Evaluating relationships among tree growth rate, shade tolerance, and browse tolerance following disturbance in an eastern deciduous forest

Lisa M. Krueger, Chris J. Peterson, Alejandro Royo, and Walter P. Carson

Abstract: Interspecific differences in shade tolerance among woody species are considered a primary driving force underlying forest succession. However, variation in shade tolerance may be only one of many interspecific differences that cause species turnover. For example, tree species may differ in their sensitivity to herbivory. Nonetheless, existing conceptual models of forest dynamics rarely explicitly consider the impact of herbivores. We examined whether browsing by white-tailed deer (*Odocoileus virginianus* Zimmermann) alters the relationship between light availability and plant performance. We monitored growth and survival for seedlings of six woody species over 2 years within six windthrow gaps and the nearby intact forest in the presence and absence of deer. Browsing decreased seedling growth for all species except beech (*Fagus grandifolia* Ehrh.). More importantly, browsing altered growth rankings among species. Increased light availability enhanced growth for three species when excluded from deer, but browsing obscured these relationships. Browsing also reduced survival for three species; however, survival rankings did not significantly differ between herbivory treatments. Our results indicated that browsing and light availability operated simultaneously to influence plant growth within these forests. Thus, existing models of forest dynamics may make inaccurate predictions of the timing and composition of species reaching the canopy, unless they can account for how plant performance varies as a result of a variety of environmental factors, including herbivory.

Résumé : Les différences interspécifiques de tolérance à l'ombre entre les espèces ligneuses sont considérées comme la principale cause de succession forestière. Toutefois, la variation de la tolérance à l'ombre peut n'être qu'une des nombreuses différences interspécifiques responsables du renouvellement des espèces. Par exemple, les espèces d'arbre peuvent se distinguer par leur sensibilité à l'herbivorisme. Néanmoins, les modèles conceptuels existants de la dynamique forestière considèrent rarement l'impact des herbivores de façon explicite. Nous avons examiné si le broutement de cerf du Virginie (*Odocoileus virginianus* Zimmermann) modifie la relation entre la disponibilité de la lumière et la performance des végétaux. Nous avons suivi la croissance et la survie des semis de six espèces ligneuses pendant 2 ans dans six trouées causées par des chablis et dans une forêt adjacente intacte en présence et en absence de cerfs. Le broutement a diminué la croissance des semis de toutes les espèces sauf dans le cas du hêtre (*Fagus grandifolia* Ehrh.). Mais surtout, le broutement a modifié le classement des espèces basé sur la croissance. Une augmentation de la disponibilité de la lumière a amélioré la croissance de trois espèces en absence de cerfs, mais le broutement a brouillé cette relation. Le broutement a aussi diminué la survie de trois espèces. Toutefois, le classement des espèces basé sur la survie n'a pas été significativement modifié par le broutement. Nos résultats indiquent que le broutement et la disponibilité de la lumière agissent simultanément pour influencer la croissance des végétaux dans ces forêts. Ainsi, les modèles existants de la dynamique forestière peuvent produire des prévisions erronées de la composition des espèces qui atteignent la canopée et du moment où elles l'atteignent, à moins qu'ils puissent tenir compte de la variation de la performance des végétaux causée par divers facteurs environnementaux, dont l'herbivorisme.

[Traduit par la Rédaction]

Introduction

Interspecific differences in shade-tolerance levels are among the primary factors causing changes in community composition during forest succession (Spurr and Barnes 1980; Shugart 1984; Pacala et al. 1994). These differences are typically accompanied by trade-offs (e.g., high shade tolerance at low light vs. rapid growth at high light) that underlie most major conceptual models of secondary succession (Clements 1916; Huston and Smith 1987; Tilman 1994).

Received 10 April 2009. Accepted 11 September 2009. Published on the NRC Research Press Web site at cjfr.nrc.ca on 15 December 2009.

L.M. Krueger[1,2] **and C.J. Peterson.** Department of Plant Biology, 2502 Miller Plant Sciences, University of Georgia, Athens, GA 30602, USA.
A. Royo. USDA Forest Service, Northern Research Station, P.O. Box 267, Irvine, PA 16329-0267, USA.
W.P. Carson. Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260, USA.

[1]Corresponding author (e-mail: lkrueger@fairchildgarden.org).
[2]Present address: Center for Tropical Plant Conservation, Fairchild Tropical Botanic Garden, 11935 Old Cutler Road, Miami, FL 33156-4242, USA.

Many studies have demonstrated physiological differences between shade-tolerant and shade-intolerant species, including differences in light compensation points, respiration rates, and photosynthetic capacity (Loach 1967; Björkman et al. 1972; Lusk 2002). Such differences have been used to parameterize simulation models of forest stand dynamics (Botkin et al. 1972; Canham et al. 1994; Kobe et al. 1995; Pacala et al. 1996). Much empirical and theoretical work has demonstrated that following a major overstory disturbance, shade-intolerant species usually increase in abundance followed by a gradual turnover to ever more shade-tolerant species, driven in part by differential species survival and growth under decreasing light levels (Bormann and Likens 1979; Bradshaw 1992; Peterson and Carson 1996; Whitmore and Brown 1996). Nonetheless, interspecific differences in shade tolerance are only one of many plant traits that influence forest succession. For example, drought may favor species with traits that promote survival under dry conditions and, thereby, shift successional trajectories compared with when precipitation is higher (Elliott and Swank 1994; Condit et al. 1995, 2004; Bunker and Carson 2005). Latham (1992) found that nutrient enrichment altered species growth rankings for six temperate species along a light-availability gradient. Thus, the outcome of succession may depend upon the environmental context present following a canopy disturbance, thereby enforcing contingency on an otherwise deterministic march to dominance by the most shade-tolerant species.

