White-tailed deer (*Odocoileus virginianus*) positively affect the growth of mature northern red oak (*Quercus rubra*) trees

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Abstract. Understanding and predicting the effects of deer (Cervidae) on forest ecosystems present significant challenges in ecosystem ecology. Deer herbivory can cause large changes in the biomass and species composition of forest understory plant communities, including early life-cycle trees (i.e., seedlings and saplings). Such changes can impact juvenile to adult transitions and the future age structure and species composition of mature forests. Changes to understory vegetation also impact flow of energy and nutrients in forest ecosystems. Studies examining the influence of deer on mature trees, however, are rare and rely on extrapolating effects from early life cycle stages of trees. We tested the hypothesis that the absence of deer would result in an increase in the growth rate of mature trees by examining the impact of white-tailed deer (*Odocoileus virginianus*) on mature canopy trees. We examined incremental growth in individuals of *Quercus rubra*, an important component of temperate deciduous forests in North America, inside and outside 16-year deer exclosures in eastern U.S. deciduous forests. We found that adult trees inside exclosures grew less than those directly exposed to deer. Our findings highlight the indirect effects of white-tailed deer on the growth of adult individuals of *Q. rubra* in a way opposite of what would be expected from previous studies based on immature or understory tree populations. We suggest the increased growth of adult trees in the presence of deer may be explained by increased nutrient inputs through deer fecal and urine deposits and the alteration of the competitive environment belowground through the reduction of understory vegetation by browsing. Underscoring the ecological and demographic importance of adult trees in forest ecosystems, results from this study suggest the direct and indirect effects of deer on mature trees should not be overlooked.

Key words: competition release; deer waste mechanism; dendroecology; forest; herbivory; Shenandoah National Park; Smithsonian Conservation Biology Institute; tree cores.

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INTRODUCTION

In recent years, deer (Cervidae) populations have increased dramatically throughout many areas of the world, including North America (Horsley et al. 2003), Europe (Apollonio et al. 2010), Asia (Tsujino and Yumoto 2004, Suzuki et al. 2008), and Oceania (Platt et al. 2004, Husheer et al. 2006). Population increases have been driven primarily by forest clearing (Dale 1997), reduction of predator populations (Mladenoff et al. 1999), and milder winter temperatures (Dumont et al. 2000). As deer populations have grown, they have increasingly impacted the biomass and species composition of understory woody plant communities in forest ecosystems. Many studies have shown that in forest ecosystems, deer have contributed to the decreased abundance and diversity of palatable herbs and tree seedlings (Gill and Beardall 2001, Kuiters and Slim 2002, McGraw and Furedi 2005, Knight et al. 2009, Heckel et al. 2010). Naturally, changes in tree seedling community can alter the future structure of adult tree communities. However, deer browsing activity also modifies the flow of energy and nutrients in forest ecosystems (Hairston et al. 1960, Pastor et al. 1993, McNeil and Cushman 2005, Pastor et al. 2006, Stritar et al. 2010).

Deer alter energy and nutrient cycles in forest ecosystems both directly and indirectly. Their browsing activity can directly reduce the quantity and quality of nitrogen (N)-rich litter inputs to the soil (Ritchie et al. 1998, Horsley et al. 2003, Rooney and Waller 2003), thereby modifying carbon (C) allocation between aboveground and belowground plant tissues (Bardgett and Wardle 2003). Changes in C allocation result in direct changes to C fixation (Ceulemans and Isebrands 1996, Giardina et al. 2003) and indirect changes in important belowground processes (Wardle et al. 2002, Persson et al. 2009) such as rates of decomposition (Wardle et al. 2002) and N mineralization (Ritchie et al. 1998, McNeil and Cushman 2005). Decreases in belowground C allocation tend to have an overall negative influence on both the cycles and availability of energy and nutrients (Epron et al. 2012). Examples where Cervidae populations have had negative effects on energy and nutrient cycles include moose (Alces alces) in boreal forests (Persson et al. 2009), red deer (Cervus elaphus) in temperate regions of Sweden (Månsson and Jarnemo 2013), Sitka black-tailed deer (Odocoileus hemionus) in coastal temperate rainforests (Vila et al. 2003), and elk (Cervus canadensis) in willow communities of the Rocky Mountain National Park in western USA (Singer and Schoenecker 2003). Positive consequences of deer on primary productivity and nutrient cycling are possible, but are less common, particularly in browsing systems (Pastor et al. 2006). Thus, through direct and indirect feedbacks with plants and soil microbial communities, deer can alter the productivity and availability of mineral resources necessary for the growth of trees and other vegetation (Rooney and Waller 2003, Bressette et al. 2012).

Despite the strong potential of deer herbivory to impact forest ecosystems, direct tests examining consequences on mature forest trees have rarely been conducted. The few studies on deer herbivory that have included mature forests in their analyses still rely on extrapolations from trees in early life cycle stages. Examples consist of herbivory impacts on seedlings and saplings that affect the transition to a mature tree population and thus affect the mature tree community over time (Chouinard and Filion 2001, Potvin et al. 2003), and also direct injuries to sapling trees, which are sometimes considered mature (Tanentzap et al. 2011). However, to obtain a complete understanding of how deer herbivory impacts the tree community, possible indirect effects must also be considered.

