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Disentangling variables that influence growth response of balsam fir regeneration during a spruce budworm outbreak

Zhuoyi Nie[a], David A. MacLean[a,*], Anthony R. Taylor[b]

[a] University of New Brunswick, Faculty of Forestry and Environmental Management, P.O. Box 4400, Fredericton, NB E3B 5A3, Canada
[b] Natural Resources Canada, Canadian Forest Service – Atlantic Forestry Centre, P.O. Box 4000, Fredericton, NB E3B 5P7, Canada

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ABSTRACT

Height increment of balsam fir (*Abies balsamea* (L.) Mill.) regeneration during a spruce budworm (*Choristoneura fumiferana* Clem.) outbreak can be affected by a variety of variables including defoliation, ground vegetation competition, canopy openness, the height of regeneration, and stand type. To disentangle how these variables interact to determine regeneration height increment, we sampled 36 plots in two regions showing contrasting climate, regional vegetation, and budworm outbreak severity. Linear mixed-effects models were used to analyze the effects of these five variables on height increment of balsam fir regeneration. In the Amqui (early defoliation) plots, height increment was significantly affected by a "cumulative defoliation × height of regeneration × hardwood content" interaction. Defoliation significantly reduced height increment when regeneration was > 30 cm tall in softwood and mixedwood plots, but regeneration < 30 cm tall in softwood and mixedwood plots and all regeneration in hardwood plots had light defoliation, which did not reduce height increment. Results were even more complex for the North Shore (late defoliation) plots, where there were three significant 3-way interactions affecting height increment: "height × hardwood content × ground vegetation cover", "hardwood content × canopy openness × cumulative defoliation", and "hardwood content × ground vegetation cover × cumulative defoliation". Canopy openness was > 25% in all softwood plots, and height increment substantially declined with increasing cumulative defoliation; however, in mixedwood and hardwood plots, canopy openness was < 25% and height increment increased with defoliation. In softwood plots, height increment declined sharply with increasing cumulative defoliation at all ground vegetation cover levels, but in mixedwood and hardwood plots, height increment increased or decreased slightly with increasing cumulative defoliation. Results showed that the variables affecting height increment have surprisingly complex interactive effects.

1. Introduction

Spruce budworm (*Choristoneura fumiferana* (Clemens)) outbreaks are an important driver of forest dynamics in eastern Canada (e.g., MacLean, 2004), affecting millions of hectares of forest every 30–40 years (Royama, 1984; Boulanger and Arseneault, 2004; Royama et al., 2005). During an outbreak, spruce budworm larvae feed on current-year shoots of balsam fir (*Abies balsamea* (L.) Mill.) and spruce (*Picea* sp.) and reduce growth and increase mortality of overstory trees across large tracts of forests (MacLean and Ostaff, 1989). Although the effects of spruce budworm infestations on the growth and mortality of mature, overstory trees are well documented (e.g., MacLean, 1980, 2016; Bergeron et al., 1995; Bouchard et al., 2006), much less is known about how outbreaks affect the dynamics of understory seedlings and saplings (i.e., regeneration), which can hinder our ability to project stand succession following outbreaks. Defoliation level, overstory canopy openness, and competition with other ground vegetation are considered important in influencing the growth response of balsam fir regeneration to budworm defoliation (Piene and Little, 1990; Morin, 1994; Kneeshaw and Bergeron, 1999) but no studies have investigated the interacting effects of these variables during a spruce budworm outbreak.

Using a manual defoliation experiment, Piene and Little (1990) showed that when balsam fir regeneration was subjected to 66% and 90% annual defoliation for 3 years, annual height increment in year 3 was reduced by 12% and 60%, respectively. However, few studies have directly observed the effect of defoliation on height increment under natural forest conditions, where the level of defoliation varies according

* Corresponding author.
E-mail address: macleand@unb.ca (D.A. MacLean).

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to severity of the spruce budworm outbreak and height of balsam fir regeneration (Nie et al., 2018). Indeed, balsam fir regeneration had 60% more cumulative defoliation in a severe outbreak (after 7 years of defoliation) than after 3 years of defoliation, and regeneration > 30 cm tall had at least 10% more defoliation than shorter regeneration (Nie et al., 2018), which may differentially affect height increment. The effects of defoliation of regeneration also vary with overstory hardwood content because during a severe outbreak, balsam fir regeneration can have up to 85% more defoliation in softwood stands than in hardwood stands (Nie et al., 2018).

Defoliation and mortality of overstory trees from spruce budworm outbreaks create extensive gaps in the overstory canopy, permitting more light to reach the forest understory (Kneeshaw and Bergeron, 1999). Height increment of advance balsam fir regeneration increased in such gaps (Baskerville, 1975; MacLean, 1988; Morin, 1994), with some studies showing balsam fir regeneration more than doubling its height increment when > 80% of overstory trees were killed by spruce budworm attack (Ghent, 1958; Batzer and Popp, 1985; Matthias et al., 2003). But this positive effect may vary with overstory hardwood content, because with high (> 80%) hardwood content, defoliation of overstory balsam fir was < 15%, while with hardwood content < 40%, the defoliation of fir was 58–71% (Su et al., 1996). The height increment response of balsam fir regeneration to overstory canopy openness also depends on the height of regeneration; for example, when regeneration was > 45 cm tall, height increment was 2 cm/year greater than that of shorter fir regeneration (Spence and MacLean, 2012).

Increased openness in the forest overstory caused by a spruce budworm outbreak may also negatively affect balsam fir regeneration, due to higher competition for light and growing space from invading shrub and herbaceous species (Fye and Thomas, 1963; Batzer and Popp, 1985; Kneeshaw and Bergeron, 1999). Shrub species, such as raspberry (*Rubus* sp.), hazel (*Corylus cornuta*), and mountain maple (*Acer spicatum*) compete strongly with balsam fir regeneration for site resources (Cornett et al., 1997; Rossi and Morin, 2011). Mountain maple and pin cherry (*Prunus pensylvanica*) have also been shown to suppress balsam fir regeneration in mixed hardwood-balsam fir stands (hereafter termed mixedwoods) (Reyes and Kneeshaw, 2008). However, level of competition from competing shrubs, herbaceous plants, and other regeneration may be related to regeneration height. For example, fir regeneration < 30 cm tall were less likely to successfully compete against shrubs for resources, while regeneration > 30 cm tall were more likely to overcome competing vegetation (Baskerville, 1961). Although we know of no direct published evidence for the competitive effects of herbaceous species on height increment of balsam fir regeneration, herbaceous plants reduced height increment of eastern hemlock (*Tsuga Canadensis*), where areas containing high herbaceous competition had 22 fewer stems/m^2 (Maguire and Forman, 1983).

