Effects of overstory and understory competition and simulated herbivory on growth and survival of white pine seedlings

Mike R. Saunders and Klaus J. Puettmann

Abstract: The interactive impact of overstory canopy closure, understory brush control, and simulated white-tailed deer (*Odocoileus virginianus* Zimmermann) herbivory (i.e., clipping) on growth and survival of underplanted white pine (*Pinus strobus* L.) seedlings was examined. Clipping was conducted in April 1996 and 1997 at three intensities (control, 0% previous year's growth removed; lightly clipped, terminal and 50% previous year's growth removed, and heavily clipped: 100% of previous-year's growth removed) and three frequencies (never clipped, clipped once, clipped 2 years in a row). Decreasing overstory canopy closure and brush competition generally increased growth of seedlings under all clipping regimes, with heavily clipped seedlings showing the least benefit of reduced competition. Although first-year height growth was stimulated after light-intensity clipping, this effect did not persist the following year, and these trees still were significantly shorter than controls at the end of the experiment. Diameter growth was reduced at any clipping intensity or frequency, and remained below controls throughout the experiment. Seedling mortality was higher without brush control and after clipping. Results suggest that increased overstory and understory competition reduced seedling growth and survival. In regards to clipping, initial height growth stimulation may result from (*i*) resource reallocation away from diameter and root growth and (or) (*ii*) hormonal redistributions from loss of apical control in the seedling. Since both high competition levels and increased herbivory reduced seedling vigor, we suggest that understory brush control and deer protection (e.g., budcapping) go hand in hand to regenerate white pine.

Résumé : Nous avons examiné l'impact combiné de la fermeture de la canopée, du contrôle de la végétation en sous-étage ainsi que de l'herbivorie simulée (coupe) par le cerf de Virginie (*Odocoileus virginianus* Zimmermann) sur la croissance et la survie de semis de pin blanc (*Pinus strobus* L.). La coupe a été effectuée en avril 1996 et 1997 à trois niveaux d'intensité (témoin, 0% de la croissance annuelle de l'année précédente; coupe légère, terminale, 50% de la croissance annuelle de l'année précédente; coupe intensive, totalité de la croissance annuelle de l'année précédente), ainsi qu'à trois fréquences (jamais, une fois, et 2 années consécutives). La diminution de la fermeture de la canopée et de la compétition avec la végétation en sous-étage ont généralement favorisé la croissance des semis dans tous les régimes de coupe expérimentale, mais les semis soumis à la coupe intensive étaient les moins favorisés par la réduction de la compétition. Même si la croissance en hauteur des semis était stimulée après la coupe légère, cet effet n'a pas persisté l'année suivante et ces plants étaient significativement moins hauts que les plants témoins à la fin de l'expérience. La croissance en diamètre était réduite à toutes les intensités et fréquences de coupe et est demeurée moindre que celle des témoins tout au cours de l'expérience. La mortalité des semis était plus élevée en l'absence de contrôle de la végétation en sous-étage et suite à la coupe. Les résultats suggèrent que l'accroissement de la compétition par la canopée et le sous-étage réduit la croissance et la survie des semis. En ce qui concerne la coupe, la stimulation initiale de la croissance en hauteur peut résulter (*i*) de la réallocation des ressources au détriment de la croissance en diamètre et des racines et (ou) (*ii*) de la redistribution hormonale découlant de la perte de contrôle apical dans le semis. Puisque le niveau élevé de compétition et l'augmentation de l'herbivorie ont réduit la vigueur des semis, nous suggérons que le contrôle de la végétation en sous-étage et la protection contre les cerfs (ex., protection des bourgeons) aillent de pair pour protéger la régénération du pin blanc.

[Traduit par la rédaction]

Introduction

In natural systems, browsing is often detrimental to plants as it removes resources needed for growth. However, low to intermediate browsing levels may stimulate growth and increase fitness of some plants, eventually leading to compensation for tissues lost during the browsing episode (e.g., Metzger 1977; Welch et al. 1992; Edenius et al. 1993). This compensatory growth pattern is species specific and generally confined to those deciduous tree species that have

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M.R. Saunders[1] and K.J. Puettmann. University of Minnesota, Department of Forest Resources, 115 Green Hall, 1530 North Cleveland Avenue, St. Paul, MN 55108–6112, U.S.A. e-mail: saund011@maroon.tc.umn.edu and kpuettma@forestry.umn.edu

[1]Author to whom all correspondence should be addressed.

heterophyllous shoots within their buds (Metzger 1977; Hjältén et al. 1993; Canham et al. 1994). Furthermore, some studies have found that increased shade, usually a result of increasing intraspecific and (or) interspecific competition, will decrease the compensatory ability of some species (Hjältén et al. 1993; Canham et al. 1994; Shabel and Peart 1994). Compensatory growth is also highly dependent on the timing and frequency of browsing. While seedlings may overcompensate for tissue browsed during the dormant season, they may not compensate for tissue lost while a plant is actively growing (Canham et al. 1994; Bergström and Danell 1995). With few exceptions (see Krefting et al. 1966), compensatory ability declines as the number of successive years of browsing increases, particularly on longer (5–10 years) time scales (Mitscherlich and Weise 1982). These factors suggest that compensatory growth responses are highly affected by physiological characteristics of a species (e.g., deciduous versus evergreen, or hardwood versus conifer), environmental and competitive conditions near the plant, and the seasonal and historical distributions of browsing pressure.

The presence of compensatory growth could significantly influence management of some forest species. For example, white pine (*Pinus strobus* L.) management can be very costly because it often requires multiple entries into a stand to protect seedlings (usually by budcapping) from white-tailed deer (*Odocoileus virginianus* Zimmermann) herbivory. Furthermore, white pine is commonly grown or planted under shelterwoods to protect seedlings from temperature and moisture extremes that may promote formation of white pine blister rust or attack from white pine tip weevil (Jones 1992; Sauerman 1992). This same environment, however, favors formation of dense understories that will increase competition for light and nutrient resources and reduce growth of the seedlings (Lancaster and Leak 1978; Smidt and Puettmann 1998). Although in some cases, dense understories may reduce herbivory by hiding seedlings from deer (Saunders and Puettmann 1999), dense understories of palatable species will attract more deer to an area. Therefore, white pine management requires a delicate balance to maintain understory and overstory densities at a level that protects young white pine from pathological concerns, yet provide enough light and nutrients for rapid growth that will quickly get terminals above the deer browse line.

