Spatiotemporal patterns of large-scale defoliation caused by the spruce budworm in Ontario since 1941

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Abstract: Survey records of spruce budworm (Choristoneura fumiferana Clem.) defoliation in Ontario, taken annually since 1941, were analysed using geographic information systems (GIS), spatial statistics, and time-series methods. Cumulative frequency maps indicated that the 41 × 10^6 ha of Ontario that had been defoliated in at least one year since 1941 could be split into three zones of frequent defoliation separated by two approximately 100 km wide, longitudinally oriented corridors of lower frequency. Analysis of annual records of the total area defoliated showed that the fluctuations in this time series are the result of a basic oscillation of approximately 36 years, which is modified by secondary fluctuations and occasionally by sharp drops. The secondary fluctuations are at least partially due to asynchrony in otherwise remarkably similar long-wave oscillations in the eastern (25.5 × 10^6 ha) and western (9.6 × 10^6 ha) zones of frequent defoliation. Analysis of this asynchrony showed that outbreaks in the eastern zone occurred 5 or 6 years before outbreaks in the central (6.6 × 10^6 ha) and western zones, which were synchronous. These observations contradict previous reports of the large-scale spread of outbreaks from west to east.

Résumé: Les relevés d’inventaire de défoliation causée par la tordeuse des bourgeons de l’épinette (Choristoneura fumiferana Clem.) en Ontario, effectués annuellement depuis 1941, ont été analysés à l’aide de systèmes d’information à référence spatiale (SIRS), de statistiques spatiales et de méthodes de séries temporelles. Des cartes de fréquence cumulative indiquent que les 41 × 10^6 ha du territoire ontarien ayant été défoliés pendant au moins une année depuis 1941 peuvent être divisés en trois zones de défoliation fréquente, séparées par deux corridors d’une largeur approximative de 100 km, orientés longitudinalement et où les fréquences sont plus basses. L’analyse des relevés annuels de la superficie totale défoliée montre que les fluctuations de cette série temporelle résultent d’une oscillation de base d’une durée approximative de 36 ans, modifiée par des fluctuations secondaires et, à l’occasion, par des chutes abruptes. Les fluctuations secondaires sont causées, du moins en partie, par un asynchronisme des oscillations de base, par ailleurs remarquablement similaires, dans les zones de défoliation fréquente de l’est (25.5 × 10^6 ha) comparativement à celles de l’ouest (9.6 × 10^6 ha). L’analyse de cet asynchronisme révèle que les épidémies dans la zone orientale se sont déclenchées 5 à 6 ans avant les épidémies des zones centrale (6.6 × 10^6 ha) et occidentale, lesquelles se sont développées de façon synchrone. Ces observations vont à l’encontre de comptes rendus antérieurs faisant état de la propagation à grande échelle des épidémies de l’ouest vers l’est en Ontario.

Introduction

Whether measured by total area infested, length, and frequency of outbreaks or volume and numbers of trees killed, the spruce budworm, Choristoneura fumiferana Clem. (Lepidoptera: Tortricidae), is North America’s most damaging forest insect (Hardy et al. 1986). It attacks principally balsam fir, Abies balsamea (L.) Mill., and spruce, Picea spp., and can kill almost all the trees in dense, mature stands of fir during uncontrolled outbreaks. These periods of high population densities and heavy defoliation typically last 5–15 years; between such outbreaks the budworm can remain at low population levels for 20–100 years (Blais 1985).

The economic impact of budworm outbreaks prompted a number of industrial foresters and natural resource agencies to begin aerial reconnaissance of budworm-infested areas within their jurisdictions in the 1930s. The Forest Insect and Disease Survey (FIDS) of the Canadian Forest Service was founded in 1936 for this role (Sippell 1983), and by 1941 the FIDS was mapping all areas of large-scale defoliation throughout Ontario each year. As the annual defoliation maps accumulated over time, they were studied to see if certain general patterns might be found in the spatial and temporal dynamics of large-scale defoliation events.

