

Changes in radial increment of host and nonhost tree species with gypsy moth defoliation

R.M. Muzika and A.M. Liebhold

Abstract: Ring widths from 1458 trees from Massachusetts, New York, and New Jersey were measured to determine the influence of gypsy moth (*Lymantria dispar* L.) defoliation on both hosts (primarily oaks (*Quercus* spp.)) and nonhosts. Previous year's defoliation negatively influenced radial increment in all oak species. Defoliation also negatively affected radial growth of pitch pine (*Pinus rigida* Mill.), an intermediate host. There was little or no effect of defoliation on increment of trembling aspen (*Populus tremuloides* Michx.) and bigtooth aspen (*Populus grandidentata* Michx.), but both are preferred hosts. Defoliation of host trees in mixed stands resulted in increased increment in the nonhosts tulip-tree (*Liriodendron tulipifera* L.) and ash (*Fraxinus* spp.) in the year following defoliation. The effect of defoliation was also evident in the relative production of earlywood and latewood with a pronounced dominance of earlywood production in host trees during the same year as defoliation and often in the following year.

Résumé : La largeur des cernes annuels de 1458 arbres situés dans les États du Massachusetts, de New York et du New Jersey a été mesurée pour déterminer l'influence de la défoliation par la spongieuse (*Lymantria dispar* L.) chez des espèces hôtes, principalement des chênes (*Quercus* spp.), et non hôtes. La défoliation de l'année précédente a influencé négativement la croissance radiale de toutes les espèces de chênes. La défoliation a aussi affecté négativement la croissance radiale du pin rigide (*Pinus rigida* Mill.), un hôte intermédiaire. La défoliation a eu peu ou pas d'effet sur l'accroissement du peuplier faux-tremble (*Populus tremuloides* Michx.) ou du peuplier à grandes dents (*Populus grandidentata* Michx.) bien qu'ils soient deux hôtes préférés. La défoliation des arbres hôtes dans les peuplements mélangés a provoqué une augmentation de la croissance du tulipier de Virginie (*Liriodendron tulipifera* L.) et du frêne (*Fraxinus* spp.), deux espèces non hôtes, l'année suivant la défoliation. La défoliation a également eu un effet visible sur la production relative de bois de printemps et de bois d'été, avec une dominance marquée pour la production de bois de printemps chez les arbres hôtes l'année même de la défoliation et souvent l'année suivante.

[Traduit par la Rédaction]

Introduction

Dendroecological techniques have been used to assess the effect of insect outbreaks and to reconstruct historic patterns of outbreaks (Fritts and Swetnam 1989). Such analyses could be useful in determining periodicity of outbreaks, radial growth losses, and changes in stand structure. In western North America, western spruce budworm (*Choristoneura occidentalis* Freeman) outbreak histories have been well defined (Thomson and VanSickle 1980; Swetnam and Lynch 1989, 1993; Weber and Schweingruber 1995) and extensive chronologies developed to determine the long-term impact of defoliation on host trees and susceptible forests. Brubaker (1978), Wickman (1980), and Mason et al. (1997) also examined radial growth losses relative to Douglas-fir

tussock moth (*Orgyia pseudotsugata* (McDunnough)) defoliation and abundance in the western United States.

In eastern North America, opportunities for chronologies longer than 150 years are limited given that many of the eastern forests are less than 100 years old. However, Jardon et al. (1994a, 1994b) have examined historic patterns of larch sawfly (*Pristiphora erichsonii* (Htg.)) outbreaks over three centuries in northern Quebec using dendrochronology and many others (e.g. Blais 1965, 1983; Krause 1997) have reconstructed spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks. Few studies have used dendrochronology to examine effects of hardwood defoliators in the eastern United States. With the exception of research by Baker (1941) and Campbell and Garlo (1982), there is a noticeable absence of dendrochronological research to detect insect outbreaks and determine effects of defoliation on deciduous trees. Hardwood forests in eastern North America tend to be diverse, with 10 or more species of dominant trees present, thus, causal relationships between defoliators and hosts are not easily demonstrated as in western forests with fewer overstory species.

The gypsy moth (*Lymantria dispar* L.) may be considered the most problematic defoliator of eastern deciduous forests.

Received July 10, 1998. Accepted April 12, 1999.

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Table 1. Species composition and basal area contribution of major species (A) and percent annual defoliation (B) at each of six areas in the gypsy moth IPS network.

(A) Species and basal area.					
	Western Massachusetts	Northeastern New York	East-central New York	Northwestern New Jersey	Coastal New Jersey
Total basal area (m ² /ha)	21.4	24.7	21.1	29.0	19.1
% of total basal area					
<i>Quercus alba</i>	13.8	16.9	5.5	12.9	16.6
<i>Quercus coccinea</i>	8.9	0	0	2.9	23.4
<i>Quercus prinus</i>	0	9.0	0.4	5.2	26.8
<i>Quercus rubra</i>	22.6	34.2	21.0	15.8	9.4
<i>Quercus velutina</i>	12.5	0	4.2	25.5	9.3
<i>Acer</i> spp.	12.0	5.8	8.5	7.4	0
<i>Pinus</i> spp.	10.6	11.2	11.7	0	20.7
<i>Populus tremuloides</i>	7.6	0	14.3	0	0
<i>Populus grandidentata</i>	3.6	0	17.8	0.5	0.5
<i>Fraxinus</i> spp.	0.2	3.4	0.1	1.5	0
<i>Liriodendron tulipifera</i>	0.1	0	0.2	4.2	0
(B) Defoliation (%).					
Year	Western Massachusetts	Northeastern New York	East-central New York	Northwestern New Jersey	Coastal New Jersey
1972	39.4	13.0	12.4	9.1	67.3
1973	16.9	8.3	2.7	28.3	86.4
1974	9.5	2.7	1.1	8.3	21.9
1975	0.7	0.1	0.6	5.3	15.0
1976	2.8	1.0	0.0	3.4	3.4

Note: Both basal area and defoliation values are means of five to eight sites per area with each site consisting of five 0.4-ha plots.

