

## Effects of Twenty Years of Deer Exclusion on Woody Vegetation at Three Life-History Stages in a Mid-Atlantic Temperate Deciduous Forest

Jennifer C. McGarvey<sup>1,2</sup>, Norman A. Bourg<sup>1</sup>, Jonathan R. Thompson<sup>1,\*</sup>,  
William J. McShea<sup>1</sup>, and Xiaoli Shen<sup>1</sup>

**Abstract** - Chronic browsing by *Odocoileus virginianus* (White-tailed Deer) has potential to alter the life history of trees within Mid-Atlantic forests, including seedling size and abundance in the short term to overstory composition in the long term. Most studies quantify the effects of deer browse using small plots (<1 ha) and short time frames (<10 years), which may misrepresent larger-scale and longer-term impacts. We maintained a 4-ha deer exclusion plot for 20 years in a mesic northern Virginia temperate deciduous forest to examine the impacts of browsing on forest trees at multiple life-history stages. We compared the abundance and species composition, as well as seedling height, of woody stems across the seedling, small-sapling, and large-sapling size classes inside the deer enclosure and within an adjacent reference area. There were no significant differences in seedling abundance or community composition, but seedling height was on average 2.25 times greater in the enclosure than the reference plot. Small-sapling (1–5 cm DBH) stem count was 4.1 times greater inside the enclosure, with all species more abundant in the enclosure except *Asimina triloba* (Pawpaw) and *Carya tomentosa* (Mockernut Hickory). Differences were smaller in the large-sapling size class (5–10 cm DBH), with relative total large-sapling stem count only 1.25 times greater in the enclosure. Browsing pressure appeared to influence the composition and size structure of smaller stems in the past 20 years, but has had little effect on larger stems. While the lack of replication limited the scope of inference of our study, our findings suggest that natural delays in mature tree recruitment in a closed-canopy forest may mask the full impact of deer herbivory for decades.

### Introduction

In many temperate forests of the eastern United States, populations of *Odocoileus virginianus* Zimmermann (White-tailed Deer) have increased dramatically over the past 50 years (McShea et al. 1997). Suggested reasons for their population growth include hunting restrictions, a decline in the number of hunters due to social, ecological, and political challenges associated with deer population management, reduced predator populations, and improved habitat (Brown et al. 2000, Côté et al. 2004, Rooney 2001). High White-tailed Deer densities have been shown to affect short-term vegetation dynamics in deciduous forests of the eastern United States by manipulating nutrient cycles and availability (Hobbs 1996), facilitating the spread of exotic species (Eschtruth and Battles 2009), and reducing understory and woody species abundance (Rooney and Dress 1997).

---

<sup>1</sup>Smithsonian Institution, Smithsonian Conservation Biology Institute, 1500 Remount Road, Front Royal, VA 22630. <sup>2</sup>Department of Environmental Sciences, University of Virginia, Clark Hall, Charlottesville, VA. \*Corresponding author - thompsonjr@si.edu.

Short-term effects of deer browsing on woody vegetation may compound over time, eventually causing alternate stable states in woody vegetation communities (Stromayer and Warren 1997) and re-directing successional trends (Liang and Seagle 2002).

The vast majority of stems regenerating under a closed canopy fail to reach the overstory due to insufficient light, water, or nutrients (Mladenoff and Stearns 1993, Peet and Christensen 1987). In addition, intense browsing by deer has the potential to influence long-term successional dynamics by limiting seedling survival and sapling growth. At an individual level, browsing of leaves and shoots delays aboveground growth of seedlings, consequently reducing seedling survival rates and densities (Dzieciolowski 1980, Gill and Beardall 2001, Healy 1997, König 1976, Putman et al. 1989). High deer densities may further inhibit seedling survival and growth by facilitating invasion of weedy forbs and grasses that compete with native seedlings (Horsley and Marquis 1983). Deer browsing has a similarly direct effect on small-sapling growth and survival by reducing photosynthetic capability, increasing mortality risk (Tripler et al. 2002), and inhibiting vertical recruitment (Liang and Seagle 2002). Selective browsing on palatable species at these two life-history stages potentially influences successional dynamics by altering the composition, density, and diversity of the understory layer (Horsley et al. 2003, Matonis et al. 2011, Rooney and Waller 2003, Stoeckeler et al. 1957). Healy (1997) predicted that loss of *Quercus* spp. (oak) seedlings due to chronic deer browsing in an oak-dominated forest in central Massachusetts eventually would cause the elimination of oaks from the overstory. Intense browsing on seedlings and small saplings may further impact successional status by changing stand structure to one where large saplings and mature trees are disproportionately represented (Anderson and Loucks 1979, Côté et al. 2004, Potvin et al. 2003, Stromayer and Warren 1997, Tilghman 1989). Finally, deer browsing may accelerate the rate of change to late-successional species. For example, Liang and Seagle (2002) predicted that the increased mortality of shade-intolerant *Liriodendron tulipifera* L. (Tulip Poplar) due to browsing by deer would cause stands in a riparian forest in Maryland to more quickly succeed to the shade-tolerant *Fagus grandifolia* Ehrh. (American Beech). Overall, deer may inhibit colonization, growth, and survival of seedlings and saplings, to eventually alter forest succession (Côté et al. 2004, Hobbs 1996, Ritchie et al. 1998).

Other enclosure studies indicate the challenge of detecting the long-term effects of chronic deer browsing within the constraints of short-term study durations. Apsley and McCarthy (2004) observed a significant increase in woody stem height following the exclusion of deer for two years after harvest in southern Ohio mixed oak forests, but no difference in community composition or density, suggesting it was too early to detect a significant effect of deer browsing on woody vegetation regeneration. After twelve years of deer exclusion, hemlock seedlings were able to re-establish in a northern Wisconsin forest, but there were no detectable changes in sapling regeneration (Anderson and Katz 1993). Similarly, following eighteen years of deer exclusion in a mixed-oak forest in Pennsylvania, Abrams and Johnson (2012) observed an increase in tree seedling

number, but no stimulation of oak regeneration and sapling recruitment. Overall, the long-term influence of persistent deer browsing on forest stand dynamics is not well understood, as previous studies typically have been spatially and temporally limited with deer exclosures smaller than 1 ha or experiments often lasting less than ten years (Bowersox et al. 1995, Long et al. 2007, Rossell et al. 2005, Sage et al. 2003, Tilghman 1989).

We quantified the impacts of intense deer browsing on tree composition and structure by contrasting a 20-year, 4-ha deer exclosure with a comparable forest area within the same stand of a Mid-Atlantic temperate deciduous forest subjected to persistently high deer densities. Specifically we asked: Do woody seedling species abundance, height, and composition differ between the deer-excluded and reference areas? Also, does the composition of small and large saplings differ between the treatment and reference areas?

