The Severity of Budworm-Caused Growth Reductions in Balsam Fir/ Spruce Stands Varies with the Hardwood Content of Surrounding Forest Landscapes

Elizabeth M. Campbell, David A. MacLean, and Yves Bergeron

Abstract: Tree-ring data collected from balsam fir (Abies balsamea [L.] Mill.) in 31 spruce (Picea spp.)/firdominated stands in northern New Brunswick were used to evaluate how radial growth reductions during the last spruce budworm (*Choristoneura fumiferana* Clem.) outbreak (1972–1992) varied according to the hardwood content of surrounding forest landscapes, insecticide spray history and elevation. Stepwise regression analysis was used to build 12 models describing relationships between mean percent growth reduction (i.e., deviation from mean tree growth averaged over the lifespan of all trees in a stand) and the explanatory variables for years when >80% of stands had growth reductions (1976–1978, 1982–1984, 1990, 1991, and 1994) and for three growth reduction periods (1972–1980, 1981–1985, and 1986–1993). The hardwood content of surrounding forest landscapes entered into all significant regression models (P < 0.05), explaining 12–41% of the variance in budworm-caused growth reductions. Differences in growth reductions among stands were greatest during the initial years of the budworm outbreak (1972–1980), particularly in 1976 when mean reductions were $\sim 40\%$ in stands with <50% hardwood and content and $\sim20\%$ in stands in which surrounding hardwood content was >50%. Relationships between variation in growth reductions among stands and elevation or insecticide spray history were weak and less consistent than with landscape hardwood content. Our findings suggest that increasing the hardwood content of forest landscapes could help to reduce the impact of outbreaks on timber supplies. FOR. SCI. 54(2):195-205.

Keywords: budworm impacts, defoliation, dendroecology, insect outbreaks

ERIODIC SPRUCE BUDWORM (Choristoneura fumiferana Clem.) (Lepidoptera: Tortricidae) outbreaks occur about every 35 years in the boreal and mixedwood forest regions of eastern North America (Royama 1984, Jardon et al. 2003). During outbreaks, repeated annual defoliation by budworm larvae reduces tree growth and often kills its hosts, particularly balsam fir (Abies balsamea [L.] Mill.), over vast areas (MacLean 1980, Hardy et al. 1986, Bergeron et al. 1995). Although budworm outbreaks are natural forest disturbances that play a critical role in directing large-scale ecological processes (e.g., forest succession and nutrient cycling), they also reduce timber supplies and generate substantial socioeconomic losses. From 1977 to 1987, 17–22% of the annual timber harvest level was lost to spruce budworm in Canada (Sterner and Davidson 1982, Power 1991, National Forestry Database 1995).

During the spruce budworm outbreaks of the 1970s, 1980s, and early 1990s, aerial application of insecticide was used throughout much of eastern Canada to reduce budworm damage and economic losses. Broad-spectrum chemical insecticides (e.g., fenitrothion), as well as the biological insecticide Bacillus thuringiensis (B.t.), were applied. Although chemical insecticides are no longer considered an environmentally acceptable option for controlling insect outbreaks in Canada, B.t., and the insect growth regulator, Mimic, can be used to reduce budworm populations during outbreaks to protect foliage and prevent host deaths. Past management efforts to reduce the impact of spruce budworm outbreaks in eastern Canada have relied heavily on the application of insecticides, but given concern about the potential negative ecological impacts of spraying B.t., for example, dramatic reductions of Lepidoptera that could significantly alter forest insect communities and affect a range of other species and ecosystem processes (Crawford and Jennings 1989, Miller 1990), additional approaches to reducing the economic impacts of budworm outbreaks are necessary.

The fact that damage caused by spruce budworm outbreaks varies with forest species composition has long been recognized. On the basis of these observations, researchers

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Elizabeth M. Campbell, Centre d'Étude de la Forêt and Département des Sciences Biologiques, C.P. 8888, Succ. Centre-ville, Université du Québec à Montréal, Québec H3P 3P8, Canada. Current address: Research Branch, British Columbia Ministry of Forests and Range, PO Box 9519, Stn Prov Govt, Victoria, BC V8W 1N1, Canada—Phone: (250) 387-6712; Fax: (250) 387-0046; elizabeth.m.campbell@gov.bc.ca David A. MacLean, Faculty of Forestry and Environmental Management, University of New Brunswick, PO Box 44555, Fredericton, New Brunswick E3B 6C2, Canada. Yves Bergeron, Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Université du Québec en Abitibi-Témiscamingue, C.P. 700, Rouyn-Noranda, Québec J9X 5E4, Canada.

