

RESPONSE OF NORTHERN RED OAK, BLACK WALNUT, AND WHITE ASH SEEDLINGS TO VARIOUS LEVELS OF SIMULATED SUMMER DEER BROWSING

Robert C. Morrissey, Douglass F. Jacobs, and John R. Seifert

Abstract.—Understanding the response of tree seedlings to browsing by white-tailed deer (*Odocoileus virginianus* Zimmerman) is critical to the management of high value hardwood plantations in the Central Hardwood Forest Region. One-year-old black walnut (*Juglans nigra* L.), northern red oak (*Quercus rubra* L.), and white ash (*Fraxinus americana* L.) bareroot seedlings were outplanted into a replicated experimental design on a field planting site in southern Indiana at Purdue University's Southeast Purdue Agricultural Center in April 2003. Five simulated summer browse treatments were applied to 15 seedlings of each species within each of five blocks, plus a control treatment for each, and were monitored for two growing seasons. Northern red oak exhibited the highest mortality rates in both years; only the most intense clipping treatment resulted in reduced mortality in year 2 in contrast to the control treatment. Seedlings with clipped terminals exhibited no height or root collar diameter (RCD) growth differences in any species. Treatments that removed leaf biomass resulted in reduced height and RCD growth in both years in contrast to control treatments, but exhibited few differences across intensity of treatments, although trends indicated that multiple clippings in a single season exhibited lower growth rates. Our findings suggest that browsing could cause significant variation in growth rates among these species, and that species composition may be altered as a result of repeated browse events.

INTRODUCTION

The effects of browsing on plantation seedling performance are believed to negatively impact their growth, form, height, and to reduce survival. The response of seedlings varies by species, the timing, intensity, and frequency of browsing, and the available resources for seedling growth; these factors may ultimately result in altered species composition (Metzger 1977, Anderson and Loucks 1979, Marquis and Brenneman 1981, Frelich and Lorimer 1985, Pastor and others 1988, Rossell and others 2005). Morphological traits, such as heterophyllous shoots within buds (Metzger 1977), and physiological traits, including carbohydrate storage and allocation patterns (Kays and Canham 1991), may contribute to the varied responses to browsing. Winter browsing results in the loss of structural material used to support growth in the following growing season, although plants may be more tolerant of browsing because carbohydrate reserves are stored throughout the plant tissue. While seedlings browsed during the summer may lose both leaf area and woody tissue required to produce carbohydrate reserves at a time when reserved stores are low, they may be more sensitive to browse during the growth period. Low to intermediate levels of browse have been shown to result in increased height growth in some species (Metzger 1977, Welch and others 1992, Edenius and others 1993), while more extreme levels of browsing have been shown to result in decreased growth and survival (Campa and others 1992). Successive years of browsing seem to decrease a seedling's ability to respond to browse (Canham and others 1994). While the response of seedlings to browsing under variable site conditions is not fully understood (Belsky 1987, Maschinski and Whitham 1989, Oesterheld and McNaughton 1991), it is expected that seedling responses will exhibit variation in the type and degree of response to browsing across different sites.

¹Research Associate (RCM), Associate Professor (DFJ), Purdue University, Department of Forestry and Natural Resources, 715 W. State Street, West Lafayette, IN 47907; DFJ is corresponding author: to contact, call (765)494-3608 or email at djacobs@purdue.edu.

The response of browsed seedlings is critical to the management of high-value hardwood plantations in the Central Hardwood Forest Region (CFHR). White-tailed deer (*Odocoileus virginianus* Zimmerman) are of particular concern in the region because of the large population densities found today (McCabe and McCabe 1984) and shrinking traditional forest foraging sites, such as early successional forest communities. Most browsing occurs in the dormant season (fall, winter, and spring), when carbohydrate reserves are stored throughout the plant. However, though typically less common, summer browsing may prove to be particularly harmful to seedlings. Canham and others (1993) observed that seedlings not shaded by adjacent shrubs and herbs had a higher probability of being browsed, thus making plantation settings particularly vulnerable. They speculated that they may be more tolerant of browse because of high rates of photosynthesis in low-competition and high-light environments. Monocultures of certain species may be devastated by repeated browsing. Mixed plantations will likely exhibit a varied species response, possibly resulting in altered species composition, spatial distribution, and competitive pressures.

