

Radial Growth Losses in Preferred and Avoided Tree Species During Gypsy Moth Outbreaks

Robin Naidoo and Martin J. Lechowicz, *Department of Biology, McGill University, 1205 Dr. Penfield Ave., Montréal, Québec, Canada H3A 1B1.*

ABSTRACT: *We investigated the effect of gypsy moth larval density on radial growth of preferred and avoided trees: northern red oak and white ash, respectively. Individual trees were censused for gypsy moth larvae from 1979 to 1992 at a site where several outbreaks occurred. Annual growth rings were measured from 1950 to 1992 on increment cores taken from these same trees, as well as from trees at a nearby site that had not experienced any outbreaks. Regression models of growth at the outbreak site on growth at the nonoutbreak site were developed to isolate the influence of gypsy moth defoliation from other factors such as climate. These were then used to generate expected values for radial growth in the absence of gypsy moth at the outbreak site. During the first year of the first gypsy moth outbreak, there was a mean reduction in radial growth of 46% in red oak, a loss similar to what has been reported in other studies. Growth of white ash was much higher than predicted in 2 yr during and subsequent to the first outbreak. Yearly larval counts from 1979 to 1992 on red oak at the outbreak site were negatively correlated with oak radial growth after correcting for climate, suggesting that nonoutbreak levels of gypsy moth may reduce radial growth more than has previously been thought. Larval counts on ash were uncorrelated with ash growth after correcting for climate. *North. J. Appl. For.* 16(1):11–18.*

The gypsy moth (*Lymantria dispar* L.) is an introduced forest insect that has become the most serious defoliator of hardwood trees in northeastern North America (Montgomery and Wallner 1988). As a “sustained eruption” insect (*sensu* Berryman 1987), outbreaks can cover large areas and can persist in a particular area for several years before the population returns to endemic levels. During these prolonged and widespread outbreaks, defoliation by larvae can have severe socioeconomic (e.g., Liebhold et al. 1995) and ecological (e.g., Campbell and Sloan 1977) consequences. Despite this, the effect of gypsy moth defoliation on radial growth of host trees in northeastern North America has not been adequately investigated.

Several studies have compared the average radial growth over a certain time period before gypsy moth defoliation to average growth after defoliation (Minott and Guild 1925, Baker 1941, Kulman 1971, Brown et al. 1979, Wargo 1981,

Campbell and Garlo 1982). Reduction of growth in the postdefoliation period compared to the predefoliation period was attributed to gypsy moth defoliation. The weakness in this method is that potentially confounding differences in climatic conditions between periods are not accounted for, making the effects of climate and defoliation on growth difficult to separate.

More recent studies using dendroecological techniques (Fritts and Swetnam 1989) have often used radial growth chronologies of nonhost species, or of nondefoliated trees of the same species, to estimate losses due to insect defoliation. Any large depressions in the growth chronology of defoliated trees relative to undefoliated trees can be attributed to defoliation, since responses to macroclimatic conditions should be similar if the trees are growing in the same general environment (e.g., Kulman 1971, Swetnam and Lynch 1989, Mason et al. 1997). This approach has not been used to quantify the effect of gypsy moth defoliation on growth of hardwood trees in northeastern North America.

This paper will discuss the use of chronologies of nondefoliated trees in determining the effect of defoliation by a known density of gypsy moth larvae on radial growth. Our method involved the use of two nearby stands with different histories of outbreaks and consequent defoliation. One stand was severely defoliated by gypsy moth on two separate occasions during a 13 yr period. The second stand did not suffer heavy defoliation during the initial outbreak at the site, although its subsequent defoliation history is unclear. Radial

NOTE: Robin Naidoo is the corresponding author and his current address is Sustainable Forest Management Network, G-208 Biological Sciences Bldg., University of Alberta, Edmonton AB T6G 2E9—Phone: (403) 492-7048; Fax: (403) 492-6547; E-mail: robin.naidoo@ualberta.ca. The authors thank Benoit Côté, Danielle Charron, and Yves Bergeron for the use of their microscope. Charles Mercier provided stellar assistance in the field. We thank Kurt Gottschalk for his comments on an earlier version of the manuscript. Three anonymous reviewers provided insightful comments on an earlier version of the manuscript. The research was supported by NSERC and FCAR grants to MJL. Finally, we are grateful to McGill University for allowing us to conduct this research at the Mont St-Hilaire Biosphere Reserve.

growth patterns of host trees at these two sites were compared to gypsy moth population density data to determine if any differences in growth could be attributed to the gypsy moth.

Methods

Study Area

The study area was located in a 1200 ha tract of old-growth forest at Mont St-Hilaire, Québec, Canada (45°32'N, 73°09'W). Two sites were selected for sampling. The Lake Hill site is on the outer face of Mont St. Hilaire, while the second site, called Sunrise, is a hill within the interior basin of the mountain that is 1.5 km northwest of Lake Hill. Both sites cover an area of approximately 25 ha. The sites have similar physical characteristics: dry, rocky, south-facing slopes, with stony and shallow soil that has an average depth of 65 cm to bedrock. Red oak (*Quercus rubra* L.) is the dominant tree species in both stands. Ironwood (*Ostrya virginiana* [Mill.] K. Koch) and sugar maple (*Acer saccharum* Marsh.) are other important species, while white ash (*Fraxinus americana* L.), basswood (*Tilia americana* L.), and American beech (*Fagus grandifolia* Ehrh.) are minor components. The lower slope and slope foot of both sites consists mostly of sugar maple and beech; at increasing elevation, red oak becomes the predominant species while beech disappears entirely. In many places the uppermost slopes are covered with small and slow-growing oak trees with open canopies; scree slopes where leaf litter is sparse are also common. Maycock (1961) provides a thorough description of the vegetation and geology of Mont St-Hilaire.