Here we test whether the exclusion of deer from a forest affects the growth of mature canopy trees. Given potentially profound effects of deer on the forest understory and the soil environment, which controls key biotic and abiotic forest ecosystem processes (Wardle and Bardgett 2004), we expected to see repercussions of deer not only on early-stage trees, but also on mature canopy trees. Because we expected N and C cycling to be slower in the presence of deer (Ritchie et al. 1998, McNeil and Cushman 2005), we hypothesized that areas from which deer had been excluded would have greater productivity, nutrient cycling and consequently greater growth of mature trees than in areas with deer. We measured the incremental growth of adult individuals of northern red oak (Quercus rubra) associated with

a set of large, long-term white-tailed deer (*Odocoileus virginianus*) exclusion plots in the temperate deciduous forest of northern Virginia (USA). The construction of deer exclusion fences 16 years prior to this study allowed the development of a dense understory of woody and herbaceous species inside the fenced areas that differs greatly in species composition, height, and density as well as in soil nutrient status from control areas open to white-tailed deer grazing (Heckel et al. 2010, Bressette et al. 2012).

METHODS

Study sites

This study was carried out at four sites in large, continuous forest tracts located within 25 km of Front Royal, Virginia USA (38°55′ N, 78°10′ W, 200 m a.s.l.), in the Shenandoah National Park (SNP; sites: Hilltop, Keyser, and Matthews Arm) and at the Smithsonian Conservation Biology Institute (SCBI; site: Posey). At each site, a long-term 200 m × 200 m (i.e., 4 ha) deer exclusion treatment plot was paired with an equally sized control treatment plot, 200–600 m away, with free access by white-tailed deer (the only expected large herbivore) and other large mammals (e.g., American black bear [*Ursus americanus*]). Sites were initially selected based on similar understory vegetation as quantified in 1990. Sites were separated by 4–21 km (Appendix: Fig. A1). Deer exclusion plots were erected in 1990 using a combination of 1.5 m high mesh farm fencing (grid size 25 cm × 25 cm) on the bottom and barbed wire above, creating a 2.4 m high fence that excludes all large mammals but allows smaller animals to circulate freely. Fences have been maintained since their establishment and while generally effective, all fences experienced small breeches in integrity during the 16 years of the study.

The forest communities were composed primarily of mature northern red oak (*Quercus rubra*), hickory (*Carya* spp.), white ash (*Fraxinus Americana*), yellow poplar (*Liriodendron tulipifera*), and white oak (*Q. alba*), with understory shrubs *Cornus florida*, *Lindera benzoin*, and *Cercis canadensis*. Meteorological data collected from 1960–2009 at NOAA's Woodstock, VA station (38°54′ N, 078°28′ W, 201 m a.s.l., approximately 50 km from our study sites), shows the mean annual precipitation as 930 mm, mean annual summer (Jun–Aug) temperature as 21.8°C, and mean annual winter (Dec–Feb) temperature as 0.3°C. Other environmental site characteristics are included in Table 1.

Mature tree and sapling communities

To determine the species composition of the mature tree communities within each plot, we gathered tree data using the point-quarter method (Krebs 1989). Briefly, we established five parallel 200-m transects in each plot, placing transects systematically at 20, 60, 100, 140, and 180 m from one side of each plot. A total of 50 points were sampled per plot, with points along each transect separated by 20 m. At each of the 50 points, tree species identity and diameter at breast height (dbh) were recorded. We included all individuals with dbh >10 cm. Smaller individuals, dbh ≤10 cm, were classified as saplings and were not included in the analyses of overstory tree communities (see *Statistical analyses* below).

To describe the effects of deer on the woody understory, we quantified the tree seedling and sapling communities. We randomly located ten 5 m × 5 m quadrats per plot. In each quadrat, we recorded the number, height, and species identity of all tree saplings ≤10 cm dbh. We treated the tree seedlings and saplings as a single stratum in the forest community and for clarity refer to them collectively as saplings.

White-tailed deer abundance

We quantified relative site differences of recent, local white-tailed deer activity using fecal pellet abundance as an index of deer abundance. Fecal pellet group counts (Campbell et al. 2004) were conducted in either 10 (at the Keyser and Matthews Arm sites) or 15 (at the Hilltop and Posey sites) randomly located, circular sampling areas of 5.64 m radius (100 m²) in each control plot. Mean white-tailed deer density at the SCBI in 2007 was 33 white-tailed deer km⁻² (95% CI = 19–56 white-tailed deer km⁻²) based on distance sampling estimates (Thomas et al. 2010) conducted by the staff at the SCBI (W. McShea, *personal communication*). White-tailed deer density in the SNP is considered to be similar (NPS 2009).

Table 1. Site characteristics of long-term deer exclusion sites and paired control sites open to deer in the Shenandoah National Park and the Smithsonian Conservation Biology Institute in northern Virginia, USA. Significant differences ($\alpha = 0.05$) between deer treatments at a given site highlighted by an asterisk.

Site	Treatment	Elevation (m)	Aspect (degrees)	Slope (%)	Soil pH Mean	SE	Fecal groups ha^{-1} Mean	SE
Hilltop	no deer	856	220	16	5.99*	0.14		
	deer	914	218	11	5.31*	0.10	3.4	1.1
Keyser	no deer	858	141	13	4.58	0.14		
	deer	872	150	14	4.34	0.17	2.8	1.1
Matthews Arm	no deer	792	325	6	5.94*	0.24		
	deer	829	18	21	5.43*	0.10	1.3	0.3
Posey	no deer	311	257	10	5.47*	0.40		
	deer	317	269	11	4.88*	0.14	5.3	1.5

Soil samples

As an index of soil nutrient availability, we quantified total soil carbon (C) and nitrogen (N), but not plant available N. Soil samples from 20 randomly chosen points per exclusion and control plot were collected from the organic soil layer (top 10 cm) using a 2.2-cm wide soil corer during spring 2008. Samples were air dried and combined into 10 composite samples for analysis at the Utah State University Analytical Lab for processing on a TruSpec C/N autoanalyzer (LECO Corporation, St. Joseph, MO, USA). Data are reported as percent by mass. Soil pH was measured using a 3:1 (v/v) mixture on a subsample from the 10 composite samples per plot.

