Legacy of Insect Defoliators: Increased Wind-Related Mortality Two Decades After a Spruce Budworm Outbreak

Sarah L. Taylor and David A. MacLean

Abstract: Effects of spruce budworm (Choristoneura fumiferana Clem.) outbreaks on growth and survival of balsam fir (Abies balsamea [L.] Mill.) and spruce (Picea spp.) are well documented, but few studies extend beyond 10 years after defoliation ceased. We used inventory data from 106 permanent sample plots in >50-year-old balsam fir stands in northern New Brunswick, Canada, to determine legacy effects of the 1969–1993 budworm outbreak on stand development up to 29 years after defoliation ceased. Defoliation data were from annual aerial surveys from 1945 to 1993 and plot ground sampling from 1985 to 1993. Plots were stratified into net stand volume development categories (decreasing, stable, and increasing 1985–2005 stemwood volume) and related to outbreak phases (outbreak, direct 1–10 years after defoliation ceased, and legacy >10 years), outbreak severity (1–4 [low], 5–8 [medium], and 9–12 [high] years of defoliation), and stand age (mature and overmature). Stand age was an important factor influencing outbreak severity (e.g., $r^2 = 0.383, P < 0.01$). Trend and rate of volume development over time were related to past outbreak severity and increased rate of postoutbreak wind-related mortality, which peaked at 11 m$^3$/ha/yr 11–15 years after defoliation ceased. Results indicate that aging postoutbreak stands are more vulnerable to wind disturbance events, effecting rapid stand decline. FOR. SCI. 55(3):256–267.

Keywords: balsam fir, Choristoneura fumiferana, spruce, stand dynamics, tree growth

Disturbance events contribute to spatial heterogeneity of vegetation patterns, which in turn affect subsequent patterns and effects of disturbances (Mladenoff and Baker 1999, Radeloff et al. 2000, Kuklewski and Veblen 2007). Because many areas are prone to multiple kinds of disturbances over different temporal and spatial scales, focusing on a single disturbance type may not fully capture a site’s disturbance history (Furyaev et al. 1983). Indeed, interactions between different disturbances are probably the rule rather than the exception (Fleming 2000), and because the disturbance “signal” can remain for many years (MacLean and Andersen 2008), interactions may be temporally delayed; hence, there is a need to consider long-term, indirect or “legacy” effects of disturbance events.

Insect outbreaks are an example of a disturbance event with a large spatial extent and long temporal duration, thereby increasing opportunities for interactions with other disturbances. In Canada, a total of 709 million ha of forest sustained moderate to severe defoliation (>30% removal of current-year foliage) or beetle-killed trees from 1975 to 2000 (Canadian Council of Forest Ministers 2002, MacLean 2005), double the 295 million ha of forest available for commercial forestry activities (Natural Resources Canada 2008). Almost two-thirds of the defoliation was caused by spruce budworm (Choristoneura fumiferana Clem.) during major outbreaks in the 1970s and 1980s. Insect outbreaks typically occur over periods up to 10 years or more, resulting in repeated defoliation of the same areas. Historically, large spruce budworm outbreaks occur every 35 years (Royama 1984) and are the major driving force of stand development in balsam fir (Abies balsamea [L.] Mill.)–spruce (Picea spp.) forests (Baskerville 1975). Defoliation reduces growth and survival of balsam fir and spruce by up to 90% (MacLean 1980, Erdle and MacLean 1999), and mortality rates remain elevated for 5–10 years after defoliation ceases (e.g., Baskerville and MacLean 1979, MacLean 1980, Blais 1981, Ostaff and MacLean 1989, Erdle and MacLean 1999). A severe spruce budworm outbreak that results in extensive tree mortality considerably modifies forest structure and composition, resulting in long-lasting legacy effects, which in turn can reduce vulnerability to future budworm attack for 50 years or more (Blais 1981, Erdle and MacLean 1999, Bouchard et al. 2006). MacLean and Andersen (2008) observed long-term effects of defoliation on stand development and rate of stand break-up continuing up to 35 years after an outbreak in an immature balsam fir stand, as a result of differential spruce budworm-caused mortality in the 1950s.

Spruce budworm outbreaks also create conditions more susceptible to blow down (Morin 1994), as slender trees previously protected from wind by a closed canopy may be vulnerable to wind-related damage (e.g., uprooting and stem breakage) in more open postoutbreak stands. Wind-related breakage of dead budworm-killed trees (Stocks 1987, Ostaff and MacLean 1989, Bergeron and Leduc 1998, Taylor and MacLean 2007a) further opens up the canopy. In addition, surviving trees are more susceptible to Armillaria root rot.

