Compensatory growth of three herbaceous perennial species: the effects of clipping and nutrient availability

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Abstract: The continuum of responses model (CRM) and the growth rate model (GRM) make conflicting predictions about the effects of soil nutrient availability on the resilience of plants to herbivory. A factorial experiment was conducted in the understory of the boreal forest to examine the effects of fertilization and simulated herbivory on the rate and amount of regrowth of three herbaceous perennial species (Achillea millefolium L., Festuca altaica Trin., and Mertensia paniculata (Aiton) G. Don.). As clipping intensity increases various measures of plant performance decrease. Fertilization reduces the ability of clipped plants to compensate for biomass loss regardless of species and growth measure. Under natural soil fertility levels in this study, M. paniculata is more likely to compensate for leaf loss than A. millefolium and F. altaica. Contrary to the findings of previous field studies, the compensatory responses of the three species studied were most consistent with the predictions of the GRM. Plants in our study sites grow in nutrient-poor soils, whereas the majority of compensatory studies have been carried out on herbaceous or woody plants in temperate regions. Resources are generally more abundant in temperate zones than in boreal forest zones, and the GRM may be a better predictor of compensatory ability of plants growing in naturally nutrient-deficient soils.

Key words: herbivory, regrowth, fertility level, clipping intensity, compensation.

Introduction

The ability of a plant to regrow after an episode of herbivory is an important aspect of its ecology and provides a tolerance strategy against herbivory. The amount of regrowth depends on environmental conditions such as soil nutrient availability (Verkaar et al. 1986; Chapin and McNaughton 1989; Hik and Jefferies 1990), defoliation intensity (McNaughton 1979; Painter and Detling 1981), the presence of competitors (Lee and Bazzaz 1980; Crawley 1990; Weiner 1993), and on internal plant traits such as growth rate (Hilbert et al. 1981; Whitham et al. 1991). Several models predict the compensatory responses of plants under a range of conditions. Two of these models, the continuum of responses model (CRM) and the growth rate model (GRM), consider soil nutrient availability, timing and intensity of de-
folliation, and plant growth rates, but they sometimes make conflicting predictions about the range of plant compensatory responses to herbivory as indicated below.

The CRM predicts that a plant is more likely to compensate for tissue loss when soil nutrient availability is high and when the plant is defoliated earlier in the growing season (Maschinski and Whitham 1989). Soil nutrients facilitate the (re)growth of plant tissues, therefore plants growing in nutrient-rich habitats potentially have an adequate supply for the replacement of lost tissues. In contrast, plants growing in nutrient-limited soils will have less nutrients available for regrowth. It has been suggested that if plants are primarily dependent on external nutrient sources, then the later in the season that a herbivory event occurs, the less likely a plant will compensate because there is limited time to recover before the end of the growing season (Crawley 1983; Oesterheld and McNaughton 1991).

The GRM predicts that a lightly defoliated plant, growing in nutrient-poor soils, with competitors, is more likely to compensate for tissue loss (Hilbert et al. 1981). Plants experience an initial increase in relative growth rate (RGR) of leaf tissue following defoliation. Plants with low relative growth rates at the time of defoliation require only small increases in RGR to compensate for lost tissue. In high-nutrient, low-competition environments, plants will be growing at rates closer to their maximum potential RGR. Defoliated plants will require large increases in growth rate to compensate. A nondefoliated plant growing in the same soil will be growing so rapidly that the defoliated plant cannot easily achieve a comparable final size.

The CRM makes no predictions based on the intensity of defoliation, but the GRM predicts that a heavily defoliated plant is less likely to compensate for tissue loss than a lightly defoliated plant. Heavily defoliated individuals require a larger increase in RGR to replace lost tissues and achieve a final size comparable to undefoliated controls.