Dendroecology

To explore the effects of deer on mature tree growth, we measured ring width increments from tree cores in canopy individuals of *Q. rubra* at the beginning of the growing season in 2008 (Posey, Keyser, and Matthews Arm) and 2009 (Hilltop). We choose *Q. rubra* because of its ecological importance in the temperate deciduous forests of eastern North America (McShea and Healy 2002, MacDougall et al. 2010) and because it is present as a dominant tree species both inside and outside of all four exclusion sites (Appendix: Table B1). In each plot, cores were collected from 45 randomly chosen individuals with dbh >10 cm. Tree cores were extracted at breast height from the cross-slope sides of the trunk using a 5-mm increment borer (Suunto; Sylvan Lake, MI, USA). Some cores were inadvertently broken during transport and processing, resulting in a total sample of n = 322

(Table 2). Cores were dried, mounted, and planed with progressively finer sandpaper (100–800 grit) until growth increments were clearly visible (Speer 2010), and then scanned at 1200 dpi (Epson Expresso 1600; Long Beach, CA, USA). Ring width measurements were made on scanned images using WinDendro software version 2008b (Regent Instruments Inc., Quebec, Canada). Ring width boundaries were verified using a dissecting microscope when necessary.

To estimate the total annual cross-sectional area built by individuals over the duration of the experiment, ring width increments were transformed to basal area increments by assuming circular tree trunks (Speer 2010). Basal areas (BA) of all individuals were calculated using the dbh recorded in 2008. From the 2008 dbh, annual ring width increments were subtracted, allowing the calculation of annual BAs from 1860 until 2008. Total BA growth over the 16 consecutive years before fence construction was compared to the 16 consecutive years after fence construction. Detrending is a common technique in dendroecology to remove long-term growth trends in annual ring-width series data due to natural aging (larger trees accumulate less width annually because of the greater stem volume), low-frequency variation due to stand dynamics, and climate (Speer 2010). We do not present detrended ring-width series because it is the growth trends that we want to investigate, and detrending may obscure any treatment response. Additionally, including only the growth increments for the 16 years before and after fence construction obviated the need for detrending (Speer 2010). To enable comparisons between individuals of different sizes and ages, relative BA growth

Table 2. Characteristics (means and standard errors) of mature (>10 cm dbh) *Q. rubra* trees including diameter at breast height (dbh), tree height, age of individuals, and number of trees included at long-term deer exclusion sites and paired control sites open to deer in northern Virginia. Significant differences ($\alpha = 0.05$) between deer treatments at a given site highlighted by an asterisk.

Site	Treatment	dbh (cm)		Height (m)		Age (years)		
		Mean	SE	Mean	SE	Mean	SE	n
Hilltop	no deer	39	3	16	1	60	1	47
	deer	49	4	20	1	51	2	38
Keyser	no deer	48	2	22	1	77	5	35
	deer	35	2	21	1	81	4	42
Matthews Arm	no deer	49*	3	26	1	71	2	36
	deer	25*	2	17	1	66	2	37
Posey	no deer	44	4	23	1	74	3	47
	deer	45	3	23	1	78	2	40

values were calculated as follows. The percentage of total BA growth over the 16 years prior to fence construction (1974–1989) of each individual *Q. rubra* tree was calculated by dividing its BA (in cm^2) in 1989 by its BA (in cm^2) in 1973 and multiplying by 100. Percentage of total BA growth over the 16 years following fence construction (1991–2006) was calculated similarly by dividing the total BA (in cm^2) in 2006 of each individual by its BA (in cm^2) in 1990, the year of fence construction, and multiplying by 100.

Additionally, to highlight annual differences in BA between deer treatments at each site, a second response variable, the mean annual BA increase, was examined. This was computed by dividing the BA (in cm^2) of each individual in year t by the BA (in cm^2) of the same individual in year $t - 1$. This standardization was done for each of the 16 years before and after fence construction.

Statistical analyses

To examine the effect of white-tailed deer presence on the total growth of mature individuals of *Q. rubra* over time, we compared the total BA growth of the exclusion and control treatments for the 16 years prior to fence construction and, in a separate analysis, for the 16 years following fence construction. The before and after time periods were analyzed separately to make clear the treatment response to deer exclusion and to avoid confounding temporal trends before and after fence construction. We used a two-way ANOVA, treating site as a random effect nested within treatment, with the total BA growth of an individual 16-years as the response variable followed by Tukey's HSD test to determine treatment differences among sites. We used a similar ANOVA model to test for differences between sapling densities, soil %N, %C, C/N ratio and pH, the number of fecal pellet groups, and tree dbh, height, and age. Response variables did not violate assumption of normality.

