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Author(s): Joäkim Hjalten, Kjell Danell, Lars Ericson

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EFFECTS OF SIMULATED HERBIVORY AND INTRASPECIFIC COMPETITION ON THE COMPENSATORY ABILITY OF BIRCHES¹

JOAKIM HJÄLTÉN,² KJELL DANELL

Department of Animal Ecology, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden

LARS ERICSON

Department of Ecological Botany, University of Umeå, 901 87 Umeå, Sweden

Abstract. To improve our knowledge regarding plant responses to herbivory we subjected juvenile birches (*Betula pubescens*) to different types of simulated herbivory, i.e., removal of the top (1 cm) of the main stem or defoliation (including removal of main stem top), and to different levels of intraspecific competition (i.e., three stand densities). Treatments were also repeated during the following year.

Birch responses to these treatments were measured as changes in plant height and dry mass. Defoliated plants showed reduced growth irrespective of the level of intraspecific competition. Topped plants in the low-density plots showed enhanced growth, i.e., overcompensation, whereas topped plants growing in the high- and medium-density plots were unaffected by the treatments.

Our results indicate that we should expect a continuum of plant responses to herbivory. Thus, there is little value in asking whether herbivory has a positive or negative effect on plant growth. Instead, emphasis should be placed on identifying conditions under which we would expect different responses.

Further, we suggest that overcompensation should not generally be considered as an adaptive response that has evolved as a consequence of natural selection due to herbivory, but rather as an indirect consequence of selection for competitive ability. Because apical dominance (assumed to be an adaptation to competition) restricts growth, the growth rate will increase if apical dominance is removed.

Key words: *Betula pubescens*; birch; browsing; compensatory growth; defoliation; herbivory; overcompensation; plant–animal interactions; plant competition; plant–plant interactions; Sweden.

INTRODUCTION

Although herbivores generally have a negative impact on their food plants (e.g., Harper 1977, Crawley 1983, Louda 1984, Edwards 1985), there are reports of plants responding to herbivory with increased growth, i.e., overcompensation (McNaughton 1976, 1979, Owen 1980, Cargill and Jeffries 1984). Between these extremes are reports of herbivores having no effect on their food plants (e.g., Karban and Courtney 1987). The question of whether herbivores can increase plant growth, and possibly even enhance plant fitness, has been intensely debated (e.g., Belsky 1986, 1987, McNaughton 1986, Crawley 1987). Recent studies suggest that an increase in plant growth following herbivory, at least in some cases, can also result in increased plant fitness (Paige and Whitham 1987, Maschinski and Whitham 1989).

It is also known that responses to damage vary, depending on prevailing abiotic and biotic conditions

(e.g., Jameson 1963, McNaughton 1986, Maschinski and Whitham 1989). However, it is less clear how specific growth conditions influence the ability of the plant to compensate for lost tissues. Belsky (1987) and Maschinski and Whitham (1989) suggest that plants are more likely to overcompensate when water and nutrients are abundant, whereas Hilbert et al. (1981) and Oosterheld and McNaughton (1991) predict that overcompensation should tend to occur when plants are under stress. Furthermore, the type of herbivory often determines the type of response. For example, winter browsing and summer defoliation can differ in their effects on the size and chemical composition of birch (*Betula* spp.) leaves (Bryant et al. 1991). The time, intensity, and frequency of herbivore attack are also important factors governing plant responses (e.g., Jameson 1963, Kulman 1971). We can therefore expect that a given plant species will show great variation in the type and magnitude of responses to injury caused by herbivores.

Moreover, plant taxa and life-forms differ in their response to herbivory. Most studies dealing with overcompensation have been conducted with grasses or herbs. Thus knowledge is limited regarding the ability of other plant groups, e.g., woody plants, to compensate

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² Present address: Department of Biological Sciences, Northern Arizona University, P.O. Box 5640, Flagstaff, Arizona 86011-5640 USA.

for tissue loss. Since woody plants grow relatively slowly, it has been suggested that their ability to compensate should be less than that of faster growing plant types (Whitham and Mopper 1985, Maschinski and Whitham 1989).