OBJECTIVES

The objective of this study was to evaluate the effects of varying intensity of summer browse levels, as simulated by mechanical clipping, on the growth and survival of three important tree species of high value hardwood plantations in the CHFR.

STUDY AREA

The study site was located at the Southeast Purdue Agricultural Center in Indiana (39°01' N, 85°35' W). Soil is primarily classified as a Muscatatuck series (fine-silty, mixed, active, mesic, Fragic Hapludalf) (USDA NRCS Pedon I.D. S021IN-079-001), formed in forest vegetation with a visible plow layer (Soil Survey Staff 2004).

METHODS

One-year-old bareroot seedlings (1+0) grown in 2002 under standard nursery cultural practices at the Indiana Department of Natural Resources State Tree Nursery near Vallonia, IN (38°85' N, 86°10' W) were planted in April 2003. Three tree species were selected for study—black walnut (*Juglans nigra* L.), northern red oak (*Quercus rubra* L.), and white ash (*Fraxinus americana* L.)—because all are commonly used in plantations throughout the CHFR. Their abundance and value make them appropriate species for examination. LaGory and others (1985) indicated a lack of selectivity in woody species selection by foraging deer in natural regeneration settings during winter; thus, it is assumed all species are equally susceptible to browse pressure.

Seedlings from the resultant 18 treatments (three species x six simulated browse treatments) were machine planted into a randomized complete block design replicated in five blocks. Fifteen seedlings from each treatment were planted into each block (1.22-m spacing) for a total of 1,350 seedlings in the experiment. Treatments consisted of: 1) control treatment with no clipping (CTRL); 2) clipped terminal bud before leaf out (CT); 3) 50-percent reduction in leaf biomass early in the growing season (50RLB); 4) 75-percent reduction in leaf biomass early in the growing season (75RLB); 5) 25-percent reduction in leaf biomass early in the growing season and another 50-percent reduction in remaining leaf biomass in the middle of the growing season (25-50RLB); and 6) 50 percent reduction in leaf biomass early in the growing season and another 75 percent reduction in remaining leaf biomass in the middle of the growing season (50-75RLB) (Table 1). Seedlings were clipped using a hand pruner at varying levels of intensity in both growing seasons. An electric deer fence was installed immediately after planting and maintained throughout the experiment.

Table 1.—Simulated browse treatment codes, descriptions, and application dates

Code	Description	2003	2004
CTRL	no browse		
CT	Clipped terminal prior to leaf-out	10-Apr	21-Apr
50RLB	Post leaf-out 50% reduction in leaf biomass	21-May	7-Jun
75RLB	Post leaf-out 75% reduction in leaf biomass	21-May	7-Jun
25-50RLB*	Post leaf-out 25% reduction in leaf biomass; later in the season another 50% reduction in leaf biomass	16-Jul	12-Jul
50-75RLB*	Post leaf-out 50% reduction in leaf biomass; later in the season another 75% reduction in leaf biomass	16-Jul	12-Jul

*Dates listed apply to the second clipping within that year; first clipping treatments were administered on the same day as the 50RLB and 75RLB treatments.

Table 2.—Analysis of variance for height and root collar diameter growth, and survival for the randomized complete block design using species (SP) and clipping treatments (TRT) as factors

Year	Source of variation	P > F		
		Height	RCD	Survival
1	SP	< 0.0001	0.0838	< 0.0001
	TRT	< 0.0001	0.0245	0.2820
	SP x TRT	< 0.0001	0.0177	0.5165
2	SP	< 0.0001	< 0.0001	< 0.0001
	TRT	< 0.0001	< 0.0001	0.0475
	SP x TRT	< 0.0001	< 0.0001	0.5678

Glyphosate (Round-up®, 3.5 L ha⁻¹), and simazine (9.35 L ha⁻¹) were applied annually to attain maximum weed control and minimize competition for moisture and nutrients from non-crop vegetation. Seedling field survival, total height (ground level to base of last surviving bud), and root collar diameter (RCD) were measured immediately after planting and at the end of each of the two growing seasons reported in this study.

