

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

Received 26 January 2007; received in revised form 13 June 2007; accepted 19 June 2007

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.

© 2007 Elsevier B.V. All rights reserved.

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 (Stoekler 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,

^{*} Corresponding author. Present address: Department of Biology, McGill University, 1205 rue Docteur Penfield, Montreal, Quebec, Canada H3A 181.

E-mail address: zachary.long@mail.mcgill.ca (Z.T. Long).

1989). Currently, deer populations exceed 12 deer/km² 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 β_0 was the estimated intercept and β_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^{β_0} and e^{β_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.,

1997). While the above growth–mortality relationships were analyzed using data for seedlings from 20 to 200 cm in height found in 1996–2000, for the repeated measures analysis of total seedling density we used individuals between 50 and 200 cm found over the 9 years of the experiment. We limited this analysis to this size class because only this size class was sampled in the final year. We also conducted separate repeated measures ANOVAs on sugar maple, ash, beech, and black cherry. These four species were the only species that occurred in at least four of the six paired controls and exclosures in the 50–200 cm size class and therefore we limited our analyses of individual species to this group. All density data were natural log transformed prior to analyses. Finally, we conducted a repeated measures ANOVA on tree species richness in this size class to determine if deer influenced this broad measure of composition. We selected the most appropriate covariance structure for the analyses on individual species and richness as described above for total stem density.

3. Results

3.1. Overall forest composition

Point quarter sampling revealed that the canopy assemblage differed significantly from the seedling assemblage ($P < 0.001$, Fig. 1). This difference was due to the increase in relative importance in the understory of black cherry (*Prunus serotina*) and American beech (*Fagus grandifolia*) and a concomitant decrease in the understory of sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), hickory species (*Carya* spp.), white oak (*Quercus alba*), and red oak (*Quercus rubra*) (Fig. 1). In fact, we found no seedlings of hickory species or white oak in any of the 344-point quarter quadrats (Fig. 1).

3.2. Growth–mortality relationships

We found significant relationships between relative growth and the probability of mortality in the absence of deer for the six species tested ($P < 0.001$; note that the relationship for oak was only marginally significant, $P = 0.075$, Fig. 2). We found significant relationships between relative growth and the probability of mortality in the presence of deer for only three species: black cherry, sugar maple, and beech ($P < 0.001$, note

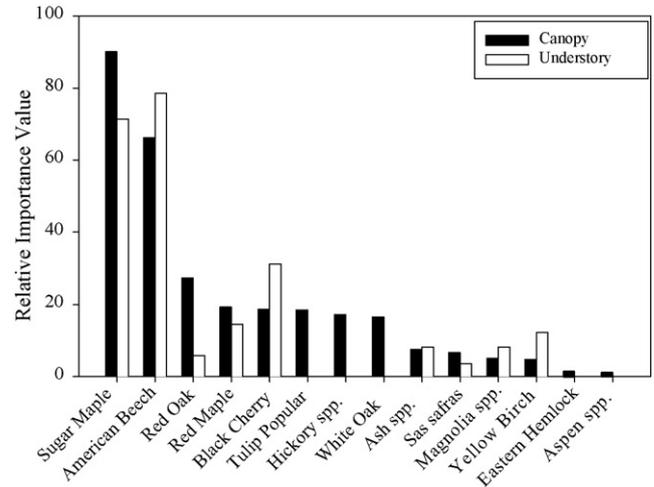


Fig. 1. Relative importance values of canopy and understory species based on point quarter sampling of 86 points along 11 transects. The P -value refers to a goodness of fit test (Chi-square = 64.19, d.f. = 10, $P < 0.001$).

that the relationship for beech was only marginally significant: $P = 0.083$). Thus, for three species (red maple, oak, and ash), in the presence of deer, higher rates of growth in the understory did not lead to higher survivorship.

In the control plots, beech had the lowest probability of mortality at lower rates of growth (i.e., lowest intercept in Fig. 2), followed by sugar maple and black cherry, though only beech and cherry were significantly different (Table 1). While beech again had the lowest mortality–growth intercept with deer excluded, ash, maples (both sugar and red), oaks, and black cherry followed sequentially, although the majority of 95% confidence intervals of these species overlapped. Only beech had a significantly lower probability of mortality than the oaks and black cherry, and the maples lower than black cherry (Table 1).

