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Competitive hierarchies of temperate tree species: Interactions between resource availability and white-tailed deer[1]

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Abstract: Rankings of species-specific juvenile tree growth and survivorship define competitive hierarchies that play a central role in forest dynamics and may also vary in response to herbivory. We conducted an experiment to examine species-specific rankings of sapling growth and survival for six common tree species in temperate forests of the northeastern US as a function of both resource availability and herbivory by white-tailed deer (*Odocoileus virginianus*). Juveniles of six tree species were planted in the presence and absence of deer, in high and low light neighbourhoods dominated by each of two different tree species known to both reflect and alter soil resource availability. Under closed canopy conditions, survival and radial growth of most species was low. Under high light conditions, red oak and eastern hemlock saplings inside exclosures grew significantly faster when protected from deer, and eastern hemlock saplings grew faster in red oak- than red maple-dominated neighbourhoods. Browsing significantly decreased survival under high light for all species except beech. Rank order of species-specific growth and survival within treatment combinations changed dramatically. For example, beech saplings had the second highest survivorship under high light / + deer neighbourhoods, but fell to the lowest rank when deer were excluded. These rank-order changes in growth and survivorship indicate that both light availability and herbivory act in concert with gap-phase dynamics to regulate tree population dynamics in eastern deciduous forests.

Keywords: competitive hierarchies, deer herbivory, forest dynamics, neighbourhood dynamics, rank order, resource availability.

Résumé : Les taux de croissance et de survie des jeunes arbres créent une compétition hiérarchique qui jouent un rôle central dans la dynamique de la forêt. Ils peuvent aussi varier en fonction de l'herbivorisme. Nous avons mené une expérience pour étudier le succès relatif des gaules de six espèces d'arbres communes des forêts tempérées du nord-est des États-Unis, en fonction des ressources disponibles et du broutement par le cerf de Virginie (*Odocoileus virginianus*). Les gaules des six espèces ont été plantés dans des lieux fréquentés ou non par les cerfs et en des endroits plus ou moins éclairés dominés par l'une ou l'autre de deux espèces d'arbres. Ces deux espèces donnent de bons indices quant à la disponibilité des ressources qui se trouvent dans le sol et peuvent altérer ces mêmes ressources. Lorsque la voûte forestière est fermée, la survie et la croissance radiale de la plupart des espèces étaient faibles. En milieu ouvert, les gaules du chêne rouge et de la pruche plantés dans des exclos (donc protégés des cerfs) ont grandi beaucoup plus rapidement. Les gaules de pruche ont grandi également plus rapidement dans les peuplements dominés par le chêne rouge que dans ceux dominés par l'érable rouge. En milieu ouvert, le broutement a diminué de façon significative le taux de survie de toutes les espèces à l'exception du hêtre. La performance relative des espèces a varié beaucoup selon les combinaisons de traitements. Par exemple, les gaules du hêtre se classent en deuxième position en ce qui concerne leur taux de survie dans des conditions de forte luminosité et en présence de cerfs, mais offrent la moins bonne performance lorsque le cerf est absent. Ces performances variables au niveau de la croissance et de la survie indiquent que l'abondance de la lumière et l'herbivorisme agissent de concert avec la dynamique des trouées pour influencer la composition et la structure des forêts décidues.

Mots-clés : disponibilité des ressources, dynamique du voisinage, dynamique forestière, herbivorisme du cerf, hiérarchies compétitives, rang.

Nomenclature: Nowak & Paradiso, 1983; Gleason & Cronquist, 1991.

Introduction

Tradeoffs between juvenile tree performance (growth and survival) in low *versus* high light are well documented in forest ecosystems (Spurr & Barnes, 1980; Lorimer, 1981; Walters & Reich, 1996; Wright *et al.,* 1998; Beaudet *et al.,* 2000; Walters & Reich, 2000). These tradeoffs reflect widely studied ecophysiological and morphological constraints (Küppers, 1994; Kozlowski & Pallardy, 1997), and they give rise to competitive hierarchies (rankings of growth and survival) among tree species that play a major role in community dynamics (Pacala *et al.,* 1996; but see Clark *et al.,* 2003). Rankings of interspecific differences in high light growth play an important role in the success of tree species

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following disturbance (Marks, 1975; Canham & Marks, 1985). Shade tolerance rankings based on interspecific differences in low light growth and survival play an even greater role in determining patterns of species turnover during succession (Shugart, 1984; Glitzenstein, Harcombe & Streng, 1986; Kobe *et al.,* 1995; Kobe, 1996; Pacala *et al.,* 1996).

Interspecific shifts in the ranking of growth and survival of seedlings and saplings along soil nutrient gradients are an important component of niche differentiation among tree species (Grime, 1979). Well-documented variation in tree species abundance in forests on different soils in southern New England is correlated with site-specific variation in shade tolerance (*i.e.,* sapling survival under low light: Kobe *et al.,* 1995; Kobe, 1996). At the within-stand scale, analyses with SORTIE, a spatially-explicit model of forest dynamics, have demonstrated that coexistence of late successional species at Great Mountain Forest in southern New England can be maintained by limited dispersal in the absence of such heterogeneity (Pacala *et al.,* 1996). We now know, however, that niche differentiation in response to fine-scale heterogeneity in soil nutrient availability (particularly calcium availability) is a more likely explanation for the observed co-occurrence of sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) as late successional dominants and of white ash (*Fraxinus americana*) and red oak (*Quercus rubra*) as early successional dominants within these forests (van Breemen, Finzi & Canham, 1997; Bigelow & Canham, 2002).

Models of resource competition among plants typically assume that resource supply is a fixed feature of the environment (Tilman, 1982) and that plants alter resource availability primarily through uptake (Goldberg & Novoplansky, 1997). While this is an apt description of competition for light, it is clearly inadequate for soil nutrients (Pastor, 2003) because it does not account for the pervasive effects of plant species on the supply of soil nutrients through a wide range of ecosystem processes, including nutrient return in litterfall and root exudates, species control over nutrient mineralization rates, and redistribution of nutrients vertically within the soil. Tree species deplete available pools through direct uptake, but also through effects of litter chemistry on leaching of nutrients below the rooting horizon (Dijkstra *et al.,* 2001). These species effects on soil nutrient availability can be summarized phenomenologically as a function of the dominant tree species in the immediate neighbourhood (Boerner & Koslowsky, 1989; Finzi, Canham & van Breemen, 1998; Finzi, van Breemen & Canham, 1998). For example, net nitrogen mineralization rates beneath the canopies of white ash and sugar maple at Great Mountain Forest can be twice as high as beneath the canopies of nearby beech, red oaks, and hemlocks (*Tsuga canadensis*) (Finzi, van Breemen & Canham,1998). However, effects of elevated N on sapling growth at this site are weak (Finzi & Canham, 2000) and mostly limited to growth at high light (Tripler *et al.,* 2002). At low light, some tree species sequester nitrogen in their tissue through luxury consumption (Tripler *et al.,* 2002). While these internal stores of nitrogen may have selective benefits if the sapling is exposed to high light following a canopy disturbance, high tissue N concentrations expose saplings to significantly higher risks of being browsed by herbivores such as white-tailed deer (Mitchell & Hosley, 1936; Tripler *et al.,* 2002).

