Effects of the frequency, timing, and intensity of simulated browsing on growth and mortality of tree seedlings[1]

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Field exclosure studies have shown that mammalian browsers such as white-tailed deer (*Odocoileus virginianus*) can have pervasive effects on forest dynamics in eastern North America. Direct experimental tests of the effects of browsing on growth and survival of a wide range of tree species, however, have yielded conflicting results. This study was designed to assess the effects of variation in the frequency, seasonal timing, and intensity of browsing (simulated by mechanical clipping) on the growth and mortality of three of the major tree species of the Hudson Valley, New York. The clipping treatments were applied to seedlings grown under two different light regimes (full sun and 8% of full sun) to examine seedling responses under different levels of shade-induced carbon stress. Our results demonstrate that even 2 successive years of heavy winter clipping (75% of new shoot growth removed) has little immediate effect on growth or survival of any of the three species. It is possible that winter browsing only has significant negative effects when seedlings are browsed repeatedly over long periods of time. However, comparable levels of summer browsing for only 2 years significantly reduced both growth and survival of all three species. While most natural browsing occurs in the dormant season, our results suggest that it is the less frequent browsing during late spring and early summer that has the greatest immediate effect on tree seedlings. Shading reduced growth and increased mortality in all three species; however, there was only a limited interaction between light level and the simulated browsing treatments. The effects of browsing on survival were similar in all three species; however, the effects of browsing on cumulative height and annual growth varied enough among the species to suggest that browsing could cause significant variation among these species in their rate of invasion in old fields and rights of way, and their rate of regeneration following logging or disturbance of forests.

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Des études d'exclos ont démontré que des mammifères brouteurs tel que le cerf de Virginie (*Odocoileus virginianus*), pouvaient avoir un impact important sur la dynamique des forêts de l'Est de l'Amérique du Nord. Toutefois, des études expérimentales portant directement sur les effets du broutage sur la croissance et la survie d'un grand nombre d'essences, ont produit des résultats contradictoires. Cette étude a été structurée de façon à évaluer les effets de la fréquence et de l'intensité du broutage (simulé par une taille mécanique), ainsi que du moment où il survient pendant la saison sur la croissance et la mortalité des trois principales espèces d'arbres de la vallée de la Hudson, dans l'état de New-York. Les traitements de taille ont été appliqués à des semis cultivés sous deux régimes de lumière (plein soleil et 8% du plein soleil) pour examiner leur réponse suivant deux niveaux de déficience en carbone induite par l'ombre. Nos résultats démontrent que deux années consécutives de taille hivernale sévère (la taille de 75% des pousses de l'année) avaient peu d'effet sur la croissance ou la survie des trois essences. Il est possible que le broutage hivernal n'ait d'effets négatifs significatifs que lorsqu'un broutage répété se fait sur une longue période. Cependant, des niveaux comparables de broutage estival sur seulement deux ans, ont significativement réduit la croissance et la survie des trois essences. Bien que la plus grande partie du broutage naturel se fasse pendant la période de dormance, nos résultats suggèrent que c'est le broutage moins fréquent à la fin du printemps et au début de l'été qui a l'effet immédiat le plus marqué sur les semis forestiers. L'ombrage a réduit la croissance et augmenté la mortalité chez les trois espèces. Toutefois, il n'y avait qu'une faible interaction entre le niveau de lumière et les traitements de broutage simulé. Les effets du broutage sur la survie étaient similaires pour les trois espèces. Cependant, les effets du broutage sur la hauteur cumulative et la croissance annuelle diffèrent suffisamment entre les espèces pour suggérer que le broutage pourrait causer des variations significatives dans leur rythme d'invasion des champs abandonnés et des zones de servitude et dans leur taux de régénération suite à des coupes ou à d'autres perturbations de la forêt.

[Traduit par la rédaction]

Introduction

Field exclosure studies have demonstrated dramatic effects of woody browsing on the dynamics of temperate forests in eastern North America (e.g., Jordan 1967; Marquis 1975, 1978; Anderson and Loucks 1979; Pastor et al. 1988). However, direct experimental tests of the effects of browsing (usually simulated by clipping) on the growth and mortality of tree seedlings have yielded conflicting results. Some studies have shown no significant reduction in performance when seedlings are clipped (i.e., Jacobs 1969), or a reduction in growth or survival only when the amount of woody tissue removed is extremely severe (e.g., Campa et al. 1992). The wide range of results encountered in these experiments suggests that the direct effects of browsing on seedling performance depend on both environmental factors and the

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physiological and morphological traits of individual species. Winter browsing represents both an immediate damage that must be repaired, and the loss of structural material and the buds and reserves contained within those woody tissues that would have otherwise been used to support growth in the next growing season. Summer browsing has the additional effect of removing leaf area and potentially reducing growth during the current growing season.

The ability of seedlings to recover from herbivory should be influenced by the availability of resources (e.g., light, water and nutrients) that determine site quality and potential growth. For example, shading significantly increases the mortality of gray birch (*Betula populifolia* Marsh.) saplings that have been cut at the base (Kays and Canham 1991). Similarly, the responses of blue oak seedlings (Quercus douglasii Hook. & Arn.) in California to simulated browsing are strongly influenced by levels of drought stress (Welker and Menke 1990). Differences among species in both the physiology and morphology of shoot growth also appear to have significant effects on seedling response to loss of woody tissue. Differences in the seasonal timing of clipping can have a dramatic effect on regrowth because of differences among species in the seasonal timing of the movement of carbohydrate reserves into roots for storage (Kays and Canham 1991). The effects of winter browsing on regrowth the next spring also depend on the nature and distribution of buds along a woody shoot, and the degree of flexibility in the ability of lateral buds to develop if the terminal leader is removed (Metzger 1977).