The applicability of these models under natural conditions requires investigations of plant growth responses. Only a few studies have attempted to investigate the interactive effects of environmental and internal factors on plant regrowth in the field and the evidence is conflicting. Even fewer have considered the compensatory responses of more than one species at a time (but see Alward and Joern 1993; Zellmer et al. 1993). The present study attempts to test some of the conflicting predictions of the two models by quantifying regrowth in response to different intensities of clipping (as a surrogate for herbivory) by three herbaceous plant species, Achillea millefolium var. borealis, Festuca altaica, and Mertensia paniculata, growing under different nutrient regimes. The three species are commonly eaten by snowshoe hares (Seccombe-Hett 1999).

A factorial experiment was conducted in the field to examine the effects of species, fertilization, and clipping on the rate of (re)growth and the amount of (re)growth of individual plants. Plants were collected from areas with either high soil fertility (fertilized annually with N, P, K for five of the previous 9 years) or low soil fertility (no history of fertilization), planted in a common garden in the field and subjected to one of three possible simulated herbivory events (no clipping, 50% leaf loss and 100% leaf loss) and one of two fertilizing treatments (no fertilizer and a high N-P-K fertilizer addition). Thus, there were two fertilization treatments in the design – fertilization history, and fertilizer application during the experiment referred to as short-term fertilization.

Materials and methods

Study area
The study was conducted near Kluane Lake, Yukon Territory, Canada (61°02'N 138°22'W). The climate is classified as subarctic, continental and is characterized by long, cold winters and short, dry summers (Wahl et al. 1987). The ground is snow-covered from mid-October to mid-April, resulting in a short growing season of about 100 days. The boreal forest vegetation is dominated by white spruce (Picea glauca Voss), interspersed with stands of trembling aspen (Populus tremuloides Michx.) and balsam poplar (Populus balsamifera L.). Open areas of shrub habitat contain dwarf birch (Betula glandulosa Michx.), grey willow (Salix glauca L.), and soapberry (Shepherdia canadensis (L.) Nutt.). Herbaceous understory plants include yarrow (Achillea millefolium L. var. borealis (Bong.) Farwell), anemone (Anemone parviflora Michx.), fescue (Festuca altaica Trin.), Arctic lupine (Lupinus arcticus S. Wats.), and bluebells (Mertensia paniculata (Aiton) G. Don.).

Soil nutrients, especially nitrogen, are often limiting to the productivity of boreal forest vegetation (Bonacci and Shugart 1989; John and Turkington 1995; Turkington et al. 1998). Low soil temperatures and low annual precipitation combine with the acidic nature of spruce leaf litter, to limit decomposition. As a result mineral nutrients remain unavailable for plant use (Dymes et al. 1986).

Study species
The plant species selected for this study were Achillea millefolium, Festuca altaica, and Mertensia paniculata. Each occurs in the understory and makes up a large proportion of the summer diet of the snowshoe hare (Lepus americanus Erxleben) diet (Wolff 1978; Seccombe-Hett 1999) which is the dominant herbivore in this system (Krebs et al. 1992). Where hare population densities are high, large amounts of aboveground biomass are consumed.

Experimental design and procedure
The experiment was a four factor split-plot design, with 12 replicate plots of 36 experimental units per treatment combination (three species × two long-term fertilizations [history] × three clipping intensities × two short-term fertilizations). Each plot was 2.5 × 2 m, protected by a 1-m high chicken wire fence (2-cm gauge) to reduce herbivory, and cleared of existing aboveground vegetation by hand to eliminate potential effects of competition. To ensure that the fertilizer applications affected only target plants, each plot was divided into two subplots (fertilized and unfertilized), separated by a 50-cm corridor. The placement of the remaining 18 treatment combinations (three species × two long-term fertilizations [history] × three clipping intensities) was randomly assigned within each half. To ensure no interactions between transplants in each half plot, they were planted approximately 30 cm apart.

