

Trembling aspen responses to drought and defoliation by forest tent caterpillar and reconstruction of recent outbreaks in Ontario

Barry J. Cooke and Jens Roland

Abstract: We investigated the long-term effects of drought and defoliation by forest tent caterpillars on trembling aspen radial growth in the province of Ontario using a dendroecological approach. Drought, as measured by Hogg's climate moisture index (CMI), was found to have no discernible impact on aspen radial increment in either northeastern or northwestern Ontario during the study period 1930–2003. Forest tent caterpillar outbreaks were strongly decadal in periodicity in both regions and resulted in similar patterns of periodic variation in tree ring-width chronologies, indicating that, in humid environments prone to spatially synchronized tent caterpillar outbreaks, herbivory is the main factor limiting aspen radial growth. We show that the major decadal outbreak cycles of forest tent caterpillar can, by filtering with the computer program OUTBREAK, be reliably reconstructed from raw aspen ring-width chronologies. We determine the filtering parameters that give the most reliable reconstruction fit to observed patterns of outbreaks in each region. We show that the periodic outbreak signal is present even in areas where aerial surveyors frequently failed to detect significant levels of defoliation, and that the outbreak signal necessarily includes minor defoliation episodes that occur in between the major decadal outbreak cycles.

Résumé : Nous avons étudié les effets à long terme de la sécheresse et de la défoliation causée par la livrée des forêts sur la croissance radiale du peuplier faux-tremble dans la province d'Ontario à l'aide d'une approche dendroécologique. Nous avons trouvé que la sécheresse, mesurée par l'indice d'humidité du climat de Hogg, n'a pas eu d'impact discernable sur l'accroissement radial du peuplier faux-tremble, ni dans le nord-est, ni dans le nord-ouest de l'Ontario au cours de la période considérée dans l'étude, soit de 1930 à 2003. Les épidémies de livrée des forêts ont eu une périodicité fortement décennale dans les deux régions et ont produit des patrons semblables de variations périodiques dans les chronologies de largeur de cernes annuels, indiquant que dans les milieux humides sujets à des épidémies de livrée des forêts synchronisées dans l'espace, l'herbivorisme est le principal facteur qui limite la croissance radiale du peuplier faux-tremble. Nous montrons que les principaux cycles décennaux d'épidémie de livrée des forêts peuvent, en filtrant avec le programme informatique « OUTBREAK », être reconstitués de façon fiable à partir des chronologies brutes de largeur de cernes de peuplier faux-tremble. Nous avons déterminé les paramètres de filtration qui permettent d'ajuster de façon la plus fiable la reconstitution avec le patron des épidémies observé dans chaque région. Nous montrons que le signal des épidémies périodiques est présent même dans les régions où les responsables de l'inventaire aérien ont souvent omis de détecter des niveaux significatifs de défoliation et que le signal d'une épidémie inclut nécessairement des épisodes mineurs de défoliation qui surviennent entre les cycles décennaux d'épidémie majeure.

[Traduit par la Rédaction]

Introduction

Insects can have a large impact on net primary productivity, especially in the boreal forest, where large-scale, recurrent outbreaks of various species of forest Lepidoptera sometimes have devastating consequences (Mattson and Addy 1975). There are a number of reasons why precise estimates of the influence of insect herbivores on forest productivity are needed, including the need for accurate carbon accounting methods, and the need for accurate timber inventory projections. Insect disturbance, however, is a very dynamic process, in that: (i) each species tends to exhibit its

own particular dynamic; (ii) the pattern of impact varies substantially in space and time, in ways that are neither purely systematic nor purely random; (iii) factors such as climate and forest structure, which strongly influence key population regulatory processes, vary continuously over multiple time scales (Cooke et al. 2007). Enviroclimatic change (e.g., climate warming, forest fragmentation), in turn, is a major challenge for insect disturbance modeling, because (i) the magnitude and nature of change is not known; (ii) the number of interacting population processes that are affected by both weather and vegetation is large; (iii) the basic processes governing insect population fluctuations (competition, predation, weather, etc.) are at best only

Received 2 June 2006. Accepted 9 January 2007. Published on the NRC Research Press Web site at cjfr.nrc.ca on 28 September 2007.

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partly understood (Fleming and Volney 1995; Volney and Fleming 2000).

Given these sources of uncertainty, one of the most important areas of research is the characterization of past disturbance regimes. By reconstructing, as accurately as possible, past climates, landscapes, and outbreaks, one can hope to find empirical associations that help in (i) forecasting future disturbance and (ii) formulating testable hypotheses regarding disturbance-generating mechanisms. Hence the rise, and importance, of insect dendroecology in forestry (e.g., Blais 1983; Swetnam and Lynch 1993). Short-term population studies can provide significant insight into a system's dynamic behaviour (Roland 2005); however, long-term, large-scale retrospective approaches are essential, because forest insect systems are under the influence of a broad array of randomly varying biotic and abiotic mortality agents (Royama 1992).

It is in this context that we consider the case of the forest tent caterpillar, *Malacosoma disstria* Hübner, a defoliator of trembling aspen, *Populus tremuloides* Michx., across the boreal forest region of North America. Outbreaks of forest tent caterpillar have occurred periodically in east-central Canada for at least a couple of centuries (Sippell 1962). At the landscape scale, outbreaks usually last only a few years, but local infestations may persist for a decade (Shepherd and Brown 1971; Witter et al. 1975; Millers et al. 1989).

The reason why outbreaks vary in extent and duration over time and space is not well understood, although it is clear that forest landscape structure and climate are among the key variables (Roland 1993; Roland et al. 1998; Cooke and Roland 2000). In terms of causal mechanisms, forest structure is known to affect organisms that parasitize tent caterpillars (Roland and Kaupp 1995; Roland and Taylor 1997; Rothman and Roland 1998), while extreme cold or variable temperatures during the overwintering period can result in the collapse of outbreaks over large areas (Blais et al. 1955; Witter and Kulman 1972; Cooke and Roland 2003).

The forest tent caterpillar is known to cause substantial and prolonged reductions in aspen foliar area, live-crown volume (Hodson 1981), and annual radial increment (Duncan and Hodson 1958; Rose 1958; Kulman 1971). In theory, long-term tree-ring reconstructions could be used to study the influence of enviroclimatic change on long-term outbreak dynamics; however, there are several challenges with this system. First, the primary host, trembling aspen, is a fast-growing, short-lived species, which limits its usefulness for long-term dendrochronology. Although living stems over 200 years old have been encountered in the western United States (Jones and Schier 1985) and in eastern Canada, these are rare. In north-central Alberta, aspen stands originating in the 1830s are not uncommon, and tree disks there frequently show characteristic signs of recurring attacks by defoliating insects (Cooke 2001). Second, in dry climate regions, the influence of drought on growth can be strong enough to mask the defoliation signal contained in annual tree ring widths (Hogg et al. 2005). Third, although it is possible in theory to amplify the outbreak signal in a host tree by contrasting it with the climatic signal contained in a nearby nonhost tree species (Nash et al. 1975), the reality is that nonhost trees can be rare in some forest types. For

example in the aspen parkland region of westcentral Canada, the forest tent caterpillar has such a wide-ranging diet that there is a serious lack of nonhost tree species (e.g., spruces, pines, and firs) to use as climate-sensitive and (or) insect-insensitive controls.

In this paper we use a historical dendroecological approach to calibrate the ring-width response of trembling aspen to drought and defoliation by forest tent caterpillar over the period 1930–2003 in the Great Lakes mixed boreal forest region of Ontario. We attempt to reconstruct the pattern of tent caterpillar outbreaks using only host–species ring-width data, and we use sensitivity analysis to examine the accuracy of these reconstructions as a function of varying filtering parameters. Our goal is to provide a solid baseline for future dendroecological research on this system in other bioclimatic regions.

