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Patterns of growth compensation in eastern white pine (*Pinus strobus* L.): the influence of herbivory intensity and competitive environments

Abstract To investigate complex growth compensation patterns, white pine (*Pinus strobus* L.) seedlings were clipped to simulate different herbivory levels. Seedlings were growing with different understory competition levels (created through monthly weeding vs no brush control) under a range of overstory canopy closures. Compensation patterns varied for the different growth and size measures. After one growing season, seedlings did not fully compensate for lost biomass regardless of the competitive environments of the seedlings. Although relative height growth was stimulated by light intensity clipping (20–40% of last-year shoots removed), relative diameter growth, total biomass, and biomass growth of seedlings declined sharply with increasing clipping intensity. Likewise, all growth parameters declined with increasing interspecific competition. Results showed that seedlings in highly competitive environments showed smaller growth loss due to clipping than those in competition-free environments, presumably because seedlings experiencing high interspecific competition devoted more energy to maintaining apical dominance and a balanced shoot-root ratio. While competition from canopy trees altered compensatory patterns, competition from understory vegetation only altered the magnitude, but not the patterns, of compensatory growth. We suggest that compensatory growth follows a complex pattern that will vary with the parameters measured, competitive conditions, and clipping intensities. Our results support the assertion that overcompensation may be an adaptation to competitive ability, rather than a response to herbivory itself.

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Introduction

Plants have developed a variety of chemical and physical defenses to discourage browsing by mammals (Strauss and Agrawal 1999). Often, these defenses reduce the palatability of the plant, usually either by preventing access to the plant (i.e., thorns) (Myers and Bazely 1991) or by reducing the nutritional value of the plant matter [i.e., increasing the lignin content of the tissue or introducing secondary metabolites that specifically interfere with digestion of the plant (Bryant et al. 1991a, 1991b, 1992)]. Plants also may display "alternative defense traits" (Strauss and Agrawal 1999). Such traits may include a plant's increased ability to reproduce and/or regrow after herbivory. This phenomenon, called tolerance to herbivory or compensatory growth, was first suggested by Dyer (1975) and is fairly well documented for grass dominated ecosystems (McNaughton 1979; Detling and Painter 1983; Du Toit et al. 1990; Frank and McNaughton 1993; Painter and Belsky 1993). This phenomenon has also been proposed for woody perennials (Belsky 1987; Hjältén et al. 1993; Canham et al. 1994), but has been found to be species and study specific. Several authors suggest that overcompensation is more likely in environments with high moisture and nutrient availability (e.g., Maschinski and Whitham 1989), while others found the opposite effect (e.g., Mutikainen and Walls 1995). The degree of compensation was also influenced by timing of herbivory and competition. Generally, plants seem more likely to overcompensate after early season herbivory (Maschinski and Whitham 1989) and in areas with low competition (Maschinski and Whitham 1989; Irwin and Aarssen 1995). Alternatively, many authors have found the herbivore-plant relationship to be either antagonistic, i.e., any level of herbivory results in reduced plant vigor (e.g., Ehrlich and Raven 1964; Levin 1976; Crawley 1983; Marquis 1984; Rhoades 1985; Zimov et al. 1995),

or to follow a threshold model, i.e., herbivory does not affect plant growth and fitness until a threshold level of herbivory is reached (McNaughton 1979; for examples see Linzon 1958; Roy 1960; Metzger 1977; Pastor et al. 1988; Gill 1992).

Most papers supporting the compensatory plant growth hypothesis used a broad definition that referred to any positive response of the plant to injury as compensatory growth (Belsky 1986, 1987). Belsky (1986, 1987) suggested that the use of the term be limited to measures of dry weight and defined overcompensation, exact compensation, and undercompensation as when the cumulative dry weight (including removed tissue) of the grazed or clipped plants was greater, the same, or less than the total dry weight of the control plants, respectively. Other authors define overcompensation as when damaged plants having a greater fitness than undamaged plants (Strauss and Agrawal 1999). Thus, inconsistencies in interpretation of the pattern of plant response to herbivory and compensatory growth may be due to the differences in the measure (e.g., height, diameter or biomass) and the specific study conditions (Belsky 1986; Strauss and Agrawal 1999). To sort out some of these inconsistencies, we present the results from an experimental study that analyzed different measures of compensatory growth with regard to variable herbivory intensity and competitive conditions.