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spruce budworm outbreak zones (south, middle, and north) Uplands, and Central Uplands ecoregions (Figure 1). Three the Appalachian Mountains, in the Highlands, Northern outbreak zone (Royama et al. 2005) in the rugged terrain of stands of the northern New Brunswick spruce budworm analyzed 106 plots in unmanaged spruce budworm host 1989 throughout the province (Porter et al. 2001). We permanent sample plot network established from 1985 to from the New Brunswick Department of Natural Resources forests (Rowe 1972) of New Brunswick, Canada, using data Methods

Study Area, Budworm History, and Plot Data

This study was carried out in the boreal and Acadian forests (Rowe 1972) of New Brunswick, Canada, using data from the New Brunswick Department of Natural Resources permanent sample plot network established from 1985 to 1989 throughout the province (Porter et al. 2001). We analyzed 106 plots in unmanaged spruce budworm host stands of the northern New Brunswick spruce budworm outbreak zone (Royama et al. 2005) in the rugged terrain of the Appalachian Mountains, in the Highlands, Northern Uplands, and Central Uplands ecoregions (Figure 1). Three spruce budworm outbreak zones (south, middle, and north) broadly delineate differences in timing and severity of historical defoliation during the 20th century, based on annual maps of budworm egg-mass densities (Royama et al. 2005). For the purposes of this study, defoliation refers to events in which >30% of current-year foliage has been removed by budworm, as this is the threshold for significant budworm-caused reduced growth and mortality (e.g., Erdle and MacLean 1999). During the last budworm outbreak, defoliation generally began in the 1970s, although defoliation was continuous throughout the 1960s in the middle zone (Royama et al. 2005) and ended in the late 1980s in the south and in 1993 in the north (Porter et al. 2004). Hence plots were restricted to the north zone to avoid confusing differences in outbreak patterns. Plots were selected to have ≥1 year(s) of defoliation, ≥3 measurements, and the following criteria at plot establishment in 1987–1989: >50 years old, >70% softwood, >60% balsam fir, <30% of red spruce (P. rubens Sarg.) and black spruce (P. mariana (Mill.) BSP.) combined, and <30% nonbudworm host species. Criteria were selected to identify the most susceptible and vulnerable budworm host stands. Hennigar et al. (2008) noted that white spruce (P. glauca [Moench] Voss), red spruce, and black spruce had approximately 72, 41, and 28% as much defoliation as balsam fir, respectively, regardless of defoliation severity or other stand variables tested. Mature balsam fir stands experience 43–72% more mortality than spruce stands, decreasing as hardwood content exceeds 30% (MacLean 1980, Su et al. 1996).

At plot establishment, ≈5.1 cm dbh trees in the circular 400-m² (0.04-ha) fixed-area plots were assigned numerical tags. Spruce, jack pine (Pinus banksiana Lamb.), and bal-
sam fir trees >9.0 cm dbh that had died within the past 5 years were also recorded and assigned to one of eight cause of death categories (broken top, insect, overmaturity, stem

Figure 1. Distribution of 106 plots in ≥50-year-old balsam fir–spruce stands across the New Brunswick north spruce budworm outbreak zone (Royama et al. 2005) by outbreak severity (low, 1–4 years; medium, 5–8 years; and high, 9–12 years of defoliation). Letter d indicates 41 plots with decreasing volume development for 1985–2005, of which 16 were overmature (>70 years old) at the end of the last outbreak (letters do on map); numbers indicate ecoregions (1, Highlands; 2, Northern Uplands; 3, Central Uplands; 5, Valley Lowlands; and 6, Eastern Lowlands).
balsam fir trees: the model of Kleinschmidt et al. (1980) for undefoliated mass for a given age of foliage (up to 5 years old), based on defoliation (C) in a given year (defoliation sequences by weighting estimates of current excessive years of defoliation (Taylor and MacLean 2008). As balsam fir foliage is retained for about 5 years, current defoliation does not gauge the cumulative impact of successive years of defoliation (nil-light, 0–30%; moderate, 31–70%; severe, 71–100%) from 1945 to 1993 (Carter and Lavigne 1993) for years before plot establishment or when no plot data were available. To ensure compatibility between the two survey techniques, ground-sampled individual tree defoliation estimates were weighted by basal area, which is proportional to tree crown size, to approximate the relative contribution of different-sized trees to an aerial estimate (MacLean and MacKinnon 1996). Use of aerial survey data was justified by high accuracy levels in relation to ground survey estimates (MacLean and MacKinnon 1996) and strong association with variability in annual growth (Taylor and MacLean 2008).

Both aerial sketch mapped and plot defoliation estimates were a measure of damage to the current year foliage only. As balsam fir foliage is retained for about 5 years, current defoliation does not gauge the cumulative impact of successive years of defoliation (Taylor and MacLean 2008). Yearly annual cumulative defoliation (CD) was calculated from the combined plot ground and aerial sketch mapped defoliation sequences by weighing estimates of current defoliation (C) in a given year (t) by the relative foliage mass for a given age of foliage (up to 5 years old), based on the model of Kleinschmidt et al. (1980) for undefoliated balsam fir trees:

\[
CD_t = 0.28C_t + 0.26C_{t-1} + 0.22C_{t-2} + 0.13C_{t-3} + 0.08C_{t-4} + 0.03C_{t-5}.
\]

Defoliation history was assessed in terms of factors affecting budworm-caused growth reduction and mortality: time since cessation of defoliation, number of years of defoliation, and cumulative defoliation levels (e.g., MacLean 1980). Years since cessation of current defoliation were used to determine three budworm phases: outbreak (≤0 years), direct effect (1–10 years), and legacy effect (>10 years). The 10-year threshold between direct and legacy effects was based on temporal trends identified by MacLean (1980) for budworm-caused mortality and reduced growth. Total number of years of moderate-severe (>30%) budworm defoliation were used to infer three outbreak severity classes: low (1–4 years), medium (5–8 years), and high (9–12 years), because the number of years of defoliation is strongly correlated with growth reduction (Ostaff and MacLean 1995). Defoliation continuity (i.e., isolated defoliation events versus successive defoliation events) was not incorporated into the outbreak severity rating as preliminary analysis revealed no effect on growth rates. Breaks in severe defoliation do not affect total number of years between initial defoliation and tree death (Blais 1958). Summed current defoliation, which is related to balsam fir mortality (e.g., Blais 1958, 1981, MacLean and Ostaff 1989), was used to gauge cumulative defoliation across the entire outbreak.