Methods

Defoliation data

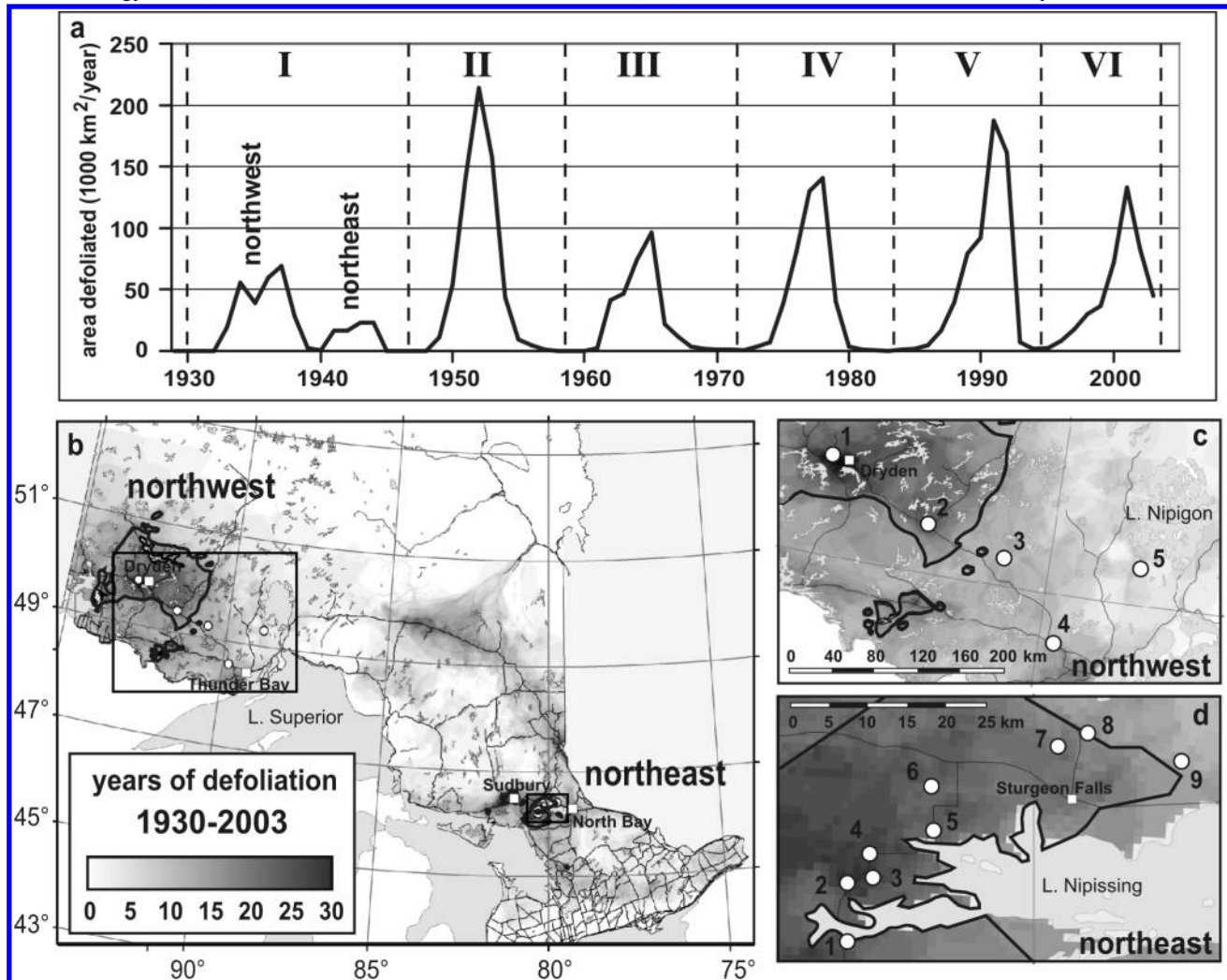
Annual Canadian Forest Service defoliation maps for the forest tent caterpillar for the period 1930–2003 were digitized and overlaid in a GIS database. In a preliminary computation, the number of hectares of forested land defoliated by forest tent caterpillar was computed for each year, and this variable was found to exhibit six distinct outbreak cycles (Fig. 1a). The number of years of defoliation during each outbreak cycle was summed for each cell in the GIS raster. We identified those areas where at least 1 year of defoliation was recorded in all six provincewide outbreak cycles, and found there to be two areas where all six outbreak cycles occurred: one near the town of Dryden, in the northwestern region (NW), and the other east of Sudbury, in the northeastern region (NE) (Fig. 1b). Moving outward from these core areas, the total number of years in which defoliation was recorded tended to decline smoothly, producing a radial gradient in the apparent duration and frequency of outbreaks. The gradient on outbreak frequency and duration was then used to structure the tree-ring sampling design. The goal of the design was to identify spatial variation in aspen radial growth across the gradient.

Tree-ring data

In each of these two outbreak regions (NW and NE), a single transect was positioned to extend from the core area where tent caterpillar outbreak cycles always occurred out to the surrounding area where outbreaks were infrequent. The NW transect, installed in the autumn of 2004, comprised five dendrochronology sites (NW-1 to NW-5), spaced at distances of roughly 100 km (Fig. 1c). The NE transect, installed in the summer of 2002, comprised nine dendrochronology sites (NE-1 to NE-9), spaced at distances of roughly 5 km (Fig. 1d). All sites were located within 50 m of a primary or secondary road, and sampled stems were located at least 20 m from the forest edge.

Because it was installed 2 years later, the scaling of the NW transect could be optimized on the basis of information obtained from the NE 2002 study. The NW site locations were determined on the assumption that five evenly spaced points along the defoliation gradient (ranging from 6 to 28 years of defoliation out of 73 total possible years) would

Fig. 1. Defoliation by forest tent caterpillars during six outbreak cycles in Ontario from 1930 to 2003: (a) summed by year over all locations and (b) summed by location over all years. Close-ups of defoliation gradients are shown in the (c) northwestern and (d) northeastern regions. Dendrochronology sites (NW 1–5, NE 1–9), ○. Thick black outlines in (b–d) indicate areas where all six outbreak cycles I–VI occurred.



be the minimum necessary to resolve the tree's response to variable levels of defoliation over time. The endpoints, NW-1 and NW-5, were located near the town of Dryden and at Black Sturgeon Lake (the conifer-dominated area studied by Ghent (1958)). Stands selected for study were chosen primarily on the basis of their proportion of aspen, the size of dominant stems, and ease of access.

From each site, three stems were selected for destructive sampling — except at NW-1, where six stems were sampled. Individual stems within stands NW-1 to NW-4 were selected on the basis of size, perceived age, and state of decay. Basal disks were cut at stump height and submitted to dendrochronological analysis (described in the following). Stems within stand NW-5, near Black Sturgeon Lake, were selected using similar criteria, with the idea of trying to resample the 1880s aspen cohort originally studied by Ghent (1952). The scientific value of this overmature stand prohibited destructive sampling. Consequently, 11 cores were taken from overstorey trees, yielding a total of $6 + 3 + 3 + 3 + 11 = 26$ samples from the NW region.

The experimental design of the NE study is somewhat

more complex, as dendrochronological analysis was only one component of a larger project. During the week of 28 June to 3 July 2002, in the midst of a severe forest tent caterpillar outbreak, a total of 51 stems of trembling aspen were sampled from among the nine NE sites. The number of stems per site varied from 3 to 14. Sites and stems were selected on the basis of their age, state of decay, and the amount of current-year defoliation caused by forest tent caterpillar. In selecting stems, we tried to balance the competing objectives of selecting the oldest stems (useful for dendrochronology) versus stems with a low incidence of heart decay (a constraint imposed by the larger project). Aspen stands in the Lake Nipissing area were generally young — the product of reinvasion after abandonment of marginal agricultural land.

From each stem, a basal disk was taken and subjected to dendrochronological analysis. The earlywood–latewood boundary is not easy to distinguish in the pale wood of trembling aspen, so we chose to use disks rather than increment cores, wherever possible. Disks were sanded to a fine polish using increasingly fine sandpapers up to 320 grit. We

chose a transect across each disk that was representative of the average ring-width patterns contained in the entire disk. This approach is advantageous for examining ring-width variation in trembling aspen, as its annual rings do not conform well to a concentric circular model because of its exploitive growth habit.

