

Effects of Simulated Rodent Herbivory on Carey's Balsamroot (*Balsamorhiza careyana*): Compensatory Leaf Growth

Abstract

Herbivores typically have negative effects on plant fitness, but many plants can compensate for herbivory by reallocating resources to replace lost tissue. We tested whether a common herbaceous plant of the shrub-steppe could compensate for leaf removal by rodents during spring when resource demands are high because plants are simultaneously growing leaves and flower stalks. We compared leaf and flower stalk production by Carey's balsamroot (*Balsamorhiza careyana*) on control and experimentally clipped plants (0, 20, or 40% of leaves removed). Clipped plants grew more new leaves than controls, catching up in total number of leaves by six weeks after clipping. The number of flower stalks did not differ, but a higher proportion of flower heads on clipped plants were broken off by herbivores or wilting. One year after clipping, control and clipped plants did not differ significantly in leaf number, leaf area, or flower production. Our data suggest that Carey's balsamroot can compensate for partial leaf removal by herbivores early in the growing season. Energy and nutrient storage in the stout taproot of Carey's balsamroot may contribute to its ability to replace lost tissues. Despite the apparent ability of this shrub-steppe herb to tolerate typical levels of rodent herbivory, plants attacked by rodents may be more susceptible to premature flower loss, thus lowering reproductive capacity.

Introduction

Despite a heated debate about whether herbivores have positive or negative effects on the plants they eat (e.g., Owen 1980; Dyer 1980; McNaughton 1979, 1983; Belsky 1986; Paige and Whitham 1987; Paige 1992; Crawley 1993), a recent review (Bergelson et al., 1996) has provided substantial evidence that herbivores typically have negative effects on their food plants. In addition to the obvious effect of removing photosynthetic tissue, herbivores can negatively affect plants by altering their resource allocation. Plants whose tissues are removed by herbivores may have less energy and resources available for reproduction, causing a decrease in seed output (e.g., Marquis, 1984), or may allocate more resources to defense (Zangerl and Bazzaz, 1992).

Although the effects of herbivory are usually negative, some plants can compensate for lost tissue. That is, they show enhanced growth in response to removal of photosynthetic tissues by herbivores. There are two basic ways in which plants might do this: either by reallocating energy from storage to produce new tissues

(McNaughton, 1983), or by increasing their photosynthetic rates (Nowak and Caldwell, 1984; Senock et al. 1991).

The ability to compensate varies considerably, both among and within species, as well as within individuals over time (Maschinski and Whitham, 1989). Water and nutrient availability (Chapin and McNaughton 1989, Houle and Simard 1996), the type and distribution of herbivore damage among plant tissues (Inouye 1982, Tolvanen et al. 1992, Hjalten et al. 1993, Lehtila 1996) and the phenological stage of the plant (Blaisdell and Pechanec 1949; Escarre et al. 1996) all influence the extent to which plants are able to compensate for tissues lost to herbivores.

Most studies of compensation have investigated responses of grasses, woody perennials, or short-lived species with single reproductive events. Herbaceous perennials with multiple reproductive events per lifetime have received less attention (Doak 1991), and may respond differently due to their different life history and morphological characteristics (e.g., above-ground tissues die back each winter).

In this paper, we address whether an herbaceous perennial in an arid environment can compensate for herbivory by rodents. Carey's balsamroot (*Balsamorhiza careyana*, Compositae) is a perennial herb that inhabits arid regions of

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the inland northwestern U.S. At our study site, rodents (probably mainly montane voles) sometimes chew off balsamroot leaves. Preliminary observations suggested that plants with extensive rodent herbivory responded by producing more new leaves, and that these plants remained green longer into the summer dry season than plants that had not experienced rodent herbivory (Ernest, pers. obs.). Thus, balsamroot may be able to compensate for rodent herbivory.