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have proposed that silvicultural activities altering forest species composition could help to reduce the impact of budworm outbreaks (Westveld 1946, Baskerville 1976, Blais 1983, Blum and MacLean 1984). Whereas Miller and Rusnock (1993) suggested that there was little evidence to support this "silvicultural hypothesis," citing fallacious assumptions and logistical problems associated with developing large-scale experimental tests, MacLean (1996) argued strongly against their conclusions, indicating that although budworm outbreaks cannot be prevented (Royama 1984, Royama et al. 2005), damage caused during outbreaks can be reduced through silviculture, and outcomes of various large-scale forest management scenarios can be tested, particularly with decision support systems that use empirical data to model budworm population dynamics, forest dynamics, and stand vulnerability. MacLean (1996) has proposed that alterations to forest composition to reduce budworm impacts could be attained through planting nonhost softwood species (e.g., jack pine Pinus banksiana Lamb.), selective harvesting of balsam fir in stands to increase the content of nonhosts or less vulnerable species (e.g., spruce), and clearcutting to break up balsam fir forests that are contiguous across landscapes.

Many recent studies that describe and quantify relationships between forest composition and budworm impact support the position of MacLean (1996). They indicate that stands dominated by balsam fir are more vulnerable to budworm outbreaks than stands dominated by spruce (Harper et al. 2003, Bouchard et al. 2005) or stands in which hosts are mixed with nonhost softwoods such as white cedar (Thuja occidentalis L.) and jack pine. The presence of various hardwoods in stands is also related to lower budworm impacts (Bergeron et al. 1995, Su et al. 1996), possibly because the natural enemies of spruce budworm are more abundant in mixed forests than in pure softwood stands (Cappuccino et al. 1998). In addition to local-scale effects of stand composition, a number of studies have proposed that the composition of surrounding forest landscapes can also influence the impact of budworm outbreaks in stands (Bergeron et al. 1995, Cappuccino et al. 1998, Kouki et al. 1997). None of these studies, however, described or quantified relationships between outbreak impacts and the hardwood content of the surrounding landscapes. The objective of our work was to build on standlevel findings regarding the influence of hardwoods (Bergeron et al. 1995, Su et al. 1996) and test the hypothesis that the impact of budworm outbreaks varies among stands according to the hardwood content of surrounding landscapes. In our analysis we also compare the effects of hardwood content with insecticide spraying. Whereas all of the aforementioned studies measured the impact of budworm outbreaks in terms of host defoliation or mortality levels in stands, we measured impacts in terms of average growth losses incurred among individual balsam fir trees in a stand. Growth losses of individual trees are directly related to the proportion of foliage removed by the budworm (Erdle and MacLean 1999) and can reflect budworm population densities on individual trees. Traditionally, budworm impacts have been expressed as a spatially integrated landscape-scale measure of the extent of damage (i.e., hectares

of defoliation calculated from aerial surveys) (e.g., Hardy et al. 1986). Studies such as this one and others that quantify stand-level impacts on the basis of measurements of individual trees (e.g., MacKinnon and MacLean 2004) better reflect local budworm population densities and thus provide an improved basis for understanding relationships between forest composition, outbreak impacts, and the mechanisms that drive budworm population dynamics. This information could have significant implications for the way in which forests are managed to reduce future socioeconomic losses caused by budworm outbreaks.

Methods

Study Area

Thirty-one stands were sampled in northern New Brunswick. Most stands occurred within the Northern Uplands bioclimatic ecoregion, but a few stands occurred in the Highlands and the Central Uplands ecoregions (Figure 1). Elevations ranged from 177 to 549 m, with a mean of 335 m. The Northern Uplands is climatically intermediate to the colder Highlands and the warmer, wetter Central Uplands (TECWG 2003). Mean annual, seasonal, and monthly climate conditions were calculated for each stand using interpolated weather station data (from the four nearest weather stations) measured from 1970 to 1998. Mean annual temperatures ranged from 1.7 to $3.4^{\circ}C$ (average = 2.4°C), and mean annual precipitation ranged from 1,010 to 1,139 mm (average = 1,054 mm). The number of consecutive days without frost ranged among stands from 82 to 121 days (average 104) and minimum winter temperatures ranged from -19 to -16°C. Mean summer precipitation ranged from 466 to 567 mm (average = 500 mm), with the least precipitation occurring in May and June (mean ~ 95 mm).

While forest landscapes of the Highlands are characteristically boreal—balsam fir dominates forests and occurs in stand mixtures with lesser components of white spruce



Figure 1. Map of the study area showing the location of 31 stands sampled in northern New Brunswick.

(*Picea glauca* [Moench] Voss), black spruce (*Picea mariana* [Mill.] BSP), and paper birch (*Betula papyrifera* Marsh.)—the Northern Uplands and Central Uplands are mixedwood landscapes containing large expanses of tolerant hardwoods such as sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britt.) that occupy upper slopes. Balsam fir dominates forests of mid to low slopes, and these forests contain lesser components of red maple (*Acer rubrum* L.), beech, and yellow and paper birch, as well as other conifers such as white spruce, white cedar, and eastern hemlock (*Tsuga canadensis* [L.] Carrière).