Rates of browsing by white-tailed deer vary widely for different tree species (Drolet, 1974; Van Vreede *et al.,* 1989; Weckerley & Kennedy, 1992), and the effects of differing levels of tissue removal by herbivores can vary significantly among tree species (Augustine & Jordan, 1998; Saunders & Puettman, 1999). Thus, selective herbivory by white-tailed deer has the potential to significantly alter the competitive hierarchies of tree species within a community. Moreover, both the patterns of browsing and the plants' response to browsing can be expected to vary significantly as a function of light and soil resource availability, so the effects of deer on competitive hierarchies can be expected to vary in different environments.

We conducted an exclosure experiment with saplings of six tree species found in northeastern US forests to test the hypothesis that browsing by white-tailed deer causes shifts in competitive hierarchies through changes in growth or survival. In addition, we asked if the net effects of browsing on competitive hierarchies interact with resource availability. To test the hypothesis that the effects of herbivory on competitive hierarchies varied as a function of light and soil resource availability, we stratified the experiment in sites that differed in light availability (closed canopy *versus* open canopy) and in neighbourhoods dominated by two canopy tree species [red maple (*Acer rubrum*) and red oak] that have been shown to differentially affect nutrient availability, specifically, soil nitrogen (Finzi, van Breemen & Canham, 1998).

Methods

STUDY SITE AND TREE SPECIES

We conducted this study at the Great Mountain Forest (GMF), an area of approximately 2,800 ha in Norfolk, Connecticut (41° 57' N, 73° 15' W). The forest is located on the Canaan Mountain plateau at elevations ranging from 350 to 500 m. The soils of GMF are spodsols and acidic inceptisols on glacial till derived from schist/gneiss bedrock (Hill, Sautter & Gunick, 1980). Deer occupy all major habitat types at GMF, which range from xeric oak/hickory ridgetops to bottomland red maple/hemlock forests. Densities of deer populations at GMF vary considerably, ranging from < 1 deer·km^{-2} to > 45 deer·km^{-2} in some years. We estimated deer populations in each year at our sites to be between 8 and 15 deer·km^{-2} using a modified deer pellet count method (Neff, 1968). Regulated hunting pressure at GMF has not likely altered deer density or distribution substantially, with culling rates averaging 15 deer per year over the entire 2,800 ha.

We used two sites for our experiment, each approximately 9 ha in area. The first site was selectively cut in 1991, removing 90% of the overstory and leaving a residual basal area of approximately 4 m^2·ha^{-1} (J. Bronson, pers. comm.). The site had been dominated by a mix of eastern hemlock, red oak, and red maple. In uncut stands adjacent to the study stand with nearly identical tree composition, overall basal area was 38-44 $m^2 \cdot ha^{-1}$ (C. D. Canham, unpubl. data). Basal area consisted of 33.9% (12.8 $m^2 \cdot ha^{-1}$) red oak, 26.3% (10 $m^2 \cdot ha^{-1}$) red maple, and 24.5% (9.2 $m^2 \cdot ha^{-1}$) eastern hemlock, with other species, such as American beech, black cherry, and yellow birch, contributing less than 4.0% (< 1.2 $m^2 \cdot ha^{-1}$) of total basal area. Each tree was individually removed from the site by surface dragging logs to a collection area or using a logging truck equipped with a boom arm to remove cut logs. In either case, disturbance was restricted, in most cases, to a single side of the stump. We erected exclosures in places next to stumps that were > 2-5 m away from the skidding road, where the ground was flat and did not appear to have any major disturbance. We dug holes at each site to accommodate the root boles of the individual saplings; hence, soil around planted saplings was disturbed in a similar manner.

The second site was located about 2 km north of the logged site along the same ridge line, slope, and soil type, and consisted of adult red oak and red maple trees ranging in diameter at breast height (DBH) from 30 to 45 cm (comparable in size to the DBH of the stump trees in the recently logged site). Previous studies at GMF have documented light levels ranging from approximately 4-6% of full sun under canopies of shade-tolerant species (Canham *et al.,* 1994; Finzi & Canham, 2000) to 15% of full sun under canopies of early successional species (Canham *et al.,* 1994; Finzi & Canham, 2000) to 60-80% of full sun for selectively cut stands similar to our recently logged site (C. D. Canham, pers. comm.). Since our intention was to use "closed canopy" *versus* "open canopy" as a discrete, categorical variable, light was not measured for this experiment.

We chose six focal tree species for our exclosure experiment, representing a range of shade tolerance. Following Kobe *et al.* (1995), the shade tolerances of the six species, ranked from least to most shade tolerant, were white ash, red oak, red maple, sugar maple, eastern hemlock, and beech. With the exception of red maple, saplings used in this study were obtained from a commercial nursery near Albany, New York. We chose nursery sapling stock over saplings growing at GMF because 1) nursery stock saplings are unlikely to have a history of deer herbivory and 2) nursery stock is grown under favourable conditions of light and nutrient availability, which would increase the saplings' chance of transplant survival into field conditions. Nursery stocks of red maple saplings were unavailable in 1994 and 1995, but we found a sufficient stock of naturally occurring saplings in a small area of GMF that had a history of low deer activity. We assumed that any death of saplings within the first year after planting into the field was due to transplant shock and not herbivory. Hence, these individuals were not counted in our survival calculations.