This study investigated how competition and simulated deer herbivory affected the growth and mortality of white pine seedlings. Unlike previous work in this arena, we focused on the interactions between clipping and interspecific competition from several sources (overstory and understory vegetation) in a field setting. We hypothesized (*i*) that increasing overstory and understory competition will reduce seedling height and diameter growth and increase seedling mortality; (*ii*) that increasing browsing intensity and frequency will reduce seedling height and diameter growth and increase seedling mortality; (*iii*) that increasing browsing intensity and frequency will reduce seedling growth and increase seedling mortality proportionally more in highly competitive environments as opposed to noncompetitive environments; and (*iv*) that seedling recovery will change over time as seedlings shift resource partitioning in response to clipping and competition.

Methods

Site description

This experiment was conducted in a 3-year-old, white pine underplanting located approximately 19 km west-southwest of Grand Rapids, Minn.., U.S.A., in southwestern Itasca County (approximately 47°10′N, 93°46′W). The 8.4-ha site lies on a gently sloping, upland area formed from a glacial till plain. Soils were predominantly Itasca silt loam, with pockets of Talmoon silt loam in a few shallow depressions found on the site. In 1992, the stand was strip thinned to a residual basal area of 12 m^2/ha. The residual overstory was comprised of northern hardwoods (Eyre 1980) and dominated by basswood (*Tilia americana* L.), sugar maple (*Acer saccharum* Marsh.), and paper birch (*Betula papyrifera* Marsh.), constituting 43, 25, and 24% of the basal area, respectively. Other canopy species included northern red oak (*Quercus rubra* L.), quaking aspen (*Populus tremulodes* Michx.), bur oak (*Quercus macrocarpa* Michx.), yellow birch (*Betula alleghaniensis* Britton), black ash (*Fraxinus nigra* Marsh.), and balsam fir (*Abies balsamea* (L.) Mill). Basal area averaged 14.1 m^2/ha (range: 1–22 m^2/ha) and canopy conditions ranged from open to closed (0–80% cover). Understory cover averaged 47% (range 2–90%) with extensive patches of beaked hazel (*Corylus cornuta* Marsh.), Canadian thistle (*Cirsium arvense* (L.) Scop.), currant and gooseberry (*Ribes* L. sp.), and sugar maple and basswood sprouts.

After strip thinning, containerized white pine were underplanted in May 1993 throughout the stand at 1520 seedlings/ha in disked trenches. Seedlings have been budcapped every winter since, and as a result, very little deer damage had occurred to seedlings on the site. Seedling height and basal diameter averaged 55.0 ± 0.8 cm (mean ± SE) and 8.38 ± 0.12 mm, respectively, in April 1996.

Experimental design

In April 1996, we randomly located 60 plots with the consideration to distribute plots under a wide range of competitive conditions on the site (Table 1). Plots were no closer than 10 m apart, averaged approximately 40 m^2, and consisted of six seedlings with little or no signs of prior deer damage. Within each plot, two seedlings were randomly assigned to one of three clipping treatments that simulated natural winter browsing: (*i*) a nonclipped control; (*ii*) a lightly clipped treatment that removed the terminal leader and 50% of the previous year's shoots; and (*iii*) a heavily clipped treatment that removed the terminal leader and 100% of the previous year's shoots. In the lightly clipped treatment, all previous year's shoots within two randomly chosen, but adjacent, quadrants were removed. Clippings were distributed vertically on the seedling, and in cases where laterals were concentrated on one side of the seedling, quadrants were expanded or narrowed so that only 50% of the previous year's shoots would be clipped. This selection simulated actual patterns seen on browsed seedlings in the area (M.R. Saunders, personal observation), in contrast to dispersing clipping damage throughout the crown of the seedling (see Edenius et al. 1993).

In June 1996, one half of the plots were randomly chosen for understory brush control (BRUSH) (Table 1). This was prescribed to create a wider range of understory competition levels within the experiment. All aboveground vegetation within 2 m of each seedling was cut to ground level and removed from each selected plot.

To examine the influence of multiple-year clippings on seedling growth and survival, one third of the plots were reclipped again in 1997 (Table 1). Each reclipped seedling received the same treatment as in 1996, with the exception that at least one unclipped quadrant (not clipped in 1996 or 1997) was left on each lightly clipped seedling. All clipping treatments were applied in late April before shoot elongation.

Table 1. Number of plots distributed among overstory conditions and plot treatments.

Treatment	Overstory condition Open (<9 m^2/ha)	Intermediate (9–15 m^2/ha)	Closed (>15 m^2/ha)	Totals
No brush control				
Clipped only in 1996	8	6	6	20
Clipped in 1996 and 1997	4	3	3	10
Brush control				
Clipped only in 1996	6	10	4	20
Clipped in 1996 and 1997	3	5	2	10
Totals	21	24	15	60

For each six-tree plot, basal area (m^2/ha) was measured with a 1 m^2/ha BAF prism and dominant overstory species were recorded. For each seedling, total height was measured to the nearest 1 cm using a ruler, and basal diameter at 5 cm above the ground was measured to the nearest 0.1 mm using dial calipers. Seedlings were measured before clipping in April 1996 and after the growing season in October 1996 and 1997.

Quantification of competition levels

After full understory and overstory canopy expansion, light conditions for each seedling were measured with the LI-COR® LAI-2000 Plant Canopy Analyzer. This instrument calculates diffuse non-interceptance (DIFN), which is an indicator of "canopy structure or openness" (LI-COR, Inc. 1992; Puettmann and Reich 1995). Readings above understory brush and above the terminal of each seedling were taken either when the skies were completely overcast or when solar elevations were low (i.e., the early morning and late evening). A 270° view lens cap restricted the view of the instrument from a 90° arc, which allowed the operator to "hide" from the instrument. Similarly, readings were restricted to a 43° cone to limit measures to trees that influence a seedling's light environment (Puettmann and Reich 1995) and to reduce the influence of sun flecks on measurements which might otherwise negatively bias the results (Chason et al. 1991; Grantz et al. 1993; Strachan and McCaughey 1996). Readings were taken for each seedling in July 1996.