Ring widths were measured to the nearest 0.01 mm using a Velmex measuring table (Velmex Inc., Bloomfield, New York). Samples were cross-dated using skeleton plots. Statistical cross dating was not used because spreading outbreaks are expected to lead to sharp growth reductions in different years in different stand chronologies.

The aspen ring-width data were compiled to create 14 mean ring-width chronologies, one for each site. Ring-width series were not detrended, because we wanted to preserve low-frequency variation that could be a product of nonstationary forest tent caterpillar population dynamics.

For each of the 14 dendrochronology sites, a binary defoliation history time series (moderate to severe defoliation versus no defoliation, in each year t) was assembled using the GIS defoliation maps (i.e., sampled sites were categorized as either defoliated or not defoliated in a given year). Thus, we were able to analyze the relationship between ring-width variability and defoliation histories at multiple spatial scales, from the level of the whole province, to regions, to individual sites within regions.

Climate data

Daily weather data for the province of Ontario were used to calculate, for the years 1930–2003, an annual seasonal climate moisture index (CMI) for two point locations in northwestern and northeastern Ontario: Ignace (NW, 49°25'N, 91°39'W) and Sturgeon Falls (NE, 46°25'N, 80°7'W). Hogg's (1999) CMI, which is computed for the "precipitation/growing year" (1 September in year $t - 1$ to 31 August in year t) rather than the calendar year, has been proven to be a strong predictor of interannual fluctuations in aspen growth rates in western Canada (Hogg et al. 2005); hence, our decision to use it over other possible techniques.

Statistical analysis

The response of trembling aspen growth to drought and defoliation by forest tent caterpillar was measured first by time-series multiple regression, using ring widths in year t as the dependent variable and CMI and defoliation in year t as independent variables. More complex models were also built, which included the potentially lagged effects of CMI and defoliation in year $t - 1$. This analysis was conducted at two spatial scales: between regions (with annual defoliation among sites being averaged within regions) and among sites within each region (with CMI, as a regional-scale variable, being fixed within regions). As not all 14 of the site-level chronologies extended back to 1930, only those 5 that did (NW-1, NW-2, NW-4, NW-5, and NE-4) were selected for site-level analysis.

Two contrasting types of time-series regression models were employed. The first, based on the assumption that ring-width observations were independent from one year to the next, was fit by ordinary least squares (OLS). The second, which allowed for autocorrelated observations, was fit using a maximum likelihood estimation (MLE) method.

With this second method, the degree of temporal autocorrelation among observations within time series, symbolized by parameter ϕ , is estimated after the regression parameters, which are interpreted as in ordinary regression. One interpretation of ϕ is as a measure of the degree of "physiological preconditioning" (Fritts 1976) resulting from endogenous carryover effects associated with the tree's intrinsic growth processes. However, ϕ may also represent the residual effect of any autocorrelated exogenous drivers (including lagged responses, positive or negative, to specified drivers) that are not included among the independent predictor variables.

Alternative approaches to modeling annual growth increment are possible, and a common one is autoregressive modeling, whereby autocorrelation effects are internalized by regressing annual increment in year t directly against annual increment in year $t - 1$. We specifically avoided the autoregressive approach because of the potentially complex behaviour of herbivory as a cyclic driver of tree growth. First, periodic insect defoliators are themselves driven by a second-order autoregressive annual recruitment process (Royama 1992), and because insect defoliation is not always easy to detect, a defoliation index may therefore be subject to autocorrelated measurement error — error which, being absent from any predictive defoliation variables, could lead to residual autocorrelation in the modeled growth signal above and beyond any physiological preconditioning effects. Second, in addition to an immediate, within-year response to early-season defoliation, host trees often exhibit a 1 year lagged response (Hogg et al. 2002b), suggesting that there are at least two intercorrelated cyclic processes mediating growth, neither of which is fully represented by error-prone defoliation indices. The autoregressive approach thus risks misidentifying any of these sources of autocorrelation as being the product of physiological preconditioning when it may in fact be a hidden product of herbivory.

Temporal patterns of cyclicality in regionally averaged aspen ring widths and defoliation histories were quantified using autocorrelation analysis and spectral analysis. The purpose of autocorrelation analysis is to identify the degree of association between observations measured at different time points. If a process is cyclic, then the autocorrelation function tends to cycle. If the cycle is caused by an autoregressive quasi-cyclic process, such as a herbivore population cycle, then the first-order partial autocorrelation should be positive, the second-order partial autocorrelation should be negative, and higher-order terms should be nonsignificant (Royama 1992). Autocorrelation analysis is well-suited to low-order, unifrequential processes (i.e., where periodicity is well-described by a single parameter), but is less useful for high-order, multifrequential, or nonstationary processes. One of our questions was whether, in addition to the expected decadal periodicity in ring-width fluctuations resulting from major and well-studied forest tent caterpillar outbreak cycles, there were higher-frequency periodic fluctuations that might be associated with minor defoliation episodes. We used spectral analysis to identify components of variability in ring-width and defoliation series occurring at different time scales. We used cross-spectral analysis to determine the extent to which regional-scale correlations between ring widths and defoliation time series were

caused by strong coherence at decadal and subdecadal time scales.

A second analysis examined the regional-scale response of ring widths to variation in moisture availability strictly during nonoutbreak years. Froelich et al. (1956) used this data-censoring approach on Minnesota tree-ring data, reasoning that the apparent response to drought should be boosted by removing the data for years in which outbreaks were known to occur. All statistical modeling and analysis was done using the R statistical software package (Ihaka and Gentleman 1996), version 2.00.

Gradient analysis and anomaly detection

The dominant source of climatic variability in ring widths having been removed by regression analysis, we compared patterns of ring-width fluctuations at either end of the two defoliation gradient transects, that is, sites NW-2 versus NW-5 and NE-1 versus NE-9. We substituted NW-2 (originating in 1915) in place of NW-1 (originating in 1950) because NW-2 spanned the full range (1930–2003) of the environmental data set.

It is well known that weather patterns affecting tree growth tend to be spatially autocorrelated at regional spatial scales (Fritts 1976). If periodic insect outbreaks are synchronized at similarly regional spatial scales (e.g., Peltonen et al. 2002), then site chronologies within a region should exhibit very similar patterns in ring-width fluctuations. Major dissimilarities among sites within a region therefore indicate the action of a locally acting disturbance process, such as a localized weather anomaly (e.g., ice storm, wind gust, etc.), or a defoliation “anomaly”. We sought to identify any such anomalies and to analyze their pattern of occurrence, in relation to known outbreaks of forest tent caterpillar, and in relation to one another. In our search, we looked specifically for two kinds of discrepancies indicating asynchronously acting, local-scale disturbance effects: (i) major, decadal growth reductions in infrequently defoliated areas at a time when defoliation was not observed locally but was observed in the frequently defoliated areas; and (ii) growth reductions at both ends of the gradient, within 1 or 2 years of one another, but not at the same time, and not coincident with a major decadal outbreak. The first type of discrepancy would indicate where surveyors missed an outbreak. The second would indicate a nonclimatic, defoliating disturbance of lesser magnitude, which may or may not be the result of localized infestations of forest tent caterpillars.

Outbreak reconstruction and validation

Outbreak reconstruction in dendroecology is accomplished via a multistage filtering process that is designed to (1) enhance the host-specific signal associated with insect outbreaks and (2) diminish the signals associated with extraneous factors, such as (i) high-frequency variation resulting from random weather fluctuations and (ii) nonstationarity attributable to gap successional dynamics. The methods used to diminish these extraneous signals are (i) climate correction, through either “response function” analysis (Fritts

1976) or use of a climatically comparable nonhost (Nash et al. 1975) and (ii) detrending, typically using stiff cubic splines (Cook and Peters 1981). The task of enhancing the insect-related signal in the host chronology is accomplished by filtering the host chronology using a multiparameter filter (e.g., Swetnam and Lynch 1993), such as the one represented by the computer program OUTBREAK (R.L. Holmes and T.W. Swetnam, unpublished operating manual (on file at the Laboratory of Tree-Ring Research, University of Arizona); also see Swetnam et al. 1995).