Browsing by white-tailed deer (*Odocoileus virginianus* Zimmermann) lowers growth and reproduction of plant species (Alverson and Waller 1997; Augustine and Frelich 1998; Long et al. 1998; Stange and Shea 1998) and can alter plant population structure and community composition (Harlow and Downing 1970; Bowers 1993; Horsley et al. 2003; Long et al. 2007), thus affecting the rate and direction of succession. Deer browsing preferences (Whitney 1984; Horsley et al. 2003) and herbivory tolerance (Anderson and Loucks 1979) vary among tree species, and species that are highly resistant or tolerant to damage span the range from shade tolerant to shade intolerant (Horsley et al. 2003). Thus, herbivory can potentially interact with light availability in a complex fashion and alter succession trajectories in ways that are not anticipated by either fixed shade-tolerance hierarchies or simple herbivore-preference rankings. For example, Tripler et al. (2005) concluded that shade tolerance and herbivory collectively drove forest dynamics in a selectively cut hemlock–oak–maple forest because browsing altered the growth and survival rankings for five of six common tree species in high-light environments but not in low-light environments. Long et al. (2007) found that deer herbivory eliminated the relationship between growth and survival for three tree species in a beech–maple forest in Pennsylvania. Few other studies have examined the relationship between tolerance to herbivory and shade tolerance (Runkle 1982). Without the explicit consideration of herbivory, existing models that examine forest stand dynamics risk confounding shade tolerance with herbivore tolerance, thereby potentially attributing compositional change to incorrect mechanisms, particularly in areas with elevated herbivore populations.

The objective of our study was to determine whether deer browsing alters the relationship among light availability, growth, and survival of six tree species across a canopy openness gradient. We hypothesized that species performance hierarchies would differ between seedlings exposed to deer herbivory and those excluded from deer as a result of interspecific differences in browsing sensitivity (see Horsley et al. 2003).

Materials and methods

Study sites

We conducted this study within the Allegheny National Forest (ANF) in northwestern Pennsylvania. The ANF has a humid continental climate with a mean annual precipitation of 1540 mm (NADP 2006) and a mean annual temperature of 8 °C (Bjorkbom and Larson 1977). The Allegheny Plateau is characterized by broad plateaus separated by steep river valleys. Within our study sites, elevations ranged from 514 to 585 m a.s.l. See Bjorkbom and Larson (1977) and USDA Soil Conservation Service (1985, 1993) for further details regarding soils, climate, and topography. The dominant canopy tree species are black cherry (*Prunus serotina* L.) and red maple (*Acer rubrum* L.); American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), and sugar maple (*Acer saccharum* Marsh.) are also common (Morin et al. 2006). The understory is dominated by beech and sugar maple saplings. Nomenclature follows Gleason and Cronquist (1991).

Deer have been abundant on the ANF since the 1920s (Bramble and English 1948) and by the 1930s had altered the abundances, height, and species composition for those plants within reach of deer (Lutz 1930; Leopold et al. 1947; Hough 1949). Based on modified deer pellet counts conducted in 2007, the mean deer density across our study areas was 4.21 ± 0.7 deer·km^{-2} (mean ± SE; T. Ristau, USDA Forest Service, Northeastern Research Station, Irvine, Pennsylvania, and J.A. Rodrigue USDA Forest Service, Bradford Ranger District, Bradford, Pennsylvania, personal communication, 2007), which is low compared with historical estimates of 9–15 deer·km^{-2} from the 1950s to the 1980s (Marquis 1981).

A severe thunderstorm in July 2003 created >200 windthrow gaps (Evans et al. 2007). We selected six of these gaps that ranged in size from 0.4 to 42.0 ha, with damage severities ranging from 38.5% to 69.5% basal area down.

Field methods

During the summer of 2005, we haphazardly selected individual seedlings (25–150 cm tall) of six tree species and then randomly assigned them to either exclosure or nonexclosure control treatments. Seedlings were either within our study gaps or within the intact adjacent forest, thereby providing a wide range of canopy openness levels. The species included eastern hemlock, red maple, black cherry, pin cherry (*Prunus pensylvanica* L.f.), American beech, and yellow birch (*Betula alleghaniensis* Britton). These species differ in either their degree of shade tolerance or white-tailed deer browse preference within this region (Horsley et al. 2003; Table 1). Although sugar maple is a common canopy species within the ANF, seedlings of this species were nota-

Table 1. Deer food preference and shade-tolerance ratings for six tree species within the Allegheny National Forest (adapted from Horsley et al. 2003) and the numbers of exclosed and nonexclosed seedlings in the study.

Species	Food preference by deer	Shade tolerance	No. of nonexclosed seedlings	No. of exclosed seedlings
Pin cherry	High in all seasons	Very intolerant	36	35
Black cherry	Low in all seasons	Intolerant	29	30
Yellow birch	High in late autumn; otherwise, moderate or low	Intermediate	56	58
Red maple	Moderate or low in all seasons; high in winter	Tolerant	34	34
American beech	High in winter and late spring; otherwise, low	Very tolerant	68	68
Eastern hemlock	Moderate across all seasons; heavier in winter	Very tolerant	28	29
Total			251	254

bly absent at the time of this study and, therefore, were not included in the sampling.

We used a two-way factorial design with exclosure treatment and species as independent variables and height growth, survival, and browse damage as response variables. Canopy openness was used as a covariate. Seedling numbers varied (28–68) among habitats and species because some species were sparsely or very patchily distributed, particularly within the intact forest (Table 1). A total of 251 nonexclosed seedlings and 254 exclosed seedlings (i.e., 254 exclosures total, one for each exclosed seedling) were included in the study. Table 1 summarizes the number of seedlings within each species that were exclosed and nonexclosed. We used 0.5 in. (1 in. = 2.54 cm) mesh hardware cloth, rebar (steel reinforcing rods 1 cm diameter), and wooden posts to construct the seedling exclosures. Exclosures were tubular and open topped to reduce shading effects caused by the hardware cloth. Exclosure size varied slightly according to seedling size. However, the exclosures were constructed to be taller than the seedlings, and too narrow for deer to jump inside; therefore, branches of seedlings were not exposed to deer at any time during the study.

We measured initial browse damage and heights for each seedling in July 2005 and measured each seedling annually (June 2006 and July 2007) for height, browsing, and survival for an additional 2 years. Browsing was examined in two ways: (*i*) browsing frequency and (*ii*) browsing damage. To quantify browsing frequency, we examined each seedling for the presence or absence of browsing and tallied frequency by species and deer preference category. We used a paired *t* test to determine if browse frequency differed between years 1 and 2 of the study, for nonexclosed individuals of each species. We also determined the cumulative (i.e., over the 2 year period) browse frequency of nonexclosed seedlings to see if this pattern differed from annual frequency. We quantified browse damage on nonexclosed seedlings by counting the number of branch tips that were browsed and not browsed on each seedling each year and then calculating the percentages of branch tips that were eaten by deer across the 2 years for each seedling.