Although the gypsy moth is highly polyphagous, feeding extensively on many species, e.g. oaks, (*Quercus* spp.), aspen (*Populus* spp.), basswood (*Tilia* spp.), there are species that it feeds on more rarely, primarily when populations of the insect are great, e.g., pitch pine (*Pinus rigida* Mill.) or paper birch (*Betula papyrifera* Marsh.). The latter are considered intermediate or resistant hosts. Other species, e.g. tulip-tree (*Liriodendron tulipifera* L.), ash (*Fraxinus* spp.), or magnolia (*Magnolia* spp.), are considered immune and are never defoliated (Montgomery et al. 1990; Liebhold et al. 1995). While some information is available about growth declines in primary hosts during outbreaks, little is known about the applicability of dendrochronology in identifying outbreaks of the gypsy moth in the northeastern United States nor is much information available comparing the effects of defoliation on hosts versus nonhost trees. The purpose of this study was to evaluate if dendrochronological analysis could be used to identify gypsy moth outbreaks, and to determine the relative effect of gypsy moth defoliation on hosts and nonhosts in several forests in the northeastern United States, among a range of defoliation levels.

Methods

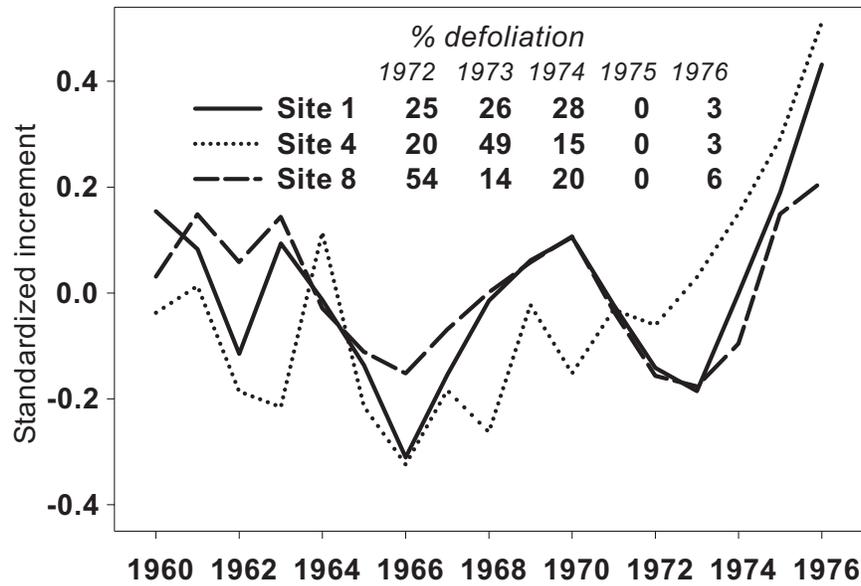
The data used in this study were collected as part of the USDA Forest Service Intensive Plot System (IPS) from 1972 to 1978 (Reardon 1976). The objectives of the IPS study included understanding gypsy moth population dynamics and forest-wide effects of defoliation, based on data collected at seven locations throughout the northeastern United States. Each of these seven areas con-

sisted of five to eight sites that were relatively homogenous in soil type and overstory species composition. Within each site, there were five 0.04-ha plots from which data were collected on a wide array of parameters relative to gypsy moth populations, individual tree defoliation, and crown condition. All trees within the plots were identified, height and diameter were measured, and vigor and defoliation were evaluated. Defoliation was determined as percentage loss of canopy and was estimated following gypsy moth feeding in the summer. In all, data were collected on nearly 10 000 trees. In this study we used data from five of these areas: western Massachusetts, northeastern New York, east central New York, northwestern New Jersey, and coastal New Jersey. The remaining two areas had inadequate numbers of tree cores to examine effect of defoliation on radial increment. Overstory tree species composition varied among the areas, but oaks were a major component throughout, and thus the forests were highly susceptible to gypsy moth outbreaks (Table 1).

In the winter of 1976–1977, an increment core was taken from each living tree on every plot. The ring widths were measured at Virginia Polytechnic Institute and State University soon after they were extracted. Most of the cores were measured through the most recent 25 years, although a few had longer series. Only species with at least 10 individuals per site were retained for analysis, making a total of 1458 usable series. Total radial increment was measured on all trees, and earlywood and latewood were differentiated on 1387 cores. The basis for distinguishing earlywood and latewood was wood color and change in vessel size.