### Site Description

The 4-ha deer exclosure was erected in 1990. It is located within a 25.6-ha Smithsonian Institute Global Earth Observatory (SIGEO; [www.si.sigeo.edu](http://www.si.sigeo.edu)) forest dynamics plot at the Smithsonian Conservation Biology Institute (SCBI), a 1295-ha research facility located 3 km SE of Front Royal, VA (38°54N, 78°09W). A 2.4-m wire fence surrounds the exclosure. The fence is maintained through regular inspections for fallen tree limbs or trunks. Any deer that gain entry into the exclosure are pushed out through a southwest-facing gate. The SIGEO plot is located in a mature secondary mixed deciduous forest, with overstory tree ages ranging from 84 to 124 years (J.R. Thompson and J.C. McGarvey, unpubl. data). The canopy is dominated by Tulip Poplar, *Quercus alba* L. (White Oak), *Q. rubra* L. (Northern Red Oak), *Q. prinus* L. (Chestnut Oak), *Q. velutina* Lam. (Black Oak), *Fraxinus americana* L. (White Ash), *Carya glabra* Mill. (Pignut Hickory), *C. tomentosa* (Lam. ex Pior.) Nutt. (Mockernut Hickory), and *Nyssa sylvatica* Marsh. (Blackgum). Prominent understory components include *Lindera benzoin* L. (Spicebush), *Asimina triloba* L. (Pawpaw), *Carpinus caroliniana* Walter (American Hornbeam/Ironwood), *Cercis canadensis* L. (Eastern Redbud), and *Cornus florida* L. (Flowering Dogwood). The plot is composed primarily of Myersville and Montalto series soils, which are stony, steep, and well-drained. The mean annual temperature for the area based on a nearby site is  $12.7 \pm 0.66$  °C and the mean annual cumulative precipitation is  $96.2 \pm 15.8$  cm (D.E. Carr, University of Virginia, Charlottesville, VA, 2011 unpubl. data). Elevation ranges from 273 to 338 m. The deer exclosure is on an average slope of 10° (range = 4–17°) with a western aspect (average = 267°, range = 228–332°). Since the exclosure was constructed, estimates of deer density in the entirety of SCBI have fluctuated at around 30 to 40 deer/km<sup>2</sup> (Heckel et al. 2010, McShea 2000, McShea and Schwede 1993) based on distance sampling methods and match estimates for the past 20 years.

In January 2011, we identified a similarly sized area subjected to deer browse to compare to the exclosure. We selected this “reference plot” on the criteria that it was within the SIGEO plot, and had similar: (1) size, (2) overstory composition,

and (3) topographic setting to the enclosure. To objectively make this selection, we classified each of the six hundred forty 20- x 20-m (400-m<sup>2</sup>) quadrats that form the SIGEO plot to a group based on its overstory composition (i.e., basal area by species) following Ward's method of hierarchical cluster analysis with a Euclidean distance matrix using the *vegan* library (Oksanen et al. 2011) within the R statistical language (R Development Core Team 2010). Ward's method minimizes group sites by reducing the distance from each site to the centroid of the group and is a robust method of classifying ecological community data (McCune and Medford 1999). While Sørensen is a preferred measure of compositional dissimilarity (and is what we used elsewhere in our analysis), it is incompatible with Ward's method; Euclidean distance, in contrast, is reliable and effective for use in clustering (McCune et al. 2000). By examining the resulting dendrogram and the percentage of information remaining after the formation of each cluster, we settled on eight groups and mapped them on the SIGEO plot. We then identified the proportion of quadrats assigned to each group within the deer enclosure and found an approximately equal-sized area with the most similar overstory compositional distribution. The identified site was 4 ha, and closely matched the enclosure in terms of overstory composition (Fig. 1), land-use history, slope (mean = 11°, range = 1–20°), and aspect (mean = 260°, range = 4–360°).

Neither the deer enclosure nor the reference area was replicated. Therefore, our samples of seed rain and our seedling plots that were randomly distributed throughout the two areas (as described below) were pseudoreplicates (*sensu* Hurlbert 1984). Similarly, our analyses of the small and large saplings (1–10 cm DBH [diameter-at-breast-height; also described below]) is based on a complete census of the areas and no greater inference is implied or warranted.

## Methods

We examined seed rain composition within the enclosure and reference area to further evaluate our rationale for comparing the two sites (i.e., that similar overstory would result in similar seed production and, in turn, similar regeneration potential). Seed rain was monitored from April 2009 to April 2011 in randomly placed 0.5-m<sup>2</sup> traps with a minimum of 20-m between each trap. Traps were distributed based on habitat types, with a set number of traps in each type. Samples were collected biweekly from the traps within the enclosure ( $n = 38$ ) and the reference plot ( $n = 32$ ), with the exception of monthly collections from December 2010 to March 2011 and no collections from January to April 2010 due to heavy snow accumulations. Sampling efforts varied between collection dates due to trap damage, and so relative annual seed abundances (seeds/total seeds/m<sup>2</sup>/year) rather than total seed counts (seeds/m<sup>2</sup>/year) were used in the analysis to account for variability. Traps were elevated off the ground and frequently sampled to reduce risk of seed predation. All seeds and fruits collected were identified to species whenever possible. Counts of individuals per species during each sampling period were categorized into four bins: 1, 2–5, 5–20, and >21 individuals. The mid-point values for each of the first three bins, and the minimum value for the fourth bin, were then used to estimate abundance for each species. Because

seeds still attached to multi-seeded fruits were not physically removed and counted, fruits and seeds were considered equivalent during analysis. We tested for differences in overall community composition between the enclosure and the reference using a permutation-based MANOVA (i.e., PerMANOVA; Anderson 2001), with a Sørensen's distance matrix and 9999 permutations as implemented in the *adonis()* function of the Vegan library (Oksanen et al. 2011) within the R statistical language (R Development Core Team 2010). In addition, we compared absolute and relative (seeds/m<sup>2</sup>/basal area m<sup>2</sup>/yr) seed abundance by species between the enclosure and the reference area by identifying any overlap in the 95% confidence intervals of the means based on the Student's *t*-distribution.

We surveyed seedlings from July to August 2010, and re-surveyed from June to August 2011. Seedlings were defined as woody tree stems <1 cm DBH. We identified to species and measured the height of all seedlings in three 1-m<sup>2</sup> sub-plots placed 2 m away to the east, west, and south of randomly-selected seed rain traps within the enclosure (*n* = 30) and the reference area (*n* = 17). The proximity of the seedling plots to the seed traps allowed for accurate evaluation of seed-to-seedling transitions. Data from the three sub-plots at each seed trap were pooled