New Brunswick has a 300- to 400-year history of land clearing for agriculture and timber harvesting. Historically, catastrophic fire disturbances were infrequent in this region. On European settlement in the area, however, fires became more frequent and have had a more important influence on forest composition (Wein and Moore 1977). Spruce budworm outbreaks have occurred about every 35 years in the study area (Royama 1984). The last outbreak started in 1971, and insecticides were widely applied to minimize the impacts of budworm defoliation.

Stand Selection and Sampling

Given that previous studies have shown that budworm outbreak impacts (i.e., host defoliation and mortality) vary with stand hardwood content (Bergeron et al. 1995, Su et al. 1996), we attempted to control for this effect by sampling mature balsam fir-dominated stands (i.e., those with $\geq 80\%$ balsam fir) that contained $\leq 20\%$ hardwoods. We first sampled 12 balsam fir-dominated stands (mostly in softwood landscapes) that were previously studied by MacKinnon and MacLean (2003, 2004). MacKinnon and MacLean initially selected these stands through a stratified random process. The remaining 19 stands sampled were systematically selected through a series of steps. The geographic information system software ARC/INFO was first used to query the New Brunswick Department of Natural Resource forest inventory database and extract all stands in our study area that were composed of at least 80% balsam fir. For each of these stands, ARC/INFO was then used to calculate the proportion of the landscape (within a 1-km radius of the balsam fir stand centroid) that was covered by plantations or recently logged forests, the percentage of the forested landscape (within a 1-km radius of the balsam fir stand) that was covered by stands composed of >75% hardwood species, and distance to the closest road. Among the initial population of balsam fir stands selected, we eliminated those for which >25% of the surrounding landscape was covered by plantations or recently logged forests. The remaining balsam fir stands were then classified into three groups: coniferous landscapes (0-25% hardwood stands), mixedwood landscapes (26-75% hardwood stands), and hardwood landscapes (76–100% hardwood stands). Distance from the nearest road was used to prioritize stands for sampling in each group. A total of 31 stands, representing a gradient in hardwood landscape composition from 2 to 87%, were sampled during 1998, 1999, or 2000.

A 20 \times 20 m sampling plot was located at the centroid

of each stand. Within this plot, the diameter of all trees (living and dead) taller than >1.3 m was tallied into 5-cm diameter classes. In each stand, two increment cores were extracted from opposite sides and at the base (<30 cm from the germination point) of 10 balsam fir trees. The 10 largest, and presumably oldest, trees closest to the stand centroid were sampled. Basal disks were also collected from up to 10 dead balsam fir.

Using ARC/INFO, the location of each stand sampled was intersected with digitized annual aerial survey maps of forest defoliation and spray blocks. Based on these intersections, we assigned a percent defoliation value to each stand (i.e., the midpoint of defoliation classes assigned during aerial surveys: nil [0-10%]; light [11-30%], moderate [31-70%], and severe [71-100%]). Similarly, the cumulative number of times a stand was sprayed was determined from annual overlays of spray blocks. These data were summarized over all stands.

Chronologies of Radial Growth

All increment cores and basal disks collected from stands were prepared in the laboratory following standard dendrochronology procedures (Swetnam et al. 1985). After sanding and mounting samples, each tree ring on a core was assigned a date (i.e., year of formation) and measured to the nearest 0.001 mm using a Velmex Uni Slide Micrometer connected to a computer. The program COFECHA (Holmes 1983) was used to verify dating. Tree-ring series that did not cross-date well with other samples in the stand (i.e., r <0.350 with the stand mean chronology) were checked for dating or measurement errors. Series that remained poorly correlated with other samples were eliminated from the dataset of each stand.

The computer program ARSTAN (Cook 1985) was used to produce a standardized chronology of mean annual ring widths for balsam fir in each stand. Raw tree-ring series were standardized through a double detrending method sensu Krause and Morin (1999) (i.e., a negative exponential or straight line and a cubic spline function with the degree of smoothing fixed at 50% frequency response of 60 years, which conserves 99% of the variation in ringwidth for wavelengths of 1-20 years) to extract variability in individual tree-ring series attributable to tree age/size or vitality and remove shared low-frequency trends in annual growth so that shorter periods of budworm-caused growth reductions were highlighted. This detrending process transformed ring widths for individual trees into dimensionless index values. Index values of 1 represented the average growth of a tree over its lifespan. Index values >1 indicated above average annual growth, whereas values <1 indicated below average (i.e., reductions) in annual growth. Index values for each year were averaged over all core samples to produce a standardized mean chronology of annual growth for each stand. This mean chronology was then used to calculate average annual growth reductions (%) for each stand by subtracting the index values for each year from 1 (which represents normal/mean tree growth over its lifespan) and multiplying them by 100. Years with index values >1 were assigned a percent reduction value of 0. For all stands

sampled, the mean percent reduction in radial tree growth was calculated for each year of the last budworm outbreak in northern New Brunswick (1971–1998). Mean annual growth reductions among stands were summarized graphically and compared with defoliation and insecticide spray data. The years in which at least 80% of stands exhibited reductions in growth were selected for subsequent regression analyses, primarily because they were the only years in which the range in growth reduction data was normally distributed (frequent zero values in other years substantially skewed the distributions of growth data).