All cores consisted of at least 25 annual growth rings. Although some extended to 50 years, the most reliable chronologies existed for the period 1952–1976. We graphically cross-dated each series and eliminated series that may have had missing rings. The raw tree ring series were standardized to correct for an age-related

Fig. 1. Average standardized increment and defoliation for *Quercus rubra* from three sites in western Massachusetts.



growth trend (Cook et al. 1989). Because of the relative shortness of the series, we fit unique linear regressions to the raw data and used the residuals as the standardized increment. Detrending eliminated the effect of individual tree age and resulted in a series that represented the relative growth level for each year.

We initially examined the effect of defoliation on radial increment using site averages; detrended ring-widths were averaged for each species at each site. Averages from sites with fewer than 10 trees of a given species were excluded from the analysis. Defoliation data were available for only the last 5 years of each series (1972–1977). Overall, there were five species, four oaks (white oak, *Quercus alba* L.; scarlet oak, *Quercus coccinea* Muenchh.; chestnut oak, *Quercus prinus* L.; northern red oak, *Quercus rubra* L.) and pitch pine, for which there were adequate data, i.e. number of sites and number of individual series. For each species, we examined the effect of defoliation using stepwise linear regression. The independent variables in the regression were (i) average defoliation in the same year as the increment (referred to as defoliation) and (ii) defoliation in the previous year (lag defoliation). The response was average detrended radial increment. A *P* value of 0.05 was used as the criterion for including either defoliation or lag defoliation in the regression model.

We also examined defoliation effects using radial increment values from individual trees, i.e., all data from all sites were pooled. Prior to this analysis, we examined autocorrelation functions and found no consistent significant autocorrelation, justifying our treatment of sequential years as independent observations. We used stepwise linear regression to test the effect of defoliation on radial increment. The dependent variable was normalized, detrended increment for each tree in each year. Increment was normalized by dividing the detrended (residual) increment by the standard deviation of the detrended values. Normalization was performed to remove among-tree variation in increment variance. There are a variety of factors affecting variance in increment (e.g., canopy dominance, tree age, stand age), and they may obscure the effects of defoliation (Twery 1987). Independent variables used in the stepwise regressions were (i) individual tree defoliation in the same year as increment (defoliation), (ii) individual tree defoliation in the prior year (lag defoliation), (iii) average plot-level defoliation in the same year as defoliation (plot defoliation), and (iv) plot-level defoliation in the previous year (lag plot defoliation). Average defoliation of all trees in the plot was included as a term in these regressions because we expected that some species (espe-

cially nonhosts) may exhibit increased growth resulting from increased light and nutrients following defoliation of other trees in the same plot.

With the subset of data consisting of earlywood and latewood measurements, we calculated the proportion of earlywood and used it as the dependent variable in stepwise regression for all trees of a given species pooled across all sites. We used the same independent variables as described above. The proportion of earlywood was transformed, then detrended because of the influence of age on early- and late-wood width (Zhang et al. 1994).

Results

Defoliation was highly variable among areas (Table 1). There was an obvious outbreak in 1972 in coastal New Jersey and a moderate outbreak in western Massachusetts. In the other areas, defoliation levels rarely exceeded 20% during the course of the study. Defoliation of individual species was high in some cases despite only moderate site- and area-level defoliation. For example, for one site in western Massachusetts the average defoliation was 36% in 1972, but defoliation of red oak alone was 67% in that site.

Defoliation of oaks generally resulted in a decline in radial increment. This relationship is illustrated by the increment chronology for red oak in western Massachusetts (Fig. 1). A decline in increment associated with gypsy moth defoliation occurred in the period 1972–1974. An earlier decline in growth was evident during the years 1965–1967. While individual tree records of defoliation in this site were not available for that earlier decline period, aerial sketch maps of defoliation collected by the Massachusetts Department of Environmental Management indicated that an outbreak was present in this area during that time (C. Burnham, personal communication).

Stepwise linear regressions using site averages indicated that increment of host species was negatively affected by defoliation (Table 2). The parameter estimate indicates the direction of the relationship; thus for all oaks tested, except red oak, defoliation in the same year was negatively correlated with increment. Only the direction of the parameter

Table 2. Results of stepwise regression of increment on defoliation using area averages.

Host species	No. of sites	r^2	Variable	Parameter estimate	P
<i>Quercus alba</i>	25	0.47	Defoliation	-1.775	0.0004
<i>Quercus coccinea</i>	25	0.58	Defoliation	-2.263	0.0001
		0.76	Lag defoliation	-0.804	0.0369
<i>Quercus prinus</i>	26	0.88	Defoliation	-2.255	0.0001
<i>Quercus rubra</i>	30	0.27	Lag defoliation	-2.737	0.0050
<i>Pinus rigida</i>	20	0.72	Defoliation	-2.589	0.0001

Note: The sample size represents the number of sites that had at least 10 individuals per species and corresponding defoliation data. See text for explanation of variables. A P value of 0.05 was used as the criterion for retaining a variable in the regression.

Table 3. Results of stepwise regression of radial increment on defoliation using individual tree data.