While browsing has usually been examined from the perspective of tree regeneration in forests, browsing may also have significant effects on the rates of tree invasion in old fields. In a separate study of the dynamics of tree invasion of old-field communities along utility rights of way, we have found significant variation in rates of browsing among tree species, community types, seasons, and landscapes (Canham et al. 1993). Seedlings that are not shaded by adjacent shrubs and herbs have a higher likelihood of being browsed (Canham et al. 1993); however, they may be much more tolerant of browse damage because of their high rates of photosynthesis in high light environments. In contrast, seedlings shaded by adjacent vegetation have a lower probability of being browsed, presumably because the vegetation makes the seedlings less apparent to the herbivores (Canham et al. 1993). However, shaded seedlings may be more sensitive to browse damage because of their slow potential growth rates under low light conditions. Similarly, most browsing occurs in the dormant season (fall, winter, and spring), when seedlings may be more tolerant of stem removal (because carbohydrate reserves are stored throughout the plant). While summer browsing is much less common than winter browsing, seedlings may be very sensitive to summer browsing because levels of stored reserves are low, and browsing removes both woody shoots and the leaves required to produce new reserves (e.g., Kays and Canham 1991).

The general objective of this study was to assess the effects of variation in the frequency, intensity, and seasonal timing of browsing (simulated by mechanical clipping) on the growth and survival of three of the major species of trees in the Hudson Valley of New York. The simulated browsing treatments were applied to seedlings grown under two different light regimes (full sun and 8% of full sun) to examine seedling responses under different levels of shade-induced carbon stress.

Methods

Study species

Three tree species, red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.), and black cherry (*Prunus serotina* Ehrh.), were selected for this study because they provided a range of shade tolerances and growth forms, and because all three are common woody invaders of old fields in the region (Canham et al. 1993). One-year-old seedlings of red maple and white ash were purchased from a local nursery, and the black cherry seedlings were germinated from locally purchased seeds the previous year and grown for 1 year in a lathhouse (and then stored overwinter in a cold storage facility). All seedlings were 10–20 cm tall at the time of planting, and were planted as bare-root stock.

Experimental design

The seedlings were planted into an old field that had been maintained by mowing at 1–2 year intervals. The approximately 1 ha experimental area was laid out into 30 blocks (arranged in four rows of eight blocks each, with two unused areas). Each block consisted of six plots approximately 2 × 2 m in size, separated by 2 m. Because of a shortage of usable seedlings, only 24 of the 30 blocks were used for black cherry. Herbaceous vegetation in each plot was removed through the use of an herbicide (glyphosate) prior to the start of the experiment, and the plots were kept weeded throughout the study. The six plots within each block were randomly assigned to one of the six possible factorial combinations of three tree species (red maple, white ash, or black cherry) and two light levels (full sun or 8% full sun) (i.e., each plot was planted with one tree species and received one of the two light levels). The 8% full sun light treatment was created by constructing shade tents over each of the appropriate plots, using 92% black shade cloth. The shade tents were removed each fall and set up again in the spring to avoid damage from snowfall. Nine seedlings of the appropriate species were planted in each plot in a grid with approximately 50-cm spacing. All seedlings were planted between 29 May 1988 – 10 June 1988. The nine seedlings in each plot were randomly assigned as either a control (no clipping treatment) or to one of the eight clipping treatments (Table 1). The seedlings were watered several times after planting to ensure successful establishment. The entire field was enclosed in an electrified fence to prevent uncontrolled browsing by either white-tailed deer or rabbits. The fence was not completely effective, and a total of 21 of the 1512 seedlings were removed from the experiment because of either heavy rabbit damage, or damage during weeding of the plots.

Two levels of simulated browsing were used: 75% of the current year's shoot length was removed in the heavy browsing treatment and 25% was removed for the light browsing treatment (Table 1). We restricted clipping to current-year growth because of our field observations that most browsing was restricted to those portions of the shoot. We removed a fixed percentage of new shoot growth (i.e., 25 or 75%) to provide a clipping intensity that was independent of plant size. This technique also avoided confounding of clipping intensity and the shade treatments (e.g., removing a fixed total length of shoots from the slower growing seedlings in the shade treatments would have represented a far more severe treatment than removing the same total shoot length from the much larger seedlings growing in full sun).

The appropriate length was clipped from each first-order branch on a seedling, rather than concentrated on only a few branches or the leader. The clipping was done with pruning shears (Snap-Cut Inc.). Growing season ("summer") clipping was done in late August to early September of 1988 and 1989. The dormant season ("winter") clipping was done in late November to early December of 1988 and 1989. For seedlings clipped in both seasons, the winter clipping amounts were calculated from the shoot length remaining after the summer clipping, plus any late season

TABLE 1. Clipping treatments used in this study

Code	Description	FREQUENCY	SEASON	INTENSITY
CTRL	Control (no clipping)	0	N	N
LWC	Light winter clipping		W	L
HWC	Heavy winter clipping	2	W	H
LSC	Light summer clipping		S	L
HSC	Heavy summer clipping	2	S	H
LSWC	Light summer and winter clipping		B	L
HSWC	Heavy summer and winter clipping		B	H
HWO	Heavy winter clipping in 1st year only	1		
HSC	Heavy summer clipping in 1st year only	1		

NOTE: "Light" clipping treatments consisted of removal of 25% of new shoot length, while 75% of new shoot length was removed for the "heavy" clipping treatments. Also indicated are the groupings of treatments used in planned contrasts for (*i*) FREQUENCY (0, 1, or 2 years); (*ii*) SEASON (N, none; S, summer; W, winter; B, both); and (*iii*) INTENSITY (N, none; L, light; H, heavy) of browsing.

flushing of new shoots following the summer clipping. Our studies of tree seedling invasion in old fields (Canham et al. 1993) indicate that seedlings browsed in 1 year have a higher than random chance of being browsed in the next year. Thus, the main clipping treatments were applied for 2 successive years (Table 1). Two of the "heavy" clipping treatments (HSO and HWO) were done only in the 1st year to allow comparison of the effects of 1 versus 2 years of browsing.