For a closer examination of annual differences in BA between deer treatments and the contributions of site and year to the growth of mature individuals of *Q. rubra*, we used a repeated measures ANOVA, with the mean annual BA increase as the response variable, again treating site as a random effect nested within treatment. We again carried out two separate analyses, one examining the mean annual BA increase over the 16 years before the fences were erected, and the other after. Our data violated the assumption of sphericity associated with a repeated measures analysis (i.e., the requirement that variances between levels of treatment and time be equal at each time point). Consequently, denominator degrees of freedom were corrected using the Greenhouse-Geisser epsilon (Greenhouse and Geisser 1959). We also used a simple linear regression to examine the temporal trend in mean annual BA increase since fence construction, using years since fence construction as the independent variable and mean annual BA increase as the dependent variable; separate analyses being carried out for trees exposed and not exposed to deer. All analyses were done using R (version 2.13.1) (R Development Core Team 2011).

RESULTS

Site comparisons

The mature tree community structure was similar among the four sites and between deer treatments, with no differences in total basal area or overall tree density of all trees having a dbh >10 cm (Appendix: Table B1). Although the species composition of mature trees differed somewhat among sites, *Q. rubra* was consistently a dominant species, and its density in particular did not differ among sites or between deer treatments (Appendix: Table B1). Measurements of mean dbh, height, and age of *Q. rubra* populations were also not different between the two deer treatments except at the Matthews Arm site, where mean dbh was greater outside the fence than inside (Table 2). Fecal pellet groups outside fences indicated no significant differences in white-tailed deer abundance among the four sites (Table 1).

Impact of deer exclusion

Deer exclusion impacted both soil characteristics and understory vegetation somewhat differently among sites. Areas from which deer had been excluded were characterized by significantly lower total soil N and C at the Matthews Arm and Hilltop sites, but there were no such differences between deer treatments at the Keyser or Posey sites (Fig. 1A, B). At the Matthews Arm site only, the C/N ratio was significantly greater outside the exclosure fence (Fig. 1C). Additionally, soil pH (Table 1) and the density and height of tree saplings were all significantly greater in areas without deer at all sites except Keyser (Fig. 2).

Deer and growth of Q. rubra

Growth of adult *Q. rubra* individuals was reduced in the absence of deer. We found a significant main effect of deer treatment for the 16 years after fence construction (Fig. 3A). Examining each site individually, there was greater tree growth with deer at all sites but Posey, where no differences were observed (Fig. 3B). This difference in tree growth between fenced plots and those exposed to herbivory contrasts with the 16 years before fence construction, when there was no pre-treatment difference in growth for these same trees (Fig. 3A, B). When
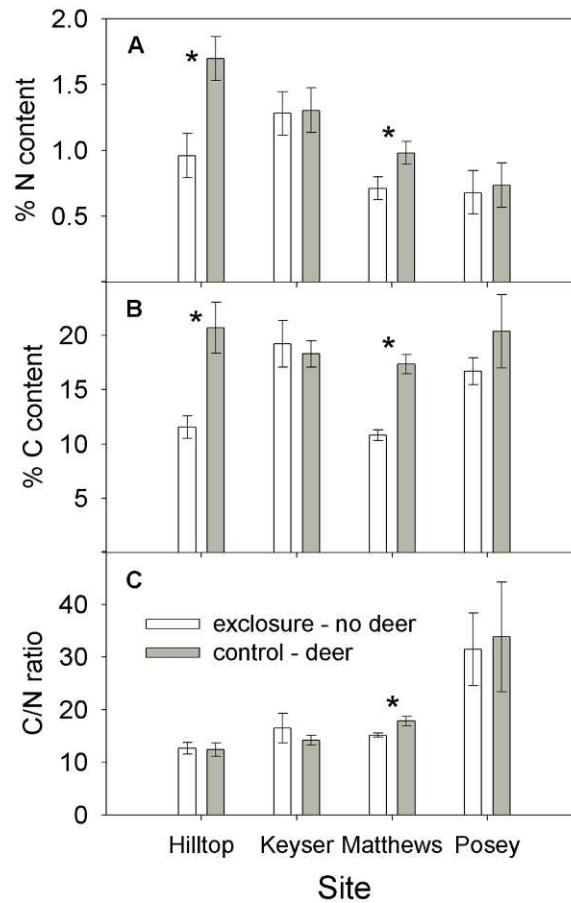

Fig. 1. Soil quality in 4-ha deer exclusion and control areas at the Shenandoah National Park and Smithsonian Conservation Biology Institute. Means and standard errors for (A) % N content by mass; (B) % C content by mass; and (C) C/N ratio. Sites with significant differences are highlighted with an asterisk.