Substantial gypsy moth defoliation was first noted on Mont St-Hilaire in 1977, when 10 ha of an oak stand on Burned Hill (a small peak adjacent to Lake Hill) were severely defoliated (Jobin 1978). In 1978, the area of heavy defoliation on Mont St-Hilaire increased to 195 ha (Lechowicz 1983). Photos from aerial surveys conducted by the Canadian Forest Service showed severe defoliation on the south slope of Lake Hill; most trees appeared to be completely stripped of foliage. Several other sites on the mountain were also heavily defoliated in 1978, but Sunrise was not among these (Jobin 1978). This type of patchiness, in which outbreaks develop only in certain stands of the infested area, is typical of gypsy moth infestations (Jones 1991, Liebhold and McManus 1991). The first outbreak at Lake Hill ended in 1980 and was followed by a number of years during which no gypsy moth defoliation was observed. A second outbreak on Mont St-Hilaire occurred in 1989 and 1990. Lake Hill trees experienced moderate to severe defoliation during these 2 yr, although the level of defoliation was not as high as during the first outbreak (M.J. Lechowicz, pers. observ.). The level of defoliation at Sunrise during this second outbreak is uncertain; reports based on ground surveys conducted in 1990 indicated that Sunrise was not heavily defoliated, but no such surveys were conducted in 1989. The available information is thus summarized as follows: during the first outbreak at Mont St-Hilaire, Lake Hill was heavily defoliated, and Sunrise was not defoliated. During the second outbreak, Lake Hill experienced moderate to severe defoliation, while defo-

liation at Sunrise may have occurred in 1989 but was not present in 1990.

In 1979, 24 permanent 500 m² circular quadrats were established along 5 altitudinal isoclines at Lake Hill to monitor gypsy moth density. Each isocline had from 3 to 7 quadrats, and isoclines were separated by approximately 25 m. The average distance between quadrats was about 200 m. Within these quadrats, all trees > 8 cm dbh were tagged and identified to species. Each summer from 1979 to 1992, gypsy moth larvae resting under tarpaper bands around the trunk of each tagged tree were counted on three to five separate occasions. Tarpaper bands are used as daytime hiding places by late-instar larvae (Liebhold et al. 1986), and these late instars consume more foliage than all other instars combined (Leonard 1981). The number of pupae and egg masses were also recorded for each tree.

Collection and Analysis of Radial Growth

We selected two species with contrasting host preferences to examine the influence of gypsy moth defoliation on radial growth. Northern red oak is a preferred host of the insect, while white ash is avoided (Lechowicz and Mauffette 1986). At the Lake Hill site, two increment cores were taken from 39 ash and 41 oak trees for which records of gypsy moth larvae existed. At Sunrise, two cores were collected from each of 41 oak and 44 ash that were randomly sampled from 3 altitudinal transects. Transects were run perpendicular to the slope and continued along the entire south side of the slope, so that the whole area was sampled with approximately equal intensity. Trees less than 8 cm dbh were not sampled. All cores were taken at breast height and at a 90° degree angle to each other, with one core taken from the upslope side of the tree.

Cores were air-dried, mounted onto wooden backings, and cross-dated visually by using signal years (Stokes and Smiley 1968); narrow rings in 1953, 1971, 1978, 1979, and 1988, and large rings in 1981 made unambiguous cross-dating possible in almost every oak and ash core. After cross-dating, ring widths were measured to the nearest 0.01 mm using a dissecting microscope with a sliding vernier scale. The years 1950 to 1992 were measured on all cores; this time period allowed the longest chronology among the largest sample of trees.

A standardized ring index chronology was calculated for each species/site combination by dividing annual growth values of each core by the core's mean annual radial growth, then averaging these values over all trees. We used the mean, instead of values from a hypothetical growth curve, to preserve as much growth trend as possible. The focus of many dendrochronological studies is purely the year-to-year climate effects, and so in these studies growth curves are fit to the raw chronologies to remove as much nonclimatic growth trend as possible (e.g., Graumlich 1993, Payette et al. 1996). In our case, we wanted to preserve potential trends, since it is possible that the arrival of the gypsy moth at Mont St-Hilaire would cause a long-term growth response in its hosts. By dividing ring widths by the mean, this is accomplished, while at the same time overall growth rate differences (i.e., fast-growing versus slow-growing trees) are removed.

Statistical Analysis

Parametric statistics were used for all statistical tests when the appropriate assumptions were met. In cases where one or more of these assumptions were violated, the equivalent nonparametric test was used. The SAS software package (SAS Institute Inc. 1985) was used for all analyses.

To investigate the effect of defoliating gypsy moth larvae on growth, we divided both the Lake Hill and the Sunrise chronologies into "pre-gypsy-moth" and "post-gypsy-moth" periods. The pre-gypsy-moth period was set from 1950 to 1975. We selected 1975 as an endpoint because gypsy moths may have been present at low numbers on Lake Hill just prior to the first outbreak in 1978. To assess the similarity of radial growth between sites in the absence of gypsy moth, we constructed regression models of Lake Hill growth based on Sunrise growth for both ash and oak in the pre-gypsy-moth period. These pre-gypsy-moth regression equations were then used to generate expected values of radial growth in the post-gypsy-moth period, 1978–1992. If gypsy moths were influencing radial growth, we would expect actual growth values to be lower than those predicted for a defoliation-free environment, especially during outbreak years.