We assessed canopy openness from hemispherical photographs taken above each seedling using a Nikon Coolpix880 digital camera and a fish-eye lens (Nikon FC-E8). Images were taken in summer 2005 and, again, in 2007 to account for any changes in canopy openness that occurred from canopy closure. Photographs were analyzed with Gap Light Analyzer software to quantify openness (Frazer et al. 2000).

To test if exclosures could alter light availability to seedlings, we constructed 10 similar exclosures in a nearby open field and measured light levels under cloudless conditions using a Sunfleck Ceptometer (SF-80, Decagon, Pullman, Washington). On each of three different days, we took six light measurements per exclosure; three inside at 25 cm aboveground and three above the exclosure at 1.7 m with the sensor wand oriented at 0°, 120°, and 240° from north. Mean light levels above versus inside the exclosures were compared using a paired *t* test.

Statistical analysis

We converted height data to absolute growth rates (AGR) using

$$\text{AGR} = [\ln(\text{size}_{\text{final}}) - \ln(\text{size}_{\text{initial}})]/\text{time}$$

where $\text{size}_{\text{initial}}$ was the initial height measured for the seedling and $\text{size}_{\text{final}}$ was the height measured for that seedling the following year. We calculated AGRs for each year of the study and then averaged the two annual AGRs for each seedling for use in our analyses. We analyzed AGR using an analysis of covariance (ANCOVA) with exclosure, species, and exclosure × species as fixed effects. The canopy openness values for 2005 and 2007 were averaged for use as a covariate. We followed significant treatment effects with Tukey post hoc analyses to identify pairwise differences. Furthermore, we explored significant covariate effects with separate regressions on each species × treatment combination to determine whether relationships between height AGR and canopy openness differed in the presence or absence of deer. Natural log transformation was applied as needed to meet assumptions of normality and homoskedasticity of variance; in one case, transformation did not yield homoskedastic variances and normality, and we used Spearman rank order correlation analyses in place of linear regression. If a significant regression occurred within a species, we conducted an analysis of variance (ANOVA) to test for an exclosure treatment × canopy openness interaction effect.

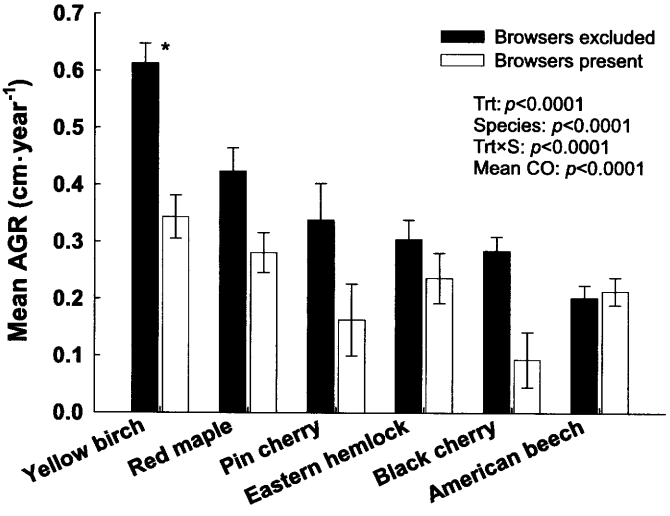
We further examined the nonexclosed seedling data only to determine how level of browsing damage affected growth. We performed an ANCOVA where species and browse damage (percentage of branch tips browsed per seedling) were the main effects, and canopy openness was the covariate. We also ran multiple linear regression analyses on the nonexclosed seedling data for each species with AGR as the

Table 2. Annual browse frequency (annual percentages of nonexclosed seedlings browsed), cumulative browse frequency (percentages of nonexclosed seedlings browsed over the 2 year period), and browse damage (percentages of branch tips that were eaten by deer across the 2 years for individuals that were browsed) for six tree species.

Species	Annual browse frequency (% seedlings)	Cumulative browse frequency (% seedlings)	Browse damage (% branch tips)
Pin cherry	63±9	72a	44±7a
Yellow birch	55±1	79b	34±4a
Red maple	41±2	53c	38±5ab
Black cherry	37±7	52cd	37±7ab
Eastern hemlock	34±2	46cd	15±4bc
American beech	18±4	31d	15±3c

Note: Values for annual browse frequency and browse damage are means ± SEs. Values with different letters within a column have significantly different browse frequency or browse damage at $p < 0.05$ among species.

Fig. 1. Mean annual height absolute growth rates (AGRs) for six species in the Allegheny National Forest, Pennsylvania, in the presence and absence of deer. Error bars are SEs. The p values within the figure show the results of the analysis of covariance. Trt, individual seedling exclosures; Trt×S, treatment × species interaction; CO, canopy openness. Asterisks show significant treatment effects within species at $p = 0.05$ based on Tukey post hoc analyses.



dependent variable and canopy openness and browse damage as the independent variables.

We determined if overall seedling survival was differentially distributed across species within each herbivory treatment group (exclosed or nonexclosed) using G tests of homogeneity. We followed each G test with the simultaneous test procedure for homogeneity of replicates tested for goodness of fit to identify species groups that were significantly different in their survival within each treatment group (Sokal and Rohlf 1995). Separate G tests of homogeneity were used to examine exclosure effects on survival within each species. We also conducted logistic regressions on overall survival and mean canopy openness data to determine if light availability influenced seedling mortality over the 2 years of the study. These analyses were conducted for all treatment × species combinations unless no individuals within a treatment group died during the study.

We analyzed species effects on browse damage levels using an ANOVA followed by Tukey post hoc analyses to identify pairwise differences between species. Variation in cumulative browse frequency among species was analyzed using a G test of homogeneity followed by the simultaneous test procedure for homogeneity of replicates tested for goodness of fit to identify pairwise differences in browsing frequency among species.