In order to address the gaps in knowledge of previous research, in this paper we investigate the individual and interacting effects of five variables influencing the response of balsam fir regeneration to spruce budworm outbreaks. More specifically, we quantified the effects of cumulative defoliation, canopy openness, ground vegetation cover, regeneration height, and overstory hardwood content on height increment of balsam fir regeneration in 36 forest plots with light to severe defoliation. Plots were sampled across a gradient in balsam fir-hardwood overstory composition because previous studies have shown that overstory defoliation and mortality and regeneration defoliation vary with hardwood content (MacLean, 1980; Bergeron et al., 1995; Su et al., 1996; Nie et al., 2018). We tested four hypotheses: (1) taller balsam fir regeneration will experience a greater negative effect of defoliation on height increment than shorter regeneration because taller regeneration will sustain higher levels of defoliation (i.e., there will be a significant "height × defoliation" interactive effect); (2a) increased canopy openness will release balsam fir regeneration (especially tall balsam fir regeneration), resulting in increased height increment, because canopy openness allows more light to reach the forest understory, or alternatively (2b) contrary to the previous hypothesis, increased canopy openness would reduce height increment of balsam fir regeneration because greater light availability in the understory also promotes understory shrub and herbaceous species growth, which would increase competition for site resources; (3) with similar canopy openness, high ground vegetation cover would have a greater negative effect on height increment of shorter balsam fir regeneration than of taller regeneration, because shorter regeneration is more affected by understory competition; and (4) increasing hardwood content (across the gradient of balsam fir-hardwood stands) will result in lower defoliation of balsam fir, which in turn will result in lower overstory canopy openness and ground vegetation competition.

2. Methods

2.1. Plot establishment and sampling

The same plots were used in this study as in Nie et al. (2018). Twenty-seven plots (three in each of nine stands) were located near Amqui, Quebec, representing light to moderate annual defoliation of overstory balsam fir (3 years of defoliation; termed 'early defoliation' plots), and nine plots (three in each of three stands) were located on the Quebec North Shore, north of Baie Comeau, representing moderate to severe annual defoliation (7 years of defoliation; termed 'late defoliation') (QMRNF, 2016). Stand locations are shown in Nie et al. (2018). All plots were selected to represent a gradient in overstory hardwood-balsam fir content, with 12 plots in each of 0–25%, 40–65%, and 75–95% hardwood, with the remainder balsam fir, representing softwood, mixedwood, and hardwood overstory types, respectively (Zhang et al., 2018). Percentage hardwood was used as a continuous variable in analyses to represent forest type. Plots were sampled in July-August 2015, as clusters of three randomly located circular 0.05-ha plots at least 50 m apart in 12 different stands (Zhang et al., 2018).

Four transects were selected in each plot, radiating out from the plot center along northwest, northeast, southeast, and southwest directions. Three 2 m × 2 m quadrats were randomly located along each transect, for 12 quadrats per plot. In each 4-m^2 quadrat, we tallied regeneration by species and by 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) (Spence and MacLean, 2011). For simplicity, in this paper, height classes will be shown as 0–5, 5–15, 15–30, 30–45, 45–60, and > 60 cm.

To determine how spruce budworm defoliation directly affects height increment, 10 balsam fir regeneration stems (seedlings and saplings) per height class per plot were sampled. One regeneration stem per height class was selected in each quadrat (if present), and if necessary, additional regeneration stems were randomly selected outside the quadrats but inside the plot. Height increment in 2015 (cm/year), determined as the inter-whorl distance of the leader, and percentage defoliation of the 2013, 2014, and 2015 age-classes of foliage were measured on each sampled balsam fir regeneration stem (Nie et al., 2018). All data were collected in 2015 after defoliation was complete. Defoliation was visually estimated on each of 25 annual shoots per sampled balsam fir regeneration stem per foliage age class (3 years of defoliation), using seven defoliation classes (0%, 1–20%, 21–40%, 41–60%, 61–80%, 81–99%, 100%). Because spruce budworm backfeed on previous year's foliage only after all current year foliage has been consumed (Graham, 1935; Blais, 1952), the level of defoliation assessed on the 2014 and 2013 shoots provided an approximation of the level of defoliation in those years. Midpoints of defoliation classes of the 25 sampled shoots were used to calculate mean defoliation of each foliage age class per sampled regeneration stem. We summed the mean current defoliation from 2013 to 2015 per stem to calculate cumulative defoliation, because cumulative defoliation influences growth more than annual defoliation (Ostaff and MacLean, 1995; MacLean et al., 1996).

To determine canopy openness, we used hemispherical (fisheye) photography to measure the canopy cover percentage in each plot. A

Table 1
Mean, standard error (SE) and range of cumulative defoliation of regeneration (%), canopy openness (%), and ground vegetation cover (%) sampled in softwood (0–25% hardwood), mixedwood (40–65% hardwood), and hardwood (75–95% hardwood) stand types in A. Amqui (27 early defoliation plots), and B. North Shore (9 late defoliation plots) study areas.

	Softwood			Mixedwood			Hardwood		
Variable	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
A. Amqui									
Cumulative defoliation	19.5	1.1	0.0–154.8	23.8	1.2	0.0–135.0	26.9	1.4	0.0–180.0
Canopy openness	19.7	0.8	11.9–33.7	16.4	1.1	8.3–34.7	11.1	0.4	7.1–16.2
Ground vegetation cover	27.8	1.9	0.2–99.8	54.2	2.4	1.2–146.5	81.5	2.2	39.0–169.0
B. North Shore									
Cumulative defoliation	153.0	5.4	0.0–269.6	14.9	2.1	0.0–220.4	16.6	1.9	0.0–165.0
Canopy openness	37.8	2.7	25.3–53.9	10.4	1.0	4.9–18.2	11.9	0.6	8.8–14.0
Ground vegetation cover	36.8	5.1	0.3–127.1	25.9	1.9	0.8–65.3	45.4	3.8	2.7–124.0