Data were analyzed using analysis of variance (ANOVA) to determine if mean (\pm standard error) annual survival, height, and RCD growth data differed among treatments. Initial height and RCD were tested using ANOVA for each species by treatment with no significant differences detected. When factor effects were significant, means were ranked according to Tukey's honestly significant differences test; differences were considered significant at $P \leq 0.05$. All data were analyzed using SAS Version 9.1 (SAS Institute Inc. Cary, NC 2004).

RESULTS

Seedling Survival

Mean seedling survival differed among species in both years ($P < 0.0001$), but differed among treatments only in year 2 ($P < 0.0269$) (Table 2). Northern red oak had the highest mortality rates of all species in both years, 7 ± 1 percent in year 1 and 16 ± 3 percent in year 2 (data not shown), while black walnut and white ash exhibited considerably less mortality overall. In year 2, there were no differences among clipped

Table 3.—Mean height, root collar diameter, and seedling mortality by species and treatment after two growing seasons. Different lower case letters within each species indicate significantly different means between treatments

Treatment	Height (cm)		RCD (mm)		Mortality (%)	
Black walnut						
CTRL	103.9	a	23.6	a	4.0	a
CT	85.2	ab	19.8	ab	10.6	a
50RLB	97.0	a	22.9	ab	1.4	a
75RLB	71.6	bc	18.5	b	9.4	a
25-50RLB	50.7	cd	13.1	c	6.8	a
50-75RLB	44.9	d	12.5	c	12.2	a
Northern red oak						
CTRL	59.0	a	8.8	a	9.2	a
CT	46.8	ab	8.0	ab	17.4	a
50RLB	37.5	bc	6.7	bc	16.0	a
75RLB	39.3	bc	6.9	bc	30.8	a
25-50RLB	36.7	bc	6.7	bc	25.4	a
50-75RLB	30.6	c	5.8	c	33.2	a
White ash						
CTRL	158.6	a	27.1	a	0.0	a
CT	123.9	ab	23.0	ab	1.4	a
50RLB	93.3	bc	17.3	bc	5.4	a
75RLB	102.2	bc	19.2	bc	1.4	a
25-50RLB	74.1	c	15.0	c	1.4	a
50-75RLB	67.0	c	14.7	c	5.4	a

seedlings, but the most intense browse treatment, 50-75RLB, had higher mortality compared to the control treatment. Although the species and treatment interactions were not considered significant in year 2, trends would seem to indicate that northern red oak had greater mortality within all treatments (Table 3).

First Year Seedling Growth

Species, treatment, and their interaction resulted in differing seedling height growth in year 1 (all $P < 0.0001$), while treatment effects and interactions between species and treatments yielded differences in RCD growth ($P = 0.0245$ and $P = 0.0177$, respectively) (Table 2). Northern red oak exhibited very limited height growth in year 1; all treatments, with the exception of the clipped terminal treatment, displayed reduced growth rates in contrast to the control seedlings (Fig. 1). Northern red oak RCD exhibited no positive growth within any treatments in year 1, including seedlings that were not clipped (Fig. 2). Black walnut height growth rates were also low in year 1 and showed no differences among treatments in year 1 growth rates (Fig. 1); RCD growth showed very mixed growth rates and no differences across all treatments in year 1 (Fig. 2). White ash height growth rates in year 1 were generally greater (averaging 21.2 ± 2.4 cm) than both black walnut and northern red oak (5.3 ± 1.2 cm and -1.2 ± 0.83 cm, respectively) among all treatments. Reduced growth rates occurred in only those treatments where leaf biomass was removed (Fig. 1), and all treatments that removed leaf biomass showed no positive RCD growth rates in white ash in year 1 (Fig. 2).

