per regeneration, using seven defoliation classes (0, 1–20, 21–40, 41–60, 61–80, 81–99, or 100%). Because spruce budworm only feeds on the current year shoots unless populations are very high, level of defoliation assessed on previous year shoots provides a good approximation of that year's level of defoliation (Graham, 1935; Blais, 1952). Defoliation of each sampled balsam fir was calculated for each foliage age class (year) using the midpoints of defoliation classes of all 25 sampled shoots. Mean defoliation was then calculated per plot, height class, and year.

To determine whether differences in defoliation of balsam fir regeneration with height were caused by different spruce budworm densities, we measured number of larvae per regeneration on five balsam fir sampled from the two tallest height classes (45–60 cm and > 60 cm), randomly located outside each plot. Each sampled balsam fir was cut at the base, measured for height, and the number of spruce budworm larvae by life stage (instar) was determined.

2.3. Data analyses

Because defoliation level, tree condition, and dispersal behavior of spruce budworm larvae all differ with outbreak severity and duration of the outbreak (Miller, 1975), we conducted separate analyses for the Amqui (3 years of outbreak) and North Shore (7 years of outbreak) plots. In order to characterize the tree regeneration present across the sampled plots, density of regeneration of the main species present was plotted against overstory hardwood content gradient, and simple linear regressions were conducted to determine strength of relationships. To measure the relationship between balsam fir regeneration vulnerability to SBW-caused mortality versus overstory hardwood content, we also conducted simple linear regressions between the density of living and dead fir regeneration and hardwood content.

We used linear mixed-effects models with repeated measures to test for effects of hardwood content, regeneration height, and year of defoliation (foliage age class) on defoliation of balsam fir regeneration, within each of the Amqui and North Shore sets of plots. Mean defoliation was the response variable, fixed factors were percent hardwood content (a continuous explanatory variable), height class and year (categorical explanatory variables), and their interaction terms. Random factors were plots nested within stands and stands. A serial correlation structure CorAr1 was included in the model error term to control for temporal autocorrelation. Our null hypothesis was that no differences in defoliation would be detected at the 0.05 significance level between stands with different hardwood content and between different regeneration height classes and years. Post hoc Tukey's HSD tests were used to test for significant differences in defoliation of balsam fir regeneration between height classes and years, with hardwood content fixed, within the sets of Amqui and North Shore plots. T-tests were used to determine significance of best fitted line coefficients in each height class and year.