Different explanations for the phenomenon of overcompensation have been proposed. The first interpretation was that overcompensation had evolved as an adaptive response to herbivory (McNaughton 1986, Crawley 1987). By contrast, in a recent paper Aarssen and Irwin (1991) proposed that overcompensation is an indirect consequence of selection induced by competition. This latter view might improve our understanding of the compensatory growth of plants, and stresses the need for studies considering between-plant competition.

In this study we examined how juvenile woody plants, here represented by common birch (*Betula pubescens* Ehrh.), respond to two types of simulated herbivory after one and two treatments. We also investigated the effect of intraspecific plant competition on the responses to herbivory by growing birches at low, medium, and high densities. Our main questions were: (1) How do different types of herbivory influence plant growth? (2) How does repeated herbivory influence a plant's compensatory response? (3) How does intraspecific competition affect the responses of plants to herbivory?

METHODS

Plant material

Birch seeds were collected from one tree close to Skellefteå in coastal northern Sweden (64°55' N, 20°55' E) during the winter of 1987. In March 1988 the seeds were sown in a greenhouse on the University of Umeå campus (63°44' N, 20°18' E). After 1 mo the seedlings (5–10 cm in height) were planted in an outdoor experimental field situated in the vicinity of the greenhouse. All vegetation had been removed from the site prior to planting.

Experimental plots

The birch seedlings were planted in circular plots. To prevent interactions between roots of seedlings and other plants, plastic sheeting was inserted in the soil down to a depth of 25 cm around the perimeter of each plot. Twenty-four birch seedlings were planted in each plot at a spacing of 3, 5, or 10 cm, which resulted in densities of 940, 340, and 90 seedlings per m², respectively. Plot size differed accordingly, and was 18, 30, or 60 cm in diameter, respectively. These three density classes of birches are hereafter referred to as *H*, *M*, and *L* (high, medium, and low density, respectively). The experimental field was divided into 8 blocks, each consisting of 12 plots, with 4 replicates of each density class per block.

Treatments

The seedlings were allowed to grow without other treatments than the differences in plant density until late October 1988, when the first simulated herbivory treatment was made. The top 1 cm of the main stem was removed from all birches in one plot per density class and block. In early June 1989 (after leaf-burst) birches in another treatment group (also consisting of one plot per density class and block) were both defoliated and topped, i.e., all leaves were removed together with the top 1 cm of the young, growing shoot tip. These two treatment groups are hereafter referred to as *T* (topped) and *D* (defoliated) birches. The treatments were repeated on the same birches during early November 1989 (*T* birches) and early June 1990 (*D* birches). The remaining two plots per density class and block served as controls (referred to as *C* birches).

The damage to *T* birches (topping) is meant to simulate minor damage caused by the winter browsing of hare (*Lepus* spp.) or moose (*Alces alces* (L.)). The damage to *D* birches (defoliation) is meant to simulate damage caused by leaf-eating herbivores, including insects as well as leaf-stripping moose or reindeer (*Rangifer tarandus* L.). Birches, being an important food source for both hare (e.g., Lindlöf et al. 1974, Pulliainen and Tunkkari 1987) and moose (e.g., Cederlund et al. 1980) during winter, are often found to have one or more shoots bitten off. Birch leaves are eaten by many invertebrate and vertebrate herbivores during summer (e.g., Haukioja and Koponen 1975, Cederlund et al. 1980), resulting in partial or total defoliation. Although mechanical damage does not always have the same effect on plants as natural herbivory (Baldwin 1990), it does make it possible to control both the timing and type of damage. Since the birches were topped during their dormant period in winter, it seems likely to assume that the way the cut was made, i.e., by hares or scissors, should have little influence on the seedling response.

During the course of the experiment we removed weeds and grasses appearing in the plots. Moreover, the birches were occasionally watered during the driest part of the summer.