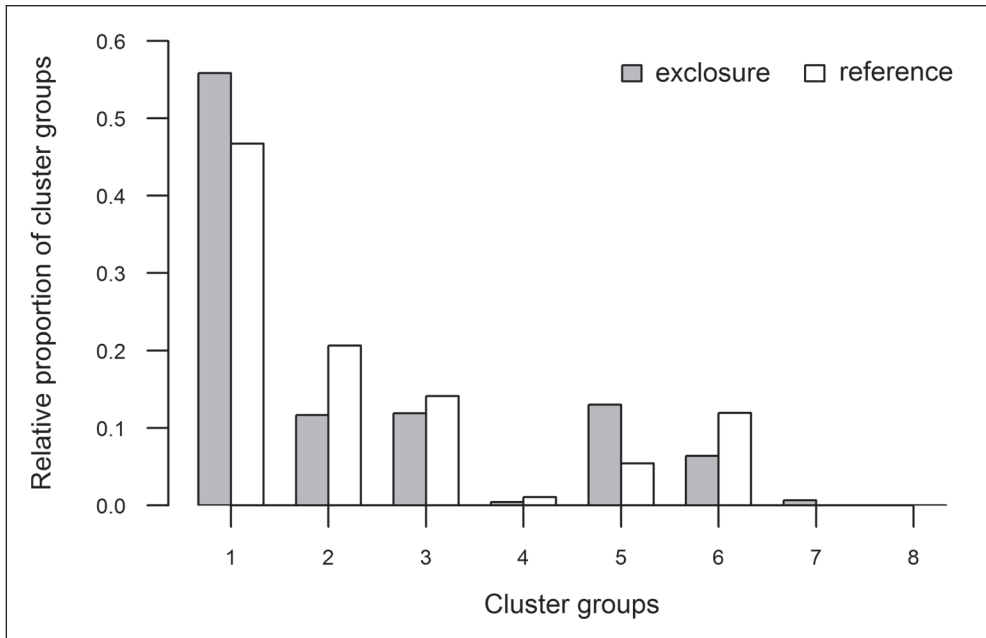


Figure 1. The relative proportion of each cluster group in the enclosure and the reference plot. The numbers refer to overstory community types using a cluster analysis based on basal area of the ten dominant tree species in each unit. Each community type is described here based on the species that make up approximately 80% of the basal area in that group, where 1 = *Fraxinus americana*, *Liriodendron tulipifera*, *Quercus prinus*, and *Carya glabra*; 2 = *L. tulipifera*; 3 = *L. tulipifera*, *Q. velutina*, *C. glabra*, and *C. tomentosa*; 4 = *Q. rubra*, *L. tulipifera*, *Q. velutina*, and *C. glabra*; 5 = *Acer rubrum*, *Nyssa sylvatica*, and *Q. prinus*; 6 = *Q. alba*, *L. tulipifera*, *Q. rubra*, and *Q. velutina*; 7 = *Q. velutina*, *L. tulipifera*, and *Q. alba*; 8 = variable.

together and averaged across the two sampling years to calculate species abundance. While woody shrubs and to a lesser extent vines were both components of the understory vegetation, our analyses focused on the understory and canopy tree species that had the physiological potential to grow into the large-sapling size class. We compared average relative seedling abundance (seedlings/m<sup>2</sup>/year), average seedling height, and small- and large-sapling density of the twenty most abundant tree species relative to their size class for the reference area and the exclosure by identifying any overlap in the 95% confidence intervals around the means (using the Student's *t*-distribution). We compared overall seedling community composition between the exclosure and reference area, again using a PerMANOVA and a Sørensen distance matrix.

The seed rain and seedling surveys were part of larger-scale studies conducted throughout the SIGEO plot. As a result, differences in sampling efforts between the reference plot and the exclosure reflect the sampling design of the larger-scale studies. Specifically, seedling plots were randomly stratified to adequately sample stream courses in the plot and the exclosure, resulting in a greater sampling effort in the exclosure than the reference area. The 95% confidence interval estimates for seed rain and seedling abundance and the subsequent analysis may reflect differences in sampling effort, as well as variability within the sample.

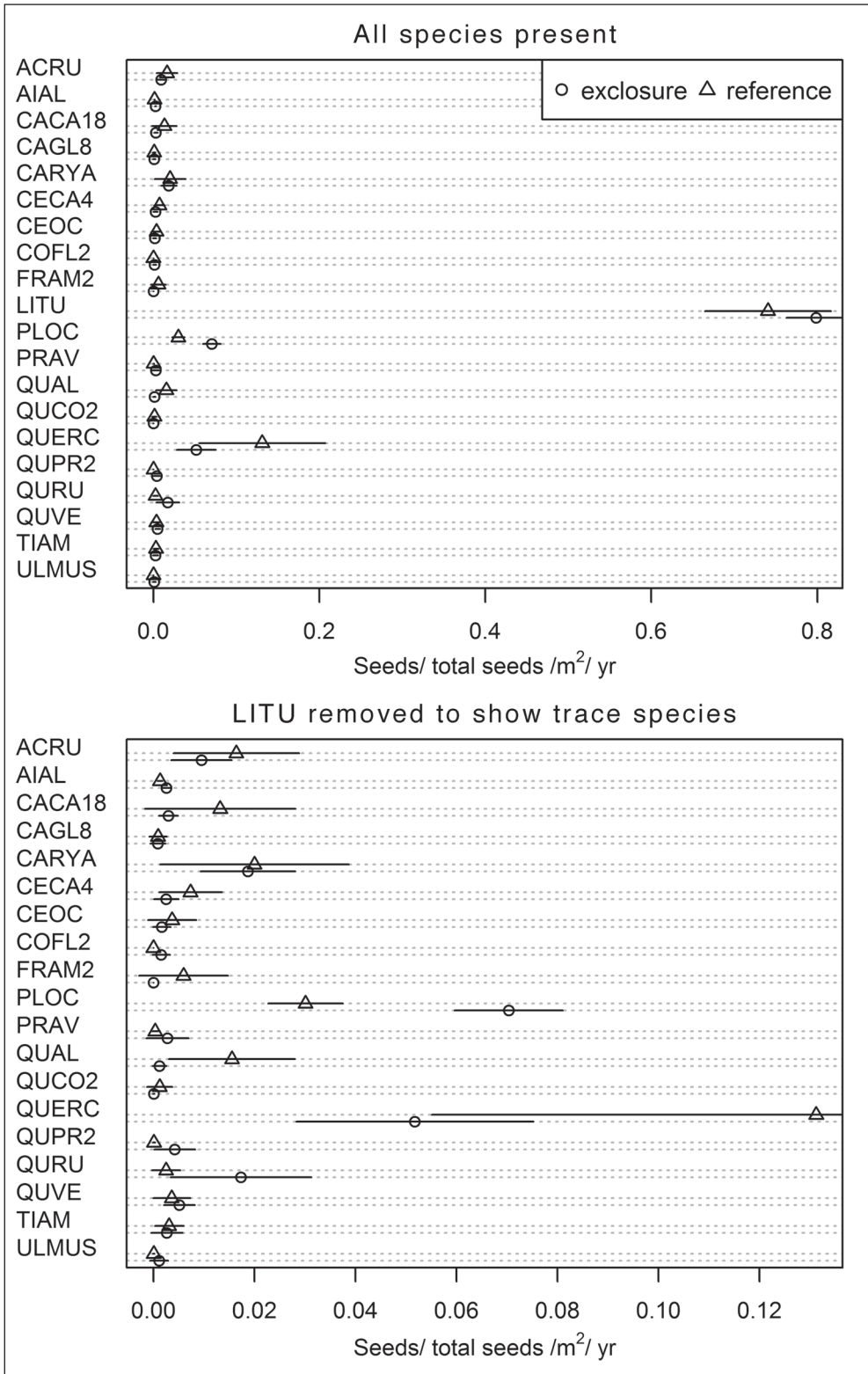
From June to December 2008, a census of all woody stems  $\geq 1$  cm DBH was completed in the SIGEO plot using the methodology of Condit (1998). All stems were identified to species, measured for DBH, tagged and mapped on a global x, y-coordinate system where any given stem was measured in meters relative to the southwest corner of the SIGEO plot. Stems ranging from 1 to 5 cm DBH were classified as small saplings, and stems ranging from 5.1 to 10 cm DBH were classified as large saplings for our analysis. Because we had a complete census of all saplings, no statistical tests were needed to compare differences between the exclosure and reference areas.