Previous work on the congeneric *B. sagittata* showed that annual leaf and flower stalk production of plants were reduced when plants were experimentally clipped to the ground the previous year, and the extent of reduction depended on the timing of clipping (Blaisdell and Pechanec 1949). Therefore, we ask whether Carey's balsamroot can compensate for herbivory if leaf removal occurs during the season in which the plant is allocating energy to reproduction, and when soil moisture is declining. If plants compensate by producing more leaves in the same growing season, does the allocation of resources toward this enhanced growth cause a decreased energy storage in the roots, and thus decreased growth or reproduction the following year? We performed field simulations of herbivory to experimentally test the hypotheses that (1) clipped plants can compensate for leaf removal by replacing lost leaves, and (2) use of energy stores for compensation causes clipped plants to suffer lower growth or reproduction in the year following herbivore attack.

Methods

Study System

Carey's balsamroot (*Balsamorhiza careyana*) is endemic to the arid regions of the inland northwestern U.S. and southwestern Canada (Hitchcock and Cronquist 1998). It inhabits shrub-steppe, where annual precipitation ranges from 15 to 50 cm (Daubenmire 1978). At our study site in central Washington (see Study Site, below), leaves begin emerging in the spring (April-May), followed very closely by growth of flowering stalks and development of floral buds. Flowers bloom in May-June before leaf maturation is complete. Leaves remain green into summer, but begin drying out by July-August. All above-ground portions of Carey's balsamroot die back by early fall.

Balsamroot is eaten by a variety of insect herbivores (Sheldon and Rogers 1978; Ernest, pers. obs.) as well as several mammals. Balsamroot leaves are nipped off at the petiole, removing the entire leaf blade and leaving diagonal cuts characteristic of rodent herbivory. Montane voles (*Microtus montanus*) are the most likely rodent herbivores of balsamroot at our study site (and were trapped near plants with clipped leaves). The number of leaves removed varies considerably among plants, ranging from 0 to 60% or more (Ernest, unpubl. data). Rodent herbivory also varies considerably among years. In April-May 1996, 28 of 30 plants had leaves removed by rodents (percent of leaves removed per plant ranging from 0 to 64, averaging 33), while in June 1999 none of 50 plants had any leaves removed (Ernest, unpubl. data). Widely fluctuating vole population densities (possibly due to climatic factors and predation) are a likely factor contributing to this temporal variability in herbivore damage levels.

Study Site

This study was carried out in shrub-steppe habitat of central Washington, on a west-facing slope in the L. T. Murray Wildlife Recreation Area, Yakima County, WA (T16N R17E S2, elevation 800-820 m). The vegetation is dominated by bitterbrush, *Purshia tridentata*. Other common plant species include lupine (*Lupinus* sp.), buckwheat (*Eriogonum* spp.), rabbitbrush (*Chrysothamnus nauseosus*), yarrow (*Achillea millefolium*), biscuitroot (*Lomatium* spp.), brodiaea (*Brodiaea* sp.), blue-bunch wheatgrass (*Pseudoroegneria spicata*) and cheat grass (*Bromus tectorum*). Precipitation in Ellensburg (approx. 26 km northeast of the study site) averages 23 cm per year, with nearly 70% falling between October and March (NOAA 1996).

Plants in the study area appear to be *B. careyana*, with multiple flower heads and the leaves sparsely hairy (Hitchcock and Cronquist 1998). Some characteristics of plants in this population, such as hairy involucre, are more typical of *B. sagittata* and hint at the possibility of hybridization. Although *Balsamorhiza careyana* hybridizes readily with several other *Balsamorhiza* species, it hybridizes with *B. sagittata* only in contact zones (Ownbey and Weber 1943). Specimens are housed in the Central Washington University herbarium.

Experimental Design

To minimize plant size effects, we selected 60 medium-sized *Balsamorhiza careyana* plants within an approximately 25m x 15m area on the hillside. Since plants were just beginning to develop new leaves when they were selected, we estimated plant size by the diameter of the previous year's leaves on the ground. Plants were numbered with aluminum plant tags, then randomly assigned to one of three treatment groups (described below).