Between May 21 and May 27, 1995, approximately 2 weeks after snowmelt, individual plants were collected from four sites (A, B, C, and D) representing the two long-term fertilization treatments. Site A had received fertilizer for 5 of the previous 9 years. For logistic reasons, annual application rates were not always consistent, but the standard was 17.5 g N m⁻² (as NH₄NO₃), 5 g P m⁻² (as H₃PO₄), and 2.5 g K m⁻² (as K₂O). In contrast, plants collected from sites B, C, and D were growing under naturally low soil nutrient conditions with no added fertilizer. To minimize initial size differences for A. millefolium and M. paniculata, individual ramets were selected with three to five leaves and a visible, central developing leaf. For F. altaica, plants with 10–15 stems (tillers) and a
maximum height of 15–20 cm were selected. Plants with obvious signs of flowering or previous herbivory were not collected. To minimize initial size differences between belowground components of each species, all plants were dug up with an intact soil plug of approximately 4.5 cm in diameter and 7 cm deep. Collected plants were transplanted into "uniform garden" plots at site B. The plots were selected because all three species occurred there naturally, and conditions of tree cover, soil moisture, and vegetation composition between plots were visually similar and likely provided similar growing conditions for all experimental units. Dead transplants were replaced until June 4, 1995. Regrowth of surrounding vegetation was removed from the plots every week.

From May 31, plants were given 30 days to establish and grow, and then clipping treatments were imposed on June 30. One third of transplants had 100% of their leaf area removed, one third had 50% removed, and the remaining one third were not clipped. Leaves were clipped with scissors at the base of the petiole, simulating the natural pattern of snowshoe hare grazing for _A. millefolium_ and _M. paniculata_ plants. Tillers of _F. altaica_ were clipped to 2 cm above ground level. During the 45-day period following clipping (June 1–July 15), half of all plants received the fertilization treatment, which was a weekly application of water-soluble N–P–K fertilizer (20:20:20) applied at a rate of 2 g 250 mL⁻¹ plant⁻¹. The remaining half received a weekly application of 250 mL of water with no fertilizer. Fifteen days after clipping, the length (L) and width (W) of all leaves were measured and used to estimate leaf areas, as described below. Forty-five days after clipping, on July 15, all plants were carefully removed using a trowel. Plant material was separated into aboveground and belowground components, air dried to constant weight, and weighed.

The product of _L_ and _W_ was used to estimate the leaf area of _F. altaica_; _W_ was set at an average width of 0.2 cm (n = 20). Because of the shape of the leaves of _M. paniculata_ and _A. millefolium_, leaf area could not be estimated using (_L_ × _W)_ alone. For both species, at final harvest, a leaf area meter was used to measure the area of a subsample of the experimental leaves (n = 35 and _n_ = 51, respectively). To determine the best predictor of leaf area for each species, area was regressed against three leaf-size variables: _L_, _W_, and (_L_ × _W_). Leaf length explained the greatest amount of variation in area for _M. paniculata_ leaves (R² = 0.82, _p_ < 0.001), and (_L_ × _W_) was the best predictor of leaf area for _A. millefolium_ (R² = 0.85, _p_ < 0.001). These values are used in eqs. 2, 3, and 4 below.

To determine the effect of experimental treatments on plant performance, the following dependent variables were measured for each expanse:

(1) Relative growth rate (RGR) of leaf area (cm²·cm⁻²·day⁻¹) plant⁻¹) was estimated over the first 15 days of postclipping growth, when plants were most likely to experience the highest growth rate increases (Hilbert et al. 1981). RGR was calculated as follows:

\[
RGR = (\ln L_{A_{15}} - \ln L_{A_{1}})/(D_{A_{15}} - D_{A_{1}})
\]

where _L_A_ was total leaf area per plant immediately after clipping and _L_A_{15} was the total leaf area per plant 15 days later. The final leaf areas of _F. altaica_, _M. paniculata_, and _A. millefolium_ were calculated as follows:

(2) final leaf area (cm²) of _F. altaica_ = \(\Sigma(4.16 \times L - 9.18)\)

(3) final leaf area (cm²) of _M. paniculata_ = \(\Sigma(0.25 \times (L \times W) + 0.442)\)

(4) final leaf area (cm²) of _A. millefolium_ = \(\Sigma(0.25 \times (L \times W) + 0.442)\)

(5) Postclipping growth of leaf area (cm²) per plant.

