Outbreak patterns of the spruce budworm and their impacts in Canada
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ABSTRACT
Historical records (1941–1998) of spruce budworm defoliation in Canada were analyzed to estimate variability in the spatial and temporal patterns of defoliation, and to determine 27 representative patterns that adequately describe the spatial and temporal variability in defoliation. Spatially referenced estimates of growth loss and mortality resulting from an outbreak of spruce budworm were obtained by subjecting a national forest inventory to the spatially defined representative patterns of defoliation. The use of these estimates in determining the status of Canada’s forests as a carbon source or sink is discussed.

Key words: spruce budworm, defoliation, growth loss and mortality, carbon source or sink

Introduction
Insect outbreaks play a significant role in the dynamics of Canada’s forests by causing tree mortality and growth reduction. Tree mortality alters the age-class distribution and species composition of the residual forest stand (MacLean 1985, MacLean et al. 2001). As a large-scale disturbance agent, insect outbreaks alter successional pathways by creating gaps (Murphy et al. 1999, Turner et al. 2001). Insect outbreaks also negatively affect wood supply and disrupt harvesting schedules (MacLean et al. 2001, Pedersen 2004).

Outbreaks also play a significant role in the carbon flux of Canada’s forests (Kurz et al. 2002) because of their frequent occurrence over vast areas. Over 51 million ha were moderately or severely defoliated by the spruce budworm in Canada in 1975, and the current outbreak of mountain pine beetle, Dendroctonus ponderosae Hopkins, covered 4.2 million ha in 2003 (Wilson 2004). Tree mortality causes a rapid shift of large carbon stores from the live organic pool to dead organic matter carbon pools (Kurz and Apps 1999). Non-lethal defoliation causes a less significant shift in carbon stores by increasing leaf litter. Transfer to the atmosphere then occurs through decomposition (Apps and Price 1996). Non-lethal defoliation also reduces tree growth, thus temporarily reducing carbon uptake from the atmosphere. Conversely, severe outbreaks replace mature and over-mature stands that accumulate carbon slowly with younger stands that accumulate carbon rapidly.

Canada’s ratification of the Kyoto Protocol means that its greenhouse gas emissions (including carbon) must be reduced below 1990 levels during the first 5-year commitment period (1 January 2008 to 31 December 2012). By 2006, Canada must decide whether or not to include forest management when tallying its greenhouse gas emissions. Work is...
ongoing (Kurz et al. 2002) to estimate the role of Canada’s forests as a source (net producer of carbon) or sink (net accumulator of carbon), and the impact of insect outbreaks is a critical factor in these estimations (Kurz and Apps 1999, Kurz et al. 2002).

The spruce budworm, *Choristoneura fumiferana* Clem. (Lepidoptera: Tortricidae), is arguably the most damaging forest insect in North America’s forests (Hardy et al. 1983). In Canada, this native defoliator occurs throughout most of the range of white spruce (*Picea glauca* (Moench) Voss), although its preferred host is balsam fir (*Abies balsamea* L. Mill.) (Miller 1963). As a result of their vast spatial extent (Hardy et al. 1986) and impact, spruce budworm outbreaks are perhaps the major natural disturbance in Canada’s boreal forest (Fleming 2000, Fleming et al. 2002). Population densities have exhibited a somewhat regular cycle of approximately 30 to 40 years over an extensive landscape for at least the last three centuries (Royama 1984, 1992). During outbreak periods, a few hundred larvae may be found on a single host branch. Between these periods, populations may be so low as to make it difficult to find a single larva among several hundred branches (Greenbank 1963a). Outbreaks occur somewhat synchronously over extensive areas (Royama 1984, Candau et al. 1998, Gray et al. 1999, Williams and Liebhold 2000), but outbreak duration varies regionally from as few as one to as many as 20 years (Candau et al. 1998, Gray et al. 1999).

Complete defoliation of the current year’s needles of balsam fir can occur by the fourth year of an outbreak (Morris 1963), and tree mortality will begin by the fifth year (Belyea 1952). Spruce species (*P. glauca* (Moench.), *P. rubens* Sarg., and *P. mariana* (Mill.) BSP) are also affected, although to a lesser degree (Greenbank 1963b, Nealis and Régnière 2004). Volume increment of balsam fir can be reduced by as much as 20% after just 1 year of defoliation (Piene 1980), and radial growth (measured at breast height) can be reduced by as much as 75% after several years of severe defoliation (Miller 1977). Approximately 45% of the host trees in eastern Canada were killed during the outbreak of the 1910s and 1920s (Swaine and Craighead 1924); mortality reached approximately 58% of the host volume in Ontario between 1943 and 1955 (Elliott 1960). Approximately one-half of all insect-caused losses in forest productivity in Canada have been attributed to the spruce budworm (Hall and Moody 1994). Growth loss and mortality from spruce budworm outbreaks will vary with outbreak duration, severity, stand composition, and stand age (MacLean 1980, Erdle and MacLean 1999).