3.3. Seedling dynamics

Over the course of the experiment, we found 18 species in the exclosures and controls (Fig. 3). The density of all species 50–200 cm in height increased over time in the exclosure (Fig. 4, significant exclosure by time interaction). For individual species, we limited our repeated measure analyses to the four species in this size class that occurred in at least four

Table 1
Estimates and the upper and lower limits of the 95% confidence intervals for the intercepts (e^{β_0}) and slopes (e^{β_1}) of the relationships between relative growth and the probability of mortality in the understory in the controls and exclosures

	Control					Exclosure						
	Red maple	Sugar maple	Beech	Ash	Black cherry	Oak	Red maple	Sugar maple	Beech	Ash	Black cherry	Oak
e^{β_0} lower limit	0.70	0.11	0.07	0.06	0.26	0.17	0.10	0.11	0.11	0.06	0.28	0.17
e^{β_0}	0.88	0.17	0.10	0.08	0.49	0.42	0.17	0.17	0.12	0.15	0.44	0.41
e^{β_0} upper limit	1.09	0.28	0.14	0.10	0.91	1.04	0.28	0.28	0.12	0.41	0.67	1.04
e^{β_1} lower limit	0.12	0.30	0.00	0.13	0.12	0.45	0.01	0.30	0.17	0.01	0.33	0.14
e^{β_1}	0.46	0.37	0.06	0.98	0.23	0.97	0.04	0.37	0.31	0.04	0.48	0.39
e^{β_1} upper limit	1.77	0.45	1.46	7.32	0.42	2.03	0.22	0.45	0.55	0.14	0.70	2.59

Bold columns indicate that the probability of mortality significantly decreased with increasing growth at a rate described by the slope (e^{β_1}).

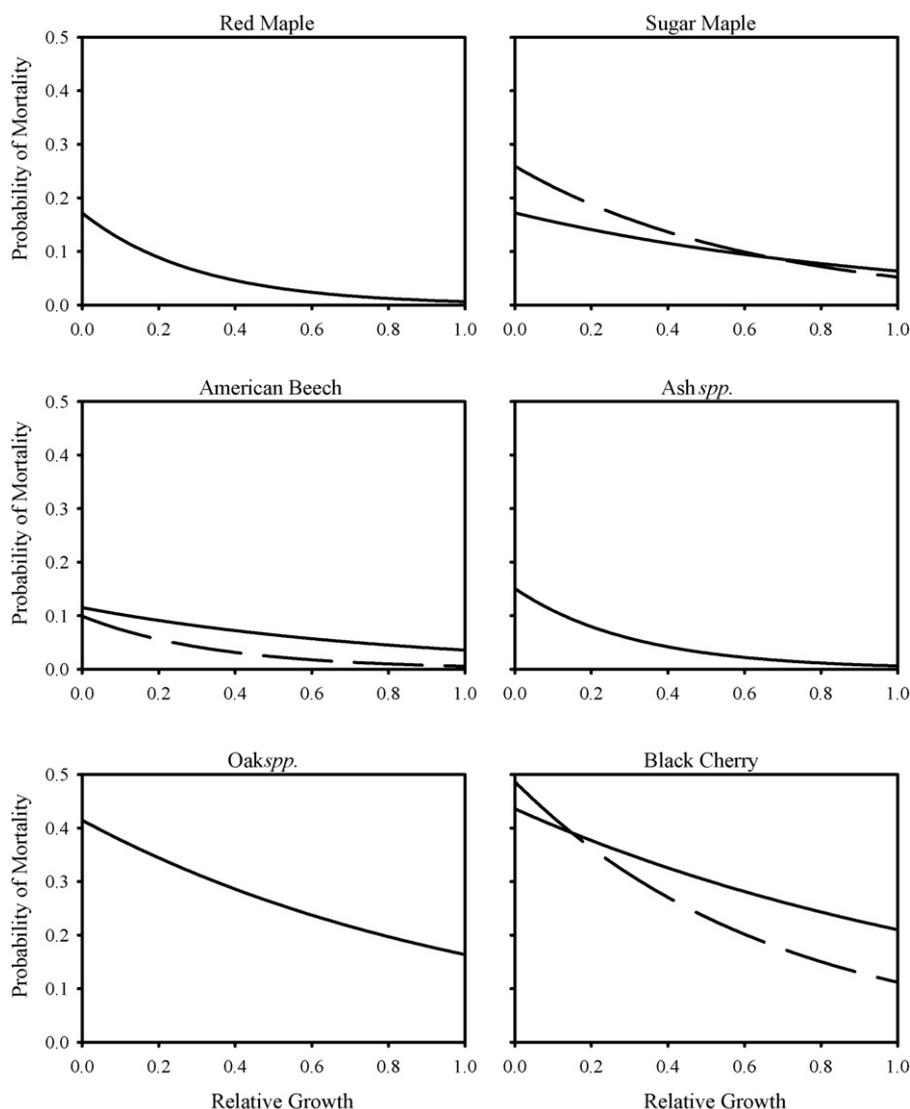


Fig. 2. Relationship between relative growth and the probability of mortality in the understory. Solid lines represent the probability of mortality in the absence of deer, dashed lines represent the probability of mortality in the presence of deer. The absence of a line indicates that there was not a significant relationship.

