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# Effects of Gypsy Moth on Radial Growth of Deciduous Trees

Robin Naidoo and Martin J. Lechowicz

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**ABSTRACT.** We investigated the effect of gypsy moth (*Lymantria dispar* L.) larval abundance on annual radial growth of preferred, intermediate, and avoided host trees: northern red oak (*Quercus rubra* L.), sugar maple (*Acer saccharum* Marsh.), and white ash (*Fraxinus americana* L.), respectively. Individual trees were surveyed for gypsy moth larvae from 1979 to 1992 in a chronically infested forest on a drought-prone site in southwestern Québec. Increment cores were collected from 156 oaks, 39 maples, and 39 ash, and annual radial growth indices from 1950 to 1992 were calculated for each species. Growth was corrected for the influence of climate using regression models. For red oak, the average number of gypsy moth larvae per tree explained 73% of the variance in growth not explained by climate. Sugar maple and white ash growth was not correlated with gypsy moth larval numbers. These results are consistent with gypsy moth host preferences and provide evidence that nonepidemic levels of gypsy moth larvae can have a significant negative effect on the radial growth of individual trees. For. Sci. 47(3):338–348.

**Key Words:** *Lymantria dispar*, dendroecology, *Quercus rubra*, *Acer saccharum*, *Fraxinus americana*.

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**T**HE IMPACT OF DEFOLIATING INSECTS ON radial growth of hardwood trees has been studied extensively in Australia (e.g., Mazanec 1968, Readshaw and Mazanec 1969, Mazanec 1974, Morrow and LaMarche 1978), Europe (e.g., Klepac 1959, Ierusalimov 1965, Ljapcenkov 1966, Rafes 1970, Magnoler and Cambini 1973, Kucherov 1990, Rubtsov 1996), and North America (e.g., Minott and Guild 1925, Baker 1941, Rose 1958, Embree 1967, Brown et al. 1979, Campbell and Garlo 1982, Gross 1991, May and Killingbeck 1995, Muzika and Liebhold 1999). Kulman (1971) provides a comprehensive review of defoliation by many insect species on the radial growth of their hosts. Dendroecological methods (Fritts 1976, Fritts and Swetnam 1991) allow one to account for abiotic and biotic conditions that affect annual radial growth in trees, such as climate and tree age, and then isolate the contribution of a single factor, such as insect defoliation, to radial growth. Several recent North American studies have used dendroecological tech-

niques to investigate the effects of defoliating insects on radial growth (Swetnam and Lynch 1989, Jardon et al. 1994, Krause and Morin 1995, Krause 1997, Muzika and Liebhold 1999, Naidoo and Lechowicz 1999, Zhang et al. 1999).

In this study, we used dendroecological techniques to determine whether long-term radial growth differences of tree species in an infested forest are related to gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae) larval counts. The gypsy moth is an introduced polyphagous folivore that feeds on the leaves of many North American trees and shrubs (Doane and McManus 1980, Liebhold et al. 1995). Gypsy moth larvae are classified as spring–early summer feeders (Hunter 1991), and generally feed on foliage from early May until the beginning of July (Jobin 1995). Because the period of growth for hardwood trees in northeastern North America is from May to August (Fraser 1956, Ahlgren 1957), we predicted that herbivory by gypsy moth larvae would result in the reduction of radial growth in the same year that

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defoliation occurred. We also predicted that growth losses would be greater in preferred tree species than in intermediate or avoided species (Muzika and Liebhold 1999). After having established growth-climate relationships for the different tree species in the absence of gypsy moths, a 14 yr time series of gypsy moth larval numbers on host trees was used to assess the impact of larval abundance on host species of varying susceptibility to gypsy moth feeding.

## Methods

### Study Area

The study site was the south slope of Lake Hill, one of seven small peaks that comprise Mont St-Hilaire (45° 32' N, 73° 09' W). Located in the St-Lawrence River Valley in the vicinity of Montréal, Québec (Figure 1), Mont St-Hilaire is covered primarily with old-growth deciduous forest and is the largest remaining tract of the Great Lakes–St-Lawrence forest type (Hosie 1990, p. 22) that covered the valley prior to European settlement. As a unique ecological and historical site, Mont St-Hilaire was accorded UN Biosphere Reserve status in 1978, and access and activities on the mountain are restricted so that its undisturbed character is maintained. Forest types on the mountain include old-growth beech-sugar maple (*Fagus grandifolia* Ehrh.–*Acer saccharum* Marsh.) stands on deep moist soils, hemlock (*Tsuga canadensis* [L.] Carrière) on steep, rocky slopes, yellow birch (*Betula alleghaniensis* Britton) and red maple (*Acer rubrum* L.) swamps in depressions, and northern red oak (*Quercus rubra* L.) forests on drier sites (Maycock 1961).

The south slope of Lake Hill exhibits many of the characteristics that Houston and Valentine (1977) ascribe to sites prone to gypsy moth infestation. The soil is shallow and sandy or rocky, with an average depth of only 65 cm over bedrock (Rouse 1970). Although the peak is only 297 m high, many areas are quite steep with open canopies, resulting in scree slopes with little leaf litter. The south slope has considerably higher air and soil temperatures and is much drier than the north slope (Rouse 1970). These differences are reflected in the forest composition, where red oak dominates the xeric forest on the south side, while on the mesic north side, the predominant species are beech and sugar maple (Lechowicz 1983). Other important species on the south slope are sugar maple and ironwood (*Ostrya virginiana* [Miller] K. Koch), while white ash (*Fraxinus americana* L.), beech, white birch (*Betula papyrifera* Marsh.), and basswood (*Tilia americana* L.) are minor components.