Predicting biological events is a risky endeavour, particularly when the dynamics of the biological system are complicated, as is the case for the spruce budworm (Royama 1984, 1992). Nonetheless, government policy-making, and forest management decision-making often rely on the “best guess” scenario. This paper describes historical outbreak patterns of the spruce budworm (defoliation levels over time), and estimates the spatial variability in volume loss that would result from a repetition of those patterns. This “best guess” scenario should contribute to the decision-making process as Canada ponders the inclusion of forest management in its Kyoto commitment.

**Methods**

**Available data – spruce budworm outbreaks**

The provinces of Canada conduct annual surveys of forest insect damage from fixed-wing aircraft. Although surveys are done according to provincial protocols, the methodologies vary only slightly. In-flight surveys use topographic maps to delineate polygons of insect damage and, in the case of spruce budworm, assign a class to their estimate of current-year defoliation within each polygon. MacLean and MacKinnon (1996) found the classification to be highly accurate in a study of defoliated stands in New Brunswick. However, classification schemes vary among provinces, and over time within certain provinces. Therefore, in order to construct a uniform data set of defoliation records, broad defoliation classes of nil–very light (≤19% defoliation), light–moderate (20%–60% defoliation), and severe (61%–100% defoliation) were created. The very light designation frequently comprised “spot” defoliation within generally undefoliated polygons. Therefore, in assigning a defoliation level to each class, the nil–very light class was assigned 0%, and the other classes were assigned the midpoint (40% or 80%) of their range. The defoliation levels (0%, 40% or 80%) were assigned to the digitized defoliation polygons from 1941–1998. The forested area of Canada was covered with a grid of 2 × 2 km cells, and the digitized defoliation polygons from each year were intersected with the cells. One defoliation level (D) was assigned to each of the 215 618 intersected cells for each year according to a rule of preponderance:

if >50% of the cell area intersected a nil defoliation polygon then D = 0;

else D = the value of the non-zero defoliation polygon whose area is greater.

Following Hardy et al. (1986), it was assumed that aerial application of insecticides had little effect on outbreak characteristics in Ontario and Quebec at the resolution and scale used here. Candau et al. (1998) cite several sources when they note that less than 2% of the moderately to severely defoliated area was sprayed in the largest Ontario spray program. Analyses by Lysyk (1990) and Fleming et al. (1984) also reported aerial application did not result in a high level of foliage protection. However, in New Brunswick, aerial application of insecticides approached 50% of the moderately and severely infested areas in many years, and significant protection was achieved (Kettela 1995). Therefore, New Brunswick data were modified in the following manner before assigning defoliation levels (D) to the 2 × 2 cells. Recorded defoliation was increased by an amount representative of the mean foliage protection (Kettela 1995) obtained by the chemical–year combination.

The last year (*Y* ) of the most recent complete outbreak from the 58-year period was defined in each cell as the most recent year with a non-zero D followed by five consecutive values of *D* = 0 (Gray et al. 1999). The first year (*Y* ) of this most recent outbreak was defined in each cell as the most recent year with a non-zero D that preceded *Y*, and was itself preceded by five consecutive values of *D* = 0. Note that, within a cell, there may be some values where *D* = 0 during the outbreak. Thus, the spruce budworm outbreak was described in each 4-km² cell by a temporal series of 0s, 40s and 80s.

**Estimating representative spruce budworm outbreak patterns**

Grouping objects by virtue of their similarity to each other, and their dissimilarity to objects of other groups, can be done by cluster analysis (Hand 1981). In pattern recognition termi-
nology, features are the characteristics that are used to distinguish the objects. Each of the \(n\) features describing an object constitutes a coordinate along a set of \(n\) perpendicular variable axes (feature space). Clustering procedures follow an agglomerative or a division procedure (Manly 1986). In the agglomerative procedure each object is initially in its own cluster (or group), and close clusters are gradually merged until there is only one cluster with all the objects. In the division procedure all objects are initially in a single cluster, and the cluster(s) is/are gradually split into two clusters until each object is in its own cluster.

Each object to be clustered must have the same number of features. Therefore, the maximum length of the outbreak was found in the data set (28 years), and enough 0s were appended to each cell where the outbreak was shorter than 28 years to give it 28 features. In this way, the defoliation sequence in each cell is an object that is entirely described by its 28 defoliation levels (features).