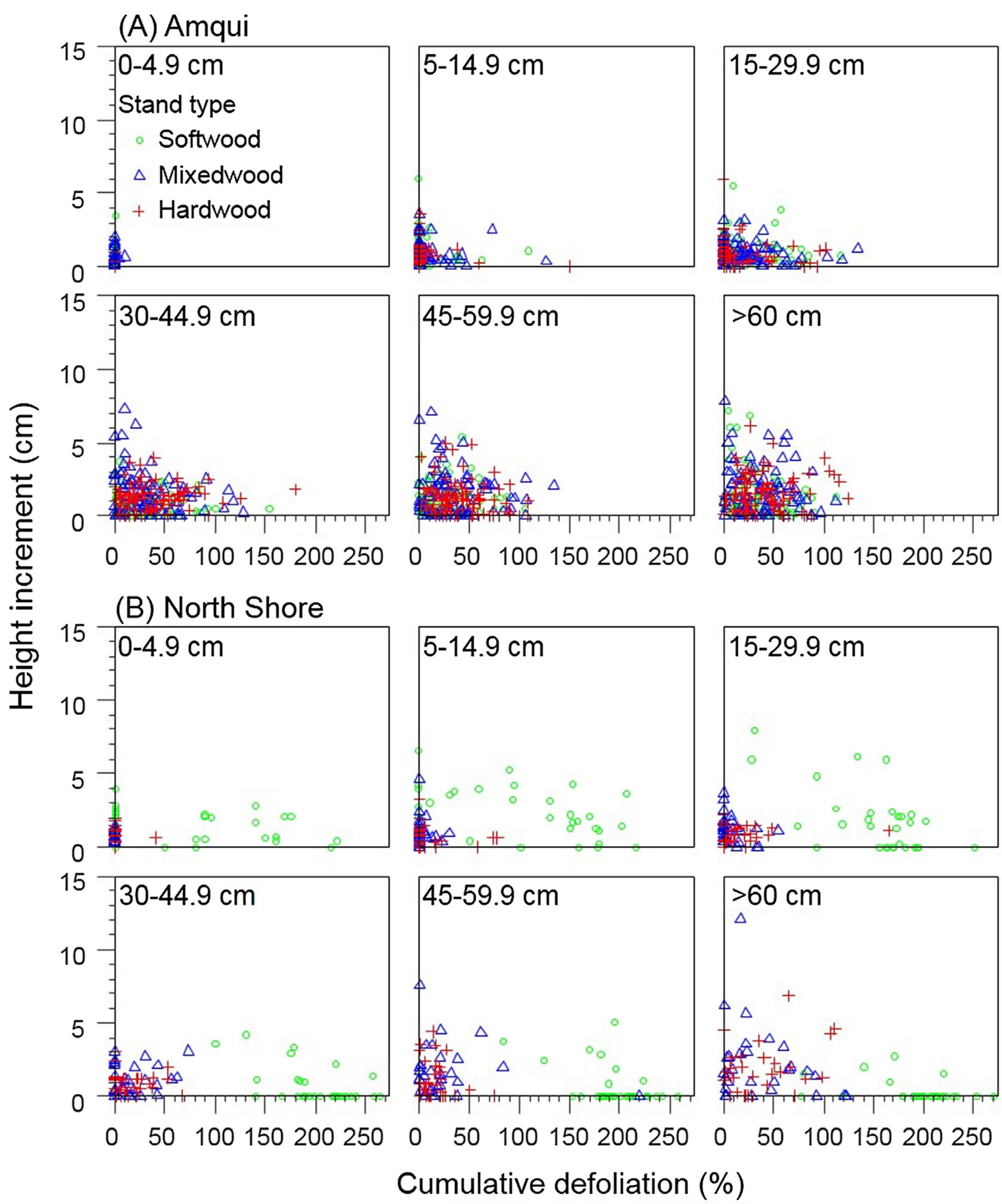

Fig. 1. Height increment of balsam fir regeneration in 2015 in six regeneration height classes plotted against summed cumulative defoliation from 2013 to 2015 (%) in (A) 27 early defoliation plots near Amqui, Quebec, and (B) nine late defoliation plots in the North Shore, Quebec.

Table 2
Results of a linear mixed-effects model testing effects of cumulative defoliation of regeneration, overstory canopy openness, ground vegetation cover, height of regeneration, and overstory hardwood content on height increment of 1503 balsam fir regeneration stems in the 27 Amqui plots. Significant differences ($p < 0.05$) are shown in bold font; four- and five-way interaction terms were not significant and were deleted from the model.

Variables	Value	Std. Error	DF	t-value	p-value
(Intercept)	0.3369032	0.2189002	1452	1.54	0.12
Height	**0.0057818**	**0.0026388**	**1452**	**2.19**	**0.03**
Hardwood content	0.0019695	0.0036853	23	0.53	0.60
Cumulative defoliation	0.0037206	0.0050573	1452	0.74	0.46
Canopy openness	0.0016625	0.0113061	1452	0.15	0.88
Ground vegetation cover	0.0005491	0.0033154	1452	0.17	0.87
Height × Cumulative defoliation	**−0.0001061**	**0.0000516**	**1452**	**−2.06**	**0.04**
Height × Canopy openness	−0.0000961	0.0001271	1452	−0.76	0.45
Height × Ground vegetation cover	0.0000343	0.0000400	1452	0.86	0.39
Height × Hardwood content	−0.0000711	0.0000383	1452	−1.86	0.06
Hardwood content × Cumulative defoliation	−0.0000018	0.0000694	1452	−0.03	0.98
Hardwood content × Canopy openness	−0.0000522	0.0002085	1452	−0.25	0.80
Hardwood content × Ground vegetation cover	−0.0000206	0.0000466	1452	−0.44	0.66
Canopy openness × Cumulative defoliation	0.0000112	0.0002439	1452	0.05	0.96
Ground vegetation cover × Cumulative defoliation	0.0000030	0.0000642	1452	0.05	0.96
Ground vegetation cover × Canopy openness	−0.0000291	0.0001504	1452	−0.19	0.85
Height × Hardwood content × Cumulative defoliation	**0.0000012**	**0.0000005**	**1452**	**2.51**	**0.01**
Height × Hardwood content × Canopy openness	0.0000033	0.0000018	1452	1.91	0.06
Height × Hardwood content × Ground vegetation cover	−0.0000002	0.0000003	1452	−0.75	0.46
Height × Canopy openness × Cumulative defoliation	0.0000017	0.0000022	1452	0.79	0.43
Height × Ground vegetation cover × Cumulative defoliation	−0.0000004	0.0000003	1452	−1.18	0.24
Height × Ground vegetation cover × Canopy openness	−0.0000007	0.0000016	1452	−0.44	0.66
Hardwood content × Canopy openness × Cumulative defoliation	−0.0000024	0.0000035	1452	−0.69	0.49
Hardwood content × Ground vegetation cover × Cumulative defoliation	0.0000000	0.0000005	1452	0.08	0.94
Hardwood content × Ground vegetation cover × Canopy openness	0.0000020	0.0000024	1452	0.81	0.42
Ground vegetation cover × Canopy openness × Cumulative defoliation	0.0000000	0.0000028	1452	−0.01	0.99

digital camera with a fisheye lens, self-leveling mount, and north direction indicator was used and set to 1.2 m above the ground. Any understory plants that could obscure the lens were pushed aside before taking pictures. In each plot, we took photos 6 m from the plot center in four directions (north, east, south, and west). At each location, eight photos were taken with different exposure (−1.3, −1.0, −0.7, −0.3, 0.0, +0.3, +0.7, +1.0) values. Hemispherical and cover images were analyzed with the WinSCANOPY (Regent Instrument, 2013) digital image analyzer. All the digital images were analyzed in the blue color channel of each 8-bit red-green-blue hemispherical image to provide the best contrast of canopy and sky (Leblanc et al., 2005; Brusa and Bunker, 2014). WinSCANOPY defined hemispherical images as canopy and sky by pixel level and adjusted percent of sky pixels by zenith angles to get real openness above the lens for each image. The exposure we used in the analysis was −0.7 to +0.7 (depending on the weather condition). All photographs were taken in early August 2015.