Eastern white pine (*Pinus strobus* L.) is a coniferous, mid-successional species that shows deterministic growth from terminal clusters of buds on the parent shoots (Wilson 1992). It is an important component of the diet of white-tailed deer (*Odocoileus virginianus* Zimmermann), especially in late winter/early spring before the vegetation "greens up" in the Lake States, and is of great commercial, wildlife, and aesthetic value. To simulate typical herbivory patterns (Hjältén et al. 1993; but see Baldwin 1990), we clipped white pine seedlings at several different intensities and under a range of competitive conditions in early spring and measured various aspects of growth response after one growing season. We addressed the following questions: How do (1) intensity of herbivory and (2) overstory and understory competition affect the compensatory growth responses of white pine seedlings herbivory? (3) How do different measures of compensatory growth or size (e.g., height, diameter, biomass) compare in their relationship to intensity of herbivory and competition? (4) Can a shift in biomass allocation patterns explain these relationships?

Materials and methods

Site description

This experiment was conducted in a 45-year-old jack pine plantation located 15 km southeast of Grand Rapids, Minnesota, in southern Itasca County (approximately 47°E 7′ N, 93°E 22′ W). The 9.5 ha site lies on a level, upland area formed from a glacial outwash plain and is 390 m above sea level. The soil type is predominately Menahga-Graycalm sandy outwash consisting of 70% sand, 20% silt, and 10% clay (unpublished data).

In 1994, the site was partially harvested using a combination of a 2.8 ha clear-cut (southeastern corner of plantation) and 6-m-wide strip-cuts (rest of plantation). This removed the overstory on approximately 50% of the site. Within the strip-cut area of the plantation, overstory basal area (BA) and cover ranged from 6 m^2/ha and 51% in strip cuts to 36 m^2/ha and 89% under the residual overstory. Understory cover was relatively sparse (0–40% cover) under residual canopy but increased dramatically within the strips and clear-cut areas (50–100% cover). Predominant understory species included bracken fern [*Pteridium aquilinum* (L.) Kuhn.], raspberry and blackberry (*Rubus* spp.), beaked hazel (*Corylus cornuta* Marsh.), chokecherry (*Prunus virginiana* L.), and aspen sprouts (*Populus* spp.).

Experimental design

During the spring of 1996, 720 3–0 white pine seedlings were planted at 1.0-m spacing within 17 plots located across the site. To ensure a range of overstory competitive conditions, two plots consisted of 90 (9 rows×10 seedlings/row) seedlings each; these were open and closed controls and located within the clear-cut and an uncut portion of the jack pine stand. The remaining plots had 36 seedlings (9 rows×4 seedlings/row) and were clustered into groups of three, for a total of five clusters across the strip-cut portion of the site. Within each cluster, one plot was located in the center of a cut strip, one was located on the edge of the cut strip under the residual overstory, and one was located in the center of an uncut strip. This provided relatively open (BA=10.3±1.1 m^2/ha (mean±SE)), intermediate (BA=22.7±3.1 m^2/ha), and closed canopy conditions (BA=31.0±2.4 m^2/ha).

Within each plot, seedlings were either weeded monthly (MON) to remove all herbaceous and woody competitors, weeded annually (ANN) to reduce cover of herbaceous competitors and remove most woody competitors, or never weeded (CTRL). Weeding treatments were randomly applied to entire rows of seedlings (4 or 10 seedlings) under the restrictions that (1) control and monthly weeding treatments could not occur in adjacent rows; and (2) the same weeding treatment could not occur in three adjacent rows. MON was applied monthly throughout 1996 and 1997 growing seasons; ANN was applied twice, in June 1996 and June 1997.

In late April and early May 1997, seedlings were assigned to one of following clipping classes: an unclipped control or the removal of the terminal and approximately 25%, 50%, 75%, or 100% of last year's shoots. To avoid artificially dispersing clipping damage throughout the crowns of the seedlings (see Edenius et al. 1993), we clipped in 1, 2, or 3 adjacent quadrants for the 25%, 50%, and 75% treatments, respectively. This distributed clippings vertically on the seedlings and, in cases where laterals were concentrated on one side of the seedling, allowed quadrants to be expanded or narrowed as needed to achieve desired clipping intensities. The timing and clipping patterns were chosen to approximate natural deer browsing as close as possible and clipping classes were used to ensure a broad range of actual clipping intensities. Two complete replications of clipping classes were installed in each weeding treatment in the 9×4 plots and three complete replications were installed in the 9×10 plots.

Field measurements

Total height, basal diameter at 1 cm above the ground, the number of last-year lateral branches in the primary flush, and number of last-year lateral branches overall were recorded for each seedling. For clipped seedlings, the number of last-year branches removed was also recorded. Seedlings were measured before clipping in April 1997 and after growth had stopped in October 1997.