of the six paired controls and exclosures. Of these, sugar maple, ash and black cherry increased in density over time with deer exclusion (Fig. 4, significant exclosure by time interactions). Although the density of beech changed over time, it was not influenced by browsing (Fig. 4). The combined density of uncommon species (i.e., species listed in Fig. 3 other than beech, sugar maple, ash, and black cherry) increased over time in the exclosures (Fig. 4, significant exclosure by time interaction). Species richness also varied over time (Fig. 5). In the presence of browsing, mean richness decreased from 6 to 3 species. Whereas in the absence of browsing mean richness remained at approximately six species, leading to a marginally significant exclosure by time interaction (Fig. 5).

4. Discussion

Numerous studies have demonstrated that selective browsing by deer can limit the recruitment, growth, and survival of preferred herbaceous and woody species in forest understories

(Anderson and Loucks, 1979; Marquis, 1981; Alverson et al., 1988; Tilghman, 1989; McShea and Rappole, 1992; Nowacki and Abrams, 1994; Kitterage et al., 1995; Abrams and Orwig, 1996; Russell et al., 2001; Horsley et al., 2003; Cote et al., 2004; Banta et al., 2005; Comisky et al., 2005) though few studies have been conducted in either beech-maple or in old-growth forests. In our point-quarter survey of this old-growth beech-maple forest, we found that the composition of the understory differed significantly from the composition of the canopy (Fig. 1). Deer were practically extirpated in the by the late 1800s but became extremely abundant throughout Pennsylvania by the late 1930s after a reintroduction program (Park, 1938; Whitney, 1984; Smith, 1989). Thus, the current old-growth canopy almost certainly developed under a lower browsing regime than the current understory which has been subjected to heavy browsing pressure (Whitney, 1984; Smith, 1989; Tilghman, 1989; Horsley et al., 2003). Indeed, in our survey we found that the understory is predominantly composed of beech and black cherry, which are not considered