Results

Browsing

The percentages of seedlings browsed (browse frequency) did not differ significantly between years 1 and 2 ($t = 1.85$, df = 5, $p = 0.12$); therefore, we report the mean percentages of individuals browsed annually (annual browse frequency; Table 2). The annual browse frequency was highest in pin cherry followed by birch, red maple, black cherry, hemlock, and beech, showing a continuum of preference by deer. Across the 2 years, the cumulative browse frequency followed a similar pattern (Table 2), although birch had a higher total percentage of seedlings browsed by the end of the study than pin cherry despite having a lower mean annual browse frequency than pin cherry. For all species, cumulative browse frequencies across the entire study are slightly higher than annual browse frequencies because some seedlings were browsed only in year 1 of the study, whereas others were browsed only in year 2

The pattern was altered slightly when we considered the relative number of branch tips removed by deer on a per total branch tips basis (browse damage) (Table 2). When seedlings were browsed, deer did the most damage to pin cherry, followed by red maple, black cherry, yellow birch, hemlock, and beech. Thus, even though black cherry was browsed less frequently than yellow birch and red maple, the deer actually caused similar amounts of damage to black cherry, yellow birch, and red maple seedlings.

Height absolute growth rate

Browsing decreased seedling growth rate and plant height over the 2 years of the study ($F_{[1,435]} = 41.46$, $p < 0.0001$; Figs. 1 and 2, Table 3) for all species except beech. Note

Fig. 2. Mean seedling heights for six tree species within the Allegheny National Forest, Pennsylvania, in the presence and absence of deer. The 2005 heights are the heights at the initiation of the study. Error bars are SEs.

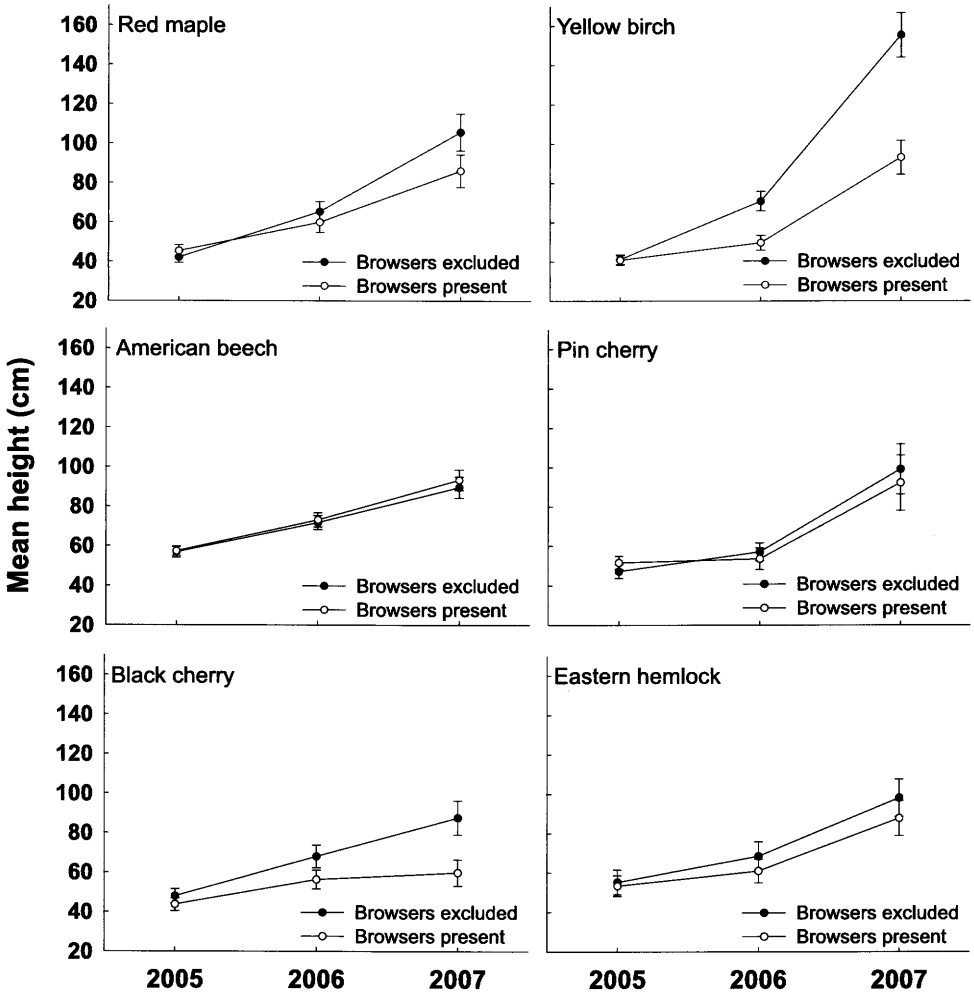


Table 3. The impact of browsing on height absolute growth rate (AGR) rankings for seedlings of six tree species within the Allegheny National Forest, Pennsylvania.

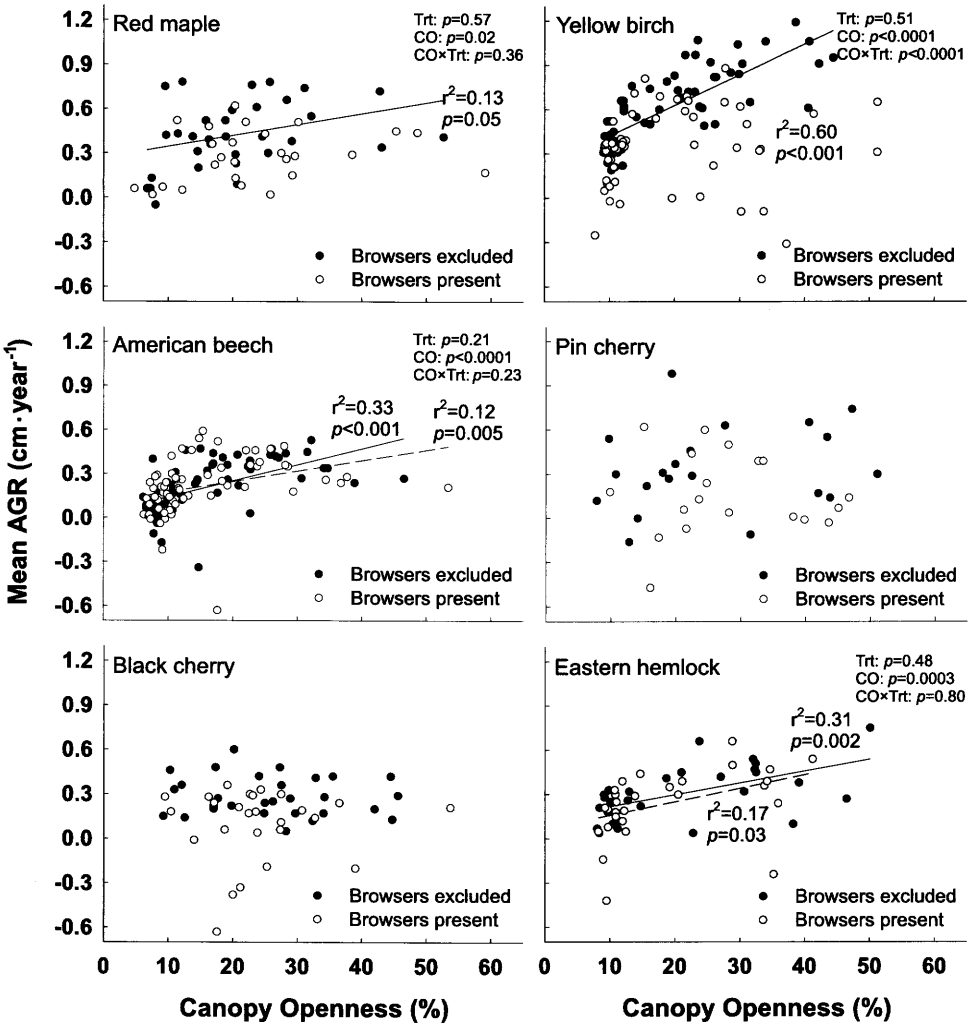
	Height AGR rank	
Tree species	Browsers present (control)	Browsers excluded (treatment)
Yellow birch	1a	1a
Red maple	2ab	2b
Eastern hemlock	3abc	4bc
American beech	4ab	6c
Pin cherry	5bc	3bc
Black cherry	6c	5bc

