Effects of Gypsy Moth Defoliation in Oak-Pine Forests in the Northeastern United States

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ABSTRACT Dendrochronology data from two oak-pine (*Quercus-Pinus*) forests in the northeastern United States (New Jersey and Massachusetts) were examined to understand the influence of defoliation on radial ring width of highly preferred trees (*Quercus*) and slightly less preferred trees (*Pinus*). Over a 5-year period, defoliation from gypsy moth (*Lymantria dispar* L.) ranged from 2.4% to 86.4% and mortality was nearly 50% of *Q. alba* stems in Massachusetts. The effect of individual tree defoliation, although generally negative, differed slightly among all the oak species. Stand-level defoliation negatively influenced growth of oaks and pines on both sites. There was no compensatory response apparent in the radial growth of pitch pine. 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.

AS A NON-NATIVE, polyphagous species in North America, the gypsy moth (*Lymantria dispar* L.) can negatively influence many forest types. Its preferred host are oaks (*Quercus* spp.), the dominant overstory tree species in the eastern United States. Pines (*Pinus* spp.) generally are considered less likely to be defoliated by gypsy moth than oaks (Liebhold et al. 1995), although defoliation of pines has been widely observed and documented (Brown et al. 1988, Gottschalk and Twery 1989, Montgomery et al. 1990). When gypsy moth larval densities are high and defoliation is widespread, shifting to a less preferred host is common. Oak-pine forests, therefore, may be classified as susceptible to gypsy moth. Oak-pine forests are also typically found on the most xeric portion of the landscape capable of supporting forests.

Site factors may exacerbate defoliation-related stress and may account for increased mortality in forests with high defoliation. Although some research findings support this assumption, Davidson et al. (1999) suggest that the evidence is contradictory, and that at least an equal number of studies have demonstrated that trees growing on poor sites have less mortality than those on good sites. Gansner (1987) suggested that poor quality trees were physiologically adapted to stress conditions and therefore could endure defoliation.

Dendroecological techniques can be useful in assessing the effect of insect outbreaks, but have been used primarily to reconstruct historic patterns of outbreaks (Fritts and Swetnam 1989). In western North America, western spruce budworm (*Choristoneura occidentalis* Freeman) outbreak histories have been developed through many studies (Thomson and VanSickle 1980; Swetnam and Lynch 1989, 1993; Weber and Schweingruber 1995). Extensive chronologies have been developed to determine the long-term impact of defoliation, such as radial growth losses of trees and forests (Brubaker 1978, Wickman 1980, Mason et al. 1997).

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Few studies have used dendrochronology to examine the effects of hardwood defoliators in the eastern United States. With the exception of research by Baker (1941), Campbell and Garlo (1982), and Muzika and Liebhold (1999), there is a noticeable absence of dendrochronological research examining the effects of defoliation on deciduous trees. In this paper, we use data from a study conducted in the 1970s to examine the effect of gypsy moth defoliation on both pines and oaks in two areas of the northeastern United States.

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). Data were collected in six areas throughout the northeastern United States. For this study, however, we focused on the two areas that were dominated by oak-pine forests. Area 1 was located on Cape Cod, Massachusetts, and Area 2 was located along the Atlantic coast in New Jersey. These areas contained coastal stands that were dominated by white oak (*Quercus alba*), scarlet oak (*Q. coccinea*), and pitch pine (*Pinus rigida*). Each area consisted 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 measured as a percentage loss of canopy and was estimated following gypsy moth feeding in the summer (Table 1).

Table 1. Defoliation estimates (%) of overstory trees for the two study areas for each of 5 years. Defoliation estimates represent averages across the sites at each area.

Year	Massachusetts	New Jersey
1972	79.7	67.3
1973	56.3	86.4
1974	10.6	21.9
1975	4.7	15.0
1976	2.4	3.4

In the winter of 1976-1977, an increment core was taken from each living tree on every plot. Ring widths were measured at Virginia Polytechnic Institute and State University soon after the cores 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. Total radial increment was measured on all trees and earlywood and latewood were differentiated.

