# ON THE DURATION AND DISTRIBUTION OF FOREST TENT CATERPILLAR OUTBREAKS IN EAST-CENTRAL CANADA

B. J. COOKE[1], F. LORENZETTI[2], J. ROLAND[3]
Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre,
5320 - 122nd Street, Edmonton, Alberta, Canada T6H 3S5
email: bcooke@nrcan.gc.ca

**Abstract** *J. ent. Soc. Ont.* 140: 3-18

An analysis of forest tent caterpillar (*Malacosoma disstria* Hbn.) defoliation records from Ontario and Quebec indicates that outbreaks recur periodically and somewhat synchronously ($r = 0.51$) in the two provinces, with six inter-provincial-scale cycles having been observed over the period 1938-2002. When the entire spatiotemporal range of observed defoliation is considered, it appears that, at the local stand level, individual outbreaks tend to last for less than a year on average. Within the three core areas where all six cycles were observed (Dryden, Sudbury, Temiscamingue), individual outbreaks tended to last for 2.6 ± 0.5 years. The seemingly small difference between two versus three years of detectable defoliation at the local stand level appears to be critical, as this determines whether annual rates of stem mortality are sufficient to produce obvious signs of forest decline. Infestations lasting three years or longer normally occur in ~45% of the stands within the relatively small core outbreak areas. However not all infestations behave "normally", in the sense of being the product of a regionally synchronized population cycle. For example, we show how a reversing, traveling wave of forest tent caterpillar outbreaks in northern Ontario in the 1990s generated an unusually long-lasting infestation along the Highway 11 corridor – an outbreak which resulted in a regional-scale decline of trembling aspen. This demonstrates how incomplete synchronization of forest insect population cycles can lead to overlapping waves of outbreak that may result in large-scale forest disturbance.

*Published November 2009*

[1] Author to whom all correspondence should be addressed.
[2] Université du Québec en Outaouais, Département d'informatique et d'ingéniérie, Gatineau, QC and Institut Québecois d'Aménagement de la Forêt Feuillue, Ripon, QC.
[3] Department of Biological Sciences, University of Alberta, Edmonton, AB.

## Introduction

The forest tent caterpillar, *Malacosoma disstria* Hbn., is a voracious defoliator of hardwood trees throughout North America, exhibiting large-scale, periodic outbreaks on trembling aspen, *Populus tremuloides* Michx., in much of the boreal forest (Witter 1979). During a typical outbreak, detectable defoliation persists for one to many years, with the total length of outbreak varying both spatially, within an outbreak, and temporally, among outbreaks. Different authorities, reporting from different areas and over different time periods, have provided different estimates of the average duration of outbreak (Table 1); however, it is not clear why these estimates vary.

Outbreak duration undoubtedly varies among outbreaks and among jurisdictions. However estimates also vary depending on the way the subjective term 'outbreak' is defined. Sippell (1962), for example, pointed out that although the province-wide outbreak of 1948-56 in Ontario spanned "a period of nine years", infestations within "individual stands" tended to exhibit only "one or two years" of "population excess". Because local infestations do not all occur at exactly same time among stands across the province, "infestations" (i.e. local-scale outbreaks), by definition, do not last as long as landscape-scale "outbreaks". At the limit, when infestation occurrence is highly asynchronous, it becomes impossible to discern individual outbreaks – a situation which caused Hildahl and Reeks (1960) to reject the idea of forest tent caterpillar population cycling in west-central Canada.

The purpose of this paper is to provide a transparent and statistically robust answer to the question: "how long do forest tent caterpillar outbreaks tend to last?" – a question that is asked by thousands of communities each decade across the country. For example, this is the question currently being asked in Georgetown, P.E.I., where, after two consecutive years of heavy defoliation, local residents and authorities are seeking a precise answer as to the expected termination date, along with some idea of the degree of uncertainty surrounding this estimate.

To the individual on the ground who has already witnessed a year or two of severe defoliation, there is a major difference between an expected duration of "one or two years" of outbreak versus "three or more years". The variability and lack of specified precision in the estimates in Table 1 is therefore disconcerting. The tendency in the literature to characterize insect disturbance regimes in terms of their long-term, regional-scale behaviour – though understandable from a population dynamics perspective – is not particularly helpful to the individual landowner or stand-level forester facing the "here and now" of an outbreak crisis situation. Forest tent caterpillars are capable of bringing about the decline of trembling aspen trees and stands over large areas (Churchill et al. 1964, Candau et al. 2002, Hogg et al. 2002). So the penultimate question of interest to all parties concerned is how long outbreaks tend to last at the level of individual trees and stands.

Of particular concern is the fact that the outbreak duration estimates in Table 1 are all higher than the figures calculated by Simpson and Coy (1999), who summarized defoliation records in the various forest regions of Canada over the relatively short time frame 1980-1996 (Fig. 1). Their analysis suggested that the three major forest regions were quite similar, in that 95% of all infestations last for three years or less – a result that seems to be at odds with the much longer estimates suggested in Table 1. Is this discrepancy just a function of Sippell's (1962) stand vs. landscape scaling issue? Or is it because of a mismatch in the time scales of observation? Clearly, the issue of outbreak duration is one that needs to be addressed using quantitative, scale-sensitive methods if these important discrepancies are to be resolved.