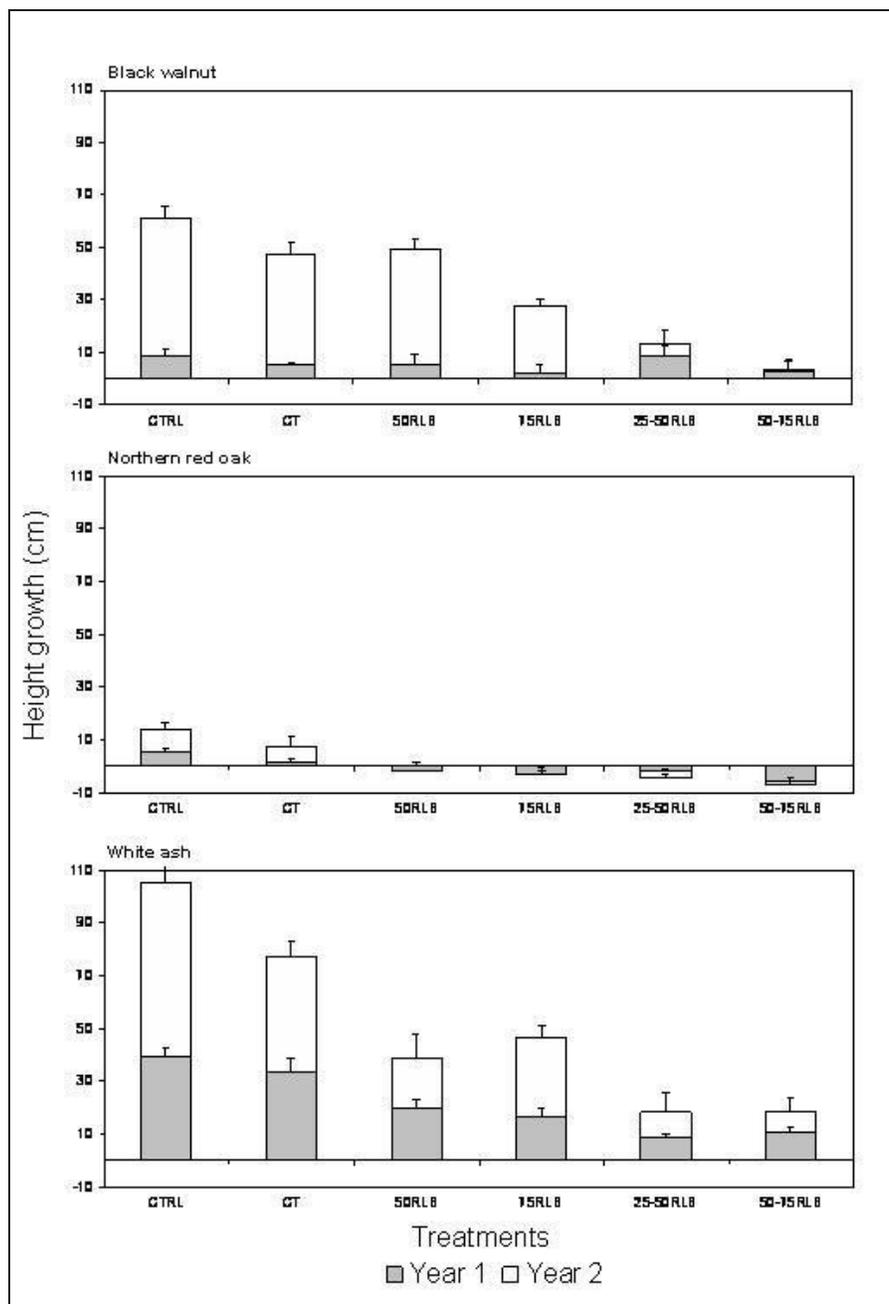


Figure 1.—Mean (\pm standard error) annual height growth rates of black walnut, northern red oak, and white ash seedlings by treatment for years one and two.

Second Year Seedling Growth

Species and treatment factors, and their interactions, in year 2 were highly significant for both seedling height and RCD growth (all $P < 0.0001$) (Table 2). Northern red oak exhibited very limited height growth again in year 2 with a similar trend of only the control and CT treatments exhibiting positive growth and no differences among all other treatments (Fig. 1). Northern red oak RCD growth rates were higher in year 2 with no differences between treatments that removed leaf biomass. Black walnut height and RCD growth rates were greater across most treatments in year 2 compared to year 1, although successive clipping treatments within year 2 resulted in lower growth rates of both measures when compared to all other treatments (Figs. 1 and 2). White ash height growth rates in year 2 appeared similar to those of year 1 across all treatments (Fig. 1), but those treatments where leaf biomass was removed exhibited lower height growth rates than white ash control treatment seedlings. RCD growth of white ash in year 2 was higher

