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Gypsy Moth Defoliation of Oak Trees and a Positive Response of Red Maple and Black Cherry: An Example of Indirect Interaction

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ABSTRACT.—We calculated relative growth rates of all species over 10 cm circumference at breast height from 1997–1999, 1999–2001 and 2001–2003 in a 70 by 100 m plot in an oak forest in southeastern Michigan. Red maple and black cherry represented most of the understory species while white and black oaks dominated the canopy. During the summer of 1999, outbreak levels of gypsy moths preferentially defoliated oaks on the plot, often resulting in 100% defoliation. The relative growth rates (RGR) of red maple and black cherry were significantly higher during the time period where gypsy moths were at outbreak levels. Oaks had lower RGR during the gypsy moth attack than in the subsequent time period. Consequently, the preference gypsy moths exhibited towards oak species indirectly resulted in a higher growth rate for understory tree species, possibly due to increased light availability and the decreased competitive capacity of the defoliated oaks. This indirect effect could accelerate the succession at which oak dominated communities become red maple forests.

INTRODUCTION

The structure of ecological communities is a complex web of interactions that includes classic notions of competition, predation and mutualism. Recently it has been acknowledged that indirect effects in these webs could be strong (Werner, 1991; Werner and Anholt, 1996) and, even if only weak, could have major consequences on overall community structure (McCann *et al.*, 1998). For example, if species A has a strong competitive effect against species B, but a predator species prefers species A, it is said that the predator has an indirect positive effect on species B. Recognized by Darwin (Vandermeer *et al.*, 1985), these indirect effects felt through the web of interactions in a community can have major consequences on the overall community behavior. Here we report on the effect of an introduced defoliator on the competitive interactions between tree species.

The abundance and size of red maples (*Acer rubrum* L.) in the forests of eastern North America dramatically increased during the 20th Century. The expanded distribution of red maples includes site conditions with varying levels of light, moisture and nutrients (Lorimer, 1984; Palik and Pregitzer, 1992; Abrams, 1998) and the species is known to prosper as both a pioneer and late successional species. However, physiological responses to environmental conditions are not sufficient to account for the increased red maple abundance (Abrams, 1998).

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Extant forest composition must reflect physical site characteristics and past disturbance. Tracing the development of eastern North American forests from pre-European settlement to current conditions may help explain the transition in species dominance (Lorimer, 1984; Abrams and Nowacki, 1992; Palik and Pregitzer, 1992; Abrams, 1998). Prior to 1900, red maple and black cherry (*Prunus serotina*) populations were apparently much lower, held in check by the periodic burnings by Native Americans, lightning strikes and logging (Abrams and Nowacki, 1992; Abrams, 1998). The dominance of oaks (*Quercus* spp.) in many eastern North American forests is now thought to be a consequence of these anthropogenic forces. During the 20th Century, fire exclusion allowed fire-sensitive red maples to thrive in forests once dominated by oaks (Lorimer, 1984; Palik and Pregitzer, 1992; Abrams, 1998). These observations suggest that red maple is a superior competitor to oaks, leading to the hypothesis that most oak dominated forests will be taken over by red maple forests if fire is excluded.

The periodic attacks of gypsy moth (*Lymantria dispar* L.) have become notorious. The species has been a forest "pest" since its introduction in the late nineteenth century. In the last 50 y, gypsy moths have expanded their range to include Michigan. It has been proposed that the differential feeding impacts of gypsy moth defoliation may also have contributed to the decline in oak dominance in eastern forests of North America (Fajvan and Wood, 1996; Abrams, 1998). Oaks are typically more susceptible to gypsy moth infestation than red maples, presumably because of the alkaloid chemicals in red maple foliage (Abrams, 1998; Davidson *et al.*, 1999). The year 1999 marked a devastating outbreak of gypsy moths in the oak forests of southeastern Michigan (Vandermeer *et al.*, 2001).

