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OVERCOMPENSATION IN RESPONSE TO MAMMALIAN HERBIVORY: THE ADVANTAGE OF BEING EATEN

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There are two major opposing views of the effects of herbivores on plant growth and reproduction (McNaughton 1983). The most common view is that herbivory is detrimental to plants (Mattson and Addy 1975; Morrow and LaMarche 1978; Simberloff et al. 1978; Kinsman and Platt 1984; Whitham and Mopper 1985) and represents a selective pressure for the evolution of plant defenses. In sharp contrast is the view that plants can benefit from being eaten because they respond by overcompensating, ultimately achieving greater fitness. Although this idea is certainly espoused by a minority, it is implicit or explicit in a number of studies (Vickery 1972; Chew 1974; Dyer 1975; Dyer and Bokhari 1976; McNaughton 1976, 1979; Owen and Wiegert 1976; Porter 1976; Simberloff et al. 1978; Stenseth 1978; Hendrix 1979; Owen 1980; Hilbert et al. 1981; Inouye 1982).

On close examination of the 40 or more studies presenting experimental evidence in support of this view, Belsky (1986) concluded that there is as yet no convincing evidence that herbivory increases plant fitness under natural conditions. Although several of the studies have demonstrated increases in plant biomass following herbivory, how biomass relates to seed production and subsequent survival is ambiguous. Measuring plant fitness is difficult for two major reasons. First, the total reproductive effort of perennials must be accumulated over the multiple bouts of reproduction that occur during their lifetimes. Second, many plants have multiple pathways of reproduction, and it is difficult to compare the ecological and evolutionary value of a sexually derived seed with an asexually derived ramet or rosette. Consequently, annual and biennial plants that die after first reproduction represent ideal candidates for quantifying herbivore impacts on reproductive success.

We experimentally demonstrate that under natural field conditions plants can benefit from the effects of herbivory. When mammalian herbivores remove 95% or more of the aboveground biomass of the biennial scarlet gilia, *Ipomopsis aggregata*, relative fitness in terms of seed production and subsequent seedling survival averages 2.4 times that of the uneaten controls.

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STUDY SITES, ORGANISMS, AND OBSERVATIONS

Studies of the effects of mammalian herbivory on scarlet gilia were conducted during the summers from 1984 through 1986 at Northland Press, near the Museum of Northern Arizona (elevation 2133 m) and Fern Mountain (elevation 2500 m) near Flagstaff, Arizona. Scarlet gilia, *Ipomopsis aggregata* (Polemoniaceae), is a red-flowered herb of western montane regions that flowers from early July through late September (Paige and Whitham 1985). Following germination, scarlet gilia develops into a leafy rosette approximately 12 cm in diameter. After 1–8 yr of vegetative growth (Inouye, pers. comm.), up to 250 flowers are produced per paniculate-racemose inflorescence. Elongation of the inflorescence is completed before flowering (Hainsworth et al. 1985). Although usually monocarpic (Hainsworth et al. 1985), scarlet gilia may become polycarpic under certain conditions (Paige and Whitham 1987). In this study all plants were monocarpic and died after flowering.

Browsed and unbrowsed plants were compared in terms of the number of shoots produced, plant height, number of flowers produced, number of fruits produced, number of seeds per fruit, seed weight, percent germination success, percent seedling survival, total plant biomass, stem and leaf biomass, and root biomass. Additionally, censuses were conducted to determine the seasonal patterns of ungulate herbivory by mule deer, *Odocoileus hemionus*, and elk, *Cervus elaphus*. Censuses were conducted by randomly selecting 100 plants per site (early and late in the season) and documenting the level of herbivore damage on each.

The probability of plants being browsed by ungulates during the flowering season is high; on the average 72% of all plants (n = 600) were fed on sometime during the flowering season. Of these, 63% were exposed to high levels of herbivory, in which 95% or more of the entire aboveground biomass was consumed.

No ungulate herbivory occurs before inflorescence elongation when scarlet gilia is a leafy rosette. Most herbivory occurs early in the season during and just following the period of stem elongation before flowering. During this period, 91% of all feeding by deer and elk occurred.