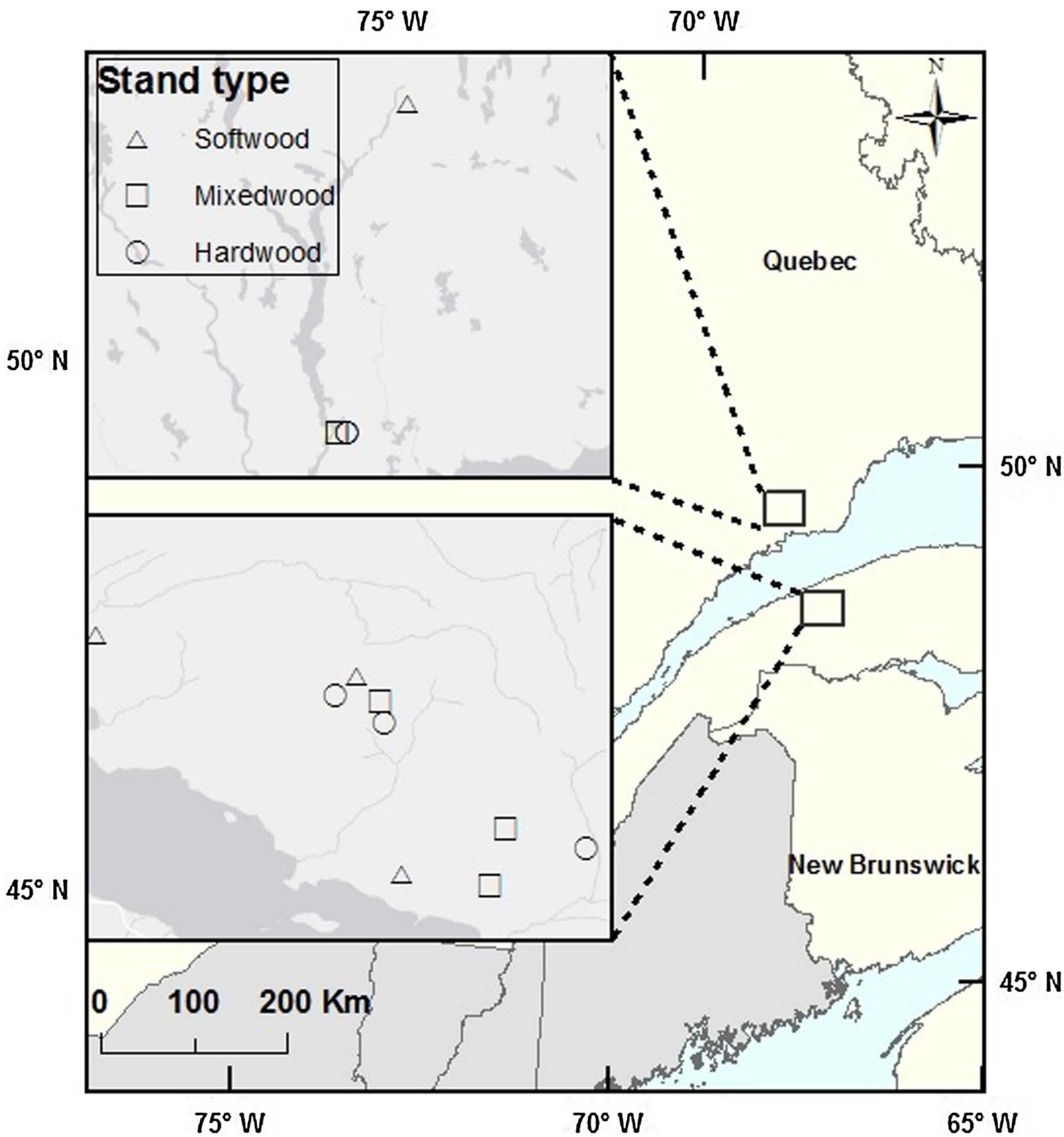

Fig. 1. Location of the study area: nine stands (27 plots) were sampled near Amqui, Quebec, and three stands (nine plots) were sampled in the North Shore of St. Lawrence River area, north of Baie Comeau.

ANCOVA and post hoc Tukey's HSD tests were used to test for significant differences between stand types. We also conducted t-tests of the best fitted line coefficients to determine whether height of balsam fir regeneration affected density of spruce budworm larvae present. This was done to explore the reason why regeneration height may influence defoliation levels in different stand types.

All data analyses were conducted using R 3.3.1 (R Development Core Team, 2016). The "nlme" package (Pinheiro et al., 2017) was used to run linear mixed-effects model analyses; "stats" package (R Development Core Team, 2016) for simple linear regression, *t*-test, and ANCOVA analyses; and "lsmeans" package (Lenth, 2016) for post hoc Tukey's HSD tests.

3. Results

3.1. Regeneration composition, density, and mortality

Sampling plots across the hardwood gradient resulted in trends of regeneration composition with overstory hardwood content (Fig. 2). For the 27 plots near Amqui, balsam fir regeneration density declined and sugar maple (*Acer saccharum* Marsh.) density increased with increasing overstory hardwood content (Fig. 2A). Balsam fir regeneration density averaged 26,430, 8240, and 3900 stems ha^{-1} in classes categorized as softwood, mixedwood, and hardwood (0–25%, 40–65%, and 75–95% overstory hardwood, respectively) (Fig. 2A). Sugar maple regeneration density ranged from 5000 to 7500 stems ha^{-1} for plots with < 50% hardwood, but was prolific with 15,000–93,000 stems ha^{-1} for plots with > 50% hardwood. Density of the third major regeneration species present, red maple (*Acer rubrum* L.), was not significantly related to hardwood content (Fig. 2A).