Design of the experiment

At the low light site we chose areas beneath the crowns of 30 adult red maple and 30 adult red oak trees to serve as treatment locations (referred to as "core trees"). Red maple and red oak do not differ significantly in transmission of photosynthetically active radiation through their canopies (between 4-6%, Canham *et al.,* 1994), but soils beneath their crowns do differ significantly in a number of ways, including measures of soil nitrogen availability (Finzi, van Breemen & Canham, 1998). While the exact mechanism through which species are so strongly associated with differences in soil chemistry has not been described, evidence from field studies suggests that interspecific differences in litter quality are the primary agent in the determination of mineralization dynamics (Prescott, 2002). We chose red maple and red oak as our focal species because previous research in adjacent stands showed nearly three times the amount of nitrification and nearly two times the amount of total pools of N under canopies of red maple compared with red oak (Finzi, van Breemen & Canham, 1998). At the high light site we used an equivalent number of stumps of the same species as the core trees. Because of the variation in the number of soil resources that can influence sapling growth in these forests, we used the neighbourhood designation as a categorical variable (red oak *versus* red maple core tree). This designation takes into account the loss of litter inputs from the canopy of these trees, but it also allows us to ascertain whether long-term influences from these species are maintained post-harvesting. When sapling growth rates differed between individuals growing next to stumps of the core tree treatments under similar light conditions, we interpreted this result as being likely attributable to long-term pervasive effects of adult tree species on soil resources.

In June 1994, we built 1.4- × 1.4- × 1.25-m-high deer exclosures next to each of these core trees, no more than 2 m from the base of the tree. Exclosures were built using 1.5-m fibreglass T-stakes for the corners covered with a non-light-inhibiting polypropylene Gardeneer Deer-X® deer restriction material. We chose bare-root stock saplings to minimize the potential confounding effects of nursery-originated soils in this experiment. We randomly selected one of the six study species to be planted at each core tree location. Sapling heights varied by species at planting time, with heights ranging from 50 to 125 cm. Within each exclosure we planted five saplings of the study species at a minimum spacing of 50 cm. Outside of the exclosures, 10 saplings of the same species were planted within a 3-m radius of the core tree, with at least 1 m between any two saplings and the exclosure. We expected sapling mortality to be higher outside exclosures than inside, and therefore we doubled the number of saplings outside the exclosures to ensure an adequate sample size for growth measures. However, we did correct our statistical approach to take into account the unequal sample sizes (see Statistical analyses below). Saplings of five of the target species were planted at the beginning of the growing season in 1994; red maple saplings were planted in 1995. We allowed all saplings to acclimate to local soil and environmental conditions for 1 y before any growth measurements were taken. Hence, we did not take any growth measurements for red maple saplings until 1996.

Plant measurements

We measured live/dead status, radial growth, extension growth of the leader, and total stem length at the end of the growing season in 1995, 1996, and 1997 (except for red maple, for which measurements began in 1996). For control (outside the exclosures) saplings in which the dominant leader was browsed, we measured the extension growth of the closest unbrowsed shoot to the leader. We calculated relative extension growth by dividing extension growth by the initial stem length. We measured radial growth rates as differences in total diameter at the end of one growing season to the end on the next. We measured sapling diameter in 1996 and 1997, again for all species except red maple, which was only measured in 1997. We measured stem diameter 5 cm above the ground using a dial calliper. Radial growth was not correlated with sapling size, and therefore radial growth was reported as an absolute measure rather than a relative rate. In 1998, logging operations at the closed canopy site caused us to abandon further measurements of saplings in that site. We measured stem diameter, extension growth, and total stem length from the fall of 1995 to the fall of 1997 for saplings in the high light site and did additional analyses on the average annual growth rates over that final period (1997–2000). We also examined average annual growth rates at the high light site over the entire course of the experiment (1995–2000). At the beginning and end of each growing season, we recorded evidence of browse for saplings outside of exclosures and noted any sapling mortality. Survival was analyzed as total survival from the beginning to the end of the experiment, and for purposes of parsimony, we compared survivorship only through the fall of 1997 at both sites.

STATISTICAL ANALYSES

Each core tree at each site was treated as a replicate. The 10 saplings outside each exclosure were pooled to give average radial growth, relative extension growth, and total stem length, as were the five saplings inside each exclosure. Pooling sapling performance measures allowed us to overcome pseudo-replication design issues (Hurlbert, 1984). If all saplings in a treatment combination died for a given measurement period, growth rate variables were treated as missing (rather than true zeros). Total stem length was used to assess sapling net growth over the course of the experiment. In many cases, net growth was negative as saplings declined in height in response to a combination of browsing and dieback. Dieback can be a serious component of biomass loss, even for individuals protected from herbivory, as plants attempt to preserve only sustainable vascular tissue, as has been shown in other species (Frey *et al.,* 2004). Since sites were not replicated in this study, we only discuss the implications of the differences between sites in the Discussion section. Where applicable, we arcsine square root transformed relative extension growth and log transformed radial growth data to conform to assumptions of normality before analysis.

Extension growth rates and total stem length from 1995 to 1997 for all species except red maple were analyzed using repeated measures analysis of variance (ANOVA), using SYSTAT (1998), with time as the within-subject factor and herbivory and core tree neighbourhoods as between-subject factors. The variances of the differences between all pairs of trials are assumed to be homogenous, the Huynh-Feldt criterion, and violations of this assumption can be corrected for by calculating the Greenhouse-Geiser epsilon term, which adjusts the degrees of freedom (Wilkinson, Blank & Gruber, 1996). We used the more conservative Greenhouse-Geiser corrected probability statistic for interpreting within-subjects output from the repeated ANOVAs. Red maple was analyzed using simple two-way ANOVA because growth was only measured for two time periods. Because there were only two measurement periods for radial growth rates, they were also analyzed using simple two-way ANOVA, with herbivory and core tree neighbourhood as the factors. Separate analyses were done for each species in each of the two time periods (one for red maple) and each of the two sites. At the high light site, we used a simple two-way ANOVA with each of the six species to test for effects of herbivory and core trees on 1997–2000 extension growth, total stem length, and radial growth. We conducted Bonferroni *post hoc* tests to assess significant pairwise differences among treatment groups.

After an arcsine transformation of the survival data, we ran two-way ANOVAs to assess effects of herbivory and core trees within each of the six species and within each of the two sites. To test if species differed in their rank order in radial growth, extension growth, and cumulative survival, we ran one-way ANOVAs for each of the response variables using species as the main factor. If the ANOVA was significant, we ran a Bonferroni *post hoc* test to detect significant differences among species. Survival differences of all the species under each light condition and +/- deer were examined using a chi-square significance test.