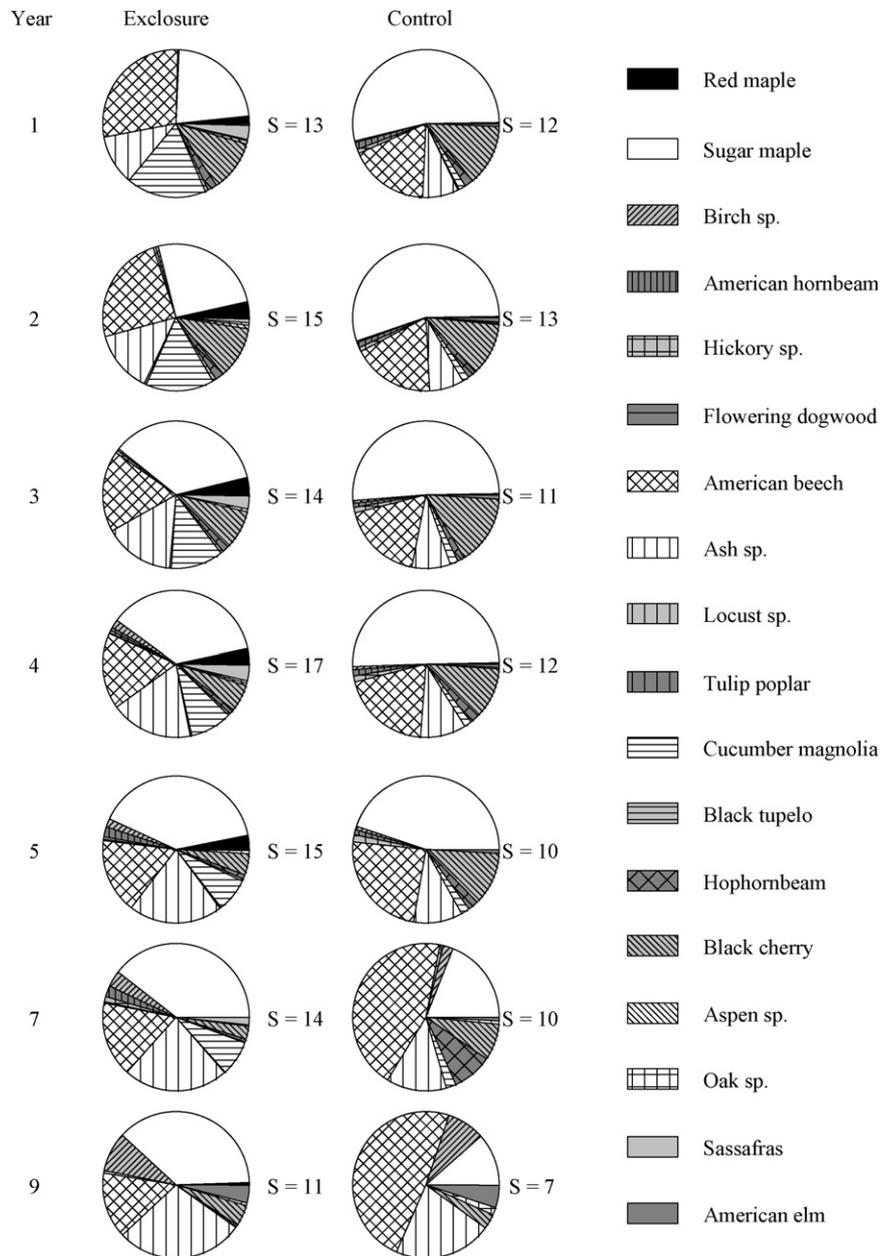


Fig. 3. Densities of each species found in the controls and exclosures over the duration of the experiment. The size of the pie slice is equivalent to the number of stems of that species relative to the total number of stems found across all controls or across all exclosures in that year. S refers to the total number of species found across all controls or all exclosures in that year.

preferred browse, and sugar maple, which is considered browse tolerant (Stoekler et al., 1957; Anderson and Loucks, 1979). The relative importance of beech and black cherry was higher in the understory than in the overstory. They were two of only five species that showed this pattern, and the magnitudes of their differences between understory and overstory importance were substantially greater than the other three species (ash sp., magnolia sp., and yellow birch). Sugar maple had a high relative importance value in the understory, but its relative importance in the understory was less than in the overstory. At least in some regions, sugar maple is heavily browsed and benefits if protected from deer (Stoekler et al., 1957; Tierson et al., 1966; Tilghman, 1989). Sugar maple may have persisted and remained relatively abundant in the understory because it

tolerates repeated browsing better than other species (Stoekler et al., 1957; Anderson and Loucks, 1979). Preferred browse such as red oak decreased in abundance while white oak, tulip poplar, and hickory species were functionally eliminated from the understory (Tierson et al., 1966; Ross et al., 1970; Runkle, 1981; Whitney, 1984; Tilghman, 1989). Thus, the differences between the canopy and understory importance values were consistent with patterns that would be generated by persistent deer browsing.

4.1. Growth–mortality relationships and shade tolerance

Relationships between growth and mortality among species play a major role in driving forest dynamics because these