Measurements of birch height and biomass

In October 1988 (before the treatment of *T* birches, but after leaf-fall and cessation of growth) we measured the height of six randomly selected birches in each plot and noted whether they were still alive. These six birches were selected from among the 12 birches growing in the center of the plot in order to exclude birches that had been exposed to slightly different growing conditions around the outermost part of the plot. The measurements of height and status were repeated in October 1989, and after the last scoring, in October 1990, we harvested the six selected birches in each plot to determine the dry mass of their below- and above-

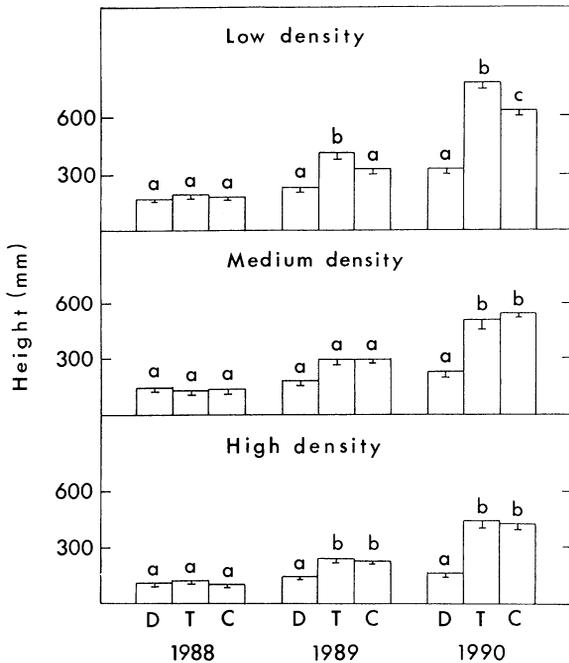


FIG. 1. Height of birches before treatment (1988) and after one (1989) and two (1990) growing seasons and herbivory treatments (D = defoliation, T = topping, and C = control) at three plant densities. Values represented by histogram bars with different letters are statistically significantly different ($P < .05$, Tukey test). Narrow vertical bars show 1 SE for eight replicates.

ground tissues. Biomass data are given as grams of dry mass after drying to constant mass at 40°C.

Definitions

The ability of the plant to compensate for tissue loss, as defined here, can be divided into three response types. "Overcompensation" was considered to have occurred when a damaged plant produced more biomass than undamaged conspecifics. "Equal compensation" and "undercompensation" were considered to have occurred when damaged plants produced equal or less biomass, respectively, compared with undamaged plants. In some studies the term "partial compensation" has been used (e.g., Belsky 1986) to describe damaged plants that produce more new biomass than undamaged ones, but not enough to fully compensate for the tissue loss.

Statistical analysis

Mean values of height and biomass for the six selected birches within each plot were used in the statistical analyses. There were two control plots per density treatment in each block, but for the statistical analysis a mean value of the duplicates was used.

To assess the degree to which treated plants compensated for tissue loss during different years, we calculated the relative height growth per year of birches in the different treatments. Relative height growth was

TABLE 1. Effect of block, treatment, and density on height (1988 to 1990) and shoot and root mass (1990) of juvenile birches.

Source of variation	ss	df	F	P
Height				
1988 (Pretreatment)				
Block	27858.890	7	3.497	.004
Treatment	2607.926	2	1.146	.326
Density	45381.009	2	19.936	.000
Treat × Density	4453.287	4	0.978	.427
Error	62598.703	55		
1989				
Block	43859.368	7	1.510	.183
Treatment	132945.431	2	16.020	.000
Density	183002.441	2	22.051	.000
Treat × Density	20528.375	4	1.237	.306
Error	228220.532	55		
1990				
Block	95825.611	7	1.929	.081
Treatment	848527.798	2	60.125	.000
Density	657901.378	2	46.602	.000
Treat × Density	140026.267	4	4.959	.002
Error	388228.603	55		
Shoot mass				
1990				
Block	11.215	7	1.093	.381
Treatment	144.484	2	49.285	.000
Density	221.534	2	75.562	.000
Treat × Density	67.023	4	11.431	.000
Error	80.618	55		
Root mass				
1990				
Block	2.481	7	1.004	.439
Treatment	29.569	2	41.869	.000
Density	89.236	2	126.368	.000
Treat × Density	12.750	4	9.028	.000
Error	19.419	55		

calculated as the ratio obtained by dividing the height growth of treated plants in a specific year by the height growth of controls the same year.