**Data Analyses**

**Assessment of Outbreak Phase and Severity**

The broad spruce budworm outbreak zones of Royama et al. (2005) do not account for variation in defoliation resulting from insecticide spray programs, nonuniformity of defoliation, and local site conditions, and therefore stand-level defoliation can differ considerably in a given year (Taylor and MacLean 2008). Hence, outbreak history was based on plot ground defoliation surveys from 1985 to 1993, supplemented with aerial sketch mapped annual defoliation (nil-light, 0–30%; moderate, 31–70%; severe, 71–100%) from 1945 to 1993 (Carter and Lavigne 1993) for years before plot establishment or when no plot data were available. To ensure compatibility between the two survey techniques, ground-sampled individual tree defoliation estimates were weighted by basal area, which is proportional to tree crown size, to approximate the relative contribution of different-sized trees to an aerial estimate (MacLean and MacKinnon 1996). Use of aerial survey data was justified by high accuracy levels in relation to ground survey estimates (MacLean and MacKinnon 1996) and strong association with variability in annual growth (Taylor and MacLean 2008).

Defoliation continuity (i.e., isolated defoliation events versus successive defoliation events) was not incorporated into the outbreak severity rating as preliminary analysis revealed no effect on growth rates. Breaks in severe defoliation do not affect total number of years between initial defoliation and tree death (Blais 1958). Summed current defoliation, which is related to balsam fir mortality (e.g., Blais 1958, 1981, MacLean and Ostaff 1989), was used to gauge cumulative defoliation across the entire outbreak.

**Assessment of Volume Development and Stand Dynamics**

Height and volume regression models for ≥9.1 cm dbh commercial species (Porter et al. 2001) were used to calculate live merchantable volume, periodic mortality (MORT), survivor growth (SG) and ingrowth (IG), from which periodic annual increment (PAI) was calculated as

\[
PAI = SG + IG - MORT.
\]

Periodic growth data for 18 plot measurement periods with intervals >5 years were excluded from analyses. Total mortality, budworm-caused mortality (insect cause of death), and wind-related mortality (wind throw, broken top, and stem breakage causes of death) were determined from all plot trees that died since establishment and up to 5 years before plot establishment. Total budworm-caused mortality is a minimum estimate of budworm impact, as stands were established toward the end of the outbreak and therefore not all budworm-caused mortality was captured. Three legacy phase wind damage classes were assigned: nil (0 m³/ha/yr), intermediate (>0–5 m³/ha/yr), and severe (>5 m³/ha/yr wind-related mortality). The overall pattern of volume development was assessed from yield curves of live merchantable volume against year and categorized as decreasing, stable, or increasing live merchantable volume from 1985 to 2005. The stable category included stable (net volume change < ±1 m³/ha/yr) and fluctuating volume development patterns of Taylor and MacLean (2005). Stand age at the end of the outbreak was projected from stand age data gathered at plot establishment.

**Statistical analyses**

Plots were stratified by three factors: outbreak severity (low, medium, or high), outbreak phase (outbreak, direct, or legacy), and volume development (decreasing, stable, or increasing); supplementary analyses evaluated effects of stand age and legacy phase wind damage class. Analyses
were restricted to >3 plots/stratum; data are essentially at the plot level, with only one plot per stand, but with plots stratified by stand variables. Statistical tests using Minitab (release 14 for Windows; Minitab, Inc., State College, PA) for each of the results sections below were as follows:

1. **Budworm outbreak history.** Relationship between last year of defoliation and number of years of defoliation was assessed using a Pearson product moment correlation. One-way analyses of variance (ANOVA) were used to assess differences in budworm outbreak severity measures among outbreak severity classes.

2. **Relationship between outbreak severity and stand characteristics.** Relationship between stand age at the end of the outbreak and outbreak severity were assessed using regression analysis. Budworm outbreak characteristics were compared between mature and overmature plots with decreasing volume development from 1985 to 2005 using a two-sample t test. Two-way ANOVAs were used to assess effects of stand characteristics on outbreak severity, outbreak phase, and an outbreak severity × phase interaction term for mature stands aged 51–70 years at the end of the outbreak.

3. **Stand development relative to the 1969–1993 budworm outbreak.** Stand and outbreak characteristics were compared across volume development categories for the legacy phase. \( \chi^2 \) analysis of plot frequency data was used to test for association between volume development and outbreak severity, and two-way ANOVAs were used to test differences in stand characteristics by volume development category, outbreak severity, and a development category × outbreak severity interaction term. Post hoc Tukey’s tests \( (P = 0.05) \) were used to identify significant pairwise comparisons.