## Results

There was no significant difference between the exclosure and the reference site in overall community composition of the seed rain, whether scaled by basal area or not ( $df = 70$ ,  $P = 0.09$  and  $0.95$ , respectively). Of the twenty most abundant tree species, average yearly relative seed rain abundance was significantly different for only *Platanus occidentalis* L. (American Sycamore) and White Oak. American Sycamore was significantly more abundant inside the exclosure (exclosure =  $0.07 \pm 0.011$  seeds/total seeds/m<sup>2</sup>/year, reference =  $0.030 \pm 0.007$  seeds/total seeds/m<sup>2</sup>/year) and in the reference for White Oak (exclosure =  $0.001 \pm 0.001$  seeds/total seeds/m<sup>2</sup>/year, reference =  $0.015 \pm 0.012$  seeds/total seeds/m<sup>2</sup>/year) (Fig. 2). Only two species had significantly different average relative seed

---

Figure 2 (opposite page). Mean annual relative seed abundance of the 20 most abundant tree species (top) and with LITU removed to show minor species (bottom). In both graphs, error bars represent 95% confidence intervals around the mean based on *t*-distribution. See Appendix A for definitions of species codes.



production, with *Acer negundo* L. (Box Elder) (exclosure =  $0.029 \pm 0.020$  seeds/m<sup>2</sup>/basal area m<sup>2</sup>/yr, reference = 0.0 seeds/m<sup>2</sup>/basal area m<sup>2</sup>/yr) and *Ailanthus altissima* Mill. (Tree-of-heaven) (exclosure =  $0.124 \pm 0.042$  seeds/m<sup>2</sup>/basal area m<sup>2</sup>/yr, reference = 0.0 seeds/m<sup>2</sup>/basal area m<sup>2</sup>/yr) having greater relative seed production in the exclosure than the reference (Fig. 3). Notably, while seed rain overall was an accurate predictor of canopy composition, a major portion of the American Sycamore and Tree-of-Heaven seeds likely came from off the plots, as there are few American Sycamores and no mature Tree-of-Heaven individuals in either the exclosure or the reference plots.

Mean seedling height was nearly 2.25 times greater in the exclosure than in the reference area (exclosure =  $18.0 \pm 1.0$  cm, reference =  $8.76 \pm 0.39$  cm). In contrast, there were few differences in seedling abundances. Specifically, there were no differences in species-level abundance, and the rank abundance for the top ten species were the same in the exclosure and reference area (Fig. 4). The tests for difference in overall community change were insignificant with a marginal *P*-value (*df* = 69, *P* = 0.06).

In the census of the twenty most abundant small tree saplings (1–5 cm DBH), total stem count for all species was 4.1 times greater in the exclosure than the reference area. With the exception of Pawpaw and Mockernut Hickory, all species were more abundant in the exclosure (Fig. 5A). There was a less notable difference in large-sapling (5.1–10 cm DBH) abundance than small-sapling abundance. Stem count was only 1.25 times greater for large tree saplings. Only eighteen species occurred in this size class in both the exclosure and the reference area, and seven of these species were more abundant in the exclosure (Fig. 5B).