Species	No. of trees	r^2	Variable	Parameter estimate	P
Hosts					
<i>Betula papyrifera</i>	24		None		
<i>Betula populifolia</i> Marsh.	28		None		
<i>Ostrya virginiana</i>	70		None		
<i>Populus grandidentata</i>	30		None		
<i>Populus tremuloides</i>	57	0.04	Lag defoliation	0.442	0.0081
<i>Quercus alba</i>	363	0.09	Defoliation	-0.579	0.0001
		0.10	Lag defoliation	-0.171	0.0001
<i>Quercus coccinea</i>	211	0.19	Defoliation	-0.709	0.0001
		0.22	Lag defoliation	-0.271	0.0001
<i>Quercus prinus</i>	249	0.26	Defoliation	-0.771	0.0001
		0.27	Lag defoliation	-0.169	0.0014
<i>Quercus rubra</i>	194	0.08	Defoliation	-0.633	0.0001
		0.06	Lag defoliation	-0.685	0.0001
<i>Quercus velutina</i>	83	0.14	Defoliation	-0.750	0.0001
		0.15	Lag defoliation	-0.292	0.0122
<i>Tilia americana</i> L.	25		None		
Nonhosts					
<i>Pinus rigida</i>	107	0.20	Plot defoliation	-0.014	0.0001
<i>Pinus strobus</i>	178	0.03	Lag plot defoliation	-0.011	0.0001
<i>Tsuga canadensis</i> (L.) Carr.	40		None		
<i>Acer rubrum</i> L.	224		None		
<i>Acer saccharum</i> Marsh.	58		None		
<i>Betula lenta</i>	24		None		
<i>Carya</i> spp.	40		None		
<i>Fagus grandifolia</i> Ehrh.	46		None		
<i>Fraxinus</i> spp.	24	0.03	Lag plot defoliation	0.016	0.0344
<i>Liriodendron tulipifera</i>	21	0.05	Lag plot defoliation	0.014	0.0474
<i>Nyssa sylvatica</i> Marsh.	20		None		
<i>Prunus serotina</i> Ehrh.	15		None		
<i>Sassafras albidum</i> (Nutt.) Nees	13		None		

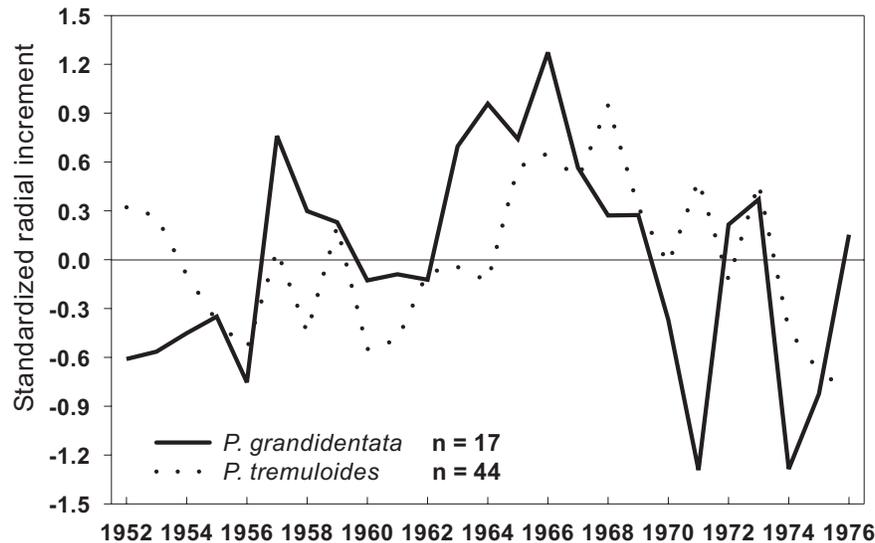
Note: The sample size represents the number of individuals per species used in the analysis. Each tree was used with four observations corresponding to defoliation data for the years 1972–1976. See text for explanation of variables. A P value of 0.05 was used as the criterion for retaining a variable in the regression. If “none” is listed in the variable column, no variables were found to be significant.

estimate is important, the magnitude of the parameter estimate is not relevant to the interpretation of the relationship. Increment of red oak and scarlet oak was negatively affected by defoliation in the previous year. The lack of a significant effect of defoliation in the current year in red oak may have resulted in part from colinearity with lag defoliation.

When analyzed at the site level, adequate numbers of

sample trees were available for analysis of defoliation effects on increment for four oak species and pitch pine (see Table 2). The use of individual tree records, however, in stepwise regressions allowed the inclusion of several additional host species and nonhosts in the analysis (Table 3). With individual tree records, the results for oaks were similar to the results obtained from area averages in that defoliation

Fig. 2. Average standardized increment and defoliation for *Populus grandidentata* and *Populus tremuloides* in western Massachusetts. Defoliation values for the years 1972–1976 for *P. grandidentata* were 25, 14, 5, 8, and 6%. For *P. tremuloides*, defoliation was 78, 19, 5, 5, and 4% for 1972–1976, respectively.



was significantly and negatively correlated with increment growth. Defoliation in the previous year was also negatively associated with increment for all five oak species (white, scarlet, red, chestnut, and black oak (*Quercus velutina* Lam.)), using individual tree records. Using individual tree records, the r^2 values were generally low. Although the parameter estimates may be significant, the independent variables we tested account for only a minimal variation in the relationship.

The relationship between individual tree defoliation and increment appeared weaker for other (nonoak) host species (Table 3). For aspen (Fig. 2), there is no clear relationship. Trembling aspen (*Populus tremuloides* Michx.) was defoliated more severely than bigtooth aspen (*Populus grandidentata* Michx.), yet the severity of the defoliation appeared to have had no noticeable effect on overall growth. Furthermore, the regression results indicated that the previous year's defoliation had a positive influence on radial increment of trembling aspen (Table 3). The extremely low increment evident in bigtooth aspen in 1971 was apparently unrelated to defoliation. Furthermore, we did not detect any relationship between increment and defoliation for several other host species such as paper birch, ironwood (*Ostrya virginiana* (Mill.) K. Koch), and basswood (Table 3).