Given that no published studies have ever validated the use of OUTBREAK in reconstructing known outbreaks, we wanted to test its ability to simulate recorded patterns of known forest tent caterpillar outbreaks. Consequently, we systematically varied the program’s filtering parameters to determine which values gave the best fit to observed patterns of outbreaks. We specifically wanted to determine the best possible reconstruction that could be obtained using raw aspen ring-width data, unadjusted for any climatic effects. A secondary goal, given that aerial survey programs are not infallible, was to identify potential defoliation episodes that might not have been recorded by the surveyors. We predicted that the match between observed and reconstructed outbreaks would be generally strong, except for the odd mismatch that might result from surveyor insensitivity or reduced survey effort in nonoutbreak years. Specifically, we expected that (i) defoliation events known to occur at the severe end of the defoliation gradient during an outbreak cycle would be recorded as a growth reduction in trees at the light end of the defoliation gradient, regardless of whether or not surveyors detected defoliation there; and (ii) minor growth reductions occurring in between the major decadal outbreak cycles were severe enough at the level of individual stems to be interpreted as localized defoliation events.

We submitted the 80 tree ring-width chronologies (29 northwest and 51 northeast) to the filtering program OUTBREAK using as fixed parameters, 2 and 6 years, for the minimum and maximum assumed length of a forest tent caterpillar outbreak.² We varied the “maximum growth reduction threshold” parameter systematically from -0.58 standard deviations to -1.56 standard deviations, in steps of -0.14 — low-threshold values being more discriminating, and higher-threshold values being more permissive. A value of -1.28 is the standard default that has been used, for example, in reconstructing outbreaks of western spruce budworm (Swetnam and Lynch 1993) and tussock moth (Swetnam et al. 1995) on Douglas-fir. We also varied the “rate-of-increase in growth reduction” parameter systematically from 0.3 to 1.0 (the default value) in steps of 0.35, but focus on results obtained using a fixed value of 1.0.

Each reconstruction was analyzed two ways. First, correlations were computed between observed patterns of outbreaks and the reconstructed “proportion of trees affected” by outbreaklike growth reductions. Second, spectral analysis was used to determine if the reconstructed outbreak sequences were unifrequential and decadal periodic, as

²The choice of 2 and 6 years as thresholds is somewhat arbitrary, but similar to the choice made by Swetnam et al. (1995), who used the OUTBREAK program to reconstruct outbreaks of Douglas-fir tussock moth, a species that, like the forest tent caterpillar, exhibits decadal outbreaks lasting 2–6 years at the landscape scale.

one would expect based on the highly periodic defoliation time series (i.e., Fig. 1a).

Results

Temporal response

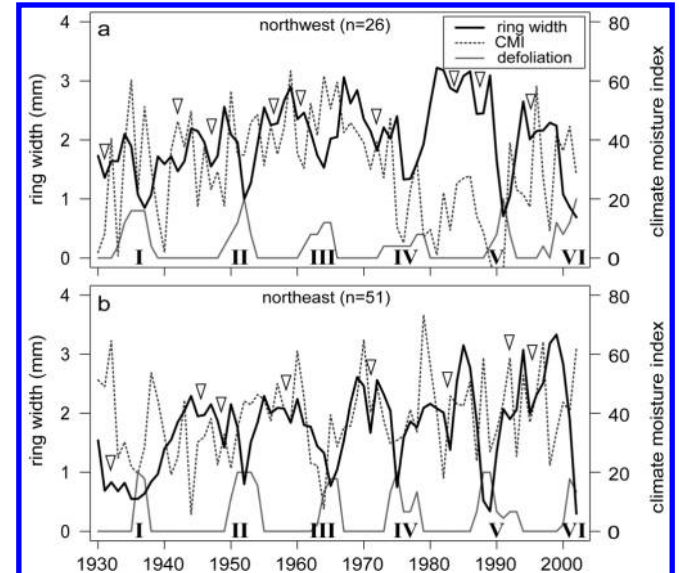
In both regions, trembling aspen ring widths tended to decline during years of forest tent caterpillar outbreak (e.g., 1937–1938, 1951–1953, 1963–1966, 1976–1978, 1989–1991, and 1999–2002), but not during years of moisture stress, as inferred from Hogg's CMI (Figs. 2a and 2b). Aspen ring widths exhibited a high degree of decadal variability, with peak periodic variability in the 13–14 year range (Figs. 3a and 3b, solid arrows). In addition, there was some higher-frequency (i.e., midfrequency) variability in the 6–7 and 4–5 year ranges in both regions (Figs. 3a and 3b, light arrows), attributable to brief and mild growth reductions occurring in between the major decadal dips. The regional defoliation time series also exhibited multiple frequencies, but not as much as did the aspen ring widths (Figs. 3a and 3b; compare black versus grey lines). This subdecadal variability was due to minor, asynchronous pulses of defoliation in the mid- versus late-1970s (NW and NE), the late 1980s versus early 1990s (NE), and the mid- versus late-1990s (NW) (Figs. 2a and 2b).

Ring-width chronologies were positively correlated between the two regions ($r = 0.36$), as were the regional defoliation time series ($r = 0.52$). In contrast, CMI was not correlated between regions ($r = -0.18$). Cross-spectral analysis indicated that the high correlation between ring-width and defoliation time series was due to decadal periodicity in each variable (Figs. 3a and 3b) and exceptionally strong coherence ($0.6 < r < 0.95$, 95% confidence interval) in the decadal frequency range (Figs. 3c and 3d). Ring-width data exhibited stronger subdecadal variability than did the defoliation time series, with strong spectral peaks near 6–7 years being bracketed by strong spectral troughs near 8–9 and 5–6 years (Figs. 3a and 3b, grey versus black lines in the vicinity of the white arrows).

The periodic variability identified through spectral analysis was confirmed by autocorrelation analysis. In both regions, autocorrelation functions were moderately periodic for the ring-width chronologies and strongly periodic for the defoliation history time series, peaking in the 13–14 year range (Fig. 4). Partial autocorrelation functions indicated strongly positive first-order autocorrelation and moderately negative second-order autocorrelation, hallmarks of a low-order, autoregressive (i.e., quasi-cyclic or feedback-driven) process.

The high degree of autocorrelation in ring-width series suggested that ring width was not independent from one year to the next, possibly a result of the tree's internal growth dynamics. Thus, we employed the two forms of the time-series multiple regression model: OLS without autocorrelation ($\phi = 0$) and MLE with autocorrelation ($\phi > 0$). When these were fit to the two regional time series (data in Figs. 2a and 2b), defoliation history was always a significant predictor of aspen ring width ($p < 0.001$), while the climate moisture index ($p > 0.1$) was not (Table 1). In every case, the effect of defoliation, measured by the defoliation coefficient, was strongly negative. The MLE model produced co-

efficients that were slightly lower in magnitude in both regions (-0.85 ± 0.24 versus -1.28 ± 0.21 in the northwest region and -0.78 ± 0.19 versus -0.93 ± 0.20 in the northeast region). The use of the MLE model appeared justified, as the endogenous first-order autocorrelation (symbolized by ϕ) was estimated at ~ 0.6 for both regions, regardless of what terms were included in the model. When the time-series regression analysis was conducted using site-level data, very similar results (not shown) were obtained.