### Collection of Gypsy Moth Data

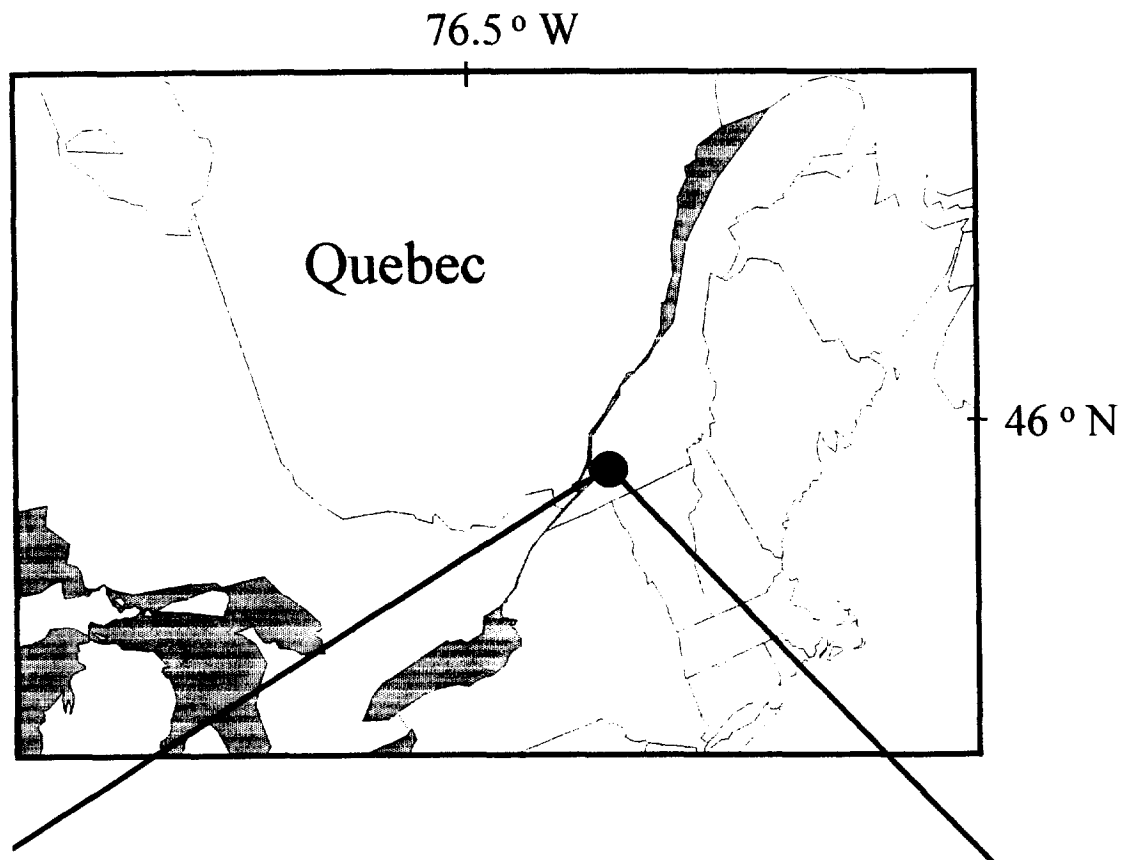
The arrival and establishment of the gypsy moth in southwestern Québec and at Mont St-Hilaire have been well documented. Widely scattered patches of gypsy moth defoliation were observed in 1972 in parts of western Québec near Mont St-Hilaire (Jobin 1995), but the first area-wide outbreak was in 1977. The first record of gypsy moth infestation at Mont St-Hilaire was also in 1977, when 10 ha of Burned Hill (a small peak adjacent to Lake Hill) were defoliated (Jobin 1978). In 1978, the area of defoliation increased to 259

ha and spread from Burned Hill to adjacent Lake Hill, where 123 ha were severely defoliated (Lechowicz 1983). The first outbreak at Lake Hill ended after 1980, as indicated by no further visible defoliation (M.J. Lechowicz, personal observation), and the very low number of larvae recorded on red oak, the preferred host at the site (see below for information on larval monitoring). This outbreak was followed by a number of years during which gypsy moth larval numbers were low but gradually increasing. Larval counts (see below) and severe defoliation of the canopy, as determined by ground observations (M.J. Lechowicz, personal observation) indicated that a second outbreak occurred at Lake Hill in 1989 and 1990.

The Lake Hill study site was established in 1979, the year after the first severe gypsy moth defoliation. Twenty-four 500 m<sup>2</sup> circular quadrats were randomly placed along four altitudinal isoclines on the south and southeast slopes of Lake Hill (Figure 1). Each isocline had from 3 to 7 quadrats, and the average distance between quadrats was about 200 m. In each quadrat, all trees with a dbh (diameter at breast height, 1.37 m) greater than 8 cm were tagged and identified to species. A tarpaper skirt was placed around the trunk of each tree; such artificial hiding places are used by late-instar gypsy moths as daytime hiding places (Liebhold et al. 1986). The number of larvae under the tarpaper bands was recorded, usually on four separate occasions, when late instars were present, each summer from 1979 through 1992. The number of gypsy moth egg masses present on each tree was also determined by visually inspecting each tree trunk on one occasion in late summer.

### Collection and Analysis of Radial Growth Data

We selected three tree species with contrasting host preferences to examine the influence of gypsy moth larvae on radial growth. Northern red oak is a preferred host of the gypsy moth, white ash is avoided, and sugar maple is intermediate in susceptibility (Lechowicz 1983, Lechowicz and Jobin 1983). For each species, two increment cores were collected from all trees with gypsy moth records in the twenty-four quadrats. The DBH of each tree was also measured. Cores were air dried and then mounted onto wooden backings. To make the rings more visible, ash and oak cores were planed, and maple cores were sanded. Cores were crossdated visually (Stokes and Smiley 1968, p. 47); narrow rings in 1953, 1971, 1978, 1979, and 1988, and large rings in 1981 made unambiguous crossdating possible in almost every oak and ash core. Unequivocal crossdating of maple cores was more difficult due to extreme suppression in some trees, and missing or additional rings in others. Any core that was damaged or that could not be crossdated was removed from the analysis; 14 oak, 19 maple, and 12 ash trees thus had chronologies based on only one core. After cross-dating, ring widths were measured to the nearest 0.01 mm using a dissecting microscope with a sliding vernier scale. The age of the tree (at breast height) was also recorded. For some cores, estimating the age was not possible, either because the tree's center was rotten or because the core was too far off the pith. Trees with only one age estimate were removed from the analysis. The years 1950 to 1992 were measured on all cores;