Root starch analysis

For each of the three species, a 10-cm piece of a major lateral root was collected at the end of the first growing season from five individuals (four for black cherry) in each of the six combinations of two shade treatments and three clipping treatments (none, light, or heavy, which were applied only during the first summer) to examine the effects of intensity of summer browsing on carbohydrate reserves. These individuals were dropped from further growth measurements and analyses because of the damage associated with root sampling. Root samples were immediately placed in plastic bags and frozen in a cooler with dry ice to minimize respiration losses. All samples were stored in a freezer at −18°C upon returning to the laboratory.

The frozen root material was removed from the freezer within 30 days and the outside bark and fine roots were removed by scrubbing with a kitchen scouring pad. The roots were then sliced into thin segments to facilitate drying, and put into a drying oven for 72 h at 70°C. After drying, the root material was ground in a Wiley mill to pass a 0.5 mm sieve screen, and stored in a drying oven until it was analyzed.

An enzyme digestion procedure was used to measure starch levels in the roots (Kays and Canham 1991). One-half gram of the dried root material was put in a centrifuge tube with 25 mL of acetate-buffer solution and 50 μL Termamyl 120L (Tecator Inc.). It was then placed in a boiling water bath for 30 min to gelatinize the starch. After cooling, 0.15 mL of amyloglucosidase was added and the samples were put in a shaking water bath at 60°C for 60 min to convert the gelanitized starch to glucose. The samples were then centrifuged for 10 min at 1500 rpm to settle out the residual root material. One milliliter of the supernatant was mixed with 19 mL of distilled water so that the values of the glucose concentrations would fall within the range of a set of glucose standards. One milliliter of the dilute solution was mixed in a vial with 2 mL distilled water and 2 mL of glucose oxidase reagent. The vials were placed in dark incubation for 60 min at 20°C, and then absorbance was measured with a spectrophotometer at 650 nm. The concentration (grams) was calculated per gram of root material, and expressed as a percentage (grams starch per gram of root material). The total quantity of starch reserves is obviously a function of both the root starch concentration and the total mass of the root system, as well as the quantity of reserves stored in shoots aboveground. Thus, root starch concentrations provide a relative index of carbohydrate reserves that is scaled independently of plant size.

Statistical analysis

After 2 full years of the clipping treatments (1988–1989), we evaluated the responses of surviving seedlings at the end of the 1990 (third) growing season by measuring (*i*) total sapling height, (*ii*) current-year extension growth of the leader (defined operationally as the tallest shoot), and (*iii*) the total dry mass of new shoots (excluding leaves). Note that for seedlings in the two treatments that were clipped only once (HWO and HSO; Table 1), the 1990 growing season was the second growing season following cessation of the clipping treatments. Thus, the single versus multiple clipping treatments allowed comparison of growth of the two groups in the same growing season, but the single clipping treatment group had the previous year to recover from clipping effects. Seedlings in the shaded treatments remained shaded during the final (unclipped) 1990 growing season.

Growth of surviving seedlings was analyzed with analysis of variance (ANOVA) of the blocked, split-plot design, with block (BLOCK), tree species (SPECIES) and light level (SHADE) as main plot factors, and clipping treatment (CLIPPING) as a within-plot factor (SAS Institute Inc. 1987). Because of the split-plot design, F-statistics for the main-plot effects of BLOCK, SPECIES, and SHADE were calculated using the BLOCK × SPECIES × SHADE interaction term as the mean squared error. Significance of the subplot factor (CLIPPING) was tested using the residual mean squared error as the denominator for the F-statistic. We also tested the significance of the three possible two-way interactions between SPECIES, SHADE, and CLIPPING. Each of the three interactions has a specific, clearly defined interpretation. The SPECIES × SHADE interaction (tested using the BLOCK × SPECIES × SHADE interaction as the error term) effectively provides a test of differences among the species in their shade tolerance (i.e., differences among the species in their response to shade). The SPECIES × CLIPPING interaction provides a test of the degree to which there are species-specific differences in the responses of seedlings to browsing. The SHADE × CLIPPING interaction tests the degree to which the responses of seedlings to browsing differ as a function of light level. Both of these latter two interactions were tested against the residual mean squared error.

We used different groupings of the nine treatments to compare the effects of (*i*) the intensity of browsing (INTENSITY: none, light, or heavy), (*ii*) season of browsing (SEASON: none, summer, winter, or both), and (*iii*) the frequency of browsing (FREQUENCY: none, 1 year, or 2 years) (Table 1). Treatment means for both main plot factors (SPECIES and SHADE) and the planned comparisons were compared using Tukey's HSD test to control the experimentwise type 1 error (SAS Institute Inc. 1987). Treatment effects on survival (assessed at the end of the 1990 growing season) were tested using linear categorical modeling (SAS

TABLE 2. Analysis of variance for total seedling height, extension growth, and new shoot biomass for the blocked, split-plot design

Source	df	MSE	*F*	*P*
Height (cm)				
BLOCK	29	2 490.738	1.162	0.307
SPECIES	2	77 939.373	36.360	0.000
SHADE	1	575 249.807	268.367	0.000
SPECIES × SHADE	2	98 181.981	45.804	0.000
BLOCK × SPECIES × SHADE	58	2 143.518		
CLIPPING	8	52 861.460	41.201	0.000
SPECIES × CLIPPING	16	4 145.816	3.231	0.000
SHADE × CLIPPING	8	1 825.625	1.423	0.182
ERROR	998	1 283.015		
Extension growth (cm/year)				
BLOCK	29	770.674	1.045	0.432
SPECIES	2	13 708.731	18.580	0.000
SHADE	1	117 910.806	159.814	0.000
SPECIES × SHADE	2	11 651.578	15.792	0.000
BLOCK × SPECIES × SHADE	58	737.802		
CLIPPING	8	10 608.295	24.960	0.000
SPECIES × CLIPPING	16	1 378.394	3.243	0.000
SHADE × CLIPPING	8	634.804	1.494	0.155
ERROR	997	425.009		
Total mass of new shoots (g)				
BLOCK	29	6 131.695	0.953	0.545
SPECIES	2	93 660.069	14.555	0.000
SHADE	1	1 050 057.067	163.182	0.000
SPECIES × SHADE	2	366 941.488	57.024	0.000
BLOCK × SPECIES × SHADE	58	6 434.891		
CLIPPING	8	77 756.289	15.799	0.000
SPECIES × CLIPPING	16	36 131.961	7.342	0.000
SHADE × CLIPPING	8	14 316.222	2.909	0.003
ERROR	995	4 921.518		

NOTE: The *F* statistics for main plot effects (BLOCK, SPECIES, and SHADE) and the SPECIES × SHADE interaction were tested with the BLOCK × SPECIES × SHADE interaction mean squared error (MSE) as the error term. Within-plot effects (CLIPPING) and the two-way interactions between CLIPPING and the main plot factors were tested against the residual error (ERROR).