Results

During the course of the experiment 99% of the saplings of the five species other than beech planted outside of exclosures (control saplings) were browsed. Only 75% of the control beech saplings were browsed, and only these saplings were used in the analyses for comparisons with saplings inside the exclosures. We chose to limit our analyses to browsed saplings to avoid confounding secondary effects of non-herbivory factors on growth and survival when comparing control and exclosed saplings. Sapling survival was generally low regardless of treatment or site. Of the 1,802 saplings planted, approximately 37% of the saplings remained alive by the end of the experiment. We report the results from the exclosure experiments conducted under the closed canopy first, and then the results from the exclosure experiments conducted under an open canopy. We emphasize that these are two distinct sets of experiments, and any differences drawn between these two experiments are for qualitative purposes only.

EFFECTS OF HERBIVORY AND TREE NEIGHBOURHOODS UNDER LOW LIGHT

RADIAL AND EXTENSION GROWTH

Under closed canopy conditions, radial growth did not differ significantly as a function of deer exclusion or core tree neighbourhood for any of the six species in either of the two time periods (1995–1996 or 1996–1997) ($P > 0.1$, two-way ANOVA results not presented). Extension growth of all six species was low regardless of the presence/absence of herbivory, presumably as a result of low light levels.

Extension growth did not consistently increase or decrease over time for any species, nor were there detectable species-specific differences, and low sample sizes due to high mortality rates by the end of the experiment did not allow for effective comparisons of extension growth across treatment groups (ANOVA results not presented). The lone exception was sugar maple, which had a significantly higher extension growth from 1995 to 1997 in neighbourhoods dominated by red maple ($F = 43.718$; df = 1,2; $P = 0.022$).

MEAN (TOTAL) STEM LENGTH

Although there were no significant effects of herbivory on average radial or extension growth rates at the closed canopy site, seedling heights (total stem length) were significantly affected by core tree and exclosure treatment over the course of the experiment. High mortality rates resulted in large numbers of missing values for treatment combinations after the first year, reducing our ability to test for differences later in the experiment. Sugar maple, white ash, red oak, and hemlock saplings in exclosures had significantly longer stem lengths than control saplings at the end of the first year (1995; Figure 1b,c,e,f). The effect was still present for sugar maple, white ash, and hemlock at the end of 1996, but by the end of 1997 we were only able to detect an effect of herbivory on white ash stem lengths, largely due to very small sample sizes in other treatment combinations (Figure 1c). Sugar maple was the only species to show an additional effect of core tree on sapling stem length, and this effect only appeared in 1996 (Figure 1b). Red maple saplings suffered high mortality and did not have a sufficient number of saplings in each of the treatment conditions to assess the effect of deer herbivory on sapling stem length. Regardless of the presence or absence of herbivory, sapling mean stem lengths under low light conditions declined for all of the species except beech over the course of the experiment due to stem dieback (Figure 1).

SURVIVORSHIP

Overall sapling survival from 1995 to 1997 was extremely low at the closed canopy site (Table I). Over the three years, control sapling survivorship did not differ among five of the six sapling species, with survivorship ranging from 2 to 9%. White ash had significantly higher survival than the other species (32%; Table I). Overall species survivorship was higher in the deer exclosures ($\chi^2 = 13.375$; df = 1; α-level < 0.005), and there were more significant differences among the species (Table I). Hemlock saplings inside exclosures had a three-fold increase in survivorship over control saplings, and hemlock survival was significantly higher than red oak and red maple, but was not significantly different from beech or sugar maple survivorship. Survivorship did not differ among red maple, red oak, sugar maple, and beech saplings, with the percent surviving very similar to that of controls (ranging from 2 to 14%; Table I). Again, white ash had the highest survival among species, with half of all enclosed saplings surviving until the end of the 1997 growing season (Table I), which was significantly higher than all other species in the study. White ash also showed an increase in survival as a function of the interaction between core tree and deer herbivory ($F = 4.95$; df = 1,5; $P = 0.041$; Table I).

EFFECTS OF HERBIVORY AND CANOPY TREE NEIGHBOURHOODS UNDER HIGH LIGHT

RADIAL AND EXTENSION GROWTH

Only two of the six species, red oak and hemlock, showed significant increases in radial growth in response to protection from deer ($P \leq 0.05$; Table II). There was also a significant effect of the core tree species on radial growth of hemlock saplings ($P = 0.035$; Table II). The results of the repeated measures ANOVAs showed few and inconsistent results across species and time. For example, radial growth of red oak saplings was greater for control saplings in 1995-1996, but greater for enclosed saplings in 1996-1997.

Extension growth also did not increase uniformly across species or treatments, with repeated measures analysis of relative extension growth showing inconsistent results across species and time. For example, average extension growth was significantly greater for control red oak and hemlock saplings compared with enclosed (Table II), with 22% and 14% of variance explained by treatment effects, respectively.

MEAN (TOTAL) STEM LENGTH

From 1995 to 1997 stem length of red maple, sugar maple, and beech saplings did not significantly differ among treatments (Figure 2a,b,d). Stem lengths for white ash, red oak, and hemlock saplings were significantly greater inside exclosures than controls ($P < 0.05$; Figure 2c,e,f). At the end of the experiment in 2000, red maple and white ash saplings demonstrated no significant differences in stem lengths across treatment groups. Sugar maple saplings were significantly taller when grown next to red maple core stumps (ANOVA; $P = 0.027$; Figure 2b), and saplings growing inside enclosures next to red maple core trees had significantly longer stem lengths than controls growing next to oaks ($P < 0.05$; Figure 2b). Similarly, beech saplings growing next to red oak stumps had significantly longer stem length than those saplings growing next to red maple stumps ($P = 0.036$; Figure 2d), and control saplings growing next to red oak core trees had significantly longer stem lengths than saplings growing inside enclosures ($P < 0.05$; Figure 2d). Red oak and eastern hemlock saplings had significantly longer stem lengths inside enclosures than control saplings ($P < 0.001$; Figure 2e,f).