On 3 May 1998, we clipped 0% (control), 20%, or 40% of the leaves of each plant to simulate rodent herbivory. Leaves were clipped with scissors along the petiole, approximately 6 cm above the ground, removing the entire leaf blade. Natural levels of rodent herbivory on balsamroot on plants in a nearby area ranged from 0 to 64% (mean = 33%) of leaves removed in April-May 1996 (Ernest, unpubl. data), so the 20% and 40% clipping treatments are within the range of herbivory experienced by balsamroot plants in the study area. We did not cage plants, leaving them in their natural habitat and exposed to herbivory by rodents as well as by insects. We monitored new rodent damage as well as insect herbivory on the leaves of all plants.

We counted the number of leaves eaten by rodents (number of leaves clipped at the petiole), number of uneaten green leaves, number of dead leaves, number of flowering stalks, and number of flowering stalks broken near the flower head (either by herbivores or from wilting) on May 19 and June 12, 1998. These dates represent approximately 2 and 6 weeks, respectively, after the clipping treatment. Total leaf production (used in the numerator for the percent of initial number of leaves) included both intact leaves and those clipped by rodents. We also recorded number of leaves with insect feeding damage on May 19.

The year following the experimental treatment, we continued to assess leaf growth and reproduction to see if there were lagged effects of the clipping. No treatment was applied in 1999, and no natural rodent herbivory was found on any plant. On 3 June 1999, we counted the number of flowering stalks and the total number of flower heads. We recorded the level of insect herbivory on each plant as none, <1%, 1-10%, 10-30%, or >30% of leaves with visible damage by chewing insects. On 9 July 1999, we counted the number of leaves

and measured leaf size, using a LiCor portable leaf area meter, for 10 randomly-selected leaves on each plant. From these data, we calculated leaf area per plant (# leaves x average leaf area).

Despite our attempt to select medium-sized plants for this study, the number of leaves per plant varied considerably because our estimate of plant size (diameter of the circle of previous year's dead leaves on the ground) was not a good indicator. To retain our initial goal of comparing only medium-sized plants (since plant response can vary with plant size and age) and to keep plant size similar among the three treatment groups, we eliminated 8 plants (the smallest and largest) from the analysis as outliers in size. In addition, we calculated number of leaves as a proportion of the initial number (on 3 May 1998, before clipping) to enable comparison of response to clipping among plants of different sizes. Final sample sizes were 49 in 1998 (16, 16, and 17 for control, 20%, and 40%, respectively) because of the plants deleted from analysis as outliers in size, and 41 (11, 14, and 16) in 1999 because rodents chewed off some plant tags over the winter.

Statistical Analyses

One-way ANOVAs showed no significant differences among the three treatment groups in number of leaves or number of flowering stalks before the clipping treatment was applied.

We performed parametric analyses on all 1998 data. We log-transformed the number of leaves (% of initial) to improve the fit to a normal distribution and homogeneity of variances. Because we counted numbers of leaves, intact flowering stalks, and broken flowering stalks on two dates in 1998, we performed a separate Repeated Measures ANOVA (Systat, SPSS 1997) for each dependent variable, with treatment (control vs. 20% clipped vs. 40% clipped) as the main factor and date as the repeated factor. Where the main treatment effect was significant, we applied a one-way ANOVA to each date, and used planned contrasts of control vs. clipped (20% and 40% pooled) and 20% vs. 40% to test for differences among the treatment levels. We used a one-way ANOVA for the 1998 insect herbivory levels.

For the 1999 data, we performed one-way ANOVAs for number of leaves, leaf size, and total leaf area per plant. Log-transformation of number of flowering stalks and number of flower heads

in 1999 did not improve the distribution or the variances, so these data were analyzed with non-parametric Kruskal-Wallis tests. The insect herbivory levels for 1999 were recorded as categorical data, so we used a Goodness-of-fit test for independence between level of insect herbivory and treatment. To maintain sufficient cell frequencies for the G-test, we combined adjacent categories (<1% of leaves damaged combined with 1-10% to form "low"; 10-30% and >30% combined to form "high").