The North Shore plots differed from the Amqui plots in having lower overall regeneration density, less hardwood regeneration, and more shade-intolerant hardwood species instead of sugar maple (Fig. 2B). There was also substantial dead balsam fir regeneration present. In the North Shore plots, there were averages of 12,000, 5500, and 2000 stems/ha of dead fir regeneration in the softwood, mixedwood, and hardwood plots (Fig. 2B). These plots were in the seventh year of the budworm outbreak, and had annual overstory defoliation of balsam fir > 70% for 7 successive years since 2009 (QMRNF, 2016). Proportions of dead fir regeneration were 24%, 26%, and 17% in softwood,

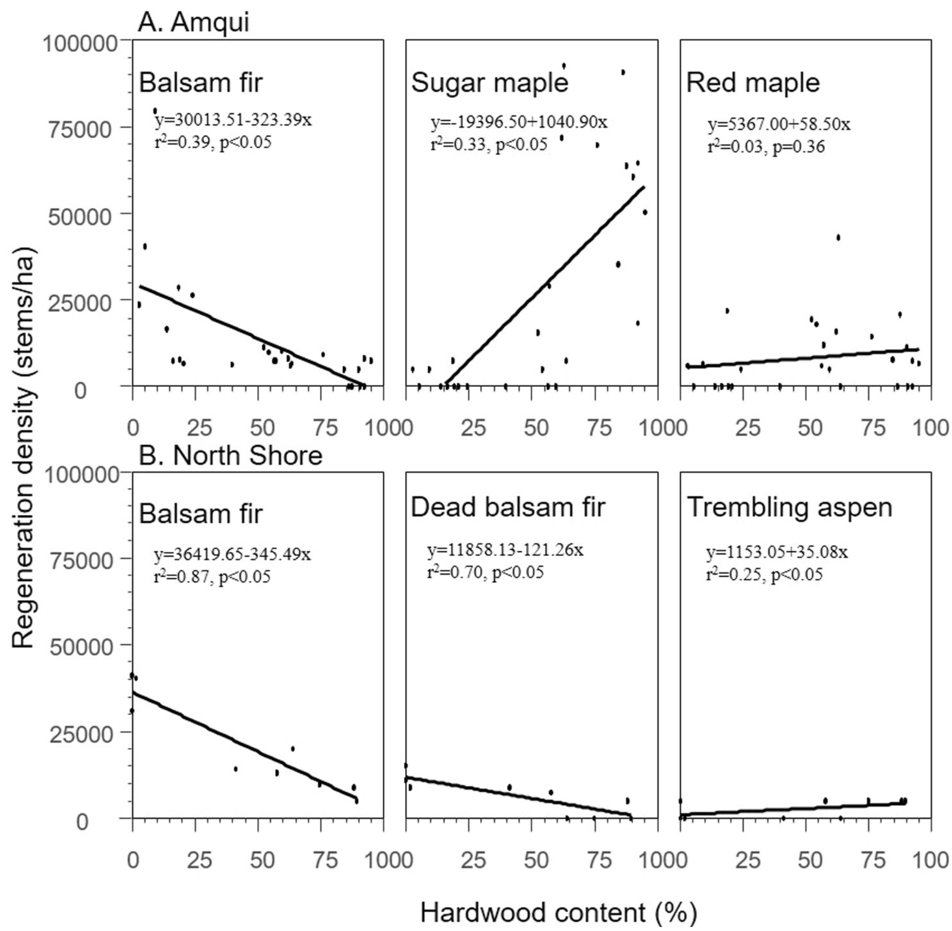

Fig. 2. Regeneration density of the main merchantable species and of dead balsam fir in A. 27 plots near Amqui and B. nine plots in the North Shore, representing two stages of spruce budworm outbreak and a hardwood content gradient.

mixedwood, and hardwood plots, respectively (Fig. 2B). The proportion of dead fir regeneration decreased with hardwood content but the relationship was not significant. Both dead and living balsam fir regeneration density were significantly, negatively related to hardwood content ($r^2 = 0.70$–0.87; Fig. 2B). Trembling aspen (*Populus tremuloides* Michx.) regeneration ranged from 0 to 5000 stems/ha, and was significantly, positively related to overstory hardwood content (Fig. 2B).