It has long been recognized that spruce budworm outbreaks are very large-scale events, typically consisting of many infestations that occur in different localities within a region at approximately the same time (Prebble 1975). A number of authors (e.g., Wellington et al. 1950; Greenbank 1956; Pilon and Blais 1961; Greenbank et al. 1980; Blais 1985; Régnière and Lysyk 1995) have reported that, in general, the large areas of spruce budworm defoliation seem to
shift from the west to the east during an outbreak. Blais (1985) succinctly states one widely held view of the relevance of this observation to theories of outbreak spread: “The general progress of outbreaks from west to east indicates that spread is attributable, at least in part, to the dispersal of moths by prevailing westerly winds.” In other words, spruce budworm outbreaks are analogous to disease epidemics (Morris 1963) with dispersing moths acting as agents of contagion.

A difficulty with these previous analyses of the large-scale, dynamical pattern in spruce budworm defoliation over time is that they are the result of subjective, eyeballed impressions from a series of complex, detailed maps. In this paper we use geographic information system (GIS) techniques and spatial statistics to provide a more objective approach to determining the general dynamical patterns of spruce budworm defoliation in Ontario from 1941 to 1996.

Methods

Our general approach to characterizing spruce budworm disturbance regimes in Ontario relies on a sequence involving three different types of methodology: aerial survey, GIS methods, and statistical methods. In brief, the “raw” data were the annual defoliation maps produced by the FIDS during aerial surveys. These maps, which delineate areas of Ontario within which the spruce budworm had caused defoliation that year, were digitized. GIS methods were subsequently applied to these digitized maps to perform various manipulations and rearrangements of the data. After error proofing and data verification, various statistical methods were applied to reveal general, large-scale patterns over space and time in the defoliation caused by the spruce budworm.

Aerial surveys

The FIDS has been conducting aerial reconnaissance of large-scale defoliation events throughout Ontario’s productive, exploitable forest since 1941. Ideally, the reconnaissance flights begin as soon as the current season’s defoliation is completed, usually in mid to late July. Survey planes generally fly along lines 6–10 km apart at speeds of about 170 km/h with their height varying between 360–600 m. In the aircraft, FIDS personnel delineate areas within which defoliation has occurred on 1 : 250 000 maps. These maps are later compiled and the information transferred to smaller scale base maps (e.g., 1 : 600 000). Al- len et al. (1984), Dorais and Kettela (1982), and Sanders (1980) provide additional technical details about aerial sketch mapping.

The FIDS relies on the telltale signs of spruce budworm infestation in conducting their annual defoliation surveys (Sippell 1983). During their most active feeding stages (i.e., fourth to sixth instars), budworm larvae lay down a fine silk thread as they crawl about the foliage of their host conifer, and when they stop to feed, the larvae tie up the surrounding needles in their silk. As this silk dries, it contracts, pulling the needles together to form a sort of shelter for each feeding larva. The larvae feed on the new shoots, cutting off needles near their base rather than consuming all the green tissue. The severed needles are prevented from falling by the silken webbing which attaches them to the tree. These severed needles slowly develop the brick red colour which provides the distinctive tinge to trees defoliated by the spruce budworm that is so evident from the air.

There are a number of potential sources of error in aerial surveys of spruce budworm defoliation (Sippell 1983). Survey timing is important because heavy rain can wash away dead foliage causing defoliated trees to lose their distinctive reddish brown hue very quickly. A second reason for underestimating defoliation occurs in the first year of heavy defoliation on white spruce (Picea glauca (Moench) Voss) when the proportion of the total foliage that becomes discoloured is so small that it is barely detectable from the air. The scale of the infestation also affects survey accuracy. Observers typically map with less relative, but greater absolute, error when an infestation is extensive (e.g., over 800 000 km2) than when it is small (e.g., under 200 km2). The phase of an outbreak also has an influence on survey accuracy. Budworm damage is more conspicuous during the peak than during either the build-up or the collapse: large flower or cone crops and injuries caused by other pests and frosts can all create difficulties. Another possible source of error occurs when cumulative defoliation is heavy; then, it can be difficult to ascertain the species of the attacked trees (Sippell 1983).