Results

Untreated *Balsamorhiza careyana* plants had on average 42 leaves with an average leaf size of 104 cm² and an estimated total leaf area per plant of 4374 cm². Natural levels of rodent herbivory were low during the study. Rodents clipped 2.9% (range 0 to 16%) of leaves per plant on 5/19/98, 0.4% (range 0 to 8%) on 6/12/98, and no leaves in 1999.

Clipped plants, compared with controls, grew more new leaves following the experimental treatment in 1998 (Figure 1). As expected, the clipping treatment initially created significant differences in number of leaves among the three treatment groups (one-way ANOVA, $n = 49$, $P = 0.000$). The number of leaves still differed significantly among treatment groups on 19 May, two weeks after clipping (Table 1). Control plants had significantly more leaves than clipped plants, and plants with 20% of leaves clipped had significantly more leaves than plants with 40% of leaves removed. Within six weeks (by 12 June), clipped plants caught up with controls in number of leaves, showing no significant differences (Table 1).

Number of flower stalks (Figure 2) did not differ among treatments in 1998 (Repeated Measures

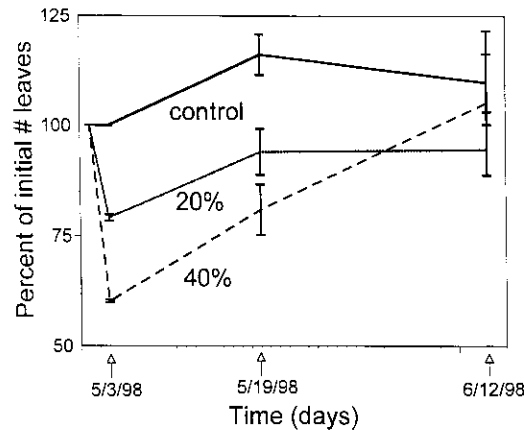


Figure 1. Mean number of leaves (\pm standard error), as percent of initial leaf number, on control plants and treatment plants (20% or 40% of their leaves clipped on 5/3/98). Number of leaves differed significantly among all three groups immediately (0 weeks) and 2 weeks after treatment, but not at 6 weeks post-treatment.

ANOVA, $P = 0.859$). However, a higher proportion of flower stalks was broken on clipped plants than on controls (Figure 3). Clipped plants were beginning to show more broken stalks by two weeks post-clipping, but the difference was not significant until six weeks post-clipping (Table 2). The proportion of broken flower stalks did not differ significantly between the 20% and 40% treatments. The level of insect herbivory (percent of leaves with insect chewing damage) did not differ among treatments (ANOVA, $P = 0.348$).

In 1999, we detected no significant differences between clipped and control plants in number of leaves, leaf size, total leaf area per plant (Table 3), number of flower stalks, total number of flower heads per plant (Table 4), or level of insect herbivory ($G = 1.78$, 2 d.f., $P > 0.25$).

TABLE 1. Statistical analysis of number of leaves in 1998 (as proportion of initial). Clip represents main effect of the clipping treatment.

ANOVA	Source	df	F	P
Repeated Measures	clip	2,46	9.034	0.000
	date	1,46	1.648	0.206
	date x clip	2,46	3.320	0.045
One-way, 5/19	clip	2,46	12.279	0.000
	planned contrasts			
	control vs. clip	1,46	19.599	0.000
	20% vs. 40%	1,46	4.622	0.037
One-way, 6/12	clip	2,48	0.914	0.408