Institute Inc. 1987), with the same three sets of planned comparisons for effects of intensity, season, and frequency of clipping on seedling mortality.

Results

As expected, there were significant differences among the three species in overall mortality and growth at the end of the experiment (mortality: $\chi^2 = 52.91$, df = 2, $p < 0.0001$; growth: see SPECIES in Table 2). Total heights of control seedlings in unshaded plots at the end of the 1990 growing season were 107.7 ± 7.5 cm (mean ± SE) for red maple, 138.3 ± 6.8 cm for white ash, and 194.1 ± 12.8 cm for black cherry. There was very little mortality of unshaded, control seedlings during the experiment (i.e., none of the 30 ash seedlings, one of 24 cherry seedlings, and two of the 30 maple seedlings) (Fig. 1). Shading also caused clear and expected differences in average mortality and growth of seedlings (mortality: $\chi^2 = 106.73$, df = 1, $p < 0.0001$; growth: see SHADE in Table 2). Final heights of control seedlings in the shade (8% full sun) treatment were 52.5 ± 5.9 cm for red maple, 101.2 ± 6.3 cm for white ash, and 85.0 ± 8.7 cm for black cherry. Of the three species, the black cherry seedlings were least shade tolerant; they had the highest cumulative growth rate in full sun, but the largest percent reduction in growth in shade (43.8% of full-sun height), and the highest rate of cumulative mortality of shaded control seedlings (41.7% mortality). Red maple seedlings had intermediate reductions in final height (48.7% of full sun) and mortality (23.3% mortality in shade vs. 3.3% mortality in full sun). White ash seedlings were the most shade tolerant of the three species, with the smallest percent reduction in final height in the shade treatment (i.e., 73.2% of full-sun height), and the lowest rate of mortality of shaded control seedlings (3.3%). The SPECIES × SHADE interaction terms were significant in the analyses of mortality ($\chi^2 = 33.73$, df = 2, $p < 0.0001$) and all of the growth variables (Table 2), confirming that the three species clearly differed in their effective shade tolerance.

Effects of intensity of summer browsing on root starch reserves

Root starch reserves at the end of the first growing season varied significantly in response to clipping intensity ($F = 15.58$, df = 2, 77, $p = 0.0001$). Root reserves were also marginally significantly different in the three species ($F = 9.15$, df = 2, 2, $p = 0.0985$, using the SPECIES × SHADE interaction as the error term) and between the two light levels ($F = 14.76$, df = 1, 2, $p = 0.0616$, again using the SPECIES × SHADE interaction as the error term). For both red maple and black cherry, even heavy clipping of unshaded seedlings in late summer did not reduce subsequent fall root reserves, while light clipping of unshaded seedlings resulted in slightly elevated

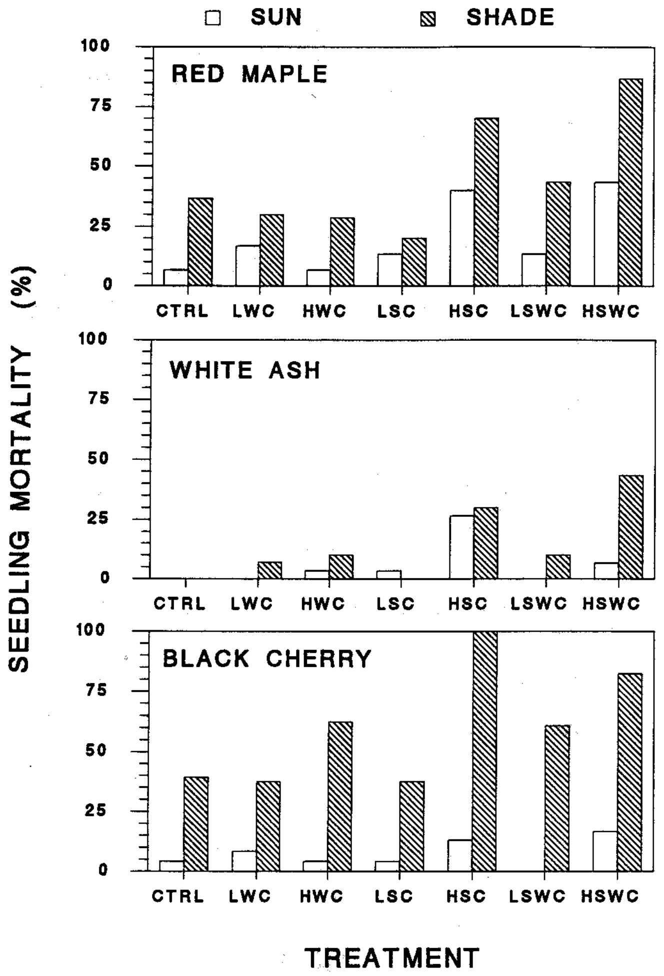

FIG. 1. Cumulative seedling mortality (%) at the end of the growing season following cessation of the clipping treatments. See Table 1 for a description of the treatment codes. Mortality rates are shown for both full sun (open bars) and shade (8% of full sun; shaded bars) treatments. To simplify the figures, data for the two treatments clipped heavily only during the 1st year (HWO and HSO, Table 1) are not shown in Figs. 1 and 3–5 because growth rates for those treatments were not significantly different than the treatments clipped for 2 years (HWC and HSC).