Note: The AGR rankings were determined using the mean of the height AGRs for 2005–2006 and 2006–2007. Rankings with different letters within a column represent significantly different AGRs at $p < 0.05$ among species.

that seedlings for all species started out at similar heights in 2005 in each treatment (Fig. 2). Browsing dramatically reduced the final height and growth rate of birch (Figs. 1 and 2, Table 3). With browsers absent, birch grew significantly taller and faster than all other species, whereas birch, red maple, hemlock, and beech had equivalent growth rates and final heights with browsers present (Figs. 1 and 2, Table 3). Browsing caused black cherry to grow significantly more slowly than birch, red maple, hemlock, and beech; inside exclosures, the growth rate of black cherry was equivalent to red maple, pin cherry, hemlock, and beech. Furthermore, with browsers present, beech had equivalent growth rates with all species except the slower growing black cherry. Without browsers, beech grew more slowly than both birch and red maple. Perhaps most importantly, browsing changed interspecific ranks in growth rate among species (Table 3). Two species (beech and pin cherry) shifted two positions in the hierarchy.

There was a significant effect of canopy openness on mean AGR for all species combined (ANCOVA, $F_{[1,435]} = 57.10$, $p < 0.0001$). With browsers absent, we found a significant positive relationship between canopy openness and growth rate for red maple ($p = 0.05$, $r^2 = 0.13$), birch ($p < 0.001$, $r^2 = 0.60$), beech ($p < 0.001$, $r^2 = 0.33$), and hemlock ($p = 0.002$, $r^2 = 0.31$; Fig. 3). Browsing negated this positive relationship for birch and red maple. Furthermore, with browsers present, canopy openness explained far less variation in growth rate for beech ($p = 0.005$, $r^2 = 0.12$) and

Fig. 3. Mean annual height absolute growth rates (AGRs) for six tree species across a canopy openness gradient within the Allegheny National Forest, Pennsylvania, in the presence and absence of deer. The AGR for seedlings within each species treatment combination was regressed against the mean of 2005 and 2007 canopy openness values. The r^2 and p values are given for significant regression analyses. Solid lines are significant regression lines for exclosed seedling data, and broken lines are significant regression lines for nonexclosed seedling data. The p values within the figure are the results of the ANOVAs. Trt, exclosure treatment; CO, canopy openness; CO×Trt, canopy openness × treatment interaction.



hemlock ($p = 0.03$, $r^2 = 0.17$; Fig. 3). Data for black cherry were not normally distributed and could not be transformed to meet statistical assumptions, thus ruling out regression analyses; although we did not find a significant correlation between canopy openness and growth for black cherry using Spearman rank order correlation analysis.

For seedlings exposed to browsers, the level of browse damage also had a significant effect on mean AGR for all species combined (ANCOVA, $F_{[1,183]} = 35.05$, $p < 0.0001$). Red maple, yellow birch, pin cherry, and hemlock had significant negative relationships between browse damage (percentage of branch tips browsed per seedling) and growth rate (Table 4). Furthermore, when browse damage was included in the regression model, a significant relationship was evident between AGR and canopy openness for both yellow birch and hemlock (Table 4). Conversely, variation in beech growth rate was related to canopy openness but not browse damage levels (Table 4). A Spearman rank order correlation analysis showed no significant correlations between black cherry AGR, browse damage, and canopy openness.

Survival

Excluding browsers increased survival for red maple by 18% ($G = 4.48$, df = 1, $p < 0.05$), black cherry by 10% ($G = 4.43$, df = 1, $p < 0.05$), and birch by 7% ($G = 5.84$, df = 1, $p < 0.025$; Table 4). Survival varied significantly among five species both outside ($G = 34.23$, df = 4, $p < 0.001$) and inside exclosures ($G = 49.21$, df = 4, $p < 0.001$). This variation was driven by low survival of pin cherry both inside and outside exclosures. Analyses of only gap seedlings (to compare our results with Tripler et al. 2005) also showed low pin cherry survival in both nonexclosed ($G = 18.36$, df = 4, $p < 0.01$) and exclosed ($G = 38.89$, df = 4, $p < 0.001$) seedlings.

There were not enough data to conduct logistic regression analyses on survivorship and mean canopy openness for four of the six species because survivorship in both treatments

Table 4. Results of multiple linear regression analyses on mean annual absolute growth rate versus browse damage (percentages of branch tips browsed per seedling) and canopy openness for seedlings in the presence of browsers of five tree species within the Allegheny National Forest, Pennsylvania.

	p value		
Species	Browse damage	Canopy openness	r^2
Red maple	0.01	0.25	0.28
Yellow birch	<0.001	0.03	0.37
American beech	0.30	0.006	0.13
Pin cherry	0.03	0.96	0.27
Eastern hemlock	0.004	0.004	0.41

was always >90% (Table 5). However, exclosed red maple and nonexclosed and exclosed pin cherry had high enough levels of mortality to run the analyses. Mean canopy openness did not significantly influence the survival of either pin cherry nor red maple.