Since spruce budworm larvae feed preferentially on the new shoots, the FIDS measures defoliation in terms of the new foliage lost. (During heavy infestations, the new shoots may be destroyed before larvae complete their feeding and then the larvae may “back feed” on needles produced in previous years). Depending on the percentage of new foliage lost, the FIDS classifies defoliation as light (0–25%), moderate (26–75%), or severe (76–100%) in its aerial surveys. Light defoliation is almost inconspicuous from the air (Sippell 1983), and therefore rarely reported (Hardy et al. 1986), so we consider only the moderate and severe categories as “defoliation” below. In this sense, our approach differs from that of Hardy et al. (1986) who considered all three defoliation classes in their cartographic analysis of aerially mapped spruce budworm defoliation in eastern North America. These authors were concerned that aerially mapped defoliation “may be slightly conservative” in Quebec, New Brunswick, and Maine where protection spraying “provided excellent foliage protection in some years” between 1970 and 1980. In an attempt to offset this bias, they mapped every class of reported defoliation, including light, which is generally not reported in Ontario.

There is reason to suspect that, as Hardy et al. (1986) imply, spraying generally has had little effect on the large-scale patterns of spruce budworm defoliation in Ontario. The largest spray program occurred in 1986 (Howse et al. 1995), but this amounted to only 1.7% of the 8.75 × 106 ha of moderate and severe defoliation that year (Howse 1995). Furthermore, Lysyk’s (1990) analysis of Ontario survey data from 1968 to 1988 indicated that “sprays... overall, did not confer a high level of foliage protection.” Similar results have been reported for some other jurisdictions (e.g., Fleming et al. 1984).

The FIDS also reports the presence of tree mortality caused by spruce budworm. Observers look for totally grey trees from the air. Subsequent ground checks (for brown cambium on both sides of some boles) are needed for confirmation, however, because trees appearing grey from the air are not necessarily dead; they may have only dead crowns (Sippell 1983).

Geographic information system (GIS) methods

The 56 maps of annual (moderate and severe) defoliation from 1941 to 1996 were digitized and stored in a GIS (Arc/Info) with each map represented by a “layer.” In each layer, each area experiencing moderate or severe defoliation was depicted by a polygon.

Several arithmetic manipulations were then performed on the digitized maps. Summing the areas of the polygons of defoliation in a layer gave the total area defoliated that year for the entire province or within specified zones of the province. The frequency of defoliation from 1941 to 1996 for each small area was also calculated. This involved determining the union of the 56 layers of annual defoliation in the database. The result was a new data layer of many small polygons, with a number associated with each polygon indicating the cumulative frequency of defoliation for the corresponding area.
Statistical methods

Analyses of time series

Classic time series methods (Box and Jenkins 1970) and the more recently developed phase coherence techniques (Lindström 1997) were applied to the time domain of the historical records. These complementary approaches can be distinguished by considering a finite, stationary time series, say \( \{z_n\} = z_1, z_2, \ldots, z_k \), which is assumed to be a single realization of an unknown stochastic process.

The focus of the classic time series methods is the auto-correlation function (ACF) which can be estimated as

\[
\hat{r}_k = \frac{\text{Cov}(z_i, z_{i+k})}{\text{Var}(z_i)}
\]

where \( k \) is a (time) lag interval (Box and Jenkins 1970). In practice, \( r_k \) is plotted against \( k \) to form the correlogram. The shape of the correlogram reveals how the correlation between two values in the time series changes with their separation in time, and this provides a means of characterizing the underlying stochastic process which gave rise to the series. The \( r_k \) are statistically significant when their absolute magnitude exceeds that of the 95% Bartlett’s band (Box and Jenkins 1970) on the correlogram. The calculation of the location of this band is based on the convergence of the sample correlation coefficients to a normal distribution. Because such convergence often does not occur for short time series, alternative approaches have been sought.

Phase coherence analysis (Lindström 1997) is a more powerful tool than the ACF for detecting periodicity in short time series. For a time lag \( k \), the series \( \{z_n\} \) is transformed into the \( k \) subsets:

\[
Q_i = \{z_i, z_{i+k}, z_{i+2k}, \ldots\} \quad (i = 1, 2, \ldots, k)
\]

Each subset is then centred about its mean and the standard deviation, \( s_k \), is calculated on the transformed time series. Substantial reductions in the standard deviation are expected for the values of \( k \) corresponding to periods of the original time series.