TABLE 1. Outbreak duration, estimated in a variety of ways across a range of jurisdictions, according to several authors. In some cases detailed estimation methods are given in the original source. In others the estimate is based on informed opinion.

| Authority | Jurisdiction | Duration (yrs) | Type of estimate |
|---|---|---|---|
| Cerezke & Volney 1995 | Prairie provinces | 3-6 | qualitative |
| Witter 1979 | Minnesota, USA | 3-4 | qualitative |
| Sippell 1962 | Ontario | 3-9 | semi-quantitative |
| Roland 1993 | eight districts in Ontario | 1.7-3.3 | quantitative |

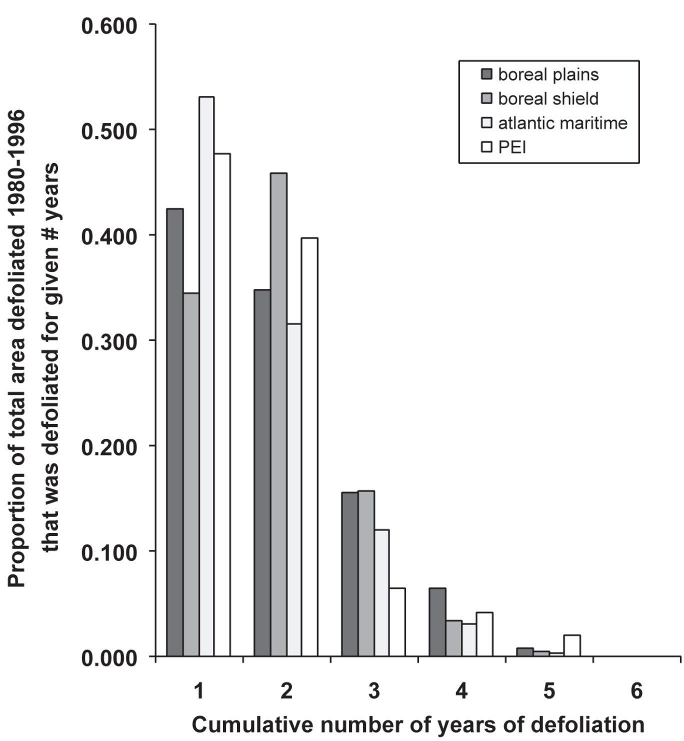


FIGURE 1. Outbreak duration in three major forest regions of Canada, according to Simpson and Coy's (1999) Table 4.

## Materials and Methods

We analysed the duration of forest tent caterpillar outbreaks over the seven decades for which Canadian Forest Insect and Disease Survey records exist for the provinces of Ontario and Quebec, an area which corresponds roughly to the "boreal shield" region reported on by Simpson and Coy (1999). The source data, described by Fleming et al. (2000) for Ontario and Cooke and Lorenzetti (2006) for Quebec, consist of digitally rasterized aerial survey sketch maps of areas exhibiting moderate to severe defoliation attributable to forest tent caterpillar. Spanning 65 years (1938-2002) and two of the country's largest provinces, this is the largest-scale study to date of long-term tent caterpillar outbreak dynamics.

Since 1938 there have been six distinct inter-provincial-scale outbreak cycles in east-central Canada, with moderate to severe defoliation occurring at periodic intervals of 9-13 years (Cooke and Lorenzetti 2006, Cooke et al. 2007). For each outbreak cycle, the number of consecutive years of moderate to severe defoliation at a given "point" was summed, and plotted in a histogram. This variable is henceforth referred to as "local-scale outbreak duration", and is intended to represent the average duration of outbreaks at the "stand" level. In actuality these "points" were cells in a data raster, each cell spanning 1 $km^2$ in Ontario and ~58 $km^2$ in Quebec, the coarser resolution of the Quebec data being a function of the way these defoliation maps were rasterized by the province at a resolution of 15 minutes of latitude and longitude.

## Results

Forest tent caterpillar outbreaks in Ontario and Quebec tend to exhibit similar periodic patterns of occurrence ($r = 0.51$ between provincial time-series), with the extent of annual defoliation being more variable in Quebec (C.V. = 216%) than in Ontario (C.V. = 139%) (Fig. 2, top). In both provinces there are a few core locations where defoliation is much more frequent than in surrounding areas (Fig. 2, bottom).

A map of local-scale outbreak duration during each of the six inter-provincial outbreak cycles reveals that the number of consecutive years of defoliation is highly spatially variable, lasting anywhere from 0 to 9 years depending on location (Fig. 3). A duration of "zero years" may seem paradoxical. However this is a natural result of the fact that individual outbreaks in Ontario and Quebec tend to span only 43 ± 7% (s.e.) and 37 ± 13% (s.e.) of the insect's total (i.e. 1938-2002) outbreak range (Fig. 3). In other words, during a typical 12 year long population/outbreak cycle, 60% of the stands located within the area amenable to outbreak, for some reason, will not experience moderate-to-severe defoliation. It is in this sense that a regionally defined outbreak event can be said to have a duration of zero years in some locales.

How, then, to characterize the distribution of the number of years of defoliation at a given location during a typical outbreak cycle? In particular, should the zero values from non-defoliated areas be included in the analysis, or should they be excluded, as in Simpson and Coy's (1999) analysis (e.g. Fig. 1)? Excluding them would clearly bias the outbreak duration estimate upward.