To expand beyond an earlier study (Saunders and Puettmann 1999), which was limited to measuring height and diameter response, and investigate compensatory growth sensu Belsky (1986) (i.e., with total biomass, including removed plant parts), we col-

Table 1 Models used to estimate initial biomass values of fall 1997, harvested seedlings. Models were developed from unclipped seedlings harvested before budbreak in spring 1997

Initial biomass model: $Y=\alpha\,(HT_{ini,bc})^\beta\,(DIA_{ini})^\delta$	n	Parameter			MSE	F	P	R^2_{ADJ}
		α	β	δ				
Aboveground	65	0.091**	0.251*	2.067**	1.586	208.97	<0.001	0.867
Leaves	65	0.083**	0.141[ns]	2.038**	0.926	111.17	<0.001	0.775
Stems	65	0.017**	0.453**	2.083**	0.191	334.18	<0.001	0.912
Belowground	41	0.082**	0.336*	1.408**	0.332	67.62	<0.001	0.769
Total	41	0.162**	0.231[ns]	1.958**	2.329	197.58	<0.001	0.908

lected all clipped material and harvested some seedlings and their roots before the experiment began and some after one growing season. In April 1997, we harvested 41 randomly selected unclipped seedlings to model initial biomass of all treated and untreated seedlings. To estimate final seedling biomass, we harvested a total of 91 seedlings (14–21 seedlings from each clipping class) in October 1997; these were randomly selected from all available seedlings within the CTRL and MON weeding treatments. All clippings and harvested seedlings were labeled and, upon returning to the laboratory, stored in a freezer at –16°C. As soon as possible, samples were removed from the freezer, cleaned of foreign matter and soil, and put in a drying oven for 72 h at 70°C. After being removed from the oven, samples were separated into roots, stems, and needles and immediately weighed to the nearest 0.001 g using a digital scale.

In late July 1997, overstory canopy structure above each seedling was measured with the LICOR LAI-2000 Plant Canopy Analyzer. Readings were taken with two instruments. One was placed in an adjacent open area to measure "above canopy" conditions. The second measured light levels immediately above each seedling. Both readings were taken 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 instruments from a 90° arc; this allowed the operator to "hide" from the instruments. Similarly, readings were restricted to a 43° cone to reduce the influence of sun flecks on measurements that might otherwise negatively bias the results (Chason et al. 1991; Grantz et al. 1993; Strachan and McCaughey 1996). The readings from both instruments were integrated to calculate DIFN, an indicator of "canopy openness" (LI-COR 1992; Puettmann and Reich 1995; Saunders and Puettmann 1999) that has been shown to be related to light availability (Gendron et al. 1998). Overstory canopy closure (OCC) was then calculated as:

$$OCC\,(\%)=(1-DIFN)\times100 \tag{1}$$

and average plot values for OCC were calculated.

Statistical analyses

Statistical analyses were conducted on (1) relative height growth, (2) relative diameter growth, (3) absolute above ground, below ground and total biomass growth and (4) needle, stem, root, and total biomass of seedlings after one growing season. All analyses used actual clipping intensity (CLIP) as a variate, as defined by the proportion of last-year shoots including the terminal, removed during the clipping treatment. This approach was taken because it was difficult to remove exactly 25%, 50%, or 75% of last-year shoots; these young seedlings often had only a few last-year shoots and treatments would sometimes remove more or less than the desired percentage of shoots (e.g., a 25% clipping could remove at least 33% of last-year shoots if only two laterals and one terminal were present on the seedling).

Analyses for (1) and (2) were conducted on relative growth instead of absolute growth since the growth of a tree is related to its initial size (Puettmann and Reich 1995). Relative height growth (RHG) was defined as:

$$RHG=(HT_{fin}-HT_{ini,\,ac})\,/\,HT_{ini,\,bc} \tag{2}$$

where HT_{fin} is final seedling height, $HT_{ini,\,ac}$ is initial seedling height after clipping, and $HT_{ini,\,bc}$ is initial seedling height before clipping. Relative diameter growth (RDG) was defined as:

$$RDG=(DIA_{fin}-DIA_{ini})\,/\,DIA_{ini} \tag{3}$$

where DIA_{fin} is final seedling diameter and DIA_{ini} is initial seedling diameter. Effects of competing vegetation and clipping on relative growths were tested using a weighted analysis of covariance (ANCOVA), with OCC and CLIP as covariates and the weeding treatment (WEED) as a factor. In order to reduce heteroscedasticity in the ANCOVA model, the natural logarithms of RDH and RDG were used in analysis as suggested by the Box-Cox transformation testing procedure (Neter et al. 1983).