(6) Total biomass (g) at the end of the experiment.

(7) Vegetative reproduction (no. of ramets or tillers) at the end of the growing season.

Statistical analysis

For each of the variables, a four-way ANOVA was used to test for main effects and for interactions of species, fertilization history, clipping intensity, and fertilizer addition. The use of a split-plot design imposed restrictions on randomization of the fertilization treatment. Therefore, analysis of this treatment effect used the mean square error of the block x fertilization term and its corresponding degrees of freedom to calculate the F-ratio denominator. Prior to analysis, data were tested for normality and homogeneity of variances. Proportional data for postclipping growth, final leaf area, aboveground and total biomass were log(x + 1) transformed to reduce heteroscedasticity. Vegetative reproduction data were log transformed. Data were analyzed using the general linear models procedure in SAS (SAS Institute Inc. 1988), and the Bonferroni adjustment was applied. Significance testing (_p_ < 0.05) used type III sum of squares. Orthogonal contrasts were used to compare the combined effects of selected treatment means (Little and Hills 1978).

Results

Relative growth rate (RGR)

The relative growth rate of leaf area was greater for clipped plants than for unclipped plants (Table 1). Planned contrasts (df always = 1) of clipping means, showed that 100% leaf loss increased RGR significantly more than the 50% leaf loss treatment (_F_ = 1403.76, _p_ = 0.0001) which in turn was greater than 0% leaf loss (_F_ = 20.66, _p_ = 0.0001). Fertilization caused an increase in RGR, but the difference in RGR between plants with 0 and 100% leaf loss was significantly greater for unfertilized plants than for fertilized plants (_F_ = 8.22, _p_ = 0.0044) (Figs. 1A, 1B, and 1C). This increase was greater for _M. paniculata_ than for either _F. altaica_ (_F_ = 6.66, _p_ = 0.0103) or _A. millefolium_ (_F_ = 8.37, _p_ = 0.0041).

Fertilization history had minimal effects on RGR (Figs. 1D, 1E, and 1F) with or without clipping. However, _A. millefolium_ from the fertilized sites had a significant increase in RGR when clipped compared with the unclipped plants.

The increase in RGR caused by fertilization was significantly greater for plants without a fertilization history (Figs. 1G, 1H, and 1I). The magnitude of this difference was significantly greater for _A. millefolium_ than for _M. paniculata_ (_F_ = 8.65, _p_ = 0.0035), which accounts for the significant interaction of fertilization x fertilization history x species, in the ANOVA (Table 1), and these were not different from _F. altaica_ (_F_ = 2.21, _p_ = 0.1382).

Postclipping growth

The change in postclipping growth caused by 100% leaf loss was significantly greater for fertilized than for unfertilized plants (_F_ = 19.92, _p_ = 0.0001). The 100% leaf loss reduced postclipping growth for all fertilized plants (_F_ = 8.44, _p_ = 0.0039), caused a slight reduction in unfertilized _A. millefolium_ and _F. altaica_ (Figs. 2A and 2B), and an increase

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Table 1. The F-probabilities (Pr > F) for seven dependent variables using ANOVA and Bonferroni adjustment.

