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Soil nitrogen availability, plant luxury consumption, and herbivory by white-tailed deer

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Abstract N is often cited as a limiting factor for sapling growth in northeastern USA forests. However, under conditions of elevated soil N, seedlings and saplings of some tree species exhibit luxury consumption of N, leading to elevated tissue N concentration. While this pool of plant N may have benefits for saplings if light levels change, it may also increase the risk of herbivory by white-tailed deer (*Odocoileus virginianus* L.). We conducted a field fertilization experiment to test the hypothesis that saplings increase stem tissue N when soil N availability is elevated. We fertilized saplings of nine tree species under closed and open canopies. Two of the nine species, yellow birch (*Betula alleghaniensis*) and black cherry (*Prunus serotina*), had significant increases in radial growth when fertilized under high light. Six of the nine species showed increased stem N concentration under either low light or high light conditions. Under low light conditions, black cherry and sugar maple (*Acer saccharum*) had significantly higher concentrations of stem N when fertilized. Regardless of fertilization treatment, yellow birch had significantly greater stem N in saplings under low light conditions when compared with saplings found in high light conditions. Under high light conditions, fertilization resulted in increased stem N in saplings of white ash (*Fraxinus americana*) and eastern hemlock (*Tsuga canadensis*). There was a trend for saplings of red maple (*Acer rubrum*) and white ash to show

elevated stem N concentration when fertilized under low light. Red oak (*Quercus rubra*), American beech (*Fagus grandifolia*) and white pine (*Pinus strobus*) did not show any evidence of luxury consumption. We compared browse frequency of fertilized and unfertilized saplings within similar forest types. Browse frequency was consistently higher on fertilized saplings. When averaged across all species, however, the difference between treatments was not significant. In contrast, we found significantly higher browse rates for fertilized saplings that had been previously identified as luxury N consumers. Our results indicate that increased soil N availability has positive effects on at least some of the species under high light, but, has potentially negative indirect effects on a larger group of species under both high and low light due to a higher risk of herbivory.

Keywords Deciduous forest · Fertilization · Forest dynamics · Saplings · Tree growth

Introduction

White-tailed deer (*Odocoileus virginianus* L.) can have severe impacts on sapling survival and growth in northeastern USA forests (Curtis and Rushmore 1958 ; Ross et al. 1970 ; Harlow and Downing 1970 ; Hanley and Taber 1980). Deer can reduce a sapling's ability to flush spring growth, and hence, decrease overall photosynthetic output, perhaps leading to an increase in mortality. Differences in the amount of N sequestered in over-wintering sapling buds and stems are likely to influence whether a deer chooses to browse a particular sapling over another. Tissue N concentrations play an important role in the palatability and nutritional quality of woody stems as an over-winter food resource for white-tailed deer (Holter et al. 1979 ; Van Soest 1982 ; Robbins 1993). In one of the earliest studies on mineral nutrition of northeastern tree species, Mitchell and Hosley (1936) observed an increased frequency of browse on saplings in plots fertilized with N.

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N has been shown to limit sapling growth in some northeastern tree species, particularly under high light levels (Burke et al. 1991 ; Canham et al. 1996 ; Fahey et al. 1998 ; Finzi and Canham 2000). However, under the low light conditions of a closed canopy, saplings may be unable to utilize available N for growth during the growing season. Under these conditions, saplings of some tree species appear to take up available N from soils beyond their current needs and store it in stems and roots (“luxury” consumption, van den Driessche 1974). While luxury consumption may have significant benefits for saplings, particularly if light levels change suddenly due to disturbance, it could have negative effects if it leads to increased rates of herbivory.

Studies from a broad range of forests have shown that adult trees influence the local availability of soil resources through uptake of water and nutrients, interception of throughfall, and deposition of litter (Zinke 1962 ; Zinke and Crocker 1962 ; Challinor 1968 ; Alban 1969 ; Lodhi 1977 ; Boerner and Koslowsky 1989 ; Boettcher and Kalisz 1990 ; Finzi et al. 1998a). Gosz et al. (1972) found that interspecific variation in litter quality was an important component in the spatial variation of soil N availability in forests. In a closed canopy forest, most of an individual tree’s litter falls close to its base (Ferrari and Sugita 1996). Hence, forest neighborhoods dominated by trees of high litter quality are characterized by high soil N availability (Melillo et al. 1982 ; Boerner and Koslowsky 1989 ; Scott and Binkley 1997 ; Finzi et al. 1998a). Thus, sapling N concentration and palatability to white-tailed deer may vary as a function of both site differences and composition of the local canopy tree neighborhoods.