### Table 1. Statistical comparison of 1969–1993 spruce budworm outbreak severity measures and budworm-caused mortality and associated growth and volume by outbreak severity and outbreak phase, for 74 permanent sample plots in balsam fir–spruce stands aged 51–70 yr at end of outbreak

<table>
<thead>
<tr>
<th>Outbreak severity (years of defoliation)</th>
<th>ANOVA</th>
<th>F (_{df})</th>
<th>( P^b )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low (1–4)</td>
<td>Medium (5–8)</td>
<td>High (9–12)</td>
<td>( F_{df} )</td>
</tr>
<tr>
<td>Outbreak severity measures</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sum current defoliation (%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>245 ± 13</td>
<td>457 ± 14</td>
<td>722 ± 36</td>
<td>128.52</td>
</tr>
<tr>
<td>No. years of current defoliation (years)</td>
<td>3.3 ± 0.2</td>
<td>6.4 ± 0.2</td>
<td>9.9 ± 0.4</td>
</tr>
<tr>
<td>First year defoliation</td>
<td>1975.2 ± 0.4</td>
<td>1973.2 ± 0.3</td>
<td>1972.1 ± 0.3</td>
</tr>
<tr>
<td>Last year defoliation</td>
<td>1984.5 ± 0.3</td>
<td>1987.5 ± 0.4</td>
<td>1988.9 ± 0.4</td>
</tr>
<tr>
<td>Outbreak duration (years)</td>
<td>10.1 ± 0.6</td>
<td>15.3 ± 0.5</td>
<td>17.8 ± 0.5</td>
</tr>
<tr>
<td>Stand characteristics over time relative to budworm outbreak phase</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Budworm-caused mortality (m(^3)/ha/yr)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Outbreak</td>
<td>1.5 ± 1.5</td>
<td>3.4 ± 1.8</td>
<td>2.3 ± 0.5</td>
</tr>
<tr>
<td>Direct</td>
<td>1.1 ± 0.4</td>
<td>0.7 ± 0.2</td>
<td>1.0 ± 0.3</td>
</tr>
<tr>
<td>Legacy</td>
<td>0.0 ± 0.1</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td>Total mortality (m(^3)/ha)</td>
<td>10.2 ± 3.5</td>
<td>14.1 ± 3.3</td>
<td>34.6 ± 17.9</td>
</tr>
<tr>
<td>Survivor growth (m(^3)/ha/yr)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Outbreak</td>
<td>8.0 ± 1.8</td>
<td>4.8 ± 0.5</td>
<td>3.2 ± 0.4</td>
</tr>
<tr>
<td>Direct</td>
<td>5.2 ± 0.2</td>
<td>4.5 ± 0.2</td>
<td>4.0 ± 0.3</td>
</tr>
<tr>
<td>Legacy</td>
<td>5.5 ± 0.3</td>
<td>5.3 ± 0.6</td>
<td>7.5 ± 2.3</td>
</tr>
<tr>
<td>Live merchantable volume (m(^3)/ha)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Outbreak</td>
<td>236 ± 4.6</td>
<td>218 ± 8.6</td>
<td>175 ± 12.1</td>
</tr>
<tr>
<td>Direct</td>
<td>218 ± 7.5</td>
<td>204 ± 8.6</td>
<td>171 ± 12.7</td>
</tr>
<tr>
<td>Legacy</td>
<td>224 ± 8.8</td>
<td>179 ± 16.0</td>
<td>195 ± 25.2</td>
</tr>
</tbody>
</table>

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^a^ Analysis restricted to years with moderate–severe defoliation (>30%).

^b^ ANOVAs performed where there were ≥3 plots per defoliation severity class. Asterisks indicate significant at \( P < 0.05 \) (*), \( P < 0.001 \) (**), ns, not significant. Letters indicate significant pairwise comparisons between outbreak severity classes: low (L), medium (M), and high (H).

^c^ Mean ± 1 SE.

^d^ Outbreak duration (number of years) calculated as difference between first and last year of the outbreak.

^e^ Budworm outbreak phases are during outbreak (outbreak), 1–10 years after outbreak (direct), or 11–25 years after outbreak (legacy).

^f^ Includes budworm-killed trees that died up to 5 years prior to plot establishment in 1987–1989.

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**Figure 2.** Spruce budworm defoliation history for stands experiencing low (1–4 years), medium (5–8 years), and high (≥9 years of defoliation) severity outbreaks. Vertical dotted line indicates end of budworm outbreak; horizontal dashed line indicates end of budworm outbreak; horizontal dashed line 30% threshold between nil-light (N-L) and moderate–severe (M-S) defoliation.
Postoutbreak dynamics: insect versus wind-related mortality. \( \chi^2 \) analysis on plot frequency data was used to test for association between outbreak severity and legacy phase wind damage class. Two-way ANOVAs were used to test differences in stand characteristics by outbreak severity, wind damage class, and an outbreak severity × wind damage interaction term for stands in the legacy phase.

Results

Budworm Outbreak History

A synchronous pulse of defoliation occurred between 1970 and 1978, with a maximum of 82% of 106 plots experiencing defoliation in 1975, followed by only 5–10% of plots in 1977–1978, after which defoliation patterns became asynchronous in the 1980s. Figure 2 illustrates patterns of annual cumulative defoliation relative to the end of the outbreak (shown by the dotted line) for the three outbreak severity classes. Year of cessation of defoliation ranged from 1975 to 1993 and was strongly positively correlated with total outbreak defoliation \( (r = 0.618, P < 0.001) \). About two-thirds (59%) of defoliation occurred in the last 10 years of the outbreak. Low severity outbreaks (1–4 years of defoliation) were significantly shorter in duration (10 years versus 15–18 years) and completed earlier (1984 versus 1987–1989) than more severe outbreaks (Table 1). Outbreak severity varied spatially by ecoregion (Figure 1), with plots in the Northern Uplands experiencing the most severe outbreak conditions (93% of 30 plots had ≥5 years of defoliation) and plots in the Central Uplands experiencing the least severe outbreak conditions (59% of 28 plots had ≤4 years of defoliation).