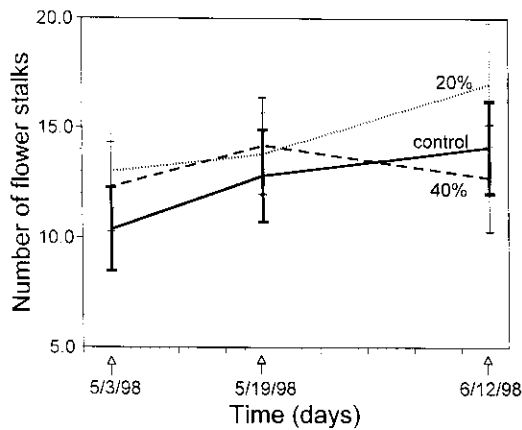


Figure 2. Mean number of flowering stalks (+/- standard error) produced by control plants and treatment plants (20% or 40% of their leaves clipped on 5/3/98). No significant differences among treatment groups at any date.

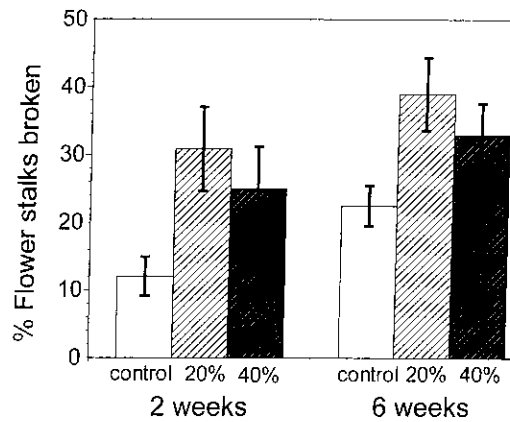


Figure 3. Mean (+/- standard error) percent of flowering stalks broken or wilted on control plants and treatment plants (20% or 40% of their leaves clipped). Clipped plants had significantly higher proportion of stalks broken than control plants both 2 and 6 weeks after treatment, but there was no difference between the two treatment levels.

TABLE 2. Statistical analyses of percent of flower heads broken in 1998. "Clip" represents the main effect of the clipping treatment.

ANOVA	Source	df	F	P
Repeated Measures	clip	2,43	4.051	0.024
	date	1,43	7.013	0.011
	date x clip	2,43	0.293	0.748
One-way, 5/19	clip	2,43	2.898	0.066
One-way, 6/12 planned contrasts	clip	2,45	3.529	0.038
	control vs. clip	1,45	6.109	0.017
	20% vs. 40%	1,45	0.858	0.359

TABLE 3. Summarized data and statistical analyses of plant growth traits measured on 7/9/99. All are one-way ANOVA's (with no planned comparisons since main effects were not significant).

Plant trait	Means (\pm se)			ANOVA results		
	Control (n=11)	20% clip (n=14)	40% clip (n=16)	df	F	P
no. leaves	48.6 \pm 6.9	52.3 \pm 4.9	45.9 \pm 5.9	2,38	1.029	0.367
leaf size (cm ²)	97.7 \pm 8.6	99.7 \pm 6.2	89.8 \pm 5.9	2,38	0.619	0.544
total leaf area (cm ²)	4742.8 \pm 755.1	5346.4 \pm 658.8	4359.7 \pm 702.0	2,38	0.666	0.520

TABLE 4. Summarized data and statistical analyses of plant reproductive traits measured on 6/3/99.

Plant trait	Means (\pm se)			Kruskal-Wallis tests		
	Control (n=10)	20% clip (n=13)	40% clip (n=12)	df	K-W	P
no. flower stalks	12.5 \pm 4.5	11.2 \pm 2.3	8.0 \pm 2.6	2	1.578	0.454
no. flower heads	16.1 \pm 6.6	15.2 \pm 3.8	11.5 \pm 4.0	2	1.354	0.508

Discussion

This study provides evidence that balsamroot can compensate for rodent herbivory in spring by growing back more leaves to replace those that are lost. This apparently has no effect on number of leaves or total leaf area the following year. Nor does it seem to affect number of flowers produced in the same year or the following year. Plants clipped at the higher treatment level (40%) showed trends toward smaller leaves and fewer flower stalks and flower heads. While these were not significant, small sample sizes in 1999 may have precluded detection of any real differences. The higher percent of broken flower stalks on clipped plants suggests that plants attacked by mammalian herbivores may be more susceptible to loss of flowers due to herbivory or wilt, and thus may suffer lower seed production.