Data Analyses

Multiple linear regression analysis was used to construct models describing relationships between mean balsam fir radial growth reductions in stands (%) (the dependent variable) and the following explanatory variables: the percentage of the forest landscape within 1 km of sample stands that is covered by hardwood forests; elevation (m); and spray history. A forward selection process was used, with explanatory variables entering the regression model if the F ratio was >1.0. Elevation was included as an explanatory variable in stepwise regression analyses to account for variation in budworm impacts associated with climatic variations along elevation gradients (largely temperature) and to remove a potential shared gradient in elevation and surrounding forest hardwood content. Regression analyses were run and presented separately for each of the years in which at least 80% of stands sampled had growth reductions: 1976–1978, 1982–1984, 1990, 1991, and 1994. Even after data transformations, least-squares regression conducted for years in which < 80% of stands had growth reductions generated unreliable results (i.e., the assumptions of least-squares regression analysis were not be satisfied) and were not presented. In addition to analyses on individual years, regressions were also done for each distinct growth reduction period: 1972-1980, 1981-1985, and 1986-1993. The explanatory variable describing spray history was categorical for analyses on individual years (i.e., sprayed or not sprayed) and continuous for analyses on growth reduction periods (i.e., cumulative number of years sprayed over the period). As the budworm outbreak and insecticide spraying ceased after 1992, spray history was not included as a variable in 1994 analyses.

Before each of these regressions was undertaken, however, we considered the possibility that any statistically significant relationship between host growth reductions during budworm outbreaks and the explanatory variables of interest, particularly forest hardwood content, could be a spurious result of coincidental variation in the explanatory variable with some other unmeasured factor that varied spatially across the study area—climate, for example. To control for this possibility, any potential spatial component of variability in the dependant and independent variables was removed through partial regression analysis following Legendre and Legendre (1998). First, we computed a multiple regression of growth reduction onto a spatial matrix of explanatory variables generated by a third-order polynomial of stand coordinates (i.e., latitude and longitude, measured in decimal degrees). A third-order polynomial was chosen as we felt it was of sufficient complexity to explain any unmeasured, and potentially influential, factors that varied along latitudinal and longitudinal gradients in our study area (cf. Legendre and Legendre, 1998). The residuals of this multiple regression, which represent variations in budwormcaused growth reductions that remain after spatial gradients in the dependent and explanatory variables were removed, were then used to compute subsequent multiple regressions (i.e., partial regressions) that tested the effects of landscape hardwood content, elevation, and insecticide spray history (as described above).

Results

Stand Characteristics

Although we extracted stands from the forest inventory database with >80% balsam fir, basal area calculations from tree diameter data collected in each stand indicated that the actual percentage of balsam fir in stands was much more variable, ranging from 24 to 90% (Table 1). However, balsam fir was the dominant species in all stands except stands 24 and 18, which had slightly more spruce and white cedar (a nonhost softwood species), respectively. The large discrepancy between the percentage of balsam fir indicated on forest inventory polygons and what was calculated from stand survey data is probably due partly to photo interpretation error in distinguishing among conifer species (especially balsam fir and white spruce) on the aerial photographs used to make inventory maps as well as within-stand variability. We thought that the larger than expected variation in the balsam fir content of stands could generate a significant gradient in growth reductions (with reductions being higher among stands with more balsam fir) that would confound regression analyses used to test the effect of surrounding forest composition. Because of this, we included the percent balsam fir content of stands (i.e., [(balsam fir basal area, $m^2 ha^{-1}/total$ tree basal area, $m^2 ha^{-1}$ × 100] as a covariable in regression analyses.

Calculations of stand hardwood content [(hardwood basal area/total tree basal area) \times 100] from diameter data collected in each stand corresponded well to the mapped forest inventory data we used to design this study. Hardwood species comprised <25 per cent of total tree basal area in all stands except 18, 19, and 28, which had slightly more (Table 1). The fact that stand hardwood content corresponded better to mapped forest inventory data than balsam fir content of stands is probably due simply to the fact that observers can more readily distinguish between hardwood and softwood trees than among softwood species on the aerial photographs used to make the inventory maps. Thus, we are confident that our calculations of landscape hardwood content within 1 km of each stand, which were based on mapped forest inventory data and ranged from 2 to 87% (Table 1), are reasonably accurate.

Aerial survey data indicated low levels of budwormcaused defoliation (mapped as nil and recorded here as 0-10%, midpoint 5%) (MacLean and MacKinnon 1996) from 1960 to 1970 in the stands we sampled (Figure 2a).