Browsed plants produced four times more flowering stalks than plants that were not browsed. Under natural conditions, browsed individuals produced an average of 4.07 ± 0.37 new inflorescences per plant, whereas the uneaten controls produced only single inflorescences (1.00 ± 0.0, Student-Newman-Keuls multiple-range test, $P < 0.05$, table 1). The difference in inflorescence number is the result of herbivory; the removal of the single inflorescence stimulates the production of multiple flowering stalks from dormant lateral buds at the base of the stem (fig. 1). This pattern of plant response to herbivory has been consistent over a 3-yr period.

Herbivore-induced differences in plant architecture correlate highly with flower and fruit production. Browsed plants with multiple inflorescences produced 2.76 times as many flowers and 3.05 times as many fruits as unbrowsed plants (Student-Newman-Keuls multiple-range test, $P < 0.05$, table 1).

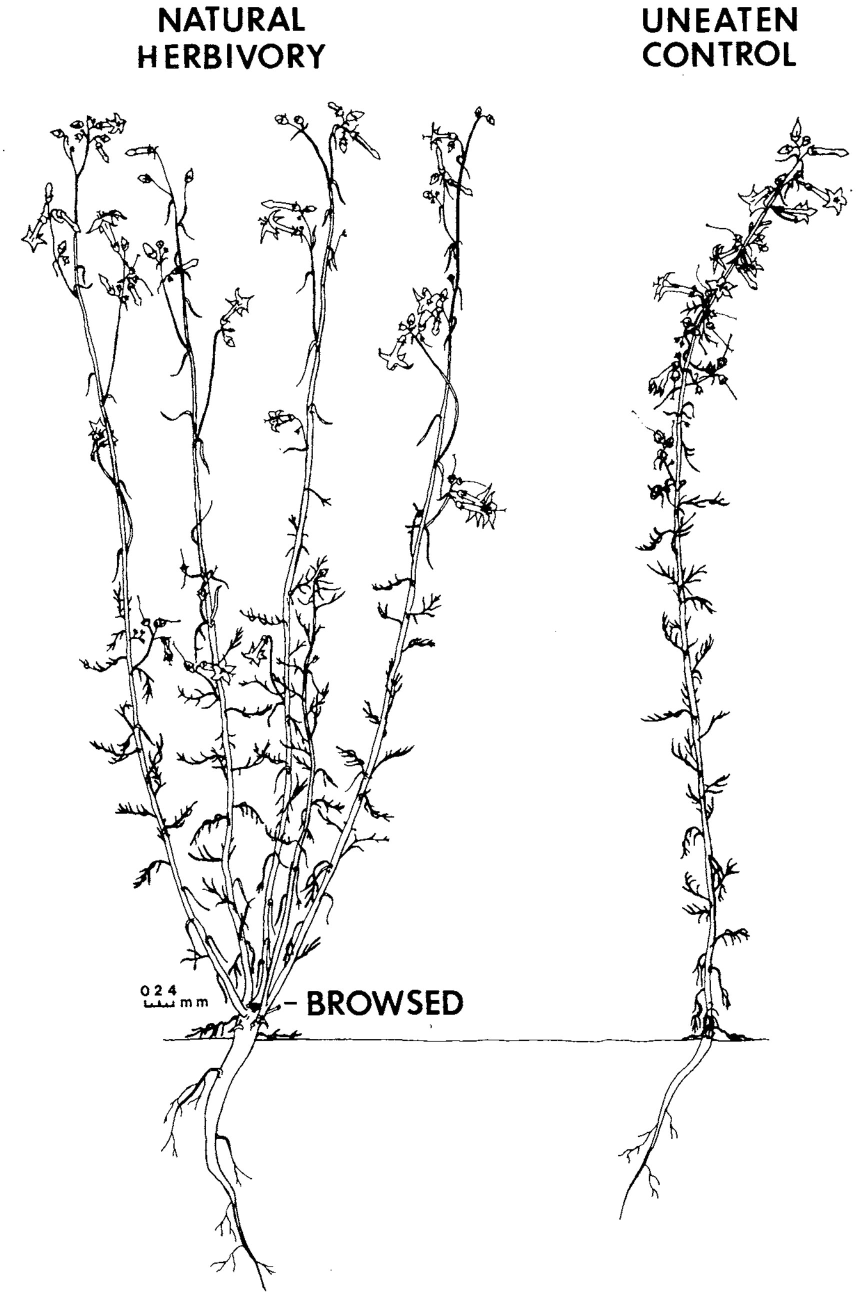

FIG. 1.—Illustration comparing browsed plants and uneaten control plants of scarlet gilia. Individuals experiencing high herbivory overcompensate by producing multiple inflorescences and up to three times as many flowers, fruits, and seeds as uneaten controls. "Browsed" indicates the position at which the original inflorescence was cut by the herbivore.

TABLE 1

COMPARISONS OF NINE MEASURES OF RELATIVE FITNESS FOR *Ipomopsis aggregata*

Fitness Measure	Natural Herbivory	Simulated Herbivory	Control (No Herbivory)	F*	df	P
Flowers per plant	102.30^a (19,15)	68.90^b (8.5,20)	37.00^c (4.2,20)	13.13	2,52	<0.001
Fruits per plant	57.70^a (14,15)	44.90^a (5.8,20)	18.90^b (2.5,20)	9.77	2,52	<0.001
Seeds per fruit	9.25^a (.73,8)	9.57^a (1.4,7)	9.00^a (1.1,7)	0.05	2,19	>0.25
Seed weight (mg)	1.18^a (.41,15)	0.95^a (.06,14)	1.14^a (.09,13)	1.94	2,39	>0.15
Plant biomass (g)	10.37^a (1.6,10)	7.69^a (1.1,15)	4.91^b (.44,15)	5.19	2,37	<0.02
Root biomass (g)	3.24^a (.80,10)	2.68^a (.40,14)	1.56^b (.16,15)	4.11	2,36	<0.03