Overstory canopy closure (OCC) was calculated as

$$[1] \qquad \mathrm{OCC} = 1 - \mathrm{DIFN_a}$$

where $\mathrm{DIFN_a}$ is integrated from simultaneous "above-canopy" readings and readings above the understory brush layer. OCC is closely correlated to light availability on a site (J.L. Machado and P.B. Reich, unpublished data). Understory canopy closures (i.e., understory cover) were calculated as

$$[2] \qquad \mathrm{UCC} = 1 - \mathrm{DIFN_b}$$

where $\mathrm{DIFN_b}$ is integrated from simultaneous readings taken above the understory brush layer and below the understory brush layer (i.e., at seedling height). Analysis of these variables showed that OCC was highly correlated to ln (basal area) (R^2 = 0.778, p < 0.001) and could be used as a covariate in growth models. UCC was negatively correlated to basal area (R^2 = 0.170, p < 0.001). Brush control treatments significantly reduced average understory cover by 55–57% across the range of observed basal areas (t = 10.57, p < 0.001).

Statistical analyses

After two growing seasons (1996 and 1997), we evaluated the effects of competing vegetation and clipping treatments on both average annual height growth and average annual diameter growth by using a split-plot analysis of covariance (ANCOVA). This type of analysis assumes different-sized experimental units for different treatments and allows partitioning of error into among-plot and within-plot errors (Kuehl 1994). In our experiment, understory brush control (BRUSH) was a whole plot treatment, while clipping treatments (CLIPPING) were subplot treatments. OCC was included as a whole plot covariate within the analysis because available light and nutrient resources were spatially autocorrelated for seedlings within a plot (Sen and Srivastava 1990). Furthermore, initial seedling height (INIHT) and diameter (INIDIA) were used as subplot covariates in analyses for annual height and diameter growth, respectively, since seedling growth is related to its initial size (Puettmann and Reich 1995). Specific effects of clipping, namely the clipping intensity (INTENSITY) and clipping frequency (FREQUENCY), on the two growth parameters had to be analyzed in parallel split-plot ANCOVAs since the design was disconnected in regards to these factors (Searle 1987). Therefore, interactions involving both INTENSITY and FREQUENCY were tested using orthogonal contrasts between treatment means in the general clipping treatment models (i.e., those using CLIPPING as a factor, instead of INTENSITY or FREQUENCY).

Because stress-induced seedling mortality is often delayed by several years (Waring 1987), ANCOVA-type analysis was not powerful in detecting effects of both competing vegetation and clipping treatments within the same model. We used contingency table analysis and chi-square tests of independence (Ott 1988) to individually assess seedling survival in regards to BRUSH, INTENSITY, and FREQUENCY. Effects of OCC, a continuous variable, on mortality were analyzed using logistic regression.

Recovery effects on height and diameter growth were tested by comparing means for 1996 growth with 1997 growth. Analyses of recovery effects were limited to seedlings that had survived both growing seasons and had not been reclipped in spring 1997. Split-plot ANCOVA analyses were also conducted on each year's growth using only OCC, BRUSH, INTENSITY, and either INIHT or INIDIA, as covariates or factors.

Comparisons among treatment means were tested using the Tukey–Kramer honest significant difference (HSD) test to control for experimentwise type I errors (Kuehl 1994). All tests were considered significant if p < 0.05 and marginally significant if p < 0.10. All statistical analyses were calculated with either JMP® 3.2.2 (SAS Institute Inc. 1996) or MacAnova 4.0.

Results

Effects of competing vegetation on seedling growth and mortality

Overstory canopy closure (OCC) had significant effects on both seedling height and diameter growth (Table 2). High canopy closure generally resulted in seedlings that were much smaller, both in height and diameter, and did not grow as quickly as seedlings in the open, regardless of clipping

Table 2. Split-plot analysis of covariance for the effects of initial seedling height or diameter, overstory canopy closure, understory brush control, and clipping treatments on mean annual height and diameter growth.

Source	df	MS	*F*	*P*
Height growth (cm/year)				
OCC	1	3784.6	34.78	<0.0001
BRUSH	1	113.2	1.04	0.3121
OCC × BRUSH	1	8.2	0.07	0.7853
Error (WP)	56	108.8		
INIHT	1	2988.6	70.88	<0.0001
CLIPPING	4	3335.7	79.12	<0.0001
OCC × CLIPPING	4	121.3	2.88	0.0237
BRUSH × CLIPPING	4	86.8	2.06	0.0871
OCC × BRUSH × CLIPPING	4	12.3	0.29	0.8826
Error	223	42.2		
Diameter growth (mm/year)				
OCC	1	24.53	13.63	0.0005
BRUSH	1	22.60	12.56	0.0008
OCC × BRUSH	1	3.05	1.69	0.1985
Error (WP)	56	1.80		
INIHT	1	31.66	58.18	<0.0001
CLIPPING	4	47.76	87.77	<0.0001
OCC × CLIPPING	4	2.80	5.15	0.0005
Brush × CLIPPING	4	1.39	2.56	0.0395
OCC × BRUSH × CLIPPING	4	0.93	1.70	0.1509
Error	223	0.54		

or understory treatments (Fig. 1). There were no interactions between OCC and brush control (BRUSH), but there were interactions between OCC and clipping treatments (CLIPPING) for both height and diameter growth (Table 2). This indicated (*i*) that understory competition levels did not significantly change a seedling's response to canopy conditions and (*ii*) that a seedling's recovery from herbivory would suffer proportionally more in shady, closed-canopy conditions than in sunny, open-canopy conditions. Seedling mortality, on the other hand, was not affected by overstory conditions (χ^2 = 1.37, df = 1, p = 0.241) and averaged 16% across the site.