<table>
<thead>
<tr>
<th>Source</th>
<th>Relative growth rate of leaves</th>
<th>Postclipping growth of leaves</th>
<th>Final leaf area</th>
<th>Aboveground biomass</th>
<th>Belowground biomass</th>
<th>Total biomass</th>
<th>Vegetative reproduc.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block (B)</td>
<td>0.0785</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.3396</td>
<td>0.0099</td>
<td>0.0001</td>
</tr>
<tr>
<td>B × F*</td>
<td>0.1675</td>
<td>0.0525</td>
<td>0.4037</td>
<td>0.0089</td>
<td>0.5801</td>
<td>0.4575</td>
<td>0.0076</td>
</tr>
<tr>
<td>Clipping (C)</td>
<td>0.0001</td>
<td>0.3752</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0119</td>
<td>0.0001</td>
<td>0.0001</td>
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<tr>
<td>Fertilization (F)*</td>
<td>0.0001</td>
<td>0.0055</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.2433</td>
<td>0.0021</td>
<td>0.0001</td>
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<tr>
<td>History (H)</td>
<td>0.5976</td>
<td>0.0001</td>
<td>0.0003</td>
<td>0.0001</td>
<td>0.0841</td>
<td>0.0001</td>
<td>0.0001</td>
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<tr>
<td>Species (S)</td>
<td>0.0001</td>
<td>0.4077</td>
<td>0.0001</td>
<td>0.2492</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
</tr>
<tr>
<td>C × F</td>
<td>0.0008</td>
<td>0.2531</td>
<td>0.0003</td>
<td>0.0001</td>
<td>0.2285</td>
<td>0.0161</td>
<td>0.1038</td>
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<tr>
<td>C × H</td>
<td>0.0016</td>
<td>0.3511</td>
<td>0.7030</td>
<td>0.0499</td>
<td>0.8394</td>
<td>0.5679</td>
<td>0.0733</td>
</tr>
<tr>
<td>C × S</td>
<td>0.0001</td>
<td>0.7972</td>
<td>0.0166</td>
<td>0.1133</td>
<td>0.2783</td>
<td>0.1015</td>
<td>0.0232</td>
</tr>
<tr>
<td>F × H</td>
<td>0.0011</td>
<td>0.9766</td>
<td>0.2392</td>
<td>0.0077</td>
<td>0.1153</td>
<td>0.8761</td>
<td>0.0309</td>
</tr>
<tr>
<td>F × S</td>
<td>0.0005</td>
<td>0.2312</td>
<td>0.0001</td>
<td>0.1000</td>
<td>0.0085</td>
<td>0.0040</td>
<td>0.0001</td>
</tr>
<tr>
<td>H × S</td>
<td>0.0425</td>
<td>0.1718</td>
<td>0.0002</td>
<td>0.0036</td>
<td>0.0744</td>
<td>0.9086</td>
<td>0.0060</td>
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<tr>
<td>C × F × H</td>
<td>0.9334</td>
<td>0.5995</td>
<td>0.5973</td>
<td>0.3380</td>
<td>0.1054</td>
<td>0.0818</td>
<td>0.9536</td>
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<tr>
<td>C × F × S</td>
<td>0.0001</td>
<td>0.6293</td>
<td>0.2948</td>
<td>0.0916</td>
<td>0.7546</td>
<td>0.8279</td>
<td>0.4567</td>
</tr>
<tr>
<td>C × H × S</td>
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<td>0.1536</td>
<td>0.9306</td>
<td>0.2769</td>
<td>0.9496</td>
<td>0.7121</td>
<td>0.2755</td>
</tr>
<tr>
<td>F × H × S</td>
<td>0.0059</td>
<td>0.2578</td>
<td>0.4379</td>
<td>0.0844</td>
<td>0.1599</td>
<td>0.0489</td>
<td>0.7602</td>
</tr>
<tr>
<td>C × F × H × S</td>
<td>0.2036</td>
<td>0.2065</td>
<td>0.9497</td>
<td>0.5289</td>
<td>0.0366</td>
<td>0.4617</td>
<td>0.3513</td>
</tr>
</tbody>
</table>

Note: Bold values indicate significant effects (p < 0.05).
*Because of restrictions in randomization imposed by the split-plot design, tests of hypotheses for the fertilization treatment use the mean square for B × F as an error term.

in *M. paniculata* (Fig. 2C). The difference in postclipping growth between 0 and 100% leaf loss, in fertilized compared with unfertilized plots, was significantly greater for *M. paniculata* than for *A. millefolium* (F = 4.32, p = 0.0385). The response of *F. altaica* did not differ significantly from the responses of either *A. millefolium* (F = 1.03, p = 0.3112) or *M. paniculata* (F = 1.05, p = 0.3052).