We initially used Ordinary Least Squares (OLS) regression to estimate regression parameters. However, portmanteau Q-tests (Proc ARIMA, SAS Institute Inc. 1993) revealed significant first-order autocorrelation in the residuals for both the oak and ash pre-gypsy-moth regression models. This autocorrelation invalidates the use of OLS regression, due to violation of the assumption of independence in the residuals. We thus used Proc AUTOREG of the SAS/ETS module (SAS Institute Inc. 1993) to compute regression parameter estimates. Proc AUTOREG computes parameter estimates for regression models where the data are time series and the error terms from OLS regression are autocorrelated. The iterative methods used to estimate regression parameters are described in detail in Harvey (1990); we used the Maximum Likelihood estimation method as this may be more efficient in estimating parameters for small sample sizes. The regression models for both species can be formulated as follows:

$$y_t = Ax_t + B + AR(1) + \epsilon_t \quad (1)$$

where

y_t = growth at Lake Hill at time t

x_t = growth at Sunrise at time t

A = regression coefficient (slope)

B = intercept

$AR(1)$ = first-order autoregressive process up to lag p (Box and Jenkins 1970)

$$= \phi \epsilon_{t-1} + \phi^2 \epsilon_{t-2} + \phi^3 \epsilon_{t-3} + \dots + \phi^p \epsilon_{t-p}$$

and

ϵ_t = error term at time t

ϕ = autoregressive coefficient

The pattern of oak and ash residual growth in the post-gypsy-moth period (i.e., expected growth values subtracted from actual values, or the variance in Lake Hill growth not explained by Sunrise growth) was examined with respect to gypsy moth population density. The maximum number of larvae recorded during one of the summer counts was averaged over all conspecific trees for each year, and this measure was used as a surrogate for annual gypsy moth defoliation for each species. Larval counts were log transformed to normalize the data. We predicted a negative relationship between growth residuals and gypsy moth numbers, especially for oak, the preferred host.

Results

The larval counts, combined with previous studies, confirmed that the gypsy moth population at Lake Hill was at outbreak levels during 1978–1980 and 1989–1990 (Table 1). The first outbreak lasted until 1980, after which larval densities on oak declined to levels slightly higher than those on ash. The population also reached outbreak levels in 1989 and 1990 before crashing once again. The average number of larvae on sampled trees varied greatly between species. Oaks hosted high densities of gypsy moth larvae during the two outbreaks, averaging 113.0 larvae per tree, while ash averaged only 3.1 larvae per tree. In the years between the two outbreaks, oak averaged 8.0, and ash 0.5, larvae per tree.

Ring Chronologies

The ring index chronologies for Lake Hill and Sunrise are shown in Figures 1 (oak) and 2 (ash), and Table 2 contains mean ring index values for the pre- and post-gypsy-moth periods. In the pre-gypsy-moth period, there was no significant difference in the mean ring index between Lake Hill and Sunrise for either oak (t -test; $t = 0.35$, $P = 0.73$) or ash ($t = 0.14$, $P = 0.89$). There were also no significant differences in mean ring index between Lake Hill and Sunrise during the post-gypsy-moth period (oak: t -test, $t = -0.38$, $P = 0.71$; ash: Mann-Whitney Rank Sum test, $T = 218$, $P = 0.56$). However, the mean ring index for oak was lower in the post-gypsy-moth period than in the pre-gypsy-moth period for both Lake Hill and Sunrise (Table 2). The reduction in growth in Sunrise oaks during the post-gypsy-moth period as compared to the pre-gypsy-moth period suggests that either: 1) gypsy moth defoliation is not the sole factor in the reduced growth of Lake Hill oaks from 1978–1992; and/or 2) Sunrise oaks were also defoliated by gypsy moth during this period.

Growth Models

The regression models of Lake Hill ring index on Sunrise ring index for 1950 to 1975 (pre-gypsy moth) are shown in Figure 3A (oak) and 3B (ash). Parameter estimates for the models are given in Table 3. For both oak and ash, regression models of Lake Hill on Sunrise were highly significant. The observed ring index values in the post-gypsy-moth period were then compared to expected values generated from the pre-gypsy-moth regression equations. (Figures 4A and 4B). For both ash and oak there was no significant correlation between expected and observed values, indicating that the pre-gypsy-moth regression models were unable to predict

Table 1. Larval numbers and defoliation levels on Lake Hill, Mont St-Hilaire, from 1978 to 1992. Two outbreaks occurred at Lake Hill, the first from 1978–1980, and the second from 1989–1990. Larval numbers in intervening years were very low.

Year	Mean gypsy moth larvae per tree		Defoliation level	Source
	Red oak	White ash		
1978	—	—	High	Jobin 1978, Lechowicz 1983
1979	51.7	1.78	High	This study
1980	85.9	2.56	High	This study
1981	2.75	0.08	Very low	This study
1982	1.95	0.04	Very low	This study
1983	7.76	0.36	Very low	This study
1984	1.12	0.02	Very low	This study
1985	0.78	0.00	Very low	This study
1986	5.05	0.38	Very low	This study
1987	11.8	0.26	Very low	This study
1988	34.9	0.44	Very low	This study
1989	127.5	2.72	Moderate-high	This study / M.J. Lechowicz pers. obs.
1990	187.8	5.32	Moderate-high	This study / M.J. Lechowicz pers. obs.
1991	2.81	0.10	Very low	This study
1992	0.32	0.06	Very low	This study

radial growth at Lake Hill after the invasion of the gypsy moth. The residuals from the ash post-gypsy-moth growth model were not correlated with larval densities on ash (Spearman correlation coefficient, $r = 0.09$, $P = 0.77$), suggesting that gypsy moth larvae were not feeding on the avoided host. However, residuals from the oak model were negatively correlated with oak larval densities (Figure 5; Spearman correlation coefficient, $r = -0.64$, $P = 0.01$).

Discussion

Pre-Gypsy-Moth Growth

Between-site radial growth of both red oak and white ash was highly correlated in the pre-gypsy-moth period, indicating that trees at both sites were responding similarly to

climatic conditions and had similar growth patterns before the arrival of the gypsy moth. This suggests that the two sites do provide comparable growing conditions for trees, and thus the use of Sunrise as a reference site for estimating the effect of gypsy moth defoliation on Lake Hill trees seems reasonable. Since climatic conditions during both the pre- and post-gypsy-moth periods were similar (Naidoo 1997), the application of the regression model developed in the pre-gypsy-moth period to the post-gypsy-moth period also seems reasonable.