Results for the range of nonhosts were highly variable. Pitch pine is an intermediate host (Montgomery et al. 1990; Liebhold et al. 1995), and late-instar gypsy moth larvae may cause extensive defoliation of this species during outbreaks. In general, however, intermediate species are less preferred than hosts such as oak. The effect of defoliation on pitch pine was strongly dependent on level of analysis. Site average data (Table 2) for pitch pine indicated a negative effect of defoliation (of pitch pine) on increment. Individual tree data, however, indicated that plot defoliation (i.e., defoliation of all species) negatively influenced increment of pitch pine (Table 3). Defoliation alone was not significant in the regression of individual tree data. Individual species defoliation and plot-level defoliation are probably highly correlated, and this may explain the latter effect.

The nonhosts, ash and tulip-tree, exhibited a significant positive effect of plot defoliation in the previous year on increment in individual tree data (Table 3). Increases in increment in tulip-tree occurred during an episode of defoliation of oaks from 1972–1974 and the chronologies also indicated an episode of increased growth during a probable outbreak from 1964–1966 (Fig. 3).

To further assess the influence of defoliation on radial increment, we examined the proportion of earlywood to latewood as a dependent variable using stepwise regression. We anticipated that defoliation effects on earlywood would be minimal since earlywood production is well underway by the time defoliation by gypsy moth occurs. Contrary to our expectations, there were significant positive effects of defoliation on the proportion of earlywood in all oak species in the year of defoliation and, for most oaks, in the year following defoliation (Table 4). Since total increment was reduced (Tables 2 and 3), a positive effect on earlywood proportion indicated a relatively severe negative effect on latewood. Latewood production would be directly influenced by both current and previous year's defoliation, corresponding to the results of the stepwise regression. Proportion of earlywood in chestnut oak was significantly related to defoliation in the current year only. There were no significant effects of defoliation on the proportion of earlywood in nonhosts.

Discussion

Moderate to severe gypsy moth outbreaks may be detected as declines in average oak increment (e.g. Fig. 1), indicating that historical increment data may be used to reconstruct chronologies of gypsy moth outbreaks in a manner similar to other defoliating insect species (e.g., Fritts and Swetnam 1989; Swetnam and Lynch 1993; Krause 1997). The lack of response or increased increment in nonhosts (Fig. 3) during periods of increment decline in hosts may be used as another indicator of a gypsy moth outbreak. For

Fig. 3. Average standardized increment for the nonhost, *Liriodendron tulipifera*, and the hosts, *Quercus alba*, *Q. rubra*, and *Q. velutina* from northwestern New Jersey.

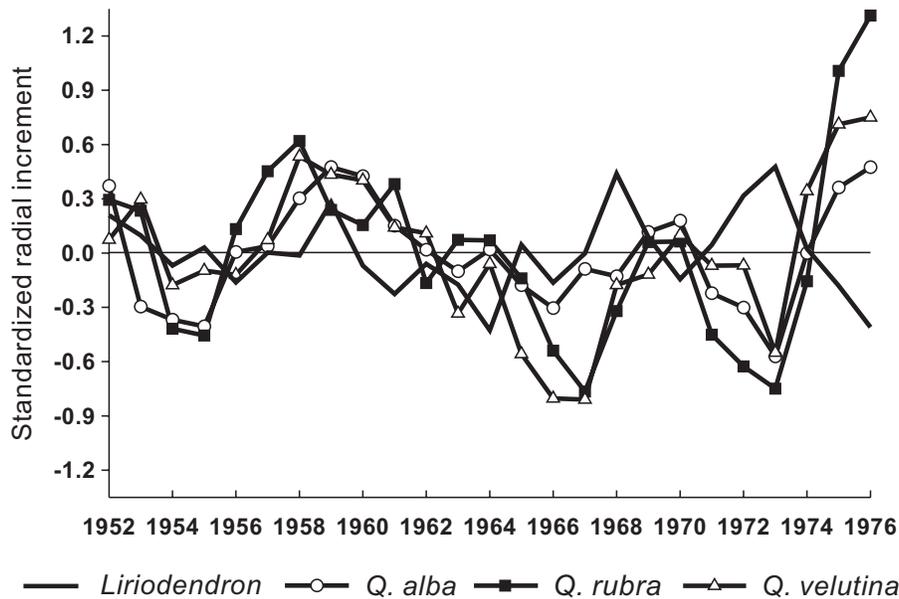


Table 4. Results of stepwise regression of earlywood proportion of total increment on defoliation using individual tree data.