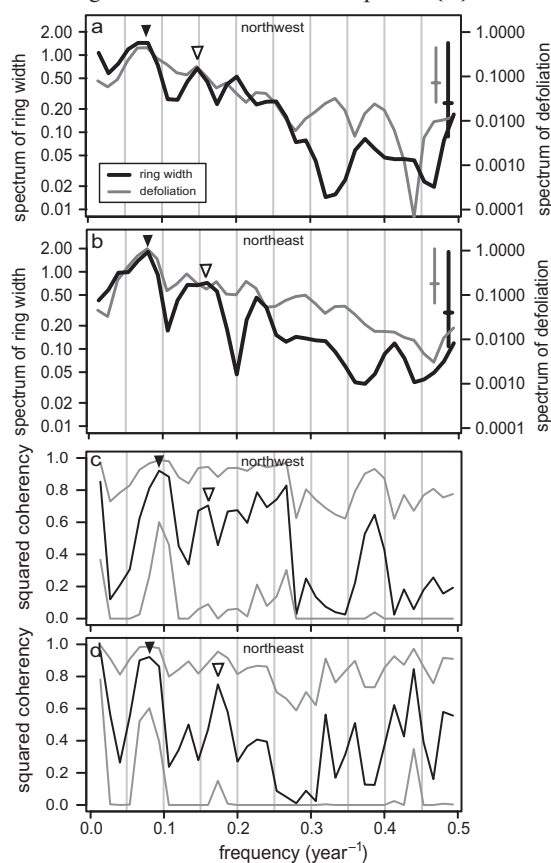


including a lagged defoliation history term did not improve any of the fitted models substantially. However, according to the MLE model, the lagged defoliation term itself was significant in both regions. Defoliation in both current and previous years had a strongly negative impact on ring width. Regardless of which model was used, the effects were similar for both regions. In the northwest region, defoliation in the previous year had a stronger impact than did defoliation in the current year. In the northeastern region, the current-year impact of defoliation was stronger than the lagged effect.

When higher-order lagged CMI terms were included in each model, none turned out significant (full analysis not shown, but see regional models 2 and 4 in Table 1). Similarly, when the regional-scale analysis was restricted to include only nonoutbreak years ($n = 40$ and 47 in NW and NE, respectively), CMI was unrelated to ring width (Table 2).

A comparison of observed ring width to values fitted by OLS and MLE regression indicated that the statistically significant first-order autocorrelations had biological significance in terms of their ability to account for both positive and negative growth anomalies in between the known, re-

Fig. 3. Spectral analysis of raw ring widths (black line) and defoliation (grey line), for northwestern (*a*) and northeastern (*b*) data in Fig. 2, along with 95% confidence intervals. Corresponding cross-spectral coherence between ring widths and defoliation in (*c*) and (*d*), along with 95% confidence intervals. Black and white arrows on spectra and cross-spectra indicate dominant, decadal variability (74 years/6 cycles = 12.3 years/cycle) and subdominant, subdecadal variability (6–7 years) occurring at the regional scale. All spectra smoothed using Daniell smoother with a span of {3}.

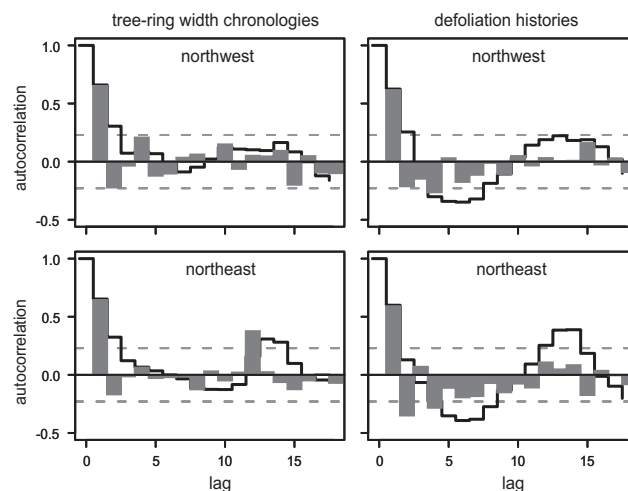


corded outbreaks (Fig. 5). These included rebounding growth following outbreak (Fig. 5, inverted triangles) and mild growth reduction both before and after recorded outbreaks (Fig. 5, up arrows). These first-order autocorrelation coefficients were therefore functional, by being associated with relatively high-frequency periodic variability that (*a*) is not removed by low-frequency detrending methods, such as time-series differencing and (*b*) has an interpretable biological cause.

Gradient analysis

Despite the high degree of phase synchrony among regional defoliation histories (Fig. 2), the transect end points differed in terms of both the total number of years of defoliation (6 and 10 years of defoliation on the light end of the gradient versus 20 and 18 years on the severe end) and timing of outbreaks (Figs. 5*a* and 5*b*). This was particularly evident during cycles III (1962–1966) and IV (1975–1979), during which no defoliation was recorded at NW-5 (Fig. 6*a*), and only 1 year of defoliation was recorded at NE-9 (Fig. 6*b*). The more heavily defoliated sites (NW-2 and NE-1), in contrast, experienced 2–4 years of outbreak during each cycle. This contrast among defoliation transect

Fig. 4. Autocorrelation functions for aspen ring-width chronologies (left) and defoliation histories (right) for each region (source data in Fig. 2). Autocorrelations plotted as a step function (black). Partial autocorrelations plotted as vertical bars (grey). Broken horizontal lines indicate Bartlett 95% confidence bands.



endpoints was reflected in the corresponding width chronologies (Figs. 5*a* and 5*b*), in that aspen radial growth in NW-5 and NE-9 did not decline nearly as much as NW-2 and NE-1 during outbreak cycles III and IV. They did, however, decline a little.

Despite this variability in the frequency and duration of defoliation, all of the individual site-level ring-width chronologies indicated the same sort of decadal and subdecadal periodicity (Figs. 6*c* and 6*d*) seen in the regional chronologies (Figs. 3*a* and 3*b*). Consequently, stems in areas deemed to be “not defoliated” by aerial surveyors carried a characteristic periodic defoliation signal.

What is more remarkable is the discrepancy between ring-width and defoliation data from either end of the defoliation gradients (Fig. 5). Results during cycle III are particularly instructive. In the heavily defoliated part of the northwestern region (NW-1), defoliation was observed from 1961 to 1965, and growth reached a decadal minimum in 1964, whereas in the lightly defoliated part of the northwestern region (NW-5), no defoliation was observed, while growth reached a decadal minimum in 1968 (Fig. 6*a*). This suggests that aerial surveyors might have detected the most intense part of the outbreak at NW-1 in the early 1960s, while failing to detect the lighter damage occurring later in the 1960s at NW-5. Such an asynchronous pattern of outbreak spread during cycle III can also be seen in the defoliation and tree-ring data from northeastern Ontario (Fig. 6*b*). Defoliation was observed in 1964–1966 in the core area (NE-1), but not at all in the fringe area (NE-9). Tree ring widths in the core area declined sharply to a decadal minimum in 1966, but did so in the fringe area 3 years earlier.

Similarly, during cycle IV in northwestern Ontario, there appeared to be a 1–2 year delay between the start of the outbreak in 1976–1978 in the core area at NW-1 and the growth reduction in 1979 at NW-5, where no defoliation was recorded. This suggests a spreading of the outbreak. This growth reduction, like the one in 1968, was one of six

Table 1. Time-series regression of nondetrended aspen ring widths from 1930 to 2003 on climate moisture index (CMI_t) and defoliation history (D_t , defoliation in the current year; D_{t-1} , defoliation in the previous year) for northeastern and northwestern regions, under two regression methods: ordinary least-squares (OLS) with no autocorrelation ($\phi = 0$) versus maximum likelihood estimation (MLE) with autocorrelated ($\phi > 0$) observations and errors.