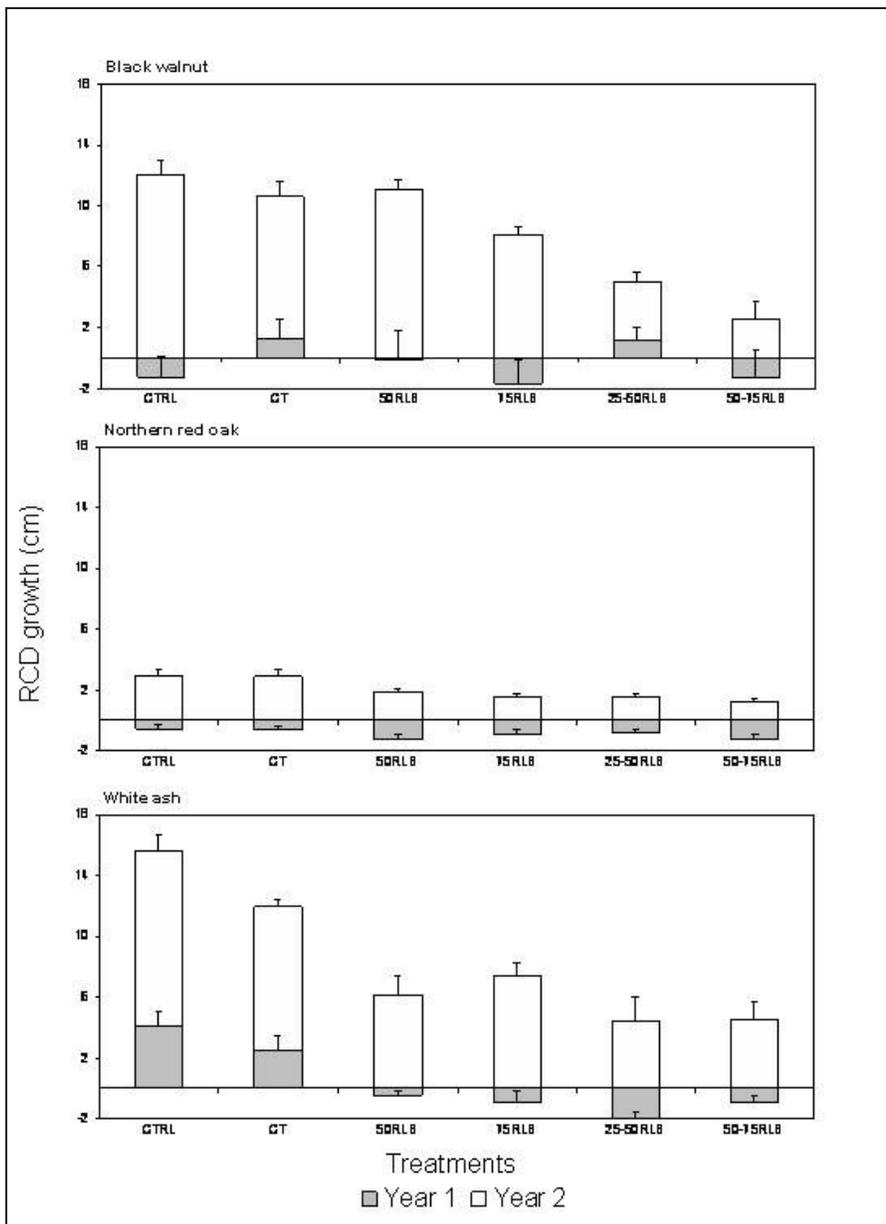


Figure 2.—Mean (\pm standard error) annual root collar diameter growth rates of black walnut, northern red oak, and white ash seedlings by treatment for years 1 and 2.

relative to year 1 across most treatments, but was lower for treatments with leaf biomass removal, with the exception of the 75-percent RLB treatment (Fig. 2).

DISCUSSION

In our study, the effects of simulated browsing had little effect on mortality, with the exception of only the most intensive browse treatment in year 2, while interspecific differences in mortality were evident in both years. Simulated browse treatments did, however, exhibit differences in total height and RCD growth, as well as annual growth rates. Although all intensities of treatments that removed leaf biomass differed from the control treatment, they typically were not different when compared to one another. This result suggests that summer browse levels that remove 50 percent or more of leaf biomass can negatively impact seedling growth for all species studied, and that each species may react differently to browse treatments.