mature tree growth following fence construction was examined for differences over time using repeated measures ANOVA, the presence or absence of deer, site location, and year all contributed significantly to the observed variation in the mean annual BA increase (Table 3). The difference between treatments in growth became more pronounced over the 16-years since fence construction (Fig. 3C). This is highlighted with a simple linear regression indicating the slope of the mean annual BA increase over time was negative in areas with no deer (slope = −0.038; $r^2 = 0.86$; $p < 0.001$) but not different from zero in areas with deer ($p = 0.821$).
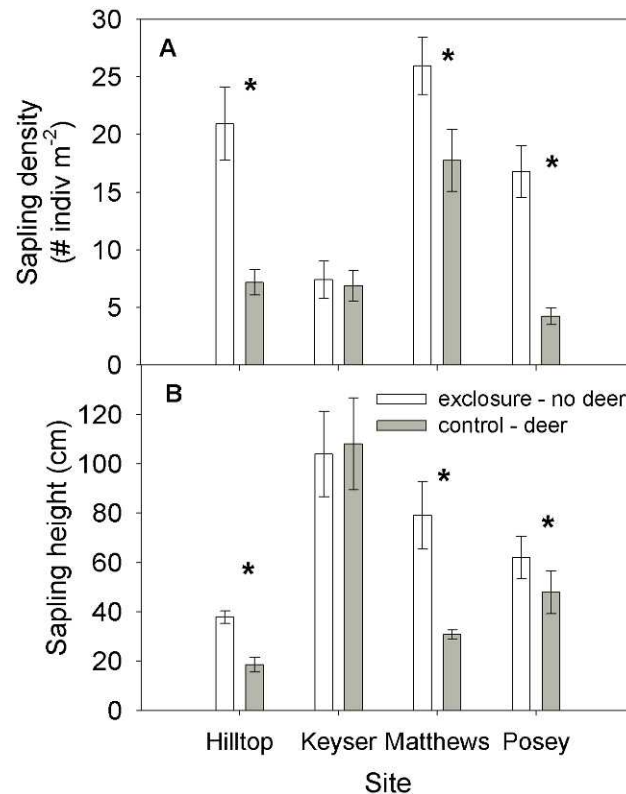
Fig. 2. Mean sapling (A) densities and (B) heights in 4-ha exclosures and control areas at the Shenandoah National Park and Smithsonian Conservation Biology Institute after 16 years of deer exclusion. Saplings represent all live individuals having a dbh ≤10 cm. Sites with significant differences are highlighted with an asterisk. Error bars are standard errors.

Tree growth appeared unresponsive to climate variation at all sites, based on visual inspection of the annual basal area incremental growth (BAI), i.e., BA increase from year t to $t + 1$, and its lack of response to extremes in annual precipitation and mean temperature (Appendix: Fig. C1).

DISCUSSION

Contrary to our initial hypothesis, this study shows that deer can have strong *positive* effects on the growth of adult individuals of *Quercus rubra* within mature deciduous forests. The basal area (BA) growth of mature *Q. rubra* trees was greater in areas exposed to deer than in areas from which deer and other large mammals had been excluded for 16 years. Differences in total BA growth or the mean annual BA increase did not exist prior to deer exclusion, and the magnitude of the growth differences continued

to increase over time. This finding suggests that differences in BA growth after fence construction were indeed due to the deer exclusion treatment, rather than spatial heterogeneity or historical artifacts. Should the differences in growth rate continue, differences will develop in the total BA of *Q. rubra* due to deer presence.

Positive effects of deer on trees contrast with previous studies that have mainly focused on forest understory and juvenile trees. Those studies mainly show that herbivory by deer and other large mammalian herbivores have strong negative effects on plant growth, reproduction, survival, and terrestrial carbon storage (Crête et al. 2001, Russell et al. 2001, Côté et al. 2004, Knight et al. 2009, MacDougall et al. 2010, Tanentzap and Coomes 2012). Herbivory on younger life cycle stage trees will eventually influence the structure of the future mature forest (Husheer et al. 2006, Long et al. 2007, Eschtruth
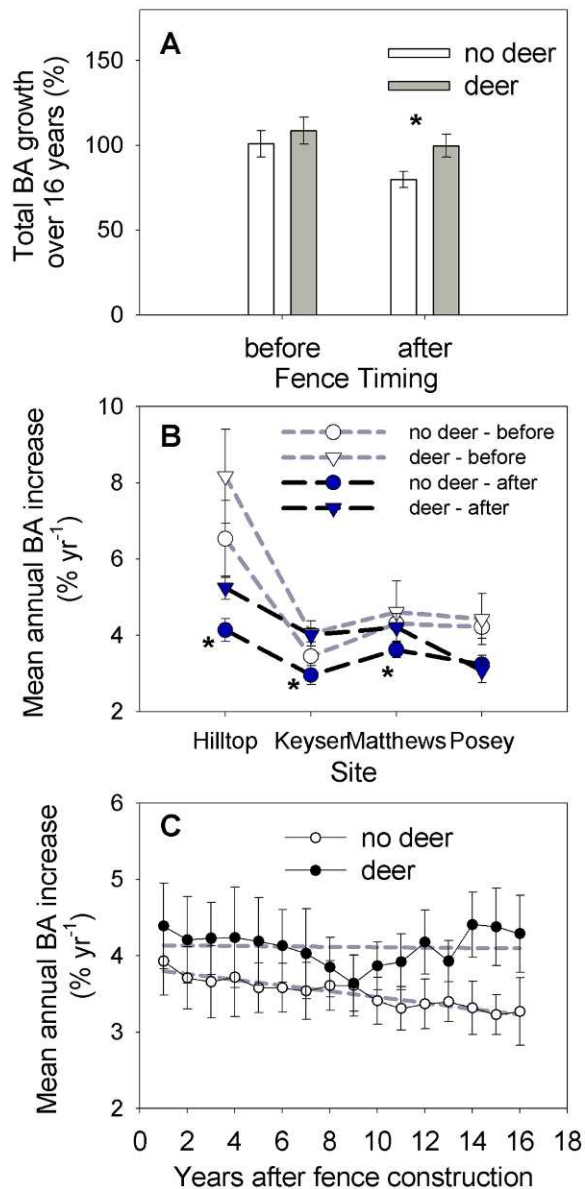
Fig. 3. Differences in the basal area (BA) growth of mature individuals of *Quercus rubra* with and without deer. (A) Total BA growth over the 16 year periods before and after exclusion fence construction. BA growth is expressed as the percent increase of an individual tree at the beginning of the period. Significant differences ($\alpha = 0.05$) indicated by an asterisk. (B) Mean annual increase of BA at each site over the 16 years before or after fence construction. Significant differences between treatments at each site are indicated by an asterisk. (C) Mean annual increase of BA averaged over all sites for the 16 year period following fence construction. Simple linear regression

and Battles 2008), but our findings highlight interactions between deer and the mature canopy trees themselves.