Exclosure shading

Light levels (measured as photosynthetic photon flux densities) inside exclosures (1138 ± 27 $\mu mol \cdot m^{-2} \cdot s^{-1}$; mean ± SE) were 7%–20% lower than outside exclosures (1368 ± 15 $\mu mol \cdot m^{-2} \cdot s^{-1}$) ($t = -9.547$, df = 8, $p < 0.001$); thus, we may have slightly underestimated the effect of browsing on growth (Figs. 1 and 2, Table 3).

Discussion

Herbivory alters critical hierarchies that are metrics of plant performance

Browsing reduced growth for five of six species over two growing seasons and changed the hierarchy of species growth rankings. Beech (a nonpreferred species) went from having the fourth most rapid AGR in the presence of browsers to having the slowest AGR in their absence. This shift in the hierarchy occurred because excluding deer increased growth rate for all species but beech. Similarly, a rapidly growing and highly preferred species, pin cherry, slipped two places in the growth hierarchy from third in the absence of browsers to fifth in their presence. Thus, browsing altered growth hierarchies by shifting a highly shade-tolerant species and a very shade-intolerant pioneer species simultaneously within the same forest.

A few other studies have also found that browsing can alter hierarchies of plant relationships that are critical metrics of plant performance. For example, Long et al. (2007) found that hierarchies of the relationship between growth and survivorship shifted among saplings for two of the six tree species they evaluated in an old-growth beech–maple forest in Pennsylvania. Similarly, Tripler et al. (2005) also found that browsing shifted survival and growth rankings for six tree species in an open-canopy, thinned forest in Connecticut.

In our study, browsing also obscured the positive relationship between growth and light availability, either negating the relationship entirely (birch and red maple) or weakening it (beech and hemlock). This is consistent with other findings that browsing obscures or negates various growth relationships. For example, Long et al. (2007) found that, in the absence of browsing, there was a significant positive relationship between growth and survivorship for saplings of six tree species within an old-growth beech–maple forest (black cherry, sugar maple, red maple, beech, white ash (*Fraxinus americana* L.), and oak (*Quercus* spp.)). Browsing negated this relationship for red maple, white ash, and oaks (red oak (*Quercus rubra* L.) and white oak (*Quercus alba* L.)).

Table 5. Percentages of seedlings alive at the end of the study for six species in the presence and absence of browsers within the Allegheny National Forest, Pennsylvania.

Species	Browsers present (control) (%)	Browsers excluded (treatment) (%)
Eastern hemlock*	100	100
American beech	96a	97a
Yellow birch†	93a	100a
Black cherry†	90a	100a
Red maple†	76ab	94a
Pin cherry	53b	57b

Note: Values with different letters within a column indicate significant differences at $p < 0.05$ among species.

*Species was not included in the analyses because of 100% seedling survival.

†*G* test indicated a significant exclosure treatment effect within a species at $p < 0.05$.

Surprisingly, we could not detect any relationship between canopy openness and absolute growth rate for pin cherry and black cherry. This suggests that enemies (other than browsers) or resources other than light may be limiting plant growth (cf. Finzi and Canham 2000). For example, an unknown leaf pathogen was pervasive on pin cherry in 2005–2006 and appeared to cause high mortality in the following year (L.M. Krueger, University of Georgia, personal observation). This would explain why we never detected a relationship between canopy openness and either growth or survivorship for this rapidly growing pioneer species.

One other explanation may exist for why we saw no increase in growth with canopy openness when browsers were excluded for pin cherry and black cherry. Canopy openness values within the study were ≤60%. Thus, light levels may not have been high enough for us to see a growth response in the shade-intolerant species, whereas they were high enough for the more shade-tolerant species to respond. In support of this, red maple, which is a less tolerant species than beech and hemlock, did not have a significant treatment × canopy openness interaction effect, even though canopy openness significantly affected growth when browsers were excluded and not when browsers were present. The results suggest the relationship between growth and canopy openness is on the borderline of detection for red maple at the levels of canopy openness used in this study.

Is shade tolerance confounded with browse tolerance?

Our results suggest that, within the ANF, the two most shade-tolerant species (beech and hemlock) are also the most browse insensitive because they alone maintained a positive relationship between canopy openness and growth in the presence of browsers. They also had the highest survivorship in the presence of browsers (see also Liang and Sea-

gle 2002). Similarly, Long et al. (2007) found that white ash, beech, and sugar maple (shade-tolerant species) all had high survivorship within a low-light forest understory both in the presence and absence of browsers. Typically, species that are classified as shade tolerant have seedlings and saplings with a suite of correlated traits (persistence in shaded understories, dense wood, well-defended leaves, low photosynthetic capacity, and slower growth), which confer an advantage both in the shade and under conditions of prolonged exposure to herbivores in the understory (Coley 1983; Coley et al. 1985; Kursar and Coley 1999; Sagers and Coley 1995). In the literature, shade tolerance has come to mean the ability to survive in the understory for long periods of time. This trait or strategy could be due to varying combinations of the ability to survive at low light and the ability to survive (tolerate, defend, or avoid) prolonged periods of browsing. Thus, it is not clear whether these species persist in the understory because they are browse tolerant or shade tolerant or the degree to which these traits are correlated. Indeed, Long et al. (2007) found that red maple had very high survivorship in the shade (equivalent to sugar maple) but only when protected from browsers. Therefore, marked differences in seedling survival in shaded understories may be a result not only of shade tolerance, but also of the local abundance of browsers. We term this apparent shade tolerance and apply it to species that when enemies are in high abundance, appear to persist in the understory because of shade tolerance when, in fact, persistence may also require enemy tolerance. These enemies could be browsers, insect herbivores, or pathogens.

How much browsing pressure is required to shift hierarchies?