Northern red oak had the highest mortality rates of all species in both years; while in year 2 the most intense simulated browse treatment, 50-75RLB, exhibited higher mortality than seedlings that were not clipped. Short-term effects of simulated browse indicate that resultant reduced growth rates and interspecific differences of mortality will likely result in altered species composition of mixed species plantations. Similar results have been documented in natural stands. Rossell and others (2005) concluded that white-tailed deer browsing altered structure and species composition across several forest types over a 5-year period in Virginia, with red and white oak group members greatly reduced, while ash and black cherry (*Prunus serotina* Ehrh.) remained abundant.

Simulated browsing resulted in different responses between species and treatments. Those treatments involving removal of leaf biomass generally resulted in decreased growth rates of height and RCD among all species, most noticeably in year 2. The clipped terminal treatment (CT) resulted in no differences in any species for height and RCD growth in either year 1 or year 2 (Figs. 1 and 2) or final height and RCD (Table 3), when compared to seedlings that were not clipped. Hjältén and others (1993) found similar results in juvenile downy birch (*Betula pubescens* Ehrh.) after varying levels of simulated browse treatments. While the removal of the terminal may break apical dominance, Aarssen and Irwin (1991) suggested that the removal of the terminal bud may in fact act as a benefit to a tree grown in a low-density situation, such as a plantation setting. Temporarily, these trees are apically indeterminate and could branch to fully utilize the available growing space. Aarssen and Irwin's (1991) hypothesis may explain the lack of differences between control seedlings and seedlings with clipped terminals. However, the differences observed, most noticeably in year 2 and in the more intense clipping treatments, may be related to the more intense leaf biomass removal treatments that resulted in less leaf area and photosynthetic capacity, and thus, reduced ability to respond to simulated browse. The timing of the initial browse events (Table 1) would also leave less time for recovery and result in reduced growth, most notably in those seedlings clipped twice within a single growing season.

The capacity for seedlings to recover from browse damage is strongly related to the timing of damage and the type of damage incurred (Jameson 1963, Maschinski and Whitham 1989, Hjältén and others 1993). Successive defoliation treatments of all species within year 1, 25-50RLB and 50-75RLB, resulted in no significant differences in height and RCD growth when compared to the less intense leaf biomass removal treatments, 50RLB and 75 RLB. However, in year 2, black walnut showed reduced growth rates of height and RCD with successive defoliation. This response implies that black walnut could not compensate for the continual heavy losses of photosynthetic capacity. Both northern red oak and white ash exhibited no differences when compared to the single defoliation treatments, although all leaf biomass removal treatments resulted in lower growth rates and smaller final height and RCDs compared to unclipped seedlings. With the exception of black walnut in year 2, the lack of differences among treatments within species in height and RCD growth implies that simulated browse events that remove 50 percent or more of leaf biomass, either in a single or two separate browse events throughout the summer, will result in reduced growth rates. The translocation of nutrients from the leaves of hardwood seedlings to the roots at the end of the growing season would also be limited in proportion to the amount of leaf biomass lost, thus contributing to reduced nutrient storage and growth rates in the following year. Although there were few differences between treatments within species in the short-term, trends indicate that more intensive treatments, 25-50RLB and 50-75RLB, exhibit lower growth rates, which would likely become more significant in the future as the effects are compounded over time.

Under low-intensity browse treatments, CT, 50RLB, and 75RLB, white ash exhibited more height growth than black walnut and northern red oak in year 1. In year 2, black walnut and white ash showed no significant differences. Slower-growing species, such as northern red oak relative to black walnut and white ash, generally tolerate browsing less than fast-growing species, especially under repeated browse events (Côté and others 2004). Trends in our data would seem to confirm such differences.

Our findings suggest that northern red oak seedlings in plantation settings subject to moderate to heavy browsing exhibit lower rates of growth. Repeated browsing may serve to alter the relative competitive success of seedlings of varying species to grow above the level of browsers such as white-tailed deer, in turn altering composition of plantations in the future as other more browse-resistant species, such as white ash, continue to grow. Our findings suggest that browsing could cause significant variation among these species, and that species composition may be altered as a result of continuous browse events. Depending on landowners' objectives and site factors, some form of seedling protection (e.g., fencing, tree shelters) may be warranted to enhance the prospects of successfully establishing planted seedlings.

