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The impact of deer on relationships between tree growth and mortality in an old-growth beech-maple forest

Zachary T. Long *, Thomas H. Pendergast IV, Walter P. Carson

Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260, United States

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Abstract

White-tailed deer have been at high levels in the northeastern forests of the United States for decades and have strongly influenced forest dynamics. In this long-term study, we found that the composition of the overstory and understory assemblages of an old-growth beech-maple forest differed significantly. We used exclosures to test the hypothesis that deer contributed to these differences by differentially influencing the relationship between growth and mortality among seedlings of the six most abundant tree species. In the absence of deer, we found that the mortality of the six species decreased with increased growth and that interspecific differences in the relationships between growth and mortality coincided with previously observed shade-tolerance rankings. In the presence of deer, mortality decreased with growth only for the browse tolerant species (American beech, black cherry, and sugar maple). Mortality did not decrease with growth for preferred browse species (oak species, ash species, and red maple), rather, this relationship was eliminated in the presence of deer. The changes in growth and mortality relationships in the presence of browsing generally corresponded to observed changes in seedling density following the removal of deer. Sugar maple, ash, black cherry, and total stem density increased in the absence of deer. Our results suggest that the relationship between survival and growth in the understory, a metric of shade tolerance, is a fairly plastic response that varies depending upon the presence and absence of herbivores. Our results indicate that deer have contributed to the differences between understory and overstory vegetation, with browse tolerant species increasing in abundance at the expense of preferred browse species.

Keywords: Growth–mortality; American beech; Herbivory; Old-growth forest; Shade-tolerance; Sugar maple; White-tailed deer

1. Introduction

In the northeastern United States, high abundances of white-tailed deer can create dramatic changes in forest understory species compositions (Russell et al., 2001; Cote et al., 2004). For white-tailed deer to change forest understory compositions, their impact on seedling and sapling mortality must be distributed unequally among species. Deer may differentially impact species because they either preferentially browse certain species (Tierson et al., 1966; Ross et al., 1970; Runkle, 1981; Whitney, 1984; Tilghman, 1989) or some species are more tolerant to repeated browsing (Stoeckler et al., 1957; Anderson and Loucks, 1979). We suggest that browsing may unequally influence the relationship between mortality and growth across species in the shaded forest understory. Typically, a negative relationship occurs between growth and mortality, such that individuals with positive growth rates have a lower probability of mortality (Givnish, 1994; Kobe et al., 1995; Pacala et al., 1996; Kobe and Coates, 1997). Indeed, our most complete models of forest dynamics are largely based on this relationship and on differences in the shapes of such relationships among species (Pacala et al., 1994, 1996; Kobe et al., 1995; Kobe, 1996; Kobe and Coates, 1997; Caspersen and Kobe, 2001).

We investigated whether white-tailed deer are contributing to changes in the understory composition of an old-growth beech-maple forest and to what degree browsing modified growth–mortality relationships. First, to investigate whether white-tailed deer are causing compositional shifts in this forest, we compared the composition of the canopy to that of the understory (arguably, the future canopy, Oliver and Larson, 1996). Deer were locally extirpated in the early 1900s due to unregulated hunting, and recovered to abundances comparable to their current abundance in the 1930s (Park, 1938; Smith,

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* Corresponding author. Present address: Department of Biology, McGill University, 1205 rue Docteur Penfield, Montreal, Quebec, Canada H3A 1B1.
E-mail address: zachary.long@mail.mcgill.ca (Z.T. Long).

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1989). Currently, deer populations exceed 12 deer/km^2 in more than half of the counties east of the Mississippi river (Quality Deer Management Association, 1999). Thus, some trees in the present canopy could have recruited under lower browsing pressure compared to the browsing regimes over the last 50 years that created and maintain the current understory (Horsley et al., 2003). Indeed, we found that the composition of the canopy and understory were significantly different. To determine if deer contributed to the observed differences between the understory and overstory, we established replicated exclosures in the understory of an old-growth beech-maple forest in northwestern Pennsylvania. Specifically, we tested whether deer differentially influenced the relationships between growth and mortality of different species. Then, we investigated whether these relationships correspond to the observed changes in the densities of seedlings in the understory over 9 years of deer exclusion.