3.2. Effects of hardwood content and height on defoliation of balsam fir regeneration

Defoliation of balsam fir regeneration was substantially higher in the North Shore balsam fir dominated plots (< 25% hardwood) than in any of the Amqui plots (Fig. 3). Linear mixed-effect model results showed that in both Amqui and North Shore plots, defoliation differed significantly with hardwood content, height class, and year (Table 1). There were significant interaction terms in all cases for the Amqui plots and for hardwood x height class and hardwood x year for the North Shore plots, which suggest that the relationship between defoliation level and overstory hardwood content differed significantly between years and height classes (Table 1). Post hoc Tukey's HSD tests showed that, for most regeneration height classes, defoliation was not significantly different between the three years for the Amqui plots (Table 2A, Fig. 3A), while defoliation was significantly higher in 2013 and 2014 than in 2015 for the North Shore plots (Table 2B, Fig. 3B). These reflect differences in stage of the budworm outbreak, with Amqui in the third year of defoliation and North Shore in the seventh year of defoliation, with declining spruce budworm populations.

Post hoc Tukey's HSD tests showed that defoliation of fir regeneration > 30 cm was significantly greater than smaller regeneration in the Amqui plots in 2013 (Table 2A, Fig. 3A) and in all three years in the North Shore plots (Table 2B, Fig. 3B). Defoliation of regeneration > 15 cm was significantly greater than smaller regeneration in 2015 in the Amqui plots (Table 2A, Fig. 3A). Defoliation of fir regeneration > 30 cm tall in the Amqui plots increased significantly with overstory hardwood content in 2013 and 2014 (Fig. 3A; asterisks indicate significance of relationships), albeit at low defoliation levels (< 20%), while defoliation of fir regeneration < 30 cm tall was not significantly related to hardwood content (Fig. 3A). In 2015, regeneration > 15 cm tall in the Amqui plots had significant higher defoliation than in 2013 or 2014 (Table 2A, Fig. 3A), and slope of the defoliation versus hardwood content relationship was negative (Fig. 3A), while regeneration < 15 cm had no significant relationship with hardwood content (Fig. 3A).

In the North Shore plots in 2013 and 2014, when spruce budworm populations and defoliation were high, defoliation of all balsam fir regeneration height classes was significantly negatively related to hardwood content (Fig. 3B). However, in 2015, when defoliation was lower, only regeneration 30–60 cm tall had significant negative relationships between defoliation and hardwood content (Fig. 3B). Defoliation of regeneration in the North Shore plots showed strong negative relationships with hardwood content in 2013 and 2014, but relationships had lower slope in 2015 (Fig. 3B).

For balsam fir regeneration taller than 30 cm, defoliation in 2015 in the Amqui plots and in all years in the North Shore plots decreased with increasing hardwood content (Fig. 3). However in 2015, only balsam fir regeneration 30–60 cm tall in the North Shore plots had a significant decreasing relationship with hardwood content (Fig. 3B). Defoliation averaged 10%, 9%, and 7% among regeneration > 60 cm tall in softwood, mixedwood, and hardwood Amqui plots (Fig. 3A), versus 28%, 11%, and 14% among regeneration > 30 cm in the North Shore plots (Fig. 3B). In the North Shore plots in 2013 and 2014, the only