The probability of occurrence of any particular reduction is established by computer generation of repeated randomizations of the observed time series. A set of \( s_k \) is then calculated for each randomized time series. We used 1000 randomizations and the fifth percentile of the resulting distribution of the \( s_k \) as our criterion for statistical significance.

Synchrony

The synchrony of outbreaks in different parts of the province was measured by comparing the shape of the corresponding time series of defoliation (Geisselbrecht et al.1995). To assess the synchrony of two time series, each was considered as an \( n \)-dimensional vector \( \mathbf{v} \), with \( n \) being the number of years when the FIDS conducted surveys. The two vectors (time series) were considered to be perfectly similar if one was a multiple of the other (i.e., if the two vectors were parallel). Thus the degree of similarity, \( 0 \leq S \leq 1 \), in the shapes of the time series curves being compared was measured by the cosine of the angle between their corresponding vectors:

\[
S = \cos(\mathbf{v}_1, \mathbf{v}_2)
\]

The probability of the observed similarity, \( S \), occurring by chance alone was assessed by applying a Monte-Carlo randomization procedure. According to the null hypothesis in this procedure, the similarity between the two vectors holding the observations is no different than the similarity between two test vectors obtained by random permutations of the elements of the original vectors. One thousand pairs of such test vectors were used to produce a distribution for \( S \), and the 95th percentile of this distribution was used as the critical value (\( \alpha = 0.05 \)) for \( S \).

A time (or phase) shift between two series can be detected by moving one series by time lags of one to several years forward (or backward) and measuring the similarity as indicated above. The magnitude of the shift is given by the smallest lag which results in a statistically significant value of \( S \). One degree of freedom is lost for every lag when applying this procedure.

Results

The defoliation belt, zones, and “hot spots”

Figure 1 summarizes the spatial distribution of the cumulative frequency of defoliation caused by the spruce budworm between 1941 and 1996. Areas defoliated at least 1 year extend over a continuous east–west “defoliation belt” of 41 303 000 ha in which a wide range of different forest types and climates exist (Halliday 1937; Mackey et al. 1996). The cumulative defoliation frequencies were used to guide the decomposition of this belt into three biologically defined “defoliation zones” (Fig. 1). From west to east these zones encompass the regions of Lac Seul (9.6 × 106 ha), Lake Nipigon (6.6 × 106 ha), and Algoma (25.5 × 106 ha). Each zone is centred around “hot spots” or areas where defoliation has frequently been recorded (i.e., in over one third of all years observed). These hot spots are surrounded by approximately radial gradients of decreasing defoliation frequencies. Two narrow corridors of about 100 km in width were relatively infrequently defoliated. These corridors (indicated by A and B in Fig. 1) run approximately from north to south and separate the central zone (Lake Nipigon) from the other two.

Outbreak periodicity

The historical records of total area defoliated by the spruce budworm (Fig. 2A) suggest a basic, long-wave, oscillatory trend. Smaller, nonperiodic fluctuations (corresponding to the peaks found in 1942, 1945, 1948, 1955, 1957, 1972, 1976, 1983, 1985 and 1992) are superimposed on this basic oscillation.

In Ontario, the basic oscillation has two separate intervals (outbreaks) when extensive defoliation occurred, with maxima in 1945 and 1980. In 1941 when the FIDS began their full aerial surveys of Ontario, 10.5 × 106 ha were already defoliated, so the first outbreak presumably began earlier. In fact, Turner (1953) traces this first outbreak back to 1938. There are only 3 years on record (1964–1966) when no defoliation was recorded anywhere in the province.