In this study, total biomass (BIO_{tot}) was defined as the cumulative dry weight of a seedling including removed (i.e., clipped) tissue or:

$$BIO_{tot}=BIO_{fin}+BIO_{clip} \tag{4}$$

where BIO_{fin} is the dry weight of the seedling after one growing season and BIO_{clip} is the dry weight of material removed during the clipping treatment (Belsky 1986). Stem (BIO_{stem}), root (BIO_{root}) and needle (BIO_{needle}) biomass were calculated using the same approach. Total, above, and below ground biomass growth (BG_{total}, BG_{above}, and BG_{below}) could not be defined in terms of measurable parameters. Therefore, initial biomass (BIO_{ini}) of fall-harvested seedlings had to be modeled from the biomass of spring-harvested seedlings using non-linear least squares regression. Models for each plant component are presented in Table 1. BGs could then be parameterized as:

$$BG=BIO_{fin}-BIO_{ini} \tag{5}$$

To isolate the effects of competition and clipping on the various BIOs and BGs, unweighted ANCOVA analyses were conducted using OCC and CLIP as variates and WEED as a factor (with only two levels – no weeding and monthly weeding). To reduce heteroscedasticity in the BIO and BG models, response variables (y_o) were transformed by: $y=\ln(y_o+b)$, with constant ($b=10$) included in only the BG models to avoid undefined values (i.e., $y_o=0$).

Interaction among variates and factors in all ANCOVA models was tested using sequential sums of squares and F-ratios. Comparisons among treatment means were tested using the Tukey honestly significant difference (HSD) to control for experiment-wise 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 JMP 3.2.1 (SAS 1996) and SPSS 6.3.1.

Results

In general, the compensatory patterns differed between growth measures and were influenced by the treatments and study conditions. Specifically, clipping intensity (CLIP) significantly influenced compensatory patterns of
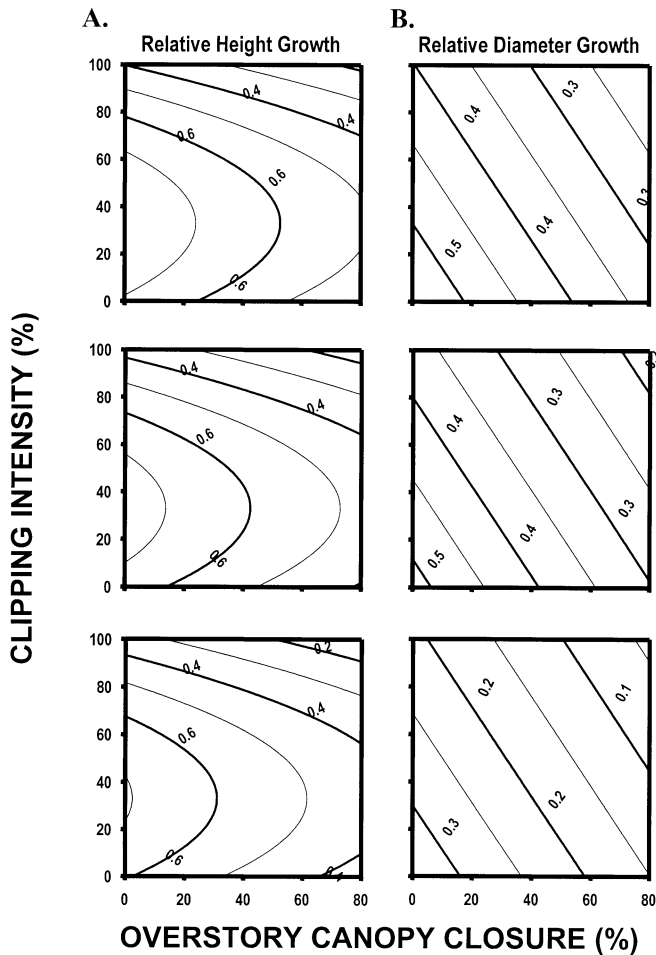
A.

Relative Height Growth

B.

Relative Diameter Growth

CLIPPING INTENSITY (%)

OVERSTORY CANOPY CLOSURE (%)

Fig. 1 Contour plots of relative height (**A**) and diameter (**B**) growth models as a function of overstory canopy closure (*OCC*) and clipping intensity (*CLIP*) for the three different weeding (*WEED*) treatments. Weeding treatments included monthly weeding (*top*), annual weeding (*middle*) and control (*bottom*). Clipping intensity is measured as the proportion of last-year shoots, including terminal, removed. Relative growth was calculated according to Eq. 2

Table 2 Analysis of covariance for the effects of initial biomass (by component), overstory canopy closure (*OCC*), percentage of last-year shoots removed (*CLIP*), and understory brush treatments (*BRUSH*) on final biomass of fall 1997, harvested seedlings. Initial biomasses were calculated from equations in Table 1