Relationship between Outbreak Severity and Stand Characteristics

Number of years of spruce budworm defoliation, which was used as an indicator of outbreak severity, was weakly positively correlated with stand age for plots with decreasing and stable volume development patterns (Figure 3). Therefore, analyses relating outbreak severity to stand characteristics were restricted to mature stands aged 51–70 years at the end of the outbreak (Table 1). Survivor growth was 1.2 m\(^3\)/ha/yr less during the direct phase and total budworm-caused mortality was 24.4 m\(^3\)/ha more for high than low outbreak severity classes (Table 1). Survivor growth was the only stand characteristic with statistically significant differences between outbreak severity classes, outbreak phases, and the outbreak severity × phase interaction term (Table 2). Budworm-caused mortality also varied significantly by outbreak phase, but not for the outbreak severity × phase interaction term (Table 2). Stands with low outbreak severity had 61 and 47 m\(^3\)/ha more live merchantable volume in the outbreak and direct phases, respectively, than those with high outbreak severity (Table 1), but the outbreak severity × phase interaction term was not statistically significant (Table 2).

Stand Development Relative to the 1969–1993 Budworm Outbreak

Figure 4 shows live merchantable volume over time yield curves for representative plots in decreasing, stable,
and increasing volume development categories relative to the end of the spruce budworm outbreak, with symbol shading indicating outbreak severity. Of the 106 balsam fir-dominated plots, 39% had decreasing volume development over time, 27% were stable, and 34% had increasing volume development. The Northern Uplands had the largest proportion of plots with decreasing volume development (50% of 30 plots), denoted by the letter d on Figure 1. Live merchantable volume ranged between 0 and 297 m$^3$/ha for decreasing, 129–295 m$^3$/ha for stable, and 93–354 m$^3$/ha for increasing volume development categories (Figure 4). Volume decline in stands with decreasing volume development was greatest in the medium and high outbreak severity classes (Figure 4a). Live merchantable volume <100 m$^3$/ha occurred in plots with decreasing volume development, and all but 1 of 15 decreasing plots with <100 m$^3$/ha experienced medium to high outbreak severity (Figure 4a).

There was a significant association ($\chi^2 = 6.681$, df = 2, $P < 0.05$) between past outbreak severity (low, medium, and high) and trends of volume development from 1985 to 2005 (decreasing versus nondecreasing) for 68 plots measured during the legacy phase (>10 years after budworm outbreak ended). The proportion of plots that experienced medium to high outbreak severity was higher in stands with decreasing volume development (79%) than for those with stable or increasing volume development (41–55%). Declining stands experienced the longest outbreak duration, but other measures of outbreak severity were not significant (Table 3). The age of stands in the legacy phase increased across the outbreak severity classes (e.g., 74, 87, and 108 years, respectively, for decreasing stands with low, medium, and high severity outbreaks), and there was a significant volume development × outbreak severity interaction ($F_{4,67} = 5.43, P < 0.001$). Stands with decreasing volume development that were >70 years had 159% more summed current defoliation (544 versus 385%; $T = -2.69$, df = 15, $P < 0.05$) and 1.9 years more defoliation (7.4 versus 5.5 years; $T = -2.35$, df = 15, $P < 0.05$) than 51- to 70-year-old stands. However, there were no significant differences in stand characteristics between stands aged 51–70 and >70 years (e.g., $P = 0.484$ for live merchantable volume).

During the outbreak phase, decreasing, stable, and increasing volume development categories had similar live volume (206–235 m$^3$/ha, $P = 0.178$); however, by the direct phase, the decreasing volume development category had 17 m$^3$/ha less volume ($F_{2,248} = 3.39, P < 0.05$), and the difference widened further to 88–108 m$^3$/ha less by the legacy phase (Table 3). In all volume development categories and outbreak severity classes, balsam fir proportion declined, whereas hardwood increased over time. For example, during the outbreak, balsam fir constituted 80% and hardwood only 7% of stand volume for decreasing volume plots, but by the legacy phase these had changed to 68 and 17%, respectively. However, stand composition did not differ significantly among volume development categories in the legacy phase (Table 3).

During the legacy phase, decreasing plots had 2 m$^3$/ha/yr lower survivor growth and 7.5 m$^3$/ha/yr higher mortality than increasing plots. Periodic annual increment was +4.5 m$^3$/ha/yr for increasing versus −5.0 m$^3$/ha/yr for decreasing plots (Table 3). Ingrowth was negligible and did not significantly differ among the volume development categories (Table 3). Periodic annual increment was lowest in the direct budworm phase for all volume development categories (Figure 5a–c), reflecting elevated mortality and reduced growth rates (Table 1). Stable and increasing volume development categories were unaffected by outbreak severity class (Figure 5b and c). In contrast, stands with decreasing volume and low outbreak severity had increasing periodic annual increment over time, approaching zero in the legacy phase, whereas those with medium outbreak severity had depressed periodic annual increment, which did not start to recover until 15–20 years after defoliation ceased (Figure 5a). Prolonged negative periodic annual increment began during the outbreak at −3.5 m$^3$/ha/yr and continued for up to two decades, at −9.2 to −3.0 m$^3$/ha/yr for plots with medium outbreak severity (Figure 5a) and was associated