We conducted a set of field fertilization experiments to address questions about sapling responses to soil N availability, and to determine how those responses might influence rates of herbivory by white-tailed deer in forests of southern New England. Specifically, we asked:

1. Is there evidence that N is a limiting resource for the nine major tree species at our sites?
2. Do saplings growing under closed canopies increase N storage over-winter when N-availability is increased?
3. Does luxury consumption of N put species at increased risk of herbivory?

Materials and methods

Study site

The experiments were conducted at Great Mountain Forest (GMF) on Canaan Mountain in northwestern Connecticut, USA (42°00’N, 73°15’W). The soils at this site are sandy, acidic inceptisols and spodosols. The study site is primarily a second-growth transitional conifer-hardwood forest dominated by a mix of nine species: red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), American beech (*Fagus grandifolia* Ehrh.), white ash (*Fraxinus americana* L.), white pine (*Pinus strobus* L.), black cherry (*Prunus serotina* Ehrh.), red

oak (*Quercus rubra* L.), and eastern hemlock [*Tsuga canadensis* (L.) Carr.]. These nine species represent a broad range of shade tolerance and differ widely in litter quality and effects on soil nutrient availability (Pacala et al. 1994 ; Kobe et al. 1995 ; Finzi et al. 1998a, 1998b).

Fertilization of individual saplings

In the spring of 1997, we located saplings of four species: red maple, sugar maple, red oak, and white ash, under high and low light levels. We chose saplings that ranged in height from 50–150 cm from an area of approximately 3 km². Saplings were no closer than 2 m. Saplings in the “low light” treatment (~<10% full sun) were found growing under mixed canopies of white pine, red oak, red maple, and sugar maple; saplings in the “high light” treatment (>50% full sun) were found growing in either logged areas that were over 10 years old (GMF staff, personal communication) or large gaps created by wind disturbance. We flipped a coin to assign the fertilization treatment randomly to ten saplings of each species under each light regime, for a total of 160 saplings in the experiment. In the spring of 1999, we repeated the experimental procedure using beech, black cherry, eastern hemlock, white pine, and yellow birch and a supplementary set of 20 (five of each treatment) oak saplings, for a total of 260 saplings.

In mid June 1997, we removed the top layer of fresh leaf litter within a 50 cm radius around the saplings and applied 25.4 g of 41% urea-N (Agway, slow release, 10.4 g N) evenly over the 0.785-m² area of exposed soil. This application rate was chosen to approximately double the amount of available growing season N, based on previous studies of mid-summer N mineralization at our sites (Finzi et al. 1998a). After adding the N, we carefully replaced the leaf litter. Leaf litter was disturbed around control saplings in a similar manner. We followed the same procedure for the sapling study in the spring of 1999, except that fertilization occurred in the last week in May. These fertilization treatments occurred after the canopy had been closed for about 2 weeks. Work in forests similar to GMF has shown that this time period corresponds to a decrease in soil N availability associated with plant uptake (Pastor et al. 1984).

At the end of the growing season in 1997 and 1999, we recorded the gain in height over the season (“extension growth”) and total height of each sapling. We calculated relative extension growth as height gain divided by total height. In 1999, we measured sapling radial growth as the increase from May to December in stem diameter approximately 2 cm above the ground. Whole saplings were harvested in December of 1997 and 1999, removing as much of the root mass as possible. We retained needles for white pine and eastern hemlock stems because we were interested in N concentration of these stem tissues as seen from the perspective of a herbivore. Apical stems from the past year’s growth were removed, weighed, and dried for 5 days at 80°C. Dried stems were ground with a micro-Wiley Mill (no. 40 mesh sieve). Triplicate samples of ground material were analyzed for total N (inorganic and organic forms of N) on a dry weight basis on a Carlo-Erba model 1500 CHN combustion analyzer.