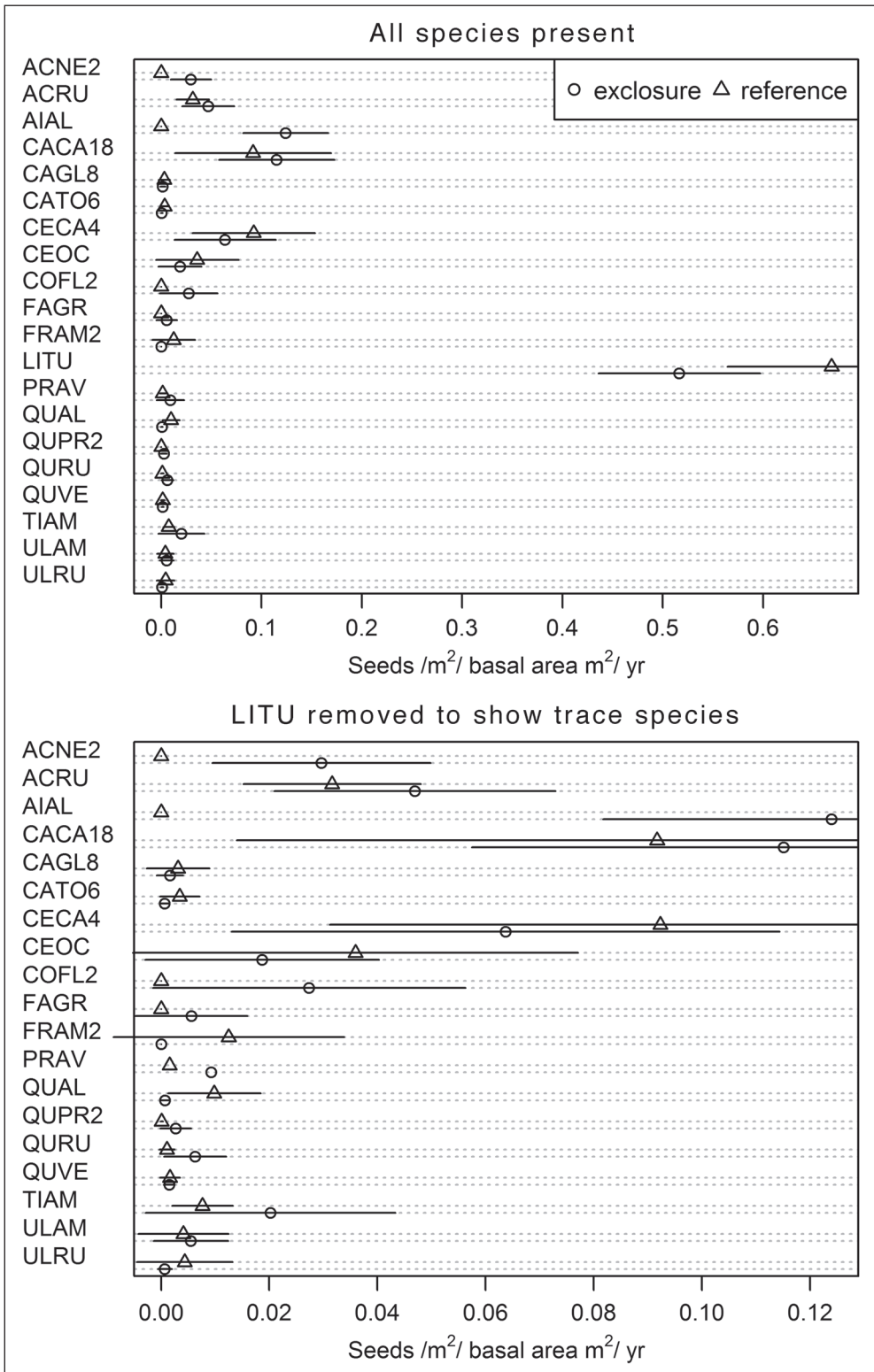
## Discussion

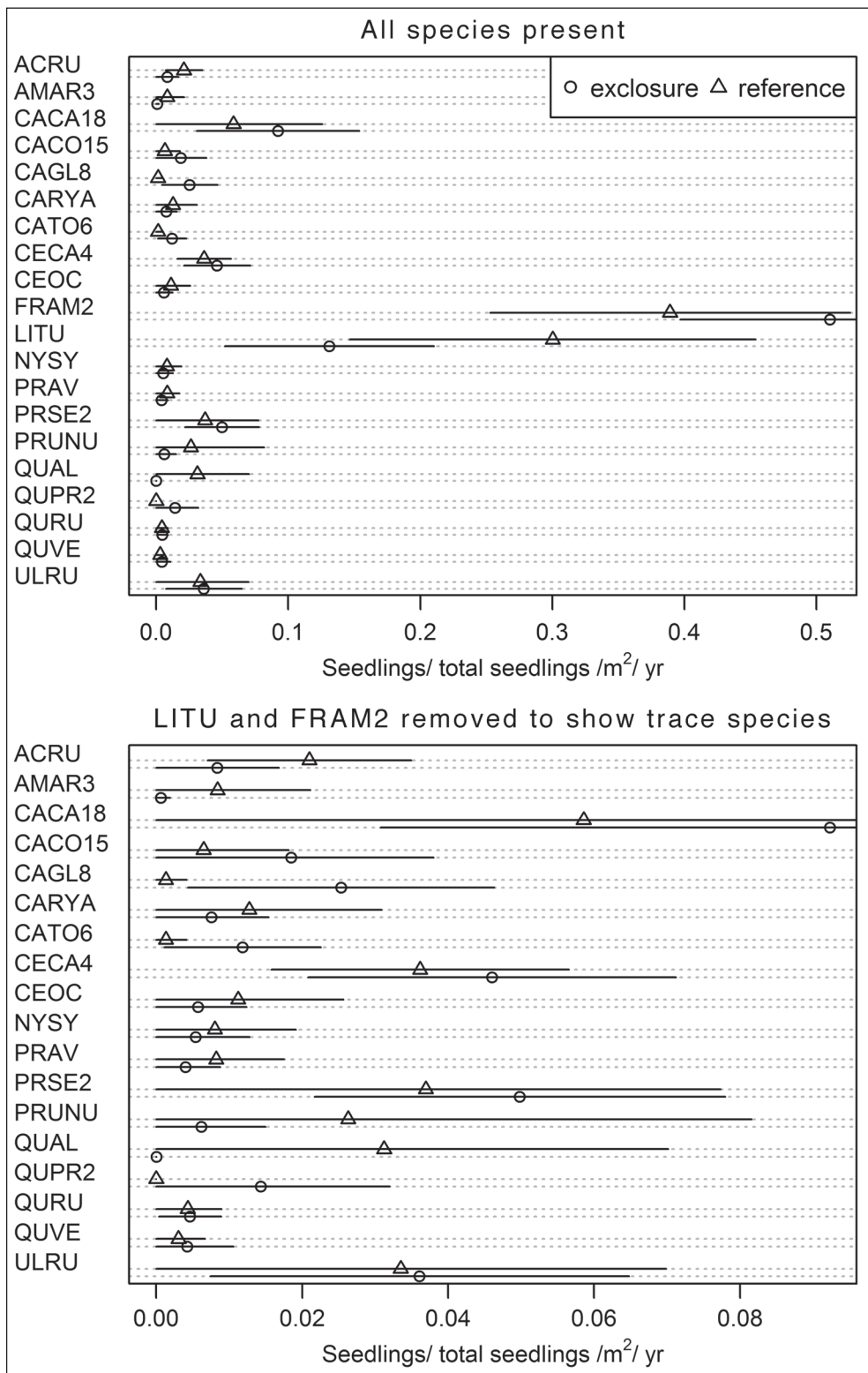
Of the four life-history stages examined, seedling height and small-sapling abundance were most notably reduced by deer browsing. Seedling height was over twice that in the exclosure than in the reference plot. Previous studies have observed similar effects of deer browsing on seedlings. Apsley and McCarthy (2004) found no differences in the seedling densities of ten hardwood species (with the exception of Blackgum) in southern Ohio mixed oak forests following two years of deer exclusion, but seedlings were on average approximately 16.1% shorter in the non-excluded areas. This effect of deer browsing on seedling height in the SIGEO plot and at other deciduous forest sites also has been documented for herbaceous species (Anderson 1994, Fletcher et al. 2001, Goetsch et al. 2011, Heckel et al. 2010). Inhibiting stem growth at this stage has the potential to alter species composition and stand structure. Limiting seedling height may increase mortality risk through competition with other understory vegetation, thereby

---

Figure 3 (opposite page). Mean annual relative seed production of the 20 most abundant tree species scaled by basal area of tree species (top) and with LITU removed to show minor species (bottom). In both graphs, error bars represent 95% confidence intervals around the mean based on *t*-distribution. See Appendix A for definitions of species codes.







altering future species composition (Tilghman 1989). While these implications are compelling, greater seedling height in the exclosure will only be advantageous, in successional terms, if other resources (i.e., water, light, and nutrients) are also available to the seedling.

Similar seedling abundances suggest that factors other than deer browsing determine seedling establishment and short-term survival. Two possible factors may be light availability and leaf-litter depth. Light availability is widely considered a key factor in determining species composition, favoring early-successional seedlings in high light levels and to a lesser extent in low levels (Beaudet and Messier 1998, Cornelissen et al. 1996, Walters et al. 1993). Similarly, leaf-litter depth may affect seedling species richness (Xiong and Nilsson 1999). Litter accumulation is correlated with reduced species diversity, inhibiting seedling establishment by acting as a barrier to seeds accessing soil moisture (Kota et al. 2007). Above all, seedling mortality frequently is unpredictable because of considerable annual variability in both precipitation and seed production by canopy trees (Boerner and Brinkman 1996). This variability may mask effects of deer browsing on seedling abundance.

We observed a delayed effect of deer herbivory on species abundance between the seedling and small-sapling size classes. Small saplings were overwhelmingly more abundant in the exclosure than in the reference area for all species, with the exception of Pawpaw and Mockernut Hickory (Fig. 5A). Our results support findings from smaller-scale exclosure studies, with deer browsing having the most notable effect on woody stems at this life-history stage (Rooney et al. 2000). Pawpaw is unpalatable to deer (Asnani et al. 2006), perhaps explaining why it was more successful in the reference plot. We do not know why Mockernut Hickory was slightly more abundant in the reference plot as it is palatable, and previous studies have identified herbivory as a primary factor limiting Mockernut Hickory seedling establishment (e.g., McCarthy 1994, Myster and McCarthy 1989).