<table>
<thead>
<tr>
<th>two-way ANOVA</th>
<th>$P^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Budworm-caused mortality (m$^3$/ha/yr) Outbreak severity</td>
<td>0.39, 124</td>
</tr>
<tr>
<td>Outbreak phase</td>
<td>4.71, 124</td>
</tr>
<tr>
<td>Outbreak severity × phase interaction term</td>
<td>0.60, 124</td>
</tr>
<tr>
<td>Survivor growth (m$^3$/ha/yr) Outbreak severity</td>
<td>3.21, 124</td>
</tr>
<tr>
<td>Outbreak phase</td>
<td>5.33, 124</td>
</tr>
<tr>
<td>Outbreak severity × phase interaction term</td>
<td>2.87, 124</td>
</tr>
<tr>
<td>Live merchantable volume (m$^3$/ha) Outbreak severity</td>
<td>5.57, 124</td>
</tr>
<tr>
<td>Outbreak phase</td>
<td>0.54, 124</td>
</tr>
<tr>
<td>Outbreak severity × phase interaction term</td>
<td>1.11, 162</td>
</tr>
</tbody>
</table>

ANOVA performed where ≥ 3 plots per combination class.

Asterisks indicate significant at $P < 0.05$ (*), $P < 0.01$ (**), ns, not significant. Letters indicate significant pairwise comparisons between outbreak severity classes: low (L), medium (M), and high (H); and outbreak phases: outbreak (O), direct (D), and legacy (Le). Outbreak severity and outbreak phase classes are defined in Table 1.
Mortality in stands with decreasing volume development exceeded that in stands with stable or increasing volume, by 6–8 m$^3$/ha/yr in the direct phase ($F_{2,204} = 28.23, P < 0.001$) and by 5–7 m$^3$/ha/yr in the legacy phase (Table 3).

**Postoutbreak Dynamics: Insect Versus Wind-Related Mortality**

By the legacy phase, total spruce budworm-caused mortality was 5.8 m$^3$/ha higher in decreasing than in increasing plots, but differences were not statistically significant (Table 3). Overall, trees recorded as budworm-killed made up 43% of trees dead at plot establishment in 1987–1989. Budworm-killed trees constituted 49–60% of total mortality during the outbreak phase, declining to 18–37% 1–5 years, to 4–7% 6–10 years, and to 0–1% 11–15 years after defoliation ended. In contrast, wind-related mortality increased from 21–25% of total mortality during the outbreak, to 21–57% during the direct phase, and to 35–67% during the legacy phase. The resultant wind-related mortality pulse lasted more than 20 years and was greatest in stands with decreasing volume development that experienced medium outbreak severity (Figure 5d). In stands with low and medium outbreak severity, wind-related mortality peaked at 3.1 m$^3$/ha/yr, 6–10 years after defoliation ceased, and at 6.5 m$^3$/ha/yr, 11–15 years after defoliation ceased, respectively. By 21–25 years after defoliation ceased, wind-related mortality had declined to 1.7 m$^3$/ha/yr, but this still exceeded that during the outbreak (1.1 m$^3$/ha/yr). There were insufficient data to determine wind mortality trends in stands that experienced high outbreak severity (i.e., 9–12 years of defoliation).

During the legacy phase, plots with decreasing volume had 6.2 m$^3$/ha/yr and 60.5 m$^3$/ha more total wind-related mortality than plots with increasing volume. Broken top was the least common form of wind-related tree death, constituting only 19 and 12% in low and medium outbreak severity classes, respectively. Stem breakage exceeded wind throw (51 versus 30% of wind-related deaths) in stands with low outbreak severity, but not in stands with medium outbreak severity (47 versus 41%, respectively). There was no association between legacy phase wind damage and outbreak severity ($\chi^2 = 2.067, df = 4, P < 0.723$), but stand age increased with wind damage intensity (76 versus 84 years for nil and severe wind damage classes, respectively), and there was a significant outbreak severity $\times$ wind damage interaction for stand age ($F_{4,56} = 3.31, P < 0.05$). Suppression and overmaturity caused $\sim$0.4 m$^3$/ha/yr mortality and did not differ significantly among volume development categories.

**Discussion**

**Legacy Effects of Budworm Outbreaks**

The long-term data set used in this study is unique in that it spans up to 10 years of direct postbudworm outbreak effects and up to 15 years of longer term legacy effects 11–25 years after cessation of defoliation. Our data demonstrate that effects of spruce budworm outbreaks on stand dynamics extend far beyond the commonly documented 10-year period of budworm-caused mortality after cessation of defoliation, affecting subsequent stand decline and
Compounding Effects of Insect and Wind-Related Disturbance Events

Balsam fir becomes susceptible to a variety of environmental stresses, notably wind, as it approaches maturity at ~60 years (Sprugel 1975). Ruel (2000) observed that vulnerability of balsam fir to wind throw increased with age from 36% for 50-year-old stands to 55% for 90-year-old stands, based on a study of wind throw associated with severe November 1994 storm events in Quebec. In this study, the level of postoutbreak wind-related mortality was influenced by spruce budworm outbreak severity, budworm outbreak phase, and volume development pattern (Figure 5d–f). Budworm-caused mortality and defoliation open the

Table 3. Statistical comparison of budworm outbreak history and stand characteristics by volume development category, for 68 permanent sample plots measured in the legacy phase >10 yr after cessation of defoliation