SURVIVORSHIP

Overall sapling survivorship was greater inside exclosures ($\chi^2 = 81.983$; df = 1; α-level < 0.005). All species other than beech had significantly higher survivorship when protected from herbivory in the high light site ($P < 0.05$; Table I). Beech survivorship declined from 32 to 20%, but this decline was not significant (Table I). Survivorship ranged from a two-fold increase in hemlock (36 to 72%) to a 25-fold increase for red maple saplings (2 to 50%; Figure 3). Under ambient conditions of deer herbivory, the six species separated into three significantly different survivorship groupings, in declining order of survivorship: 1) hemlock and beech, 2) red oak, white ash, and sugar maple, and 3) red maple. When deer herbivory was removed, there were no significant differences in survivorship among species with the exception of

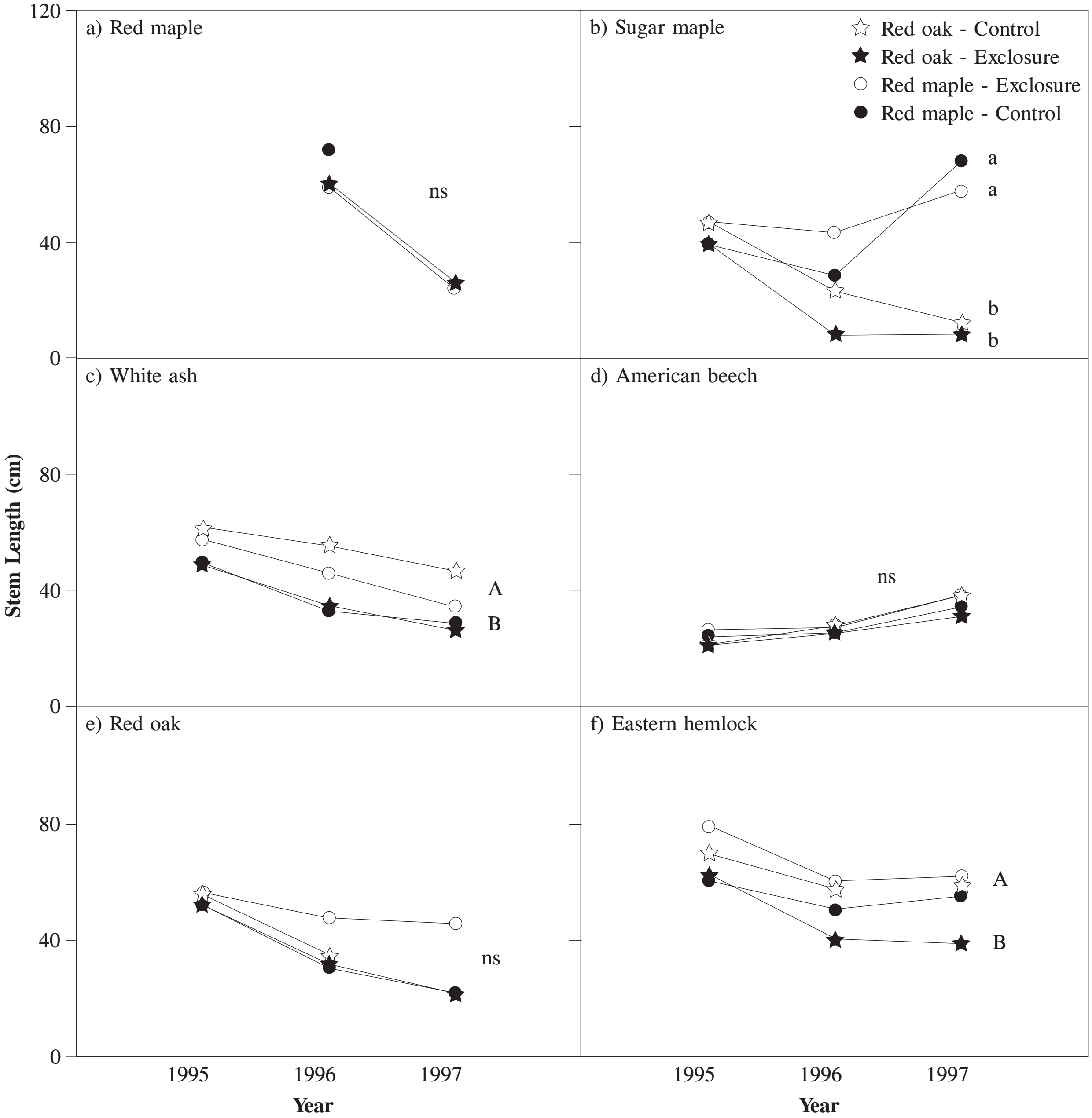

FIGURE 1. Closed canopy: Mean stem length (cm, standard error bars left off for clarity of presentation) for saplings next to red maple or red oak core trees from 1995 to 1997 inside (- deer) and outside exclosures (+ deer). No significant within-subjects comparisons were found for saplings growing under closed canopy conditions. Red maple (a) and American Beech (d) did not have any significant differences in mean stem length. By the end of the experiment, white ash (c) and eastern hemlock (f) saplings inside exclosures had significantly longer stem lengths than those saplings outside (controls) as indicated by different capital letters to the right of each panel. Sugar maple (b) saplings had significantly longer stem length growing next to red maples than red oaks regardless of exclosure treatment as indicated by different lower case letters. Treatments with different letters to the right of plotted 1997 data are significantly different at $P < 0.05$.

beech, which had a significantly lower survivorship than any of the other five species (Table I; Figure 3).

EFFECTS OF HERBIVORY ON COMPETITIVE HIERARCHIES UNDER LOW AND HIGH LIGHT

Previous studies have highlighted the importance of quantitative differences in low light survival for tree population dynamics at Great Mountain Forest (Kobe *et al.,* 1995; Pacala *et al.,* 1996). In our study, rankings of survival under low light did not change in response to herbivory (Table I). With the exception of anomalously high survival of white ash saplings, the rank order of survival fit expectations based on previous studies of shade tolerance in these species (Kobe *et al.,* 1995). While the rank order among species did not shift in response to herbivory, the scale of separation among species did change, with more pronounced variation among species in low light survival in the absence of herbivory (Table I).

Herbivory's effect on sapling survival rankings under high light was largely due to the insensitivity of beech survival to the presence of herbivory (Table I). Hemlock sap-

TABLE I. Species ranking in survivorship at the end of the growing season for saplings +/- deer herbivory under closed canopy from 1995 to 1997 and open canopy from 1995 to 2000. Values in parentheses represent percent alive at the end of those respective growing seasons. Different subscripted letters within a column indicate significant differences among species under that combination of treatments. Except for white ash, core treatment had no significant impact on survivorship and is not reported here. Superscript symbols within a row indicate significant differences for a species within the given site and not across sites treatments: † indicates a significant difference in +/- deer treatment at the $P \leq 0.05$; ‡ indicates a significant interaction between neighbourhood and +/- deer treatment at the $P \leq 0.05$.