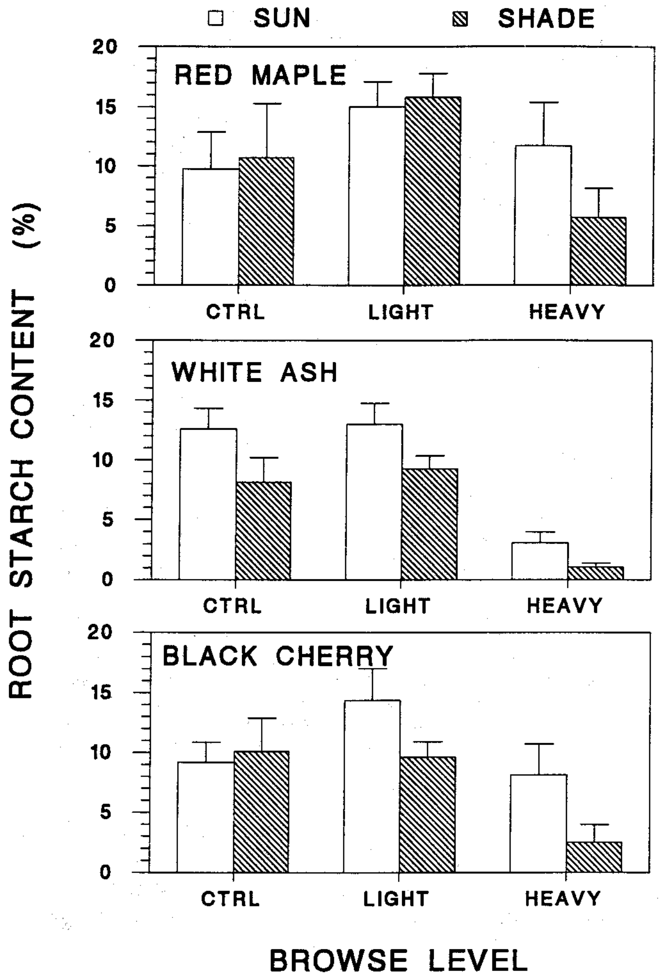

FIG. 2. Concentration of starch reserves in roots (% by weight) in the fall following the first summer clipping treatments (CTRL, control; LIGHT, 25% of shoot growth removed; HEAVY, 75% of shoot growth removed). Results are presented for seedlings in both full sun (open bars) and shade (8% of full sun; shaded bars).

levels of root reserves (Fig. 2). In contrast, root reserves of white ash seedlings were severely reduced by heavy clipping in late summer, regardless of light level (Fig. 2).

Effects of timing of browsing on seedling growth and mortality

The seasonal timing of clipping (SEASON) had significant effects on both cumulative mortality ($\chi^2 = 37.18$, df = 3, $p < 0.0001$) and all three growth responses (final height, extension growth, and new shoot biomass) (Table 3, Figs. 1 and 3–5). In general, growth and mortality of seedlings that had been clipped in the winter for the 2 previous years were not significantly different than in the control seedlings. Winter-clipped seedlings actually averaged 10.8 cm more extension growth in the final summer than the control seedlings ($p < 0.05$, Tukey's HSD test). For both red maple and white ash, seedlings clipped heavily in the winter had the highest new shoot biomass of any of the treatments (Fig. 5). In contrast to the effects of winter clipping, both growth rates and survival of seedlings clipped in the two preceding summers were significantly lower than the controls ($p < 0.001$ for all three growth variables in pairwise comparisons of summer clipping with controls in Tukey's HSD test; $\chi^2 = 11.92$, df = 1, $p < 0.001$ for mortality). Summer clipping generally produced high mortality only when the intensity of clipping was high (Fig. 2). The combination of both summer and winter clipping did not result in a significant additional reduction in growth or survival (Figs. 2–5). In general, new shoot biomass of the summer-clipped seedlings was 50–75% lower than in winter-clipped seedlings (Fig. 5), while the summer-clipped seedlings averaged 8.6 cm less extension growth than the controls ($p < 0.05$, Tukey's HSD test).

The SEASON × SPECIES and SEASON × SHADE interaction terms were significant for the three growth variables (Table 3), but not for cumulative mortality. Thus, the effects of the seasonal timing of clipping on growth vary as a function of both light level and tree species. However, the immediate effects of the seasonal timing of clipping on mortality were independent of both tree species and light levels. Summer clipping generally had a greater effect on survival and growth of red maple and white ash than in black cherry (Fig. 1). The reduction in growth and survival of summer-clipped

TABLE 3. Analysis of variance for the effects of season of clipping (SEASON: none, summer, or winter) on total height, leader extension growth, and new shoot biomass

Source	df	F	P
Height (cm)			
SEASON	3	40.46	0.000
SPECIES × SEASON	6	2.59	0.017
SHADE × SEASON	3	4.91	0.002
ERROR	773		
Extension growth (cm/year)			
SEASON	3	33.14	0.000
SPECIES × SEASON	6	2.11	0.050
SHADE × SEASON	3	3.03	0.029
ERROR	772		
New shoot biomass (g)			
SEASON	3	17.16	0.000
SPECIES × SEASON	6	4.61	0.000
SHADE × SEASON	3	7.51	0.000
ERROR	771		

NOTE: See Table 1 for a list of the specific treatments included in the seasonal comparisons. Statistics for the main plot effects in the full split-plot design (BLOCK, SPECIES, and SHADE) and the SPECIES × SHADE and BLOCK × SPECIES × SHADE interaction terms are given in Table 2, therefore statistics for those terms are not listed below, although the terms were included in the models used to calculate the statistics given below.

seedlings (relative to the controls) was generally higher for seedlings in full sun than in shade (Figs. 1 and 3–5). Thus, we did not observe a synergistic effect in which the combination of summer clipping and shade stress led to greater than additive effects on growth and survival.