The large number (215,618) of cells required us to first conduct a FASTCLUS procedure (SAS Institute Inc. 1999) to identify initial clusters as seeds. We choose 200 seeds, as this number explained over 91% of the feature space \((r^2 > 0.91)\), and each addition seed cluster increased \(r^2\) by less than 0.001. We then subjected the 215,618 cells to agglomerative hierarchical clustering (PROC CLUSTER) using the 200 seeds as the starting point. We used Ward’s minimum variance method, which minimizes the within-cluster sum of squares over all clusters (SAS Institute Inc. 1999). We tested the significance of the clusters (i.e., the probability \(\alpha\) that each cluster was unique) by comparing the probability of obtaining an equal or greater pseudo \(F\) (Calinski and Harabasz 1974) to the Bonferroni-corrected level

\[
\alpha' = \frac{\alpha}{k \times (k-1)/2},
\]

where \(\alpha\) was our desired significance level \((0.01)\) and \(k\) was the number of clusters compared (Legendre and Legendre 1998).

The 200 seed clusters explained more than 91% of the feature space, and were statistically unique. However, 11 seeds comprised 10 or fewer observations each, and the loss of one cluster reduced \(r^2\) (the proportion of feature space variance accounted for by the clusters) by less than 0.0005. This degree of separation was deemed excessive for our purposes. Therefore, we plotted \(r^2\) against the number of clusters, in order to judge how many clusters would be appropriate to represent the feature space. The relationship illustrates the increasing loss in \(r^2\) that results from each elimination of a cluster during agglomeration (Fig. 1). A maximum acceptable loss of 0.005 was used as a criterion for eliminating a cluster, and 27 clusters were saved that still explained 72% of the feature space variance.

Once the clusters were constituted, the representative defoliation pattern of each cluster was constructed by calculating the mean defoliation and standard error of the mean defoliation for each year of the sequence from the cells belonging to each cluster.

The effect on tree growth and mortality of spruce budworm feeding depends, in part, on the annual sequence of defoliation levels. MacLean et al. (2001) calculated cumulative defoliation \((CD)\) as a weighted average of the defoliation levels over the current and previous 5 years:

\[
1) \quad CD_t = 0.28D_t + 0.26D_{t-1} + 0.22D_{t-2} + 0.13D_{t-3} + 0.08D_{t-4} + 0.03D_{t-5}
\]

where \(CD_t\) is the cumulative defoliation in year \(t\), and \(D_{t-i}\) is the defoliation (%) in year \(t - i\). Average cumulative defoliation \((ACD)\) values were calculated for each 5-year period of the 27 representative defoliation patterns, in accordance with MacLean et al. (2001). For purposes of visual display, the representative defoliation patterns were grouped into seven outbreak classes based on their sum of \(ACD\) (90%–99%; 50%–99%; etc).

Available data — forest composition

The growth loss and mortality caused by a given cumulative defoliation value depend on species composition and age (MacLean 1980, Erdle and MacLean 1999). The Canadian Forest Inventory (CanFI) (Gray and Power 1997) was used, because of its uniform national format, to determine composition and age. Records in the CanFI database describe the species composition \((m^3/ha)\), age, total volume \((m^3/ha)\), and area \((ha)\) of each stratum within each mapsheet. Mapsheets vary in size \((\mu=175^2 \text{ km}; \sigma = 324^2 \text{ km})\), and are spatially referenced. However, individual strata within mapsheets are not spatially referenced. MacLean et al. (2001) described 54 classes of stand type based on their susceptibility to spruce budworm defoliation. Their budworm impact classes (BICs) are defined by “a combination of percent spruce–fir content, species composition, age class, and silvicultural treatment” (Table 2: MacLean et al. 2001). We determined the BIC for each forest stratum within each CanFI mapsheet.

\[4\text{A stratum is a unique combination of 26 attributes, including such things as jurisdiction, ecoregion, ownership, stocking class, } m^3/ha \text{ of each species, etc. The area (ha) of a stratum is the sum of the areas of individual stands that share the 26 attributes. Thus, a single stratum may comprise many identical stands within the mapsheet, and a stratum has no location within the mapsheet.} \]
Fig. 2. Mean (± SE) annual defoliation (%) of the 27 representative defoliation patterns of a spruce budworm outbreak. Note that some SEs are too small to be seen in the figure. Cluster numbers correspond to those in Table 1.
Table 1. Mean annual defoliation (%) (top) and standard error (bottom) for the 27 representative outbreak patterns.