	Closed canopy survivorship 1997		Open canopy survivorship 2000	
Rank	+ deer	- deer	+ deer	- deer
1	White ash‡ (0.32)	White ash $(0.50)_{a}$	Eastern hemlock† $(0.36)_{a}$	Eastern hemlock $(0.72)_{a}$
2	Eastern hemlock $(0.09)_{b}$	Eastern hemlock $(0.28)_{b}$	Beech $(0.32)_{a}$	Red oak $(0.58)_{a}$
3	Sugar maple $(0.09)_{b}$	Beech $(0.14)_{bc}$	Red oak† $(0.13)_{b}$	White ash $(0.52)_{a}$
4	Beech $(0.07)_{b}$	Sugar maple $(0.10)_{bc}$	White ash† $(0.12)_{b}$	Sugar maple $(0.52)_{a}$
5	Red oak $(0.05)_{b}$	Red oak $(0.08)_{c}$	Sugar maple† $(0.07)_{b}$	Red maple $(0.50)_{a}$
6	Red maple $(0.02)_{b}$	Red maple $(0.02)_{c}$	Red maple† $(0.02)_{c}$	Beech $(0.20)_{b}$

TABLE II. Average radial growth and rankings in average radial growth under +/- deer and red oak/red maple neighbourhoods under high light conditions. Values in parentheses indicate average annual radial growth (mm) from 1995 to 2000 or relative growth rate from 1995 to 2000. Different subscripted letters within a column indicate significant differences. Superscript symbols within a row indicate significant differences for a species within the given deer + neighbourhood treatment. Subscripted 0 indicates that the overall ANOVA was not significant and therefore *post hoc* comparisons were not conducted. * indicates a significant difference in neighbourhood treatment at the $P \leq 0.05$. † indicates a significant difference in +/- deer treatment at the $P \leq 0.05$. No significant interactions between neighbourhood and +/- deer treatment were observed.

	Red maple		Red oak	
Rank	+ deer	- deer	+ deer	- deer
AVERAGE ANNUAL RADIAL GROWTH, 1995-2000				
1	Beech (1.410)	Eastern hemlock $(1.210)_{a}$	Beech $(1.550)_{a}$	Eastern hemlock $(2.140)_{a}$
2	Red oak† $(0.400)_{b}$	Red oak $(0.980)_{ab}$	Eastern hemlock $(0.810)_{c}$	Beech $(1.150)_{b}$
3	Sugar maple $(0.370)_{b}$	White ash $(0.750)_{b}$	Red maple (0.400)	Red oak $(0.530)_{c}$
4	Eastern hemlock*,† $(0.350)_{b}$	Sugar maple $(0.590)_{bc}$	White ash $(0.250)_{b}$	White ash $(0.490)_{c}$
5	Red maple (0.325)	Beech $(0.550)_{bc}$	Sugar maple $(0.210)_{bc}$	Sugar maple $(0.380)_{c}$
6	White ash $(0.160)_{b}$	Red maple $(0.263)_{c}$	Red oak $(0.180)_{b}$	Red maple $(0.340)_{c}$
RELATIVE EXTENSION GROWTH, 2000				
1	White ash $(0.258)_{0}$	White ash $(0.171)_{a}$	Beech $(0.181)_{a}$	Beech $(0.174)_{a}$
2	Red oak (0.173)	Sugar maple $(0.122)_{ac}$	Eastern hemlock $(0.159)_{a}$	Sugar maple $(0.149)_{ab}$
3	Beech (0.169)	Red oak $(0.112)_{bc}$	Red oak $(0.136)_{ab}$	Eastern hemlock $(0.142)_{a}$
4	Eastern hemlock (0.135)	Beech $(0.109)_{ab}$	White ash $(0.072)_{b}$	White ash $(0.127)_{ab}$
5	Sugar maple (0.067)	Eastern hemlock $(0.085)_{bc}$	Sugar maple $(0.061)_{b}$	Red oak $(0.078)_{b}$
6	Red maple (0.023)	Red maple $(0.062)_{b}$	Red maple $(0.053)_{b}$	Red maple $(0.070)_{b}$

lings had the highest survival regardless of exposure to deer, and the rankings of red oak, white ash, sugar maple, and red maple survival did not change in response to herbivory. All five of these species showed significant and often dramatic declines in survival when exposed to deer. Survival of beech saplings, on the other hand, did not respond significantly to herbivory, and was relatively lower inside the exclosures. As a result, beech moved from the lowest survival rate in the absence of herbivory to the second highest survival in the presence of herbivores (Table I).

Discussion

EFFECTS OF RESOURCE AVAILABILITY AND HERBIVORY ON COMPETITIVE HIERARCHIES

Shifts in rankings of species performance as a function of variation in light have been widely documented, and they reflect well-known ecophysiological and architectural tradeoffs (Canham & Marks, 1985; Poorter *et al.,* 2003). Clark *et al.* (2003) point out that tradeoffs based on estimates of average species performance hide considerable variability in performance at the individual plant level and that the tradeoffs may not be as important for species coexistence as is commonly assumed by theoretical models. Nonetheless, competitive hierarchies (as measured by static rankings of species-specific average growth and survival) have been frequently shown to correlate well with both the relative abundance of species and the long-term dynamics of succession at a site (Shugart, 1984; Pacala, Canham & Silander, 1993; Pacala *et al.,* 1996; Kobe, 1996). Our results demonstrate that competitive hierarchies can vary markedly in response to foraging by a common vertebrate herbivore, at least under high light conditions. Under high light, survival of five of the six species declined significantly in the presence of herbivory, while one species, beech, had lower rates of browsing and showed no significant decline in survival when browsed. As a result of the very high tolerance of browsing by beech, its survival moved from the lowest rank in the absence of herbivory to being tied for the highest rank in the presence of herbivory (Table I).

These results mirror other studies showing both low utilization of beech by deer and relatively high tolerance of beech to browsing (Webb, King & Patric, 1956; Liang & Seagle, 2002). We did not measure offtake rates (*i.e.,* amounts of plant material removed by deer), but it is possible that the high apparent tolerance of browsing in beech saplings is actually due to low rates of consumption of beech shoots on any individual sapling because of low overwinter nitrogen contents relative to other species at our sites (Tripler *et al.,* 2002) and/or high quantities of tannins and lignins, both of which would tend to minimize the amount of plant material taken by deer (Robbins *et al.,* 1987a,b).