Stem and leaf mass (g)	5.05^a (.85,10)	$3.43^{a,b}$ (.66,15)	2.59^b (.32,15)	3.29	2,37	<0.05
Plant height (inches)	22.66^a (2.2,10)	18.64^a (1.3,12)	21.00^a (.89,12)	1.58	2,31	>0.15
Inflorescences per plant	4.07^a (.37,15)	3.33^a (.39,15)	1.00^b (0.0,15)	47.10	2,42	<0.001

NOTE.—Some plants experienced natural herbivory by deer and elk; others were clipped to simulate herbivory; and uneaten plants served as controls. Means with the same letters show no significant difference at the 0.05 level, Student-Newman-Keuls multiple-range test. Numbers in parentheses indicate ± 1 standard error of the mean, number of plants.

* Tests were run on log-transformed or $\log(Y + 1)$-transformed data to equalize variance.

HYPOTHESES AND EXPERIMENTAL TESTS

The above correlations between herbivory, growth form, and fruit production led us to hypothesize that mammalian herbivory plays a beneficial role in the survival and reproductive success of scarlet gilia. In response to high levels of mammalian herbivory, individual plants appeared to overcompensate, increasing relative fitness. To test this experimentally, we chose 40 uneaten (single-stalked) plants of similar size and height early in the season after inflorescences had fully elongated but not yet flowered. To simulate high levels of natural herbivory by mule deer and elk, 20 plants were experimentally clipped, having over 95% of their entire aboveground biomass removed. The remaining 20 unmanipulated plants served as a control.

The growth response of experimentally clipped plants was rapid; within approximately 4 wk inflorescences on clipped plants attained heights statistically indistinguishable from those of unmanipulated controls (Student-Newman-Keuls, $P > 0.05$, table 1). In addition, these plants flowered at approximately the same time and in a few cases flowered before individuals of the control group. As predicted, experimentally clipped plants produced 1.86 times as many flowers and 2.38 times as many fruits on the average as the controls (Student-Newman-Keuls multiple-range test, $P < 0.05$, table 1).