A randomized-block ANOVA design (no interaction term between block and treatments) was used to evaluate the effect of density and treatment on plant growth characters. For within-year, pairwise comparisons we used Tukey tests. For comparisons of growth characters between years, paired-sample *t* tests were used. The data fulfilled the requirement of homoscedasticity but deviated slightly from normality. However, minor deviations from normality will not affect the validity of the analysis (Zar 1984). Due to an accident with a lawn mower, three plots were excluded from the analysis.

RESULTS

Effects of simulated topping and defoliation

At the first measurement of plant height in October 1988 (before the birches had been subjected to any simulated herbivory) no difference in height was found between plots that later belonged to different herbivory-treatment groups (Table 1; Fig. 1).

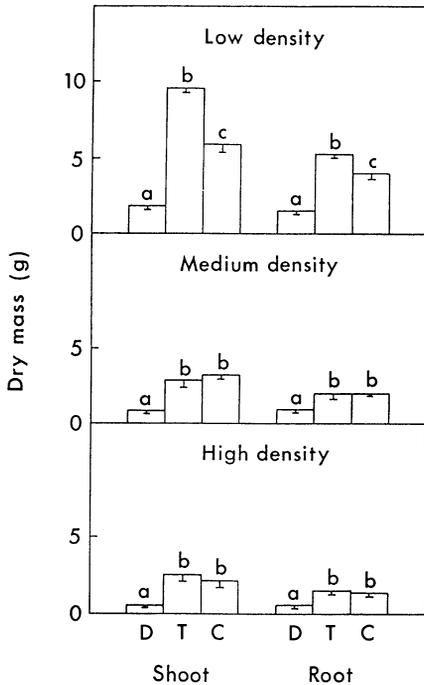


FIG. 2. Shoot and root biomass of birches in 1990 after two growing seasons, and simulated herbivory treatments (D = defoliation, T = topping, and C = control) at three plant densities. Values represented by histogram bars with different letters are statistically significantly different ($P < .05$, Tukey test). Narrow vertical bars show 1 SE for eight replicates.

Defoliated birches responded to treatment by developing many new, short shoots with many foliar buds. Topped birches did not show an increase in branching. Instead, topping resulted in an increase in growth in the uppermost shoots of the plant for a short period ($\approx 2-3$ wk, until the top shoot regained its dominance), resulting in an enlargement of the upper part of the plant (J. Hjäältén, *personal observation*).

One growth period (growing season) after the first simulated herbivory treatments (October 1989), significant differences in height were found among treatments (Table 1). The D (defoliated) birches growing at the H (high) density were significantly shorter than T (topped) or C (control) birches at corresponding density (Tukey test, $P < .001$; Fig. 1). Furthermore, the T birches growing at the L (low) density were significantly taller than D or C birches at the corresponding density (Tukey test, $P < .05$). In the other density classes, T birches did not differ significantly in height from C birches.

After two growing seasons and two herbivory treatments (October 1990) there were even greater differences in height between treatment groups (Table 1; Fig. 1). Regardless of density, D birches were shorter than C and T birches. T birches at L densities were still taller than C birches at the same density (Tukey test, $P < .01$).

There were also differences in shoot and root bio-

mass between the birch groups in October 1990 (Table 1). At all densities the shoot and root biomass were lower in the D birches than in C and T birches (Tukey test, $P < .05$; Fig. 2). T birches had more root and shoot biomass than C birches at the L density (Tukey test, $P < .01$). However, at the two higher densities no difference in root or shoot biomass could be detected between T and C birches (Tukey test, $P > .05$).

None of the plants died during the experimental period.

Effects of single and repeated herbivory

To test whether the compensatory ability of birches decreased when damaged a second time we compared the relative height growth in 1989 and 1990. T birches compensated for height loss to approximately the same degree both years (paired *t* test, $P > .05$; Fig. 3A). By contrast, D birches compensated better for tissue loss during the first growing season (1989) than during the second one (1990) (paired *t* test, $P = .007$; Fig. 3B).