Effects of deer on the growth of mature canopy trees have rarely been reported. The few studies showing impacts of deer on larger tree species include in their definition of mature individuals from young life stages or from smaller size classes with which deer can interact directly through browsing or other means. For example, scrape scars were found on 45-year-old individuals of *Abies balsamea* growing on Anticosti Island, Quebec at heights 3–3.5 m above the ground, presumably generated by white-tailed deer during times of deep snow (Querrec and Filion 2008). Also during the winter, red deer (*Cervus elaphus*) strip bark from many tree species but show a strong preference for 18–30 year old individuals of *Picea abies* (Månsson and Jarnemo 2013). Other studies reporting deer effects on mature trees defined mature trees as those being above 1.4 m (Tanentzap et al. 2011) or 1.5 m in height (Potvin et al. 2003). Consequently, the negative effects of deer reported on mature trees may have been manifested in smaller size classes.

We suggest two non-mutually exclusive explanations for why deer positively affected the growth of mature, canopy individuals of *Q. rubra*. The first we refer to as the deer waste mechanism. Deer can contribute substantial nutrients to ecosystems through the deposition of fecal and urine deposits (Christenson et al. 2010, Jensen et al. 2011). When deer consume food rich in N, they excrete excess N in their urine as urea, a form of N readily available to plants (Mengel and Kirkby 2001, Pastor et al. 2006). In contrast, when deer consume food low in N, they retain as much N as possible, and N excretion is primarily in fecal material which may mineralize even more slowly than soil organic matter (Pastor et al. 1993, Pastor et al. 2006). When deer waste deposits result in the concentration of higher quality nutrients than autochthonous pools, plant litter and soil organic

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(dashed lines) indicated the slope of the mean annual BA increase over time was negative in areas with no deer (slope = -0.038; $r^2 = 0.86$; $p < 0.001$) but not different from zero in areas with deer ($p = 0.821$). Error bars are standard errors.

Table 3. Factors contributing to the variation in the annual basal area (BA) growth of *Q. rubra* over the 16 years following the construction of the exclusion fences. Results are from a repeated measures ANOVA on the mean annual BA increase. Site is treated as a random effect nested within deer exclusion treatment. Denominator degrees of freedom are corrected using the Greenhouse-Giesser epsilon (0.3755) to account for sphericity.

Source	df	F	P
Deer treatment	1, 2.3	70.4	0.01
Deer treatment(site)	6, 1886.3	56.1	<0.001
Year	15, 1886.3	1.8	0.03
Deer treatment × Year	15, 1886.3	0.8	0.65
Deer treatment (site) × Year	90, 1886.3	0.8	0.86
Residuals	5024		

matter, N cycling is positively affected (Ritchie et al. 1998, Pastor et al. 2006), and consequently, feeds back to positively affect plant growth (LeBauer and Treseder 2008). In other words, it is plausible that deer could positively affect plant growth if the nutrient content of their fecal and urine deposits is quantitatively greater than that mineralized from the soil organic matter. Amplification of the N cycle has been observed on Anticosti Island, Canada, where soil nitrification in clear-cut sites with high deer density was approximately 2.5 times greater than in areas with low deer density (Dufresne et al. 2009). In areas of high white-tailed deer use, nitrogenous waste inputs have been measured as high as 13 kg N ha^{-1} yr^{-1} (Jensen et al. 2011). Thus, in areas of high deer density, such as our sites, N inputs from deer waste could be important components of the ecosystem N budget and a strong control on ecosystem productivity.

Support for the deer waste mechanism driving the patterns of increased mature tree growth is seen in soil data from our sites. Concentrations of nitrate and phosphorus in forest soils at the Hilltop and Keyser sites were higher in areas with deer than those from which deer have been excluded (Bressette et al. 2012). Decomposition of soil organic matter was hypothesized to be higher in areas with deer as well (Bressette et al. 2012). If N inputs from deer have had a long-term impact on decomposition and nutrient availability, we would expect to see differences in the total N and C pools of the organic soil. Our findings of significantly greater soil %N and %C in areas with deer at the Hilltop and Matthews Arm sites are consistent with deer having long-term impacts on decomposition and nutrient availability. Significant elevations in soil %N and %C in areas with deer have also been reported at

the Keyser site (Bressette et al. 2012). No such differences in soil nutrient pools have been observed at the Posey site and may explain why there were no effects of deer on the growth of mature trees at the Posey site. Furthermore, soil pH provides a second line of support for the deer waste mechanism. Soil pH was consistently lower in areas with deer and is consistent with increased N additions (Aber et al. 1998). Low level N additions have been found to stimulate decomposition by the soil microbial community (Allison et al. 2009).