Few studies directly address the question of how low deer abundances need to be for browsing effects to become insignificant on community structure and dynamics. An enclosure study conducted in the Allegheny Plateau estimated that deer densities >8 deer·km^{-2} can significantly affect forest dynamics (Horsley et al. 2003). However, based on our results, deer population levels do not have to be that high (4.21 ± 0.7 deer·km^{-2}) to induce shifts in growth hierarchies (see also deCalesta and Stout 1997). An exact deer density threshold is difficult to suggest because of a lack of studies that specifically examine the effect different deer densities have within the same region. However, Alverson et al. (1988) suggest that densities would need to be <4 deer·km^{-2} to ensure successful regeneration and species diversity maintenance in northern hardwood stands. Our results appear to concur with this estimate; however, further work will be necessary to determine if abundances <4 deer·km^{-2} do not alter competitive hierarchies.

Implications for forest models

Interspecific differences in growth and survival in relation to light availability have often been used to parameterize model simulations that predict forest dynamics (Botkin et al. 1972; Canham et al. 1994; Kobe et al. 1995; Pacala et al. 1996). However, individual plants vary considerably in their performance because of a variety of factors, including herbivory. Our results suggest that predictions of seedling performance based solely on shade tolerance may not hold up throughout large areas of the northeastern United States where deer densities are high. Therefore, basing seedling growth and survival probabilities only on light availability is a current shortcoming of these models. We emphasize that our findings directly apply only to seedlings; once individuals reach a size refuge, they are no longer vulnerable to deer browsing. Nevertheless, all regeneration must pass through the vulnerable seedling stage, so our findings may illuminate patterns established in the seedling stages that carry over into later life stages. If species competitive hierarchies vary markedly over time in response to herbivory, projections of successional trajectories based solely on established survival and growth rankings may be inaccurate.

Acknowledgements

The authors thank the USDA Forest Service Northern Research Station in Warren, Pennsylvania, for data concerning deer populations at the study sites in the ANF and Dr. Lawrence Krueger, Joe Rodriguez, Jennie Osborne, and Cassandra Bruno for assistance in the field. We also thank Tom Pendergast for his comments concerning this manuscript. Funding for this study was provided by the Plant Biology Department, University of Georgia, Athens, Georgia.

References

Alverson, W.S., and Waller, D.M. 1997. Deer populations and the widespread failure of hemlock regeneration in northern forests. *In* The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C. pp. 280–297.

Alverson, W.S., Waller, D.M., and Solheim, S.L. 1988. Forests too deer: edge effects in northern Wisconsin. Conserv. Biol. **2**(4): 348–358. doi:10.1111/j.1523-1739.1988.tb00199.x.

Anderson, R.C., and Loucks, O.L. 1979. White-tail deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. J. Appl. Ecol. **16**(3): 855–861. doi:10.2307/2402859.

Augustine, D.J., and Frelich, L.E. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. Conserv. Biol. **12**(5): 995–1004. doi:10.1046/j.1523-1739.1998.97248.x.

Bjorkbom, J.C., and Larson, R.G. 1977. The Tionesta scenic and research natural areas. USDA For. Serv. Gen. Tech. Rep. NE-31.

Björkman, O., Boardman, N.K., Anderson, J.M., Thorne, S.W., Goodchild, D.J., and Pyliotis, N.A. 1972. Effect of light intensity during growth of *Atriplex patula* on the capacity of photosynthetic reactions, chloroplast components and structure. Carnegie Inst. Wash. Year Book, **71**: 115–135.

Bormann, F.H., and Likens, G.E. 1979. Catastrophic disturbance and the steady-state in northern hardwood forests. Am. Sci. **67**(6): 660–669.

Botkin, D.B., Janak, J.F., and Wallis, J.R. 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. **60**(3): 849–872. doi:10.2307/2258570.

Bowers, M.A. 1993. Influence of herbivorous mammals on an old-field plant community: years 1–4 after disturbance. Oikos, **67**(1): 129–141. doi:10.2307/3545103.

Bradshaw, F.J. 1992. Quantifying edge effect and patch size for multiple-use silviculture — a discussion paper. For. Ecol. Manage. **48**(3–4): 249–264. doi:10.1016/0378-1127(92)90148-3.

Bramble, W.C., and English, P.F. 1948. The forest grazing problem

created by deer in eastern forests. Proc. Soc. Am. For. **1948**: 257–263.

Bunker, D.E., and Carson, W.P. 2005. Drought stress and tropical forest woody seedlings: effect on community structure and composition. J. Ecol. **93**(4): 794–806. doi:10.1111/j.1365-2745.2005.01019.x.

Canham, C.D., Finzi, A.C., Pacala, S.W., and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can. J. For. Res. **24**(2): 337–349. doi:10.1139/x94-046.

Clements, F.E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington, Washington, D.C.

Coley, P.D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecol. Monogr. **53**(2): 209–233. doi:10.2307/1942495.

Coley, P.D., Bryant, J.P., and Chapin, F.S., III. 1985. Resource availability and plant antiherbivore defense. Science (Washington, D.C.), **230**(4728): 895–899. doi:10.1126/science.230.4728.895. PMID:17739203.

Condit, R., Hubbell, S.P., and Foster, R.B. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. Ecol. Monogr. **65**(4): 419–439. doi:10.2307/2963497.

Condit, R., Aguilar, S., Hernandez, A., Perez, R., Lao, S., Angehr, G., Hubbell, S.P., and Foster, R.B. 2004. Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. J. Trop. Ecol. **20**(1): 51–72. doi:10.1017/S0266467403001081.

deCalesta, D., and Stout, S.L. 1997. Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. Wildl. Soc. Bull. **25**: 252–258.

Elliott, K.J., and Swank, W.T. 1994. Impacts of drought on tree mortality and growth in a mixed hardwood forest. J. Veg. Sci. **5**(2): 229–236. doi:10.2307/3236155.

Evans, A.M., Camp, A.E., Tyrrell, M.L., and Riely, C.C. 2007. Biotic and abiotic influences on wind disturbance in forests of NW Pennsylvania, USA. For. Ecol. Manage. **245**(1–3): 44–53. doi:10.1016/j.foreco.2007.03.024.

Finzi, A.C., and Canham, C.D. 2000. Sapling growth in response to light and nitrogen availability in a southern New England forest. For. Ecol. Manage. **131**(1–3): 153–165. doi:10.1016/S0378-1127(99)00206-6.

Frazer, G.W., Canham, C.D., and Lertzman, K.P. 2000. Gap light analyzer (GLA), version 2.0. Bull. Ecol. Soc. Am. **81**: 191–197.