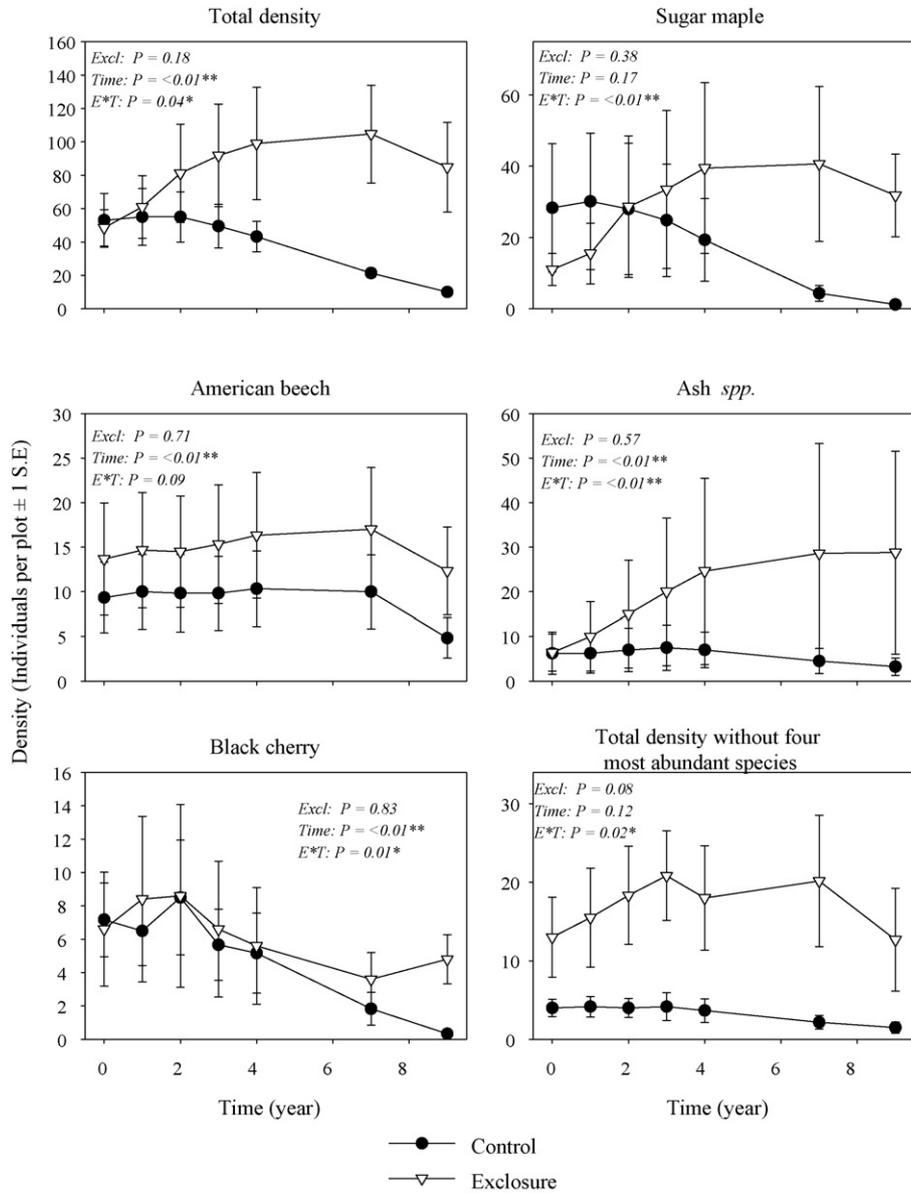


Fig. 4. Changes in stem density over time in the exclosures and controls. P -values within each graph are the results of repeated measures analyses of variance.

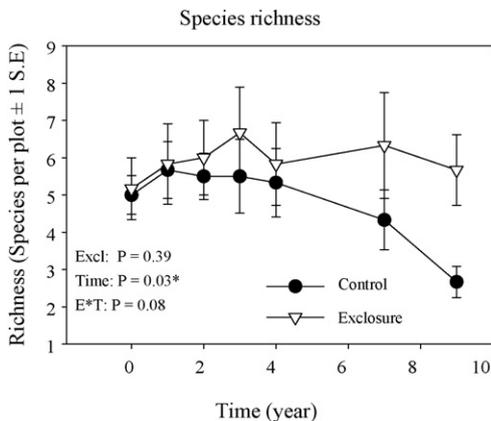


Fig. 5. Changes in species richness over time in the exclosures and controls. P -values are the results of repeated measures analyses of variance.

relationships often determine which species persist within shaded understories (e.g., Kobe et al., 1995; Kobe, 1996, 1999; Pacala et al., 1996; Kobe and Coates, 1997; Caspersen and Kobe, 2001). The observed differences in overstory and understory compositions may be explained by how browsing influences the relationships between mortality and growth of each species. In the absence of browsing, the six species we tested exhibited the same general pattern observed in other studies (Kobe et al., 1995; Kobe, 1996, 1999; Pacala et al., 1996; Kobe and Coates, 1997; Caspersen and Kobe, 2001); mortality declined with increasing growth. While this general pattern was consistent among species, there were differences in the intercepts and shapes of the growth–mortality relationships, suggesting that species differed in the probability of mortality at low rates of growth. Beech had the lowest probability of mortality at lower rates of growth (i.e., beech had the lowest intercept in Fig. 2), consistent with the previous conclusion that

beech is one of the most shade tolerant species in eastern forests (Burns and Honkala, 1990). Indeed, beech had significantly lower mortality at low growth than black cherry and oak species in the presence of deer (Table 1), species generally considered substantially less shade-tolerant than beech (Burns and Honkala, 1990). For the remaining five species, ash had the next lowest probability of mortality at low growth rates followed by red maple, sugar maple, oak, and black cherry, although the majority of 95% confidence intervals of these species overlapped. If the degree of shade-tolerance is defined as a low probability of mortality at low growth rate in shaded understories, then the rankings of these species generally corresponds to a hierarchy of shade tolerance rankings suggested by others or demonstrated empirically in previous studies (Baker, 1949; Burns and Honkala, 1990; Pacala et al., 1996). These previous studies, however, did not explicitly consider the impact of browsing on these relationships.

4.2. Browsing by deer nullified growth–mortality relationships of preferred browse species

The presence of deer created conditions where higher growth rates did not confer higher survivorship for preferred browse species (ash, oak, and red maple). Thus, deer obscured the rankings of shade tolerance discussed above and rankings that are fairly well accepted. Browsing by deer could have nullified the relationship between mortality and growth through different non-exclusive mechanisms. First, repeated browsing by deer may have decreased the range of growth over which to evaluate the growth–mortality relationships, decreasing our ability to detect statistical significance. The range of relative growth was smaller for the three species that did not exhibit a relationship between growth and mortality. Ash, oaks, and red maple had a 37%, 37%, and 72% reduction in relative growth range when deer were present, respectively. Second, the relationships would disappear if deer browse individuals to the point where the plants cannot recover. That is, deer are likely to cause mortality by over-browsing, regardless of growth rate. Irrespective of mechanism, browsing effectively nullified an important physiological relationship.