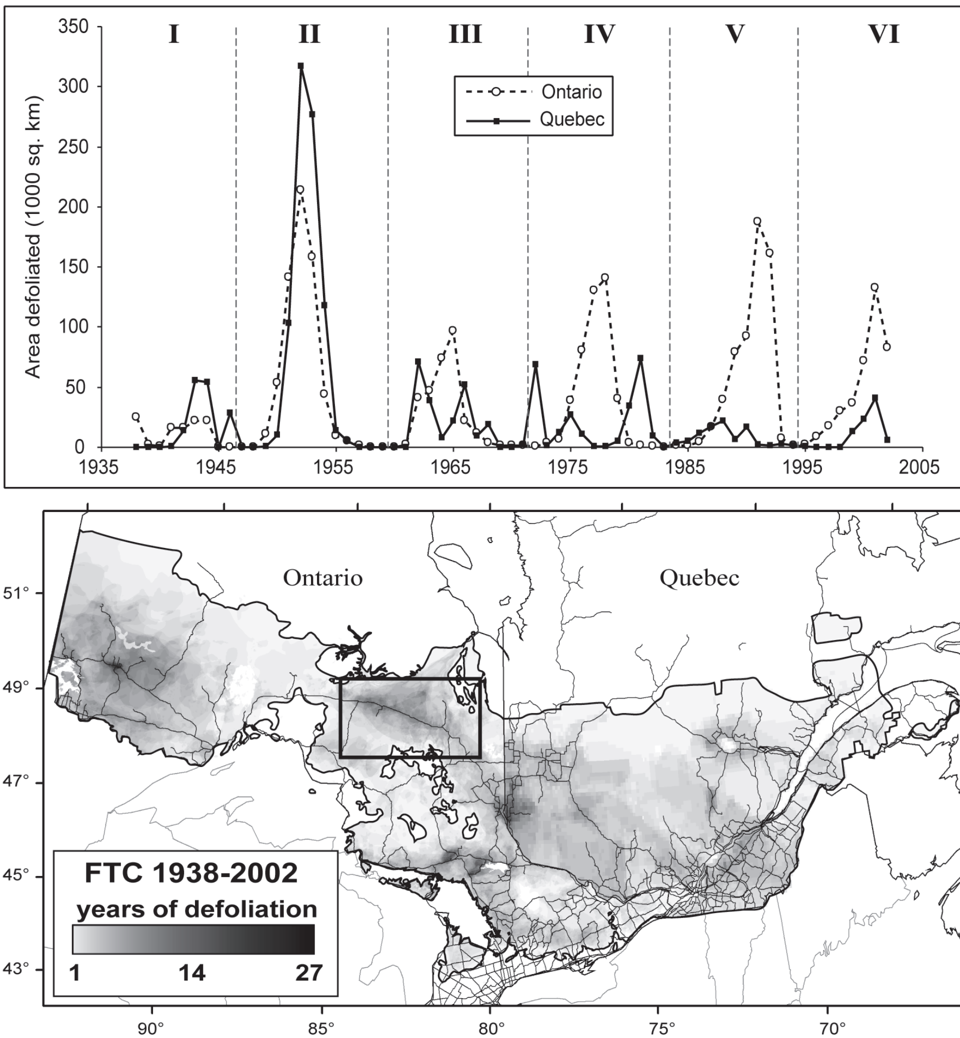


FIGURE 2. The distribution of forest tent caterpillar defoliation during six outbreak cycles in the provinces of Ontario and Quebec. Top: Outbreak cycles are fairly well synchronized between provinces, although cycles III, IV, and V appear to have been interrupted in the early stages of development in 1963, 1976, 1989 in Quebec, but not in Ontario. Bottom: Note the fairly seamless gradient across the Ontario-Quebec border, despite the different survey and data pre-processing methods. Road density (shown as dark lines) is broadly indicative of the degree of human settlement and forest fragmentation. Rectangle indicates area plotted in Fig. 6.

A second issue is spatial heterogeneity in outbreak frequency. Noting that defoliation in the Fig. 3 maps is most frequent in rural areas characterized by disturbed, semi-agricultural landscapes (Roland 1993), it would clearly be advantageous to distinguish between core areas where outbreaks are frequent *versus* fringe areas where outbreaks are infrequent.

The frequency distribution of the number of years that a given cell is defoliated during an outbreak cycle reveals that this variable is not unimodally distributed (Fig. 4). The number of zero values in these distributions is high, as expected for a random (i.e. Poisson) process with a low mean; however the spatial distribution of defoliation is clearly non-random, following a spatially autocorrelated gradient pattern (Fig. 3). Indeed, the

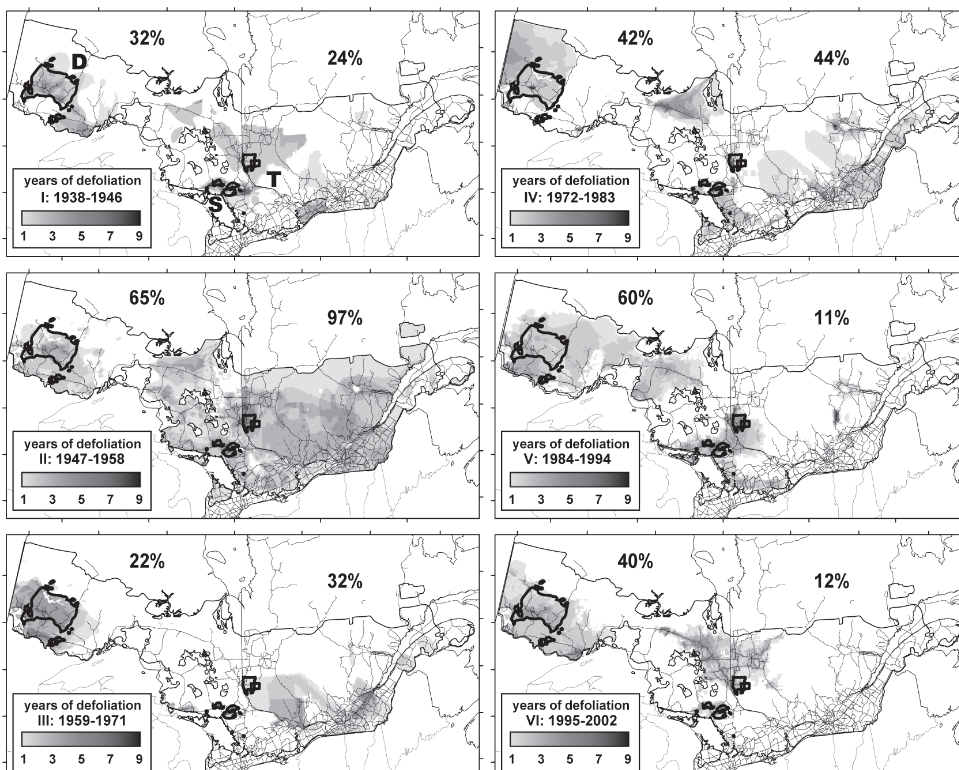


FIGURE 3. The distribution of forest tent caterpillar defoliation during each of six outbreak cycles in Ontario and Quebec. Thin and thick black outlines indicate (i) the entire outbreak range over the period 1938-2002 and (ii) the core areas where at least one year of defoliation occurred during each of all six cycles. Core areas labelled as “D” (Dryden), “S” (Sudbury), and “T” (Temiscamingue). The area between the thin and thick black outlines is referred to as the “fringe” area – the area where “zero values” for local outbreak duration are common. Percentages indicate the mean percentage of the outbreak range defoliated in each province during each cycle. Histograms of outbreak duration provided in Fig. 4.