Whole plot fertilizations

In June of 1999, we chose twelve 8×8-m plots in areas of known high deer density. The plots were positioned in pairs within 50 m of each other with similar understory structure. All plots had a closed canopy, and sapling density ranged from 30–70 plants plot⁻¹ (or 0.5–1.1 saplings m⁻²), with each pair of plots containing similar sapling densities. Saplings ranged from 30–150 cm in height. We mapped and tagged each sapling within each plot. We randomly chose one plot from each pair to be a control and the other to be fertilized. Following the method from the first experiment, we fertilized each sapling in the fertilization plots with 25.4 g of 41% N-urea spread over a 0.785-m² area. We scored browsing as any stem (terminal or lateral) that was torn in a manner consistent with deer feeding, and did not count any other dam-

age as herbivory such as browsing from lagomorphs. For each sapling, we identified any previous winter (1998–1999) deer browsing in June 1999 prior to our treatment application. In the first post-treatment census, September 1999, we scored only new browsing on saplings with special care taken for saplings that were browsed in the previous winter. In subsequent censuses, December 1999 and March 2000, we scored any new deer browsing. At the end of the study, if a sapling was browsed during any three of the post-treatment census periods, that sapling was counted as browsed. A cumulative browse frequency was then assigned to each category of sapling, luxury or constant N consumer.

Statistics

Data were analyzed using SYSTAT version 7 (SPSS 1997). Sapling N concentration and radial growth had highly skewed distributions; we log-transformed these data to make them normally distributed. We used a fourth-order power transformation to normalize the relative extension growth rate data set. Although an uncommon transformation, for proportional data with a large number of small values clumped to the left-hand side of a distribution, a power transformation is appropriate. In this case, expected vs. observed transformed points were linear; residual plots showed well-dispersed data; and the skewness and kurtosis ratios were around the suggested 2:1 ratios. We analyzed relative extension growth rate data by pooling all species, from the 2 years of the experiment, into a single data set. We analyzed saplings for changes in N concentration, radial growth and relative extension growth using general linear modeling with species, light, and fertilization treatment as main factors. We used one-way ANOVAs to compare treatment groups for each species and Bonferroni post-hoc tests across pairs of treatment groups when the ANOVA was significant. If any of the four N concentration means was significantly different from the others, for each of the six luxury N consumers, then the Bonferroni post-hoc test was applied for pairwise comparisons of the four means (within species comparison, α level=0.05).

For the plot fertilization experiments, we analyzed the summed browse frequencies of each plot type (control vs. fertilized) for each census period, using a paired *t*-test on the arcsine-square root transformed data. Since individual species were absent from some plots, we grouped species into one of the two N consumer categories, constant and luxury (see Results). We classified 52 of the saplings as constant N consumers and 356 as luxury N consumers. To test overall differences in browse frequencies between control and fertilized saplings, we analyzed the frequency of browse using a Mantel-Haenszel χ^2 (Wilkinson et al. 1996) with control versus fertilized saplings as the stratifying variable and the N consumer designation as the categorical variable. We further conducted Pearson χ^2 -tests to look for differences between constant and luxury N-consuming species within the control and fertilized plots.

Results

Sapling growth

The general linear model explained 52% of the variance associated with absolute radial growth. There were significant effects of species, light, and fertilization on radial growth (Table 1). In addition to these direct effects, there was a significant light by species interaction, and there was an indication fertilization had a marginally significant interaction with species ($P=0.070$) and light ($P=0.054$) influencing radial growth (Table 1). Radial growth of beech, white pine, black cherry, and eastern hemlock saplings was significantly greater under high light than low light ($P<0.05$, Fig. 1). Under high light

Table 1 ANOVA of absolute sapling radial growth (mm)

$R^2=0.517$					
Source	SS	df	MS	F	P
Species	2.413	4	0.603	5.847	0.000
Light	15.680	1	15.680	151.972	0.000
Fertilization	0.950	1	0.950	9.212	0.003
Light×species	3.451	4	0.863	8.361	0.000
Light×fertilization	0.386	1	0.386	3.741	0.054
Species×fertilization	0.908	4	0.227	2.201	0.070
Light×species×fertilization	0.519	4	0.130	1.257	0.288
Error	22.596	219	0.103		