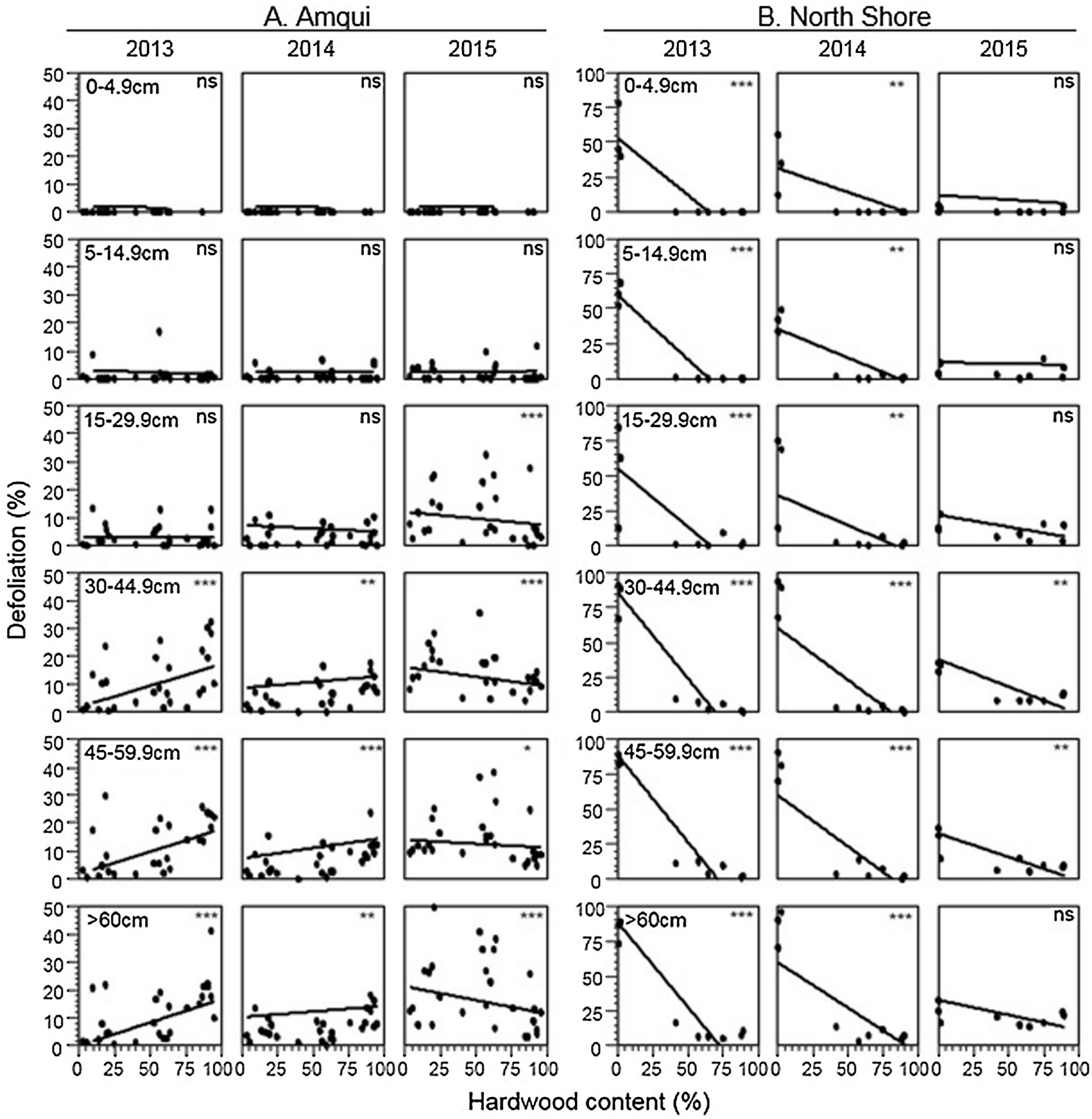

Fig. 3. Mean defoliation per plot of current-year foliage in 2013, 2014, and 2015 in six regeneration height classes plotted against overstory hardwood content in A. 27 plots near Amqui after 3 years of spruce budworm outbreak, and B. 9 plots on the North Shore after 7 years of budworm outbreak. Best fitted lines used fitted values from results of the linear mixed model analysis. Significance of best fitted lines are indicated by ns not significant, and *, **, or *** for $p < 0.05$, < 0.01, < 0.001.

significant differences in defoliation between height classes were between < 30 cm versus > 30 cm tall (Table 2B). In these years, when budworm population levels were highest, even small seedlings (0–15 cm) sustained high (40–75%) defoliation (Fig. 3B). Spruce budworm larvae strongly prefer to feed on current-year foliage and will only back-feed on older age-classes of foliage when all current-year foliage is consumed (Miller, 1963). Defoliation never reached 100% in the sampled regeneration (Fig. 3, although it did reach 80–97% on > 30 cm tall seedlings in the North Shore plots in 2013 and 2014. Therefore, defoliation sampled on the three foliage age-classes (2013–2015) during 2015 can be attributed to current-year feeding.