Brush control treatments had significant effects on diameter growth, but not on height growth (Table 2). By reducing understory competition, brush control resulted in seedlings that were only slightly taller (p = 0.139; untreated: 72.6 ± 2.4 cm (mean ± SE); treated: 77.8 ± 2.5 cm) but significantly larger in diameter (p = 0.001; untreated: 11.9 ± 0.3 mm; treated: 13.4 ± 0.4 mm, as averaged across all clipping treatments). Brush control increased annual diameter growth by 32%; untreated seedlings increased in diameter by 1.80 ± 0.09 mm/year, while treated seedlings increased by 2.38 ± 0.12 mm/year, both as averaged across all clipping treatments. BRUSH and CLIPPING significantly interacted for diameter growth (p = 0.040) and marginally interacted for height growth (p = 0.087; Table 2). Generally, clipping moderated the effect of brush control with decreasing returns as the intensity and frequency of clipping increased (Fig. 2). For instance, unclipped seedlings were, on average, 17% taller and 28% larger in diameter in areas with brush removal; lightly clipped seedlings were 7% taller and 14% larger in diameter; and heavily clipped seedlings were 8% shorter and 7% smaller in diameter. Unlike overstory cover, understory brush control significantly reduced mortality, from 21% for untreated plots to 11% for treated plots (χ^2 = 6.675, df = 1, p = 0.036). There were no significant interactions between understory brush control and any other main effects on mortality.

Effects of clipping treatments on seedling growth and mortality

Clipping treatments had significant effects on both height and diameter growth (Table 3). Increasing clipping intensity (INTENSITY: none, light, or heavy) resulted in smaller seedlings, with lightly and heavily clipped seedlings being 12.4 ± 3.4 cm shorter and 1.65 ± 0.52 mm thinner in diameter, and 42.9 ± 3.5 cm shorter and 3.84 ± 0.54 mm thinner than the control seedlings, respectively (Table 3). Lightly clipped seedlings responded by increasing annual height growth by 33% compared with controls; often, this stimulation was a result of laterals on the seedling "bending up and taking over" apical dominance of the seedling. On the other hand, annual diameter growth decreased in these seedlings by 31% compared with controls. Heavily clipped seedlings decreased height growth by 58% and diameter growth by 66% compared to controls (Table 3, Fig. 1).

OCC and INTENSITY interacted for both height and diameter growth (Table 4). This suggested that higher intensity clipping led to proportionally less reduction in growth under closed overstory conditions than in open overstory conditions (Fig. 1). For example, lightly and heavily clipped seedlings in open conditions (OCC < 0.625) averaged 34 and 68% less diameter growth than the controls, respectively, while in closed conditions (OCC > 0.750), lightly and

Fig. 1. Mean annual height and diameter growth versus overstory canopy closure (OCC) by herbivory treatment. Height and diameter growth are not adjusted for initial seedling size. Clipping treatment abbreviations are as in Table 3. The R^2 values ranged from 0.12 to 0.19 for highly significant relationships (**, p ≤ 0.01) and from 0.05 to 0.13 for significant relationships (*, $p \leq 0.05$). ns, not significant.

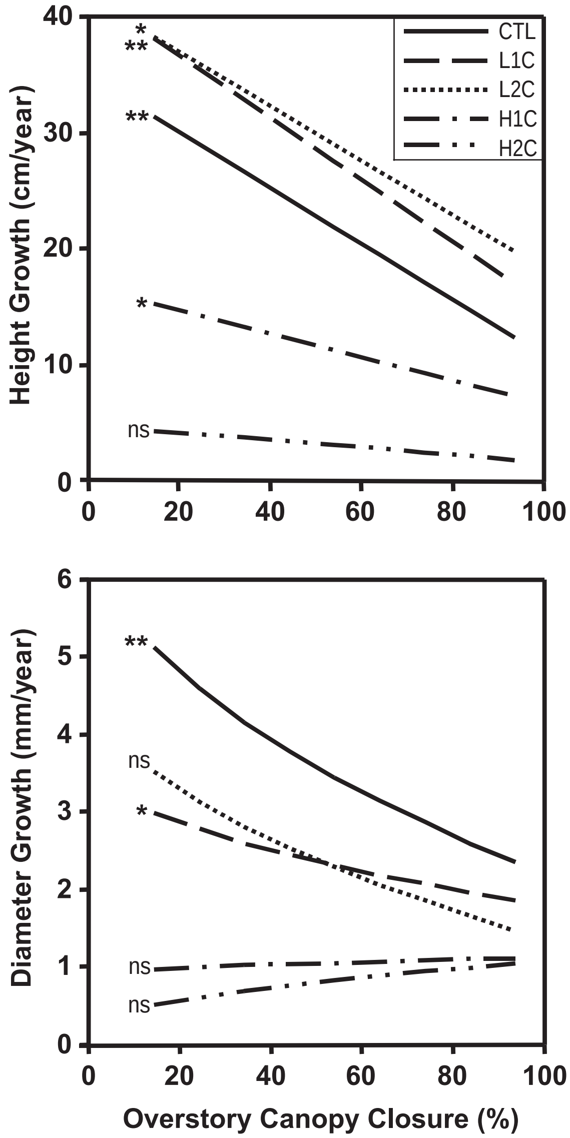
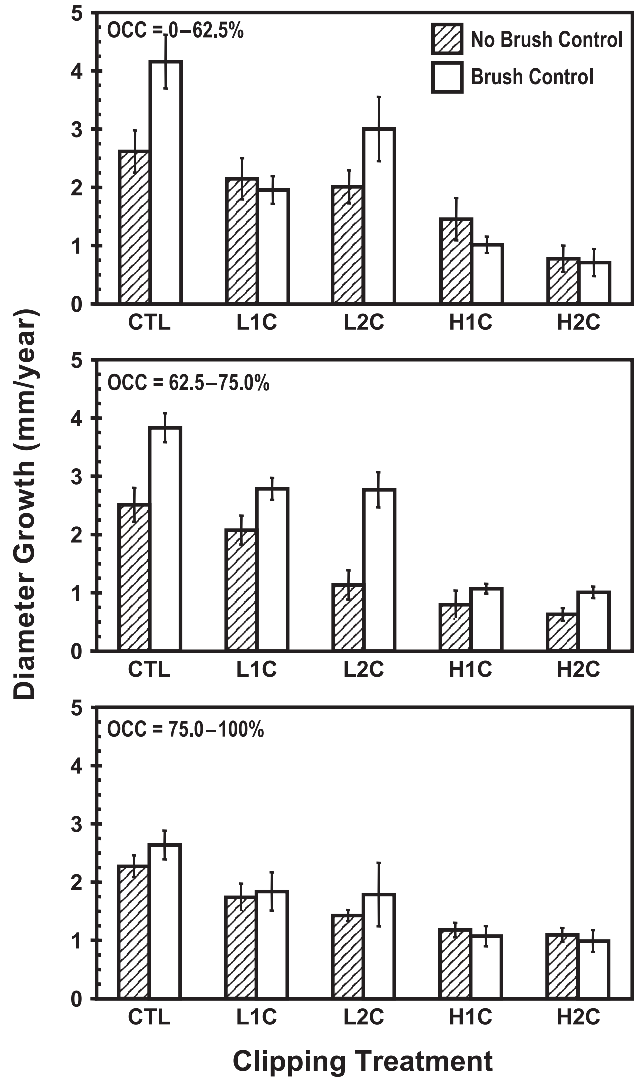