The second potential mechanism for enhanced tree growth in the presence of deer is reduced competition for belowground resources associated with the removal of understory vegetation due to browsing. Belowground competition can be intense (Casper and Jackson 1997, Bloor et al. 2008) and has been demonstrated for both saplings and adult trees in other contexts (Bloor et al. 2008, Montgomery et al. 2010). Because understory vegetation represents an important fraction of forest biomass (Knight et al. 2009, Heckel et al. 2010) and is a substantial contributor to ecosystem transpiration (Yepez et al. 2003), competition for water and nutrients may be important in structuring forest communities and could be strongly influenced by deer herbivory. Increased resource competition following reductions in deer population is suggested by a study involving muntjac deer (*Muntiacus reevesi*) in a copice woodland in England where growth, survival, and recruitment of *Corylus avellana* and *Crataegus laevigata* all significantly decreased following a reduction in the deer population (Tanentzap et al. 2012). In our study system, understory biomass is much greater in areas from which deer have been removed (McShea and Rappole 2000, Heckel et al. 2010)

and represents a substantial nutrient sink against which mature trees must compete to secure needed resources. Differences in the understory biomass are reflected in the sapling densities which were significantly greater in areas from which deer have been excluded at all sites except the Keyser site. The lack of difference in sapling density at the Keyser site is explained because at the time of fence construction, the Keyser site had a well-developed subcanopy. Saplings were initially taller, and remain so, at Keyser than at the other sites and many are tall enough to have escaped herbivory pressure by inaccessibility (Tripler et al. 2002). Additionally, shading provided by the taller saplings and canopy trees may have limited establishment of new saplings in this exclosure and thus explain the lower sapling density at this site.

Conclusions

We have shown that deer indirectly affect the growth of mature canopy trees of *Q. rubra*, in a way that is contrary to that expected from previous studies that have focused mainly on smaller or younger tree populations. Growth rates of mature trees affect the long-term population dynamics of forests, particularly because the reproductive success of long-lived organisms, such as trees, relies most heavily on adult life cycle stages (Franco and Silvertown 1996). The next logical step is to investigate the generality of the interactions between deer and mature canopy trees of other species and to understand the mechanisms driving the observed differences. We suggest two potential mechanisms, enhanced nitrogenous inputs from deer waste, or reduced belowground competition due to deer herbivory on the understory. More importantly, understanding the relative importance of these mechanisms could greatly increase our understanding of forest dynamics and help us to understand when deer may have positive or negative effects on ecosystem productivity.

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LITERATURE CITED

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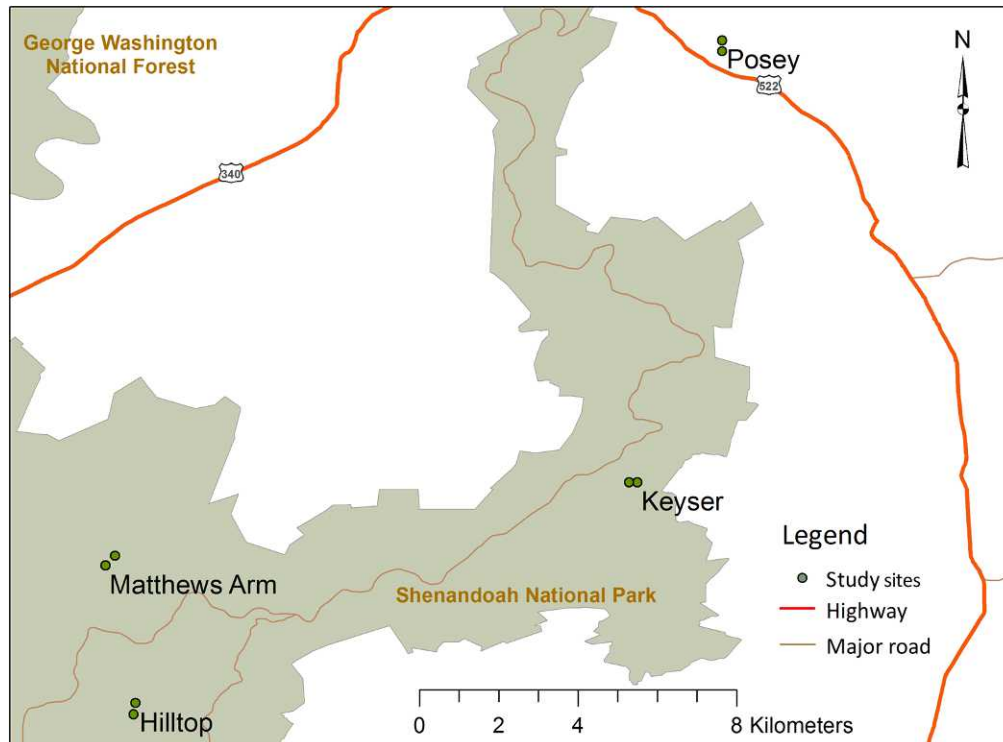
Supplemental Material

Appendix A

Fig. A1. Map of Shenandoah National Park (sites: Hilltop, Keyser, and Matthews Arm) and Smithsonian Conservation Biology Institute (site: Posey) study site locations.