Mortality decreased with growth for beech, black cherry, and sugar maple in both the presence and absence of deer. In contrast to the species above, beech and black cherry are not considered preferred browse, and sugar maple is considered browse tolerant (Stoekler et al., 1957; Anderson and Loucks, 1979). For beech, the line describing the growth–mortality relationship in the presence of deer was actually less than the line found in the absence of deer, suggesting beech may have had a greater chance of survival when deer were present, although these relationships are not significantly different from each other (Table 1). A greater chance of survival in the presence of deer could occur because deer preferentially consume other species and thereby reduce negative effects of interspecific competition on beech. Consistent with this view, black cherry and sugar maple have higher mortality at low growth rates than beech (Table 1). The significant difference between mortality at low growth between beech and black

cherry is consistent with widely held views on the shade tolerance of these two species (Baker, 1949; Burns and Honkala, 1990; Pacala et al., 1996). The significant difference between mortality at low growth between beech and sugar maple in the presence of browsing, however, is not consistent with widely held views on shade tolerance (Baker, 1949; Burns and Honkala, 1990; Pacala et al., 1996). Indeed, browsing shifted the mortality at low growth of sugar maple to where it was not significantly different from black cherry (Table 1). This suggests that in the presence of deer, the ability of species widely held as shade tolerant to tolerate low light conditions in the understory is not very different from a species widely held as shade-intolerant.

4.3. Growth–mortality relationships in the presence and absence of deer correspond to changes in seedling density

We monitored the densities of seedlings 50–200 cm in height in the exclosures and control plots to determine if relationships between mortality and growth described above correspond to changes in seedling densities observed over the 9 years of deer exclusion. Oak species and red maple were omitted from these analyses because they were not present in this size class in the presence of deer. For two of the four species that we could reliably investigate (sugar maple and black cherry), changes in density over the duration of the experiment were consistent with the view that browsing increased mortality rates across a wide range of growth rates. Higher survivorship inside the exclosures likely led to the increase in the density of sugar maple throughout the experiment and the increase in density of black cherry in the in the final year (Fig. 4, significant exclosure by treatment interaction). Similar to sugar maple and black cherry, ash density also increased in the exclosures. In contrast, increased growth rates for ash did not decrease mortality in the presence of browsing. Therefore, individuals of ash could grow and survive where protected from deer herbivory, but could not in the presence of deer, resulting in consistently low densities. Beech had low mortality across a wide range of growth rates regardless of the presence of deer and thus excluding deer had little effect on the density of the small size classes of this species. This suggests that other factors (e.g., competition, clonal associations with canopy individuals) may be more important for beech seedling dynamics.

Total seedling density showed a dramatic increase following the removal of deer. Total density included all tree species that were initially found or grew into the 50–200 cm size class (see Fig. 3 for a list of species). However, the four species discussed above comprised the majority of all of the total seedlings observed (an average of 81% across years and treatments) and therefore primarily contributed to the increase in total stem density. Species other than the four discussed above occurred relatively infrequently (on average, less than 20 individuals per exclosure or control, Fig. 4), possibly because browsing suppressed their numbers or eliminated many species prior to the start of the experiment and there has not been sufficient time for their recovery in the absence of browsing. Given the

periodicity of seed production for trees in this area, the 9 years of deer exclusion provided sufficient time for at least 2 years of abundant seed production by the relatively infrequent species. For example, abundant red maple seed crops occur every 2–3 years, and abundant oak seed production occurs every 4–5 years in this area (Horsley et al., 1994). Indeed, these seed crops may have contributed to the observed modest increase in density of the uncommon species following the removal of deer (significant exclusion by time interaction, Fig. 4, although note that there was a decrease in the final year). Such modest changes in the density of species other than the four most abundant may partly explain why we only found a marginally significant difference in species richness between the controls and exclosures over the course of the experiment. Specifically, we would expect an increase in richness to occur due to an increase in species that are not initially abundant. As described above, the increase in stem density was largely due to the response of the abundant species, with only a modest contribution from the remaining species. Thus, we attribute the lack of an increase in richness despite the removal of browsing to “the ghost of herbivory past” *sensu* Banta et al. (2005) and also called a “legacy effect.” Banta et al. (2005) suggested that deer have drastically reduced the local seed sources of many palatable herbaceous species, and because of this there may be a large time lag between the cessation of browsing and resulting changes in plant species richness (Banta et al., 2005). Here, it appears that although seed sources are still present as canopy trees, there may be a significant lapse before these species begin recruiting into the seedling layer. In this study, that time lapse is apparently longer than 9 years. Nonetheless, the mean species richness in the controls was just three species compared to six species in the exclosures by the final year, suggesting that the lack of a statistically significant difference may have resulted because of our choice of statistical analysis. Indeed, when we compare richness in the controls and exclosures in only the final year with a paired *t*-test, richness does differ ($P = 0.017$).