Fig. 2. Mean annual diameter growth for each clipping treatment by understory brush control treatment and overstory canopy closure (OCC) groupings. OCC groupings of 0–62.5% (n = 78), 62.5–75.0% (n = 109), and 75.0–100% (n = 109) correspond to basal areas of <9 m^2/ha, 9–15 m^2/ha, and >15 m^2/ha, respectively (unpublished data). Error bars are ±1SE.



heavily clipped seedlings averaged only 30 and 54% less height growth, respectively. Likewise, there was a similar INTENSITY × BRUSH interaction for diameter growth (p = 0.009), although there were no significant interactions between INTENSITY and BRUSH for height growth (p = 0.113; Table 4). Differences in diameter growth between seedlings with and without brush control decreased when intensity of clipping increased (Fig. 2). Unclipped, lightly clipped, and heavily clipped seedlings, each with brush control, grew at rates 48, 33, and –5% faster in diameter than corresponding seedlings without brush control, respectively.

Increasing clipping frequency (FREQUENCY: none, one episode, two episodes) led to shorter seedlings; one clipping episode reduced average final height by 21.8 ± 3.5 cm and two episodes by 36.6 ± 4.3 cm. Final diameter was also significantly reduced with increasing clipping frequency (Table 3), but final diameters of seedlings clipped for two successive years were not significantly different than final diameters of seedlings clipped only in the first year (p = 0.842, Tukey–Kramer HSD test). Diameter growth was significantly reduced by increasing clipping frequency (p < 0.001; Table 5). Unclipped seedlings averaged 3.05 ± 0.14 mm/year, seedlings clipped only in the first year averaged 1.65 ± 0.08 mm/year, and seedlings clipped both years averaged 1.53 ± 0.12 mm/year. However, annual height growth was not significantly affected by clipping frequency (p = 0.447; Table 5). One episode of clipping reduced height growth by 7%, and two episodes reduced height growth by 15% compared with unclipped seedlings.

An interaction between FREQUENCY and OCC was not

Table 3. Average seedling mortality, final height, annual height growth, final diameter, and annual diameter growth, as summarized by herbivory treatment.

Herbivory treatment	*N*	Mortality (%)	Final height (cm)	Height growth (cm/year)	Final diameter (mm)	Diameter growth (mm/year)
CTL	60	13.3*ab*	92.7*a*	18.4*a*	14.4*a*	3.0*a*
L1C	40	7.5*a*	84.8*ab*	23.8*b*	12.9*a*	2.2*b*
L2C	20	12.5*ab*	71.3*b*	25.6*b*	12.5*ab*	2.0*b*
H1C	40	22.5*ab*	55.5*c*	9.8*c*	10.7*b*	1.1*c*
H2C	20	27.5*b*	36.3*d*	2.7*d*	10.3*b*	0.9*c*

Note: Herbivory treatments included a control (CTL), a light clipping consisting of removal of 50% of current-year shoots and the terminal leader done either 1 year (L1C) or 2 years (L2C) in a row, and a heavy clipping consisting of removal of 100% of current-year shoots and the terminal leader done either 1 year (H1C) or 2 years (L2C) in a row. Values in each column with the same letter are not significantly different from each other ($p < 0.05$, Tukey–Kramer HSD test).

Table 4. Split-plot analysis of covariance for the effects of initial seedling height or diameter, overstory canopy closure, understory brush control, and clipping intensity on mean annual height and diameter growth.

Source	df	MS	*F*	*P*
Height growth (cm/year)				
OCC	1	3784.6	34.78	<0.0001
BRUSH	1	113.2	1.04	0.3121
OCC × BRUSH	1	8.2	0.07	0.7853
Error (WP)	56	108.8		
INIHT	1	2988.6	66.29	<0.0001
INTENSITY	2	6240.4	138.88	<0.0001
OCC × INTENSITY	2	238.4	5.29	0.0057
Brush × INTENSITY	2	99.4	2.21	0.1123
OCC × BRUSH × INTENSITY	2	8.8	0.19	0.8226
Error	231	45.1		
Diameter growth (mm/year)				
OCC	1	24.53	12.63	0.0005
BRUSH	1	22.60	12.26	0.0008
OCC × BRUSH	1	3.05	1.69	0.1985
Error (WP)	56	1.80		
INIHT	1	31.66	58.00	<0.0001
INTENSITY	2	94.73	173.51	<0.0001
OCC × INTENSITY	2	4.94	9.04	0.0002
BRUSH × INTENSITY	2	2.66	4.87	0.0084
OCC × BRUSH × INTENSITY	2	1.07	1.95	0.1444
Error	231	0.55		

present for height growth ($p = 0.677$) but was present for diameter growth ($p = 0.009$; Table 5). Likewise, an interaction between FREQUENCY and BRUSH was not present for height growth ($p = 0.334$), but was marginally present for diameter growth ($p = 0.051$; Table 5). These two interactions indicate that diameter growth was very sensitive to competitive conditions, particularly when the seedling had received successive years of simulated browsing.

