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Competitive balance among tree species altered by forest tent caterpillar defoliation

Danaë M.A. Rozendaal *, Richard K. Kobe

Michigan State University, Department of Forestry, Natural Resources Building, 480 Wilson Road, Room 126, East Lansing, MI 48824-1222, USA

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ABSTRACT

In northern hardwood forests with a closed canopy, tree growth is largely driven by tree size and competition with neighboring trees. Canopy defoliation during insect outbreaks temporarily increases light availability and may decrease light competition among neighboring trees. Defoliation typically reduces tree growth, but canopy defoliation could also stimulate growth of trees that maintain some leaf area. We compared the growth responses of mature trees of non-host species *Acer rubrum*, and the three host species *Acer saccharum*, *Quercus rubra* and *Tilia americana*, to defoliation by forest tent caterpillar (*Malacosoma disstria*, Lasiocampidae), a native forest insect with a ∼10-year outbreak periodicity, in a northern hardwood forest in northern lower Michigan.

We compared tree growth during the forest tent caterpillar outbreak in 2009, and in the following year, to the average growth before the outbreak in relation to the defoliation level of both the focal tree and its neighbors. Growth responses were related to focal tree defoliation, but we found little direct evidence for effects of neighborhood defoliation; relatively uniform defoliation within sites may have obscured detection of neighborhood effects. Growth of *T. americana* increased substantially in the year following defoliation, despite the growth reduction during the outbreak in 2009. *T. americana* rapidly produced new leaves after peak defoliation in 2009, which could explain increased growth in 2010. *A. rubrum*, which was not defoliated, decreased growth slightly during the outbreak. In 2010, however, one year after peak defoliation, *A. rubrum* growth was similar to pre-outbreak growth. The two other defoliated species, *A. saccharum* and *Q. rubra,* decreased growth in both 2009 and 2010. These strongly species-specific growth responses to canopy defoliation might result in changes in tree species' interactions and shifts in species advantages over time.

1. Introduction

In northern hardwood forests with a closed canopy, individual tree growth is largely driven by tree size and by competition for light with neighboring trees (e.g., Baribault and Kobe, 2011). Canopy defoliation during insect outbreaks, however, may temporarily reduce light competition among neighboring trees and stimulate tree growth, especially for trees that are lightly or not defoliated. Insect outbreaks that occur periodically, for example of forest tent caterpillar (*Malacosoma disstria*, Lasiocampidae), may have a large influence on individual tree growth. During the typically 2 to 5-year outbreaks, forest tent caterpillar defoliates most northern hardwood species, except for *Acer rubrum*, early in the growing season (Fitzgerald, 1995). Trees refoliate within a few weeks after defoliation, although leaves remain smaller during years of insect outbreaks than in non-outbreak years (Wargo, 1981). If growth responses to insect outbreaks differ across tree species, species interactions could be altered, which may lead to changes in community structure and composition. In this study, we compare the growth responses of mature trees of *A. rubrum*, *Acer saccharum*, *Quercus rubra*, and *Tilia americana* to a forest tent caterpillar (FTC) outbreak.

A direct effect of canopy defoliation of mature trees during an insect outbreak is a reduction in growth in the same year (e.g., Minott and Guild, 1925; Baker, 1941; Muzika and Liebhold, 1999; Hennigar et al., 2007; Fajvan et al., 2008), due to the loss of leaf area for photosynthesis. Growth often remains low in the years following an outbreak (e.g., Muzika and Liebhold, 1999; Fajvan et al., 2008), probably through lag effects of defoliation resulting from depletion of non-structural carbohydrate reserves (e.g., Wargo et al., 1972). On the other hand, insect outbreaks could have indirect effects on tree growth by reducing competition for

* Corresponding author. Present address: Department of Ecology and Evolutionary Biology, University of Connecticut, 75 North Eagleville Road, Storrs, CT 06269-3043, USA. Tel.: +1 860 486 7955; fax: +1 860 486 6364.

E-mail addresses: danae.rozendaal@uconn.edu (D.M.A. Rozendaal), kobe@msu.edu (R.K. Kobe).

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light among neighboring trees, as light competition influences tree growth (e.g., Canham et al., 2006; Baribault and Kobe, 2011). Trees that are lightly or not defoliated could take advantage of the increase in light and increase growth (e.g., Jedlicka et al., 2004). Insect outbreaks may not only impact light levels, but also soil nutrient levels through frass input. Changes in soil nutrient levels in response to insect outbreaks are not clear, however, as soil nitrogen levels either increased in response to defoliation (e.g., Frost and Hunter, 2004), or did not change (e.g., Christenson et al., 2002). Moreover, nitrogen from insect frass may not be available for plant uptake (Lovett and Ruesink, 1995). Thus, here we focus on changes in light availability.

For our study species, a growth response to defoliation would occur at a 1-year lag, due to a certain degree of determinate shoot growth for all species. That is, the number of leaves in the terminal bud is pre-formed and is influenced by resource conditions in the preceding growing season (Kramer and Kozlowski, 1979). *A. saccharum* is a strictly determinate species with only elongation of the pre-formed internodes in spring, *T. americana* has determinate shoot growth, although shoot-tip abortion occurs, and *Q. rubra* and *A. rubrum* are semi-determinate, thus these species can display episodic flushes of shoot growth throughout the growing season (cf. Romberger, 1963; Marks, 1975). While the number of leaf primordia is set by resource levels in the previous year, growth in the year following an outbreak is also influenced by the environmental conditions in that year. Thus, growth responses after defoliation are a balance of negative effects due to canopy defoliation, positive effects through release from competition, and the growing conditions (e.g., climate) in the year after defoliation. Although growth increases in response to defoliation of neighboring trees are expected to be of shorter duration than growth responses to canopy gaps, they may influence neighborhood competitive dynamics. Canopy defoliation by gypsy moth (*Lymantria dispar*) indeed increased growth of various non-host species (Campbell and Garlo, 1982; Muzika and Liebhold, 1999; Jedlicka et al., 2004), and forest tent caterpillar outbreaks also increased growth of non-host species in *Populus tremuloides* stands (Duncan and Hodson, 1958). Species-specific growth responses to an insect outbreak are expected to alter species interactions with respect to shading and access to light, which in turn could influence competitive balances and species composition.