The largest decline in species richness, however, occurred in the last 5 years, particularly within the control plots. This unexpected result may be due to (1) an herbivory threshold effect, (2) a recent change in deer population/resource availability, or (3) increased competitive exclusion by beech seedlings. Some species may be able to tolerate deer browsing for a number of years, but fail beyond a certain threshold. Given that deer populations are believed to be relatively stable since the 1930s (Park, 1938; Smith, 1989), this seems unlikely. However, a recent increase in deer density and/or a reduction in available resources for deer may increase browsing impact in the understory. Unfortunately, accurate deer population measures are not available for this area for the period of this study and we lack evidence of an increase in deer density. There certainly may have been a reduction in available resources, resulting in increased herbivory on less-preferred plant species—now the only individuals left in the understory. Indeed, we observed sharp declines in sugar maple, uncommon species, total, and even black cherry density in the presence of deer in the last 5 years of the experiment (Figs. 3 and 4). Beech

had high survival in the understory, likely because most individuals observed were root suckers. We acknowledge that, given the advantages provided through connections with canopy trees, beech could have also exerted strong competitive effects on other species in the understory. The high importance value of beech (Fig. 1) and the dramatic increase in relative density observed over the duration of the experiment (Fig. 3) certainly suggests this possibility. In the absence of a direct manipulation of beech density (as may occur unintentionally due to beech bark disease), we cannot determine how much this competitive effect contributes to the observed overall decline of stem density, relative to the trophic effects of white-tailed deer. The differences in richness and densities between treatments and over time predict that species ultimately recruiting into the understories and canopies will be strictly composed of deer tolerant species (i.e., beech). Our results suggest that (1) long-term experiments are going to be required to adequately address the impact of browsers on forest dynamics, and (2) deer are creating a depauperate, low density, low diversity understory and hence even moderately diverse old-growth forests in this area may be potentially replaced by only a small number of potential tree species with unknown implications for higher trophic levels.

Acknowledgements

Troy Milkey, Amy Long, and many others helped establish and maintain the exclosures. The comments of J. Anderson, D. Bunker, R. Collins, S. Kalisz, A. Long, J. Merritt, P. Morin, A. Royo, S. Schnitzer, H. Stevens, and S. Tonsor, and two anonymous referees greatly improved this manuscript. The Pennsylvania Academy of Science, Sigma Xi, and the Pymatuning Laboratory of Ecology provided financial support. This is contribution number 132 of Pymatuning Laboratory of Ecology.

References

- Abrams, M.D., Orwig, D.A., 1996. A 300 year history of disturbance and canopy recruitment for co-occurring white pine and hemlock on the Allegheny Plateau, USA. *J. Ecol.* 84, 353–363.
- Albert, P.S., McShane, L.M., 1995. A generalized estimating equations approach for spatially correlated binary data—applications to the analysis of neuroimaging data. *Biometrics* 51, 627–638.
- Alverson, W.S., Waller, D.M., Solheim, S.L., 1988. Forests too deer: edge effects in northern Wisconsin. *Conserv. Biol.* 2, 348–358.
- Anderson, R.C., Loucks, O.L., 1979. White-tail deer influence on structure and composition of *Tsuga canadensis* forests. *J. Appl. Ecol.* 16, 855–861.
- Baker, F.S., 1949. A revised tolerance table. *J. Forestry* 47, 179–181.
- Banta, J.A., Royo, A.A., Kirschbaum, C., Carson, W.P., 2005. Plant communities growing on boulders in the Allegheny National Forest: evidence for boulders as refugia from deer and as a bioassay of overbrowsing. *Nat. Areas J.* 25, 10–18.
- Bishop, J., Die, D., Wang, Y.G., 2000. A generalized estimating equations approach for analysis of the impact of new technology on a trawl fishery. *Aust. New Zealand J. Statist.* 42, 159–177.
- Burns, R.M., Honkala, B.H., 1990. *Silvics of North America*. U.S. Department of Agriculture Handbook, p. 654.
- Caspersen, J.P., Kobe, R.K., 2001. Interspecific variation in sapling mortality in relation to growth and soil moisture. *Oikos* 92, 160–168.