Figure 2 also shows the results of applying time series and phase coherence methods to the defoliation records. In Fig. 2B, the positive correlations (\( r_k \)) for small values of \( k \) indicate a smooth series. Since a periodic series of period \( T \) would be revealed by negative correlations for \( k = T/2 \) and positive correlations for \( k = T \) (Chatfield 1989), the correlogram displayed in Fig. 2 indicates a tendency for outbreaks to cycle with a period of \( T \approx 36 \) years. The time series is not statistically significant at lag \( k = 36 \) years, however, probably because the series is short relative to its suspected period. In Fig. 2C, phase coherence analysis (Lindström 1997) indicates a statistically significant period of between 35 and
46 years in length, thus corroborating the existence of a long-term cycle. This period is similar to the average cycle lengths found by Royama (1984) in budworm populations in New Brunswick (35 years (in records of over 210 years)) and Quebec (38.5 years (in over 270 years)).

The left side of Fig. 3 gives the time series of total area defoliated for each defoliation zone (in $10^6$ ha and as a percentage of the zone’s total area). The corresponding correlograms are given on the right side of the figure. Vertical bars indicate the autocorrelation for the corresponding time lag (years). The horizontal lines above and below the horizontal axes represent Bartlett’s bands of statistical significance. Autocorrelations are significant for lags at which the length of the vertical bar exceeds the height (or depth) of Bartlett’s bands.

**Outbreak synchrony**

Figure 4 shows the results of the pairwise analysis of time series similarity for the different defoliation zones. The lag represents the number of years by which the phase of the outbreak cycle in one zone follows that in the other. Values of similarity, $S$, which lie above the solid horizontal line in each plot are statistically significant ($\alpha = 0.05$). The degree of synchrony between the two curves being examined is indicated by the smallest lag at which the similarity ($S$) becomes statistically significant.

The comparison between east and centre (Fig. 4A) indicates asynchrony (with a statistically significant lag of 5 years). This may appear to contradict Fig. 3 where the first outbreak occurs at approximately the same time in both zones. However, in this analysis, the greater duration of the second outbreak gives it more weight, and hence the overall result indicates asynchrony. Figure 4B also indicates statistically significant ($\alpha = 0.05$) asynchrony: the outbreak cycle in the western zone follows that in the eastern zone by about 6 years. The comparison of outbreak cycles in the central and western zones (Fig. 4C) produces a statistically significant lag at 0 years so these cycles can be considered synchronous. This last result is likely due to the synchrony of the second outbreak in both zones (Fig. 3) and the fact that the greater duration of this second outbreak gave it more weight than the first outbreak in this analysis of time series synchrony.

**Discussion**

**The defoliation belt, zones, and hot spots**

The northern limits of the defoliation belt (Fig. 1) are thought to be due to a relative scarcity of the insect’s
preferred host species (white spruce and balsam fir are replaced by jack pine, *Pinus banksiana* Lamb., and black spruce, *Picea mariana* (Mill.) BSP, in the west and black spruce in the east) and less favourable climatic conditions (Hardy 1986). At the southern boundary the forest becomes predominantly deciduous, and the spruce budworm is restricted to pockets of its host species where substantial defoliation is unusual.

When an outbreak reaches its peak and environmental conditions become exceptionally favourable, defoliation can occur well outside its usual limits. This was the case in 1979 when defoliation was recorded on white spruces located near the Missinaibi, Mattagami, and Abitibi rivers. This accounts for the wedge of defoliation in Fig. 1 which emerges from the eastern part of the northern boundary and extends as far northeast as James Bay.

The cumulative frequency of defoliation can be considered a rough indication of the historical threat of budworm to the local forest (Hardy et al. 1986). With similar data to that illustrated in Fig. 1, but at a much coarser scale and over fewer years, these authors applied budworm–temperature relationships to distinguish different zones of defoliation. Accordingly, they divided Ontario’s defoliated area into three parallel transects running east–west at different latitudes. By contrast, the FIDS data (Fig. 1) suggest a different type of zonation: a division into three zones centred around hot spots of frequent defoliation, which are separated longitudinally by two corridors where defoliation is rarer. The areas of very frequent defoliation, the hot spots (Fig. 1), tend to occur where budworm host trees are reported to comprise relatively high proportions of the local forest (Blais 1985; Halliday et al. 1943; Turner 1953).