In contrast to our results under high light conditions, herbivory by deer had no significant effect on interspecific rankings of growth or survival under the low light levels

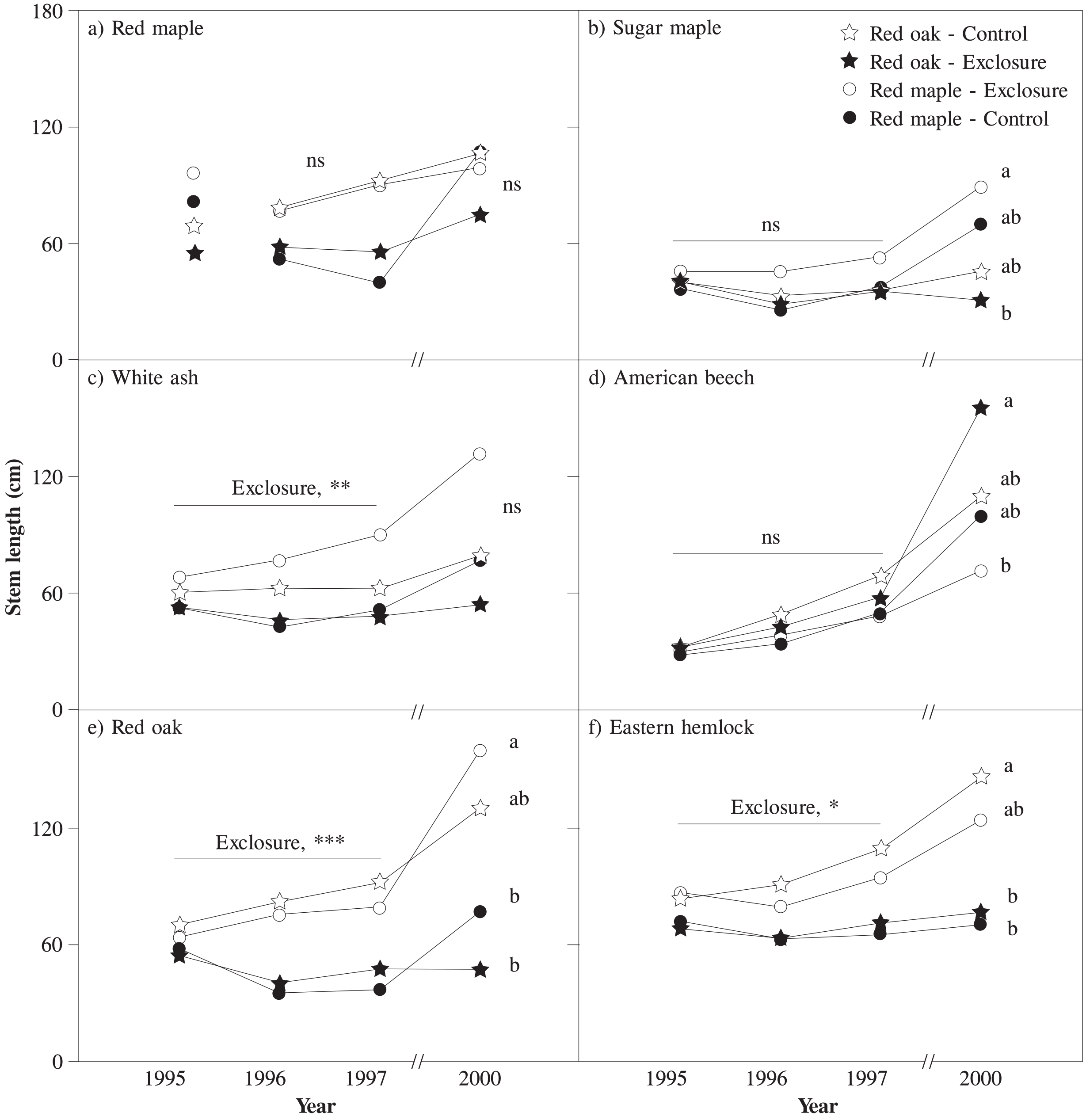

FIGURE 2. Open canopy: Mean stem length (cm, standard error bars left off for clarity of presentation) for saplings planted next to red maple or red oak core trees from 1995 to 2000 inside (- deer) and outside exclosures (+ deer). Repeated measures ANOVA were not significant for red maple, sugar maple, and beech, as indicated by ns (not significant) over data from 1995 to 1997. Exclosure treatments were significant for the repeated measures ANOVA for white ash, red oak, and eastern hemlock as indicated by asterisks above the line for data from 1995 to 1997 (*$P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). One-way ANOVAs performed on 2000 data. ns indicates a non-significant ANOVA. Treatments with different letters to the right of plotted 2000 data are significantly different at $P < 0.05$.

in our closed-canopy site. Our rankings of interspecific variation in low light survival (Table I) were remarkably insensitive to the presence/absence of browsing. Our ability to detect significant effects of browsing on growth at the closed canopy site was limited by the very low rates of survival at that site and the resulting small numbers of saplings alive at the end of the experiment. With the exception of the anomalously high survival of white ash saplings, the interspecific variation in survival was consistent with well-documented variation in shade tolerance of the species at this site (Kobe *et al.,* 1995).

Our results are consistent with the recently reported study by Horsley, Stout, and deCalesta (2003) in which closed-canopy sites showed only minor responses to experimental manipulation of deer density over a 10-y period. While the competitive hierarchy under low light did not change in response to herbivory, the absolute magnitudes of survival rates were consistently lower for saplings exposed to browsing. The overall differences in survival are large enough that we would expect significant effects of browsing on the abundance of advance regeneration of even the most shade-tolerant species (beech, hemlock, and sugar maple) (Liang & Seagle, 2002).