<table>
<thead>
<tr>
<th>Status of 1969–1993 budworm outbreak</th>
<th>Decreasing (D)</th>
<th>Stable (S)</th>
<th>Increasing (I)</th>
<th>ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sum current defoliation (%)</td>
<td>441.3 ± 30.4**</td>
<td>377.5 ± 41.1</td>
<td>337.0 ± 31.0</td>
<td>2.70</td>
</tr>
<tr>
<td>No. years of current defoliation (years)</td>
<td>6.2 ± 0.4</td>
<td>5.3 ± 0.6</td>
<td>4.7 ± 0.4</td>
<td>2.79</td>
</tr>
<tr>
<td>Total outbreak duration (years)**</td>
<td>14.6 ± 0.9</td>
<td>12.7 ± 0.9</td>
<td>11.6 ± 0.8</td>
<td>3.26</td>
</tr>
<tr>
<td>Stand age (years)</td>
<td>86 ± 2.9</td>
<td>74 ± 1.5</td>
<td>72 ± 1.3</td>
<td>11.39</td>
</tr>
<tr>
<td>Live merchantable volume (m³/ha)</td>
<td>129 ± 12.9</td>
<td>217 ± 10.3</td>
<td>237 ± 12.6</td>
<td>23.45</td>
</tr>
<tr>
<td>Balsam fir (% volume)</td>
<td>68.3 ± 4.4</td>
<td>78.4 ± 3.9</td>
<td>75.8 ± 2.8</td>
<td>1.83</td>
</tr>
<tr>
<td>Spruce (% volume)</td>
<td>14.9 ± 2.9</td>
<td>9.0 ± 2.2</td>
<td>14.5 ± 2.2</td>
<td>1.39</td>
</tr>
<tr>
<td>Hardwood (% volume)</td>
<td>16.8 ± 4.0</td>
<td>11.3 ± 3.7</td>
<td>8.4 ± 2.2</td>
<td>1.58</td>
</tr>
<tr>
<td>Survivor growth (m³/ha/yr)</td>
<td>3.4 ± 0.5</td>
<td>6.8 ± 0.7</td>
<td>5.5 ± 0.3</td>
<td>12.16</td>
</tr>
<tr>
<td>Ingrowth (m³/ha/yr)</td>
<td>0.2 ± 0.1</td>
<td>0.3 ± 0.1</td>
<td>0.1 ± 0.0</td>
<td>1.94</td>
</tr>
<tr>
<td>Mortality (m³/ha/yr)</td>
<td>8.6 ± 1.8</td>
<td>3.4 ± 0.8</td>
<td>1.1 ± 0.3</td>
<td>8.57</td>
</tr>
<tr>
<td>Wind-related mortality (m³/ha/yr)</td>
<td>7.8 ± 1.8</td>
<td>1.9 ± 0.5</td>
<td>0.7 ± 0.3</td>
<td>9.53</td>
</tr>
<tr>
<td>Periodic annual increment (m³/ha/yr)**</td>
<td>−5.0 ± 2.0</td>
<td>3.6 ± 0.9</td>
<td>4.5 ± 0.4</td>
<td>13.95</td>
</tr>
</tbody>
</table>

* Asterisks indicate significant at P < 0.05 (*), P < 0.01 (**), and P < 0.001 (***), ns, not significant. Letters indicate significant pairwise comparisons between volume development categories: decreasing (D), stable (S), and increasing (I).
* Mean ± 1 SE.
* Duration is the total number of years between the first and last year of >30% current defoliation.
* Total budworm-caused mortality observed over period of assessment (1982–2005), which includes budworm-killed trees that died up to 5 years before permanent sample plots establishment in 1987–1989.
* Periodic annual increment = survivor growth + ingrowth − mortality.

break-up. Budworm outbreaks resulted in altered stand characteristics, in the form of lower live merchantable volume during the direct budworm phase and an increased proportion of nonbudworm host species in the legacy phase. Significant differences in 1969–1993 budworm outbreak severity were observed among 1985–2005 volume development categories (Table 3). Higher outbreak severity was associated with the decreasing volume development category, lower live merchantable volume (Figure 4a), and higher levels of postoutbreak wind-related mortality (Figure 5d–f). Thus, it would appear that stands hardest hit by the outbreak, which have the highest budworm-caused mortality rates, were also the hardest hit in terms of wind-related mortality for up to 20 years after defoliation ceased. This finding contrasts with findings by MacLean and Andersen (2008) that plots with high levels of budworm-caused mortality in an immature balsam fir stand in the 1950s had lower mortality 10–20 years later. However, these conflicting results could reflect an age effect.