Species	No. of trees	r^2	Variable	Parameter estimate	P
<i>Pinus rigida</i>	114		None		
<i>Pinus strobus</i>	57		None		
<i>Carya</i> spp.	127		None		
<i>Fraxinus</i> spp.	56		None		
<i>Quercus alba</i>	649	0.06	Defoliation	0.074	0.0001
		0.09	Lag defoliation	0.047	0.0001
<i>Quercus coccinea</i>	322	0.14	Defoliation	0.100	0.0001
		0.15	Lag defoliation	0.025	0.0005
<i>Quercus prinus</i>	412	0.17	Defoliation	0.118	0.0001
<i>Quercus rubra</i>	537	0.06	Defoliation	0.107	0.0001
		0.09	Lag defoliation	0.046	0.0023
<i>Quercus velutina</i>	94	0.16	Defoliation	0.102	0.0001
		0.22	Lag defoliation	0.056	0.0004

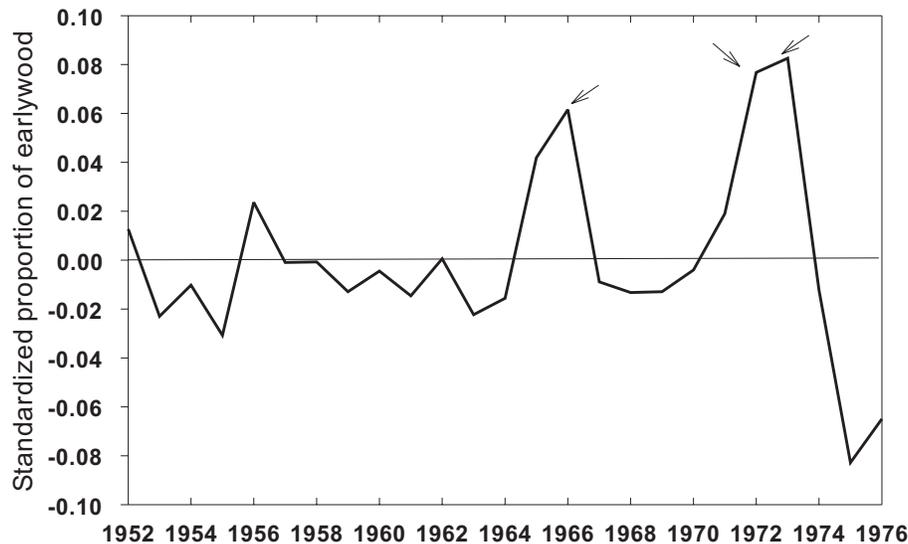
Note: See text for explanation of variables. A P value of 0.05 was used as the criterion for retaining a variable in the regression. If "none" is listed in the variable column, no variables were found to be significant.

example, ash and tulip-tree are considered immune species and are never defoliated by gypsy moth, even when insect populations are at outbreak densities. Therefore, increases in growth in these species during periods of gypsy moth defoliation represent plot-wide effects of defoliation. Defoliation of hosts in the same plot would result in increased light and nutrients, thus enhancing growth of nonhosts and explaining the positive relation between plot-level defoliation and increment in these species (Wickman 1980).

Our findings are in general agreement with previous studies describing how defoliation by gypsy moth and other insect species affect tree growth. Earlier research characterizing the influence of gypsy moth on tree growth indicated that increment loss was proportional to defoliation. Spe-

cifically, Minott and Guild (1925) found that, in years of 100% defoliation, oaks may lose 52% of radial growth relative to previous years. With 33% average defoliation over a 10-year period oaks lost one third the normal diameter growth. The analysis, however, consisted of nonstandardized chronologies, and defoliation effects were not separated from other influences to tree growth such as competition, tree age, or climate. Furthermore, Minott and Guild (1925) found that the effect of defoliation on increment appeared to be greatest in the same year as defoliation, but there may also be a decline in growth in the year following defoliation. Similarly, Baker (1941) demonstrated that throughout a 10-year period of repeated gypsy moth defoliation, reductions in growth were strongest in the year during defoliation; there

Fig. 4. Standardized proportion of earlywood to total increment in *Q. rubra* from western Massachusetts. Arrows indicate known defoliation years.



was a noticeable, although less pronounced, lag effect, i.e., reduced increment in the year following defoliation.

In this study it appears that oaks respond to defoliation more consistently than other highly preferred hosts. Relatively high defoliation levels of nearly 80% seem to have little influence on increment growth of aspen. In trembling aspen defoliated by forest tent caterpillar (*Malacosoma disstria* Hb.), Rose (1958) found that defoliation caused a premature cessation of radial growth and, consequently, negatively influenced total radial growth in the year of defoliation. No cessation of growth occurred from forest tent caterpillar defoliation, however, unless individual trees were 100% defoliated. Unlike gypsy moth, which defoliates aspen after foliage has been fully expanded, forest tent caterpillar feeds concurrently with the production of new foliage, relatively early in the growing season. Since gypsy moth defoliation doesn't interfere with the first flush of foliage from aspen, radial growth maybe unaffected early in the growing season. Refoliation by aspen then provides an opportunity for compensatory growth. The lack of response of defoliation on other hosts such as birch, basswood, and ironwood is difficult to explain but may also in part explained through the refoliation response. It is possible that the apparent lack of significance may be a function of inadequate sample size, or it may reflect minimal levels of defoliation on these hosts.