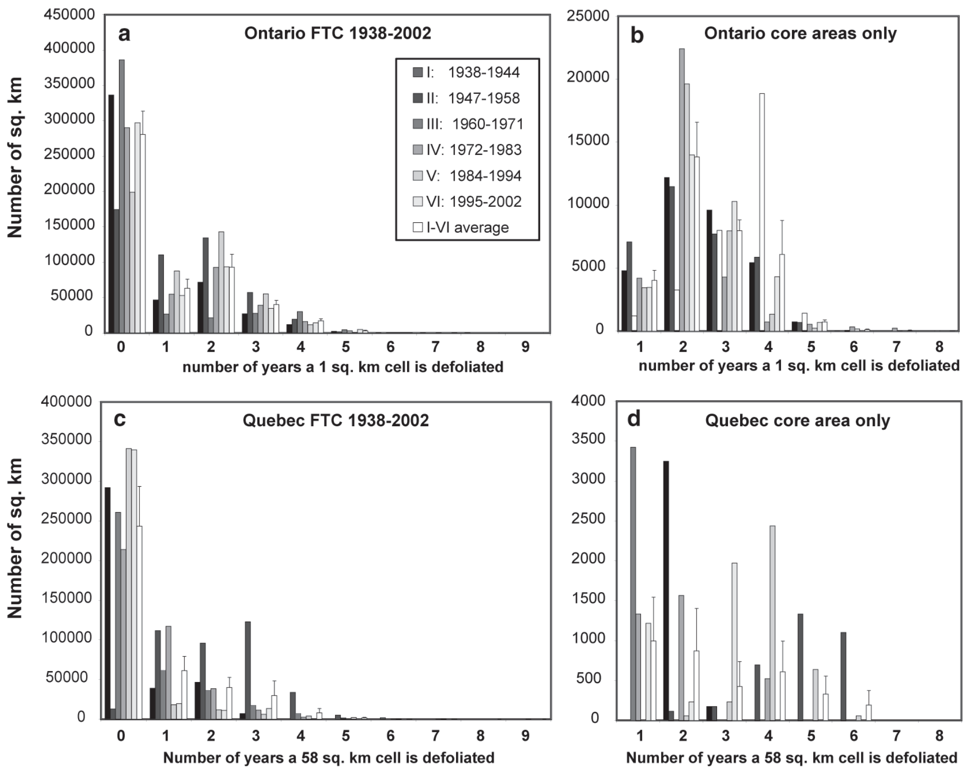


FIGURE 4. Frequency distribution of the number of years a given cell is defoliated during each of six outbreak cycles in Ontario (a,b) and Quebec (c,d), both across each province (a,c), and in "core" areas only (b,d), as defined in Fig. 3. The core area in northwestern Quebec is smaller than the core area in northwestern Ontario, and outbreak duration is much more variable among cycles.

TABLE 2. Average number of years of FTC defoliation expected during a "typical" outbreak cycle in a given cell in east-central Canada (based on n=6 cycles, 1938-2002; data in Fig. 3). Condition "d ≥ 3" symbolizes the area experiencing three or more years of defoliation during a 12y outbreak cycle. Its relevance will become clear in Fig. 4. Note that these estimates include "zero values" – cells which were not defoliated during the (regionally defined) outbreak cycle. Also note that the core areas are areas which, by definition, did not exhibit any zero values during any outbreak cycle.

| | Entire outbreak range | | | Core area only | | |
|---|---|---|---|---|---|---|
| | mean ± s.e. | range | % area d ≥ 3 | mean ± s.e. | range | % area d ≥ 3 |
| Ontario | 0.92 ± 0.11 | 0-9 | 12.3 | 2.58 ± 0.47 | 1-8 | 45.6 |
| Quebec | 0.40 ± 2.20 | 0-9 | 10.4 | 2.70 ± 0.61 | 1-6 | 45.5 |

bimodality in many of the Fig. 4 distributions suggests a composite distribution resulting from non-stationarity in the spatial distribution of outbreak.

Summary statistics of the mean and range of local-scale outbreak durations for the two provinces are provided in Table 2. Mean outbreak duration is comparable in the two provinces, although Quebec appears to offer a more variable environment, with outbreak duration exhibiting twice the variance as in Ontario. This is because the fringe area is estimated to comprise a much larger portion of the insect's range in Quebec than in Ontario. The higher variability in outbreak duration in Quebec appears to be exacerbated by the unusually large extent of defoliation during cycle II. Excluding cycle II from the calculation, the average extent of outbreaks relative to the total area amenable to outbreak would be 39 ± 6% (s.e.) in Ontario and 24 ± 6% (s.e.) in Quebec.

In the three "core" areas of northwestern Ontario (near Dryden), northeastern Ontario (near Sudbury), and northwestern Quebec (near L. Temiscamingue) outbreaks tend to last for 2.6 ± 0.6 (s.e.) years. These are rural, populated areas where forest tent caterpillars are highly likely to encounter humans. In the "fringe" areas, which are more conifer-dominated, more remote, and are dominated by forest industry activity, outbreaks tend to last for only 0.8 ± 0.1 (s.e.) years in Ontario, and less than this in Quebec. Reporting bias may therefore help to explain why the literature tends to overestimate the duration of outbreaks at something greater than two years: in conifer-dominated boreal landscapes there are fewer observers making fewer reports to fewer readers.

A key question is the probability that a given outbreak will persist for three years or longer. In both provinces, infestations lasting three years or longer will occur in ~11% of the outbreak range. Within core areas where populations oscillate with regular periodicity, this figure jumps to ~45% – still, less than half.

## Discussion

### 1. Duration of Outbreaks

Despite the large extent of forest tent caterpillar outbreaks in east-central Canada, 60% of the area theoretically available for defoliation does not actually experience any significant defoliation during a typical 12-year outbreak cycle. For the purposes of computing an average outbreak duration, it matters a great deal whether one chooses to include these "zero values" in the computation. In the "core" areas where all n=6 outbreak cycles occurred this is a moot point because there are no such zero values. Beyond the "fringe" area there are nothing but zero values. If tent caterpillars can be found there, their populations never reach the level of causing aerially detectable defoliation. It is thus within the transition region of the fringe area that this question becomes relevant.