Effect of Nonoutbreak Level Larval Densities

Larval counts were significantly correlated with Lake Hill residual growth over the 1979–1992 period. This agrees with results from Naidoo (1997), in which counts were highly

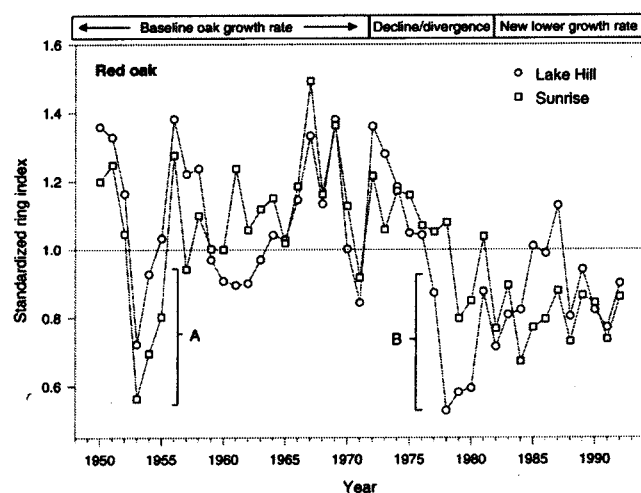


Figure 1. Growth chronology (ring indices) for red oak at Lake Hill and at Sunrise, 1950 to 1992. The timeline at the top of the figure highlights three different periods of growth: initially, growth between sites was fairly synchronous, including during a tent caterpillar outbreak in 1953(A); subsequently, divergence and a steep growth reduction in the Lake Hill oak chronology during the first gypsy moth outbreak(B); and finally, growth at both sites re-equilibrated to a new, lower level from 1981–1992.

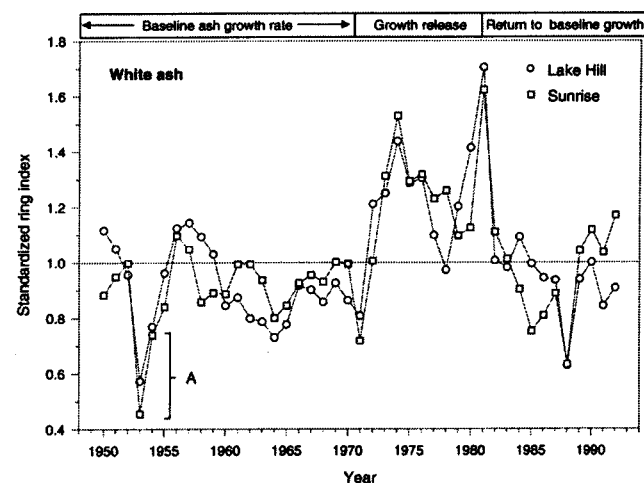


Figure 2. Growth chronology (ring indices) for white ash at Lake Hill and at Sunrise, 1950 to 1992. The timeline at the top of the figure highlights three different periods of growth: growth at both sites was fairly poor from 1950–1971, including during a tent caterpillar outbreak in 1953(A); between 1971 and 1981 ash at both sites experienced increases in growth; finally, growth returned to pre-increase levels from 1982–1992. Unlike red oak, white ash chronologies between sites were highly synchronous throughout the 1950–1992 chronology.

Table 2. Ring index means for pre- (1950 to 1975) and post- (1978 to 1992) gypsy-moth periods, and the first-order autocorrelation in the pre-gypsy-moth period.

Chronology	Mean ring index	
	1950–1975	1978–1992
Lake Hill oak ring index	1.107	0.819*
Sunrise oak ring index	1.088	0.838*
Lake Hill ash ring index	0.964	1.038
Sunrise ash ring index	0.957	1.039

* Mean ring index in post gypsy moth period significantly lower than the index in the pre-gypsy-moth period (*t*-test, $P < 0.0001$).

correlated with growth of Lake Hill oaks, once the effect of climate on growth had been removed by means of a multiple regression model including climate variables. Of note, however, is that Lake Hill oaks were actually growing *faster* than Sunrise oaks in most years of the post-gypsy-moth period. Some possible explanations for this phenomenon are given below (see “Growth losses in second outbreak” section). One possibility that should not be discounted is that nonoutbreak and undetectable levels of defoliation were occurring at Sunrise, thus reducing growth at Sunrise and increasing the Lake Hill:Sunrise growth ratio.