Differences in large-sapling abundances were less apparent than those observed in the small-sapling class (Fig. 5B). Once the leader stem is out of the browse zone (approximately 2 m), deer-caused mortality is less likely (Vila et al. 2002). These larger saplings might have reached this height prior to the installation of the deer exclosure, and so did not benefit from the reduced browsing pressure. However, another explanation might be that deer had no role promoting or inhibiting the transition of stems from small to large saplings; rather, other environmental variables determined the survivorship of small saplings. Without knowing the age of the larger saplings, we cannot determine whether they generated before the exclosure installation, and so were subjected to deer browsing, or

---

Figure 4 (opposite page). Average annual relative abundance of the 20 most abundant tree seedlings (top) and with LITU and FRAM2 removed to show minor species (bottom). In both graphs, error bars indicate 95% confidence intervals around the mean based on a *t*-distribution. See Appendix A for definitions of species codes.

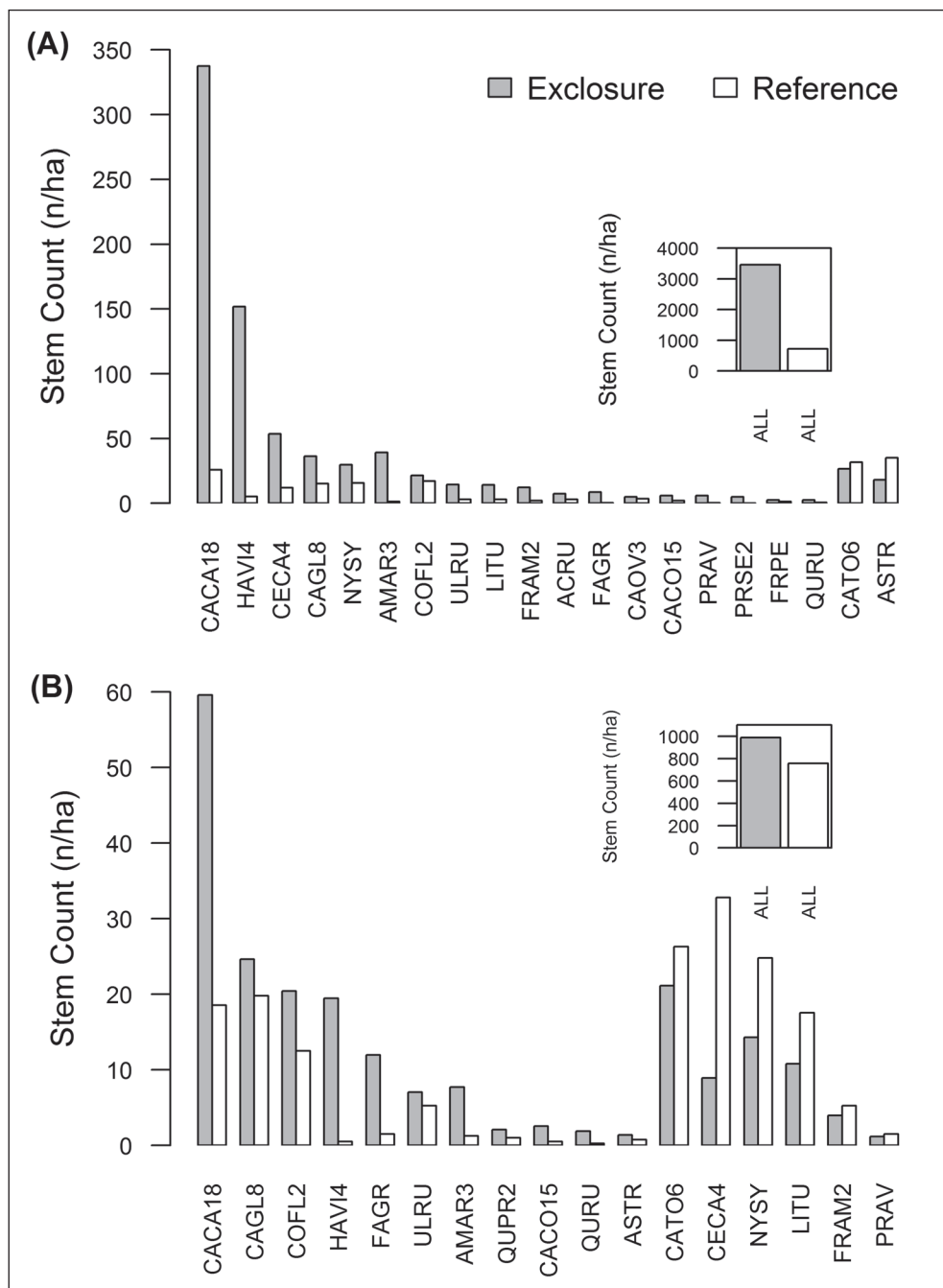


Figure 5. (A) Census of the 20 most abundant small saplings (1–5 cm DBH). (B) Census of the 18 most abundant large saplings (5.1–10 cm DBH). Graphs sorted by the most abundant species in the exclosure followed by species most abundant in the reference area. The inset graphs are of the sum total of the 20 most abundant tree saplings. Confidence intervals and *P*-values were not calculated because we had a complete census of stems >1 cm DBH. See Appendix A for definitions of species codes.

afterwards, implying large-sapling abundance was controlled by other variables. We addressed this age question post hoc by sampling large saplings ( $n = 30$ ) from along the northern and eastern edge of the SIGEO study area in November 2011. We did not collect sapling cores from inside the reference or enclosure in order to preserve the integrity of other on-going studies. The overstory in this ancillary sampling area had a similar species composition and age to the reference and enclosure. We selected both potential canopy and understory tree species to reflect the sapling species composition seen in the enclosure and reference area. On average, saplings were notably older than 20 years ( $47 \pm 5.5$  years), and so were well-established at the time of the enclosure installation. This result supports our first conclusion, that many of the large saplings in both the reference and enclosure were subjected to the same browsing pressure in the small sapling stage. It also implies that the predominant size-class transition to occur since the installation of the deer enclosure was from seedling to small sapling.

### Conclusions

After 20 years of excluding deer, we found more than a two-fold difference in average tree seedling height and a four-fold increase in the abundance of small saplings, with significant increases found across nearly all sapling species. In contrast, we found little difference in seedling abundance or seedling community composition, and only a small difference in the abundance of large saplings. Given the differences in understory seedling height, the most significant impact of deer browse will only be realized through interactions with gap-scale disturbance. Clearly, whether or not advanced regeneration is present to utilize newly available resources is dramatically affected by chronic browsing. Relative to the complete absence of White-tailed Deer, deer browsing has been shown to negatively influence woody vegetation height and species richness at densities as low as 4 deer/km<sup>2</sup>, a substantially lower deer density than observed at SCBI and in most eastern forests (Horsley et al. 2003). Nonetheless, as stated by Mladenoff and Stearns (1993) regarding hemlock in the Northern Great Lakes region, deer herbivory is only one of several pertinent factors that determine regeneration. There are many other variables, including climate, life-history characteristics, and particularly disturbance, that also influence regeneration.