Source	df	MSE	F	P
Final leaf biomass (g)[a]				
INILEAF[a]	1	9.345	59.307	<0.001
OCC	1	4.735	30.050	<0.001
CLIP	1	4.257	27.019	<0.001
OCC×CLIP	1	1.369	8.688	0.004
BRUSH	1	4.856	30.816	<0.001
ERROR	83	0.158		
Final stem biomass (g)[a]				
INISTEM[a]	1	14.848	114.848	<0.001
OCC	1	3.011	23.289	<0.001
CLIP	1	3.495	27.034	<0.001
OCC×CLIP	1	1.141	8.824	0.004
BRUSH	1	4.276	33.072	<0.001
ERROR	83	0.129		
Final root biomass (g)[a]				
INIROOT[a]	1	7.702	69.486	<0.001
OCC	1	1.684	15.192	<0.001
CLIP	1	0.692	6.242	0.015
OCC×CLIP	1	0.419	3.782	0.055
BRUSH	1	1.966	17.734	<0.001
ERROR	83	0.111		
Final total biomass (g)[a]				
INITOTAL[b]	1	9.908	98.359	<0.001
OCC	1	3.148	31.249	<0.001
CLIP	1	2.652	26.330	<0.001
OCC×CLIP	1	1.011	10.041	0.002
BRUSH	1	3.478	34.528	<0.001
ERROR	83	0.101		

[a] To stabilize variances, model was linearized with a natural logarithm transformation

[b] Transformed by natural logarithm to maintain scale

relative height growth. The relationship between relative height growth and CLIP was quadratic ($P<0.001$), with relative height growth greatest when approximately 30% of the last-year shoots were removed (Fig. 1). At higher clipping intensities, the benefit of clipping declined and at the highest clipping intensity (100% of last year shoots removed) the seedlings were undercompensating. However, since we also removed the terminal, this growth stimulation at low to intermediate clipping intensities did not result in trees that were taller than trees in the controls after one growing season. For example, as averaged across all overstory conditions and weeding treatments, unclipped trees were 40.0±0.9 cm (mean±SE) in height, while trees with 20–40% of last-year shoots removed were only 31.4±1.6 cm tall.

Unlike relative height growth, relative diameter growth showed undercompensation at any clipping intensity. The degree of undercompensation was linearly related to the clipping intensity ($P<0.001$, Fig. 1). There-fore, clipping at any intensity reduced final seedling diameter; unclipped trees averaged 6.44±0.16 mm in diameter, while trees with 40–60% of last-year shoots removed and 100% of last-year shoots removed averaged 5.95±0.15 mm and 5.80±0.24 mm, respectively. There were no interactions between CLIP and either OCC or WEED for either relative height growth or relative diameter growth ($P>0.10$). This suggested that height and diameter growth were affected only additively in the short term (i.e., one growing season) by the multiple stresses imposed on the seedlings.

Clipping intensity also significantly influenced total final biomass (Table 2) and total biomass growth (Table 3) of harvested seedlings. Total seedling biomass dramatically decreased with increasing clipping intensity (Table 2, Fig. 2a). For example, seedlings with 40–60% and 100% of last-year shoots removed averaged 74% and 64%, respectively, of the biomass of unclipped seedlings. Likewise, clipping at any intensity reduced biomass growth of seedlings (Table 3, Fig. 2b). Biomass growth declined from 6.53±1.57 g/year in unclipped