There are at least two types of processes that may explain the approximately radial gradients of decreasing defoliation frequencies surrounding the hot spots (Fig. 1). First, as suggested above, environmental conditions for budworm may (gradually or abruptly) deteriorate outside the hot spots. This may be due to gradients in physical variables (e.g., soil moisture) that affect the budworm only indirectly by causing changes in certain aspects of the insect’s environment (e.g., the composition of nonhost tree species, which in turn may affect other factors such as natural enemy populations). Alternatively, deterioration of more immediate components of the budworm’s environment such as the loss of host species

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**Fig. 2.** Time-series analysis of the annual defoliation in Ontario from 1941 to 1996. (A) Historical records of the total area defoliated (×10⁶ ha). (B) Corresponding correlogram with 95% confidence bands. (C) Phase coherence function (broken line) and 95% confidence interval (solid line).
through harvesting may underlie the defoliation gradients. For instance, in corridor A (Fig. 1) extensive logging and fires have replaced fairly dense stands of balsam fir (observed prior to the first outbreak in 1941) with a much fragmented forest with stands of jack pine and trembling aspen, *Populus tremuloides* Michx. (Belyea 1952). Second, like any process with diffusive characteristics, the population pressure provided by dispersal of egg-laying moths from a hot spot can generally be expected to decline with distance from the source in the long term. Both types of process probably play a role.

**Outbreak periodicity**

The secondary fluctuations in Fig. 2A are at least partly explained by the asynchrony in outbreak cycles among defoliation zones (Fig. 3). The peaks in total area defoliated in 1942, 1945, 1972, 1976, and 1980 (Fig. 2A) correspond to maxima of defoliation in the eastern zone (Algoma), the peaks in 1948, 1985, and 1992 to maxima of defoliation in the central zone (Lake Nipigon), and the peaks in 1955, 1957, and 1985 to maxima in the western zone (Lac Seul). Thus, the secondary fluctuations in the pooled data (Fig. 2A) are partially explained by some desynchronization of outbreak cycles among the three defoliation zones.

Other than this temporal (phase) shift, the results of the time-series analysis for the different zones are similar (Fig. 3). The periodicity and the relative amplitude (i.e., percent of the total area of the zone defoliated) of the outbreaks in the three zones are remarkably alike. The eastern and western zones, respectively, have 12 and 13 consecutive years without recorded defoliation and, according to their correlograms, periods of 34–37 and 31–34 years.

Finally, tree mortality and late spring frosts may explain some of the smaller amplitude fluctuations. The collapses of outbreaks observed in 1948, 1956, and 1976 are associated with extensive balsam fir mortality (Sippell 1984). In 1973 and 1987, snowstorms and freezing temperatures in late May in the area north and east of Chapleau (Algoma) destroyed the new shoots of balsam fir and are presumed to have directly or indirectly killed a large proportion of the spruce budworm population as well (Howse et al. 1974; Howse and Applejohn 1984).

The period between the last two outbreaks can be compared with those inferred from tree ring records for the previous century. The suppression patterns in the annual rings of old white spruce suggest that spruce budworm outbreaks started around 1800, 1832, 1862, and 1880 in Ontario (Blais 1968, 1983; Turner 1953). These approximate initial years of attack imply periods of 32, 30, and 18 years, respectively, between outbreaks. Hence, the time period between the last two outbreaks (i.e., 28 years) falls well within the range of observations from the last century. At a provincial scale,
Fig. 3 shows, the last two outbreaks have been provincewide but were resolved by considering changes in outbreak extent. As the two 20th century outbreaks greatly exceed the interval of 35 years observed between the outbreaks in the 19th century. The inter-outbreak interval of 106 years between this outbreak and the next in 1938 is slightly higher than the average of 62 years in the 19th century. The intervals between outbreaks in these zones have apparently been reduced to 32 and 38 years, respectively. In the outbreaks that have occurred since 1941, extensive defoliation was first recorded in the eastern zone and then appeared in the western zone (Fig. 3). Pairwise analysis of the time series revealed a statistically significant lag of 6 years (Fig. 4).