Effects of intensity of browsing on seedling growth and survival

Variation in the intensity of clipping (INTENSITY: none, light, or heavy) also caused significant variation in cumulative seedling mortality ($\chi^2 = 66.98$, df = 2, $p < 0.0001$). Overall, seedling mortality rates were 36.2% in the heavy-clipping treatments, 16.4% in the light-clipping treatments, and 13.9% in the control seedlings, and all three pairwise comparisons were significant ($\chi^2 > 8.29$, df = 1, $p < 0.003$). There were no significant interactions between INTENSITY and either SPECIES or SHADE for survival. Thus, while there were significant differences in seedling survival among the different species and shade treatments, we found no clear evidence of (*i*) differences among species in ability to survive heavy clipping or (*ii*) synergism in the effects of combinations of heavy clipping and shading on seedling survival.

The lightly and heavily clipped seedlings were 14.9 and 39.7 cm shorter, respectively, than the control seedlings at the end of the experiment. Most of this pattern is due to reductions caused by summer clipping (Fig. 3). Given that the control seedlings ranged from 100–200 cm in height at the end of the experiment, and that the heavily clipped seedlings had 75% of new shoot growth (including leader growth) removed for 1 or 2 successive years, these differences in total seedling height are remarkably small. In fact, black cherry and red maple seedlings that had been heavily clipped for two successive winters were still not significantly shorter than the control seedlings at the end of the experiment (Fig. 3) (pairwise comparisons using Tukey's HSD test, $p > 0.05$, controlling for experiment-wise error).

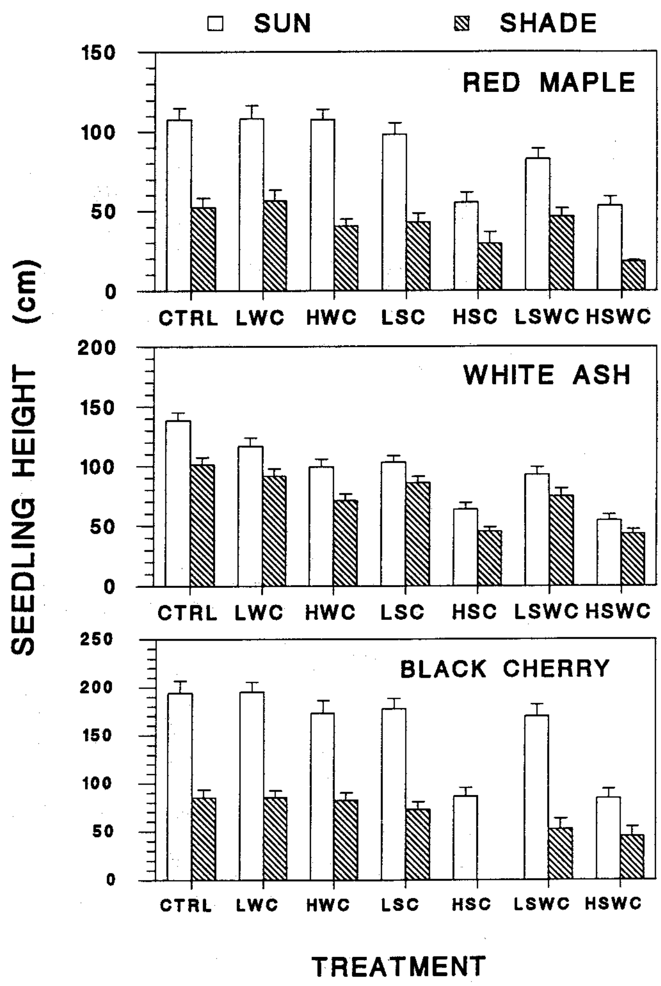

FIG. 3. Seedling height (cm) at the end of the growing season following cessation of the clipping treatments for both full sun (open bars) and shade treatments (shaded bars). See Table 1 for a description of the treatment codes.

These relatively minor differences in final seedling height reflect differences in the growth of terminal leaders versus lateral branches. The total biomass of new shoots did vary significantly in response to the intensity of clipping (Table 4). While heavy clipping significantly reduced the total mass of new shoots produced in the growing season following the cessation of the clipping treatments, the heavily clipped seedlings concentrated much of their growth in the terminal leader. As a result, extension growth of the terminal shoots of the seedlings was not affected by the previous clipping intensity (Table 4, Fig. 4). The light clipping treatments had little effect on subsequent extension growth regardless of the season in which clipping occurred (Fig. 4).

There were significant interactions between INTENSITY and both SPECIES and SHADE for all of the growth responses except extension growth (Table 4). Thus, while there were no clear interspecific differences in the effects of heavy clipping on seedling survival, the effects of heavy clipping on whole-plant carbon gain differed significantly among the species. Similarly, while there were no interactions in the effects of SHADE and INTENSITY on survival, the effects of the intensity of clipping depended on light level (Table 4). As was the case with the effects of seasonal timing, the effects of heavy clipping were proportionately greater for seedlings in full