- Comisky, L., Royo, A.A., Carson, W.P., 2005. Deer browsing creates rock refugia gardens on large boulders in the Allegheny National Forest, Pennsylvania. *Am. Midland Naturalist* 154, 201–206.
- Cote, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. *Annual Rev. Ecol. Evol. Systemat.* 35, 113–147.
- Cottam, G., Curtis, J.T., 1956. The use of distance measures in phytosociological sampling. *Ecology* 37, 451–460.
- Cox, G.W., 1996. *Laboratory Manual of General Ecology*, seventh ed. W.C.B. Publishers, Chicago, IL, USA.
- Givnish, T.J., 1994. Does diversity beget stability. *Nature* 371, 113–114.
- Horsley, S.B., Auchmoody, L.R., Walters, R.S., 1994. Regeneration principles and practices. In: Marquis, D.A. (Ed.), *Quantitative Silviculture for Hardwood Forests of the Alleghenies*. Gen. Tech. Rep. NE-183. United States Department of Agriculture Forest Service, Northeastern Forest Experiment Station, Radnor, PA.
- Horsley, S.B., Stout, S.L., Calesta, S.de, 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol. Appl.* 13, 98–118.
- Inc., S.I., 1997. *SAS/STAT Software: Changes and Enhancements through Release 6.12*. SAS Institute Inc., Cary, N.C.
- Kitterage, D.B., Marks, P., Ashton, S., 1995. Impact of deer browsing on regeneration in mixed stands in southern New England. *North. J. Appl. Forestry* 12, 115–120.
- Kobe, R.K., 1996. Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. *Ecol. Monogr.* 66, 181–202.
- Kobe, R.K., 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology* 80, 187–201.
- Kobe, R.K., Coates, K.D., 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Can. J. Forest Res.-Revue Canadienne De Recherche Forestiere* 27, 227–236.
- Kobe, R.K., Pacala, S.W., Silander, J.J.A., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5, 517–532.
- Kuss, O., 2002. How to use SAS for logistic regression with correlated data. In: *Proceedings of the 27th Annual SAS Users Group International Conference (SUGI 27)*. SAS Institute, Cary, North Carolina, USA, Paper 261–27.
- Marquis, D.A., 1981. *Effects of Deer Browsing on Timber Production in Allegheny Hardwood Forests of Northwestern Pennsylvania*. US Department of Agriculture Research Paper NE-475, Washington, D.C., USA.
- McShea, W.J., Rappole, J.H., 1992. White-tailed deer as keystone species within forested habitats of Virginia. *Virginia J. Sci.* 43, 177–186.
- Nowacki, G.J., Abrams, M.D., 1994. Forest composition structure and disturbance history in the Alan Seeger Natural Area, Huntingdon County, Pennsylvania. *Bull. Torrey Bot. Club* 121.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*. John Wiley and Sons Inc., New York.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.* 66, 1–43.
- Pacala, S.W., Canham, C.D., Silander, J.A., Kobe, R.K., 1994. Sapling growth as a function of resources in a north temperate forest. *Can. J. Forest Res.-Revue Canadienne De Recherche Forestiere* 24, 2172–2183.
- Park, B.C., 1938. Deer weights and measurements on the Allegheny National Forest. *Trans. North Am. Wildlife Conf.* 4, 261–279.
- Quality, D.M.A., 1999. *White-tailed Deer Density Map 1999*. www.qdma.com.
- Ross, B.A., Bray, J.R., Marshall, W.H., 1970. Effects of long-term deer exclusion on a *Pinus resinosa* forest in north-central Minnesota. *Ecology* 51, 108–1093.
- Runkle, J.R., 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62, 1041–1051.
- Russell, F.L., Zippin, D.B., Fowler, N.L., 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations, and communities: a review. *Am. Midland Nat.* 146, 1–26.
- Smith, T.L., 1989. An overview of old-growth forests in Pennsylvania. *Nat. Areas J.* 9, 40–44.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*, third ed. W.H. Freeman and Company, New York, N.Y., USA.
- Stoekler, J.H., Strothmann, R.O., Krefting, L.W., 1957. Effect of deer browsing on reproduction in the northern hardwood-hemlock type in northeastern Wisconsin. *J. Wildlife Manage.* 21, 75–80.
- Tierison, W.C., Patric, E.F., Behrend, D.F., 1966. Influence of white-tailed deer on the logged northern hardwood forest. *J. Forestry* 64, 801–805.
- Tilghman, N.G., 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *J. Wildlife Manage.* 53, 524–532.
- Whitney, G.G., 1984. Fifty years of change in the arboreal vegetation of Heart's Content, an old-growth hemlock white-pine northern hardwood stand. *Ecology* 65, 403–408.
- Yarowski, M., Rector, D., Eckenrode, J., Jensen, J., Grubb, R., 1979. *Soil Survey of Crawford County, Pennsylvania*. US Department of Agriculture, Soil Conservation Service, Washington, D.C..