Fertilization history did not significantly interact with clipping, but increased postclipping growth for each of three species (Fig. 3; Table 1). This increase was significantly greater for *M. paniculata* than for *A. millefolium* (F = 12.12, p = 0.0006) and for *F. altaica* (F = 10.69, p = 0.0016).

**Final leaf area**

The response of final leaf area to clipping was similar to the response of postclipping growth (Table 1). Contingent on the interaction of fertilization and species, the difference in final leaf area between 0% and 100% leaf loss was significantly greater for fertilized than for unfertilized plants (F = 19.92, p = 0.0001). This difference was significantly greater for *M. paniculata* than for *A. millefolium* (F = 4.51, p = 0.0344). The response of *F. altaica* did not differ significantly from the responses of either *A. millefolium* (F = 0.58, p = 0.4476) or *M. paniculata* (F = 1.74, p = 0.1883).

Fertilization history did not significantly interact with the clipping treatments but did so with species. Fertilization history caused an increase in final leaf area that was significantly greater for *M. paniculata* than for *A. millefolium* (F = 11.31, p = 0.0009) and resulted in a decrease in leaf area for *F. altaica*.

**Aboveground biomass**

Similar results were obtained for aboveground biomass, belowground biomass, and total biomass so only aboveground biomass is reported here.

Fertilization increased aboveground biomass for all treatment combinations (Fig. 4). For *A. millefolium* and *M. paniculata*, the increase in biomass was greater for plants that had a history of fertilizer (Figs. 4A and 4C). The response of *F. altaica* differed significantly from the response of the dicots (F = 4.87, p = 0.0279). The biomass responses of *A. millefolium* and *M. paniculata* were not different (F = 0.15, p = 0.6967).

For each species, the difference in aboveground biomass between 0% and 100% leaf loss was significantly greater for both fertilized (F = 26.7, p = 0.0001) and long-term fertilized plants (F = 5.54, p = 0.0191).

**Vegetative reproduction**

Ramets are the units of vegetative reproduction for *M. paniculata* and *A. millefolium* and tillers for *F. altaica*. Vegetative reproduction was reduced by both 50 and 100% leaf loss from the parent plant (Fig. 5). The reduction caused by 50% leaf loss was significantly greater for fertilized than for unfertilized plants (F = 2.2, p = 0.0438). Similarly, the reduction caused by 100% leaf loss was significantly greater when plants were fertilized (F = 4.31, p = 0.0387). The 100%-clipping alone, reduced vegetative reproduction by an average of 0.6 offspring and with fertilization clipping caused an average reduction of 3.17 offspring. This accounts for the significant interaction of clipping and fertilization in the ANOVA (Table 1). All species responded positively to fertilization by doubling the number of offspring (Fig. 6). The increase was significantly greater for *F. altaica*, than *M. paniculata* (F = 38.46, p = 0.0001), which in turn was significantly greater than for *A. millefolium* (F = 4.17, p = 0.0419).

For *F. altaica* and *M. paniculata* the decrease caused by 100% leaf loss was greater for long-term fertilized plants than for unfertilized plants (Figs. 7B and 7C). The responses of *F. altaica* and *M. paniculata* did not differ (F = 1.64, p = ...
Fig. 1. Mean (± 1 SE) relative growth rates of leaf area. (A–C) Unclipped (□) and 100% clipped (■) plants at two levels of short-term fertilization. (D–F) Unclipped (□) and 100% clipped (■) plants at two levels of long-term fertilization (history). (G–I) Plants without (dots) and with (hatched) a long-term history of fertilization at two levels of short-term fertilization. All measurements were taken in the first 15 days after clipping.

0.2008). In contrast, for *A. millefolium* the decrease in vegetative reproduction was reduced by fertilization history (Fig. 7A). The response of *A. millefolium* differed significantly from the response of *F. altaica* ($F = 5.02$, $p = 0.0257$), but not significantly from the response of *M. paniculata* ($F = 0.85$, $p = 0.3584$).