3.3. Spruce budworm larval density by balsam fir regeneration height

Density of spruce budworm larvae per individual balsam fir regeneration increased with regeneration height and decreased with increasing stand hardwood content (Fig. 4). The ANCOVA and post hoc Tukey's HSD test results showed that density of spruce budworm larvae per regeneration was significantly higher in softwood than in mixedwood and hardwood stands ($p < 0.05$), and larvae density in hardwood stands was significantly lower than in softwood and mixedwood stands ($p < 0.05$). Height of fir regeneration had a significant effect ($p < 0.001$) on spruce budworm density on regeneration in all stand types (Fig. 4). Best fitted line equations fit against regeneration height for each hardwood content class predicted that balsam fir regeneration 50 cm and 100 cm tall would have budworm densities of 2.9 and 7.4 larvae/regeneration in softwood, 1.7 and 5.2 larvae/regeneration in mixedwood, and 1.4 and 2.4 larvae/regeneration in hardwood stands. Therefore, results in the previous section showing that defoliation of fir regeneration decreased with overstory hardwood content and increased with regeneration height both reflect differences in budworm density.

Table 1
Results of a linear mixed model with repeated measures for differences in spruce budworm defoliation of balsam fir regeneration in the Amqui and North Shore plots, as a function of hardwood content, six height classes, and three years (2013, 2014, 2015). Significant factors ($p < 0.05$) are shown in bold font.

Source	d.f.	X^2	P
	Amqui		
Hardwood content	1	1.55	0.213
Height class	5	291.86	**< 0.001**
Year	2	82.17	**< 0.001**
Hardwood content × Height class	5	13.79	**0.017**
Hardwood content × Year	2	40.19	**< 0.001**
Height class × Year	10	49.03	**< 0.001**
Hardwood content × Height class × Year	10	25.77	**0.004**
	North Shore		
Hardwood content	1	4.45	**0.035**
Height class	5	102.98	**< 0.001**
Year	2	72.06	**< 0.001**
Hardwood content × Height class	5	58.44	**< 0.001**
Hardwood content × Year	2	250.85	**< 0.001**
Height class × Year	10	4.82	0.903
Hardwood content × Height class × Year	10	14.52	0.151

Table 2
Compact letters display showing results of Tukey's HSD tests of differences in defoliation of balsam fir regeneration, within the sets of Amqui and North Shore plots, following the linear mixed model analysis. Different letters indicate significant differences ($p < 0.05$) in defoliation among regeneration height classes and years.

	Height class (cm)					
Year	0–5	5–15	15–30	30–45	45–60	> 60
A. Amqui						
2015	a	abc	de	ef	ef	f
2014	a	ab	abc	cd	bcd	bcd
2013	a	ab	abc	de	de	de
B. North Shore						
2015	a	ab	abc	d	d	def
2014	bcd	cd	d	efgh	efgh	gh
2013	cd	de	deg	fh	fh	h

4. Discussion

Our results generally support the hypotheses that (i) balsam fir regeneration had more defoliation (and mortality) in stands with low overstory hardwood content, at least under high defoliation levels; and (ii) taller regeneration had more defoliation than smaller regeneration.