### Lake Hill - Mt. St-Hilaire, Québec

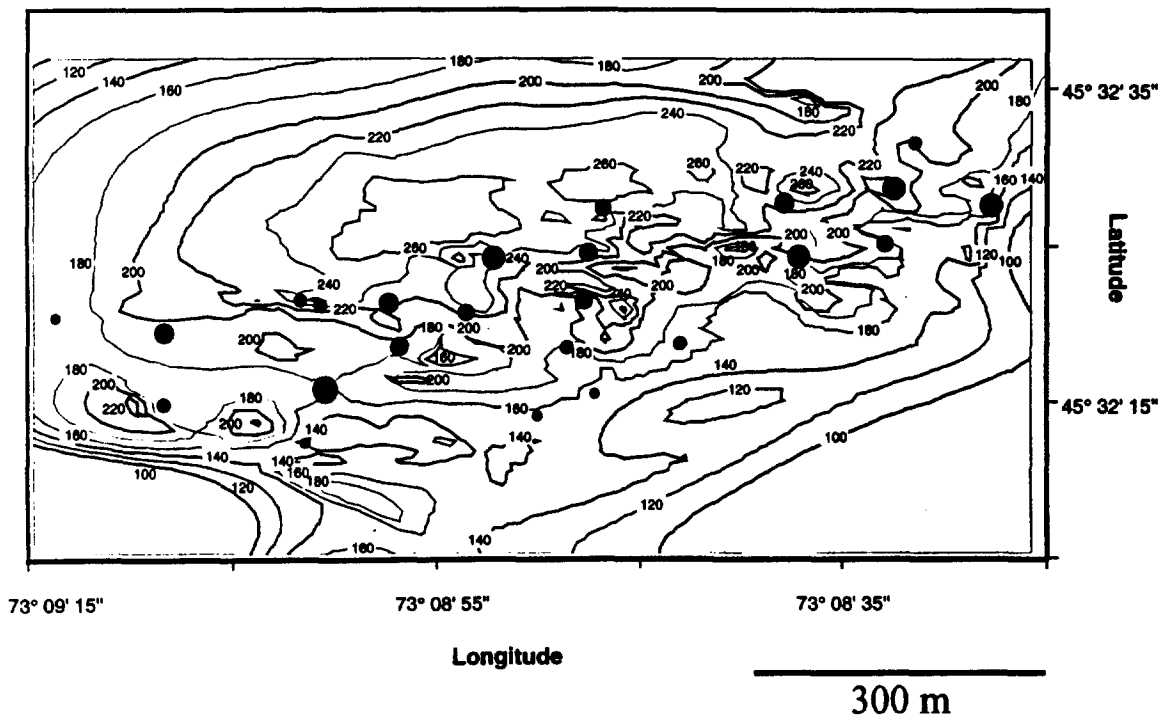


Figure 1. The Lake Hill study site at Mont St-Hilaire. In 1979, twenty-four 500 m<sup>2</sup> quadrats (represented as circles on the contour map) were established on the south-facing slope of Lake Hill to monitor the gypsy moth infestation. Allitudes are in meters. The larger the symbol, the greater the average number of larvae per tree was during 1979 to 1992. The difference in larval numbers between quadrats was mainly due to the percentage of red oak in the canopy (Pearson correlation coefficient,  $r = 0.524$ ,  $P = 0.015$ ).

1950 was the earliest year we could measure, since many trees had just grown to breast height in the preceding few years.

A standardized ring index was calculated for each core by fitting a horizontal line through the mean. The resulting series were averaged over all cores and trees for each species to give the standardized ring index chronology. We used the mean of each series (i.e., a straight line with slope = 0 and y-intercept = mean of series) instead of a more flexible hypothetical growth curve for two reasons. First, many tree-ring studies are focused on the year-to-year variation in ring width due to climate, and thus other sources of variation such as long-term growth trends must be removed (e.g., Blasing et al. 1988, Innes and Cook 1989, Graumlich 1993, Payette et al. 1996). Standardizing by the mean of a series ensures preservation of trends that may be of interest, while at the same time removes growth rate differences among individual trees and among species. Second, we used only a subset of the years that any given tree had been growing, therefore any fitted growth curves would have been biased by the lack of growth data prior to 1950. We feel this bias would have outweighed any positive effects standardization by growth curves may have had.

#### *Climate and Gypsy Moth Analysis*

All statistical analyses were conducted using SAS, Release 6.04. For each chronology, 128 candidate variables were screened with Pearson correlation coefficients to identify potential growth-limiting climatic conditions. It is important to emphasize that this stage of the analysis represented a preliminary and exploratory phase in which no hypotheses were tested, nor statistical relationships developed. Rather, the objective was to attempt to reduce the large number of variables that could potentially impact radial growth. The variables included monthly average temperatures and total monthly precipitation, precipitation during different periods of the growing season, discrete climatic conditions such as winter thaw and drought lengths, and modelled monthly values of soil water. All candidate variables were calculated for the period beginning in September of the previous year and continuing until September of the current year. Studies on the effect of climatic conditions on radial growth of trees often report different climate variables being limiting to growth, and all of the variables considered here have been correlated with growth (e.g., Fritts 1976, p. 349–351, Pilcher and Gray 1982, Graumlich 1993, Lane et al. 1993, Yin et al. 1994, Jenkins and Pallardy 1995, Payette et al. 1996). Soil water values were modeled using ForHym, a process-based model of forest soil water content with inputs of monthly precipitation and temperature data, as well as descriptive site data such as forest type and soil depth (Yin et al. 1994). All climate records were obtained from the St-Hubert airport weather station, about 20 km northwest of the study site. From 1950 to 1992 several weather stations were also in operation for short periods at Mont St-Hilaire. Data from these stations were collated and compared to St-Hubert data from the same time. Regression analysis showed that the two data sets agreed closely and correc-

tion factors for the St-Hubert data were unnecessary (Naidoo 1997).

To establish a baseline model of tree growth in the absence of gypsy moth, the period 1950 to 1975 was used to generate a regression model of radial growth based on climatic variables. The year 1975 was selected as the end of this period because the status of the gypsy moth population on Lake Hill during the years immediately preceding the first outbreak in 1978 is not known. Since it is possible that the gypsy moth was present at undetectable levels in 1976 and 1977, these years were not used in any regression analyses. The years 1978 to 1992 were used as the post-gypsy moth period; i.e., the period during which gypsy moth were known to be present at Lake Hill.