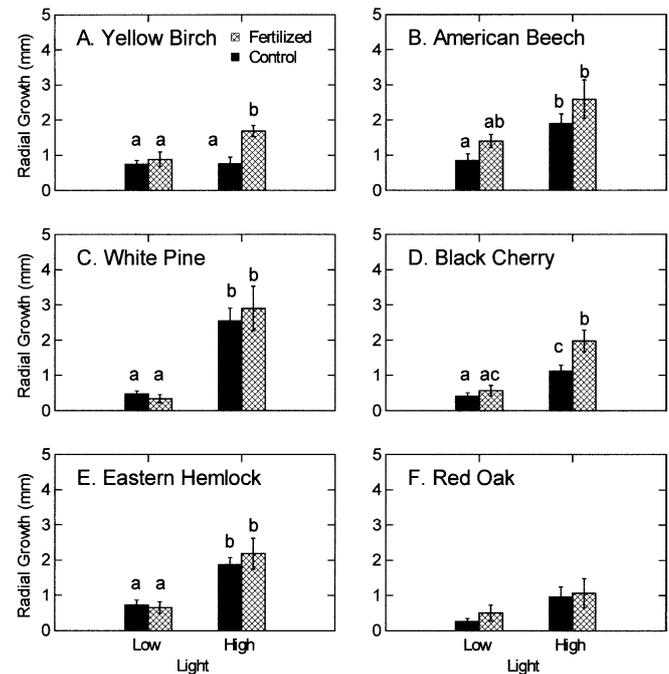


Fig. 1A–F Mean radial growth (with SEs) for fertilized and unfertilized saplings of yellow birch, American beech, white pine, black cherry, and eastern hemlock under low and high light conditions. Different letters over bars represent significant pairwise differences across all four treatment combinations (Bonferroni post-hoc tests, $P<0.05$). Lack of letters indicates no significance for any pairs. Across all species except yellow birch, mean radial growth was significantly greater under high light conditions. For red oak, differences did not exist among the four treatment groups (no letters shown), but there was a significant effect of light on radial growth

conditions, fertilization produced significant increases in radial growth for yellow birch (Fig. 1A) and black cherry (Fig. 1D). Beech, white pine, and eastern hemlock saplings had significantly greater radial growth under high light conditions when compared to yellow birch, black cherry, and red oak saplings but not when compared with each other.

Overall, relative extension growth varied significantly among species and light levels, but not in response to fertilization and there were no significant interactions

Table 2 ANOVA of sapling relative extension growth (%)

$R^2=0.401$					
Source	SS	df	MS	F	P
Species	7.999	8	1.000	21.078	0.000
Light	1.529	1	1.529	32.226	0.000
Fertilization	0.014	1	0.014	0.291	0.590
Light×species	0.421	8	0.053	1.110	0.355
Light×fertilization	0.007	1	0.007	0.147	0.701
Species×fertilization	0.430	8	0.054	1.132	0.341
Light×species×fertilization	0.497	8	0.062	1.310	0.237
Error	16.413	346	0.047		

among the three main factors (Table 2). Yellow birch saplings had significantly higher relative growth rates under high light/fertilized conditions compared with the low light controls (Fig. 2D). Fertilized black cherry saplings had lower relative extension growth under low light canopy conditions when compared with high light/fertilized saplings (Fig. 2E). Unfertilized white pine saplings had significantly higher growth rates under high light than under low light (Fig. 2H).

Stem N concentrations

We found significant differences in sapling stem N concentration as a function of species, light, and fertilization treatments (Table 3). Differences in stem N concentration also depended on the light environment in which species were found (a species-light interaction), or whether saplings were fertilized under high or low light

(a light-fertilization interaction). Beech, white pine, and red oak saplings (regardless of year) did not differ significantly in stem N concentration for any treatment combination (Fig. 3). For sugar maple and black cherry saplings, significant increases in stem N concentration were clearly seen for fertilized individuals growing under a closed canopy (Fig. 4A, B). Stem N concentration of yellow birch saplings was significantly higher under closed canopies, and was not affected by fertilization treatment (Fig. 4C). Eastern hemlock and white ash showed significant increases in stem N concentration for fertilized saplings growing under open canopies (Fig. 4D, E). Fertilized white ash saplings growing under closed canopies had a mean stem N concentration that was higher than that of unfertilized saplings, but differences were not statistically significant ($P=0.082$, Fig. 4E).

Three of the nine species – beech, eastern hemlock, and red oak – did not show luxury N consumption, had small mean differences between any light/fertilization treatments within species, and showed little variation in N concentration across treatments (Fig. 3). Beech and red oak saplings had the lowest tissue N concentrations of the nine species in this study. White pine had a relatively high concentration of N across all treatments compared with beech and oak, which may be a result of the inclusion of needles in the analysis (Fig. 3B). Nonetheless, the increase in available N did not cause differences in over-wintering tissue N in white pine. We have designated these three species as constant N consumers.