Model	Term ^a	Regression method							
		OLS, $\phi = 0$				MLE, $\phi > 0$			
		Coeff.	SE	<i>t</i> value	<i>p</i> value	Coeff.	SE	<i>t</i> value	<i>p</i> value
Northwest region									
1	CMI _t	0.0031	0.0030	1.06	0.2930	0.0009	0.0027	0.32	0.7495
	D_t	-1.1736	0.1830	-6.41	0.0000	-0.8470	0.2081	-4.06	0.0001
	Model 1 summary	$R^2 = 0.370$, $F_{2,70} = 20.6$, $p < 0.0001$				AIC = 77.0, BIC = 88.4, logLik = -33.5, $\phi = 0.51$			
2	CMI _t	0.0053	0.0027	1.96	0.0546	0.0032	0.0024	1.34	0.1828
	D_t	-0.5512	0.2175	-2.54	0.0135	-0.5231	0.1874	-2.79	0.0068
	D_{t-1}	-1.0117	0.2333	-4.33	0.0000	-1.0554	0.2008	-5.25	0.0000
	Model 2 summary	$R^2 = 0.505$, $F_{3,69} = 23.4$, $p < 0.0001$				AIC = 54.5, BIC = 68.3, logLik = -21.3, $\phi = 0.55$			
Northeast region									
1	CMI _t	0.0026	0.0054	0.48	0.6310	-0.0028	0.0037	-0.74	0.4593
	D_t	-0.9283	0.2048	-4.53	0.0000	-0.7795	0.1981	-3.93	0.0002
	Model 1 summary	$R^2 = 0.238$, $F_{2,70} = 10.9$, $p < 0.0001$				AIC = 108.4, BIC = 119.9, logLik = -49.2, $\phi = 0.66$			
2	CMI _t	0.0047	0.0055	0.85	0.3957	-0.0010	0.0034	-0.29	0.7746
	D_t	-0.6680	0.2622	-2.54	0.0131	-0.6752	0.1951	-3.46	0.0009
	D_{t-1}	-0.4117	0.2629	-1.56	0.1219	-0.4862	0.1948	-2.49	0.0150
	Model 2 summary	$R^2 = 0.264$, $F_{3,69} = 8.2$, $p < 0.0001$				AIC = 104.1, BIC = 117.9, logLik = -46.1, $\phi = 0.63$			

Note: Time-series analyzed correspond with those plotted in Fig. 2. Observed versus fitted values are plotted in Fig. 3. AIC, Akaike's information criterion; BIC, Bayesian information criterion.

^aIntercept is significant in all models, indicating a nonzero mean of chronology ring widths.

decadal minima, suggesting it could well be the result of a periodic disturbance agent, such as the forest tent caterpillar.

Close temporal and spatial proximity of these growth reductions in 1968 and 1979 in NW-5 to known outbreaks of forest tent caterpillar in 1961–1965 and 1973–1979 in the nearby core area of defoliation at NW-1 suggests defoliation by this insect.

Outbreak reconstruction and validation

The filtering program OUTBREAK performed well in simulating the known pattern of outbreaks (Fig. 7). The performance in the northwestern region was particularly good (Fig. 7, top). The reconstruction in the northeastern region, in contrast, consistently failed to pick out an outbreak cycle for 1934–1938 (Fig. 7, bottom). This is not surprising given that 50 of 51 of these samples originated after 1935, and stems less than 10 years in age do not exhibit large growth reductions during outbreaks (Batzer et al. 1995; Cooke 2001). The high fidelity of the reconstructions suggests that the choice of filtering parameters was appropriate. In particular, growth reductions lasting 2–6 years are likely attributable to episodic insect defoliation.

What is notable in these reconstructions is not just the degree of concordance with the aerial defoliation survey data, but the wide range of parameter space over which concordance is observed. Correlations between reconstructed and observed outbreaks were always >0.55 , regardless of the value chosen for the maximum growth reduction threshold parameter (Fig. 8). In the northwestern region, setting this threshold parameter ≥ -1.00 standard deviations still produced correlations >0.72 . In the northeastern region, setting this parameter ≥ -1.28 standard deviations produced correlations >0.66 .

The most curious trend to emerge as a result of varying the growth reduction threshold parameter was the increased tendency to detect minor defoliation episodes (Fig. 7, ∇) between major outbreak cycles I–VI (Fig. 7, \blacktriangledown). These minor defoliation episodes, in 1947–1948, 1971–1972, 1983–1984, and 1994–1995, represent significant growth reductions occurring in a minority of stems somewhat simultaneously in both regions. For whatever reason, aerial surveyors did not detect localized outbreaks of forest tent caterpillar during these time periods.

The reconstructed outbreaks matched the observed outbreak data, in both the time and frequency domain (Fig. 9). The strong decadal periodicity and its increasing strength with increasingly permissive filtering is no surprise. What is more interesting is that the subdecadal variability (i.e., in the 5–7 years range) increases even more in strength as the growth reduction threshold parameter is relaxed from a conservative -1.56 standard deviation to a permissive -0.58 standard deviation. In other words, the more permissive the threshold, the better the reconstruction of the major decadal outbreaks, and the more one is forced to contend with the minor growth reduction episodes occurring at subdecadal and subregional scales.

Discussion

Sensitivity of aspen to drought and defoliation

Trembling aspen ring widths in the province of Ontario appear to be far more sensitive to annual defoliation by forest tent caterpillars than to annual fluctuations in Hogg's CMI. We used a variety of manipulations in searching for the potential effects of drought including the use of higher-

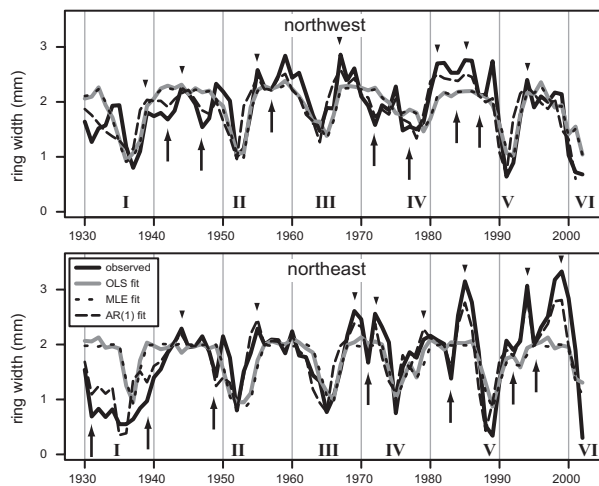
Table 2. Time-series regression analysis (using maximum likelihood estimation (MLE) model, with $\phi > 0$) of the effect of climate moisture index (CMI) on ring width for nonoutbreak years.

Region	Term ^a	Coeff.	SE	<i>t</i> value	<i>p</i> value	ϕ
NW	CMI _{<i>t</i>}	-0.00064	0.00334	-0.191	0.8497	0.575
NE	CMI _{<i>t</i>}	0.00193	0.00394	0.489	0.6270	0.785

Note: NW, northwestern; NE, northeastern.

^aIntercept significant in all models, indicating nonzero mean of chronology ring widths.

Fig. 5. Observed ring widths versus fitted values from ordinary least-squares (OLS) and maximum likelihood estimation (MLE) regressions. Dotted and broken curves represent fits from MLE regression with the autoregressive term excluded (curve labelled MLE) and included (curve labelled AR(1)), respectively. Note how the MLE model with the AR(1) term included faithfully reproduces many of the higher-frequency fluctuations associated with positive (\blacktriangledown) and negative (up arrows) growth anomalies occurring in between the primary outbreak cycles (numbered).

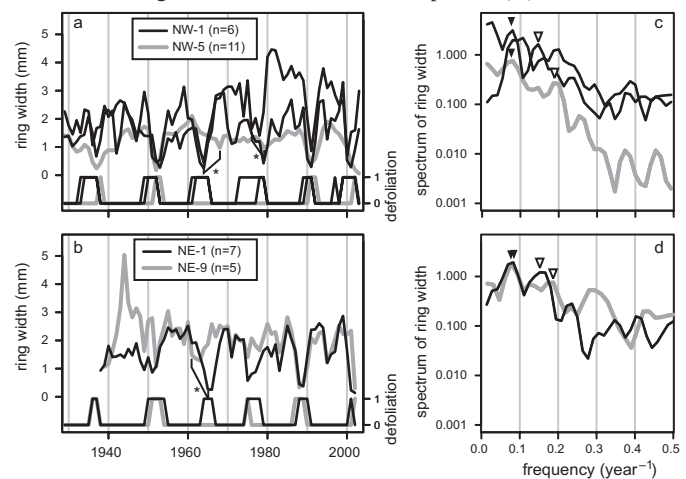


order time lags (Table 1) and censoring the data to consider only nonoutbreak years (Table 2) yet we still find no effect of drought.