From the initial set of candidate variables screened in the exploratory stage, the 20 variables having the highest Pearson correlation coefficients with each growth chronology were selected for further analysis. From this pool, a multiple regression model of growth with two climatic variables was developed for each chronology, using the SAS procedure RSQUARE (SAS Institute Inc. 1989, p.1399). The final model was selected based on: (1) a large coefficient of determination ( $r^2$ ); (2) the absence of correlation between the two climate variables; and (3) the absence of differences in the means of the two variables between the two time periods. We used *t*-tests to determine whether there were any significant differences in the means of the climate variables between the two periods. All variables used in regression models showed no significant differences between the two periods ( $P < 0.05$ ), thus climatic conditions most limiting to growth were assumed to be equivalent. The year 1953 was excluded in all regression analyses because of a known forest tent caterpillar outbreak at Mont St-Hilaire that would have weakened the climate-growth relationship [preliminary analyses indicated that growth in 1953 was significantly lower than climate-predicted values, see Naidoo (1997) for more detail].

We initially used Ordinary Least Squares (OLS) regression to estimate regression parameters for all three species. Portmanteau Q-tests (Proc ARIMA, SAS Institute Inc. 1993) were used to test for autocorrelation in the residuals of each regression model. Autocorrelation at lags 1–6 was not present in the residuals of either the oak or maple growth-climate regression models. For ash, however, there was significant first-order autocorrelation in the residuals of the growth-climate model. This invalidates the use of OLS regression, due to violation of the assumption of independence in the residuals. For ash we then constructed a regression model that incorporated a first-order autocorrelated error term using Proc AUTOREG (SAS Institute Inc. 1993). 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 is thought to be more efficient in estimating parameters for small sample sizes.

The addition of the autocorrelated error term resulted in the coefficient of one of the climate predictors for ash growth becoming non-significant, therefore this variable was dropped from the equation. The regression models can be summarized as follows:

$$y_t = A_1x_{1(t)} + A_2x_{2(t)} + B + \epsilon_t \quad (1)$$

(for red oak and sugar maple); and

$$y_t = A_1x_{1(t)} + B + AR(1) + \epsilon_t \quad (2)$$

(for white ash) where

$y_t$  = radial growth at time  $t$

$x_{1(t)}, x_{2(t)}$  = climate variables at time  $t$

$A, A_1, A_2$  = regression coefficients

$B$  = intercept

$\epsilon_t$  = error term at time  $t$

$AR(1)$  = first-order autoregressive process up to lag  $p$  (Box and Jenkins 1970, p. 9)

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

and  $\phi$  = autoregressive coefficient.

Examination of the residuals from all regression equations revealed that they were normally distributed and showed no trend (i.e., no autocorrelation was present), thus satisfying the linear regression assumptions of normality and homoscedasticity (Zar 1999, p. 332).

The pre-gypsy moth regression models were then used to generate predicted radial growth values in the post-gypsy moth period. These were plotted against actual growth values, and the residuals (predicted subtracted from actual, i.e., the component of growth not explained by climate) were regressed against gypsy moth larval numbers. For each tree, the greatest number of larvae that were recorded during one of the several summer counts was used as our measure of larval abundance. This value was averaged over all trees for each species, log transformed, and used in the regression analyses. Undoubtedly, defoliation and larval abundance or density will not always be strongly correlated (factors leading to this expectation are summarized by Mason et al. 1997). However, our measure of larval abundance on oak was highly correlated with the number of egg masses counted the previous year (Spearman's  $r$ :  $r = 0.76$ ,  $n = 13$ ,  $P = 0.002$ ), and egg mass density has explained a significant amount of the variation in subsequent defoliation in several studies (e.g., Williams et al. 1991, Liebhold et al. 1993).

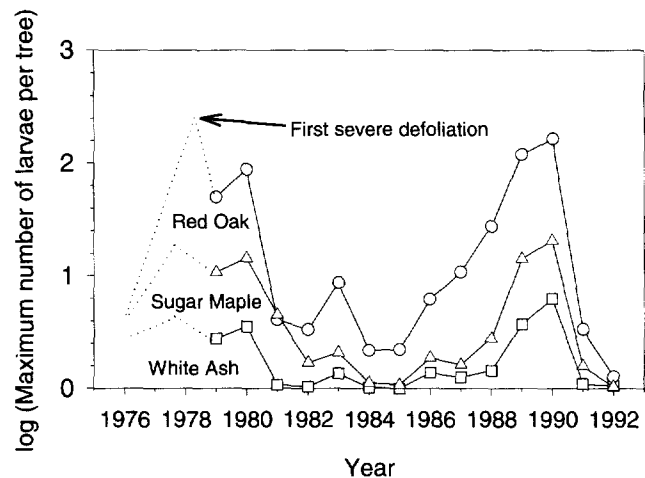


Figure 2. Gypsy moth population levels at Lake Hill, Mont St-Hilaire. Solid lines and symbols are logged values of the mean maximum larval count per tree of each species (three to five larval counts were made each summer from 1979 to 1992; the maximum larval count refers to the highest count of each summer for an individual tree). Dashed lines are estimates of the same measure, using data from Jobin (1978), Madrid and Stewart (1979), and Lechowicz (1983).

## Results

### Gypsy Moth Population

Aerial photographs of severe defoliation (Jobin 1978) indicated that the first gypsy moth outbreak at Lake Hill began in 1978, the year before larval counts on individual trees began, and continued through 1980 (Figure 2). The average number of larvae on oak trees in 1979 and 1980 was over 1.5 orders of magnitude higher than the average number of larvae on oak trees in 1984 and 1985, the years of lowest larval abundance. Larval counts on oaks increased steadily from 1985 until 1990, at which point abundance was even higher than counts in 1979–1980. The last 2 yr of the series (1991 and 1992) had very low gypsy moth larval counts.

The average number of larvae on sampled trees varied greatly between species. Oak was heavily attacked during the two outbreaks, averaging 104.5 larvae per tree (range 0–697), while maple averaged 14.0 (0–204) and ash 3.1 (0–51) larvae per tree. In the years between the two outbreaks (1981–1988), oak averaged 7.1, maple 2.5, and ash 0.5 larvae per tree.