To determine how spruce budworm-caused defoliation influences competition between other ground vegetation and regeneration, we established a 1 m × 1 m quadrat within each 4-m^2 quadrat. Percent cover by species was estimated for all herbaceous species in each 1-m^2 quadrat and estimated for all shrub species and all tree regeneration in each 4-m^2 quadrat. We used modified Daubenmire cover classes (Daubenmire, 1959) (0%, 0.005–0.049%, 0.05–0.24%, 0.25–0.99%, 1–4%, 5–14%, 15–24%, 25–49%, 50–74%, 75–94%, 95–100%) to characterize cover. Total ground vegetation cover (shrub and regeneration cover plus herbaceous cover) was calculated for each quadrat. Conspecific competition was not specifically included in the analysis because the density of regeneration was < 0.5 fir regeneration stems per m^2 (Nie et al., 2018), and we already had five variables analyzed in the statistical analyses. Given the small size of many of the regeneration stems, we deemed conspecific regeneration to be less important than overall vegetation competition, which did include the fir competition.

2.2. Data analyses

General linear mixed-effects models were used to determine the effect of (i) cumulative defoliation, (ii) canopy openness, (iii) ground vegetation cover, (iv) height of regeneration, and (v) overstory hardwood content on balsam fir regeneration height increment. Ground vegetation cover was calculated as the sum of herbaceous, shrub and regeneration cover because preliminary analysis results showed no significant relationship between height increment and herbaceous and shrub vegetation cover when analyzed separately. Height increment was the response variable (with log (x + 1) transformation), and explanatory variables were cumulative defoliation per regeneration stem, canopy openness per plot, ground vegetation cover per plot, the median value of height class, hardwood content per plot, and their interaction terms. All the variables were treated as continuous variables. As the minimal sampled unit was the seedling or sapling stem in each plot, plot was included as a random variable in the analysis. Because the sample plots were nested within stands, "stand" was also included as a random variable. The null hypotheses were that no differences in height increment would be detected at the 0.05 significance level between stands with different (i) cumulative defoliation, (ii) canopy openness, (iii) ground vegetation cover, (iv) height of balsam fir regeneration, and (v) overstory hardwood content. Analyses were conducted separately for the early and late defoliation plots because defoliation level, tree condition, and dispersal behavior of spruce budworm larvae all differ with severity and duration of the outbreak (Miller, 1975). We used R 3.3.1 (R Development Core Team, 2016) and the "nlme" package (Pinheiro et al., 2017) to run all analyses.

3. Results

3.1. Cumulative defoliation, canopy openness, and ground vegetation cover by stand type

The sampling strategy of using plots with a gradient of balsam fir-hardwood content in the two study areas was effective in providing a wide range of cumulative defoliation (0–270%), canopy openness (5–54%), and vegetation competition (0–169%) among plots (Table 1). In the early defoliation plots, mean cumulative defoliation only ranged from 20 to 27%, and was slightly lower in the softwood than in the

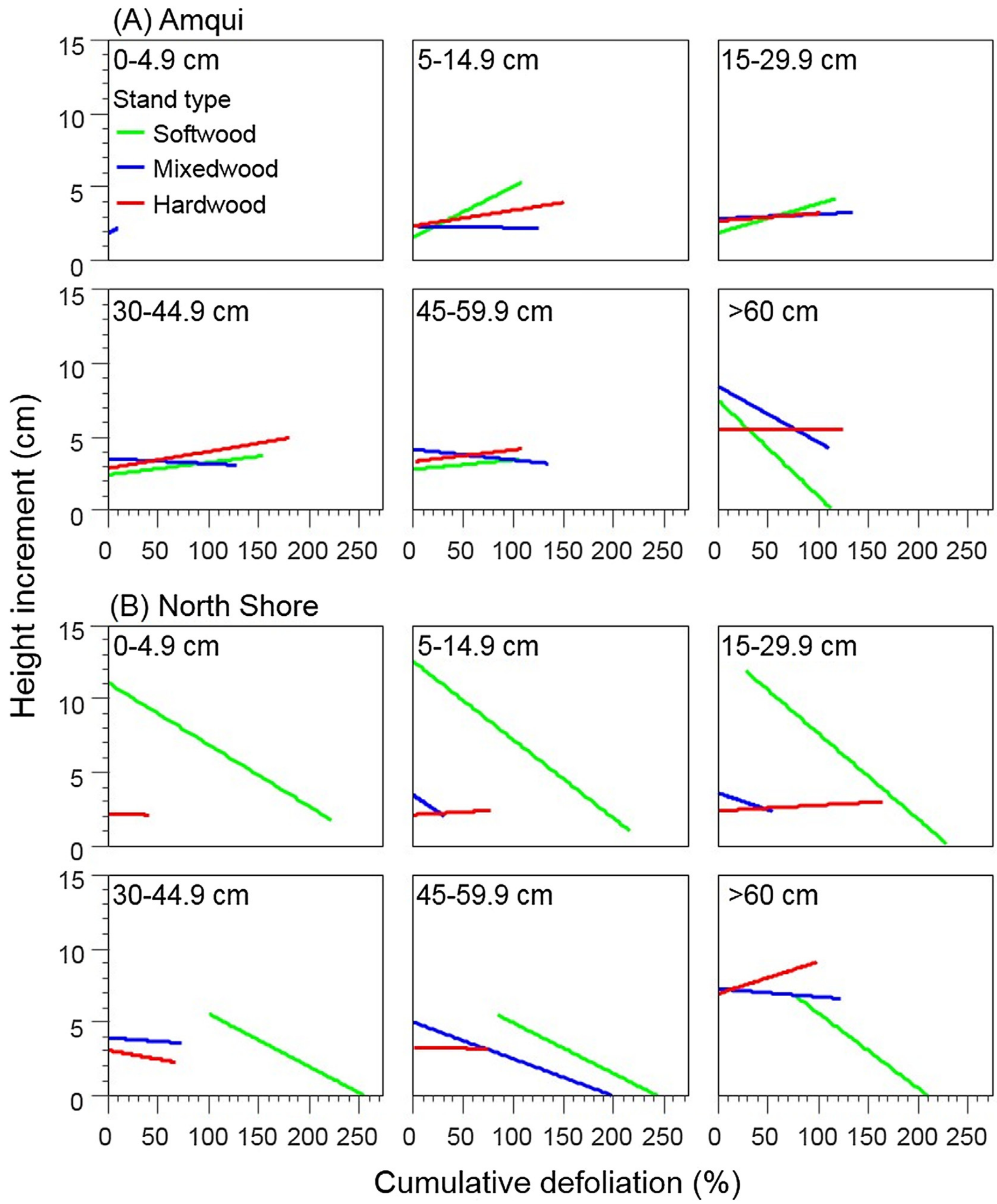

Fig. 2. Best fit lines (from a linear mixed-effects model) of height increment of balsam fir regeneration in 2015 plotted against summed cumulative defoliation from 2013 to 2015, for six regeneration height classes in softwood, mixedwood, and hardwood stand types in (A) 27 early defoliation plots near Amqui, Quebec, and (B) nine late defoliation plots in the North Shore, Quebec.

mixedwood or hardwood plots, which was contrary to expectations (Table 1A). However, in the late defoliation plots, cumulative defoliation was almost 10 times higher in the softwood than in the mixedwood or hardwood plots (Table 1B). Mean canopy openness ranged from 11 to 20% in the early defoliation plots and 10–12% in the late defoliation mixedwood and hardwood plots, but was nearly twice as high (38%) in the late defoliation softwood plots (Table 1), which sustained the greatest defoliation (Nie et al., 2018). Mean ground vegetation cover increased substantially with increasing hardwood content in the early defoliation plots, from 28% to 82% (Table 1A), and ranged from 26 to 45% in the late defoliation plots (Table 1B). The wide range of cumulative defoliation of individual sampled regeneration stems (0–270%) occurred because the sampling was by regeneration height classes, and there was much lower defoliation of small (< 30 cm tall) than of larger regeneration (Nie et al., 2018).