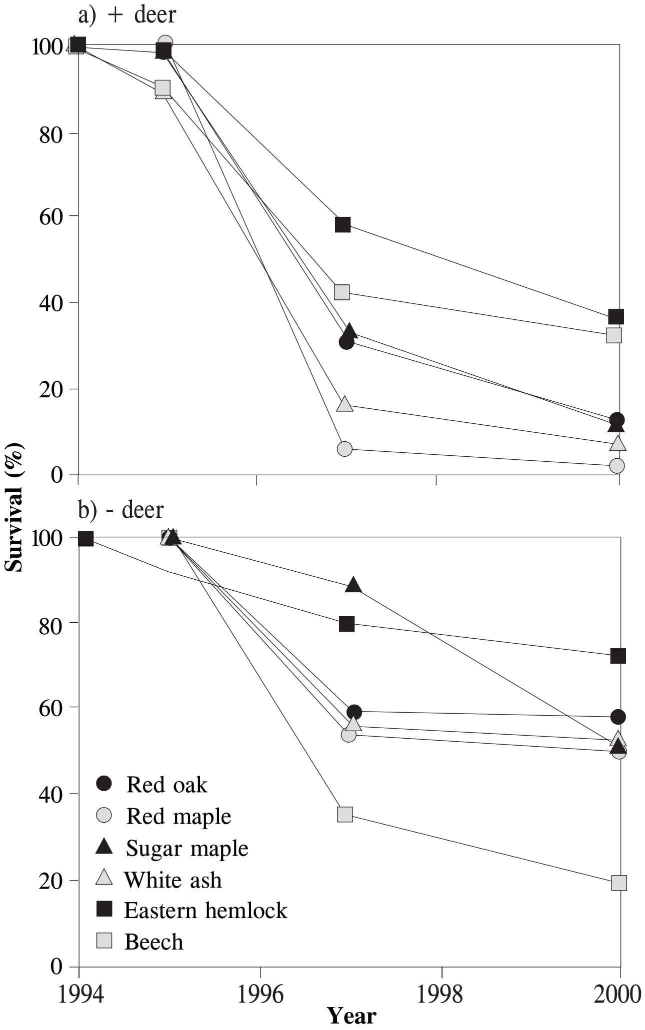

FIGURE 3. High light: Percent of saplings surviving under a) ambient levels of deer herbivory (+ deer) and b) deer herbivory removed (- deer). Trend lines included for clarity of presentation. Each species is represented by a unique symbol as indicated in legend.

TABLE III. Summary of effects of herbivory and canopy tree neighbourhoods on sapling radial growth, extension growth, stem length, and survival for the six study species under open canopy conditions. Only significant results are displayed in the table. The results are reported for 5 y of observation ending in 2000.

	Radial growth	Extension growth	Stem lenght	Survival
Beech				Increased by herbivory
Hemlock			Greater under red oak canopies	
Red maple	Reduced by herbivory		Reduced by herbivory	Reduced by herbivory
Red oak	Reduced by herbivory		Reduced by herbivory	Reduced by herbivory
Sugar maple				Reduced by herbivory
White ash			Greater under red maple canopies Reduced by herbivory	

While strong feedbacks between canopy trees and soil resource availability have been documented for GMF (van Breemen, Finzi & Canham, 1997; Finzi, Canham & van Breemen, 1998; Finzi, van Breemen & Canham, 1998), we found limited evidence of canopy-tree neighbourhood effects on sapling growth and survival, primarily under high light conditions (Tables I & III). This result is in contrast to a study done by Liang and Seagle (2002) in which they found interactions between neighbourhoods and the effects of browsing. The Liang and Seagle (2002) study contrasted neighbourhood effects of two tree species with very different shade tolerances, with the corresponding likelihood of differences in light transmission, which vary systematically as a function of shade tolerance in northeastern tree species (Horn, 1971; Canham *et al.,* 1994). Thus, the interactions between herbivory and neighbouring trees found in their study could be due to variation in light levels. For our study, we specifically selected core trees that have similar shade tolerance and light transmission characteristics (red oak *versus* red maple) (Canham *et al.,* 1994) to reduce confounding of light *versus* soil resource availability in our test of neighbourhood effects. Previous studies at our site have documented significant differences in N mineralization beneath the crowns of these two species (Finzi, van Breemen & Canham, 1998). We have shown elsewhere that foraging patterns of white-tailed deer vary in response to local variation in soil nitrogen availability (Tripler *et al.,* 2002). In particular, saplings of some of these tree species exhibit luxury consumption of nitrogen under low light and experience significantly higher rates of browsing (Tripler *et al.,* 2002). Despite these previous results, our current study revealed very little effect of neighbouring trees on response to herbivory.

IMPLICATIONS FOR COMMUNITY DYNAMICS

Deer densities in northeastern US forests have risen dramatically over the past century as a result of hunting regulations and landscape-scale changes in predator abundance and habitat quality (Porter, Coffey & Hadidian, 1994). Deer densities in many parts of the region appear to be at historic highs (McCabe & McCabe, 1997; Augustine & deCalesta, 2003). In Pennsylvania, the effects of high deer densities on tree regeneration are considered severe enough that the state Bureau of Forestry routinely fences state forestland after logging to ensure sufficient regeneration. In other states, hunting policies have been altered to try to reduce deer density, often by encouraging greater harvest rates, particularly of does (Porter, Coffey & Hadidian, 1994; Patterson *et al.,* 2002; Riley *et al.,* 2003).

One of the most direct effects of high deer densities is a reduction in the abundance of advanced regeneration under closed canopy conditions (Anderson & Loucks, 1979; Alverson, Waller & Solheim, 1988; de la Cretaz & Kelty, 2002). Our study did not reveal significant changes in competitive hierarchies under low light, but the simple reduction in survival and the constant pruning of saplings we observed reduces the density and size of understory saplings. This has a simple but profound effect on forest structure and biomass by reducing the rate of closure of gaps formed when canopy trees die. As a result, a larger percentage of a forest is in an open gap condition at any given time. Simulations suggest that this effect alone is sufficient to significantly reduce forest biomass and productivity (Jorritsma, van Hees & Mohren, 1999; Seagle & Liang, 2001).

Coomes *et al.* (2003) have raised the issue of the reversibility of the effects of high populations of introduced herbivores in forests of New Zealand. They note that heavy browsing by red deer (*Cervus elaphus scoticus*) has promoted the spread of unpalatable ferns, which appear to further reduce rates of regeneration of native tree species (Wardle, 1984). Stromayer and Warren (1997) have raised similar concerns in northeastern US forests, noting the interactions between browsing by white-tailed deer and the establishment of a dense ground layer of hayscented fern (*Dennstaedtia punctilobula*), which reduces tree seedling establishment, growth, and survival via a number of mechanisms (Hill, 1996; George & Bazzaz, 1999a,b). Exclosure studies in temperate forests of North America generally show some degree of recovery of the forest understory, but the rate of recovery may be very slow (Anderson & Loucks, 1979), and the reversibility of the effects of a half-century of very high deer densities is still uncertain (Horsley, Stout & deCalesta, 2003; Potvin, Beaupré & Laprise, 2003).

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