Discussion

Much has been written and debated concerning plant adaptations to herbivory, and whether these adaptations are mutualistic or antagonistic (reviewed by Järemo et al. 1999). This debate has been prompted by findings in some studies that plants sometimes overcompensate in response to herbivory (e.g., McNaughton 1979; Lennartsson et al. 1997, 1998). The focus of the research reported here is tangential to these questions, and we are primarily interested in those factors that influence the amount of regrowth, chiefly soil nutrient status and intensity of clipping (herbivory), and not on whether herbivory per se is beneficial to the plant.

The primary and general findings from this study are that (i) plants collected from sites that had been fertilized previously had increased postclipping growth and aboveground biomass, and this was especially true of the dicots, (ii) short-term fertilization reduces the ability of clipped plants to compensate for biomass loss, regardless of species, and reduces the subsequent vegetative reproduction of clipped plants, (iii) increased clipping intensity had increased nega-
Reproductive consequences on all measures of plant performance, including vegetative reproduction, yet all plants compensated for tissue loss to some extent. (iv) the magnitude of regrowth response was often species-specific.

Plants collected from sites that had been fertilized previously had increased postclipping growth, and one species, A. millefolium, had increased vegetative reproduction — this provides some support for the CRM. This suggests that additional nutrients are stored by the plants, presumably in the rhizomes, and after an episode of herbivory the stored nutrients are released to support new growth. This is an intriguing result, because it is quite contrary to the response of clipped plants to short-term fertilization, which generally reduces the ability of clipped plants to compensate for biomass loss. Unfertilized plants had a relatively higher increase in RGR when clipped than fertilized plants, but this is partly a mathematical argument. In absolute terms, the RGR of fertilized plants was often higher than unfertilized plants. Unfertilized plants having low relative growth rates at the time of defoliation require only small increases in RGR to compensate for lost tissue, but fertilized plants have higher RGR and therefore require larger increases in RGR to compensate for the loss due to herbivory. However, in a number of cases the absolute RGR of unfertilized plants was as high as fertilized plants, especially for M. paniculata. Other work from this study area (Turkington et al. 1998; Graham and Turkington 2000) reported that the three species in this study increased (while others decreased) in abundance in response to fertilization, but usually with a 1-year delay. It seems that a small amount of the added nutrients are used directly for growth but most are being stored by the plant to be used for additional growth in subsequent years, and to be used especially after herbivory. This result is consistent with predictions of the GRM but conflicts with the results of some previous studies. For example, Serengeti grass species show well-developed compensatory growth following defoliation in high-nutrient soils (e.g., McNaughton and Chapin 1985; Chapin and McNaughton 1989; Westoby 1989) but the grasses lose their potential for compensatory growth when soil nutrients are deficient (Chapin and McNaughton 1989). Thus, the GRM may be a better predictor of compensatory ability of plants growing in naturally nutrient-deficient soils.

Although all three species had an increase in relative growth rate in leaf area in response to clipping (see also Cargill and Jefferies 1984; Oesterheld and McNaughton 1991; Oesterheld 1992), clipping was generally detrimental to final plant performance in all species, and the effect intensified as clipping intensity increased (Olson and Richards 1988; Obeso and Grubb 1994). Nevertheless, all plants compensated for tissue loss to some extent. However, the magnitude of the response following clipping was contingent on soil fertilization level and was species-specific. In order to increase RGR after tissue loss, it is likely that root carbon reserves are initially implemented in shoot regrowth and
Fig. 4. Mean (± 1 SE) aboveground biomass at the end of the study (75 days after transplanting), of plants without (dots) and with (hatched) a long-term history of fertilization, at three clipping intensities (0, 50, and 100% leaf loss) and two levels of short-term fertilization.

A. Achillea millefolium

B. Festuca altaica

C. Mertensia paniculata

Fig. 5. Mean (± 1 SE) number of vegetative offspring per plant (summed over all clipping intensities) of short-term-fertilized (■) and unfertilized plants (□) of Achillea millefolium, Festuca altaica, and Mertensia paniculata.