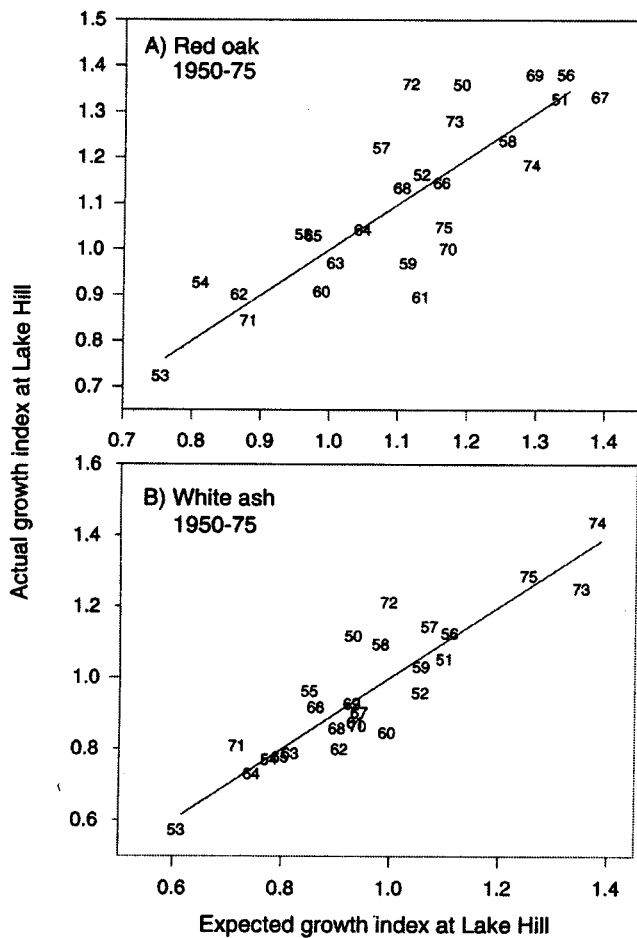


Figure 3. Observed (Y-axis) and expected (X-axis) growth at Lake Hill, 1950 to 1975, for red oak (A) and white ash (B). Symbols are years, and line of equality is shown. Expected Lake Hill growth was based on growth at Sunrise and was generated from the regression equations for each species in Table 3.

Table 3. Regression parameters for models described in equation (1).

Model	A	B	ϕ	R^2
Red oak	0.7699*	0.2724	0.6422*	0.66
White ash	0.6604*	0.3560*	0.7038*	0.64

* Parameters significantly different from 0 ($P < 0.01$ in all cases).

The effects of low-level (“nominal”) defoliation by endemic levels of outbreaking defoliators have usually not been considered when assessing impacts on trees (Mattson and Addy 1975, Seastedt et al. 1983, Schowalter et al. 1986). This could be because the sheer magnitude of outbreaks (e.g., Dunlap 1980), has overshadowed the potential effects of nominal but persistent defoliation. Most authors assume that effects of herbivory are negligible below 30% of annual foliage crop (Mattson and Addy 1975), as trees should have adapted to historic low levels of defoliation. These studies, however, have modeled systems where defoliation is due to native phytophagous insects. At our study site, low-level defoliation by the gypsy moth (an introduced nonnative phytophage) combined with that of native phytophagous insects may well push the total defoliation beyond that which red oaks are adapted to (Naidoo 1997).

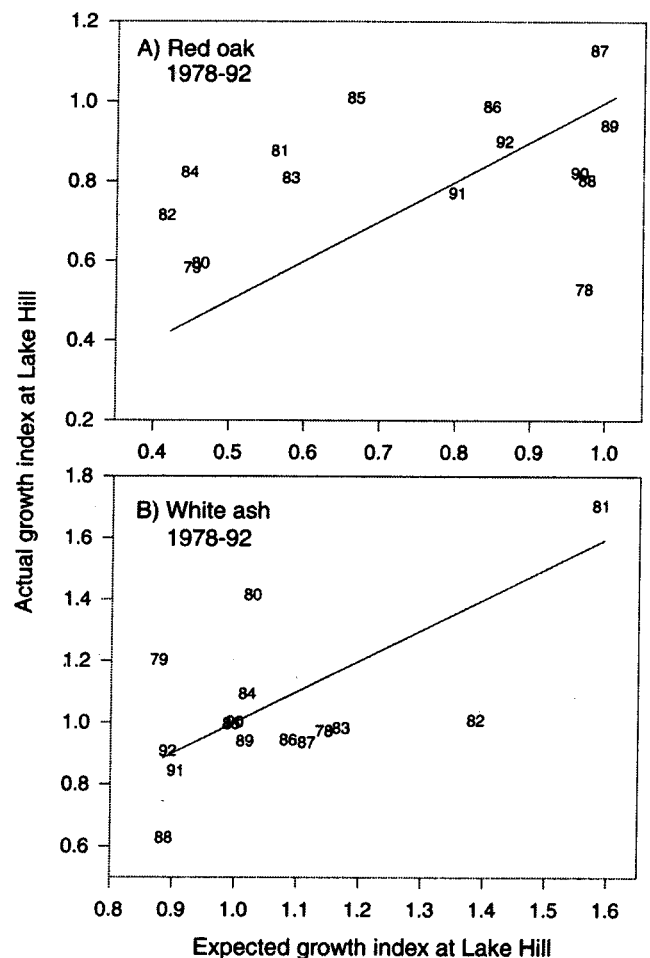


Figure 4. Observed (Y-axis) and expected (X-axis) growth at Lake Hill, 1978 to 1992, for red oak (A) and white ash (B). Symbols are years, and line of equality is shown. Expected growth values were generated using the regression equations given in Table 3.

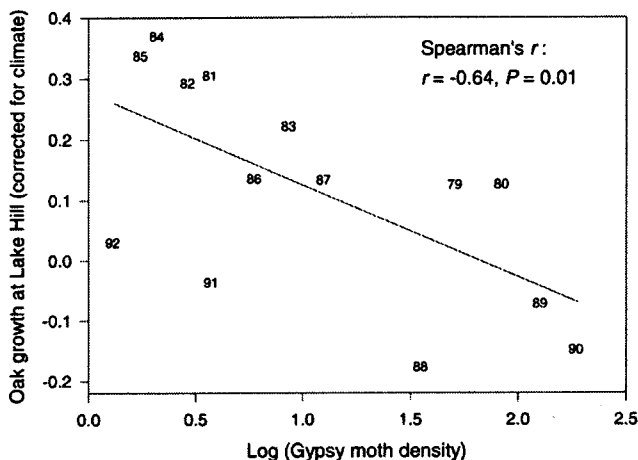


Figure 5. The effect of gypsy moth larval density on oak growth after correcting for climate.