Given that red maples are displacing oaks through competition and that gypsy moths differentially attack oaks, the effect of gypsy moths on red maple may represent a case of positive indirect interaction. Furthermore, this indirect interaction could accelerate succession. This study examined an oak/red maple forest during and after a year of extremely high gypsy moth abundance. We tested the hypothesis that red maple responds to the competitive release resulting from the negative effect of gypsy moths on oak trees.

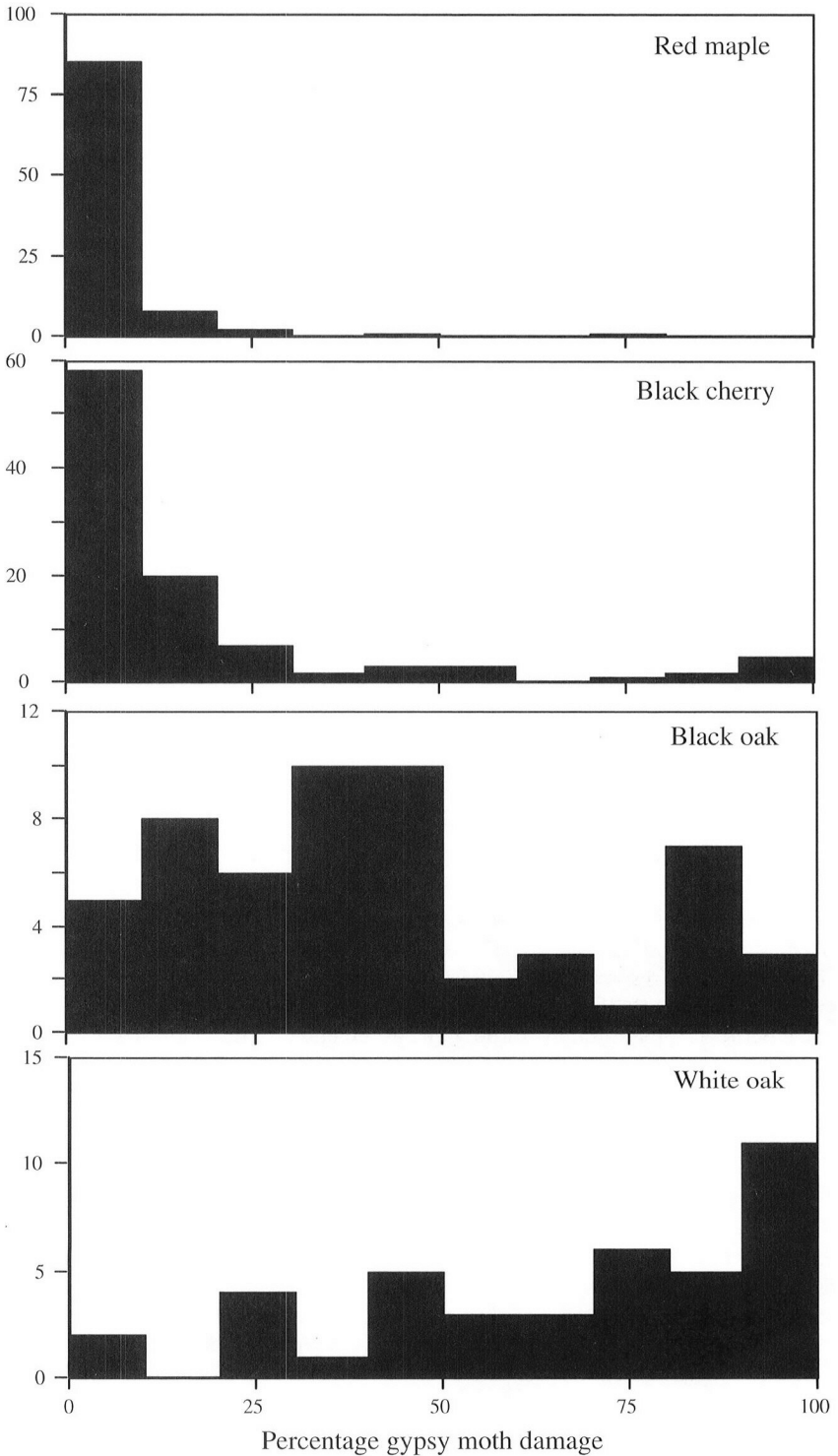
METHODS

The study was conducted on the University of Michigan's E.S. George Reserve, Livingston County, Michigan. The site is dominated by oak-hickory forest, most of which was identifiable in aerial photographs as closed canopy forest as early as 1940. The oaks in the study site are white oaks (*Quercus alba*) and hybrids between black (*Q. velutina*) and red (*Q. rubrum*) oaks (Wagner, pers. comm.). Here the hybrid is lumped into one category (referred to as black oaks). A permanent plot of 100 by 70 m was established in an old growth forest within the reserve in the fall of 1997. Every tree within the plot with a circumference at breast height (CBH) over 10 cm was permanently marked with a numbered tag. At every census those trees that reached the 10 cm CBH critical value were added as new recruits and given a new tag. This number and CBH were recorded every 2 y along with the species, tree status (alive or dead) and plot coordinates. In the early fall of 1999, percent defoliation of each tree was recorded by visual estimates after an intense gypsy moth outbreak that summer.

Censuses were completed in the summers of 1997, 1999, 2001 and 2003. For the later three censuses we calculated relative growth rates (RGR) as the difference in CBH between