The central zone appears to be more synchronized with the eastern zone during the first outbreak and with the western zone during the second outbreak (Fig. 3). Analysis of synchrony, however, revealed no statistically significant lags in the outbreak cycles between the central and western zones and a statistically significant lag of 5 years between the eastern and central zones. In either case, the time-series dynamics of the small central zone may not be entirely autonomous; they seem to be prone to entrainment by the dynamics of larger neighbouring zones.

Two hypotheses may explain the lack of synchrony observed between the eastern and western zones. First, the time lag between the defoliation observed in the zones may be a consequence of insect dispersal. For some unknown reason (perhaps climate, moth invasion from Quebec, or tree species composition), the outbreak starts in the eastern zone. As the budworm population builds up, the migration of insects propagates the outbreak to other zones. Radar studies of moth dispersal (Greenbank et al. 1980) have shown that both sexes often fly distances of 50–100 km in 1 year. The distance between the eastern and the central hot spots, however, is approximately 475 km and the time lag between outbreaks in these two areas is 5 years. This implies that, on average, each generation of moths has to cover 95 km/year (i.e., close to the observed average maximum), which is improbable considering that spruce budworms are weak flyers and that westbound flights are likely to be against prevailing winds. In addition, defoliation occurs much less frequently between the two hot spots. All of this casts some doubt in the small central zone may not be entirely autonomous; they seem to be prone to entrainment by the dynamics of larger neighbouring zones.

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Asynchrony of outbreak cycles
In both the outbreaks that have occurred since 1941, extensive defoliation was first recorded in the eastern zone and later appeared in the western zone (Fig. 3). Pairwise analysis of the two time series revealed a statistically significant lag of 6 years (Fig. 4).

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An alternative hypothesis stipulates zones are effectively independent. Accordingly, any migration of insects between zones is hypothesized to be inconsequential in its effect on the long-term dynamics of the outbreak cycles in either zone. In this case, the time lag between outbreaks in different zones is due to different dates of outbreak initiation or...
slightly different outbreak periods. In the latter case, the time lag between zones should differ from one outbreak to another.

**Summary and conclusions**

The use of GIS techniques, time-series methods, and spatial statistics revealed a number of previously unrecognized characteristics of the spatiotemporal dynamics of spruce budworm disturbance regimes. Maps of the cumulative frequency of (moderate and severe) defoliation indicated that a belt of $4.1 \times 10^6$ ha running across Ontario from east to west was defoliated at least once between 1941 and 1996. This defoliation belt consisted of three zones (of areas $25.5 \times 10^6$, $6.6 \times 10^6$, and $9.6 \times 10^6$ ha going from east to west) where defoliation occurred often. Two longitudinally oriented corridors, both about 100 km wide, were relatively rarely defoliated and separated the central zone from the other two. Each defoliation zone is centred around hot spots or areas where defoliation was recorded in over one third of all years observed. These hot spots are surrounded by approximately radial gradients of decreasing defoliation frequencies within each zone. In the two intervals of extensive defoliation recorded since 1941, large outbreaks were first recorded in the eastern zone, later became evident in the central zone, and finally appeared in the western zone.

Analysis of annual records of the total area defoliated in Ontario showed that the complex fluctuations in this time series could be decomposed into a basic oscillation of approximately 36 years, which is modified by secondary fluctuations and occasionally by sharp drops. The secondary fluctuations are at least partially due to asynchrony in otherwise remarkably similar long-wave oscillations in the three zones of frequent defoliation. (The time-series dynamics of the small central zone may not be entirely autonomous; they seem prone to entrainment by the dynamics of its larger neighbouring zones.) The occasional sharp drops in area defoliated were often associated with climatic extremes such as late spring frosts. Thus, complex temporal fluctuations at large spatial scales were explained by simpler fluctuations at smaller scales. This emphasizes the importance of the interactions between temporal and spatial relationships and the benefits of studying the same process at different scales.

Plans for the future include using climate, soil, and vegetation data to help explain why certain areas of the defoliation belt were more prone to spruce budworm defoliation than others. This would lay a foundation for developing spatially explicit models to simulate the dynamics of spruce budworm disturbance regimes in Ontario.

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