Effects of intraspecific competition

An effect of plant density on height growth had already become apparent by the first height measurement in 1988 (after one growing season, but before the simulated herbivory treatments; Table 1). The C birches growing at L density were higher than those growing

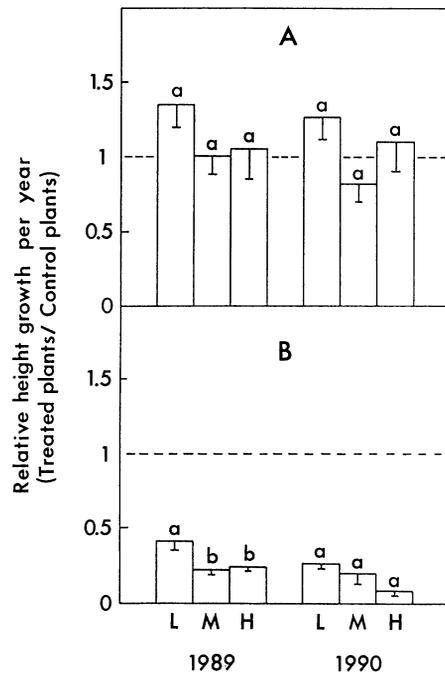


FIG. 3. Relative height growth per year (standardized to controls) of birches subjected to (A) topping and (B) defoliation after one (1989) and two (1990) growing seasons and treatments at low (L), medium (M), and high (H) densities. Values represented by histogram bars with different letters are statistically significantly different ($P < .05$, Tukey test). Narrow vertical bars show 1 SE for eight replicates.

at *H* density (Tukey test, $P < .01$; Fig. 1). These differences increased during the growing season of 1989 (Table 1; Fig. 1), and after the 1990 growing season the height of the *C* birches differed significantly among all density treatments (Tukey test, $P < .05$), with birches tallest in the low-density plots and lowest in the high-density plots (Fig. 1). In addition, for the *C* birches the shoot and root masses were higher in the *L*-density plots than in the *M*- and *H*-density plots (Tukey test, $P < .01$; Fig. 2).

In 1990, but not in 1988 and 1989, there was a significant interaction between treatment and density (Table 1), showing that the effect of the herbivore treatment changes with density. To assess the effects of intraspecific plant competition on the response to simulated herbivory, we compared the relative height growth (standardized to controls) of birches in different treatments. During the first growing season after the treatment (1989), the *D* birches growing at the *L* density were better able to compensate for biomass loss than were *D* birches growing at *M* and *H* densities (one-way ANOVA, $F = 8.30$, $P = .03$; Tukey test, $P < .01$; Fig. 3B). A similar, but not statistically significant ($F = 2.48$, $P = .11$), trend was apparent for *D* birches after the second growing season (1990) and for *T* birches in both 1989 and 1990 (one-way ANOVA, $F = 1.06$, $P = .365$ and $F = 1.83$, $P = .186$, respectively; Fig. 3A)—thus indicating that the herbivore effect increased with density.

DISCUSSION

Our results support the view that there is a continuum in plant responses to herbivory (Maschinski and Whitham 1989, Oosterheld and McNaughton 1991). From such a perspective, it is no longer meaningful to ask whether herbivory has a negative or positive effect on plant growth. Instead, emphasis should be placed on identifying circumstances under which we would expect one of the possible responses.

Long-lived, slow-growing plants have a lower ability to regenerate lost tissue compared with short-lived, fast-growing ones (Whitham and Mopper 1985, Garnier 1991). It has been suggested that biennial, short-lived, and fast-growing plant species are those most likely to show strong compensatory responses to herbivory (Maschinski and Whitham 1989). In accordance with this view, overcompensation had, prior to the present study, only been reported for fast-growing grasses and herbs (McNaughton 1986, Paige and Whitham 1987). Birches (within the browsing-height interval), with 25% or more of their current annual shoots removed, produced less shoot biomass than unbrowsed ones (Bergström and Danell 1987, Danell and Bergström 1989). However, in certain situations the shoot production of browsing-tolerant species does not differ from that of unbrowsed conspecifics (Aldous 1952, Krefting et al. 1966, Wolff 1978). Moreover, our results (*T* [topped] birches) indicate that if apical dominance

is broken and the damage degree is sufficiently low, even deciduous tree species can overcompensate.