### Radial Growth Chronologies

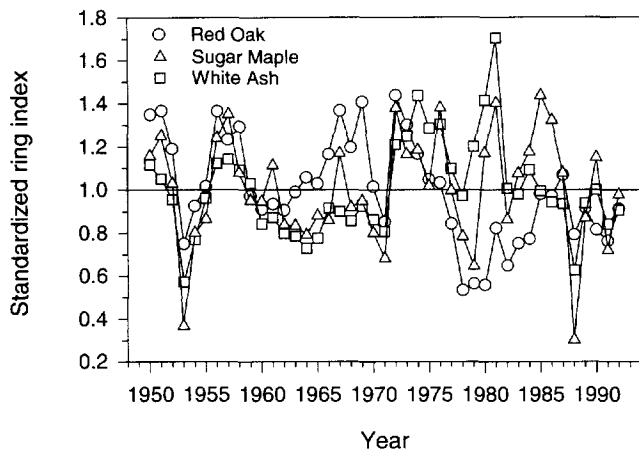
Pre- and post-gypsy moth ring index chronologies varied significantly for red oak but not for sugar maple or white ash (Table 1). Sample sizes for the three tree species varied

Table 1. Descriptive statistics for ring width chronologies of red oak, sugar maple, and white ash.

Species	Mean age (range)	Pre-gypsy moth (1950–1975)			Post-gypsy moth (1978–1992)
		Mean (SD) ring width (cm)	1st order autocorrelation*	Portmanteau Q-test: $\chi^2$ , DF (P)*	Mean (SD) ring width (cm)
Red oak ( $n = 156$ )	74 (45–171)	0.134 (0.022)	0.33	8.81, 6 (0.184)	0.093 (0.019) <sup>†</sup>
Sugar maple ( $n = 39$ )	91 (49–155)	0.113 (0.025)	0.27	11.47, 6 (0.075)	0.118 (0.034)
White ash ( $n = 39$ )	67 (44–133)	0.119 (0.026)	0.65	16.83, 6 (0.010)	0.134 (0.032)

\* First-order autocorrelation and portmanteau Q-tests for autocorrelation at lags 1–6 were for the standardized ring index chronologies.

<sup>†</sup> Significantly lower than mean of pre-gypsy moth period ( $t$ -test,  $P < 0.001$ ).



**Figure 3. Standardized ring index chronology for red oak, sugar maple, and white ash.**

because of differences in species abundance at Lake Hill and because many maple trees were excluded due to difficulties in crossdating. From 1950 to 1972, the three species show very similar growth patterns (Figure 3). All three decreased in growth in 1953, most likely due to severe defoliation by the forest tent caterpillar, *Malacosoma disstria* Hubner (Lepidoptera: Lasiocampidae) (Naidoo 1997, Martineau and Beique 1953).

After 1953, maple and ash experienced a period of slow but constant growth during the 1960s. Oak growth showed a similar pattern, although growth after 1966 was higher than that of either ash or maple. All three chronologies were significantly correlated with each other in the pre-gypsy moth period of 1950 to 1975 (Pearson correlation coefficients, oak with maple:  $r = 0.67$ ,  $n = 26$ ,  $P < 0.001$ ; oak with ash:  $r = 0.42$ ,  $n = 26$ ,  $P < 0.05$ ; maple with ash:  $r = 0.79$ ,  $n = 26$ ,  $P < 0.001$ ). Beginning in 1973, however, a different pattern emerged. From that point on, oak growth declined steeply and eventually ended with 3 yr of very low radial growth in 1978, 1979, and 1980. These years coincide with the first gypsy moth outbreak at Lake Hill. After 1980, oak growth increased and eventually stabilized at a level significantly below its pre-gypsy moth average (Table 1). Ash and maple also experienced growth declines beginning in 1973. The ash decline was much less severe than that of oak, and was also less prolonged.

Whereas oak growth was depressed from 1978 to 1980, ash growth rebounded immediately after 1978, and increased to the highest observed level in 1981. Maple exhibited a decline intermediate to that of oak and ash, and like ash did not experience a prolonged growth depression. There was no significant difference between mean ring width before and after the gypsy moth infestation for either ash or maple (Table 1). The decoupling of the species' growth chronologies is reflected in the Pearson correlation coefficients for 1978 to 1992: although ash and maple were still significantly correlated, oak and maple and oak and ash were no longer significantly correlated (oak with maple:  $r = 0.42$ ,  $n = 13$ ,  $P > 0.05$ ; oak with ash:  $r = -0.27$ ,  $n = 13$ ,  $P > 0.05$ ; maple with ash:  $r = 0.54$ ,  $n = 13$ ,  $P < 0.05$ ).

#### Climate Model

The regression models developed for growth chronologies in the pre-gypsy moth period were highly significant for all three species, with coefficients of determination ( $r^2$ ) ranging from 0.63 to 0.70 (Table 2, Figure 4). Summer soil water values (or correlates thereof) are predictors in each model, and oak was the only species to have a temperature variable included (daytime high temperature in January was a positive predictor of growth).

#### Impact of Gypsy Moth

The growth-climate relationship for red oak was not as strong in the post-gypsy moth period (1978 to 1992) as it was in the pre-gypsy moth period (Figure 5). Oak ring index values were lower than predicted in all years, and there no longer appeared to be a linear relationship between the predictor variables and growth. The greatest deviations of actual from predicted values were in outbreak years: 1978, 1979, 1980, 1989, and 1990. Growth of white ash and sugar maple was still closely predicted by the pre-gypsy moth growth equations, and the residuals from climate models of these two species were uncorrelated with log-transformed maximum larval counts (Pearson correlation coefficients, maple:  $r = -0.061$ ,  $n = 15$ ,  $P = 0.836$ ; ash:  $r = 0.202$ ,  $n = 15$ ,  $P = 0.488$ ). For red oak, however, log-transformed maximum larval counts were a significant predictor of oak residual growth (Figure 6), accounting for 73% of the variance unexplained by climate between 1979 and 1992.