Fig. 2 Contour plots of final biomass (**A**), biomass growth (**B**), and shoot/root ratio (**C**) models (see Tables 3, 4) as a function of overstory canopy closure (*OCC*) and clipping intensity (*CLIP*) for unweeded seedlings and seedlings with monthly brush control. Graphs in **A** are for final leaf, stem, root, and total biomass (top to bottom), in **B** for aboveground, belowground and total biomass growth (top to bottom). Numbers on the contours are grams and grams/year for plot (**A**) and (**B**), respectively, or the ratio of the aboveground biomass to below ground biomass (**C**). Clipping intensity is measured as the proportion of last-year shoots, including the terminal, removed from the plant
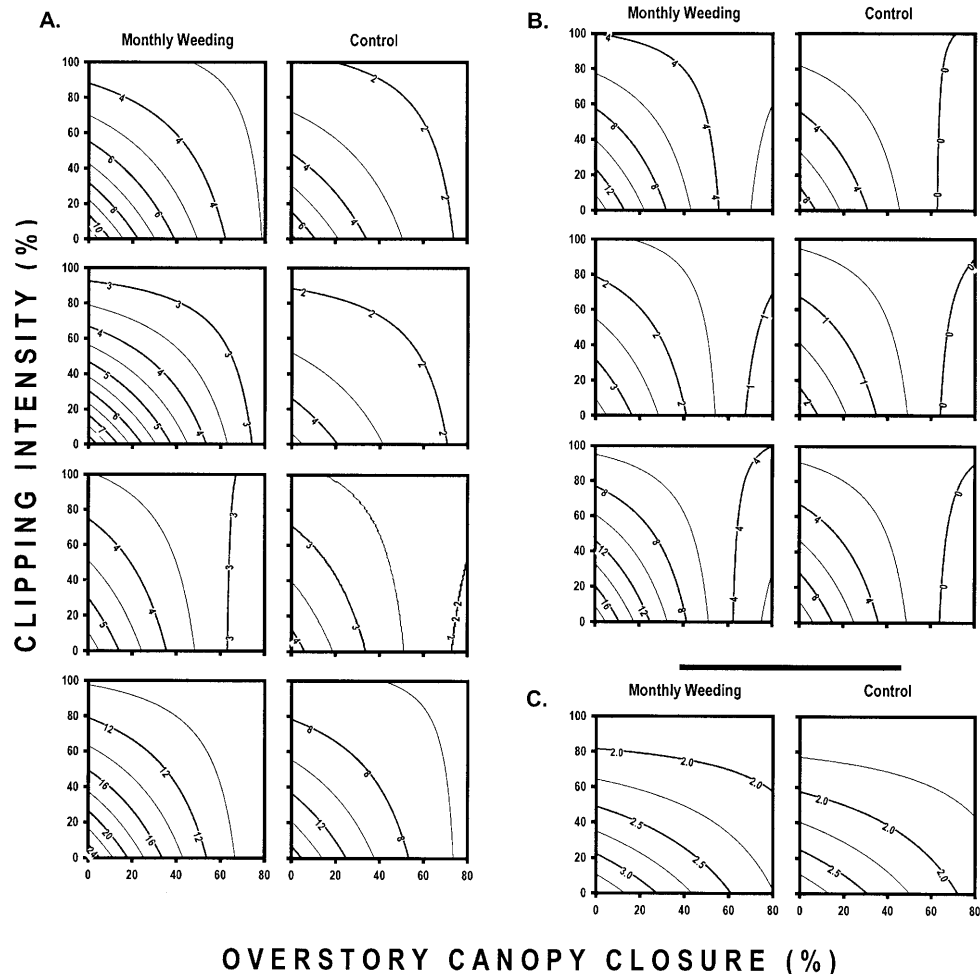

OVERSTORY CANOPY CLOSURE (%)

Table 3 Analysis of covariance for the effects of overstory canopy closure (*OCC*), percentage of last-year shoots removed (*CLIP*), and understory brush treatments (*BRUSH*) on biomass growth of fall 1997, harvested seedlings. Biomass growth was calculated as the difference between the final, measured biomass and an estimated, initial biomass using equations from Table 1

Source	df	MS	F	P
Above ground biomass growth (g/year)[a]				
OCC	1	1.755	46.828	<0.001
CLIP	1	0.980	26.125	<0.001
OCC×CLIP	1	0.597	15.924	<0.001
BRUSH	1	1.481	39.512	<0.001
ERROR	84	0.037		
Below ground biomass growth (g/year)[a]				
OCC	1	0.167	17.698	<0.001
CLIP	1	0.081	8.619	0.004
OCC×CLIP	1	0.053	5.649	0.020
BRUSH	1	0.248	26.339	<0.001
ERROR	84	0.009		
Total biomass growth (g/year)[a]				
OCC	1	2.266	40.657	<0.001
CLIP	1	1.184	21.245	<0.001
OCC×CLIP	1	0.762	13.677	<0.001
BRUSH	1	2.171	38.949	<0.001
ERROR	84	0.056		

[a] To stabilize variances, model was linearized with a natural logarithm transformation

seedlings to 2.63±1.31 g/year in seedlings with 40–60% of last-year shoots removed and to 1.71±0.97 g/year in seedlings with 100% of last-year shoots removed. However, unlike relative height and diameter growth, the OCC×CLIP interaction was marginally significant in the total biomass model and highly significant in the total biomass growth model (Tables 2, 3). In general, biomass compensatory patterns of seedlings under dense canopies (i.e., high OCC) were not affected as greatly by increasing clipping intensity as of seedlings in open, unshaded environments (a low OCC; Fig. 2). For example, seedlings with 100% of last-year shoots removed averaged only 14% of the biomass growth of unclipped controls when OCC was between 0–25%, while they averaged 93% of the biomass growth of unclipped controls when OCC was 50–75%. Thus, white pine seedlings may exhibit exact compensation under denser overstory conditions and undercompensation under more open conditions. No other interactions were significant in final biomass or biomass growth models.