The quantitative estimate of outbreak duration by Roland (1993) in Table 1 included some of these zero values, in the sense that "if a specific township suffered no defoliation during an outbreak, this was included in the estimate of mean outbreak duration". However not all zero values were included because "populations were considered to be in the outbreak phase if there was moderate to severe defoliation recorded in at least one-third of the township", which means that the time-frame for summation was defined locally, not globally. Consequently there were many instances where the lack of defoliation in a district prevented local zero values within a township (~10 x 10 km) from being included in the district sum, despite the possible presence of significant and extensive defoliation in neighbouring districts. The qualitative estimates of outbreak duration provided in Table I probably tacitly exclude such zero values. If that is the case, it may help explain why these estimates appear to be biased high.

Given the contrasting data in Tables 1 and 2, we surmise that the estimates presented in Table 1 are descriptions of the dynamics of outbreaks in core areas where (1) outbreaks occur more frequently and more regularly, (2) the probability of people encountering mass aggregations of crawling larvae is highest, (3) forests are more fragmented and the local infestations that comprise the outbreak are not particularly well-synchronized across the landscape, and (4) forest entomologists interested in quantifying hardwood timber impacts were historically most likely to focus their attention.

Given the more objective and comprehensive analysis represented in Table 2, it would clearly be a distortion to suggest that infestations of three or more years in duration are in any way normal in east-central Canada. Authors who report an average outbreak duration of anything greater than three years – as in Table 1 – therefore must be reporting on the basis of individual infestations summed across a larger regional extent, which harkens back to Sippell's (1962) original comments on the relatively short duration of local-scale infestations compared to landscape-scale outbreaks, when individual infestations occur somewhat asynchronously.

In our case, choosing to focus on local-scale infestation dynamics means that our estimates of outbreak duration are not only bias-free, they also relate more closely to (i) the locally-acting processes that are thought to govern cycling (e.g. parasitism, predation, starvation, host-plant effects, disease) and (ii) the critical outcomes of concern (e.g. probability of permanent tree damage). Our estimates are thus useful to both the small private landowner and the large forest company.

Finally, the estimates reported here may well turn out to fit other regions, such as west-central Canada and the Atlantic maritime region, because they correspond well with the larger-scale, shorter-term estimates reported by Simpson and Coy (1999) in Fig. 1. Had we focused on landscape-level outbreak duration, this might not be the case, for it is well established that forest tent caterpillar outbreaks are less well synchronized in the prairie provinces (Hildahl and Reeks 1960) than in Ontario (Sippell 1962). By focusing on the duration of local-scale infestations, we effectively avoid the issue of the degree of synchrony among infestations within the area (and time-frame) of outbreak.

**2. Forest-Insect Feedbacks**

Roland (1993) was the first to attempt a quantitative analysis of the Ontario tent caterpillar data, and what he showed (using a smaller-scale, abbreviated dataset spanning cycles II-IV from 1948 to 1984) was that forest tent caterpillar outbreaks in eight major forest districts tended to last for 2.2 years on average, consistent with what is reported here for core areas of outbreak. He further showed that there tended to be a split in outbreak duration, with outbreaks in districts where forests were heavily fragmented lasting "4 to 6 years" and outbreaks in districts where forests were intact lasting only "one or two years". A formal analysis indicated that just a single km of edge per square kilometre of forest area would increase the expected duration of outbreaks from 1.8 years to 2.7 years (see his Fig. 2). Consistent with the Ontario data, where there is a strong association between aspen defoliation and the presence of major roads (Cooke and Roland 2000), we see in Fig. 2 a similar association in the province of Quebec – especially in the northwestern region around L. Temiscamingue. Moreover, the association between disturbance and prolonged outbreaks during cycles II-IV (Roland 1993) also appears to be present during cycles I, V, and VI (Fig. 3). The relationship between forest fragmentation and outbreak duration thus appears to be quite robust.

From a forestry perspective, the foregoing analysis becomes highly significant when one considers the result of Churchill et al. (1964), who showed that among dominant, co-dominant and intermediate (i.e. non-suppressed) trees, mortality due to "an unidentifiable agent" tended to increase sharply (from 10% to 30%) as the number of years of defoliation by forest tent caterpillars increased from two to three years of heavy defoliation (Fig. 5). These authors concluded that the unidentified killing agent must have been the delayed action of forest tent caterpillar defoliation occurring during the 1950s. Notably, caterpillar-caused mortality did not happen immediately after the outbreak had started or ended (Duncan and