**Table 2. Regression models of standardized ring index on climate ( $n = 25$ ).  $\hat{Y}$  represents an annual growth ring in cm.**

Species	Predictors	Regression equation	$r^2$	$F$	$P$
Red oak	$X_1$ : Daytime Jan. temp. ( $^{\circ}\text{C}$ ) $X_2$ : Precipitation in second quarter of growing season (mm)	$\hat{Y} = 1.1186 + 0.0029X_1 + 0.0436X_2$	0.70	25.8	0.0001
Sugar maple	$X_1$ : June rain (mm) $X_2$ : July rain (mm)	$\hat{Y} = 0.4951 + 0.0035X_1 + 0.0022X_2$	0.63	18.4	0.0001
White ash	$X_1$ : Modeled July soil water (cm) $X_2$ : 1st order autoregressive process of error term	$\hat{Y} = 0.4951 + 0.0035X_1 + 0.0022X_2$	0.67	—*	—*

\* Parameters estimated by Maximum Likelihood method, therefore  $F$  and  $p$  values not available. Both  $X_1$  and  $X_2$  in the regression equation were significantly different from 0 ( $t$ -tests,  $P < 0.01$  in both cases).

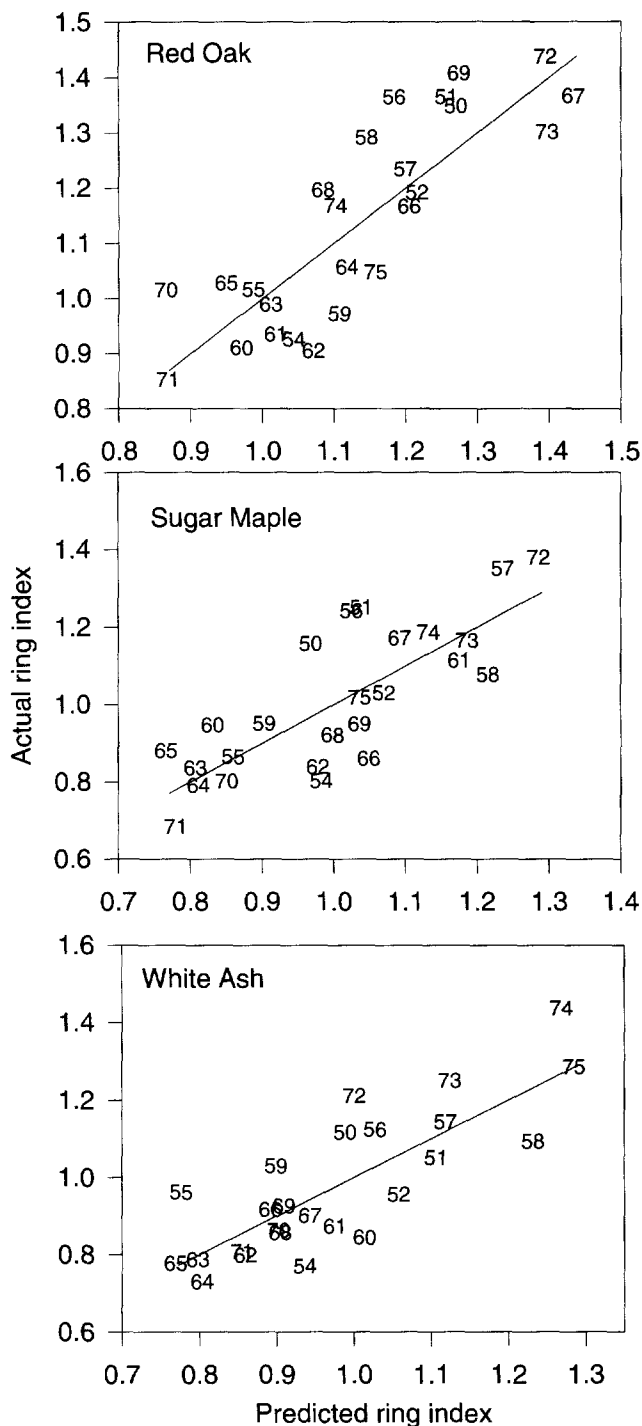


Figure 4. Actual (Y-axis) and predicted (X-axis) ring-width values (cm), 1950 to 1975, with 1953 excluded. Predicted values were generated using climate data (cf. regression equations in Table 2). Line of equality is also shown. Symbols are years.

## Discussion

### Pre-Gypsy Moth Growth

Summer soil water, or a correlate thereof, was an important predictor of radial growth for all three species in the pre-gypsy moth period. On a very dry, rocky slope such as the south slope of Lake Hill, soil water in the summer is likely to be limiting for growth. Many previous dendroecological studies have found correlates of summer soil water to be