Table 1. Characteristi	s of 31	forest	stands	sampled	in	northern	New	Brunswick
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0, 1		Total tree	Sta	nd composition	on (% basal aı	Surrounding landscape		
no.	(m)	(m ² /ha)	BF	SP	OS	HW	(% hardwood forests)	No. times sprayed†
12	249	39	84	8	0	8	2	20
15	247	47	59	2	24	13	3	17
14	210	50	72	16	5	6	5	15
7	287	56	93	4	0	3	8	17
2	505	43	78	13	0	9	10	22
9	288	39	82	1	0	17	15	19
21	177	40	78	1	4	17	15	15
23	191	49	49	20	32	0	15	15
1	361	31	81	11	0	8	17	18
29	462	47	78	16	0	6	19	9
27	511	47	74	19	0	7	23	19
10	300	43	75	17	0	9	28	18
25	302	37	69	18	0	14	28	20
17	549	45	68	21	2	8	30	18
24	198	66	31	44	2	24	40	13
31	327	51	78	6	0	15	40	17
6	265	34	72	26	0	2	54	14
26	400	33	87	8	0	5	54	12
28	384	44	67	0	0	33	55	10
8	367	36	90	4	0	6	60	10
11	283	58	89	8	0	3	67	17
30	430	40	66	14	0	20	67	13
3	350	43	69	15	0	16	70	17
4	243	52	76	13	0	11	72	7
22	443	30	57	28	0	15	72	12
20	326	34	48	23	28	0	77	3
5	378	50	81	11	0	8	81	7
13	389	46	68	15	0	18	81	5
16	378	42	81	0	0	19	81	7
18	247	41	24	18	27	31	84	3
19	344	33	63	8	3	26	87	8

BF, balsam fir; SP, spruce spp. (*P. glauca, Picea rubens, and P. mariana*); OS, other softwoods (white cedar, white pine); HW, all hardwoods (*Betula* spp., *Acer* spp., *F. grandifolia*).

* Percentage of land covered by hardwood-dominated forests within a 1-km radius of the sample stand.

[†] Total number of times sample stand was sprayed with insecticide from 1970 to 1992. Chemical insecticides were used before 1988. After 1988, biological insecticides (i.e., *B.t.*) were applied to most stands. Some stands were sprayed twice in 1 year.

Mean defoliation among stands began to increase in 1971. The highest levels of defoliation occurred in 1973, 1974, and 1975, with the mean defoliation among stands for these years being 41, 65, and 58%, respectively. Spraying of insecticide to minimize the impacts of the spruce budworm during the last outbreak began in the early 1970s and was widespread from 1975 to 1977 when 50-80% of the stands were sprayed each year (Figure 2b). As of 1977, these stands had been sprayed, on average, five times. Mean defoliation levels decreased in 1976, 1977, and 1978 but increased again in 1979, hovering between 20 and 30% until 1986, when mean defoliation decreased by another 10%. Extensive spraying occurred again from 1980 to 1983 and in 1989, when at least 50% of the stands were treated. As of 1992, stands were sprayed, on average, 13 times. Stands in hardwood-dominated landscapes tended to be sprayed with insecticides less frequently than those in landscapes with a lower hardwood forest content (r = -0.75; P < 0.001) (Table 1). Low amounts of dead balsam fir were found in all stands, but among stands in landscapes with less hardwood forests, low amounts of dead fir are presumably seen because frequent insecticide applications reduced budworm

populations and resulting defoliation levels, enough to prevent tree death.

Overall Patterns of Balsam Fir Radial Growth during the Outbreak

Based on the mean standardized chronologies of tree growth developed for each stand, we found that the percentage of stands showing an overall reduction in balsam fir growth varied from 0 to 100% in various years from 1970 to 1998 (Figure 3). Although no stands showed reductions in tree growth in 1970 or 1971, the number of stands showing growth reductions steadily increased from 1972 to 1977, and in 1977 and 1978, mean tree growth was reduced in all stands sampled. After 1978, growth reductions occurred in at least 50% of stands sampled over most years, and occurred in at least 90% of stands in 1984, 1991, and 1994.

Initially, the pattern of mean reductions in balsam fir growth (%) was similar to the frequency of growth reductions among stands—mean reductions in growth increased steadily from 1972 until 1977, when all stands had reductions in growth and mean reduction in tree growth over all



Figure 2. a, Mean annual stand of defoliation caused by spruce budworm (aerial survey data). b, Insecticide spray history over all stands sampled (n = 31, the mean cumulative number of times a stand was sprayed by insecticide is indicated by the solid black line). c, Percentage of stands with growth reductions and mean growth reduction (%) in stands from 1970 to 1998.