In the early defoliation study area, mean cumulative defoliation of all three stand types was low, averaging only 20–27%, and maximum cumulative defoliation of individual stems was 180% (Table 1). Since there was only light defoliation and no mortality of overstory balsam fir in these plots, any effect of overstory hardwood content (stand type) on canopy openness reflects differences in original canopy composition. In contrast, in the late defoliation study area, both overstory and understory balsam fir suffered more severe defoliation (Table 1B) and also mortality in the softwood plots (Nie et al., 2018). Defoliation of individual balsam fir regeneration stems ranged up to 270% (equivalent to 2.7 age classes of foliage removed), and was consistently higher in softwood than in mixedwood or hardwood plots (Fig. 1B). Plots with high overstory hardwood content had greater ground vegetation cover in both study areas in both study areas (Table 1).

Table 3
Results of a linear mixed-effects model testing effects of cumulative defoliation of regeneration, overstory canopy openness, ground vegetation cover, height of regeneration, and overstory hardwood content on height increment of 540 balsam fir regeneration stems in the nine North Shore plots. Significant differences ($p < 0.05$) are shown in bold font; four- and five-way interaction terms were not significant and were deleted from the model.

Variables	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.4755351	0.3523518	507	1.35	0.18
Height	−0.0064959	0.0057792	507	−1.12	0.26
Hardwood content	0.0004271	0.0067968	5	0.06	0.95
Cumulative defoliation	0.0022120	0.0025834	507	0.86	0.39
Canopy openness	0.0198094	0.0104709	507	1.89	0.06
Ground vegetation cover	0.0032222	0.0070206	507	0.46	0.65
Height × Cumulative defoliation	−0.0000034	0.0000357	507	−0.10	0.92
Height × Canopy openness	0.0003075	0.0002376	507	1.29	0.20
Height × Ground vegetation cover	**0.0002309**	**0.0000952**	**507**	**2.43**	**0.02**
Height × Hardwood content	0.0000552	0.0001001	507	0.55	0.58
Hardwood content × Cumulative defoliation	**−0.0001951**	**0.0000889**	**507**	**−2.19**	**0.03**
Hardwood content × Canopy openness	−0.0002499	0.0003813	507	−0.66	0.51
Hardwood content × Ground vegetation cover	−0.0000066	0.0001037	507	−0.06	0.95
Canopy openness × Cumulative defoliation	**−0.0001479**	**0.0000741**	**507**	**−2.00**	**0.05**
Ground vegetation cover × Cumulative defoliation	−0.0001091	0.0000625	507	−1.74	0.08
Ground vegetation cover × Canopy openness	−0.0000734	0.0001841	507	−0.40	0.69
Height × Hardwood content × Cumulative defoliation	0.0000004	0.0000005	507	0.76	0.45
Height × Hardwood content × Canopy openness	0.0000015	0.0000050	507	0.29	0.77
Height × Hardwood content × Ground vegetation cover	**−0.0000021**	**0.0000009**	**507**	**−2.24**	**0.03**
Height × Canopy openness × Cumulative defoliation	−0.0000011	0.0000013	507	−0.85	0.40
Height × Ground vegetation cover × Cumulative defoliation	0.0000000	0.0000004	507	0.09	0.93
Height × Ground vegetation cover × Canopy openness	−0.0000053	0.0000029	507	−1.82	0.07
Hardwood content × Canopy openness × Cumulative defoliation	**0.0000138**	**0.0000069**	**507**	**2.00**	**0.05**
Hardwood content × Ground vegetation cover × Cumulative defoliation	**0.0000014**	**0.0000007**	**507**	**2.10**	**0.04**
Hardwood content × Ground vegetation cover × Canopy openness	−0.0000020	0.0000060	507	−0.33	0.74
Ground vegetation cover × Canopy openness × Cumulative defoliation	0.0000025	0.0000015	507	1.68	0.09

3.2. Effect of spruce budworm defoliation on height increment of balsam fir regeneration

In the early defoliation plots, cumulative defoliation significantly reduced height increment of balsam fir regeneration, but it varied significantly with the height of balsam fir regeneration and with stand type (i.e., the height × hardwood content × cumulative defoliation interaction term was significant – Table 2). The decreasing height increment occurred in the tallest (> 60 cm) regeneration stems in softwood and mixedwood plots, but not in shorter height classes or in hardwood plots (Fig. 2A). The range of cumulative defoliation was generally similar for balsam fir regeneration stems in all three stand types (Fig. 1A and 2A). Height and "height × cumulative defoliation" were the only other terms that significantly affected height increment in the early defoliation plots (Table 2).

Results were more complex for the late defoliation plots. Three significant three-way interactions occurred: "height × hardwood content × ground vegetation cover", "hardwood content × canopy openness × cumulative defoliation", and "hardwood content × ground vegetation cover × cumulative defoliation" (Table 3). These suggest that the relationship between height increment and cumulative defoliation differed significantly between stand types (hardwood content), canopy openness, and vegetation cover. Regeneration stems in the late defoliation softwood plots clearly had higher defoliation than in mixedwood or hardwood plots in most height classes (Fig. 2B). The decreasing height increment with increasing cumulative defoliation was clear in all height classes in softwoods plots (Fig. 2B), and was apparent for regeneration stems in mixedwood plots in the 45–60 cm height class, but did not occur in hardwood plots or for most mixedwood height classes (Fig. 2B).

3.3. Effect of canopy openness on height increment of balsam fir regeneration

In the early defoliation plots, canopy openness did not significantly affect regeneration height increment (Table 2). Nonetheless, in all cases, the trend (slope of the best fit lines) was positive, suggesting increasing height increment with increasing canopy openness (Fig. 3A).

In the late defoliation plots, "hardwood content × canopy openness × cumulative defoliation" had a significant interactive effect on height increment (Table 3). In softwood plots, canopy openness was > 25%, and height increment substantially declined with increasing cumulative defoliation (Fig. 4A). In contrast, in the mixedwood and hardwood plots, canopy openness was < 25% and height increment increased with cumulative defoliation (Fig. 4A). The "canopy openness × cumulative defoliation" interaction term was also significant in the late defoliation plots (Table 3). The most striking result in comparing height increment against canopy openness by stand type was the clear separation of high (25–50%) canopy openness in the late defoliation study area only occurring in softwood plots (Figs. 3B and 4A). Slopes of best fit lines of height increment against canopy openness were negative for regeneration in softwood plots and positive for regeneration in all height classes in mixedwood plots (Fig. 3B).