We found clear evidence of luxury N consumption in saplings of sugar maple, black cherry, and yellow birch (Fig. 4A–C) under low light conditions; in saplings of eastern hemlock and white ash under high light conditions (Fig. 4D, E); a trend for increased stem N in fertil-

Fig. 2A–I Mean relative extension growth (with SEs) for fertilized and unfertilized saplings of nine species under high and low light conditions. For each species, different letters over bars represent significant pairwise differences across all four treatment combinations (Bonferroni post-hoc tests, $P<0.05$). Lack of letters indicates no significance for any pairs. Red oak panel represents both years (1997, 1999) summed together. Note difference in axis values for the top three graphs

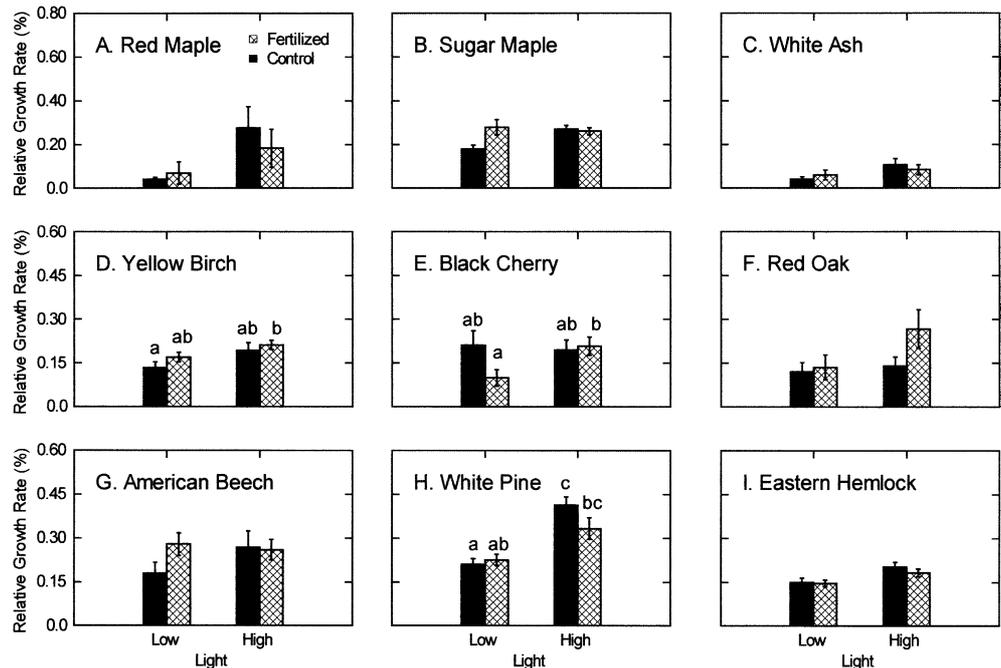
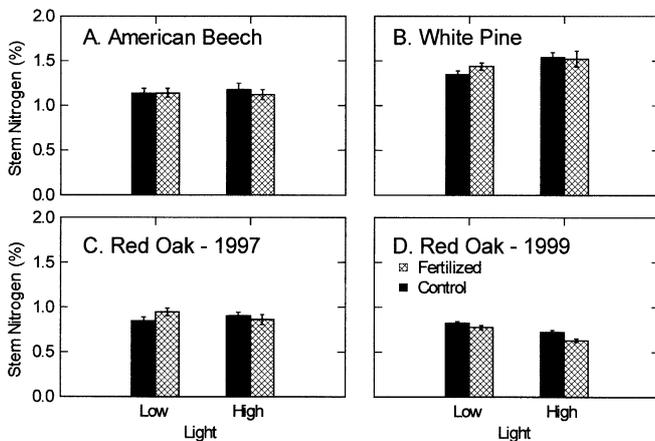