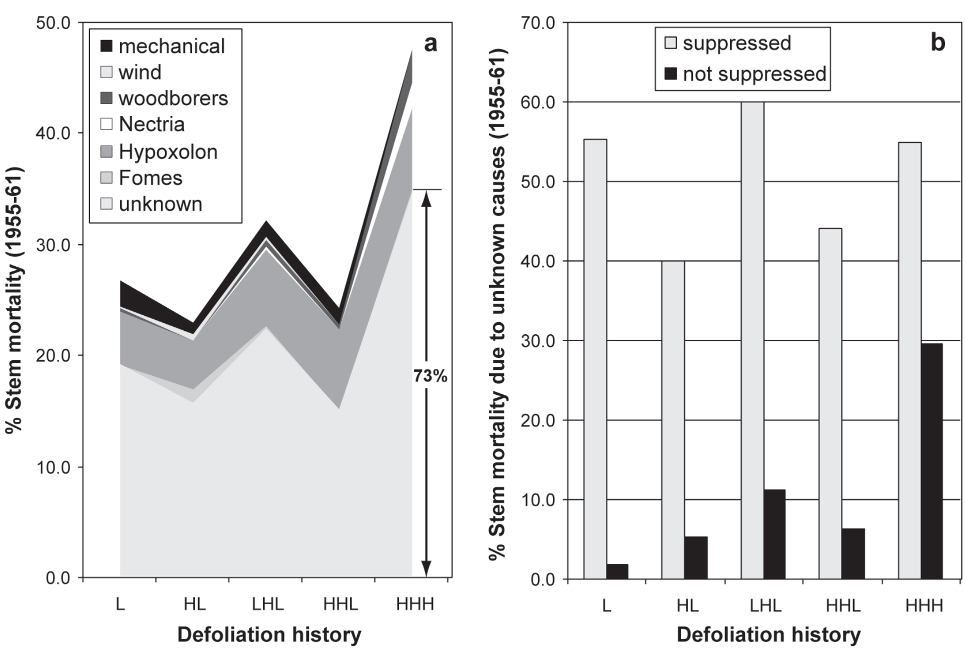


FIGURE 5. Aspen mortality in Minnesota occurring as a result of the 1951-59 forest tent caterpillar outbreak cycle (original data in Churchill et al. 1964). 'L' indicates a single year of light defoliation. 'HHH' indicates three consecutive years of heavy defoliation. (a) 73% of all mortality in the 'HHH' category is a result of "unknown" causes (i.e. delayed effects of forest tent caterpillar defoliation). (b) Trees that were "not suppressed" (all dominant, co-dominant and intermediate trees in the stand) show a clear response to defoliation intensity over time.

Hodson 1958), but occurred gradually, and in association with the growing abundance of a number of ancillary secondary agents. As time passed, the level of mortality became increasingly statistically significant and increasingly visually detectable. This is a pattern that has also been observed in western Canada (Hogg et al. 2002).

Putting the Roland (1993) and Churchill et al. (1964) results together, one may conclude that a single unit of forest fragmentation (one km forest edge per square km of forest area) can increase the probability that defoliation will intensify from 1.8 years of outbreak to 2.7 years of outbreak, which, based on Fig. 5b, would imply a two-fold increase in mortality among dominant stems, from ~12% to ~30%. In summary, although it is extremely uncommon for moderate-to-severe defoliation to last as long as 3 years or more in a given stand, (1) it clearly can happen, (2) forest fragmentation significantly increases the probability that the three-year threshold is crossed, and (3) the crossing of the three-year threshold implies significant tree mortality[1]. From this we conclude that not only are forest tent caterpillars quite capable of killing their primary host, trembling aspen, but the probability of heavy mortality increases with forest fragmentation. Notably, this implies a closed feedback loop between the effect of forest structure on insect dynamics, and the reciprocal impact of insects on the forest – a relationship that has been confirmed for two other major Canadian defoliators: the jack pine budworm (Nealis et al. 2003) and the spruce budworm (Nealis and Régnière 2004).

### 3. Overlapping Traveling Waves of Outbreak

Candau et al. (2002) suggested that forest tent caterpillars may have been the primary cause of more than 500 000 hectares of declining aspen along Trans-Canada Highway 11 in northern Ontario – an area where defoliation historically occurs rather frequently (Fig. 2, bottom). These authors showed that outbreak cycles V and VI in this region happened to occur in very close temporal proximity to one another, with consecutive outbreak peaks separated by six years, instead of ten years, which is the provincial norm (Fig. 2, top). What they did not show, however, is that the compression of these cycles in time was associated with a curious epidemiological phenomenon: a reversing traveling wave of outbreak along the corridor of Highway 11. The first wave traveled eastward from Hearst to Cochrane 1989-1995, and the second wave traveled westward from Cochrane to Hearst 1996-2004 (Fig. 6, top). Between these two locations, in the zone of overlap at Kapuskasing-Smooth Rock Falls, trembling aspen host trees, having very little respite from defoliation during the middle years 1993-1996, were exceptionally vulnerable to sudden dieback and decline (Fig. 6, bottom).

Traveling waves of insect outbreak are of interest to population ecologists because they are one of the dynamic features predicted by theoreticians to occur in spatially extended predator-prey systems (Hassell et al. 1994, Bjornstad et al. 2002). However, this particular traveling wave appears to be different from those that occur in simple theoretical models in that it reversed direction very suddenly. It is not yet clear why this outbreak progressed in the unusual way that it did, but this question is being investigated through population

[1] Note we are not suggesting that 3 years of defoliation is an ecological threshold parameter in a nonlinear mortality function. On the contrary, we expect the mortality function is a smooth linear function of the degree and duration of defoliation, and that three years is merely the amount of defoliation required to surpass an arithmetic impact detectability threshold (unpublished data, D. Marchand, F. Lorenzetti, Y. Mauffette, Y. Bergeron).