In the North Shore plots, defoliation of balsam fir regeneration was very high in 2013 and 2014, with nearly all current-year foliage consumed in the softwood plots. In both of these years, defoliation of fir regeneration of all height classes was strongly negatively related to overstory hardwood content, supporting our hypothesis. In contrast, defoliation of larger regeneration in the Amqui plots (> 30 cm in 2013 and 2014) was positively related to hardwood content, but only at low defoliation levels, generally < 20%. This result was counter to our hypothesis and might reflect higher dispersal of larvae from overstory fir trees in hardwood stands, which ended up on regeneration if they were unable to locate another overstory fir tree. However, in 2015, as outbreak severity increased to conditions of low-moderate overstory defoliation, defoliation of regeneration in the Amqui plots showed a marginal, negative relationship with overstory hardwood content. Research on plant neighborhood effects on defoliation of overstory balsam fir and black spruce near our North Shore plots (Bognounou et al., 2017) showed that there was a positive relationship between balsam fir defoliation and its conspecific neighbor dominance in balsam fir-dominated and mixed stands, as predicted by the resource concentration hypothesis. Resource concentration effects on balsam fir became stronger in balsam fir-dominated stands from 2006 to 2010, until overstory foliage resources were highly depleted (Bognounou et al., 2017). This could explain why balsam fir regeneration had more defoliation in softwood stands in the North Shore plots, later in the budworm outbreak.

Among the strongest and most consistent relationships observed in our study were higher spruce budworm larval density and higher defoliation with increased regeneration height. This may occur because, first, smaller regeneration might be covered by taller balsam fir regeneration; and second, larger balsam fir regeneration have larger crowns, and therefore budworm larvae have an increased probability of dropping on to them. More budworm larvae per regeneration is likely to result in higher defoliation (e.g., MacLean et al., 1996; Nealis and Régnière, 2004).

Level of defoliation of balsam fir regeneration is also likely related to overstory spruce budworm population and defoliation levels. In the North Shore sites, which represented the later stages of an outbreak (7 years of defoliation), defoliation of fir overstory trees in the softwood plots was > 80% in 2013 and 2014. Following consumption of most current-year foliage, budworm larvae likely dispersed downwards to obtain new food resources (Ghent, 1958; Batzer, 1968). This may have

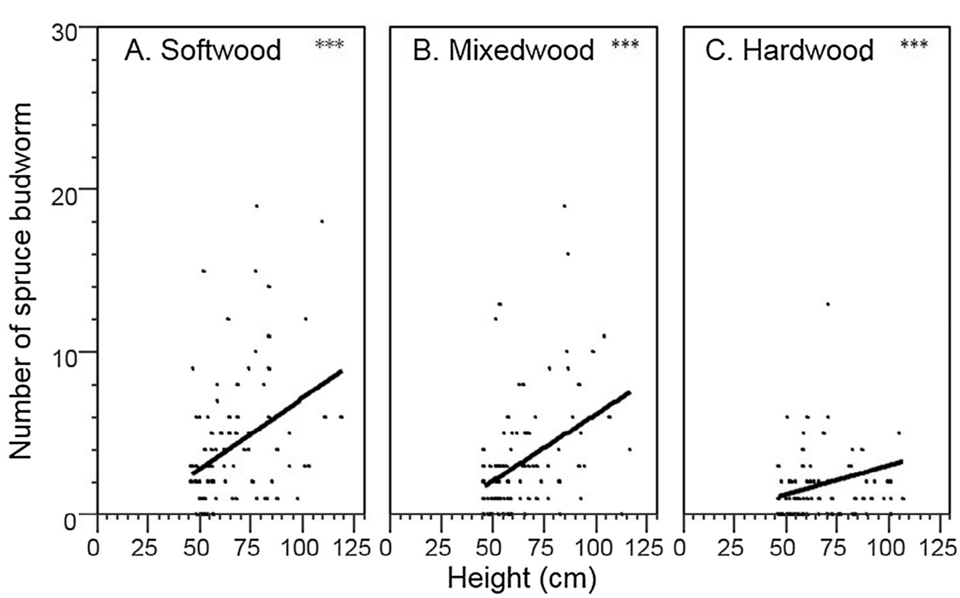

Fig. 4. Number of spruce budworm larvae (fourth to sixth instar) per balsam fir regeneration versus height, for three balsam fir-hardwood content classes. Best fitted lines used fitted values from results of ANCOVA. Significance of best fitted lines are indicated by ns not significant, and *, **, or *** for $p < 0.05, < 0.01, < 0.001$.