Table 3 ANOVA of tissue N of sapling stems

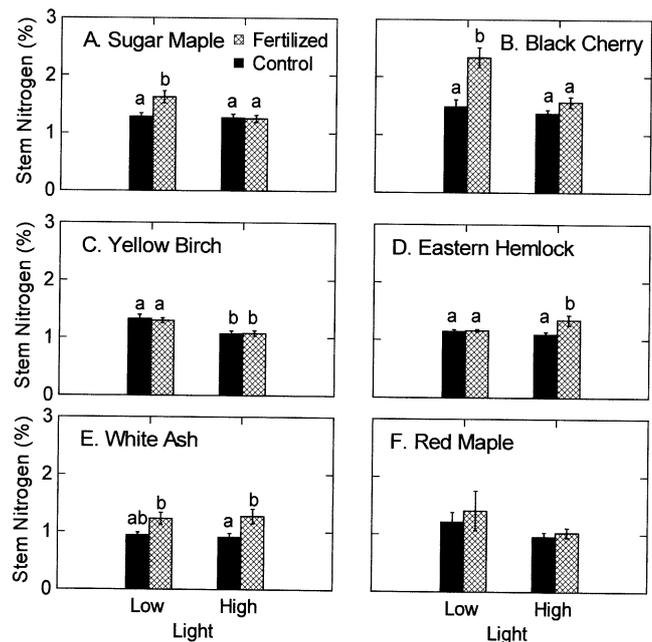
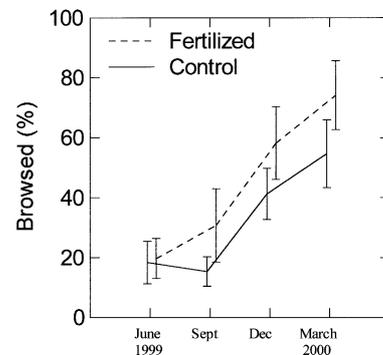
Source	SS	df	MS	F	P
Species	9.250	8	1.151	29.666	0.000
Light	0.464	1	0.464	11.967	0.001
Fertilization	0.840	1	0.840	21.667	0.000
Light×species	1.136	8	0.133	3.660	0.000
Light×fertilization	0.090	8	0.090	3.426	0.001
Species×fertilization	1.063	1	0.133	2.322	0.129
Light×species×fertilization	0.549	8	0.069	1.769	0.082
Error	12.412	320	0.039		

**Fig. 3A–D** Mean stem N concentration (with SEs) shown for American beech, white pine, and red oak (in 1997 and 1999) as a function of light and fertilization treatments. There were no significant differences associated with light or fertilization for these species

ized white ash saplings compared with controls under low light conditions (Fig. 4E); and a trend for increased stem N in red maple saplings growing under low light compared with red maple saplings under high light (Fig. 4F). We considered yellow birch a luxury N consumer even though saplings did not respond to the fertilization treatment (Fig. 4C), because saplings growing under low light had significantly higher concentrations of stem N than saplings growing under high light. Black cherry under low light had the greatest response to N fertilization, increasing stem N nearly 36% relative to control saplings. Black cherry also showed the highest average stem N concentration, over 2% N, a very high value for N concentration in woody plant material (compare to Switzer et al. 1966 ; Switzer and Nelson 1972 ; van den Driessche 1974).

Fertilization and deer herbivory

When summed across all species, browse rates did not differ significantly between control and fertilized plots in

**Fig. 4A–F** Mean stem N concentration (with SEs) shown for red maple, sugar maple, white ash, yellow birch, black cherry, and eastern hemlock as a function of light and fertilization. For each species, different letters over bars represent significant pairwise differences across all four treatment combinations (Bonferroni post-hoc tests, $P < 0.05$). Lack of letters indicates no significance for any pairs**Fig. 5** Averaged total percent (with SE bars) of browsed saplings from control ($n=6$) and fertilized plots ($n=6$) over time from June 1999 to March 2000. Sample dates were the same for fertilized and control plots; bars are offset for clarity. *Sept* September, *Dec* December

any of the individual census periods (June, $t = -0.132$, $df = 5$, $P = 0.900$; September, $t = -1.725$, $df = 5$, $P = 0.145$; December, $t = -1.971$, $df = 5$, $P = 0.106$; March, $t = 0.472$, $df = 5$, $P = 0.657$), although saplings on the fertilized plots were browsed at a higher percentage than saplings in the control plots on each of the three census dates (Fig. 5). The fertilization treatment significantly increased the amount of herbivory on luxury N consumers when compared to constant N consumers (Fig. 6). The Mantel-