31 stands reached a maximum at 44%. The fact that maximum mean defoliation levels occurred in 1974 suggests a 3-year "lag" in growth responses to defoliation by spruce budworm during population outbreaks, which really results because defoliation assessed here is for current year foliage only, whereas growth is a function of cumulative defoliation of all age classes of foliage (e.g., Ostaff and MacLean 1995, Erdle and MacLean 1999). Mean growth reductions oscillated after 1977, with peaks in growth reductions occurring again in 1984, 1991, and 1994. Although 90–100% of stands had reduced tree growth during these years, mean growth reductions were about 30–50% less than they were in 1977. More severe growth reductions may reflect the occurrence of defoliation that includes "backfeeding" on



Landscape hardwood content (%)

Figure 3. Linear relationships between the reduction in radial growth of balsam fir in stands and the hardwood content of surrounding forest landscapes (n = 31). Results are presented for individual years and time periods that showed significant relationships.

older age classes of foliage when budworm populations are very high (e.g., Ostaff and MacLean 1995).

Regression Analyses

Twelve partial regression models described relationships between residual variation in balsam fir growth reductions (%) among stands and the hardwood content of surrounding landscapes, stand elevation, and the history of insecticide spraying (Table 2). The hardwood content of surrounding forest landscapes was entered as a variable into all statistically significant (i.e., P < 0.05) regression models and explained 12–41% of the variation in growth reductions among stands during the last budworm outbreak. There were strong negative relationships between landscape hardwood content and growth reductions during the initial years of the budworm outbreak (i.e., from 1972 to 1980) (Table 2;

Table 2. Summary of partial regression analyses accounting for variation in budworm-caused balsam fir growth reductions among 31 spruce-fir stands in northern New Brunswick, after shared spatial gradients in the dependent and explanatory variables were removed

	Model statist	tics			Explanatory variables entered into model				
Growth reduction (%)	Intercept	R^2	MSE	Р	Variable*	В	Partial r^2	Р	
1976	9.03	0.46	10.16	0.0008	% hardwood—landscape -23.02		0.41	0.0010	
					% balsam fir—stand	15.67	0.02	0.1963	
					Elevation	-0.02	0.03	0.2372	
1977	6.20	0.24	7.90	0.0204	% hardwood—landscape	-12.42	0.17	0.0094	
					Insecticide spraying	4.70	0.07	0.1174	
1978	4.33	0.05	9.40	0.2476	% hardwood—landscape	-6.13	0.05	0.2476	
1972–1980	4.80	0.20	4.53	0.0110	% hardwood—landscape	-6.79	0.20	0.0110	
1982	10.49	0.05	8.07	0.2239	% balsam fir—stand	-10.42	0.05	0.2239	
1983	10.18	0.12	8.74	0.1602	Elevation	-0.02	0.07	0.1682	
					Insecticide spraying	-4.11	0.05	0.2067	
1984					No variables entered				
1981–1985	14.82	0.19	6.35	0.0514	Cumulative no. years sprayed	-0.85	0.06	0.0238	
					% hardwood—landscape	-8.84	0.13	0.0444	
1990	-4.22	0.03	10.79	0.3240	% hardwood—landscape	5.98	0.03	0.3240	
1991	-5.02	0.12	6.50	0.0574	% hardwood—landscape	7.11	0.12	0.0574	
1994	-6.05	0.05	4.94	0.2513	% balsam fir—stand	6.00	0.05	0.2513	
1986–1993	-3.17	0.19	3.16	0.0155	% hardwood—landscape	4.49	0.19	0.0155	

Regressions were computed separately for each year of the last budworm outbreak (\sim 1971–1993) if >80% of sample stands had growth reductions and then for three time periods: 1972–1980, 1982–1985, and 1986–1993. MSE, mean square error.

* To improve residual normality and reduce heteroscedasticity of residual variance, % hardwood content and % basal area of balsam fir were transformed using the following function: arcsine ($\sqrt{(\times/100)}$). Explanatory variables are listed in the order by which they were entered into models.

Figure 3) when average growth reductions were most severe and a weak negative relationship in the 1980s when average growth reductions decreased by approximately 20% (Figure 2c). Differences in annual growth reductions among stands were greatest in 1976 (Figure 3): mean growth reductions were approximately 40% in stands where the surrounding landscape hardwood content was <50% and approximately 20% where landscape hardwood content was >50%. In the following year, growth reductions among stands in hardwood-dominated landscapes rose by approximately 20%, whereas those in softwood-dominated landscapes (i.e., with a hardwood content of \sim 50%) increased by 10%. Near the end of the budworm outbreak, when budworm defoliation and growth reductions were comparatively low (Figure 2a and c), we found an unexpected weak positive relationship between balsam fir growth reductions and landscape hardwood content (Table 2; Figure 3). Although this relationship was of borderline statistical significance for 1991, the relationship was stronger for the period 1986–1993 (Table 2).

Relationships between growth reductions and stand elevation or insecticide spray history were weak (Table 2). Elevation was entered into the 1976 and 1983 regression models but did not explain a statistically significant percentage of the variation in growth reductions among stands. Similarly, although the effect of insecticide spraying was entered into regression models for 1977 and 1983, it also did not explain a significant proportion of the variation in growth reductions among stands for these years. However, there was a statistically significant, albeit somewhat weak, negative relationship between the cumulative number of times a stand was sprayed up to 1985 and average growth reductions over the period spanning 1981–1985 (Table 2). By 1985, all stands had been sprayed at least three times and approximately 60% of stands had been sprayed more than 10 times. Growth reductions were, on average, 6% less severe in stands sprayed more than 10 times.