Much of the unexplained variation in aspen ring widths could be due to climatic factors other than the drought effects simulated by the CMI. This is an area that needs to be explored further, but is beyond the scope of this paper. For the purposes of the current argument, it is sufficient to note three points: (i) large differences (e.g., 3–4 years) in the timing of major periodic growth reductions among nearby sites (e.g., tens of kilometres) are unlikely to be a product of climatic processes, which tend to be regional in scale (e.g., correlated over hundreds of kilometres); (ii) small differences (e.g., 1–2 years) in the timing of minor growth reductions among nearby sites, which were common, are unlikely to be caused by acute, spatially correlated climatic disturbances; and (iii) because they are somewhat periodic in occurrence (e.g., falling in between major decadal outbreak cycles), it is unlikely that the minor growth reductions are the result of climatic perturbations, such as late spring frosts, spring snowstorms, or annual variations in growing season length, which are strictly nonperiodic in occurrence.

The absence of a drought effect contrasts with similar

Fig. 6. Aspen ring-width chronologies (upper curves, left axis) and defoliation histories (lower curves, right axis) for the two most defoliated (black) and least defoliated (grey) plots in each region ((a) NW-1 and NW-5 and (b) NE-1 and NE-9). Plot numbers are mapped in Fig. 1. Asterisks indicate three notable “discrepancies” in timing of growth reductions during cycles III and IV that are discussed in the text. Graphs (c) and (d) are corresponding spectra for ring widths in each region. Dominant, decadal variability (12–14 years, \blacktriangledown) and subdominant, subdecadal variability (5–7 years, ∇) are indicated, occurring at the scale of individual sites. Spectra smoothed using Daniell smoother with a span of {3}.



dendroecological studies conducted ~1500 km to the west in central Alberta, which show aspen radial growth to be strongly limited by drought (Cooke 2001) and well predicted by Hogg’s CMI, despite the strong influence of aspen defoliators (Hogg et al. 2002a). This difference in aspen sensitivity to moisture is likely due to much lower levels of growing-season precipitation in western Canada. For example, annual rainfall at Edmonton, Alberta, averages 374.8 mm, as compared with 535.6 mm at Dryden, in northwestern Ontario, and 656.5 mm at Sudbury, in northeastern Ontario (Environment Canada 1971–2000 normals; available from http://climate.weatheroffice.ec.gc.ca/Welcome_e.html). Because CMI in both regions of Ontario was found to be unrelated to annual ring width (Table 1), we conclude that differences in precipitation levels across Ontario are insufficient to produce significantly different degrees of sensitivity to annual variations in precipitation. Additional sampling along the pan-Canadian east–west moisture gradient should reveal more precisely where precipitation becomes strongly limiting to aspen growth.

Despite the high degree of sensitivity of trembling aspen to defoliation by forest tent caterpillars, a substantial portion of the variation in ring widths could not be explained. The

Fig. 7. Reconstructed patterns of outbreaks using program OUTBREAK with the “maximum growth-reduction threshold” parameter varying systematically from -1.56 to -0.58 standard deviations. Roman numerals I–VI and ∇ indicate major outbreak cycles matching those in Fig. 1. ∇ indicates minor defoliation episodes where significant growth reduction occurs in a small proportion of chronologies.

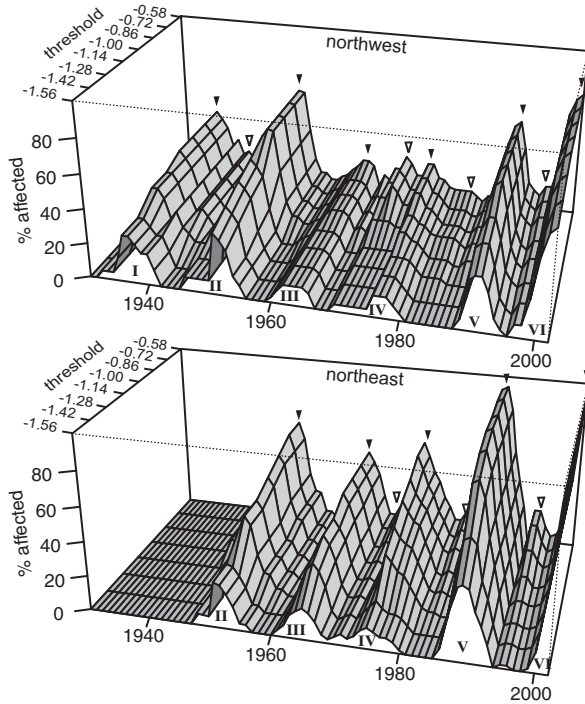
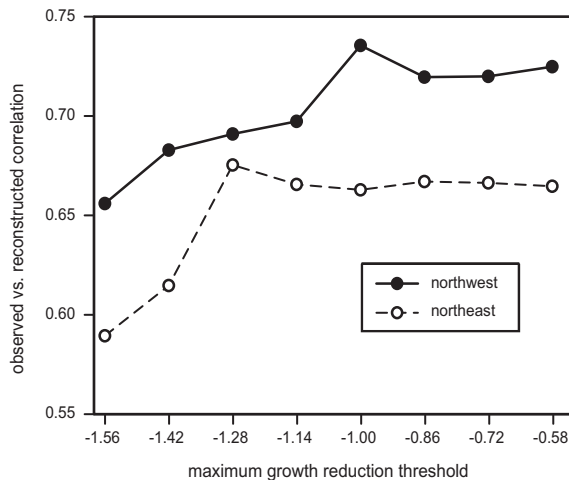


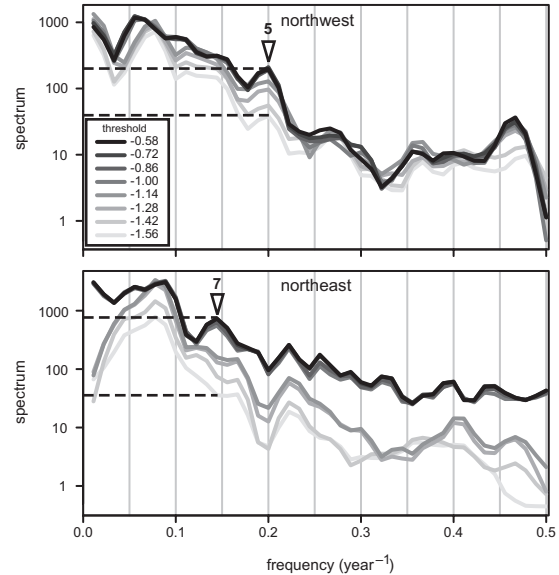
Fig. 8. Correlation between observed (Fig. 2) and reconstructed (Fig. 7) outbreak time series, as a function of the maximum growth reduction threshold parameter.



OLS models suggested that the direct and delayed effects of defoliation account for only 24%–50% of the variation in regional ring-width chronologies (Table 1), and 12%–35% of the variation in site-level ring-width chronologies (Table 2). The MLE models performed better, but still left a large portion of the total variation unexplained.

The MLE models estimated the delayed effects of defoliation to be slightly stronger than did the OLS models (D_{t-1} coefficient = -1.05 versus -1.01 in NW and -0.49

Fig. 9. Spectral analysis of reconstructed outbreaks in Fig. 8. ∇ indicates significant subdecadal (5–7 year) variability that is enhanced through increasingly permissive filtering. Broken lines indicate disproportionately large and smooth increases in subdecadal signal strength as the “maximum growth reduction threshold” parameter is increased from -1.56 to -0.58 .



versus -0.41 in NE). Indeed, the delayed effect of defoliation in the northeastern region was found to be nonsignificant using the OLS approach ($p = 0.12$), but significant using the MLE approach ($p = 0.015$) (Table 1). This highlights a major strength with the MLE approach to modeling tree ring-width time series, and a relative weakness in the OLS approach, for we know via controlled experiments that trembling aspen does in fact exhibit a lagged response in year $t + 1$ to defoliation in year t (Hogg et al. 2002b).

Gradient analysis

Whether or not a tree ring-width chronology came from the frequently defoliated end of the transects, the time-series data carried a similar characteristic signal of periodic growth reduction at both decadal and subdecadal time scales. This suggests aerial surveyors may be insensitive to defoliation occurring in those areas deemed to be infrequently defoliated. Surveyors almost certainly missed a 1961–1964 outbreak at site NE-9, and there is a possibility they missed less intense defoliation episodes in 1968 and 1979 at NW-5. It is well known that aerial defoliation mapping, in the case of spruce budworms in coniferous forests, is an imprecise science (MacLean and MacKinnon 1996). Given what we know about the crude methods of hardwood defoliation detection and mapping in the province of Quebec (Cooke and Lorenzetti 2006), a similar situation may exist in the case of tent caterpillars defoliating trembling aspen in Ontario.