Appendix B

Table B1. Species composition of all trees with dbh >10 cm expressed as a proportion of the total basal area for each site and treatment combination. There are no significant differences between deer and no-deer treatments for total basal area or overall tree density. Units of total basal area and overall density are m^2 ha^{-1} and individuals ha^{-1}, respectively.

| Species	Hilltop		Keyser		Matthews Arm		Posey	
	No deer	Deer	No deer	Deer	No deer	Deer	No deer	Deer
Acer pensylvanicum	0.02	0.03	0.04	0.03	0.01	0.03	0	0
Acer rubrum	0.02	0.06	0.23	0.09	0.08	0.06	0.14	0.14
Acer saccharinum	0	0	0	0.04	0	0.06	0	0
Acer saccharum	0.02	0	0	0	0	0	0.05	0.07
Betua lutea	0.03	0.04	0.08	0.02	0.03	0.03	0.12	0
Caprinus caroliniana	0	0	0	0	0	0	0	0.02
Carya glabra	0.03	0.02	0	0.05	0.06	0.05	0	0.08
Carya ovata	0	0.09	0	0	0.07	0.03	0.03	0.07
Carya tomentosa	0.01	0.02	0	0.07	0.10	0.04	0	0
Carya sp.	0.03	0.01	0.05	0	0	0	0.04	0.12
Celtis occidentalis	0	0.01	0	0	0	0.04	0.01	0
Cornus florida	0	0	0	0	0	0.02	0	0
Diospyros virginiana	0.16	0	0	0	0	0.02	0	0
Fagus grandifolia	0.02	0.09	0.05	0	0	0	0.03	0.04
Fraxinus americana	0.13	0.12	0.15	0.04	0	0.07	0.06	0.13
Hamemelis verginiana	0	0.01	0	0.05	0	0	0	0
Liriodendron tulipifera	0.12	0.14	0	0	0	0.01	0.10	0.13
Ostrya virginiana	0	0	0	0	0	0	0.01	0
Prunus serotina	0	0.07	0	0.08	0.02	0.01	0	0
Quercus alba	0.09	0.18	0.11	0.20	0.14	0.29	0.08	0
Quercus palustris	0.03	0	0	0	0	0	0	0
Quercus prinus	0	0	0	0.12	0	0.02	0.09	0
Quercus rubra	0.17	0.10	0.25	0.14	0.37	0.15	0.10	0.10
Quercus velutina	0.12	0	0	0	0	0	0.09	0
Robina pseudoacacia	0	0	0	0	0.01	0	0	0
Tilia americana	0	0	0	0	0.01	0	0	0
Ulnus americana	0	0.04	0.05	0	0	0	0.06	0.11
Unknown	0	0	0	0	0	0.04	0	0
Total basal area (SE)	3.17 (0.70)	2.63 (0.76)	1.63 (0.29)	1.59 (0.35)	2.86 (0.49)	1.86 (0.07)	4.15 (0.37)	4.33 (0.88)
Overall density (SE)	449 (83)	559 (153)	466 (70)	529 (26)	538 (72)	710 (83)	343 (15)	290 (51)

Appendix C
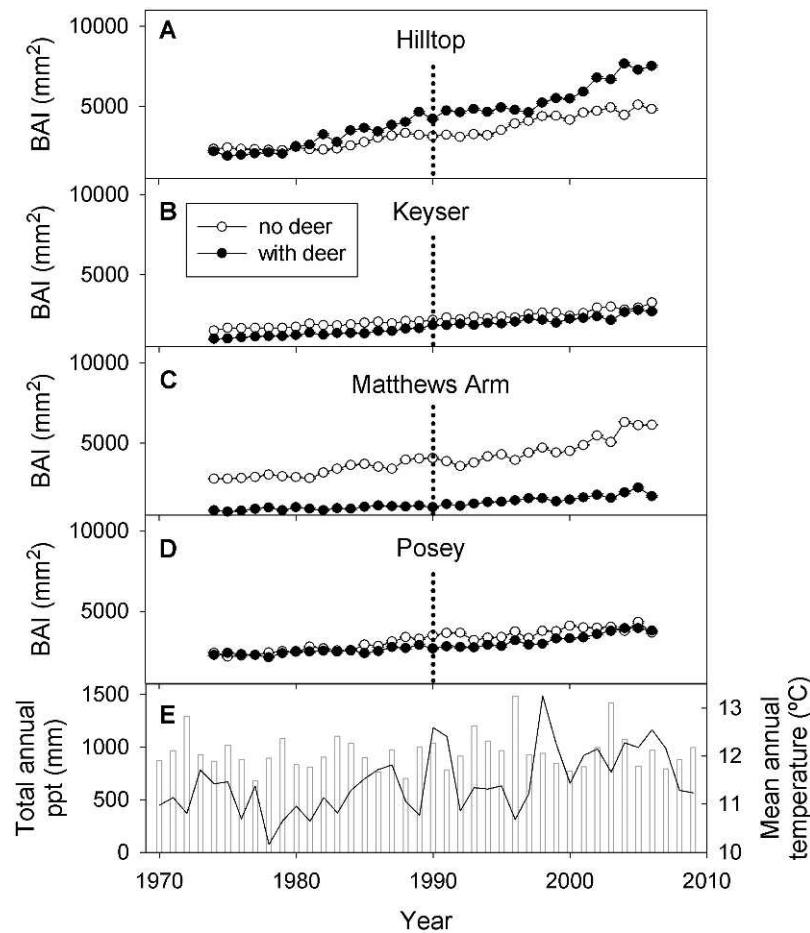
Fig. C1. Mean annual basal area increment (BAI) growth (raw) and standard deviations of adult *Q. rubra* trees growing in the canopy at four sites in Virginia (A–D) that have excluded deer herbivory since 1990 (onset of herbivory exclusion indicated with dotted vertical line) and paired controls that have allowed open access to deer continuously. Error bars are often smaller than the symbol. Exclusion plots and control plots were 4 ha in size. (E) Climate record summarizing total annual precipitation (bars) and mean annual temperature (line) from 1970 to 2009 for NOAA's Woodstock, VA site, about 50 km from study sites.