All cores consisted of at least 25 annual growth rings; the most reliable chronologies existed for the years from 1952 to 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 growth trend. Because of the relative shortness of the series, we fit unique linear regressions for each tree 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.

Detrended ring widths were used for analysis of defoliation effects; we used averages for each species at each site. Defoliation data were available for only the last five years of each series (1972 to 1977). Overall, there were five species used in the analysis (white oak, scarlet oak, chestnut oak (*Q. montana*), northern red oak (*Q. rubra*), and pitch pine). Stepwise linear regression was used 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 in order to remove among-tree variation in increment variance. Independent variables used in the stepwise regressions were: (1) individual tree defoliation in the same year as increment (defoliation), (2) individual tree defoliation in the prior year (lag defoliation, or defoliation (t-1)), (3) average stand-level defoliation in the same year as increment (stand defoliation), and (4) stand-level defoliation in the previous year (lag stand defoliation, or stand defoliation (t-1)). A *P* value of 0.05 was used as the criterion for including either defoliation or lag defoliation in the regression model.

Using 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 latewood width (Zhang et al. 1994).

Results and Discussion

Previous research indicated that both study areas were dominated by oak with 10 to 15% of their basal area in pitch pine (Montgomery et al. 1990). Defoliation estimates were comparable between the two areas and reflected gypsy moth populations in outbreak years (1972 and 1973) with a dramatic decline in populations within a few years following extensive defoliation. The temporal sequence in defoliation suggests that the outbreak occurred in Massachusetts initially and a year later in New Jersey. Among all six areas in the original study, these two oak-pine forests incurred the greatest amount of defoliation.

Mortality within each area was determined as a percentage of dead stems by species. Mortality of pine was comparable at both areas. In Massachusetts, nearly half of the white oak stems died over the 5-year period, but only 9% died in New Jersey (Table 2). As a group, the red oaks (*Q. velutina* and *Q. coccinea*) had greater mortality than white oaks in New Jersey. Overall, mortality was greater in Massachusetts than in New Jersey, despite higher levels of defoliation in New Jersey.

Stepwise regression results indicated the specific influence of each of the identified variables on ring width of each species (Table 3). Predictably, individual-tree defoliation and stand-level defoliation in a given year negatively influenced growth of pitch pine in Massachusetts and New Jersey. While that negative effect persisted in Massachusetts, previous year's defoliation did not influence pine growth in New Jersey. Similarly, stand-level defoliation in the previous year was inversely related to growth in Massachusetts but not New Jersey. As a less preferred host, pitch pine may be expected to benefit from

Table 2. Cumulative percent mortality from *L. dispar* defoliation for overstory trees over a 5-year period (1973 to 1978) at Cap Cod, Massachusetts, USA, and New Jersey, USA. "NA" indicates that no individuals of that species were present at the study area.

Species	Massachusetts	New Jersey
Pinus rigida	16.1	15.6
Quercus alba	46.3	8.7
Quercus rubra	20.4	NA
Quercus velutina	29.5	37.8
Quercus montana	NA	14.3
Quercus coccinea	NA	23.4

Table 3. Results of stepwise regression of radial increment on defoliation. Each tree had four observations corresponding to defoliation data from 1972 to 1976. See text (page 119) for an explanation of the variables. This table lists parameter estimates from the stepwise regression that indicate the direction of the relationship. A *P* value of 0.05 was used as the criterion for retaining a variable in the regression.

Species	Variables	Massachusetts	New Jersey
Pinus rigida	Defoliation	-2.201	-1.359
	Defoliation (t-1)	-0.767	*ns*
	Stand Defoliation	-1.323	-1.138
	Stand Defoliation (t-1)	-0.381	*ns*
Quercus alba	Defoliation	0.203	-0.548
	Defoliation (t-1)	-0.328	*ns*
	Stand Defoliation	0.449	-0.666
	Stand Defoliation (t-1)	-0.538	*ns*
Quercus coccinea	Defoliation	*ns*	-0.588
	Defoliation (t-1)	-1.138	-0.175
	Stand Defoliation	*ns*	-0.710
	Stand Defoliation (t-1)	-1.564	-0.216
Quercus montana	Defoliation	-	-0.793
	Defoliation (t-1)	-	*ns*
	Stand Defoliation	-	-1.045
	Stand Defoliation (t-1)	-	*ns*
Quercus rubra	Defoliation	0.227	-
	Defoliation (t-1)	-0.615	-
	Stand Defoliation	*ns*	-
	Stand Defoliation (t-1)	-0.840	-
Quercus velutina	Defoliation	*ns*	-0.417
	Defoliation (t-1)	-0.479	*ns*
	Stand Defoliation	*ns*	-0.668
	Stand Defoliation (t-1)	-0.785	*ns*