D (defoliated) birches were not able to maintain biomass production to the same degree as the *T* birches. Apical dominance was broken in both *D* and *T* birches, which is known to greatly enhance compensatory growth in plants (Maschinski and Whitham 1989, references in Aarssen and Irwin 1991). The most likely explanation for this difference is that the defoliation treatment removed more plant tissue than the topping treatment did. Moreover, these birches were defoliated in early June, by which time one third of the growing season had passed, reducing the time left for recovery. Thus, the capability to recover from herbivory depends primarily on the type of damage and when it occurs during the season (Jameson 1963, Maschinski and Whitham 1989).

Even if the poorer compensation by *D* birches after the second treatment could, at least partly, have been due to different climatic conditions the second year, repeated defoliation seemingly had a more serious impact than a single defoliation event. Belsky (1986) suggested that damage initially is a cost to the plant, and regrowth meant to replace removed tissue depletes stored reserves. However, no indications of root mass depletion was found for the overcompensating *T* birches, and these birches overcompensated even after they had been damaged a second time. Thus, even if damage is repeated, plants can nevertheless compensate (or overcompensate) for lost tissue without depleting stored reserves if the degree of damage is very low, apical dominance is removed, and the periods between damage events are relatively long.

Competition reduced height and biomass to the same degree as did the most severe type of simulated herbivory (defoliation). Furthermore, the compensatory ability of the birches decreased with density. This indicates that equal compensation and overcompensation in our experiment was more likely to occur under low-stress conditions (e.g., Belsky 1986, Maschinski and Whitham 1989) than under conditions of severe stress, as proposed by Hilbert et al. (1981).

Overcompensation has long been considered to be an adaptive response that evolved as a consequence of natural selection due to herbivory (McNaughton 1986, Crawley 1987). Using this explanation, it is, however, difficult to find situations where plants should have evolved to depend on herbivory to achieve their greatest fitness (Crawley 1987, Paige and Whitham 1987). van der Meijden (1990) defined some of the conditions required: herbivory should be restricted to a limited period in time; the probability of herbivore attack should be high; and, most importantly, it should not be possible to predict the timing of herbivory based on environmental cues.

It is doubtful that birch has evolved in an environment where herbivory is restricted to a limited period of time, nor would it appear that herbivory on birches

should be unpredictable based on environmental cues. Daylength often stimulates plants to alter their allocation schemes (Kozlowski 1971), and could act as an environmental cue for predicting herbivory. At low latitudes, where overcompensation has been reported in plants (Paige and Whitham 1987), daily differences in daylength might be too small to trigger growth (van der Meijden 1990). However, in the northern part of Europe daily differences in photoperiod are large, and this factor, together with temperature, sets plant allocation schemes (similarly for *Betula pubescens*) (Kozlowski 1971). Thus, it seems as though the conditions required for overcompensation to evolve as a response to herbivory in birches are not fulfilled. Aarssen and Irwin (1991) proposed that apical dominance in the plants, being an adaptation to competition, also invokes a cost for the plant, since it restrains the growth of the plant. The release from apical dominance will therefore result in enhanced plant growth. This view of overcompensation might better explain the results from our study. It seems unlikely that a long-lived, slow-growing tree such as birch would evolve an overcompensatory response and depend on herbivory to achieve its highest fitness. Furthermore, if birches show this type of response it is likely that overcompensatory responses could be found in other deciduous trees (and other plants), for which the conditions required for overcompensation to evolve as a consequence of herbivory may not be fulfilled either (further investigations are needed in this regard). We therefore believe that Aarssen and Irwin (1991) offer a more plausible explanation for the results in our experiment, and possibly a more universal explanation for this growth response in plants, even though there may be situations in which overcompensation could evolve as a response to herbivory (e.g., van der Meijden 1990).

However—and this should be stressed—if we accept that overcompensation is not an adaptation to herbivory, but rather reflects an inadvertent growth release of no adaptive value, there is no longer any reason to assume that overcompensation will always result in increased fitness. In fact, because overcompensation reduces stored reserves (Belsky 1986) this response might even, during some circumstances, turn out to be fatal to the plant.

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