Although an INTENSITY by FREQUENCY interaction was not present for diameter growth ($t = 0.408$, df = 1, $p = 0.683$), it was present for height growth ($t = 4.16$, df = 1, $p < 0.001$). Heavily clipped seedlings had significantly less height growth when clipped twice as compared with once (Table 3). There were no other significant higher order interactions among INTENSITY, FREQUENCY, BRUSH, and OCC for either growth parameter.

Mortality was moderately influenced by clipping treatments ($\chi^2 = 13.75$, df = 4, $p = 0.088$; Table 2) with clipping intensity positively related to mortality ($\chi^2 = 11.28$, df = 2, $p = 0.024$) and clipping frequency having no effect ($\chi^2 = 2.97$, df = 2, $p = 0.564$). No interactions among INTENSITY, FREQUENCY, BRUSH, and OCC were significant.

Recovery of seedlings changes over time

Seedling growth responses to clipping treatments were quite different when comparing growth patterns across the 2 years of the experiment. In 1996, lightly clipped seedlings averaged 34% greater height growth, and heavily clipped seedlings averaged 68% less height growth compared with unclipped seedlings (Fig. 3). However, the differences between clipping treatments had changed during 1997, the second growing season after treatment, as lightly and heavily

Table 5. Split-plot analysis of covariance for the effects of initial seedling height or diameter, overstory canopy closure, understory brush control, and clipping frequency on mean annual height and diameter growth.

Source	df	MS	*F*	*P*
Height growth (cm/year)				
OCC	1	3784.6	34.78	<0.0001
BRUSH	1	113.2	1.04	0.3121
OCC × BRUSH	1	8.2	0.07	0.7852
Error (WP)	56	108.8		
INIHT	1	2988.6	29.82	<0.0001
FREQUENCY	2	80.9	0.80	0.4474
OCC × FREQUENCY	2	39.2	0.39	0.6769
BRUSH × FREQUENCY	2	110.5	1.10	0.3338
OCC × BRUSH × FREQUENCY	2	6.9	0.06	0.9338
Error	231	100.2		
Diameter growth (mm/year)				
OCC	1	24.53	13.63	0.0005
BRUSH	1	22.60	12.56	0.0008
OCC × BRUSH	1	3.05	1.69	0.1985
Error (WP)	56	1.80		
INIHT	1	31.66	40.25	<0.0001
FREQUENCY	2	68.54	87.14	<0.0001
OCC × FREQUENCY	2	3.75	4.77	0.0093
BRUSH × FREQUENCY	2	2.37	3.02	0.0509
OCC × BRUSH × FREQUENCY	2	0.93	1.18	0.3098
Error	231	0.79		

clipped seedlings averaged 18 and 46% less height growth than controls, respectively (Fig. 3). These INTENSITY effects were significant in split-plot ANCOVA models in 1996 and 1997 (Table 6).

Diameter growth patterns also changed between 1996 and 1997. In 1996, diameter growth was significantly reduced by clipping (Table 6), with lightly and heavily clipped seedlings averaging only 61 and 38% of the growth of unclipped controls, respectively. In 1997, increased intensity of clipping still significantly reduced diameter growth (Table 6) but did not proportionally change in the same manner. For instance, in 1997, diameter growth in control seedlings increased by 25% compared with 1996 growth, while 1997 growth increased by 59% and 10% for lightly and heavily clipped seedlings, respectively.

Overstory canopy closure significantly influenced both growth variables for both years (Table 6), generally decreasing growth as overstory canopy closure increased. On the other hand, brush control affected diameter growth significantly only in the second year (Table 6). This indicated that there was a delayed response by the seedlings to the brush control treatment.

Overstory canopy closure interacted with INTENSITY for both height and diameter growth in 1996, but not in 1997 (Table 6). Likewise, BRUSH × INTENSITY interactions were not present for height growth and present only in 1996 for diameter growth (Table 6). This suggested that competitive effects had more influence on seedling response to clipping treatments early in the experiment (i.e., the first growing season; Fig. 4). For example, in 1996, brush control significantly increased diameter growth of controls by 1.18 ± 0.22 mm (t = 5.38, p < 0.001), but diameter growth of lightly and heavily clipped seedlings was not improved (t = 0.38, p = 0.698; and t = 0.66, p = 0.507, respectively). In 1997, diameter growth of seedlings with brush control improved, with decreasing returns as the intensity of the clipping treatment increased (Fig. 4). Brush control increased 1997 diameter growth by 1.15 ± 0.26, 0.85 ± 0.32, and 0.02 ± 0.34 mm/year for control, lightly clipped, and heavily clipped seedlings, respectively.

Discussion

Increasing overstory canopy closure reduced both height and diameter growth in this experiment. Generally, the relationship between OCC and height growth was linear; seedlings responded similarly to changes in overstory cover across a continuum of overstory densities. Although height responses to OCC may differ greatly on nutrient-poorer sites or under coniferous overstories (M.A. Counte and K.J. Puettmann, in preparation), this linear trend suggests that white pine seedlings may be much more shade tolerant than previously thought and can be used as planting stock under a much broader range of overstory conditions. Unlike height growth, the relationship between overstory canopy closure and diameter growth in white pine seedlings was nonlinear and similar to that reported for a variety of other species (Pacala et al. 1994; Wang et al. 1994; Puettmann and Reich 1995).

While overstory canopy closure affected both height and diameter growth, increasing cover of understory vegetation decreased only diameter growth strongly. This was not surprising since diameter growth is known to be much more sensitive to competition than height growth (Brand 1990;

Fig. 3. Mean annual height growth versus overstory canopy closure (OCC) groupings by clipping treatment and year. Trees that were clipped twice (L2C and H2C) and trees that died either in the first year or second year of the study were not included in this analysis. Clipping treatment abbreviations are as in Table 3. Error bars are ±1SE.