Recent research on two native defoliators in the northwest United States (Douglas-fir tussock moth, *Orgyia pseudotsugata* McDunnough, and western spruce budworm, *Choristoneura occidentalis* Freeman) supports the idea that defoliation by endemic levels of native phytophagous insects may be a more important factor in growth of host trees than has previously been thought. Mason et al. (1997) show that larval numbers considerably lower than the threshold needed to produce defoliation visible from aerial surveys had a negative impact on radial growth over a 22 yr period. They suggest that this is because at lower densities, larvae are feeding on a high proportion of younger, more productive foliage. At high populations, the additional larvae must shift to feeding on older, less productive foliage, resulting in a situation where larvae at lower densities may produce disproportionately higher growth losses than larvae at high densities. This situation could also occur in a gypsy moth–red oak system, since maximum gypsy moth larval growth and survival is achieved on newly emerged foliage of preferred species like red oak (Hunter and Lechowicz 1992).

Growth Losses in First Outbreak

The greatest deviation of Lake Hill oak growth from expected growth values was in 1978, the first year that severe gypsy moth defoliation occurred on oaks. We compare only the first year of the 1978–1980 outbreak, since the time series nature of our analysis will necessarily reduce the percent loss in years immediately following extremely narrow growth rings. The percent loss in growth in 1978, 46%, is slightly lower than other estimates reported for loss in radial growth due to severe (80–100%) gypsy moth defoliation in the northeastern United States. These were 52.2% (Minott and Guild 1925) and 58.0% (Baker 1941) losses for red, scarlet, black, and white oaks in New England. These older studies estimated the loss in radial growth using an average measure of growth before the outbreaks as an estimate of predicted radial growth in the absence of gypsy moth. The weakness in this approach is that it fails to account for the often combined and concomitant negative effect of drought stress on host trees (Koerber and Wickman 1970, Mattson and Haack 1987). Thus a certain percentage of the decline attributed to gypsy moth defoliation in these studies is likely due to the

associated drought stress that often coincides with outbreaks of defoliating insects. Baker (1941) described additional plots of black oak and white oak for which climatic conditions as well as growth declines were observed. On these plots, growth losses due to severe defoliation were only 33 to 43%. These lower estimates were likely due to the average or even above-average rainfall in these years, which could have mitigated the negative effects of gypsy moth defoliation.

Growth Losses in Second Outbreak

The 1989–1990 outbreak had a much lower impact on growth of Lake Hill oaks than the first year of the 1978–1980 outbreak (15% and 13% reductions in growth for 1989 and 1990, respectively). This could be because conditions preceding and during the second outbreak were more favorable for oak growth than in the first outbreak, and thus the effect of defoliation was lessened. Unlike the first outbreak, when the years of heavy defoliation were preceded by a steady decline in oak growth, growth prior to the second outbreak was actually increasing. This increase or recovery in growth among trees surviving an insect outbreak has been noted before (e.g., Campbell and Garlo 1982, Swetnam and Lynch 1989, Gansner et al. 1993), and is likely due to a release effect resulting from reduced competition and increased canopy opening by virtue of neighbor-tree mortality and reduced vigor. Climatic conditions were also very favorable for growth in 1989 and 1990; Naidoo's (1997) climate-based model for radial growth of Lake Hill oaks predicted 1989 and 1990 to be the two most favorable years for oak growth during the entire 1979–1992 period. These conditions resulted in a favorable, nonstressed environment for trees that were then defoliated by gypsy moth larvae. Studies have shown that stressed or unhealthy trees are often more subject to heavy defoliation and/or reduced vigor due to insect herbivory than are healthy ones (Koerber and Wickman 1970, Campbell and Sloan 1977, Mattson and Haack 1987). The favorable conditions for trees defoliated by gypsy moth during the second outbreak may therefore have resulted in a less severe growth reduction in Lake Hill oaks.

Effect of Gypsy Moth on White Ash Growth

Growth of ash in the post-gypsy-moth period at Lake Hill diverged from that at Sunrise. Large deviations from predicted values were evident in 1979, 1980, 1982, and 1988. While we are uncertain as to why growth at Lake Hill in 1982 and 1988 was so low, the higher than expected growth in 1979 and 1980 may have resulted from a nutrient pulse following the first gypsy moth outbreak. It has been well established that in the aftermath of an insect outbreak, large quantities of nutrients, especially nitrogen, are returned to the forest floor (Mattson and Addy 1975). This is due to the exceptionally high concentration of nutrients in larvae bodies and frass, as well as the increased fall of leaves, twigs, and branches due to larval activity in the canopy. White ash has been classified as a nitrogen-demanding tree (Stanturf et al. 1989), and has been shown to respond to nitrogen fertilization with an increase in radial growth (Ellis 1979, Stanturf et al. 1989). It is thus possible that increased availability of nitrogen in the form of a nitrogen pulse after the first gypsy moth outbreak

allowed ash to experience a time-lagged increase in radial growth. As an avoided host, ash trees suffered little if any defoliation during the first gypsy moth outbreak of 1978 to 1980, and several studies have observed growth increases in nondefoliated trees subsequent to heavy defoliation of preferred hosts in the same stand (Kulman 1971, Campbell and Garlo 1982, Twery 1987, Swetnam and Lynch 1989).

Tent Caterpillar Defoliation

As an ancillary note on insect herbivory, the steep drop in both species' growth in 1953 was most likely due to severe defoliation by the forest tent caterpillar (*Malacosoma disstria* Hubner). Starting in 1952, a region-wide tent caterpillar outbreak caused severe damage to forests in much of southwestern Québec (Martineau and Beique 1953). By 1953, Mont St-Hilaire was within a 3000 square mile area in which most deciduous trees were completely defoliated. This defoliation is the likely cause of the very narrow growth ring observed in all trees in 1953, since climatic conditions were not especially severe that year (Naidoo 1997). The same tent caterpillar outbreak also resulted in growth reductions in 1953 in sugar maple radial growth chronologies from several sites in western Québec (Payette et al. 1996) and New York State (Bauce and Allen 1991). Red oak and white ash are both preferred hosts of the forest tent caterpillar (Craighead 1950). Ash at both Lake Hill and Sunrise had very narrow growth rings in 1953. In contrast, ash radial growth at Lake Hill was unaffected by heavy gypsy moth defoliation from 1978 to 1980. After the tent caterpillar outbreak, both species at both sites rebounded to pre-defoliation levels; there was no evidence of a long-term decline due to this native folivore.