The fact that defoliation events can be so readily detected in tree rings from sites where defoliation is presumed to be infrequent leads us to speculate that space–time series of aspen ring widths may provide not only a more complete record of the historical pattern of forest tent caterpillar outbreaks, but possibly a less-biased record as well. In contrast with crudely sketched aerial defoliation records, tree-ring re-

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CORDS are spatially referenced with 100% accuracy down to the level of the individual stem. For this reason, we suggest that, used carefully, they can be helpful in spatial population dynamics research.

Imperfect synchronization of outbreak cycles

Despite the overall similarity in tree-ring signals from frequently and infrequently defoliated areas, some major discrepancies were observed, especially during outbreak cycles III and IV. These discrepancies were of two types: (i) major growth reductions occurring in infrequently defoliated areas just before a major outbreak, but with no defoliation being recorded locally (e.g., NE-9, 1961–1966); (ii) minor growth reductions occurring in infrequently defoliated areas just after a major outbreak, but with no defoliation being recorded locally (e.g., NW-5, 1968 and 1979). In contrast, when defoliation is severe and extensive (e.g., during high-amplitude cycles II, V, and VI) the aerial survey data and the tree-ring data seem to provide similar information.

Growth reductions in infrequently defoliated areas, especially during the less severe cycles III and IV, appeared to not coincide with the peaking of the major outbreak cycle in the areas where defoliation was more frequent. The difference in timing between known outbreaks in the core areas and associated growth reductions in the infrequently defoliated areas was as large as 4 years. The most parsimonious explanation for these asynchronous growth reductions is that forest tent caterpillar outbreak cycles are not as synchronous as the defoliation survey data would suggest.

Our interpretation of a 3 year delay in outbreak spread from NE-9 in 1961–1962 to NE-1 in 1964–1965 (Fig. 6b) hinges on the assumption that surveyors occasionally fail to detect locally significant (but regionally insignificant) levels of defoliation. How likely is it that the northeastern region outbreak started several years before surveyors were able to detect it, and that it started not in the core region of NE-1, but closer to the fringe region of NE-9? Considering the observations of Hodson (1977) that forest tent caterpillar populations at subregional scales can rise and peak without crossing the outbreak detectability threshold (i.e., the population density required to obtain a level of defoliation that is aerially detectable), we think it is possible.

The timing of this particular episode in the 1960s corresponds roughly with a similar breakdown in the synchrony of forest tent caterpillar defoliation cycles in the neighbouring province of Quebec. Here, a pulse of defoliation in northwestern Quebec, peaking in 1962 and declining in 1963–1964, was followed by a later pulse in southeastern Quebec, which started in 1963, declined briefly in 1964, and reached a higher peak in 1968 (Cooke and Lorenzetti 2006). Again, the ~5 year interval between the emergence of the first pulse of defoliation in 1963 and the defoliation cycle peak in 1968 is reminiscent of the subdecadal (4–7 year) variability found in both the Ontario tree-ring data and the Minnesota population data.

In addition to the examples provided here during outbreak cycles III and IV, there is also the well-documented example of cycle II in Minnesota, where the outbreak peaked in northern Minnesota in 1951–1952, and spread 100 km southward, peaking in the Duluth region in 1953–1954 (Hodson 1977) — a pattern of spread that is again reflected

in the corresponding tree-ring data (Cooke et al. 2003). In fact, cycle I in Minnesota appears to have followed much the same pattern of development (Hodson 1941). Clearly, although forest tent caterpillar population cycles may be sufficiently synchronized that they result in periodic, large-scale outbreaks, these cycles are not perfectly synchronized at all spatial scales. There are many instances where localized population and (or) defoliation pulses will emerge 4–7 years before or after the primary, decadal defoliation cycle.

Outbreak reconstruction

The lack of sensitivity of Ontario aspen to fluctuations in the annual CMI suggests that in moderately humid areas climate correction using a nonhost species (i.e., the method proposed by Nash et al. (1975)) may not be necessary to reconstruct outbreaks. We see this as an advantage, because in many parts of the boreal forest there is not a single long-lived tree species that is not attacked by some periodically erupting forest insect. In such a case the nonhost correction method runs the risk of introducing a noisy signal that is semi-periodic in nature and possibly indistinguishable from the defoliator signal one wishes to extract from the host series.

Filtering raw ring widths with the computer program OUTBREAK helped to visually emphasize the major outbreak cycles; however, the spectral properties of the outbreak reconstructions were similar to those of the raw chronologies. Outbreak reconstructions were found to closely mimic the decadal patterns of outbreaks reported by aerial defoliation surveyors, although no outbreak cycle was detected for 1934–1938 in the northeastern region, because of a lack of older (pre-1935) samples.

Sensitivity analysis of the filtering parameters brought out another feature in the reconstructed outbreak series, shared in the raw ring-width data, that may be important to consider: there is clearly a subdecadal component of variability in reconstructed outbreaks that appears to be associated with less severe defoliation episodes occurring in between the major decadal outbreaks. Indeed, the primary effect of increasingly permissive filtering is to increase one's ability to detect more localized growth reductions, which in this case are not associated with the primary, decadal outbreak cycle. The most logical interpretation is that forest tent caterpillar population fluctuations occur at multiple time scales. Some population "cycles" attain the status of "outbreak", while others, for whatever reason, do not.

Conclusion

In the province of Ontario, forest tent caterpillar defoliation is the dominant source of variation affecting trembling aspen annual ring widths; drought plays no discernible role. The lagged effects of defoliation are highly significant, even when the autoregressive nature of annual growth is accounted for using MLE time-series regression. The herbivory signal is not merely decadal periodic, it exhibits periodicity at two or more time scales. The herbivory signal is present not just in core areas of cyclicity where outbreaks always occur, but also in areas where defoliation is rarely recorded.

If it can be shown that localized defoliation episodes occurring in between the major decadal outbreak cycles are in-

deed caused by forest tent caterpillars, then one would have to conclude that their dynamics are more complex than what is commonly reported in the literature, and more complex than what is predicted by the theory of synchronizable predator-prey-caused oscillations.

As insect population growth is a continuous process, the idea of treating outbreaks as discrete, countable events is overly simplistic. If not all population cycles develop into readily detectable outbreaks, then the estimated periodicity of outbreaks inferred through standard dendroecological reconstruction techniques would be lower than the estimated periodicity of population fluctuations, and, ultimately, less informative as to the nature of the primary cycle-generating processes. In general, one should be careful not to attach too much importance to estimates of periodicity, if the systems are not all that periodic or if the periodicity is manifest at multiple time scales.

Most dendroecologists recognize the importance of large-scale, long-term ecological data. Our results emphasize the high spatial resolution of sampling that is required for multi-scale spatiotemporal analysis. Insect population processes operating at subdecadal and subregional scales (e.g., parasitism, predation, disease, and host-plant effects) are likely to lead to complex, multiscale patterns of disturbance. Sampling at too low a spatial resolution thus could result in overly simplistic, or distorted, disturbance reconstructions that fail to adequately represent the full range of dynamic behaviour exhibited by the population and (or) outbreak process.

Acknowledgments

For their assistance with field sampling, we thank Taylor Scarr, Mike Lesperance, Lincoln Rowlinson (Ontario Ministry of Natural Resources), and Louis Morneau (Ministère des ressources naturelles et faune, Quebec). From the Canadian Forest Service, Great Lakes Forestry Centre, we thank Ken Baldwin, for providing increment cores for site NW-5, and Gordon Howse, Tony Hopkin, and Ronald Fournier, for facilitating access to historical defoliation records. We thank Ted Hogg, Northern Forestry Centre, and René Alfaro, Pacific Forestry Centre, for their helpful reviews.

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