Overstory competition had significant effects on the relative growth rates of seedlings but not necessarily on the patterns of compensatory growth. While the patterns (over- vs exact vs under-compensation) were not altered by OCC, the absolute amount of growth reduction increased with increasing overstory density (*P*<0.001 for

Table 4 Final height, relative height growth, final diameter, and relative diameter growth of seedlings as summarized by understory weeding treatment. Weeding treatments included an unweeded control (*CTRL*), an annual weeding of woody competitors (*ANN*), and a monthly weeding of woody and herbaceous competitors (*MON*). Values in each column with the same letter are not significantly different from each other (*P*<0.05, Tukey-Kramer HSD test)

Understory weeding treatment	n	Final height (cm)	Relative height growth	Final diameter (mm)	Relative diameter growth
CTRL	85	29.8[a]	0.439[a]	5.29[a]	0.182[a]
ANN	85	31.3[a]	0.475[a]	6.34[b]	0.348[b]
MON	85	32.4[a]	0.504[a]	6.60[b]	0.359[b]

relative height and relative diameter growth). On the other hand, the pattern of biomass compensatory growth in relationship to clipping intensity varied between seedlings grown under different overstory conditions (see above).

Weeding treatments were also influential (Table 4) in determining the amount of growth. Generally, monthly weeded seedlings (MON) grew slightly better than annually weeded seedlings (ANN) and significantly better than unweeded controls (CTRL) (*P*=0.008 and *P*<0.001 for relative height and relative diameter growth, respectively,. For total biomass and total biomass growth, the difference between MON and CTRL was quite large, e.g., monthly weeding increased total final biomass by 86% and biomass growth by 864% over unweeded seedlings. Weeding treatments did not alter the compensatory patterns for any of the growth measures tested, however.

Biomass allocation was influenced by competitive conditions and clipping intensity. While the compensatory patterns described for total biomass and total biomass growth are consistent for all biomass components (Tables 2, 3), the absolute amounts of growth response were not identical (Fig. 2a, b). Thus, the shoot/root ratio, defined as aboveground biomass divided by below ground biomass, shows that biomass allocation varied with study conditions. Increased clipping intensity resulted in seedlings with a lower shoot/root ratio (Fig. 2c), although this effect was partially a result of the clipping treatments themselves (i.e., shoot biomass was artificially reduced by clipping in the spring and trees were still responding to it). Likewise, increasing OCC reduced the shoot/root ratio (Fig. 2c). On the other hand, the shoot/root ratio for seedlings in unweeded, control plots was lower than for seedlings in plots that received monthly weed control. For example, average shoot/root ratio for unweeded and weeded seedlings was 1.94±0.09 and 2.41±0.13, respectively.

Discussion

This study shows the complexity of plant compensatory growth response patterns. It pointed out that many factors influence white pine seedlings' responses to simulated herbivory, which may explain why general patterns regarding compensatory growth are hard to establish (Strauss and Agrawal 1999). For example, low intensity clipping stimulated relative height growth, while relative diameter growth, biomass growth, and final total biomass of seedlings declined at any clipping intensity. Typically, height growth is the most likely to exhibit overcompensation in hardwood (Hjältén et al. 1993; Canham et al. 1994; Shabel and Peart 1994; McLaren 1996) and conifer species (Mitscherlich and Weise 1982), including white pine (Wilson 1992; Saunders and Puettmann 1999). On the other hand, other studies did not find overcompensation in height growth in several hardwood species (e.g., Metzger 1977; Canham et al. 1994) and in conifer species when leaders were not removed (Mayhead and Jenkins 1992; Bergström and Danell 1995).

Diameter growth response seems to show a consistent pattern of undercompensation in hardwood (Braithwaite and Mayhead 1996) and conifer species (Mitscherlich and Weiss 1982; Mayhead and Jenkins 1992). The dichotomy in height and diameter growth responses is common in white pine; in a similar study, we observed that white pine showed compensatory height growth at medium clipping levels, but did not show compensatory diameter growth during the growing season immediately after clipping (Saunders and Puettmann 1999).

The response to herbivory in terms of biomass (overcompensation sensu Belsky 1986) has been investigated less frequently for woody plants. Our study supports an antagonistic plant–herbivore relationship, i.e., any level of herbivory will lead to reduced biomass growth and reduce total final biomass. Our results also support the hypothesis that compensatory height growth is, at least partially, a result of significant shift in biomass allocation from diameter growth and root growth within the plant. This agrees with Belsky's (1986) assertion that herbivory is a cost to the plant, and that regrowth to replace lost aboveground tissues will reduce below ground growth and deplete stored plant reserves (Mabry and Wayne 1997).