<table>
<thead>
<tr>
<th>Year</th>
<th>Cluster number</th>
<th>Very Mild Outbreak</th>
<th>Mild Outbreak</th>
<th>Mild-Moderate Outbreak</th>
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<tr>
<td>1</td>
<td>62 0.1 23 0.2 9 0.1 29 0.2 19 0.2 11 0.2 3 0.1 0 0.0 0 0.1 0 0.0</td>
<td>72 0.1 80 0.0 30 0.0 1 0.0</td>
<td>64 0.2 8 0.1 78 0.4 36 0.2 8 0.1 1 0.0 0 0.0 0 0.1 0 0.0</td>
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<td>2</td>
<td>69 0.2 30 0.3 9 0.3 23 0.3 28 0.3 33 0.3 52 0.2 46 0.3 31 0.2 8 0.2</td>
<td>70 0.1 67 0.2 79 0.1 76 0.1 58 0.3 1 0.0 0 0.0 0 0.1 0 0.0</td>
<td>62 0.2 52 0.3 57 0.3 54 0.3 56 0.3 38 0.3 1 0.1 4 0.1 1 0.1</td>
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<td>3</td>
<td>60 0.2 72 0.3 74 0.3 62 0.3 53 0.3 23 0.3</td>
<td>7 0.2 77 0.3 80 0.3 80 0.3 79 0.3</td>
<td>71 0.2 60 0.3 66 0.3 49 0.3 32 0.3</td>
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Table 1. Mean annual defoliation (%) (top) and standard error (bottom) for the 27 representative outbreak patterns (continued).

<table>
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<tr>
<th>Year</th>
<th>Cluster number</th>
<th>moderate outbreak</th>
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Fig. 3. Locations of the seven outbreak classes (defined by average cumulative defoliation (ACD)) of the 27 representative defoliation patterns of a spruce budworm outbreak. Spatial resolution = 2×2 km.

Estimating growth loss and mortality from the representative outbreak patterns
Because the spruce budworm outbreaks and representative defoliation patterns were summarized at a different spatial scale (4-km² cell) than the individual forest strata of the inventory (somewhere within the variably sized mapsheets), it is not possible to match, in a one-to-one manner, the defoliation patterns with the forest strata. Therefore, the ACD values of each representative pattern that occurred within a mapsheet were applied to each BIC that occurred within the mapsheet. The volume loss (growth loss plus mortality (m³/ha)) for each combination of defoliation pattern and BIC was calculated by the stand growth model STAMAN version 5.5.1 (Vanguard Forest Management Services Ltd. 1993, Erdle and MacLean 1999). The average volume loss for each 4-km² cell was calculated as a weighted average of the individual estimates of volume loss using the area of each BIC in the mapsheet as the weight.

The relationship between outbreak class and forest composition
The spatial coincidence between outbreak classes and forest composition was examined by conducting a step-wise multiple regression between the sum of ACD (Σ(ACD)) (which defines the outbreak class), and linear and quadratic combinations of volume (m³/ha) of host species and relative abundance (percentage of total volume) of balsam fir. An arcsine transformation was performed on the defoliation (arc sin (Σ(ACD)/600)) and on the balsam fir abundance before conducting the regression.

Results and Discussion
The earliest observation of the last spruce budworm outbreak was in 1950, and the last observation was in 1993. Approximately 85 million ha of Canada's forests were affected by this last outbreak (Fig. 2). Approximately equal areas (21.8–23.0 million ha) suffered outbreak patterns in the very mild, mild, and mild–moderate outbreak classes, whereas approximately 16 million ha experienced an outbreak in the moderate class. Less than 3 million ha experienced a moderate–severe outbreak, and only 91,000 a severe, or very severe outbreak. The mean annual defoliation levels of the patterns and their total area are illustrated in Fig. 2.

The last spruce budworm outbreak was principally confined to eastern Canada (Fig. 3), as were previous outbreaks (Blais 1983). Isolated pockets of the outbreak occurred in all provinces west of Ontario, although the outbreak pattern was in the very mild or mild outbreak class in all cases. In western Canada, the outbreak occurred as far north as approximately 64°N. Outbreak patterns were more severe in eastern Canada, and outbreak patterns of the moderate to severe classes were common. However, the outbreak did not occur north of approximately 52°N in eastern Canada. The locations of the seven outbreak classes of the 27 outbreak patterns are illustrated in Fig. 3.