Fig. 6. Mean (± 1 SE) number of vegetative offspring per plant (summed over all clipping intensities) of short-term-fertilized (■) and unfertilized plants (□) of Achillea millefolium, Festuca altaica, and Mertensia paniculata.

when new leaves begin to photosynthesize, more photosynthetic than usual is diverted into roots. This is most likely to occur following severe defoliation, when all photosynthesizing leaves are removed. But one result remains an enigma, namely, that a bite taken from a plant in high nutrient soils does more damage than a bite of the same size taken from a plant growing under low soil nutrient conditions. The bite taken from a fertilized plant results in a greater loss of tissue at the end of the growing season, compared with uneaten controls growing in the same soil type.

Clipping has been reported to increase (McNaughton 1979; Paige and Whitham 1987; Maschinski and Whitham 1989; Lennartsson et al. 1997, 1998), decrease (Inouye 1982; Louda 1984), and to have no effect on the reproductive output of plants (Lee and Bazzaz 1980). In the present study, leaf loss had a negative impact on the number of offspring produced. Apparently the plant energy budget that was to be used for reproduction was reallocated to regrowth.

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Fig. 7. Mean (+ 1 SE) number of vegetative offspring per plant of unclipped (■) and 100% clipped (■) plants of the three species at two levels of fertilization history.

A. *Achillea millefolium*

<table>
<thead>
<tr>
<th>Number of ramets</th>
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<th>Unfertilized</th>
</tr>
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<tbody>
<tr>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td></td>
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<td>2</td>
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B. *Festuca altaica*

<table>
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</tr>
</thead>
<tbody>
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<td></td>
<td></td>
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<tr>
<td>10</td>
<td></td>
<td></td>
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<tr>
<td>5</td>
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</table>

C. *Mertensia paniculata*

<table>
<thead>
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<th>Unfertilized</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td></td>
<td></td>
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of the parent plant after defoliation. In contrast, short-term fertilization increased the number of ramets produced, the size of the offspring, and the size of the parent plant, but had no effect on the proportion of total plant leaf area that was allocated to offspring. This suggests that allocation patterns are “hard-wired” by the availability of nutrients to which a plant has become adapted. Addition of nutrients increases both parent plant size and offspring size, but does not affect the allocation pattern.

The degree of compensatory growth following clipping is species-dependent. Under natural conditions of low soil nutrient availability, *M. paniculata* was more likely to compensate for herbivory, followed by *A. millefolium* and then *F. altaica*. This order of decreasing compensatory ability occurred for leaf area variables only. The extent to which a plant compensates for tissue loss may depend on species traits such as phenology and architecture (Whitham et al. 1991). Structural differences were not included in the present study but may have had an effect on the differences in compensatory ability between species.

One might imagine that if herbivory is sufficiently intense on a regular basis, then it would benefit a plant to withhold some portion of its resources normally devoted to growth and reproduction against the possibility that an initial investment will be eaten. In this scenario, the ability to regrow is a strategy for dealing with expected herbivory, and minimizing the negative effects of damage. However, the snowshoe hare population peak occurs on a recurring 10- to 12-year cycle, and during the intervening years the probability of herbivory is quite low, so it is quite surprising that herbaceous plants in this low-herbivore system have evolved any capacity to compensate after herbivory. Compensatory ability was always reduced with fertilization. Nutrient supplementation can alter the compensatory responses shown by plants (Maschinski and Whitham 1989; Hik and Jeffries 1990; Hik et al. 1991), but responses to naturally occurring levels of soil nutrients are clearly most relevant. Plants in our study sites grow in nutrient-poor soils, and it was under these conditions that plants were more likely to compensate for tissue loss. These results indicate that current models need to incorporate the natural level of resource availability that plants may be adapted to, prior to a herbivory event.

The majority of compensatory studies have been carried out on herbaceous or woody plants in temperate regions (Oresco 1993) which could account for the generally good predictive ability of the CRM. Resources are generally more abundant in temperate zones than in boreal forest zones. Future studies could compare the regrowth responses of plants of the same species, native to areas of different resource availability.

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References