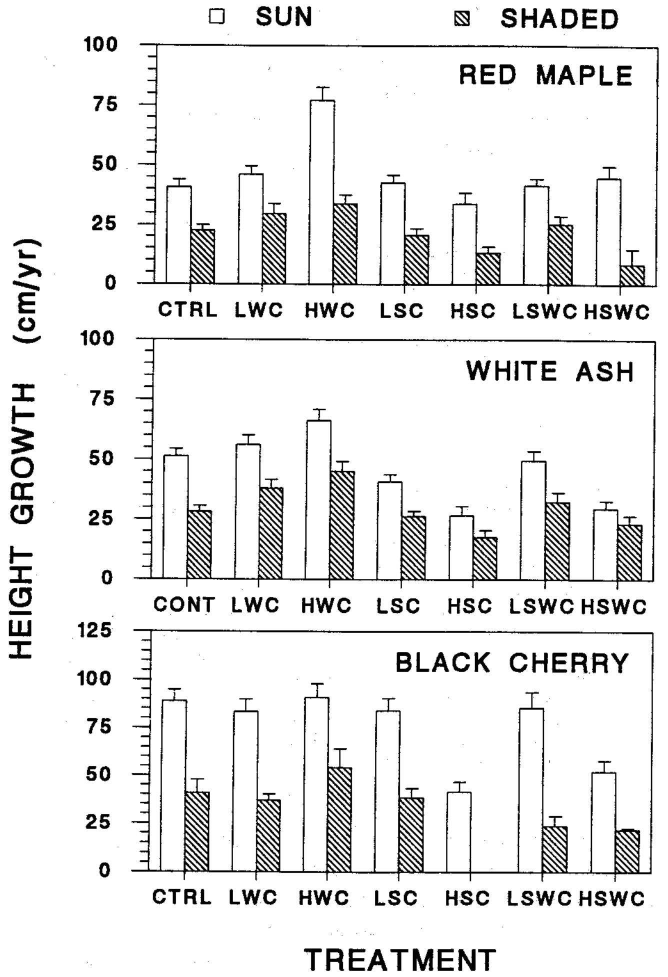

FIG. 4. Seedling extension growth (cm/year) in the growing season following cessation of the clipping treatments for both full sun (open bars) and shade treatments (shaded bars). See Table 1 for a description of the treatment codes.

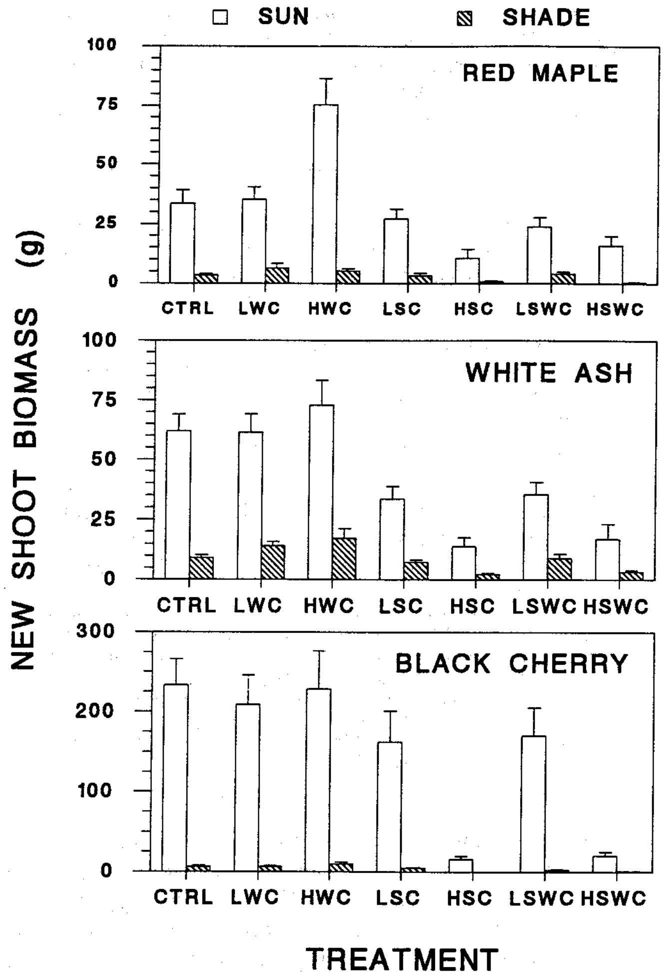

FIG. 5. Total biomass of new shoots (g dry weight) produced in the growing season following cessation of the clipping treatments for both full sun (open bars) and shade treatments (shaded bars). See Table 1 for a description of the treatment codes.

sun than for seedlings in the shade. In general, the total biomass of new shoots in the shaded seedlings was extremely low even in the control seedlings, and heavy clipping caused relatively little additional reduction in growth (Fig. 5).

Effects of frequency of browsing on seedling growth and survival

The frequency of clipping had significant effects on seedling survival ($\chi^2 = 15.16$, df = 2, $p < 0.001$) and growth (Table 5). Two episodes of clipping generally caused higher mortality than only a single clipping; however, the difference was only marginally significant ($\chi^2 = 3.17$, df = 1, $p = 0.075$). The total biomass of new shoots produced during the 1990 growing season by seedlings clipped in only the 1st year (1988) was still significantly lower than in the control seedlings ($p = 0.047$, Tukey's HSD test). However, seedlings clipped for 2 successive years did not have significantly lower new shoot biomass than seedlings clipped in only the first year ($p > 0.9$).

Discussion

Previous studies have led to widely divergent conclusions about the effects of woody browsing on growth and survival of tree seedlings. In our study, the effects of simulated browsing on seedling mortality varied in response to all of the factors considered in the experiment: (*i*) seasonal timing of browsing, (*ii*) intensity of browsing, (*iii*) frequency of browsing, (*iv*) light environment, and (*v*) tree species. This suggests that robust generalizations about the effects of mammalian browsers on tree regeneration in forests and tree invasion in old fields will require comprehensive, comparative studies with a wide range of species and habitats.

Field studies have demonstrated that browsing can alter forest composition through differences in (*i*) the timing and rates of browsing on different tree species and (*ii*) interspecific differences in the responses of seedlings to browsing (e.g., Bramble and Goddard 1953; Graham 1954; Curtis and Rushmore 1958; Metzger 1977; Anderson and Loucks 1979; Marquis and Brenneman 1981; Frelich and Lorimer 1985; Pastor et al. 1988). Our results provide limited experimental evidence of interspecific differences in seedling response to browsing. The short-term effects of browsing on seedling mortality were similar for all three species; however, there was significant variation among the three species in the effects of frequency, timing, and intensity of browsing on seedling growth rates. When seedlings of the three species were grown in the shade, black cherry seedlings showed the greatest reduction in growth as a result of browsing (although only as a result of summer browsing). In contrast, red maple seedlings had the smallest reduction in