defoliation of oak species; therefore, stand-level defoliation could result in a positive influence on pitch pine growth, as has been demonstrated with non-host species (Muzika and Liebhold 1999). In the present study, increased growth in less preferred species (pitch pine) was not observed, but this most likely resulted from the high intensity of defoliation that included less preferred species themselves and depressed their growth.

Oak species were predictably, but variously, influenced by defoliation. Only scarlet oak demonstrated a consistent and negative effect of defoliation, but only in New Jersey. Defoliation in the year of growth and the previous year, both at the individual-tree and stand level, affected scarlet oak growth increment in New Jersey. The fact that defoliation positively influenced white oak increment in Massachusetts may be explained by the high mortality rate of that species. With nearly 50% white oak mortality, the individuals that did not die also did not reduce increment, likely reflecting a different cohort, i.e. the survivors may have been considerably younger than those that died. Reductions in radial growth are uncommon in younger trees. Furthermore, stand-level defoliation positively affected white oak growth in Massachusetts, suggesting enhanced or compensatory growth of the remaining cohort. In New Jersey, where white oak mortality was lower (Table 2), individual tree defoliation and stand defoliation both negatively influenced radial growth.

Most other oak species were negatively affected by defoliation in either study area. Unexpected findings include a positive influence of current-year, individual-tree defoliation on red oak and white oak growth. The previous year's individual-tree defoliation and previous year's defoliation at the stand level both negatively affected red oak increment, however. It is possible that some mortality occurred in red oaks in the first year of defoliation, but survivors responded with increased growth. In subsequent years, however, growth was negatively influenced by defoliation from the year previous. The delayed, but negative, response in growth increment the year following defoliation was also evident in scarlet and black oaks in Massachusetts.

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 for the oak species only. 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 often reduced in these trees, 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. The proportion of earlywood in chestnut oak was significantly related to defoliation in the current year only.

Our findings are in general agreement with previous studies describing how defoliation by gypsy moth and other insect species affects tree growth and production of latewood. Earlier research characterizing the influence of gypsy moth on tree growth indicated that increment loss was proportional to defoliation. There is variation in the timing of the significant relationships, however. Minott and Guild (1925) found that the effect of defoliation on increment appeared to be greatest in the same year as defoliation, but noted that 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 was a noticeable, although less pronounced, lag effect, i.e. reduced increment in the year following defoliation.

Table 4. Results of stepwise regression of earlywood proportion of total increment on defoliation. This table includes trees from both study areas.

Species	N	Variable	Parameter Estimate	P
Quercus alba	1,905	Defoliation	0.074	0.0001
		Defoliation (t-1)	0.047	0.0001
Quercus coccinea	955	Defoliation	0.100	0.0001
		Defoliation (t-1)	0.025	0.0005
Quercus montana	1,225	Defoliation	0.118	0.0001
Quercus rubra	1,495	Defoliation	0.107	0.0001
		Defoliation (t-1)	0.046	0.0023
Quercus velutina	360	Defoliation	0.102	0.0001
		Defoliation (t-1)	0.056	0.0004

In this study, we have shown that gypsy moth defoliation negatively influences radial increment in hosts irrespective of the quality of that host. Overall, the more highly preferred oaks were negatively influenced, but the strength of the relationship differed among species. The intermediate host, pitch pine, was negatively affected by defoliation, but the lag response varied between the two areas. The consistent relationships between the two sites indicated that generalizations about the susceptibility of oak-pine forests to gypsy moth can be established and predictions about anticipated losses in radial growth or tree mortality can be made to benefit forest management efforts.

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