Discussion

We examined variations in the impact that spruce budworm outbreaks have on balsam fir/spruce-dominated stands in northern New Brunswick. Outbreak impacts can be evaluated using various measures over various scales. While we quantified impact by measuring the degree to which the radial growth of balsam fir was reduced in stands during spruce budworm outbreaks, others have quantified impact by measuring host defoliation levels among species (Nealis and Régnière 2004), in stands (MacKinnon and MacLean 2003), and over landscapes (Gray et al. 2000, Candau and Fleming 2005). Host mortality levels have also been used to measure outbreak impacts (MacLean and Ostaff 1989, Bergeron et al. 1995). Of course, variation in the impact of budworm outbreaks on hosts does not always reflect variation in budworm population densities, as others have shown (Lysyk 1990, Nealis and Régnière 2004). The sometimes weak, or nonlinear, relationship between outbreak impact and budworm abundance occurs because impact is not only influenced by budworm population densities but also by the ability of hosts to withstand the effects of a given population level of these defoliators. In many cases, therefore, budworm impacts on forests result from an interaction between these factors. Although information about budworm population dynamics must form the basis of managing outbreaks impacts over the long-term, describing and quantifying patterns of budworm impact is often of more immediate and practical relevance to forest managers as it provides a means to identify stands that are most vulnerable to outbreaks and to target management strategies (e.g., adjustments of harvest scheduling, and insecticide applications) accordingly.

We found a significant negative relationship between the hardwood content of surrounding forest landscapes (%) and mean balsam fir radial growth reductions (%) during the initial years of the last spruce budworm outbreak in northern New Brunswick. As the hardwood content of forest landscapes increased, mean growth reductions in balsam fir/spruce-dominated stands decreased. This finding is consistent with a previous stand-level study in New Brunswick (Su et al. 1996) in which defoliation caused by budworm outbreaks was much less in stands mixed with hardwood species than in host-dominated stands. It also supports a long history of studies indicating that forest composition has a significant influence on the impact of budworm outbreaks (Fauss and Pierce 1969, MacLean 1980, Bergeron et al. 1995, MacKinnon and MacLean 2003). On the other hand, our finding seems to be contradicted by another study in New Brunswick that showed no statistically significant differences in balsam fir or spruce growth reductions among stands in softwood or mixedwood landscapes (MacKinnon and MacLean 2004). However, this study did not remove the potentially confounding spatial component to budwormcaused growth reductions or forest composition, and this may explain the discrepancy in findings.

Several hypotheses can be proposed to explain why host growth reductions of balsam fir were less severe in stands surrounded by hardwood forests. Budworm populations in these stands may have been lower because fir stands isolated in hardwood landscapes are simply harder for dispersing moths to find. However, in a Quebec study, Cappuccino et al. (1998) found that moth densities did not significantly differ among balsam fir stands isolated by hardwood forests and contiguous tracts of balsam fir forests. Thus, stand isolation is an unlikely explanation for our findings. High levels of competition in small stands isolated by hardwood forests could contribute to significant losses of first- and second-instar larvae during dispersal to other hosts (Kemp and Simmons 1978). Although the stands we sampled were dominated by host trees, balsam fir or spruce, dispersal losses could be a significant contributing factor among isolated stands if the stand edge to area ratio is high (Roland 1993; Kouki et al. 1997). A favored explanation for lower budworm impacts in balsam fir/spruce stands surrounded by hardwood forests is that they contain more abundant and a more diverse complex of budworm natural enemies. Cappuccino et al. (1998) found that tachinid parasitism of larvae and ichneumonid parasitism of pupae were greater in balsam fir stands isolated by hardwood forests than in expansive tracts of balsam fir. Similarly, Quayle et al. (2003) found parasitism of eggs by a hymenopteran species was greater in balsam fir stands than in stands mixed with hardwood species. More abundant nectar sources and alternate hosts associated with hardwoods probably explain the higher parasitoid densities (Simmons et al. 1975, Houseweart et al. 1984) that help to suppress budworm populations. Larval predation by a potentially more diverse community of birds at forest edges and in mixedwoods may also be a contributing factor (Crawford and Jennings 1989, Drapeau et al. 2000). Another explanation for lower growth reductions in stands of hardwood landscapes may be related to site conditions.