Gleason, H.A., and Cronquist, A. 1991. Manual of vascular plants of northeastern United States and adjacent Canada. Van Nostrand, Princeton, N.J.

Harlow, R.F., and Downing, R.L. 1970. Deer browsing and hardwood regeneration in southern Appalachians. J. For. **68**(5): 298–300.

Horsley, S.B., Stout, S.L., and deCalesta, D.S. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol. Appl. **13**(1): 98–118. doi:10.1890/1051-0761(2003)013[0098:WTDIOT]2.0.CO;2.

Hough, A.F. 1949. Deer and rabbit browsing and available winter forage in Allegheny hardwood forests. J. Wildl. Manage. **13**(1): 135–141. doi:10.2307/3796131.

Huston, M., and Smith, T. 1987. Plant succession: life-history and competition. Am. Nat. **130**(2): 168–198. doi:10.1086/284704.

Kobe, R.K., Pacala, S.W., Silander, J.A., Jr., and Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. **5**(2): 517–532. doi:10.2307/1942040.

Kursar, T.A., and Coley, P.D. 1999. Contrasting modes of light acclimation in two species of the rainforest understory. Oecologia (Berl.), **121**(4): 489–498. doi:10.1007/s004420050955.

Latham, R.E. 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. Ecology, **73**(6): 2129–2144. doi:10.2307/1941461.

Leopold, A., Sowls, L.K., and Spencer, D.L. 1947. A survey of over-populated deer ranges in the United States. J. Wildl. Manage. **11**(2): 162–177. doi:10.2307/3795561.

Liang, S.Y., and Seagle, S.W. 2002. Browsing and microhabitat effects on riparian forest woody seedling demography. Ecology, **83**(1): 212–227. doi:10.1890/0012-9658(2002)083[0212:BAMEOR]2.0.CO;2.

Loach, K. 1967. Shade tolerance in tree seedlings I. Leaf photosynthesis and respiration in plants raised under artificial shade. New Phytol. **66**(4): 607–621. doi:10.1111/j.1469-8137.1967.tb05432.x.

Long, Z.T., Carson, W.P., and Peterson, C.J. 1998. Can disturbance create refugia from herbivores: an example with hemlock regeneration on treefall mounds. J. Torrey Bot. Soc. **125**(2): 165–168. doi:10.2307/2997303.

Long, Z.T., Pendergast, T.H., IV, and Carson, W.P. 2007. The impact of deer on relationships between tree growth and mortality in an old-growth beech–maple forest. For. Ecol. Manage. **252**(1–3): 230–238. doi:10.1016/j.foreco.2007.06.034.

Lusk, C.H. 2002. Leaf area accumulation helps juvenile evergreen trees tolerate shade in a temperate rainforest. Oecologia (Berl.), **132**(2): 188–196. doi:10.1007/s00442-002-0974-9.

Lutz, H.J. 1930. Original forest composition in northwestern Pennsylvania as indicated by early land survey notes. J. For. **28**: 1098–1103.

Marquis, D.A. 1981. Effect of deer browsing on timber production in Allegheny hardwood forests of northwestern Pennsylvania. USDA For. Serv. Northeast For. Exp. Stn. Res. Pap. NE-475.

Morin, R.S., Liebhold, A.M., Gottschalk, K.W., Woodall, C.W., Twardus, D.B., White, R.L., Horsley, S.B., and Ristau, T.E. 2006. Analysis of forest health monitoring surveys on the Allegheny National Forest (1998–2001). USDA For. Serv. Gen. Tech. Rep. NE-339.

National Atmospheric Deposition Program (NADP). 2006. NADP National Trends Network monitoring location PA29 [online]. NADP Program Office, Champaign, Ill. Natl. Res. Support Project 3. Available from http://nadp.sws.uiuc.edu/.

Pacala, S.W., Canham, C.D., Silander, J.A., Jr., and Kobe, R.K. 1994. Sapling growth as a function of resources in a north temperate forest. Can. J. For. Res. **24**(11): 2172–2183. doi:10.1139/x94-280.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Jr., Kobe, R.K., and Ribbens, E. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol. Monogr. **66**(1): 1–43. doi:10.2307/2963479.

Peterson, C.J., and Carson, W.P. 1996. Generalizing forest regeneration models: the dependence of propagule availability on disturbance history and stand size. Can. J. For. Res. **26**(1): 45–52. doi:10.1139/x26-005.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology, **63**(5): 1533–1546. doi:10.2307/1938878.

Sagers, C.L., and Coley, P.D. 1995. Benefits and costs of defense in a neotropical shrub. Ecology, **76**(6): 1835–1843. doi:10.2307/1940715.

Shugart, H.H. 1984. A theory of forest dynamics: the ecological implications of forest succession models. Springer-Verlag, New York.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry. W.H. Freeman & Co., New York.

Spurr, S.H., and Barnes, B.V. 1980. Forest ecology. John Wiley & Sons, New York.

Stange, E.E., and Shea, K.L. 1998. Effects of deer browsing, fabric mats, and tree shelters on *Quercus rubra* seedlings. Restor. Ecol. **6**(1): 29–34. doi:10.1046/j.1526-100x.1998.00614.x.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology, **75**(1): 2–16. doi:10.2307/1939377.

Tripler, C.E., Canham, C.D., Inouye, R.S., and Schnurr, J.L. 2005. Competitive hierarchies of temperate tree species: interactions between resource availability and white-tailed deer. Ecoscience, **12**(4): 494–505. doi:10.2980/i1195-6860-12-4-494.1.

USDA Soil Conservation Service. 1985. Soil survey of Warren and Forest counties, Pennsylvania. USDA Soil Conservation Service, Washington, D.C.

USDA Soil Conservation Service. 1993. Soil survey of Cameron and Elk counties, Pennsylvania. USDA Soil Conservation Service, Washington, D.C.

Whitmore, T.C., and Brown, N.D. 1996. Dipterocarp seedling growth in rain forest canopy gaps during six and a half years. Philos. Trans. R. Soc. Lond. B Biol. Sci. **351**(1344): 1195–1203. doi:10.1098/rstb.1996.0102.

Whitney, G.G. 1984. Fifty years of change in the arboreal vegetation of Heart's Content, an old-growth hemlock – white pine – northern hardwood stand. Ecology, **65**(2): 403–408. doi:10.2307/1941403.