Applications

As with other studies that have looked at defoliating insects and tree growth (e.g., Swetnam and Lynch 1989, Mason et al. 1997), our use of growth chronologies from nondefoliated trees as predictors produced a clear signal for growth losses during outbreak years in trees defoliated by gypsy moth. Since this method is simple to use, the effects of gypsy moth defoliation on radial growth of trees in other northeastern forests could be assessed in this manner. Replication of our study at other locations would also help establish the applicability of these results. Collecting increment cores and measuring growth rates at the beginning of an outbreak may also be useful in estimating the potential damage to a stand. In the first outbreak at our site, red oak growth was declining before gypsy moth densities reached outbreak levels; the subsequent outbreak led to heavy growth losses. In the second outbreak, radial growth of red oak was increasing, which may have been a factor in the minimal growth losses experienced by oaks. Appraising overall growth rates of a forest on the verge of a gypsy moth outbreak may thus be a worthwhile endeavor, as management options such as spraying may not be necessary in a forest where host trees are growing well.

If growth of preferred hosts are affected negatively by nonoutbreak densities of gypsy moth, as our results suggest, then suppression efforts may also be necessary during years between outbreaks. As noted above, however, growth of red

oaks at Lake Hill actually increased in relation to growth at Sunrise for most years following the initial outbreak at Lake Hill. Forest managers should thus consider potential losses during nonoutbreak years in models that also include variables such as growth losses during outbreaks, subsequent growth increases, and mortality (a factor which was not considered in this study).

Our results also suggest that nondefoliated trees should be of the same species as defoliated trees, especially when examining annual growth losses. The use of nonhost trees as undefoliated references has been utilized mostly in western North America, where records of defoliation by native insects such as the western spruce budworm and Douglas-fir tussock moth are longer than for the gypsy moth. Small species-related differences in annual growth are less important when chronologies from infested stands are much longer, and growth losses are assessed at the outbreak or multiyear level. Since records of gypsy moth defoliation are more likely to be on the time scale of our study, rather than the 200–300 yr time scale of some western spruce budworm defoliation records, nondefoliated tree chronologies should match defoliated tree chronologies at the annual level as much as possible. This is best achieved by using a "control" involving comparisons between trees of the same species growing under comparable conditions except for defoliation levels. Otherwise, species-related differences in annual growth may lead to excessive noise in short chronologies. For example, had we used Lake Hill white ash, instead of Sunrise red oak, in our pre-gypsy-moth regression model for Lake Hill red oak, the R^2 would have been 0.46 instead of 0.66, which accordingly would have led to a less accurate prediction for growth losses during the first outbreak.

This prediction would have been even worse had we used a simple differencing technique for the whole 1950–1992 series (e.g., Swetnam and Lynch 1989), since outbreaks that reduce growth in preferred species may actually enhance growth in avoided species. Subtracting these nonhost chronologies from host chronologies may thus produce artificially corrected indices, since the "control" trees do not accurately reflect growing conditions for the host trees in the absence of the defoliator. We therefore suggest that when using nondefoliated trees to assess growth losses in areas with relatively recent histories of gypsy moth infestations, the most accurate way to generate expected growth values for outbreak periods may be from regression models that: (1) are developed prior to the initial outbreak; and (2) incorporate nondefoliated conspecific trees from a similar but undefoliated site nearby.

Literature Cited

- BAKER, W.L. 1941. Effect of gypsy moth defoliation on certain forest trees. *J. For.* 39:1017–1022.
- BAUCE, E., AND D.C. ALLEN. 1991. Etiology of a sugar maple decline. *Can. J. For. Res.* 21:686–693.
- BERRYMAN, A.A. 1987. The theory and classification of outbreaks. P. 3–30 *in* Insect outbreaks, Barbosa, P., and J.C. Schultz (eds.). Academic Press, Inc., New York.
- BOX, G.E.P., AND G.M. JENKINS. 1970. Time series analysis: Forecasting and control. Holden-Day, Inc., San Francisco.