TABLE 4. Analysis of variance for the effects of intensity of clipping (INTENSITY: none, light, or heavy) on total height, net annual height growth, and new shoot biomass

Source	df	F	P
Height (cm)			
INTENSITY	2	66.78	0.000
SPECIES × INTENSITY	4	5.72	0.000
SHADE × INTENSITY	2	5.78	0.003
ERROR	777		
Extension growth (cm/year)			
INTENSITY	2	0.85	0.428
SPECIES × INTENSITY	4	7.15	0.000
SHADE × INTENSITY	2	2.31	0.100
ERROR	776		
New shoot biomass (g)			
INTENSITY	2	8.99	0.000
SPECIES × INTENSITY	4	8.98	0.000
SHADE × INTENSITY	2	2.93	0.054
ERROR	775		

NOTE: See Table 1 for a list of the specific treatments included in the comparisons of intensity of browsing. Statistics for the main plot effects in the full split-plot design (BLOCK, SPECIES, and SHADE) and the SPECIES × SHADE and BLOCK × SPECIES × SHADE interaction terms are given in Table 2, therefore statistics for those terms are not listed below, although the terms were included in the models used to calculate the statistics given below.

TABLE 5. Analysis of variance for the effects of frequency of clipping (FREQUENCY: none, 1 year, or 2 years) on total height, leader extension growth, and new shoot biomass

Source	df	F	P
Height (cm)			
FREQUENCY	2	27.74	0.000
SPECIES × FREQUENCY	4	2.24	0.064
SHADE × FREQUENCY	2	2.23	0.109
ERROR	517		
Extension growth (cm/year)			
FREQUENCY	2	4.40	0.013
SPECIES × FREQUENCY	4	3.09	0.016
SHADE × FREQUENCY	2	1.10	0.334
ERROR	517		
New shoot biomass (g)			
FREQUENCY	2	3.43	0.033
SPECIES × FREQUENCY	4	2.96	0.019
SHADE × FREQUENCY	2	1.37	0.256
ERROR	516		

NOTE: See Table 1 for a list of the specific treatments included in the comparisons of frequency of browsing. Statistics for the main plot effects in the full split-plot design (BLOCK, SPECIES, and SHADE) and the SPECIES × SHADE and BLOCK × SPECIES × SHADE interaction terms are given in Table 2, therefore statistics for those terms are not listed below, although the terms were included in the models used to calculate the statistics given below.

growth due to summer browsing, while winter browsing actually resulted in a significant increase in shoot growth in the summer following cessation of the clipping treatments. Even in the absence of direct interspecific differences in the effects of browsing on mortality, these interspecific differences in growth may be sufficient to allow herbivores to alter the relative competitive success of these species in both forests and old fields.

We found only limited evidence of an interaction between light level and seedling response to browsing. In particular, there was no evidence that shade stress caused a synergistic increase in mortality or reduction in growth when seedlings were clipped. On the contrary, seedlings in full sun showed larger absolute and relative declines in new shoot biomass when clipped than did seedlings in the shade. In general, growth rates in the shade treatment were very low, regardless of the clipping treatments. We suggest that the explanation for the differences in the effects of browsing on seedlings in high versus low light environments may lie in patterns of carbohydrate storage within seedlings. In particular, we propose that the limited carbohydrate reserves of shaded seedlings are stored primarily in roots rather than shoots, while more actively growing seedlings in full sun are forced to store reserves in both roots and shoots. As a result, seedlings in full sun are more vulnerable to loss of carbohydrate reserves when stems are browsed. In effect, our results indicate that stem removal in the shade treatments represented a smaller proportionate reduction in seedling carbon reserves than in the full sun treatment.

Our results indicate that 1 or 2 years of even severe winter browsing has little effect on either survival or overall height of tree seedlings of these three species, regardless of whether the seedlings are in high-light environments or in the shade. White-tailed deer consume woody stems primarily in the winter and early spring (e.g., Bramble and Goddard 1953). Thus, our results suggest that most of the browse damage observed in forests and old fields will have relatively little effect on the dynamics of tree seedling invasion if the seedlings are only browsed for 1 or 2 years. Our field studies (Canham et al. 1993) indicate that seedlings browsed in 1 year have a much higher than random chance of being browsed in the following year. Without long-term studies we do not know how consistently seedlings are browsed over longer (5–10 years) time scales. Krefting et al. (1966) found that even nine successive years of simulated browsing had little effect on mountain maple (*Acer spicatum* Lam.). However, we expect that the ability of seedlings to tolerate such prolonged periods of stem removal will vary significantly among species and environments.

Our short-term experiment revealed no immediate interaction between light levels and seedling response to clipping. For seedlings subjected to repeated browsing over successive years, however, light levels may ultimately determine whether seedlings put on enought net height growth each year to eventually escape browsing. Under closed forest canopies, the combination of low, light-limited growth rates and repeated browsing may effectively preclude the growth of saplings above the reach of browsers such as white-tailed deer. In contrast, high-light environments in old fields or forest clearings may allow saplings to grow past the effective foraging height of deer, regardless of the frequency with which saplings are browsed.

In contrast to the potentially minor effects of winter browsing, our results demonstrate that comparable levels of stem removal in the summer can cause a significant increase in seedling mortality, and a significant decrease in overall seedling height. While browsing may be less common during the summer, our results suggest that it has more serious consequences for seedling growth and survival than the much more frequent winter browsing. Bramble and Goddard

(1953) observed significant differences in the seasonal timing of browsing on red maple, black cherry, and white ash seedlings in Pennsylvania. While both red maple and black cherry were browsed primarily in the winter, white ash seedlings were browsed almost exclusively in the summer (Bramble and Goddard 1953). It is also worth noting that in our experiment, summer clipping had greater effects on fall root starch reserves in white ash seedlings than in the other two species. Taken together, these results suggest that the dynamics of white ash regeneration will be more strongly affected by browsing than in the other two species, and that the differences will be due more to differences in the seasonal timing of browsing and the physiological responses of the seedlings than to differences among the species in the proportion of seedlings browsed.

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