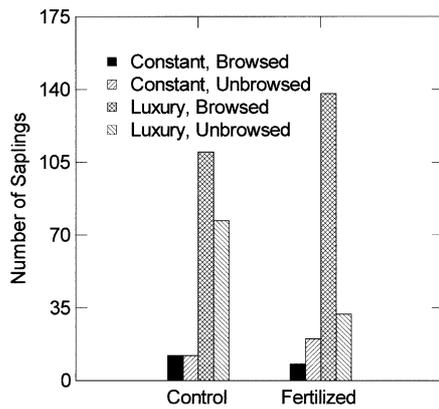


Fig. 6 Number of saplings browsed at the end of the whole-plot fertilization study. Saplings are categorized as control (i.e. unfertilized) or fertilized, and then further grouped into browsed and unbrowsed N consumer groups (i.e. constant or luxury). See text for a discussion of the significant differences

Haenszel test showed that there was a significant difference in the frequency of browsing on constant and luxury N consumers when control and fertilized saplings were compared (Mantel-Haenszel $\chi^2=20.276$, $P<0.001$). Luxury and constant N consumers did not differ significantly in their browse frequency when unfertilized (Pearson $\chi^2=0.679$, $P=0.410$), but did differ in their browse frequency when fertilized (Pearson $\chi^2=35.281$, $P<0.001$).

Discussion

We found clear evidence of luxury consumption of N by saplings of many, but not all, of the tree species in our study. Saplings could be characterized as either constant (e.g. red oak) or luxury N consumers (e.g. sugar maple) depending on the increase in stem N concentrations as a function of local light and soil N availability. Within the group of luxury consumers, species differed in whether luxury consumption occurred at low versus high light. While luxury consumption may have physiological benefits for these species, our results indicate that it may also have significant negative effects by stimulating higher rates of browsing by white-tailed deer. Our results also suggest that this important consumer is able to discern differences in stem concentrations at the individual plant level. One consequence of such fine-scale trophic level interaction is the potential for deer to influence the dynamics of forest succession. Under the current paradigm, shade-tolerant species (e.g. sugar maple) have the higher probabilities of surviving in the understory until a disturbance event occurs allowing those species to outcompete seedlings that colonize the gap. However, if deer herbivory alters the growth of the shade-tolerant species, then the differential success of any given species becomes a function of whether it was browsed. From our study, we suggest that the probability of being browsed is a func-

tion of a species' N consumption strategy and its spatial distribution relative to neighborhoods of high N availability.

Sapling growth

Both light and N can limit growth of saplings of north-eastern tree species (Sipe and Bazzaz 1995 ; Kobe et al. 1995 ; Walters and Reich 1997 ; Fahey et al. 1998 ; Finzi and Canham 2000). Canham et al. (1996) found that species differed in shoot and root biomass accumulation across varied combinations of light, water, and N treatments. Similarly, we found light limitation in radial growth for five of the six species – beech, white pine, black cherry, eastern hemlock, and red oak – and N limitation in radial growth under high light conditions for two of the six species – yellow birch and black cherry (Fig. 1).

Fertilization did not cause a consistent response in relative extension growth rates across the nine species in this study (Fig. 2). The lack of a significant effect of N on relative extension growth suggests that relative extension growth rate may be a poor measure of sapling sensitivity to N availability. This may be related to strong effects of light availability on allocation to height growth versus radial growth (Walters and Reich 2000). In contrast, radial growth appears to be a more sensitive measure of sapling performance, since species must allocate some fraction of resources to new conducting tissue (Kozlowsky and Pallardy 1997).

Over-wintering N storage

Although we elevated soil N availability to twice any values measured at GMF, we cannot rule out the possibility of high N availability in soils for control saplings. Hence, the elevated stem N concentration for the control saplings of yellow birch under low light conditions may reflect higher than predicted soil N pools below those saplings. Moreover, constant N consumers may be storing N in their roots, as has been shown for some species (Glerum 1980 ; Marmann et al. 1997). Root N concentrations have also been shown to increase with increases in net soil N mineralization (Nadelhoffer et al. 1985). Although the species in this study varied in their stem N storage response to increased soil N availability, the species categorized as constant N consumers may still luxury-consume N, but the consumed N may be stored in roots. However, N storage in roots is not likely to affect the outcome of deer herbivory on these species.