### Acknowledgments

Establishment of the SCBI SIGEO plot by William McShea and Norman Bourg was funded by the HSBC Climate Partnership, the SIGEO Initiative and the Smithsonian Institution. Numerous technicians, interns, and volunteers of the Conservation Ecology Center at SCBI were essential in assisting with plot establishment and data collection, most notably Shawn Behling, Megan Baker, Sumana Serchan, and Chris Lewis. Support for the original fence installation was provided by Friends of the National Zoo and Earthwatch. Additional thanks to Richard Lucas, John Parker, and the anonymous reviewers for *Northeastern Naturalist* for their helpful comments on later drafts of the paper.

### Literature Cited

- Abrams, M.D., and S.E. Johnson. 2012. Long-term impacts of deer exclosures on mixed-oak forest composition at the Valley Forge National Historical Park, Pennsylvania, USA. *The Journal of the Torrey Botanical Society* 139:167–180.
- Anderson, R.C. 1994. Height of White-flowered Trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. *Ecological Applications* 4:104–109.
- Anderson, R.C., and A.J. Katz. 1993. Recovery of browse-sensitive tree species following release from White-tailed Deer, *Odocoileus virginianus* Zimmerman, browsing pressure. *Biological Conservation* 63:203–208.
- Anderson, R.C., and O.L. Loucks. 1979. White-tail Deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. *Journal of Applied Ecology* 16:855–861.
- Apsley, D.K., and B.C. McCarthy. 2004. White-tailed Deer herbivory on forest regeneration following fire and thinning treatments in southern Ohio mixed oak forests. Pp. 461–471, *In* D.A. Yaussey, D.A. Hix, R.P. Long, and P.C. Goebel (Eds.). 14th Central Hardwood Forest Conference. Newtown Square, PA. US Department of Agriculture, Forest Service, Northeastern Research Station, Wooster, OH.
- Asnani, K.M., R.A. Klips, and P.S. Curtis. 2006. Regeneration of woodland vegetation after deer browsing in Sharon Woods, Metro Park, Franklin County, Ohio. *Ohio Journal of Science* 106:86–92.
- Beaudet, M., and C. Messier. 1998. Growth and morphological responses of Yellow Birch, Sugar Maple, and Beech Seedlings growing under a natural light gradient. *Canadian Journal of Forest Research* 28:1007–1015.
- Boerner, R.E.J., and J.A. Brinkman. 1996. Ten years of tree seedling establishment and mortality in an Ohio deciduous forest complex. *Bulletin of the Torrey Botanical Club* 123:309–317.
- Bowersox, T.W., G.L. Storm, and W.M. Tzilkowski. 1995. Canopy openings and White-tailed Deer influence the understory vegetation in mixed oak woodlots. General Technical Report. Proceedings, 10th Central Hardwood Forest Conference, US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, PA.
- Brown, T.L., D.J. Decker, S.J. Riley, J.W. Enck, T.B. Lauber, P.D. Curtis, and G.F. Mattfeld. 2000. The future of hunting as a mechanism to control White-tailed Deer populations. *Wildlife Society Bulletin* 28:797–807.
- Condit, R. 1998. *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots*. Springer, Berlin, Germany
- Cornelissen, J.H.C., P.C. Diez, and R. Hunt. 1996. Seedling growth, allocation, and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology* 84:755–765.
- Côté, S.D., T.P. Rooney, J.-P. Tremblay, C. Dussault, and D.M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics* 35:113–147.
- Dzieciolowski, R. 1980. Impact of deer browsing upon forest regeneration and undergrowth. *Polish Journal of Ecology* 28:583–599.
- Eschtruth, A.K., and J.J. Battles. 2009. Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. *Ecological Monographs* 79:265–280.

- Fletcher, J.D., W.J. McShea, L.A. Shipley, and D. Shumway. 2001. Use of common forest forbs to measure browsing pressure by White-tailed Deer (*Odocoileus virginianus* Zimmerman) in Virginia, USA. *Natural Areas Journal* 21:172–176.
- Gill, R.M.A., and V. Beardall. 2001. The impact of deer on woodlands: The effects of browsing and seed dispersal on vegetation structure and composition. *Forestry* 74:209–218.
- Goetsch, C., J. Wigg, A.A. Royo, T. Ristau, and W.P. Carson. 2011. Chronic over browsing and biodiversity collapse in a forest understory in Pennsylvania: Results from a 60-year-old deer exclusion plot. *The Journal of the Torrey Botanical Society* 138:220–224.
- Healy, W.M. 1997. Influence of deer on the structure and composition of oak forests in central Massachusetts. Pp. 246–266, *In* W.J. McShea, H.B. Underwood, and J.H. Rap-pole (Eds.). *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Institution Press, Washington, DC.
- Heckel, C.D., N.A. Bourg, W.J. McShea, and S. Kalisz. 2010. Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. *Ecology* 91:319–326.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological monographs* 54:187–211.
- Hobbs, N.T. 1996. Modification of ecosystems by ungulates. *The Journal of Wildlife Management* 60:695–713.
- Horsley, S.B., and D.A. Marquis. 1983. Interference by weeds and deer with Allegheny hardwood reproduction. *Canadian Journal of Forest Research* 13:61–69.
- Horsley, S.B., S.L. Stout, and D.S. DeCalesta. 2003. White-tailed Deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications* 13:98–118.
- Konig, E. 1976. Game damage and woodland regeneration. *Schweiz Z Forstwes* 127:40–57.
- Kota, N.L., R.E. Landenberger, and J.B. McGraw. 2007. Germination and early growth of *Ailanthus* and Tulip Poplar in three levels of forest disturbance. *Biological Invasions* 9:197–211.
- Liang, S.Y., and S.W. Seagle. 2002. Browsing and microhabitat effects on riparian forest woody seedling demography. *Ecology* 83:212–227.
- Long, Z.T., T.H. Pendergast IV, and W.P. Carson. 2007. The impact of deer on relationships between tree growth and mortality in an old-growth beech-maple forest. *Forest Ecology and Management* 252:230–238.
- Matonis, M.S., M.B. Walters, and J.D.A. Millington. 2011. Gap-, stand-, and landscape-scale factors contribute to poor Sugar Maple regeneration after timber harvest. *Forest Ecology and Management* 262:286–298.
- McCarthy, B.C. 1994. Experimental studies of hickory recruitment in a wooded hedgerow and forest. *Bulletin of the Torrey Botanical Club* 121:240–250.
- McCune, B., and M.J. Medford. 1999. PC-ORD for Windows. Multivariate analysis of ecological data, MjM Software Design, Gleneden Beach, OR.
- McCune, B., R. Rosentreter, J.M. Ponzetti, and D.C. Shaw. 2000. Epiphyte habitats in an old conifer forest in western Washington, USA. *Bryologist* 103:417–427.
- McShea, W.J. 2000. The influence of acorn crop on annual variation in rodent and bird populations. *Ecology* 81:228–238.