LITERATURE CITED

- Aarssen, L.W.; Irwin, D.L. 1991. **What selection: herbivory or competition?** *Oikos*. 60(2): 261-262.
- Anderson, R.C.; Loucks, O.L. 1979. **White-tailed deer (*Odocoileus virginianus*) influence on structure and composition of a *Tsuga canadensis* forest.** *Journal of Applied Ecology*. 16: 855-861.
- Belsky, A. 1987. **The effects of grazing: confounding of ecosystem, community, and organism scales.** *The American Naturalist*. 129: 777-783.
- Campa, H., III; Haufler, J.B.; Beyer, D.E., Jr. 1992. **Effects of simulated ungulate browsing on aspen characteristics and nutritional qualities.** *Journal of Wildlife Management*. 56: 158-164.
- Canham, C.D.; Hill, J.D.; Wood, D.S. 1993. **Demography of tree seedling invasion in rights-of-way.** In: Canham, C.D., ed. *Proceedings, vegetation dynamics along utility rights-of-way: factors affecting the ability of shrub and herbaceous communities to resist invasion by trees.* Final Technical Report to the Empire State Electric Energy Research Corporation, Albany, NY: 143-180.
- Canham, C.D.; McAninch, J.B.; Wood, D.M. 1994. **Effects of the frequency, timing, and intensity of simulated browsing on growth and mortality of tree seedlings.** *Canadian Journal of Forest Research*. 24: 817-825.
- Côté, S.D.; Rooney, T.P.; Tremblay, J.P.; Dussault, C.; Wailer, D.M. 2004. **Ecological impacts of deer overabundance.** *Annual Review of Ecology, Evolution, and Systematics*. 35: 113-147.
- Edenius, L; Danell, K.; Bergström, R. 1993. **Impact of herbivory and competition on compensatory growth in woody plants: winter browsing by moose on Scots pine.** *Oikos*. 66: 286-292.
- Frelich, L.E.; Lorimer, C.G. 1985. **Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, U.S.A.** *Biological Conservation*. 34: 99-120.

- Hjältén, J.; Danell, K.; Ericson L. 1993. **Effects of simulated herbivory and intraspecific competition on the compensatory ability of birches.** *Ecology*. 74(4): 1136-1142.
- Jameson, D.A. 1963. **Responses of individual plants to harvesting.** *Botanical Review*. 29: 532-594.
- Kays, J.S.; Canham, C.D. 1991. **Effects of time and frequency of cutting on hardwood root reserves and sprout growth.** *Forest Science*. 37: 524-539.
- LaGory, M.K.; LaGory, K.E.; Taylor, D.H. 1985. **Winter browse availability and use by white-tailed deer in southeastern Indiana.** *The Journal of Wildlife Management*. 49(1): 120-124.
- Marquis, D.A.; Brenneman, R. 1981. **The impact of deer on forest vegetation in Pennsylvania.** Gen. Tech. Rep. NE-65. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 11 p.
- Maschinski, J.; Whitham, T.G. 1989. **The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing.** *American Naturalist*. 134: 1-19.
- McCabe, R.E.; McCabe, T.R. 1984. **Of slings and arrows: an historical retrospection.** In: L.K. Halls, ed. *White-tailed deer: ecology and management*. Harrisburg, PA: Stackpole: 19-72.
- Metzger, F.T. 1977. **Sugar maple and yellow-birch seedling growth after simulated browsing.** Res. Pap. NC-140. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station. 11 p.
- Oesterheld M, McNaughton SJ. 1991. **Effect of stress and time for recovery on the amount of compensatory growth after grazing.** *Oecologia*. 85: 305-313.
- Pastor, J.; Naiman, R.J.; Dewey, B.; McInnes, P. 1988. **Moose, microbes and the boreal forest.** *BioScience*. 38: 770-777.
- Rossell, C.R., Jr.; Gorsira, B.; Patch, S. 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(1): 415-424.
- SAS Institute, Inc. 2004. **SAS Users Guide: version 9.1.** SAS Institute, Cary, NC.
- Soil Survey Staff, 2004. **National soil survey characterization data.** Lincoln, NE: U.S. Department of Agriculture, Natural Resources Conservation Service.
- Welch, D.; Staines, B.W.; Scott, D.; French, D.D. 1992 **Leader browsing by red and roe deer on young Sitka spruce trees in western Scotland.** *Effects on tree growth and form. Forestry*. 65: 309-330.