3.4. Effect of ground vegetation cover on height increment of balsam fir regeneration

There was no significant effect of ground vegetation cover on height increment in the early defoliation plots (Table 2), and very little difference in slope of best fit lines among the three stand types (Fig. 5A).

In the late defoliation plots, the interaction terms "height × hardwood content × ground vegetation cover" and "hardwood content × ground vegetation cover × cumulative defoliation" were significant (Table 3). The effects of ground vegetation cover on height increment varied with height and with stand type (Fig. 5B). Height increment was little affected by ground vegetation cover in all height classes in hardwood plots and for regeneration < 30 cm tall in softwood plots. However, height increment increased with ground vegetation cover in mixedwood plots, and it decreased with ground vegetation cover for regeneration > 30 cm tall in softwood plots (Fig. 5B). For regeneration < 30 cm tall, height increment was largest in softwood, intermediate in mixedwood, and smallest in hardwood plots, but when it was > 30 cm tall, height increment in softwood plots was lower than in mixedwood and hardwood plots (Fig. 5B). The significant interaction

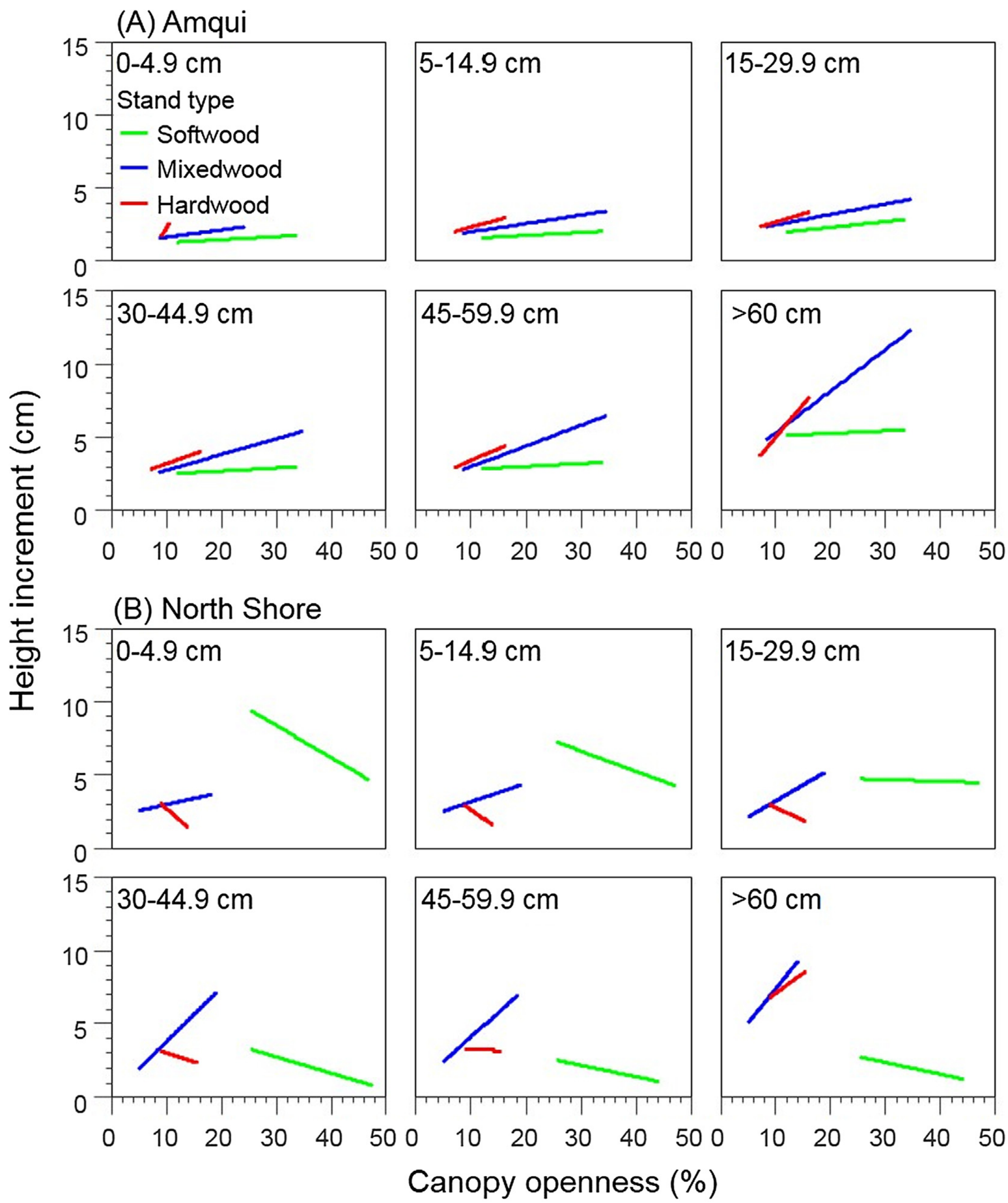

Fig. 3. Best fit lines (from a linear mixed-effects model) of height increment of balsam fir regeneration in 2015 plotted against canopy openness (%), for six regeneration height classes in softwood, mixedwood, and hardwood stand types in (A) 27 early defoliation plots near Amqui, Quebec, and (B) nine late defoliation plots in the North Shore, Quebec.

of "hardwood content × ground vegetation cover × cumulative defoliation" resulted in dramatically different patterns of height increment against cumulative defoliation relationships among stand types. At all ground vegetation cover levels, height increment sharply declined with increasing cumulative defoliation in softwood plots (Fig. 4B), whereas in mixedwood and hardwood plots, height increment increased with cumulative defoliation with low (≤50%) ground vegetation cover, increased (in hardwood) or decreased slightly (mixedwood) with 51–100% ground vegetation cover, and decreased slightly (hardwood) with > 100% ground vegetation cover (Fig. 4B).

4. Discussion

The results show that cumulative defoliation negatively affected height increment of balsam fir regeneration, but the strength of this relationship varied between the early defoliation plots (3 years of light to moderate defoliation of overstory balsam fir) and the late defoliation plots (7 years of moderate to severe defoliation). Hypothesis 1, that taller balsam fir regeneration will experience a greater negative effect of defoliation on height increment than shorter regeneration, because taller regeneration will sustain higher levels of defoliation, did occur in the early defoliation plots. As predicted, there was a significant "height × defoliation" interactive effect in the early defoliation plots, but this was significantly modified by overstory hardwood content.