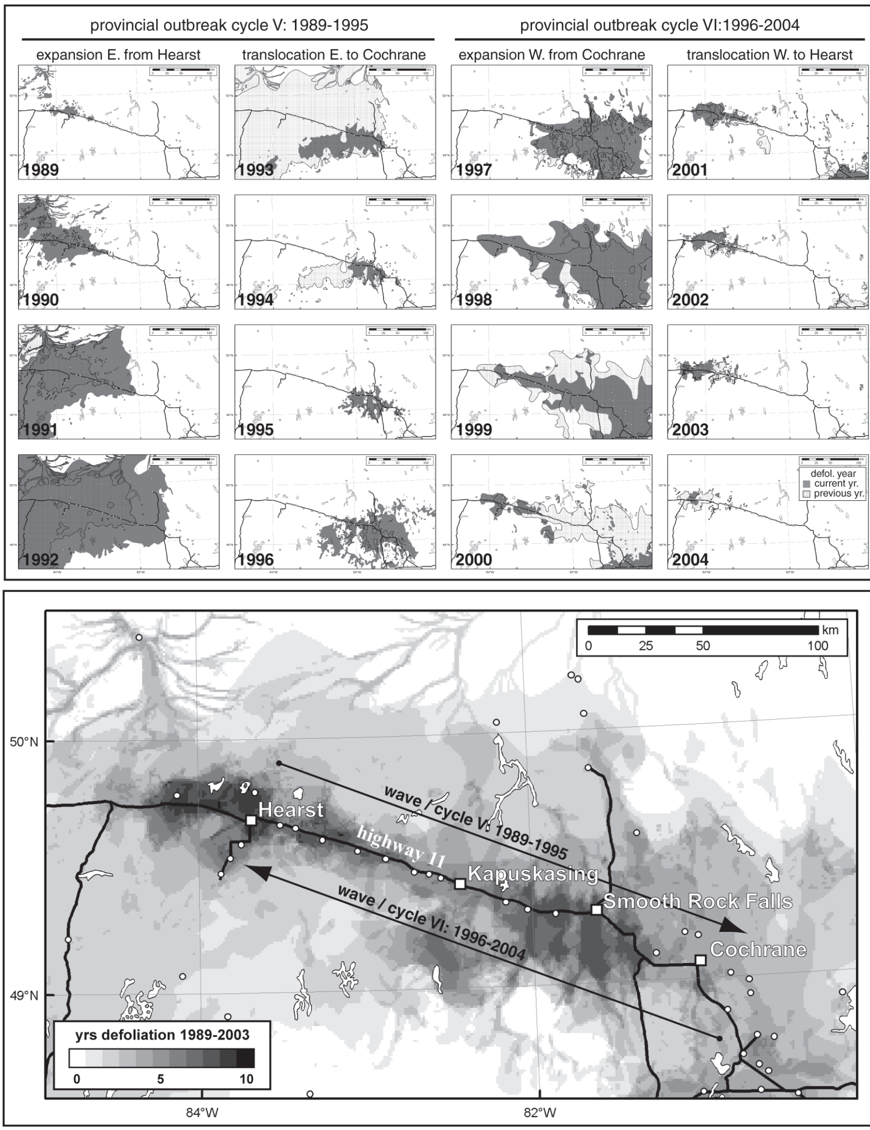


FIGURE 6. Progression of defoliation during outbreak cycles V (1989-1995) and VI (1996-2004) in northern Ontario. Top: annual displacement of defoliation between years. Outbreak V, originating at Hearst, expanded and shifted eastward toward Cochrane, while outbreak VI, originating at Cochrane, expanded and shifted westward toward Hearst. Bottom: cumulative distribution of defoliation, 1989-2003. Although Hearst and Smooth Rock Falls both experienced ~9 years of defoliation over the two outbreak cycles, it was at Smooth Rock Falls where the two population cycles occurred in such rapid succession that there was little or no respite in defoliation. This is where the highest levels of aspen decline were observed (Candau et al. 2002).

studies and simulation modeling. What we can state, however, is a clear prediction that a complex dynamic of this type can be expected to be replayed in the future. Meanwhile, it would be worthwhile trying to determine how much aspen decline might have happened in response to the overlapping waves of tent caterpillar outbreak that occurred in the boreal and aspen parkland regions of Alberta in the early and late 1980s, respectively (Cooke 2001).

Finally, this exposé reveals a demarcation problem in our attempts to quantify outbreak duration. Recalling that 1994 was the year between cycles V and VI where province-wide defoliation reached a minimum (Fig. 2), we see now that this was actually the peak year of defoliation in the out-of-phase regional oscillation at Smooth Rock Falls (Fig. 6, top). Thus our provincially defined time-frame led to a regional-scale truncation of the out-of-phase outbreak at Smooth Rock Falls, such that this single regional outbreak was treated as two separate provincial outbreaks. Outbreak duration in this instance was therefore underestimated. Estimation error due to imperfect demarcation (deciding where one outbreak cycle stops and another one starts) is clearly unavoidable when cycle synchronization is imperfect.

**4. Variability in Outbreak Duration, Extent and Timing**

Outbreaks appear to be more variable in extent in Quebec than in Ontario, although this inference is based on a limited sample of only six cycles. Excluding the unusually extensive outbreak cycle II from the Quebec data, it would appear that the two provinces exhibit similar levels of variability. However it is not clear that such dismissal is warranted. Although cycle II was unusually extensive in Quebec, it was also the most extensive outbreak on record in Ontario. Before discounting cycle II in Quebec as an outlier, it is important to know if this anomaly might be explained by some persistent feature of the environment, such as a more variable climate in Quebec.

There does not appear to be any evidence that the range of forest tent caterpillar outbreaks in east-central Canada is shifting gradually northward in response to a climate warming trend (Fig. 3). Thus it would be premature to suggest that the decline of aspen in northern Ontario in the late 1990s was facilitated by climate warming. This system does not appear to be responding as strongly to climate change as, say, mountain pine beetle in western Canada (Carroll et al. 2004). On the other hand, given that (i) weather is not the only driver of the system's dynamics, and (ii) the 20th century global warming trend has been punctuated by brief cooling phases (Smith and Reynolds 2005), it may be quite difficult to estimate the marginal effects of climate change, especially with such a short, stochastic time-series. Indeed, one of the reasons we have tried to be as quantitative as possible in estimating outbreak duration is so that future studies looking at this question will have a solid baseline from which to start. Although tent caterpillar outbreaks may last as long as 3-6 years in some areas, this is neither precise enough nor accurate enough an estimate to serve as a baseline for future studies looking at potential shifts in dynamics in response to climatic and landscape change.

The reason we are keen to continue pursuing this hypothesis is because of regional differences in outbreak occurrence, with outbreak duration being twice as variable in Quebec as in Ontario. Looking back at the provincial defoliation time-series of Fig. 2., it is striking how cycles III, IV, and V appear to have been interrupted in the early stages of development in Quebec, but not in Ontario, hence the asynchronous pattern of outbreak between the two regions during that time-period. In fact, the years of cycle interruption can be identified with some precision: 1963, 1976, 1989. It would not surprise us if it should turn out that these cycles were interrupted by cold spring or winter weather, as described by Cooke and Roland (2003), for it certainly appears that the insect's distribution in Quebec may be strongly limited by a combination of climate and topography (Cooke and Lorenzetti 2006). It is for this reason that we expect climatic change may eventually be found to have some influence on long-term tent caterpillar dynamics. However additional research on the relationship between insect survival and weather is required before the hypothesis can be refined to the point of a specific prediction.