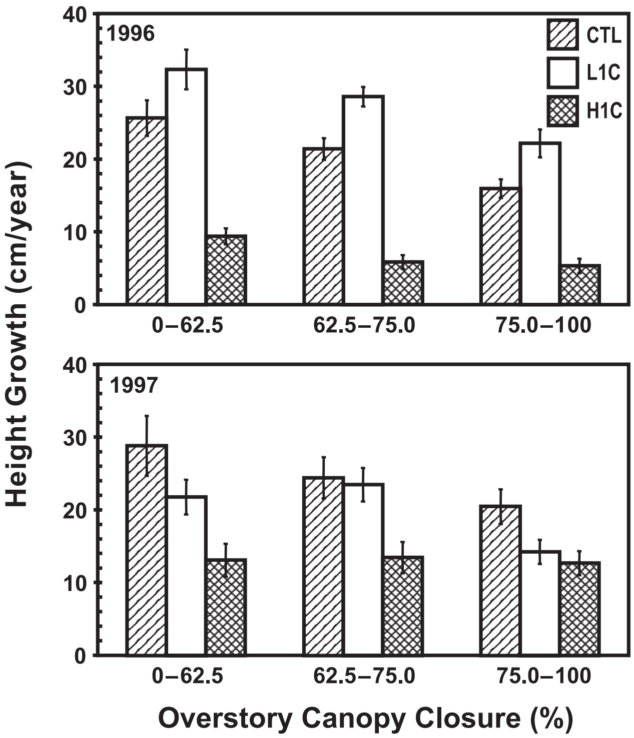
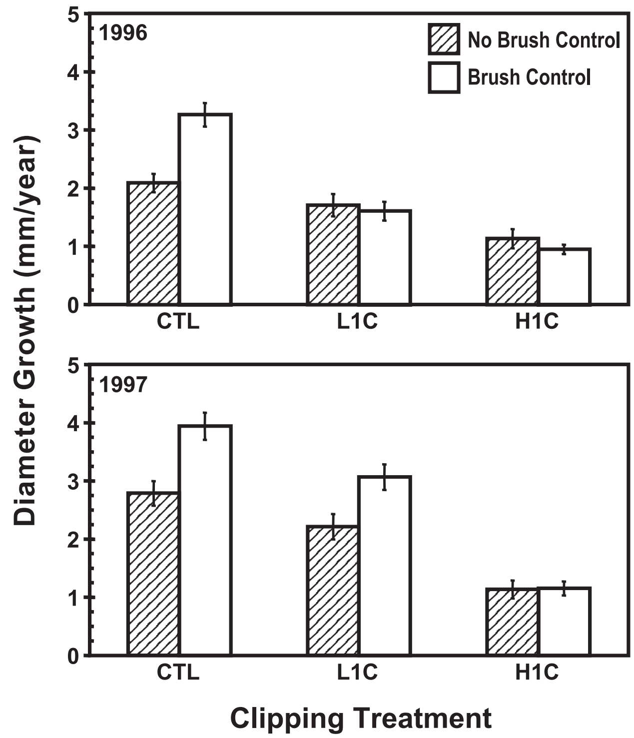


Fig. 4. Mean annual diameter growth versus clipping treatment as separated by understory brush control treatment and year. Trees that were clipped twice (L2C and H2C) and trees that died either in the first year or second year of the study were not included in this analysis. Clipping treatment abbreviations are as in Table 3. Error bars are ±1SE.



Morris et al. 1990). Furthermore, we hypothesize that the effects of overstory and understory competition on seedling growth may differ. Elliott and Vose (1994) suggest that growth of white pine will only be reduced when surrounding competitors had developed enough to shade the seedling and reduce net photosynthesis. At our site, the most severe shading of the seedlings occurred later in the growing season (i.e., June or July) after the understory flushed and developed. Since diameter growth continues later in the growing season than height growth (M.A. Counte and K.J. Puettmann, unpublished data), this may explain why understory competition only affected diameter growth. Further studies are ongoing to isolate and identify competitive effects within the neighborhood of the seedling.

Seedling response to a single understory brush control treatment was also delayed. BRUSH was only marginally significant in diameter growth models in 1996 but was highly significant in 1997. This was not unusual since current-year growth is often partially subsidized by the previous year's carbon gain. It is unlikely, however, that the effects of brush control would be felt even more strongly in the 1998 growing season. More likely, the effects would begin to fade as understory vegetation became re-established and dominant within the treated plots.

White pine did not show a compensatory growth pattern as defined by Belsky (1986). Although light-intensity clipping stimulated height growth, diameter growth decreased significantly at any clipping intensity or frequency. Assuming that a stem volume index ((basal diameter)^2 × height) is highly correlated to plant biomass (Shainsky et al. 1991), increasing clipping intensity significantly reduced plant biomass ($p < 0.001$) by an average of 35% in lightly clipped trees and by 74% in heavily clipped trees. Instead, response patterns suggest that substrate reallocation and hormonal redistribution within the plant may be responsible for altered first-year growth patterns in plants that were clipped once (L1C and H1C). For example, in relation to controls and to the previous year's growth, diameter growth slightly increased during the second growing season. Since basal diameter is a good indicator of belowground biomass under normal (i.e., nonclipped) conditions (Grigal and Kernik 1984; Shainsky et al. 1991; Thies and Cunningham 1996), this might suggest an adjustment of the root/shoot ratio. On the other hand, first-year height growth gains of lightly clipped seedlings did not continue into the second year. In 1997, lightly clipped seedlings had similar or less height growth than controls. Aarssen and Irwin (1991), Hjältén et al. (1993), and Chamberlin and Aarssen (1996) hypothesize that this response is typical for plants that lose apical control as a result of clipping and re-establish it with "bending up" of a lateral branch by the second growing season.