Compensatory increases in growth increment may be observed in some, but not all, nonhost species during outbreaks. Campbell and Garlo (1982) analyzed a subset of the IPS data to compare growth of oaks and pines; however, they did not test hypotheses statistically. They did report a sharp decline in increment of oaks during and directly after a gypsy moth outbreak. In contrast, growth of pines declined only slightly during the outbreak but increased greatly directly after the outbreak. Our results are not entirely consistent with Campbell and Garlo's conclusions. Site averages (Table 2) indicated that defoliation negatively influenced growth of pitch pine, but there was no lag effect, whereas Campbell and Garlo (1982) found that pine increased in growth after plot-wide defoliation of the more preferred oak

species. In our study, however, regressions using individual tree data (Table 3) indicated only a negative effect of plot defoliation in the previous year. We found no evidence of a positive effect of defoliation on pines as previously reported. Because we examined individual tree growth and individual tree defoliation in the stepwise regression, we feel that our analysis was more sensitive to effects of defoliation on pitch pine than the aforementioned work.

In oaks, earlywood consists of large vessels, which are an adaptation for conducting large amounts of available water early in the growing season. Latewood production, particularly the size and density of vessels, is indicative of available moisture (Woodcock 1989), and latewood induction is hastened and length of time of production is decreased by water deficits (Kozlowski et al. 1991). Water deficits modify both increment and earlywood-latewood production, and inasmuch as defoliation resembles water deficits by reducing leaf area, the effect would be similar. Earlywood production precedes defoliation by gypsy moth; thus, the effect of defoliation would be manifested in latewood production. Increases in the proportion of earlywood correspond with the defoliation periods and the loss in total increment. (Fig. 4, cf. Fig. 1). Krause (1995) found that latewood development was more sensitive than ring width to spruce budworm defoliation, and Weber (1995) concluded that a narrow latewood band is a significant indicator of defoliation by the larch budmoth. Jardon et al. (1994a) also confirmed that defoliation reduced latewood formation. Gross (1992) found that proportion of latewood decreased in the year of defoliation whereas total increment decreased the year following defoliation of jack pine (*Pinus banksiana* Lamb.) by jack pine budworm (*Choristoneura pinus pinus* Free). Findings in the previous studies strongly suggest that latewood production is reduced by defoliation, which may correspond with our finding of increased proportion of earlywood in the year following defoliation. There is a marked contrast, however, with our finding of a significant positive effect of defoliation on earlywood production in the same year. One explanation for this discrepancy is that the previous studies dealt with

coniferous tree species. Examining ring porous hardwoods, however, Zhang, et al. (1994) have shown that intertree variation and the influence of age may dampen environmental effects on early- and late-wood formation in sessile oak (*Quercus petraea* ((Matt) Liebl.)) and English oak (*Quercus robur* L.).

In this study we have shown that gypsy moth defoliation negatively influences radial increment in hosts and that plot-level defoliation positively influences the increment in immune nonhosts such as ash and tulip-tree. No change in increment occurred in most intermediate hosts (such as maples, hickories, beech) during gypsy moth outbreaks and through a range of defoliation levels. Increment of the intermediate hosts pitch pine and white pine (*Pinus strobus* L.), however, was negatively affected by defoliation, but all other preferred and intermediate hosts we analyzed were unaffected by plot-level defoliation. Temporally, reduced increment in oak occurred during the year of defoliation, but oaks also exhibit decreased growth the year following defoliation.

Overstory mortality caused by gypsy moth defoliation may eventually result in stands that are less susceptible to gypsy moth because host species are replaced by species resistant to gypsy moth (Kegg 1973; Campbell and Sloan 1977; Gansner et al. 1983; Fosbroke and Hicks 1989; Muzika and Twery 1995). Although limited long-term information is available to substantiate such claims, the findings in our study may help support them. Plot-level defoliation resulted in increased increment in the immune species that we studied, ash and tulip-tree, thus representing the successful exploitation of resources by the species that are not defoliated. Patterns of differential growth response correspond to loss of foliage of hosts and eventual mortality of hosts if outbreaks of gypsy moth are prolonged. Increased growth of nonhosts represents a competitive advantage and a potential for a shift in dominance toward resistant and immune species.

Acknowledgements

The authors gratefully acknowledge the efforts of numerous scientists and technicians who were responsible for the collection of these data and the creation of the Intensive Plot System. M. McManus, M. Montgomery, and M. Twery provided advice and information about the initial study. We thank Richard Guyette, Tom Schuler, and an anonymous reviewer for helpful suggestions to improve this manuscript.