A STAMAN simulation produces a stand table for each 5-year period of the simulation. We ran a 30-year simulation of STAMAN with, and then without, the spruce budworm defoliation pattern. The 5-year period where the difference between the runs in softwood volumes was maximum was selected as an estimate of the spruce budworm-caused volume loss.
Fig. 4. Host abundance in a CanFl mapsheet.

a. Average fir + spruce volume (m³/ha).  
b. Balsam fir percentage of host volume.
Fig. 5. The relationship between average cumulative defoliation (arcsine transformed) and host volume (m³/ha) (top) and abundance of balsam fir as a percentage of total volume (arcsine transformed) (below).
Fig. 6. Estimated volume loss (growth loss plus mortality (m³/ha)) from a spruce budworm outbreak. 

a. Spatial resolution = 2×2 km.  
b. Frequency distribution of loss.
Although there was some limited spatial coincidence between the outbreak classes (Fig. 3) and the average volume (m$^3$/ha) of host species (Fig. 4a) (see, for example, northern New Brunswick and the Gaspé Peninsula of Quebec where severe and very severe outbreak classes occur together with the highest host volumes), the host volume alone cannot explain the spatial arrangement of outbreak classes. Northern Quebec, for example, with higher host volumes, experienced outbreaks of milder outbreak classes than southern Quebec with lower host volumes. The abundance of balsam fir, as a percentage of total host volume, appears to have a mild influence on outbreak class. The higher host volumes of northern Quebec (Fig. 4a) comprise lower percentages of balsam fir (Fig. 4b), which may partly explain the occurrence of lower impact classes in that area (Fig. 3). Only 11% of the variability in $\Sigma$ (ACD) (which defines the outbreak classes) could be explained by the linear and quadratic combination of host volume and abundance of balsam fir (as a percentage of total volume) ($p < 0.0001$). No obvious non-linear trend in the relationship could be detected from plots of the observations (Fig. 5). An investigation of the effects of climate on outbreak characteristics of the spruce budworm (Gray 2007) suggested that climate also plays a significant role in determining the duration and severity of outbreaks.

Estimated volume losses caused by the last spruce budworm outbreak ranged from 3–68 m$^3$/ha. Volume losses were highest in New Brunswick and the Gaspé Peninsula, with additional pockets of very high losses in Ontario (Fig. 6a). Lower losses were more frequent than higher losses (Fig. 6b); 50% of the outbreak area accounted for only 20% of the loss.

Estimates of the growth loss and mortality from a spruce budworm outbreak rely on four component estimates: 1. spatial extent of the outbreak; 2. annual defoliation levels; 3. forest composition; and 4. species-specific vulnerability to defoliation. When the objective is to estimate the growth loss and mortality at a large regional, or national, scale, estimates of the spatial extent and annual defoliation levels must necessarily come from aerial surveys and sketch-mapping because this is the only source of data at these scales. Aerial surveys suffer from a number of issues, including the ability of observers to accurately locate a defoliation polygon on the survey map (spatial accuracy), and their ability to accurately estimate the level of defoliation in the polygon (defoliation accuracy). Despite the widespread use of the method (Simpson and Coy 1999), relatively little has been done to evaluate these two elements of its accuracy (MacLean and McKinnon 1996). Nevertheless, aerial surveys remain the only survey method used to collect defoliation data at the national level. Our method of assigning a single defoliation level to each 2×2 km cell has reduced the effect of spatial inaccuracy in the raw data. Similarly, our method of using broad classes of defoliation level has reduced the effect of defoliation accuracy in the raw data. This reduction in inaccuracy has come, however, at the cost of simultaneously reducing the precision of the defoliation estimates.

Estimating the net effect of spruce budworm on the carbon flux within Canada’s forests during the specific reporting periods of the Kyoto Protocol requires (in addition to the impact estimates provided here) an estimate of the timing of the next outbreak. A significant spatial trend in the timing of a spruce budworm outbreak has been noted in previous work (Candau et al. 1998, Gray et al. 1999, Gray 2005). A minor shift in the timing of the next outbreak could easily move the outbreak, and the resulting growth loss and mortality, from one reporting period to the next. Such a shift would have dramatic effects on the carbon flux during the reporting period in those areas with high host volumes that experience a high impact outbreak. The short duration of the Kyoto reporting periods (5 years) is most probably far smaller than our uncertainty in predicting the timing of the next outbreak. Gray et al. (1999) reported on the beginning of a spruce budworm outbreak in the Gatineau region of western Quebec. That outbreak has, so far, failed to develop into the anticipated, large-scale outbreak. A risk analysis approach is, therefore, the preferred method of addressing this question. Risk is defined (Society of Risk Analysis; http://www.sra.org) as the conditional probability of an event occurring multiplied by the consequence of the event given its occurrence. A risk analysis would combine estimates of the probabilities of the timing of the next spruce budworm outbreak with the estimated carbon flux impacts that would result from the losses estimated here.

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References