Overstory competition and understory brush control both significantly affected a seedling's ability to respond to clipping. Increasing intensity and frequency of clipping lessened gains achieved by brush control. Likewise, increasing overstory canopy closure had weak or no effects on

Table 6. Split-plot analysis of covariance for the effects of initial seedling height or diameter, overstory canopy closure, understory brush control, and clipping intensity on 1996 and 1997 mean annual height and diameter growth.

Source	df	MS	*F*	*P*
1996 height growth (cm/year)				
OCC	1	4716.0	45.37	<0.0001
BRUSH	1	49.1	0.47	0.4947
OCC × BRUSH	1	79.0	0.76	0.3871
Error (WP)	56	104.0		
INIHT	1	2339.3	48.98	<0.0001
INTENSITY	2	6946.3	145.46	<0.0001
OCC × INTENSITY	2	196.7	4.12	0.0180
Brush × INTENSITY	2	41.0	0.85	0.4255
OCC × BRUSH × INTENSITY	2	58.6	1.23	0.2955
Error	168	47.8		
1997 height growth (cm/year)				
OCC	1	4035.1	8.82	0.0044
BRUSH	1	330.0	0.72	0.3993
OCC × BRUSH	1	836.2	1.83	0.1818
Error (WP)	56	457.5		
INIHT	1	2446.8	25.05	<0.0001
INTENSITY	2	717.4	7.34	0.0009
OCC × INTENSITY	2	101.2	1.04	0.3573
BRUSH × INTENSITY	2	27.1	0.28	0.7580
OCC × BRUSH × INTENSITY	2	27.6	0.28	0.7541
Error	168	97.7		
1996 diameter growth (mm/year)				
OCC	1	16.96	6.34	0.0147
BRUSH	1	9.39	3.51	0.0663
OCC × BRUSH	1	3.13	1.17	0.2841
Error (WP)	56	149.88		
INIHT	1	2.33	2.70	0.1022
Intensity	2	84.65	49.02	<0.0001
OCC × INTENSITY	2	10.91	6.32	0.0023
BRUSH × INTENSITY	2	8.40	4.86	0.0088
OCC × BRUSH × INTENSITY	2	4.11	2.38	0.0960
ERROR	168	145.06		
Diameter growth (mm/year)				
OCC	1	27.94	8.43	0.0052
BRUSH	1	29.36	8.86	0.0042
OCC × brush	1	5.54	1.67	0.2015
Error (WP)	56	3.31		
INIHT	1	46.20	38.96	<0.0001
INTENSITY	2	80.94	68.26	<0.0001
OCC × INTENSITY	2	0.12	0.10	0.9070
Brush × INTENSITY	2	1.30	1.10	0.3354
OCC × BRUSH × INTENSITY	2	0.15	0.12	0.8830
Error	168	1.19		

seedlings under higher intensity and frequency clipping treatments. These results are not surprising; growth often declines drastically as multiple stresses are imposed on a plant (Grime and Campbell 1991; Waring 1991). However, the extent to, and direction in which competition and herbivory interact are species dependent (Edenius et al. 1993; Canham et al. 1994) and may differ widely between conifers and hardwoods. For either species group, plant recovery from browsing is hypothesized to decrease with increasing intra- and (or) inter-specific competition. Shabel and Peart (1994), for example, reported that a ratio of relative height growth of browsed pin cherry (*Prunus pensylvanica* L.) seedlings to unbrowsed seedlings declined linearly with increasing intraspecific competition. Hjältén et al. (1993) observed a threshold pattern between herbivory and competition. They observed that at densities of 340 and 940 seedlings/m^2, birch (*Betula pubescens* Ehrh.) showed no significant differences between height of topped and untopped trees after three years of growth, while at 90 seedlings/m^2, topped seedling height was significantly greater ($p < 0.05$).

Unlike growth, white pine mortality was not affected by clipping frequency or overstory density but increased with clipping intensity and decreased when brush control was applied. This suggests that the range of overstory densities and browsing frequencies might not have been sufficient in our study to document any effects. Furthermore, overstory competition and browsing frequency may act on longer time scales (e.g., >2 years) than measured in this experiment. Krefting et al. (1966), for example, found that it took 9 years of clipping of 100% of the annual growth of mountain maple (*Acer spicatum* Lam.) before mortality was observed.

In conclusion, our results suggest that white pine may be able to quickly recover from winter browsing, especially on nutrient-rich sites and when interspecific competition is low. On the other hand, white pine may not recover from summer browsing (Canham et al. 1994) or when browsing is severe or repetitive. Unfortunately, most white pine seedlings in the Lake States are subjected to severe deer pressure (>8 deer/km^2) year after year (Sauerman 1992). This pressure can lead to regeneration failures across large areas. For example, Frelich and Lorimer (1985) found that seedling depredation by white-tailed deer was a major cause of the decline of eastern hemlock (*Tsuga canadensis* (L.) Carr.) from mixed conifer–hardwood forests in northwestern Michigan and northern Wisconsin. Likewise, Davis et al. (1998) found that deer browsing prevented regeneration of eastern white cedar (*Thuja occidentalis* L.) in northeastern Minnesota forests. Coupled with competition, changing climate, interrupted disturbance cycles, and other factors (Mladenoff and Sterns 1993), deer pressure can lead to significantly reduced abundance of many plant species (Augustine and Jordan 1998).

In terms of management, increases in height growth after a browsing event may allow foresters to skip seedling protection (i.e., budcapping) for 1 year or more, especially when seedlings have not been severely browsed and they are close to the browsing limits for deer (>130 cm) (Saunders and Puettmann 1999). However, if seedlings are repetitively or severely browsed, they may not respond with increased height growth. Likewise, our results demonstrate the combined importance of understory brush control and seedling protection to maintain large growth increments and reduce mortality in young white pine regeneration. Although understory brush control will reduce light and nutrient competition, it removes horizontal and vertical cover that hides seedlings from deer, which increases the probability of a seedling being browsed (Saunders and Puettmann 1999). Alternatively, protection from deer browsing is most beneficial when seedlings have good growing conditions. High densities of competing vegetation reduce growth and increase the time that seedling terminals are vulnerable to browsing damage. Therefore, understory brush control and seedling protection should go hand in hand in the regeneration of white pine.

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