MacLean and Andersen (2008) followed the postoutbreak fate of <50-year-old immature stands, whereas in this study we followed the postoutbreak fate of >50-year-old mature and overmature stands. Our results showed that stand age was associated with increased outbreak severity (Figure 3) and had a significant outbreak severity × legacy phase wind damage interaction. Many published studies have reported higher levels of budworm-caused mortality with increased stand age, resulting in a transition from self-thinning in immature stands to stand replacement in mature stands (Baskerville 1975, MacLean 1980). For example, MacLean (1980) noted that budworm-caused mortality averaged 42% in immature stands and 85% in mature balsam fir stands. Also, balsam fir is a moderately short-lived species, which naturally starts to decline at 70–90 years of age (Bakuzis and Hansen 1965, Porter et al. 2001, Taylor and MacLean 2005). Hence, the older, less resilient stands in this study did not have the ability to recover like the younger, more adaptable stands of MacLean and Andersen (2008). The potentially modifying effects of the earlier 1950s outbreak on vulnerability of stands to later attack in the 1969–1993 outbreak, reported elsewhere by Bouchard et al. (2006), could not be determined in this study as pre-1980s forest inventory data were not available. However, aerial sketch-mapped defoliation for the 1950s indicated that outbreak duration averaged 4 years of defoliation (i.e., low outbreak severity) and did not differ between volume development categories (e.g., decreasing versus increasing, P = 0.755). The lack of difference in 1950s budworm outbreak severity between volume development classes is probably related to immature stands being less susceptible to budworm defoliation.
canopy cover of postoutbreak stands to expose previously sheltered surviving canopy trees, weakened by defoliation, to the ravages of wind. Results from this study support the hypothesis of Taylor and MacLean (2005, 2007b) that insect and wind-related disturbance events interact synergistically to effect rapid stand decline and break-up in aging stands. Other studies have also noted interactions between budworm outbreaks and wind throw (Stocks 1987, Reams et al. 1988, Morin 1994, Bergeron and Leduc 1998). Budworm defoliation exposes residual surviving trees, which tend to have a high incidence of decay (Stillwell 1956), to increased wind exposure and hence a high probability of blow down. Reams et al. (1988) suggested that budworm and blow down risk of death, although related, are somewhat exclusive.
Thus, intense budworm defoliation may kill a tree before it can blow down, or vice versa, and relationships may be further confounded by competitive status because small-crowned trees in the understory may have higher defoliation stress but lower wind exposure stress owing to a reduced wind sail.

Magnussen et al. (2005) suggested that the tendency of budworm to drop from overstory to understory trees may result in a disproportionately high defoliation stress on small-crowned trees. Baskerville and MacLean (1979) observed higher mortality of suppressed and intermediate trees (73% of 3,970 stems/ha versus 27% for dominant and codominant crown classes), which tended to be killed first, resulting in altered stand structure with a larger proportion of dominant trees. In contrast, Bergeron et al. (1995) observed higher mortality levels for >15 cm dbh balsam fir compared with 5- to 10-cm dbh class trees (74.6 versus 48.5%, respectively) and noted that the size effect decreased from hardwood- to conifer-dominated stands.

Implications for Forest Management

The status of spruce budworm as one of the most destructive insect pests in North America (Gray et al. 1998) and the importance of balsam fir in commercial forestry has resulted in detailed and exhaustive studies of the spruce budworm–balsam fir system. Our results demonstrate the need to consider the complexity of disturbance dynamics when insect outbreak systems are examined, because a single disturbance event rarely operates in isolation (Fleming 2000). Interactions with other disturbance agents can drastically increase the impact and longevity of a disturbance event in time and space. For example, climate change is predicted to result in budworm outbreaks that are on average 6 years longer with an average of 15% greater defoliation (Gray 2008). In this study, the compounding effect of wind on postoutbreak stands resulted in a pulse of wind-related mortality 20 years after cessation of defoliation. Interactions between disturbances is not a new concept, but this is the first article to quantify wind disturbance >10 years after cessation of defoliation. Previous published work has focused on the role of wind during outbreaks (e.g., Reams et al. 1988) and subsequent fall of budworm-killed trees (e.g., Taylor and MacLean 2007a).

An understanding of the impact of insects on forest structure and function is critical to forecasting timber yields and establishing priority and timing for stand management strategies, such as harvesting, silvicultural treatment, and protection (Ostaff 1985). Adoption of forest management practices that emulate natural disturbance through harvesting to reconcile cost-effective wood production with biodiversity maintenance and long-term ecosystem productivity is increasing (Bergeron and Harvey 1997). A representative study on an industrial forest in northwest New Brunswick (Amos-Binks and David A. MacLean, University of New Brunswick, pers. comm., Oct. 16, 2005) demonstrated that budworm-inspired partially harvested stands (i.e., where trees estimated to be killed by spruce budworm were harvested) had blow down 15 times higher 2–3 years later than controls (15% versus 1% basal area blow down). There are two important points here: first, we need to understand the full effects of budworm outbreaks (i.e., direct defoliation and indirect wind effects) to formulate targets for natural disturbance-based emulation; and second, emulation harvest prescriptions must be reduced by the expected postharvest blow down. Budworm-caused mortality results in much more gradual canopy opening than harvesting, which has a higher immediate edge-effect blow down (Taylor and MacLean 2007a).

Spruce budworm outbreaks have long been recognized as a severe natural disturbance in eastern spruce–fir stands. Our results indicate that effects on growth and yield, in terms of associated higher levels of wind-caused mortality, continue for 11–25 years after the cessation of defoliation. These effects should be included in stand yield forecasts using stand dynamics models (e.g., Erdle and MacLean 1999) and the Spruce Budworm Decision Support System (MacLean et al. 2001, Hennigar et al. 2007). Postoutbreak wind-related mortality could be of particular concern in New Brunswick, as there is already a projected future wood supply shortage (Erdle and MacLean 2005) and blowdown could result in reduced returns through loss of wood volume, wood deterioration, and salvage harvesting costs (Mitchell 2004). Management decisions to protect stands against spruce budworm defoliation, using the biological insecticide Bacillus thuringiensis should recognize both direct and legacy effects of outbreaks. Stand development projections and wood supply models need to take into account losses that result from interaction of disturbance events to ensure the security of future wood supplies.

Literature Cited