References

- Baker, W.L. 1941. Effect of gypsy moth defoliation on certain forest trees. *J. For.* **39**: 1017–1022.
- Blais, J.R. 1965. Spruce budworm outbreaks in the past three centuries in the Laurentides Park, Quebec. *For. Sci.* **11**: 130–138.
- Blais, J.R. 1983. Trends in the frequency, extent and severity of spruce budworm outbreaks in eastern Canada. *Can. J. For. Res.* **13**: 539–547.
- Brubaker, L.B. 1978. Effects of defoliation by Douglas-fir tussock moth on ring sequences of Douglas-fir and grand fir. *Tree Ring Bull.* **38**: 49–60.
- Campbell, R.W., and Garlo, A.S. 1982. Gypsy moth in New Jersey pine-oak. *J. For.* **80**: 89–90.
- Campbell, R.W., and Sloan, R.J. 1977. Forest stand responses to defoliation by the gypsy moth. *For. Sci. Monogr.* No. 19.
- Cook, E., Briffa, K., Shiyatov, S., and Mazepa, V. 1989. Tree-ring standardization and growth-trend estimation. *In* *Methods of dendrochronology: applications in the environmental sciences.* Edited by E.R. Cook and L.A. Kairiukstis. Kluwer Academic Publishers, Dordrecht, the Netherlands. pp. 104–122.
- Fosbroke, D.A., and Hicks, R.R. 1989. Tree mortality following gypsy moth defoliation in southwestern Pennsylvania. *In* *Proceedings of the 7th Central Hardwood Forest Conference, Carbondale, Ill.* Edited by G. Rink and C.A. Budelsky. USDA For. Serv. Gen. Tech. Rep. NC-132. pp. 74–80.
- Fritts, H.C., and Swetnam, T.W. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. *Adv. Ecol. Res.* No. 19. pp. 111–188.
- Gross, H.L. 1992. Impact analysis for a jack pine budworm infestation in Ontario. *Can. J. For. Res.* **22**: 818–831.
- Gansner, D.A., Herrick, O.W., DeBald, P.S., and Acciavatti, R.E. 1983. Changes in forest condition associated with gypsy moth. *J. For.* **81**: 155–157.
- Jardon, Y., Filion, L., and Cloutier, C. 1994a. Tree-ring evidence for endemicity of the larch sawfly in North America. *Can. J. For. Res.* **24**: 724–747.
- Jardon, Y., Filion, L., and Cloutier, C. 1994b. Long-term impact of insect defoliation on growth and mortality of eastern larch in boreal Québec. *Écoscience*, **1**: 231–238.
- Kegg, J.D. 1973. Oak mortality caused by repeated gypsy moth defoliations in New Jersey. *J. Econ. Entomol.* **66**: 639–641.
- Kozlowski, T.T., Kramer, P.J., and Pallardy, S.G. 1991. The physiological ecology of woody plants. Academic Press, Inc., San Diego.
- Krause, C. 1995. Impact of spruce budworm defoliation on the number of latewood tracheids in balsam fir and black spruce. *Can. J. For. Res.* **25**: 2029–2034.
- Krause, C. 1997. The use of dendrochronological material from buildings to get information about past spruce budworm outbreaks. *Can. J. For. Res.* **27**: 69–75.
- Liebhold, A.M., Gottschalk, K.W., Muzika, R.M., Montgomery, M.E., Young, R., O'Day, K., and Kelley, B. 1995. Suitability of North American tree species to the gypsy moth: a summary of field and laboratory tests. USDA For. Serv. Gen. Tech. Rep. NE-211.
- Mason, R.R., Wickman, B.E., and Paul, H.G. 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.
- Minott, C.W., and Guild, I.T. 1925. Some results of the defoliation of trees. *J. Econ. Entomol.* **18**: 345–348.
- Montgomery, M.E., McManus, M.L., and Berisford, C.W. 1990. The gypsy moth in pitch pine-oak mixtures: predictions for the south based on experiences in the north. *In* *Pine-Hardwood Mixtures: A Symposium on Management and Ecology of the Type.* USDA For. Serv. Gen. Tech. Rep. SE-58. pp. 43–49.
- Muzika, R.M., and Twery, M.J. 1995. Woody species regeneration following defoliation and thinning in hardwood stands of north-central West Virginia. *In* *Proceedings of the 10th Central Hardwood Forest Conference, Morgantown, W.V.* Edited by K. Gottschalk. USDA For. Serv. Gen. Tech. Rep. NE-197. pp. 326–340.
- Reardon, R.C. 1976. Parasite incidence and ecological relationships in field populations in gypsy moth larvae and pupae. *Environ. Entomol.* **5**: 981–987.
- Rose, A.H. 1958. The effect of defoliation on foliage production and radial growth of quaking aspen. *For. Sci.* **4**: 335–342.
- Swetnam, T.W., and Lynch, A.M. 1989. A tree-ring reconstruction of western spruce budworm history in the southern Rocky Mountains. *For. Sci.* **35**: 962–986.

- Swetnam, T.W., and Lynch, A.M. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecol. Monogr.* **63**: 399–424.
- Thomson, A.J., and VanSickle, G.A. 1980. Estimation of tree growth losses caused by western spruce budworm defoliation. *Can. J. For. Res.* **10**: 176–182.
- Twery, M.J. 1987. Changes in vertical distribution of xylem production in hardwoods defoliated by gypsy moth. Ph.D. dissertation, Yale University, New Haven, Conn.
- Weber, U.M., and Schweingruber, F.H. 1995. A dendroecological reconstruction of western spruce budworm outbreaks (*Choristoneura occidentalis*) in the front range, Colorado, from 1720 to 1986. *Trees*, **9**: 204–213.
- Weber, U.M. 1995. Ecological pattern of larch budmoth (*Zeiraphera diniana*) outbreaks in the central Swiss Alps. *Dendrochronologia*, **13**: 11–31.
- Wickman, B.E. 1980. Increased growth of white fir after a Douglas-fir tussock moth outbreak. *J. For.* **78**: 31–33.
- Woodcock, D.W. 1989. Climate sensitivity of wood-anatomical features in a ring-porous oak (*Quercus macrocarpa*). *Can. J. For. Res.* **19**: 639–644.
- Zhang, S.Y., Nepveu, G., and Eyono Owoundi, R. 1994. Intra-tree and intertree variation in selected wood quality characteristics of European oak (*Quercus petraea* and *Quercus robur*). *Can. J. For. Res.* **24**: 1818–1823.