Hypotheses 2a and 2b about the effects of canopy openness on height increment were not supported in the light to moderately defoliated early defoliation plots, but Hypothesis 2a was supported in the late defoliation plots, where there were significant "hardwood content × canopy openness × cumulative defoliation" and "canopy openness × cumulative defoliation" interative effects on height increment. These plots had much more severe and long-lasting defoliation, especially in the softwood stands, which had greater canopy openness than

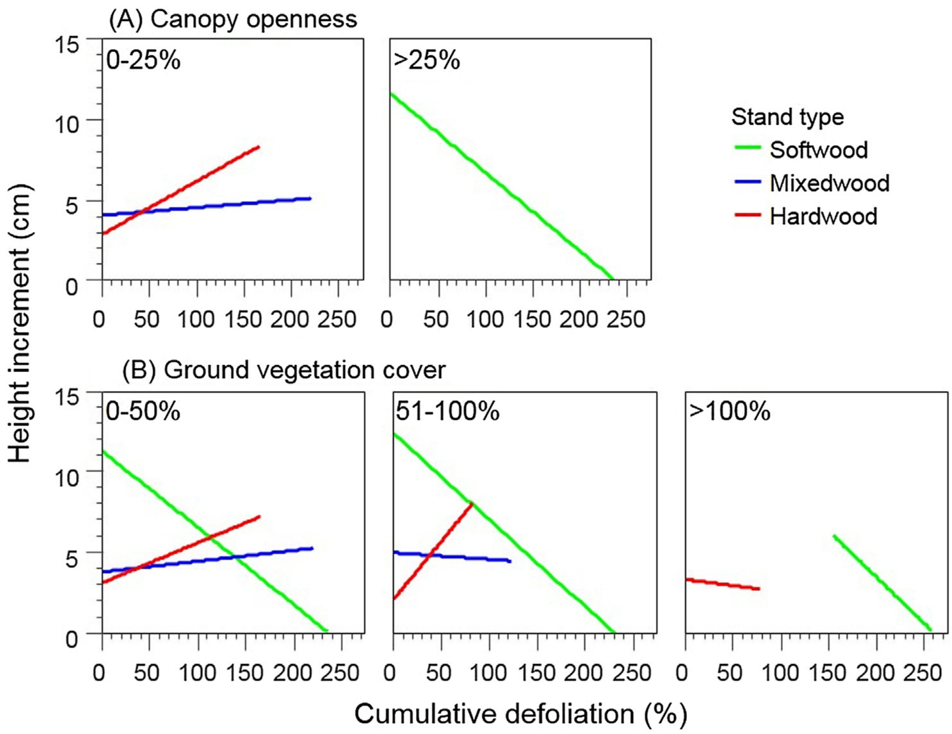

Fig. 4. Best fit lines (from a linear mixed-effects model) of height increment of balsam fir regeneration in 2015 plotted against cumulative defoliation from 2013 to 2015 (%), in softwood, mixedwood, and hardwood stand types in nine late defoliation plots in the North Shore, Quebec, for (A) two canopy openness levels, and (B) three ground vegetation levels.

mixedwood or hardwood stands, probably owing to the 7 years of repeated defoliation. There was no support for Hypothesis 2b, that increased canopy openness would reduce height increment of balsam fir regeneration because greater light availability in the understory would also promote understory shrub and herbaceous species growth, which would increase competition.

Hypothesis 3, that under similar canopy openness, high ground vegetation cover would have a greater negative effect on height increment of shorter balsam fir regeneration than of taller regeneration, because shorter regeneration is more affected by understory competition, was not supported. However, there were significant "height × hardwood content × ground vegetation cover" and "height × ground vegetation cover" interaction terms, with the biggest difference being that height increment of stems > 30 cm tall in softwood plots declined with increasing ground vegetation cover. The lack of support in the early defoliation plots conflicts with previous studies (e.g., Cornett et al., 1997; Rossi and Morin, 2011), which reported that shrubs were a strong competitor to balsam fir regeneration. However, the early defoliation plots may have had insufficient defoliation to cause canopy opening, and the late defoliation softwood plots had such severe defoliation of large regeneration that it may have overridden any potential competition effects.

Hypothesis 4, that increasing hardwood content (across the gradient of balsam fir-hardwood stands) will result in lower defoliation of balsam fir, which in turn will result in lower overstory canopy openness and ground vegetation competition, was supported in the late defoliation plots by the significant "hardwood content × canopy openness × cumulative defoliation" and "hardwood content × ground vegetation cover × cumulative defoliation" interactive effects on height increment.

4.1. Effect of cumulative defoliation on height increment

In the early defoliation softwood and mixedwood plots, defoliation reduced height increment of balsam fir regeneration. This was similar to results of Piene and Little (1990) from a laboratory manual defoliation experiment, in which balsam fir regeneration had 12%, 60%, and 78% height increment reduction after 3 years of 160%, 270%, and 300% cumulative defoliation, respectively. Loss of foliage affects the photosynthetic process and causes reductions in growth (e.g., Kleinschmidt et al., 1980). Regeneration > 30 cm tall lost a larger proportion of foliage than shorter regeneration. Cumulative defoliation did not decrease height increment in the early defoliation hardwood plots, probably because of low levels of defoliation in these plots.

In the late defoliation plots, defoliation of balsam fir regeneration had a more complicated effect on height increment. The negative effect of cumulative defoliation on height increment was significantly affected by canopy openness and hardwood content, with particularly large declines in height increment with increasing cumulative defoliation in softwood plots of high canopy openness. Previous research on young shortleaf pine (*Pinus echinata* Mill.) and loblolly pine (*Pinus taeda* L.) also found an interactive effect between defoliation and canopy openness, but with the opposite effect, i.e., when regeneration was shaded by overstory trees, mortality of stems occurred with only 50% defoliation, while with wider canopy openness, the regeneration could survive with > 75% defoliation (Beal, 1942). These differences might reflect contrasts in shade tolerance and growth of balsam fir versus pine.

4.2. Effect of canopy openness on height increment

Results from the late defoliation plots showed that increasing canopy openness resulted in greater height increment of balsam fir regeneration, but that this effect was also dependent on cumulative defoliation level and stand type. With moderate-severe defoliation on the balsam fir regeneration, the positive effect of canopy openness declined in the softwood plots. Because the effect of canopy openness was only significant in the late defoliation plots, which had suffered 7 years of moderate-severe defoliation (QMRNF, 2016), it is likely that the larger canopy openness in softwood stands was caused by spruce budworm. Regeneration had > 100% more cumulative defoliation in softwood than in mixedwood or hardwood plots, and even though regeneration might receive more light with a more open canopy, severe defoliation still suppressed the growth release (Vincent, 1962). Defoliation and