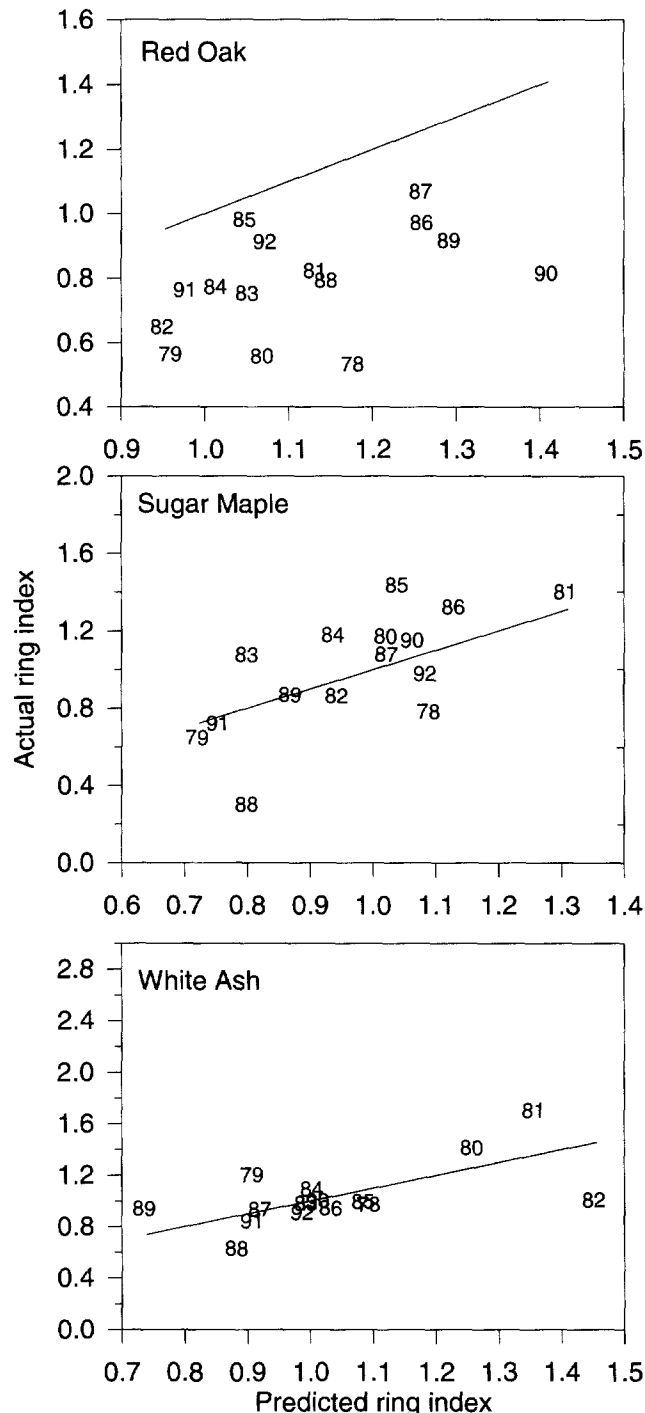
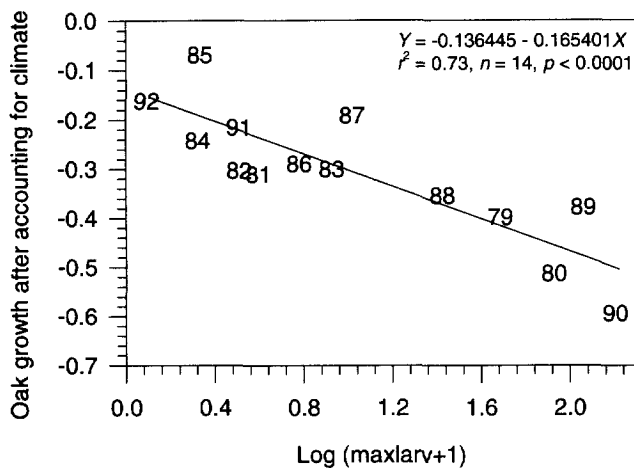


Figure 5. Actual (Y-axis) and predicted (X-axis) ring-width values (cm), 1978 to 1992. Predicted values are from regression equations in Table 2. Line of equality is also shown. For oak, percent losses in radial growth from climate-predicted values during outbreak years are: 1978—56.0; 1979—42.8; 1980—48.4; 1989—29.6; and 1990—42.0.

important predictors of radial growth (e.g., Lane et al. 1993, Yin et al. 1994, Jenkins and Pallardy 1995). Modeled soil water values were significant predictors for ash growth, but did not replace their concomitant precipitation values in climate models for oak and maple. This result is in disagreement with that of Yin et al. (1994), who found that replacing precipitation variables with modeled soil water values substantially increased the predictive power of regression equations for growth. This could be due to the ForHym model



**Figure 6. Losses in oak growth attributable to defoliation by gypsy moth after the effects of climate have been removed.**

being an aspatial model parameterized on a flat site with deep soil, whereas Lake Hill is a south-facing slope with shallow, rocky soil over impermeable bedrock. Resultant modeled soil water values may not be as accurate as those for flat sites for which the model was developed.

Differences in predictor variables of growth for the three species can be attributed to differences in life history or autecological traits, since all were growing at the same site. Of the three species, only red oak had a temperature variable as a predictor of growth. Red oak is at the northern limit of its distribution (Burns and Honkala 1990), and so may be more likely to suffer severe cold damage than sugar maple, a species with a somewhat more northerly range (Calmé et al. 1994). Higher temperatures in January may thus indicate more favorable conditions for oak, as damage due to extremely low temperatures would be less severe. A multiple regression model for earlywood width in red oak from North Carolina had December and February temperatures as significant positive predictors (Tainter et al. 1984). The coefficient of determination ( $r^2$ ) for the four-variable model was 0.464. A five-variable multiple regression model for latewood width for the same oaks included July precipitation as a significant positive predictor. This model had an  $r^2$  of 0.609. Response function analyses of the oaks *Q. robur* L. and *Q. petraea* (Mattuschka) Liebl. showed that climate accounted for between 5 and 72% of the variance in annual radial growth, with about half of the models having significant response elements for summer precipitation (Pilcher and Gray 1982). Our regression model of growth accounted for 69% of the variance in pre-gypsy moth radial growth, which is at the upper end of the range reported for *Quercus* species.

The percentage of variance in growth explained by the sugar maple model (62%) was also well within the range reported in the literature. Studies on the effect of climate on maple radial growth had climate variables explaining between 19.5–65.7% (Payette et al. 1996), 24–79% (Lane et al. 1993), 49–90% (Bauce and Allen 1991) and 83% (Yin et al. 1994) of the variance in radial growth. It should be noted that most of these growth models had far more predictor variables than our models. We chose to use only two predictors because the addition of even random variables to a multiple regression

equation can artificially inflate the amount of variance explained by the model (Draper and Smith 1966, p. 63). There was little consistency in predictor variables between literature models for maple radial growth. Many different climate variables from both the current and previous year were found to be significant predictors of growth, although six of the nine models for which standard climate variables were used did include some measure or correlate of summer soil water.

Radial growth in white ash was positively influenced by modelled soil water in July. Of the two other studies we found that modeled white ash radial growth from climate, both had some correlate of summer soil water as predictors (Luken et al. 1994, Han et al. 1991).

#### **Post-Gypsy Moth Growth**

Radial growth of both sugar maple and white ash was not substantially different in the post-gypsy moth period than in the pre-gypsy moth period. Mean annual growth rates were similar, and climate models continued to predict growth reasonably well. As both these species are nonpreferred hosts, this lack of response to the arrival of the gypsy moth on the site is not surprising. Effects of gypsy moth outbreaks on sugar maple, an intermediate host, were negligible in Muzika and Liebhold (1999). There was some evidence that white ash, an avoided host, experienced a growth increase during years during and subsequent to the first and second outbreaks (Figure 5: 1979, 1980, 1981, and 1989 are the only years that are higher than was predicted from climate). This was also supported by a different analysis of the same system reported elsewhere (Naidoo and Lechowicz 1999), where we argue that increased nitrogen transfer during and subsequent to outbreaks favoured the growth release of ash, a nitrogen-demanding tree. Working with defoliation and radial increment data from the northeastern United States, Muzika and Liebhold (1999) also found evidence that ash species showed radial growth increases in response to defoliation of nearby preferred gypsy moth hosts, in their case oaks of various species.