While all plant components (above and below ground biomass as well as root, stem, and leaf biomass growth) followed a similar trend, the absolute growth response among plant components was different resulting in a decreased shoot/root ratio for clipped seedlings, a trend also found for sitka spruce [*Picea sitchensis* (Bong.) Carr.] (Mayhead and Jenkins 1992) and non-woody plants (e.g., Welter and Steggal 1993). On the other hand, defoliation or disbudding of several annual and biennial species led to a shift in biomass allocation from roots to shoots (e.g., Mabry and Wayne 1997; Julien and Bourne 1986; Richards 1984). This trend was attributed

to reestablishment of leaf canopies and shoot/root balances (Richards 1984) or – in nutrient-limiting environments – to root mortality (Chapin and Slack 1979). In natural settings, other factors, like fertilization by the herbivores, may have resulted in the overcompensation in aboveground biomass of grass species (Hik and Jefferies 1990), even though the phenomenon also has been documented in experimental settings regardless of nutrient status (e.g., Wegener and Odasz 1997).

This study's response may be partially due to a size effect, as bigger plants usually have a higher shoot/root ratio (Johnson 1990). On the other hand, the influence of interspecific competition on biomass allocation within this study was consistent with the general trend that shoot/root ratios for trees increase in lower competitive environments (Wang et al. 1994; Mitchel and Arnott 1995).

Our study indicated that the question whether compensation is more likely under high or low competitive conditions (Strauss and Agrawal 1999) is too general and different competitive conditions need to be distinguished. Competition from overstory trees and understory vegetation appeared to affect seedlings differently. Increased overstory competition resulted in slower growth, but reduced the impacts of clipping, i.e., compensatory patterns in terms of total biomass growth shifted from under-compensation to exact compensation at low clipping intensities. Monthly weeding that removed woody perennials and herbaceous competitors increased growth significantly compared to controls, but did not influence the compensatory patterns. Results from this study suggest that seedlings in open, non-competitive environments are most affected by herbivory in absolute terms. Apparently, herbivory stress results in relatively smaller growth losses when plants are growing slowly due to competitive conditions. Edenius et al. (1993) and others concluded that overcompensation was not a specific adaptation to herbivory, but an indirect consequence to make up for lost competitive status (Belsky 1986; Edenius et al. 1993; Hjältén et al. 1993; McLaren 1996). Thus, compensatory growth may not be as advantageous, and therefore less pronounced, in less competitive environments. While this trend has been observed for a variety of other tree species (Hjältén et al. 1993; McLaren 1996), it does not suggest that seedlings in non-competitive environments can recover easily from herbivory losses, particularly when the intensity and frequency of browsing is high (McLaren 1996; Saunders and Puettmann 1999). This may possibly be due to the increasing necessity for apical dominance and maintaining a balanced shoot-root ratio in highly competitive, shady environments (McLaren 1996).

The compensatory height growth pattern may be explained by the competitive advantage of establishing apical dominance as quickly as possible (Aarson and Irwin 1991; Mutikainen and Walls 1995). A plant that concentrates its resources on increasing leader length would more likely over-top potential competitors and thus increase chances of long-term survival. On the other hand,

if a plant is not in danger of being over-topped, this response may not necessarily lead to better survival when other stresses affect plants. For example, if seedlings in a competitive environment use much of their reserves to compensate for lost foliage, they might exhibit an unbalanced shoot-root ratio and thus maybe more sensitive to future episodes of herbivory or drought periods (Hjältén et al. 1993; see also Messier et al. 1999).

Lastly, it is important to note that any response to herbivory may only be temporary. For example, by the second growing season following clipping, surviving trees had the same aboveground growth as control trees regardless of clipping intensity and competitive conditions (McLaren 1996; Saunders and Puettmann 1999), presumably because newly formed terminals had re-established apical control within the plant (Hjältén et al. 1993; Chamberlin and Aarssen 1996). Also, note that this study used hand clipping as treatment, rather than actual herbivore browsing. While growth effects of herbivore saliva have been documented in some greenhouse studies (e.g., Reardon et al. 1972), these effects could not confirmed in field studies (e.g., Reardon et al. 1974). In our study, we tried to minimize potential effects due to artificial clipping by choosing timing and distribution of clipped branches to match natural deer browsing patterns as closely as possible.

In conclusion, white pine does not appear to fully compensate (sensu Belsky 1986) for lost tissues after simulated browsing. While height growth stimulation occurs, it is limited to conditions when the intensity of simulated herbivory is light and if apical control is broken. Full compensation for lost biomass does not appear to occur in a natural setting, even if competition is precluded from the seedlings. As a result, simulated browsing and any subsequent overcompensation will almost always deplete stored plant reserves, reduce plant vigor, and increase the probability of plant mortality over time (Saunders and Puettmann 1999; Belsky 1986). The variation in compensatory response pattern related to competition from different vegetational components suggests that overcompensation may be an adaptation for competitive ability, rather than a response to herbivory per se (see also Hjältén et al. 1993).

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