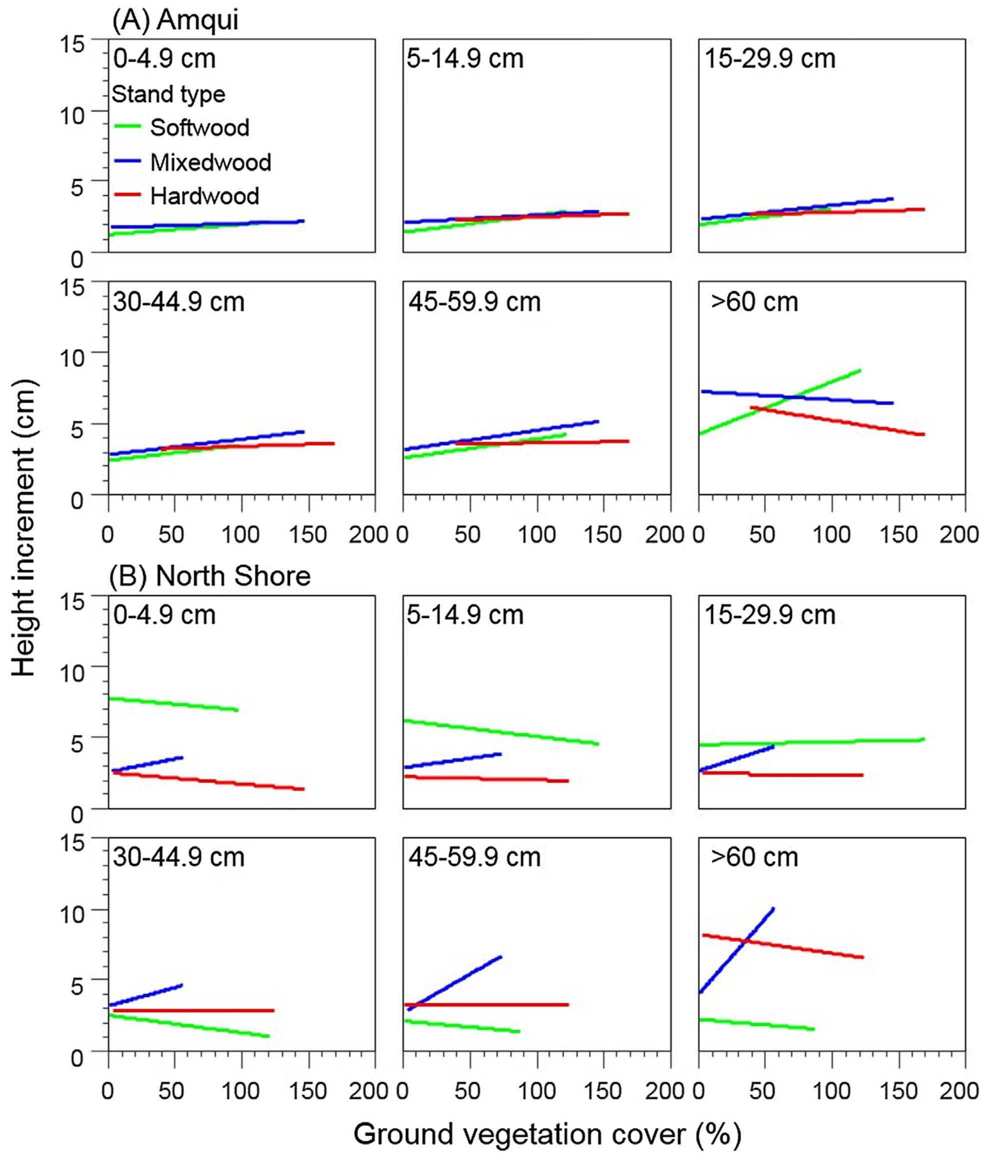

Fig. 5. Best fit lines (from a linear mixed-effects model) of height increment of balsam fir regeneration in 2015 plotted against ground vegetation cover (%), for six regeneration height classes in softwood, mixedwood, and hardwood stand types in (A) 27 early defoliation plots near Amqui, Quebec, and (B) nine late defoliation plots in the North Shore, Quebec.

mortality of overstory balsam fir trees create gaps that allow more light to directly reach regeneration on the forest floor (Kneeshaw and Bergeron, 1998). Light intercepted by fir regeneration is strongly, positively related to height increment (Duchesneau et al., 2001). Similar to our results, Fye and Thomas (1963) found that height increment of regeneration > 100 cm tall increased by 0.9 cm/year whereas regeneration < 15 cm tall increased by only 0.08 cm/year, on average, after 9 years of increasing canopy openness caused by spruce budworm in Quebec. In Nova Scotia, taller advance balsam fir regeneration (> 45 cm) had three- to five-times increases in height increment as the canopy opened (MacLean, 1988). In a study of regeneration growth release using stem analysis during the 1970–1980 s spruce budworm outbreak in Nova Scotia, Spence and MacLean (2012) found that mean annual height and radial increment increased in all seedlings > 5 cm tall, beginning 1–2 years after the start of defoliation. Larger regeneration had the earliest and greatest height response, with height increment of regeneration > 45 cm tall increasing from 2 to 3 to 9–10 cm/year after 7 years of outbreak (Spence and MacLean, 2012). The only difference between our results and those of previous research was that we did not detect differences in the relationship between canopy openness and height increment for regeneration of different height classes.

4.3. Effects of ground vegetation cover on height increment.

Several studies have demonstrated that shrubs strongly compete with balsam fir regeneration, especially under large gaps (Batzer and Popp, 1985; Morin and Laprise, 1997; Duchesneau et al., 2001). We initially tested for separate effects of competition from shrubs and herbaceous vegetation, but neither had significant effects on regeneration height increment, so we combined them. Subsequently, height increment of balsam fir regeneration was found to be significantly reduced by competition from overall ground vegetation, but only in the late defoliation study area, and mainly in the softwood plots. Height increment tended to increase or remain stable in the mixedwood and hardwood plots as ground vegetation cover increased, whereas it decreased for regeneration > 30 tall in softwood plots. When regeneration was < 30 cm tall, as ground vegetation cover increased, height increment increased more in the softwood than in the mixedwood and hardwood plots. We do not have a good explanation for the variable results observed, but response to competition may vary considerably depending on the relative height and composition of competing vegetation (Batzer and Popp, 1985; Archambault et al., 1998). The lack of any ground vegetation response in the early defoliation plots may have resulted from the lighter defoliation and earlier stage of the outbreak, with little canopy opening occurring yet.

5. Conclusions

Height increment is a good indicator to show how balsam fir regeneration responds to a spruce budworm outbreak. We examined the individual and interacting effects of cumulative defoliation and vegetation competition (negative variables), canopy openness (a positive variable), the height of regeneration, and stand type (hardwood content) on regeneration height increment in two regions. Overall, our results demonstrated that relationships between regeneration height growth and other variables are complex, with all five variables tested having significant interactive effects in the late defoliation plots with 7 years of moderate-to-severe defoliation. In the early defoliation plots, with 3 years of light-to-moderate defoliation, regeneration height, cumulative defoliation, and hardwood content had significant interactive effects on height increment. In the early defoliation softwood and mixedwood plots, 100% cumulative defoliation reduced height increment of regeneration > 30 cm tall by 85–100%. In the late defoliation plots with moderate-to-severe defoliation, at large canopy openness (≥25%), height increment in softwood plots declined approximately in proportion to cumulative defoliation, but in mixedwood and hardwood, canopy openness was < 25% and height increment increased with cumulative defoliation. In softwood plots, height increment also declined sharply with increasing cumulative defoliation at all ground vegetation cover levels, but in mixedwood and hardwood plots, height increment increased or decreased slightly with increasing cumulative defoliation. Our results reveal the complexity of forest regeneration dynamics followng disturbance, and further highlight the need to understand how regeneration responds during a spruce budworm outbreak as this is critical to predicting future stand composition and to plan effective forest management during an outbreak.

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