- BROWN, J.H., D.B. HALLIWELL, AND W.P. GOULD. 1979. Gypsy moth defoliation: Impact in Rhode Island Forests. *J. For.* 77:30-32.
- CAMPBELL, R.W., AND A.S. GARLO. 1982. Gypsy moth in New Jersey pine-oak. *J. For.* 80:89-90.
- CAMPBELL, R.W., AND R.J. SLOAN. 1977. Forest stand responses to defoliation by the gypsy moth. *For. Sci. Monogr.* 19:1-32.
- CRAIGHEAD, F.C. 1950. Insect enemies of eastern forests. USDA Misc. Publ. no. 657.
- DUNLAP, T.R. 1980. The gypsy moth: A study in science and public policy. *J. For. History* 24:116-126.
- ELLIS, R.C. 1979. Response of crop trees of sugar maple, white ash, and black cherry to fertilization. *Can. J. For. Res.* 9: 179-188.
- FRITTS, H.C., AND T.W. SWETNAM. 1989. Dendroecology: A tool for evaluating variations in past and present forest environments. *Adv. Ecol. Res.* 19:111-188.
- GANSNER, D.A., S.L. ARNER, R.H. WIDMANN, AND C.L. ALERICH. 1993. After two decades of gypsy moth, is there any oak left? *North. J. Appl. For.* 10:184-186.
- GRAUMLICH, L.J. 1993. Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great Lakes region. *Can. J. For. Res.* 23:133-143.
- HARVEY, A.C. 1990. *The econometric analysis of time series*. Ed. 2. Philip Allan, New York.
- HUNTER, A.F., AND M.J. LECHOWICZ. 1992. Foliage quality changes during canopy development of some northern hardwood trees. *Oecologia* 89:316-323.
- JOBIN, L. 1978. Historique et situation actuelle de la spongieuse au Mont St-Hilaire. Laurentian Forest Research Centre, Ste-Foy, Québec.
- JONES, C.G. 1991. What causes the patterns of gypsy moth defoliation? P. 127 in *Proc. of USDA Interagency Gypsy Moth Res. Rev.* 1990, Gottschalk, K.W., et al. (eds.). USDA For. Serv. Gen. Tech. Rep. NE-146.
- KOEBER, T.W., AND B.E. WICKMAN. 1970. Use of tree-ring measurements to evaluate impact of insect defoliation. P. 101-106 in *Tree-ring analysis with special reference to Northwest America*, Smith, J.H.G., and J. Worrall (eds.). Univ. of British Columbia Fac. of For. Res. Bull. 7, Vancouver, Canada.
- KULMAN, H.M. 1971. Effects of insect defoliation on growth and mortality of trees. *Annu. Rev. Entomol.* 16:289-324.
- LECHOWICZ, M.J. 1983. Leaf quality and the host preferences of gypsy moth in the northern deciduous forest. USDA Gen. Tech. Rep. NE-85.
- LECHOWICZ, M.J., AND Y. MAUFFETTE. 1986. Host preferences of the gypsy moth in eastern North American versus European forests. *Rev. D'Ent. Que.* 31:43-51.
- LEONARD, D.E. 1981. Bioecology of the gypsy moth. P. 9-29 in *The gypsy moth: Research toward integrated pest management*, Doane, C.C., and M.L. McManus (eds.). USDA For. Serv. Tech. Bull. 1584.
- LIEBHOLD, A.M., J.S. ELKINTON, AND W.E. WALLNER. 1986. Effect of burlap bands on between-tree movement of late instar gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae). *Environ. Entomol.* 15:373-379.
- LIEBHOLD, A.M., W.L. MACDONALD, D. BERGDAHL, AND V.C. MASTRO. 1995. Invasion by exotic forest insect pests: A threat to forest ecosystems. *For. Sci. Monogr.* 30:1-49.
- LIEBHOLD, A.M., AND M.L. MCMANUS. 1991. Does larval dispersal cause the expansion of gypsy moth outbreaks? *North. J. Appl. For.* 8:95-98.
- MARTINEAU, R., AND R. BEIQUÉ. 1953. Annu. Rep. of the For. Insect and Disease Survey, Province of Quebec. Dep. of Agric. Canada, For. Biol. Div., Ottawa, Canada.
- MASON, R.R., B.E. WICKMAN, AND H.G. PAUL. 1997. Radial growth response of Douglas-fir and Grand fir to larval densities of the Douglas-fir tussock moth and the western spruce budworm. *For. Sci.* 43:194-205.
- MATTSON, W.J., AND N.D. ADDY. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190:515-522.
- MATTSON, W.J., AND R.A. HAACK. 1987. The role of drought in outbreaks of plant-eating insects. *Bioscience* 37:110-118.
- MAYCOCK, P.F. 1961. Botanical studies on Mont St. Hilaire, Rouville County, Quebec. *Can. J. Bot.* 39:1293-1325.
- MINOTT, C.W., AND I.T. GUILD. 1925. Some results of defoliation on trees. *J. Econ. Entomol.* 18: 345-348.
- MONTGOMERY, M.E., AND W.E. WALLNER. 1988. *The gypsy moth: A westward migrant*. P. 354-377 in *Dynamics of forest insect populations: Patterns, causes, implications*, Berryman A.A. (ed.). Plenum Press, New York.
- NAIDOO, R. 1997. The effects of gypsy moth defoliation and climatic conditions on radial growth of deciduous trees. M.Sc. Thesis, McGill University, Montréal, Canada. 111 p.
- PAYETTE, S., M-J. FORTIN, AND C. MORNEAU. 1996. The recent sugar maple decline in southern Quebec: Probable causes deduced from tree rings. *Can. J. For. Res.* 26:1069-1078.
- SAS Institute, Inc. 1993. *SAS/ETS user's guide*, version 6. SAS Institute Inc., Cary, NC.
- SAS Institute Inc. 1985. *SAS user's guide: Statistics*, version 5 edition. SAS Institute Inc., Cary, NC.
- SCHOWALTER, T.D., W.W. HARGROVE, AND D.A. CROSSLEY, JR. 1986. Herbivory in forested ecosystems. *Annu. Rev. Entomol.* 31:177-196.
- SEASTEDT, T.R., D.A. CROSSLEY, JR., AND W.W. HARGROVE. 1983. The effects of low-level consumption by canopy arthropods on the growth and nutrient dynamics of black locust and red maple trees in the southern Appalachians. *Ecology* 64: 1040-1048.
- STANTURF, J.A., E.L. STONE, JR., AND R.C. MCKITTRICK. 1989. Effects of added nitrogen on growth of hardwood trees in southern New York. *Can. J. For. Res.* 19:279-284.
- STOKES, M.A., AND T.L. SMILEY. 1968. *An introduction to tree-ring dating*. University of Chicago Press, Chicago.
- SWETNAM, T.W., AND A.M. LYNCH. 1989. A tree-ring reconstruction of western spruce budworm history in the southern Rocky mountains. *For. Sci.* 35:962-986.
- TWERY, M.J. 1987. Changes in vertical distribution of xylem production in hardwoods defoliated by gypsy moth. Ph.D. Diss., Yale University, New Haven, CT.
- WARGO, P.M. 1981. Defoliation and tree growth. P. 225-240 in *The gypsy moth: Research toward integrated pest management*, Doane, C.C., and M.L. McManus (eds.). USDA For. Serv. Tech. Bull. 1584.