To reduce the level of damage caused by the last spruce budworm outbreak in New Brunswick, large insecticide spray programs were undertaken from 1972 to 1993. We found that spray history was generally a weak and inconsistent predictor of the degree to which balsam fir growth was reduced during budworm outbreaks. The lack of spray effects in individual years undoubtedly reflects the fact that host growth reductions in a given year are more strongly related to the cumulative effects of defoliation, over a number of years on all ages of foliage, than the level of defoliation that occurs in any given year (Erdle and MacLean 1999). Because spraying against budworm generally only influences current-year defoliation, it perhaps is not surprising that we found no effect during the individual years tested. The fact that cumulative defoliation levels, rather than defoliation in any one particular year, more strongly affect growth reductions is emphasized by our finding that host growth reductions from 1981 to 1985 tended to be less severe among stands that had been sprayed more often. However, the cumulative effects of spraying were not consistent, with no effect observed during the other two growth periods tested: 1972-1980 and 1986-1993. Weak relationships between budworm impact levels and spraying are reported throughout the literature. MacLean et al. (1984) found little difference in volume losses among insecticidetreated and untreated spruce, and spraying seems to have little influence on large-scale patterns of budworm defoliation (Fleming et al. 1984, Hardy et al. 1986). We suspect that the spatial scale of analysis, varying local factors that affect budworm densities (or host vulnerability), as well as spraying methods, intensity, and varying efficacy may all confound the ability to detect relationships between growth reductions and insecticide spray history, especially with a relatively small number of samples. It is also important to note that insecticide spraying in New Brunswick has been designed to prevent tree mortality rather than to minimize growth reduction (MacLean et al. 1984).

An unexpected finding of this study was the temporal trend in the influence of landscape hardwood content on balsam fir growth reductions. Su et al. (1996) recognized the potentially confounding effect that outbreak year may have on forest composition effects when their regression models indicated that stand hardwood content explained progressively less variation in defoliation levels among stands over time, in the years toward the end of the budworm outbreak (1989-1993). This temporal trend is consistent with our regression results from 1976 to 1985. However, when Su et al. (1996) followed their regression analyses with a test for a hardwood content-outbreak year interaction effect and found it to be insignificant, they proposed that increasing forest hardwood content has same proportional decrease in budworm impacts, regardless of changes in budworm population levels over time. Our results do not support this hypothesis. When average defoliation levels decreased substantially from the early 1980s onward, presumably a reflection of low budworm densities resulting from the combined cumulative effects of spraying and natural drivers of decreasing population trends, forest hardwood content explained little to no variance in growth reductions among stands in the 1980s. When budworm

population densities are low, it is possible that parasitoids are sufficiently abundant in all forests to dilute any spatial variation in budworm impacts that are mediated by forest hardwood content. This hypothesis does not preclude the idea that rates of parasitism vary with forest hardwood content, even when budworm populations are low (i.e., at endemic levels), as two studies in Quebec have shown (Cappuccino et al. 1998; Quayle et al. 2003). It simply suggests that impacts related to hardwood content, can no longer be detected when populations are low and causing little damage. A potentially interesting extension to this study might be to examine how parasitism rates vary through the course of an outbreak in relation to forest hardwood content. The positive relationship between growth reductions and surrounding forest hardwood content in the late 1980s and early 1990s is a more curious finding that may be partly related to a greater or more rapid reduction in budworm population densities among stands of firdominated landscapes that were sprayed more frequently.

Conclusions

This study showed that surrounding forest hardwood content significantly influences the severity of budwormcaused growth reductions in mature balsam fir-spruce stands. This finding lends support to the "silvicultural hypothesis," which states that forest management activities altering forest composition could be used to minimize the impacts of budworm impacts. What makes this study stand apart from others that have examined relationships between forest composition and outbreak impacts is that we measured budworm impacts on individual trees (i.e., growth loss during budworm outbreaks), rather than using some landscape-level spatially integrated measure of damage extent. Because host growth losses during budworm outbreaks directly reflect budworm population densities, this study forms a strong basis from which to make inferences about the effects of forest composition on local-scale budworm population dynamics. Of particular significance is the fact that our study shows forest composition has an active effect on budworm populations, which is probably mediated through the differences in parasitism rates related to forest hardwood content, and not just a passive effect of increasing amounts of host available for defoliation (e.g., Blais 1983). Distinguishing between active and passive effects of forest composition on budworm outbreak impacts has significant implications for how foresters might alter the composition of forest landscapes to minimize future budworm impacts. Increasing hardwood content may yield proportionately greater rewards.

Forest managers are interested in cost-effective ways to reduce the impacts of spruce budworm outbreaks on timber supplies. Although spraying insecticides has been used extensively throughout New Brunswick in the past, attaining protection objectives through widespread application of biological insecticides will be costly. We suggest that increasing the hardwood content of managed forest landscapes could help to reduce the impact of budworm outbreaks. However, forest management plans designed to minimize the impact of budworm outbreaks should combine several strategies, such as planting of nonhost softwood species, harvest scheduling and silviculture (e.g., stand thinning), and judicious use of insecticides, with ways to increase forest hardwood content. Additionally, the effects of surrounding hardwood content should be incorporated into decision support tools that predict stand vulnerability, such as the Spruce Budworm Decision Support System (Mac-Lean et al. 2001, 2002). More accurate predictions of stand vulnerability will help to target specific management strategies.

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