Increased over-wintering stem N could be a benefit if it can be mobilized quickly to produce leaves, and subsequently increase the rate of photosynthesis, before the canopy reduces available light at the forest floor (Lechowicz 1984 ; Uemura 1994). Few studies have examined whether an early leaf-out phenology is a way of avoiding competition for light and soil nutrients later in

the growing season (Kudo 1991 ; Uemura 1994 ; Bilbrough and Caldwell 1997 ; Seiwa 1998). For saplings in the forests of southern New England, there may exist a small window in which light and soil resources are not limiting to understory sapling photosynthesis (Uemura 1994). Therefore, an early flush of growth has the potential to benefit a sapling. Yet, there are clearly species, such as red oak and beech that forego luxury N consumption and subsequent storage in their stems. For these species, the cost of losing N in their stems to herbivory over-winter may not be balanced by the benefit of C gain from an early flush of leaf growth in the spring. Differences in the development of sun and shade leaves and their subsequent N demand may also help explain differences in species responses to elevated soil N (Boardman 1977 ; Eschrich et al. 1989), however an examination of the contribution of sun-shade leaves to N demand was beyond the scope of this study.

Luxury consumption and deer herbivory

We assessed the impact of an increase in soil N availability on the frequency of herbivory in neighborhood-scale plots. Browse frequencies were not significantly higher for fertilized saplings when compared to unfertilized saplings when all species were pooled across plots (Fig. 5). However, there was a significant increase in the frequency of browse on the fertilized saplings when compared with the unfertilized saplings of the luxury N-consuming species (Fig. 6). This comparison becomes more striking when one considers that under ambient field conditions (i.e. "controls") 50% of the constant N consumers and about 59% of the luxury N consumers were browsed, not a large difference in a population of thousands of saplings. However, when N availability increased, 82% of the luxury N consumers were browsed compared with 29% of the constant N consumers. Our sampling scheme did not allow us to examine these differences at the species level, but we are hopeful that further studies could help elucidate how individual species are impacted by herbivory as a function of increased N availability. We believe this information could be utilized to assign browse probabilities to saplings as a function of tree neighborhoods, in forest simulation models, which could be coupled with differential growth functions. This approach could ultimately help us refine our knowledge about the role deer play in influencing successional dynamics of eastern deciduous forests.

Site and canopy neighborhood effects on diet selection by white-tailed deer

Studies attempting to identify the feeding preferences of deer have often relied on the frequency in which deer foraged upon any particular species, and then ranked this preference (Coblentz 1970 ; Drolet 1974 ; Pekins and

Mautz 1988). Yet, deer-preference rankings for tree saplings are rarely the same in studies from different regions with similar woody species compositions [e.g. compare Healy (1971) and Drolet (1974)]. The results from our study suggest that preference rankings should vary with site quality. On a spatial scale smaller than a stand, site quality can be argued to be largely a function of the local trees (Finzi et al. 1998a, 1998b). For example, a black cherry sapling found growing under a tree associated with high litter quality is likely to have higher over-winter stem N and, hence, a higher probability of being browsed than a black cherry sapling growing under a tree associated with lower litter quality, where it would have lower stem N. Thus, two studies might differ in their preference ranking of black cherry if the studies found these saplings growing in portions of the forest with different levels of available soil N.

Implications for effects of N deposition

There is an increasing concern that elevated N deposition in northeastern U.S. forests could lead to N saturation and a complex suite of changes in ecosystem and population level processes (Aber et al. 1989, 1991 ; Aber 1992 ; Lovett and Rueth 1999). The National Atmospheric Deposition Program has recorded atmospheric deposition of inorganic N in the order of approximately 5 kg·ha⁻¹·year⁻¹ from the southeastern region of New York through southern New England (National Atmospheric Deposition Program 2000). As seen in the plot-level fertilization experiment, increases in local soil N can significantly enhance the probability that a luxury N consumer sapling is browsed. If increases in the N deposition rate elevated the amount of available soil N at GMF, there could be an increase in the frequency of browsing on luxury N consumers regardless of their local neighborhood. Moreover, if the frequency of herbivory were to increase for luxury N consumers everywhere in the forest, gap-phase replacement dynamics could be altered to favor constant N consumers. Hence, we suggest that increased soil N availability through deposition could alter successional dynamics to favor beech and oak through the indirect effect of loss or weakening of luxury N consumer competitors due to herbivory by white-tailed deer.

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