caused the observed high defoliation of smaller regeneration (< 30 cm) in the North Shore plots. In contrast, the Amqui plots, which represent an early stage outbreak (3 years of defoliation) sustained only light (generally < 30%) defoliation of regeneration. Outbreak duration was also observed to influence defoliation and mortality caused by western spruce budworm (*Choristoneura occidentalis* Freeman), where after at least 5 years of outbreak, 15% of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) regeneration had severe defoliation (up to 92%) and 5% of the severely defoliated regeneration died (Ferguson, 1988).

Overstory balsam fir mortality only occurs following multiple years of severe defoliation (e.g., MacLean, 1980), and by 2015, mortality of regeneration had only occurred in the North Shore plots. Averages of 12,000, 5500, and 2000 stems ha^{-1} of dead fir regeneration occurred in the softwood, mixedwood, and hardwood North Shore plots, representing 17–26% of the fir regeneration present. Such mortality of fir regeneration caused by budworm defoliation is relatively uncommon, except in cases of high spruce budworm population levels or spill-over from overstory trees (MacLean, 1985). Indeed, only 0.9% of fir regeneration died due to budworm defoliation in plots sampled in Ontario during the 1950s outbreak (Ghent et al., 1957). Even in the severe 1970 s–1980 s outbreak on Cape Breton Island, Nova Scotia, direct defoliation-caused mortality was low (Spence and MacLean, 2012). Our findings also showed higher mortality of fir regeneration in the softwood and mixedwood (24–26%) than in the hardwood (17%) North Shore plots. However, in contrast, Turner (1952), who studied a 1946 outbreak in Ontario, showed that during the outbreak, fir in the understory of high hardwood content stands had 20% higher mortality than in softwood stands (Turner, 1952). Swaine (1933) observed that when fir seedlings in the understory were shaded by overstory trees, mortality of regeneration occurred when the regeneration had only 50% defoliation, while under open-grown conditions regeneration could survive with up to 75% defoliation. When fir regeneration is taller than 30 cm, it can quickly respond to a canopy opening during an outbreak and have up to a 45% higher survival rate than smaller regeneration (Spence and MacLean, 2012). However, our results showed that fir regeneration taller than 30 cm had severe (up to 80%) defoliation during the peak of the outbreak and most dead regeneration were in these height classes. Competition with other understory plants or increased exposure due to low canopy closure may also contribute to mortality of balsam fir regeneration during an outbreak (Batzer and Popp, 1985; Kneeshaw and Bergeron, 1999). How spruce budworm defoliation, competition with other plants, and canopy closure interact and affect growth and survival of balsam fir regeneration remains unclear and requires further study.

5. Conclusions

Our results demonstrated significant and interacting effects of overstory hardwood content and regeneration height on defoliation of balsam fir regeneration caused by spruce budworm. Defoliation of fir regeneration was significantly higher in softwood than in hardwood stands, especially under a severe spruce budworm outbreak. Continued high defoliation levels resulted in 17–26% mortality of fir regeneration, reflecting the severity of the budworm outbreak in the North Shore plots. Regeneration > 30 cm tall generally had higher defoliation than smaller regeneration, but regeneration in all height classes had high defoliation levels during severe outbreak years. Stand succession in balsam fir and mixedwood stands damaged by spruce budworm is determined by growth and survival of existing balsam fir regeneration but also by hardwood regeneration that typically proliferates following canopy opening caused by defoliation (e.g., Kneeshaw and Bergeron, 1999; Bouchard et al., 2006; Spence and MacLean, 2012). Our results showed that most fir regeneration can survive even severe defoliation, taller regeneration will sustain higher defoliation levels, and defoliation of regeneration depends upon both overstory species composition and outbreak severity. These results increase our ability to project regeneration, stand dynamics, and succession following spruce budworm outbreaks.

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