In this study, we evaluate the effects of a forest tent caterpillar outbreak on mature tree growth of four tree species in relation to the level of defoliation of the focal tree and the defoliation level of the neighborhood. We compared mature tree growth of *A. rubrum*, *A. saccharum*, *Q. rubra*, and *T. americana* during a FTC outbreak, and in the subsequent year, to the average growth over the previous eight non-outbreak years using tree-ring measurements. We evaluated the following hypotheses: (1) growth responses to a FTC outbreak differ across species. *A. rubrum*, which was not defoliated by FTC, will increase growth at a 1-year lag in response to the outbreak. The host species *A. saccharum* and *Q. rubra* will reduce growth during the outbreak and in the year after the outbreak. *T. americana*, which was defoliated, will reduce growth during the outbreak, but will increase growth the year after the outbreak due to rapid production of new leaves during the defoliation year. *T. americana* produced new leaves within two weeks of defoliation (D.M. Minor, personal observation), which may enable it to capitalize on improved light conditions, and lead to fast growth in the year following defoliation. The other defoliated species produced new leaves ~5 weeks after defoliation; (2) tree growth during, and in the year after, the outbreak decreases with the defoliation level of the focal tree in the outbreak year; and (3) tree growth in the year following defoliation increases with increasing defoliation of neighboring trees.

2. Materials and methods

2.1. Study sites and species

The study was conducted in the Manistee National Forest (44°12′N, 85°45′W), in northern lower Michigan, USA. Six mixed hardwood stands, which were all affected by a forest tent caterpillar (*M. disstria*) outbreak from 2008 to 2010, were selected from a set of 13 mixed hardwood stands across a soil-fertility gradient (cf. Baribault et al., 2010). The six selected stands all occur on morainal, nutrient-rich, deposits in a glacial landscape, but differ slightly in soil nutrient content, and in tree species composition (Baribault et al., 2010; Table 1). Baribault et al. (2010) regarded site 12 and 13 as separate sites from the perspective of nutrient availability and productivity, but we merged both sites into site 12. The six forest stands are all between 80 and 100 years old, and the maximum distance between two sites is 30 km. In each site, all trees >10 cm diameter at breast height (dbh) were mapped in a plot of 41 m × 240 m (0.96 ha) in 1998. Peak defoliation took place during 2009, whereas in 2008 and 2010 light defoliation occurred. In 2009, two of the included sites were heavily defoliated (~75–100% of total leaf area removed), two were moderately defoliated (~25–50% of total leaf area removed), and two sites were lightly defoliated by forest tent caterpillar (<25% of total leaf area removed; Table 1). In 2010, sites 8 and 9 were lightly defoliated by forest tent caterpillar, and in site 7 *Q. rubra* was lightly defoliated by gypsy moth (D.M.A. Rozendaal, personal observation). Canopy openness of these sites, however, only slightly increased in 2010 (D.M.A. Rozendaal and R.K. Kobe, unpublished data). Four tree species were included: *A. rubrum*, *A. saccharum*, *Q. rubra*, and *T. americana*. Based on survival in the understory, *A. saccharum* is very shade tolerant, *A. rubrum* is shade tolerant, and *Q. rubra* has intermediate shade tolerance (Burns and Honkala, 1990). Burns and Honkala (1990) classify *T. americana* as shade tolerant because of its strong resprouting capacity, but we regard *T. americana* as shade intolerant because of its fast mature tree growth, low wood density, and low seedling survival in the understory. In total, the four species comprised 76–97% of the total basal area of the sites.

2.2. Tree growth measurements

We selected 77–114 trees >10 cm dbh per species, distributed across sites (Table 1). We selected trees, where possible, such that we spanned the entire range of defoliation levels and tree sizes for each species. In addition, we preferably selected trees within 10 m from a central 1 m × 200 m transect in each site to allow accurate estimation of defoliation levels of individual trees from canopy photos taken in the central transect. For each tree, we collected one increment core at a height of 1 m from October to November 2010, after radial growth had ceased. Cores were air-dried and

Table 1
Percent basal area of each species per site and the number of trees sampled per species and site. Site numbers generally correspond to the numbering in Baribault et al. (2010), except for sites 12 and 13, which we merged into one site (site 12). acru = *Acer rubrum*, acsa = *Acer saccharum*, quru = *Quercus rubra*, tiam = *Tilia americana*.

Site	Defoliation	Percent basal area				Sample size			
		acru	acsa	quru	tiam	acru	acsa	quru	tiam
8	Light	3	91	0	0		12		
9	Light	15	27	41	0	39	15	15	
12	Moderate	13	36	12	22	28	21	14	29
10	Moderate	0	44	11	28		19	17	33
7	Severe	4	35	58	0	10	20	42	
11	Severe	0	40	1	34		27		35