How does balsamroot compensate for herbivore damage to leaves? The most likely explanation is that plants whose tissues are eaten grow back new leaves by reallocating resources stored in the root. Members of the balsamroot genus have a stout taproot, ranging in diameter up to 10 cm and reaching an average depth of 1.7 m in *B. sagittata* (Weaver 1919). A fairly rapid decline in protein content of *B. sagittata* leaves through the growing season suggests that plants translocate proteins to the roots for storage (Blaisdell et al. 1952). Because we did not want to disturb plants at the end of the first season after the clipping treatment, we did not measure root mass or total proteins and carbohydrates. However, this would be an important next step to see if clipped plants showed a decrease in root mass or shift in composition as they sent resources upward into developing leaves. Compensation may also occur if balsamroot leaves that remain intact increase their rate of photosynthesis when other leaves on the plant are clipped. This type of compensation is more difficult to document because it may require days or weeks to implement (Senock et al. 1991).

Rodent herbivory may influence the susceptibility of the plant to attack by other herbivores because compensatory growth may require resources that are normally allocated to plant defense. However, level of insect herbivory did not seem to be affected by the clipping treatment. Finer measurements of insect damage on clipped and

control plants would help address this potential effect of rodent herbivory.

The only negative effect of herbivory we measured during this study was the higher proportion of broken flower stalks on clipped plants. This may be an indirect cost of compensation: if leaf regrowth taxes energy stores, plants may not send sufficient resources to flowering stalks to support these structures. Another possibility is that if clipped plants increase nutrient transfer to reproductive structures during compensation, herbivores may preferentially browse flowering stalks on these plants.

The ability of balsamroot to compensate likely varies with factors not tested here. One factor is extent of herbivore damage. *Balsamorhiza sagittata* clipped to the ground (by investigators) during the early to mid-growing season (late May – early June in Idaho) had lower yields a year following treatment than did controls (Blaisdell and Pechanec 1949). The extent of reduction in yield varied with timing of the clipping in relation to plant phenology: yield was reduced most when plants were clipped during or immediately following full bloom. Other factors that may influence compensatory capacity include plant size, age, genotype (Houle and Simard 1996), nutrient availability (Houle and Simard 1996), and water stress (Maschinski and Whitham, 1989). We tried to minimize the influence of plant size and age, and nutrient and water availability by selecting all medium-sized plants on the same hillside. Nevertheless, these factors may be important in balsamroot's compensatory response.

In this study, we have shown responses of balsamroot to manual clipping. We suggest that plants would respond in a similar fashion to actual rodent herbivory. There is considerable controversy about the effects of simulated vs. actual herbivory because patterns of damage by herbivores could be different, and herbivore saliva may have additional effects on the plants. Most of the demonstrated differences between simulated and real herbivory have been for insect herbivore systems (e.g., Hartley and Lawton 1991). An experimental assessment of the effects of bison saliva on grasses showed no effect on photosynthesis or carbon allocation (Detling et al. 1980). Birch trees respond in similar fashion to mechanical damage and moose herbivory (Danell et al. 1985).

Although we cannot discount effects of rodent saliva on balsamroot's compensatory ability, we feel that our clipping closely simulated the pattern of leaf removal by rodents.

This study shows compensation in number of leaves produced without any significant shift in leaf size, and no effect on reproduction in terms of number of flowering stalks or flower heads. We have not measured size of flower heads or seed production. Studies are in progress to assess effects of clipping on seed set and seed viability.

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