Oak radial growth after the invasion of the gypsy moth was lower than the climate-predicted values for all years between 1978 and 1992. Not only was radial growth much lower than predicted, but it was no longer linearly related to the climate variables identified as most limiting to growth in the pre-gypsy moth period. Rather, gypsy moth larval numbers seemed to be the primary influence on oak growth from 1978 to 1992. In this study we observed growth losses in outbreak years of between 29.6 and 56.0%, for an average of 43.8%. A European study that also computed climate-predicted radial growth values found that upland oaks had radial growth losses of about 40% after near-total defoliation from outbreaks of gypsy moth and other Lepidoptera (Rubtsov 1996). Both of these values are less than the 52.2% (Minott and Guild 1925) and 58.0% (Baker 1941) values reported for red, scarlet, black, and white oaks in New England following defoliation of 81 to 100% of the canopy. Overestimation of the effect of gypsy moth defoliation on growth in these studies is likely, since drought conditions which are often associated with severe outbreaks also result in poor growth, and

distinguishing between these two factors is difficult without quantifying both (Koerber and Wickman 1970). Baker (1941) also reported on additional plots of black and white oak where severe defoliation resulted in growth declines of only 33 to 43%. In these cases, however, years of heavy defoliation were not associated with drought conditions. Rainfall was average or even above-average in these years, which likely mitigated the negative effects of gypsy moth defoliation. Other studies report radial growth losses of 32 to 50%, but no mention of climatic conditions is made in these cases, therefore comparisons are difficult to make (Brown et al. 1979, May and Killingbeck 1995).

Our results suggest that endemic levels of gypsy moth larvae, presumably feeding at low intensities on the trees in which they were counted, can have a significant negative effect on radial growth of a preferred host. This underscores the potentially adverse consequences of gypsy moth infestations during nonoutbreak years. Mason et al. (1997) have reported similar reductions in growth of Douglas-fir and Grand fir due to low-intensity herbivory by Douglas-fir tussock moth and western spruce budworm. For oaks (*Quercus* spp.), only one other study could be found that attempted to relate the abundance of larval defoliators to radial growth of host trees over a number of years. In this case, the authors (Varley and Gradwell 1962) investigated the influence of temperature and rainfall on growth of *Quercus robur*, but found no significant correlations. They then constructed an index of growth, using the mean growth rate of each tree, and developed a significant regression model for growth on caterpillar density for an 8 yr period. Growth decreased linearly with increasing caterpillar density, even though only 2 of the 8 yr were years of heavy damage (i.e., outbreak years).

Muzika and Liebhold (1999) reported reduced radial growth of oaks, including red oak, in years of gypsy moth defoliation as well as in the year after defoliation. Their analysis did not correct for the effect of climate on radial growth, although their use of nonhost radial growth chronologies allowed for detection of the effects of defoliation. As their defoliation time series was only 5 yr, it is probable that trees in this time period did not experience a complete gypsy moth population cycle of outbreak, collapse, buildup, and second outbreak. Our radial growth chronologies coincided with this cycle, as indicated by the larval count data from the same trees that comprised the growth chronologies. Therefore our results complement the thorough, region-wide evaluation of gypsy moth defoliation on many different tree species of Muzika and Liebhold (1999) by providing site-specific, long-term evidence that gypsy moth larvae influences climate-corrected radial growth of a preferred host, northern red oak, over a wide range of abundance levels.

Several alternate hypotheses exist for the long-term reduction in radial growth of red oaks following the initial gypsy moth outbreak, thus potentially confusing the relationship between gypsy moth numbers and radial growth in nonoutbreak years. The first of these is that crown dieback and reduced vigor (Campbell and Sloan 1977) from the initial outbreak are causing the radial growth patterns after the first

outbreak. Heavy defoliation from the first outbreak did seem to result in prolonged growth reductions in oak, possibly due to crown dieback. Since oak trees can take up to 10 yr to recover from a severe defoliation episode (Campbell and Sloan 1977), delayed recovery and reduced crown vigor could have been responsible for the reduced growth observed in oaks between the two outbreaks (1981–1988). However, if crown dieback were the sole factor affecting radial growth in this period, there should have been a time trend in the growth chronology, such that as trees gradually recovered and began reallocating more resources to growth, the annual growth rings increased in width from 1981 to 1988. No such strict increase is noted in the oak growth chronology, although it is possible that a climate-dieback interaction was occurring. This possibility cannot be discounted, nor can it be tested with our data. However, due to the strength of the relationship between the residual growth from the climate models and the number of gypsy moth larvae on defoliated trees (Figure 6), we submit that low-intensity gypsy moth defoliation is the more likely explanation for the radial growth pattern of oaks after the initial outbreak. It should also be noted that our model of residual growth and gypsy moth numbers was based not only on the period between outbreaks, but also on larval numbers during both outbreaks and also after the second outbreak. Crown dieback would not have been an issue during the first outbreak, and presumably was of secondary importance during the second outbreak.

Another possible explanation for reduced growth in oak is the potential change in competitive relationships between species in the stand. Mortality and reduced competitive ability of oaks in relation to white ash and sugar maple could have led to a growth release of these nonpreferred species. It is possible that increased light availability and reduced root competition from dead and unhealthy oaks could have increased the competitive abilities of ash and maple and prevented oaks from increasing their growth rates back to preinfestation levels. However, this type of release due to changes in competitive status was not reflected in the growth chronologies of both ash and maple. Although ash did seem to experience a slight increase in growth after the first outbreak, maple did not. Any canopy openings should have elicited a response from sugar maple, a species readily able to exploit gaps in the canopy, as well as increase its growth once released from competition (Canham 1985). Since this did not occur, there most likely was little change in competitive status between species, and so growth reductions in oak after the initial outbreak were probably not due to increased competition by white ash and/or sugar maple.

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