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FIG. 1.—Number of individuals on the y-axis for the respective species grouped by percent defoliation measured after a gypsy moth outbreak in 1999. Individuals with no visible defoliation appear in the first column (0–10%)



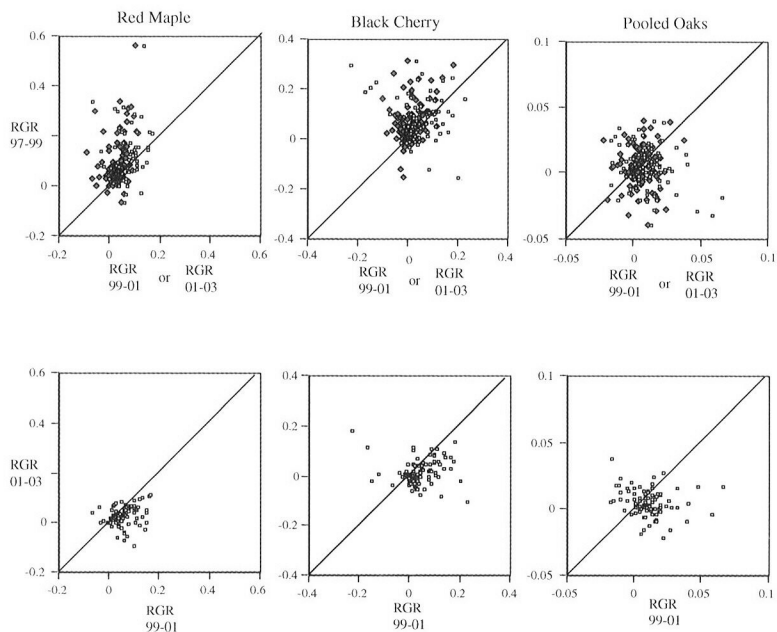


FIG. 2.—Relative growth rates (RGRs) of red maple (left column), black cherry (middle column) and black and white oaks pooled (right column). The top row compares RGRs of 1997–1999 on the y-axis (a period affected by a gypsy moth outbreak) with RGRs of non-gypsy moth periods on the x-axis. RGRs of 1999–2001 are represented by squares and RGRs of 2001–2003 by diamonds. Diagonal lines indicate equivalent RGR values. A cluster of data points above the diagonal represents increased relative growth rates during the gypsy moth outbreak period, and vice versa. The bottom row graphs RGR values from 2001–2003 on the y-axis and 1999–2001 on the x-axis. Both time periods are non-gypsy moth outbreak periods

successive samplings (2 year intervals) as a fraction of the CBH at the beginning of the interval. It is worth noting that negative RGR values could be a result of either the trees actually shrinking in response to drought or human error. Because of debate about the proper calculation of RGR (*e.g.*, Sheil *et al.*, 1995), we also calculated the RGR as the difference between the natural log of the CBH at the end and the natural log of the CBH at the beginning of the interval. There was virtually no difference in the two methods, so we use the more intuitive relative difference between the two intervals (*i.e.*, the difference divided by the value at the beginning of the time interval), with an arcsine transformation for hypothesis testing.