- McShea, W.J., and G. Schwede. 1993. Variable acorn crops, and the response of White-tailed Deer and other mast consumers. *Journal of Mammalogy* 74:999–1006.
- McShea, W.J., H. Underwood, and J. Rappole. 1997. *The Science of Overabundance: Deer Ecology and Management*. Smithsonian Institution Press, Washington, DC.
- Mladenoff, D.J., and F. Stearns. 1993. Eastern Hemlock regeneration and deer browsing in the Northern Great Lakes region: A re-examination and model simulation. *Conservation Biology* 7:889–900.
- Myster, R.W., and B.C. McCarthy. 1989. Effects of herbivory and competition on survival of *Carya tomentosa* (Juglandaceae) seedlings. *Oikos* 56:145–148.
- Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, and H. Wagner. 2011. *Vegan: Community Ecology Package*. R package. Available online at <http://CRAN.R-project.org/package=vegan>. Accessed 24 October 2011.
- Peet, R.K., and N.L. Christensen. 1987. Competition and tree death. *BioScience* 37:586–595.
- Potvin, F., P. Beaulieu, and G. Laprise. 2003. The eradication of Balsam Fir stands by White-tailed Deer on Anticosti Island, Quebec: A 150-year process. *Ecoscience* 10:487–495.
- Putman, R.J., P.J. Edwards, J.C.E. Mann, R.C. How, and S.D. Hill. 1989. Vegetational and faunal changes in an area of heavily grazed woodland following relief of grazing. *Biological Conservation* 47:13–32.
- R Development Core Team. 2010. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available online at <http://www.R-project.org/>. Accessed 24 October 2011.
- Ritchie, M.E., D. Tilman, and J.M.H. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79:165–177.
- Rooney, T.P. 2001. Deer impacts on forest ecosystems: A North American perspective. *Forestry* 74:201–208.
- Rooney, T.P., and W. Dress. 1997. Species loss over sixty-six years in the ground-layer vegetation of Heart's Content, an old-growth forest in Pennsylvania, USA. *Natural Areas Journal* 17:297–305.
- Rooney, T.P., and D.M. Waller. 2003. Direct and indirect effects of White-tailed Deer in forest ecosystems. *Forest Ecology and Management* 181:165–176.
- Rooney, T.P., R.J. McCormick, S.L. Solheim, and D.M. Waller. 2000. Regional variation in recruitment of hemlock seedlings and saplings in the Upper Great Lakes, USA. *Ecological Applications* 10:1119–1132.
- Rossell Jr., C.R., B. Gorsira, and S. Patch. 2005. Effects of White-tailed Deer on vegetation structure and woody seedling composition in three forest types on the Piedmont Plateau. *Forest Ecology and Management* 210:415–424.
- Sage Jr., R.W., W.F. Porter, and H.B. Underwood. 2003. Windows of opportunity: White-tailed Deer and the dynamics of northern hardwood forests of the northeastern US. *Journal for Nature Conservation* 10:213–220.
- Stoeckeler, J.H., R.O. Strothman, and L.W. Krefting. 1957. Effect of deer browsing on reproduction in the northern hardwood-hemlock type in northeastern Wisconsin. *Journal of Wildlife Management* 21:75–80.
- Stromayer, K.A.K., and R.J. Warren. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildlife Society Bulletin* 25:227–234.



- Tilghman, N.G. 1989. Impacts of White-tailed Deer on forest regeneration in northwestern Pennsylvania. *The Journal of Wildlife Management* 53:524–532.
- Tripler, C.E., C.D. Canham, R.S. Inouye, and J.L. Schnurr. 2002. Soil nitrogen availability, plant luxury consumption, and herbivory by White-tailed Deer. *Oecologia* 133:517–524.
- Vila, B., G. Vourc'h, D. Gillon, J.-L.M. Martin, and F. Guibal. 2002. Is escaping deer browse just a matter of time in *Picea sitchensis*? A chemical and dendroecological approach. *Trees—Structure and Function* 16:488–496.
- Walters, M.B., E.L. Kruger, and P.B. Reich. 1993. Growth, biomass distribution, and CO<sub>2</sub> exchange of northern hardwood seedlings in high and low light: Relationships with successional status and shade tolerance. *Oecologia* 94:7–16.
- Xiong, S., and C. Nilsson. 1999. The effects of plant litter on vegetation: A meta-analysis. *Journal of Ecology* 87:984–994.

**Appendix A.** Definitions of USDA-NRCS species codes.

Code	Scientific name	Common name
ACNE2	<i>Acer negundo</i>	Box Elder
ACRU	<i>Acer rubrum</i>	Red Maple
ACER	<i>Acer</i> sp.	Maple
AIAL	<i>Ailanthus altissima</i>	Tree of Heaven
AMAR3	<i>Amelanchier arborea</i> (F.Michx.) Fernald	Common Serviceberry
ASTR	<i>Asimina triloba</i>	Pawpaw
CACA18	<i>Carpinus caroliniana</i>	American Hornbeam
CACO15	<i>Carya cordiformis</i> (Wangenh.) K.Koch	Bitternut Hickory
CAGL8	<i>Carya glabra</i>	Pignut Hickory
CAOV3	<i>Carya ovalis</i> (Wangenh.) Sarg.	Red Hickory
CARYA	<i>Carya</i> sp.	Hickory
CATO6	<i>Carya tomentosa</i>	Mockernut Hickory
CECA4	<i>Cercis canadensis</i>	Eastern Redbud
CEOC	<i>Celtis occidentalis</i> L.	Common Hackberry
COFL2	<i>Cornus florida</i>	Flowering Dogwood
FAGR	<i>Fagus grandifolia</i>	American Beech
FRAM2	<i>Fraxinus americana</i>	White Ash
FRPE	<i>Fraxinus pennsylvanica</i> Marshall	Green Ash
FRAXI	<i>Fraxinus</i> sp.	Ash
HAVI4	<i>Hamamelis virginiana</i> L.	Witch Hazel
LITU	<i>Liriodendron tulipifera</i>	Tulip Poplar
NYSY	<i>Nyssa sylvatica</i>	Blackgum
PINUS	<i>Pinus</i> sp.	Pine
PIST	<i>Pinus strobus</i> L.	White Pine
PLOC	<i>Platanus occidentalis</i>	American Sycamore
PRAV	<i>Prunus avium</i> (L.) L.	Sweet Cherry
PRSE2	<i>Prunus serotina</i> Ehrh.	Black Cherry
PRUNU	<i>Prunus</i> sp.	
QUAL	<i>Quercus alba</i>	White Oak
QUCO2	<i>Quercus coccinea</i> Muenchh.	Scarlet Oak
QUPR2	<i>Quercus prinus</i>	Chestnut Oak
QURU	<i>Quercus rubra</i>	Red Oak
QUERC	<i>Quercus</i> sp.	Oak
QUVE	<i>Quercus velutina</i>	Black Oak
TIAM	<i>Tilia americana</i> L.	American Basswood
ULAM	<i>Ulmus americana</i> L.	American Elm
ULRU	<i>Ulmus rubra</i> Muhl.	Slippery Elm
ULMUS	<i>Ulmus</i> sp.	Elm