2. Methods

We conducted this study in Tryon-Weber Woods, a 10-ha old-growth beech-maple remnant in Crawford County in northwestern Pennsylvania (latitude 41°36′N and longitude 80°21′W). Tryon-Weber Woods is surrounded by several second growth forests, a 50-year-old abandoned pine plantation, and an agricultural field. This surrounding habitat (especially the agricultural field) could further increase deer abundances found in the old-growth forest. Soils are described by Yarowski et al. (1979) as Holly (HY) and Cambridge (CaB) silt loams.

2.1. Overall forest composition

In 1996, we quantified the composition of the entire forest remnant with point-quarter sampling (Cottam and Curtis, 1956). We sampled a total of 86 points along 11 transects. Each transect was separated by 30 m; points along transects were separated by 25 m. We classified individuals greater than 10 cm diameter at breast height (dbh) as canopy individuals, and individuals less than 10 cm dbh but greater than 140 cm in height as understory individuals. We calculated relative importance values for each species as the sum of relative frequency, relative density, and relative dominance, with dominance being a measure of basal area (Cox, 1996) and compared the composition of the canopy and seedling assemblages with a g-test of independence (Sokal and Rohlf, 1995).

2.2. Herbivore exclusion

In March 1996, we built six fenced exclosures located haphazardly throughout the forest to exclude large vertebrates. Each exclosure was paired with an adjacent, unfenced, control plot. Each exclosure and control plot was 20 m × 20 m, and separated by approximately 3 m. We randomly assigned treatments among paired plots. The exclosures consisted of a 2.4 m high fence, 5.1 cm × 10.1 cm mesh, to exclude deer and other large vertebrates. Evidence strongly suggests, however, that our findings reflect deer exclusion as we observed deer frequently, but only observed rabbits in the forest twice and never observed groundhogs. We established the inner 15 m × 15 m area within each subplot as a permanent sampling area. This left a 2.5 m buffer around the perimeter of each plot to reduce edge effects.

We monitored the growth and mortality of all woody seedlings 20–200 cm in height in the permanent sampling areas. We initially tagged, mapped, and recorded the species identities and heights in June through August 1996 and resampled in the summers of 1997–2000. We tagged, mapped, and monitored new individuals that grew above 20 cm every year during this time period. We resampled all plots in 2003 and 2005 but restricted our sampling to individuals 50–200 cm in height.

2.3. Growth–mortality relationships

We calculated relative growth of individuals as the difference between their initial and final height, divided by initial height. For individuals that died, we used the last recorded height as the final height. We used logistic regression to determine if the survival of an individual (a binary response) was influenced by its relative growth (continuous variable). We used a generalized estimating equation (GEE) approach to help correct for potential spatial correlations among seedling survival and growth within each paired exclosure and control (Albert and McShane, 1995; Bishop et al., 2000). We used Proc genmod with a repeated statement (using each site as the class variable) to call for the GEE analysis in SAS Version 8.02 (SAS Institute Inc., 1997; Kuss, 2002). We conducted separate analyses for each species in each exclosure and control to investigate how herbivory influenced these relationships. To aid in interpretation, we plotted the lines for each significant relationship using the formula $e^{(\beta 0 + \beta 1 \times \text{relative growth})}$, where $\beta 0$ was the estimated intercept and $\beta 1$ was the estimated effect of relative growth. This converted the estimates to more readily interpretable odds ratios, with the resulting plot now showing how the expected probability of mortality changes with increases in relative growth (Sokal and Rohlf, 1995). Additionally, we report the estimates for $e^{\beta 0}$ and $e^{\beta 1}$ and their 95% confidence limits to allow comparisons of both slopes and intercepts among species.

2.4. Seedling dynamics

We used repeated measures analysis of variance to determine if herbivory influenced total seedling density over 9 years of the experiment. We used Proc mixed in SAS Version 8.02 to include the environmental heterogeneity associated with each paired control and exclosure in our model as a random variable (SAS Institute Inc., 1997). We used Akaike's information criterion to select the most appropriate covariance structure. The covariance structures we tested between were unstructured, compound symmetry, heterogeneous compound symmetry, and first-order ante-dependence (SAS Institute Inc.,