RESULTS

Oaks had a higher percentage of gypsy moth damage than black cherries (*Prunus serotina*) and red maples (Fig. 1) during the year of the gypsy moth outbreak. The few very large damage estimates for black cherry (Fig. 1), we suspect, are probably the result of tent caterpillar damage, incorrectly identified as gypsy moth damage in the field. However, even including these data points, the difference between the oaks and the red maples and black cherries is clear.

TABLE 1.—Mean relative growth rates for all species, and for black and white oaks pooled. Means are based on raw RGR figures but significance is calculated based on paired *t*-tests with arcsine-transformed raw RGRs. For *P*-values <0.05, significance value within row is noted with different letters

Species	RGR 97–99	RGR 99–01	RGR 01–03	df
RED MAPLE	0.103 a	0.049 b	0.027 c	98
BLACK CHERRY	0.097 a	0.033 b	0.015 c	103
BLACK OAK	0.005 a	0.009 a	0.005 a	41
WHITE OAK	0.002 a	0.01 b	0.006 a	57
OAKS (POOLED)	0.003 a	0.01 b	0.005 a	98

Graphing the RGRs during the gypsy moth outbreak (1997–1999) vs. the RGR during non-gypsy moth years (1999–2001 and 2001–2003) demonstrates the quantitative difference between the oaks and the other two species (Fig. 2). The black oaks had reduced RGR during the gypsy moth years, but it was not significant (Table 1). The white oaks had higher RGR values in 1999–2001, but the difference between the second non-gypsy moth time period (2001–2003) and the RGR values during the gypsy moth period was not significant. Because of their low densities, we also pooled the black and white oaks. The pooled oaks had a reduction of RGR during the time the gypsy moths were attacking when compared to other years. However, that difference was only statistically significant for 1999–2001. The relative growth rates for both red maples and black cherries were significantly higher for the gypsy moth period (1997–1999) than for either of the two non-gypsy moth periods (Fig. 2, Table 1).

Taking the average CBH of the oaks in 2003 as an estimate of the final size expected of all species, we can make an approximate projection of the number of years it will take for red maple to dominate the forest, based on the calculated relative growth rates, under a variety of assumptions regarding gypsy moth attack. Without gypsy moth attack (averaging red maple RGRs of 1999–2001 and 2001–2003), the average CBH of red maple will reach the average size of current oaks in 72 y. If a gypsy moth outbreak were to occur every year (assuming, unrealistically, that RGRs would nevertheless remain constant over the years), the time to reach average oak size would be 28 y. With outbreaks every 5 y (a reasonable expectation) the figure is 52 y and with outbreaks every other year, 39 y.

DISCUSSION

The evidence presented here indicates that there is a significant indirect effect on both red maple and black cherry of gypsy moth larval attack on oak trees. The mechanism would seem to be the defoliation of the canopy trees (almost all of which are oaks) opening up the canopy and thus releasing the understory from shade competition of the oaks. Consequently, the red maples and black cherries that dominate the understory receive substantial amounts of light and respond with a spurt of growth. This result fully supports the disturbance mediated accelerated succession model for red maple proposed by Abrams and Nowacki (1992). These undefoliated trees could also benefit from the nutrient input of gypsy moth frass. Since the growth rate response of both red maple and black cherry with gypsy moth attack is almost double the rate without such attack, we conclude that the facilitative effect of gypsy moth on these two successional species could be substantial and that the expected takeover of oak forests by other species, such as red maple, will be accelerated with gypsy moth outbreaks. This effect could be enhanced by the weakening of the overstory oak trees by those same gypsy moth larvae.

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