## Conclusion

This note is not intended to discount other figures published in the literature, but merely to put them in context. We want to emphasize that although most forest tent caterpillar outbreaks do not last longer than 1-2 years, those rare ones that do last longer than 2 years tend to result in "significant" (i.e. readily detectable and/or economically important) mortality. The reason that forest tent caterpillars are generally thought of as benign insects is not because they are incapable of destroying a forest. Rather, it is because outbreaks are typically terminated before they reach their third year. As our analysis indicates, there are always small areas where outbreaks linger on for 4 years or longer.

Our second major point is that although it is desirable to be able to forecast population oscillations in time and space, from a forestry perspective it is not particularly useful to be able to predict cycle timing across the bulk of the outbreak range, when it is the number of years of defoliation in excess of three that determines whether or not forests survive. The real challenge lies in predicting precisely when, where and under what circumstances the number of years of defoliation will exceed the three-year threshold.

Just as meteorologists have difficulty in predicting extreme weather events, so entomologists are likely to find it challenging to obtain any success in predicting extreme entomological events. Predicting animal population fluctuations is an imprecise science. Predicting which of these fluctuations are likely to result in anomalously severe and prolonged population eruptions is going to require continuing research into the fundamentals of population dynamics. Understanding the forces that lead to imperfect synchronization of cyclic population fluctuations is one promising avenue for determining when and where waves of outbreak may overlap to produce unusually long-lasting infestations capable of causing large-scale forest decline.

## Acknowledgements

Ronald Fournier (Canadian Forest Service) and Bruno Boulet (Ministère des Ressources Naturelles et Faune du Québec) kindly provided access to forest tent caterpillar defoliation data from Ontario and Quebec, respectively.

## References

Bjornstad, O. N., M. Peltonen, A.M. Liebhold and W. Baltensweiler. 2002. Waves of larch budmoth outbreaks in the European Alps. Science 298: 1020-1023.

Candau, J.-N., V. Abt and L. Keatley. 2002. Bioclimatic analysis of declining aspen stands in northeastern Ontario. Ontario Forest Research Institute, Forest Research Report No. 154.

Carroll, A., S. W. Taylor, J. Régnière and L. Safranyik. 2004. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. p. 223-232 In: Shore et al. (Eds.) Mountain Pine Beetle Symposium: Challenges and Solutions. Inf. Rep. BC-X-399.

Cerezke, H. F. and W. J. A. Volney. 1995. Forest insect pests in the Northwest region. pp. 59-72 In: J. A. Armstrong and W. G. H. Ives (Eds.). Forest Insect Pests in Canada. Natural Resources Canada. Canadian Forest Service.

Churchill, G. B., H. H. John, D. P. Duncan and A. C. Hodson. 1964. Long-term effects of defoliation of aspen by the forest tent caterpillar. Ecology 45: 630-633.

Cooke, B. J. 2001. Interactions between climate, trembling aspen, and outbreaks of the forest tent caterpillar in Alberta. PhD dissertation, University of Alberta, Edmonton, Alberta.

Cooke, B. J. and F. Lorenzetti. 2006. The dynamics of forest tent caterpillar outbreaks in Québec, Canada. Forest Ecology and Management 226: 110-121.

Cooke, B. J., V. G. Nealis and J. Régnière. 2007. Insect Defoliators as Periodic Disturbances in Northern Forest Ecosystems. pp. 487-525 In: (E. A. Johnson and K. Miyanishi, Eds.) Plant Disturbance Ecology: The Process and The Response. Academic Press.

Cooke, B. J. and J. Roland. 2000. Spatial analysis of large-scale patterns of forest tent caterpillar outbreaks. Ecoscience 7: 410-422.

Cooke, B. J. and J. Roland. 2003. The effect of winter temperature on forest tent caterpillar egg survival and population dynamics in northern climates. Environmental Entomology 32: 299-311.

Duncan, D. P. and A. C. Hodson. 1958. Influence of the forest tent caterpillar upon the aspen forests of Minnesota. Forest Science 4: 71-93.

Fleming, R. A., A. A. Hopkin and J.-N. Candau. 2000. Insect and disease disturbance regimes in Ontario's forests. pp. 141-162 In: Ecology of a Managed Terrestrial Landscape: Patterns and Processes of Forest Landscapes in Ontario. UBC Press, Toronto, ON.

Hassell, M. P., H. N. Comins and R. M. May. 1994. Species co-existence and self-organizing spatial dynamics. Nature 370: 290-292.

Hildahl, V. and W. A. Reeks. 1960. Outbreaks of the forest tent caterpillar *Malacosoma disstria* Hbn. and their effects on stands of trembling aspen in Manitoba and Saskatchewan. The Canadian Entomologist 92: 199-209.

Hogg, E. H., J. P. Brandt and B. Kochtubajda. 2002. Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. Canadian Journal of Forest Research 32: 823-832.

Nealis, V. G., S. Magnussen and A. A. Hopkin. 2003. A lagged, density-dependent relationship between jack pine budworm *Choristoneura pinus pinus* and its host *Pinus banksiana*. Ecological Entomology 28: 183-192.

Nealis, V. G. and J. Régnière. 2004. Insect-host relationships influencing disturbances by the spruce budworm in a boreal mixedwood forest. Canadian Journal of Forest Research 34: 1870-1882.

Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. Oecologia 93: 25-30.

Simpson, R. and D. Coy. 1999. An ecological atlas of forest insect defoliation in Canada 1980-1996. Natural Resources Canada, Canadian Forest Service. Inf. Rep. M-X-206E.

Sippell, L. 1962. Outbreaks of the forest tent caterpillar, *Malacosoma disstria* Hbn., a periodic defoliator of broad-leaved trees in Ontario. The Canadian Entomologist 94: 408-416.

Smith, T. M. and R. W. Reynolds. 2005. A global merged land air and sea surface temperature reconstruction based on historical observations (1880-1997). Journal of Climate 18: 2021-2036.

Witter, J. A. 1979. The forest tent caterpillar (Lepidoptera: Lasiocampidae) in Minnesota: a case history review. Great Lakes Entomologist 12: 191-197.