The compensatory response resulting from simulated herbivory is similar to that generated by natural herbivory. Experimentally clipped plants produced approximately the same numbers of inflorescences and fruits as plants that were naturally browsed by ungulate herbivores (Student-Newman-Keuls multiple-range test, $P > 0.05$, table 1). Experimentally clipped plants, however, produced significantly fewer flowers than naturally browsed plants, and both produced significantly more than the controls (Student-Newman-Keuls multiple-range test, $P < 0.05$, table 1). Naturally browsed plants were also similar in height to experimentally clipped plants (ANOVA, $P > 0.15$, table 1).

Although plants that were naturally browsed or experimentally clipped early in the season (when 91% of feeding on *Ipomopsis aggregata* occurred) ultimately produced significantly more fruits than control plants, one might suspect that the fruits would be of poorer quality and contain fewer seeds. Comparisons between experimentally clipped, naturally browsed, and control (no herbivory) plants, however, showed no significant differences in the number of seeds produced per fruit (ANOVA, $P > 0.25$, table 1). Thus, regardless of treatment, fruit number and seed production are directly related.

Even though browsed and experimentally clipped plants produced significantly more seeds than control plants, a potential decline in the quality of seeds produced by browsed or clipped plants might offset this numerical advantage. Seed quality was examined in three ways. First, because seed weight is indicative of seed quality and the level of stored food reserves (Schaal 1980; Weis 1982; Zimmerman and Weis 1983), approximately 110 individual seeds from each group were weighed on a Cahn electrobalance to determine whether or not herbivory affects seed weight. No significant difference in seed weight could be detected (ANOVA, $P > 0.15$, table 1).

Second, if seeds varied in quality, we would expect differences in germination success; none were observed. To test this, five seeds from each of 38 plants (19 uneaten controls, 12 experimentally clipped plants, and 7 naturally browsed plants) were randomly selected and germinated. Seeds were germinated between two pieces of moistened Whatman #1 filter paper placed in petri plates (5 seeds per plate per plant) under aphotic conditions. Our results showed no significant differences between uneaten controls and plants that were naturally browsed or mechanically clipped (ANOVA, $F = 0.05$, df = 4,40, $P > 0.25$; results include replicates of experimentally clipped versus control groups, table 2). Thus, the lack of significant differences in these two measures of seed quality of browsed (natural and simulated) and uneaten controls strongly suggests that the seeds are of the same quality.

Third, if seedlings varied in quality, we would expect differences in survival; none were observed. Although few studies have tracked seedling survival and subsequent reproduction to obtain a true measure of plant fitness, our initial data collected over a 30-day censusing period suggest that survival for treatment and control groups is not significantly different (51% for natural herbivory and 58% for control; $\chi^2 = 0.42$, df = 1, $P > 0.25$). These results were also replicated with another set of seeds over a 4.5-mo period. Again no significant differences in

TABLE 2

COMPARISONS OF SEED GERMINATION AND SURVIVAL FOR NATURALLY BROWSED PLANTS, CLIPPED PLANTS, AND UNEATEN CONTROLS

Treatment	% Germination	% Survival after 30 Days*	% Survival after 4.5 Months*
Natural herbivory by mule deer and elk	43 (35,7)†	51 (45)‡	38 (21)‡
Uneaten control	44 (90,18)	58 (52)	47 (66)
Uneaten control (replicate)	48 (25,5)	—	—
Simulated herbivory (clipping)	44 (50,10)	—	48 (48)
Simulated herbivory (replicate)	40 (25,5)	—	—

* Percent survival does not include seeds that failed to germinate.

† The numbers in parentheses are the number of seeds and the number of plants.

‡ The numbers in parentheses are the number of seedlings.

survival were detected (38% natural herbivory, 48% simulated herbivory, and 47% control; $\chi^2 = 0.62$, df = 2, $P > 0.25$; table 2).

Cumulative estimates of plant performance demonstrate that browsed plants achieve a 2.4-fold increase in relative fitness over uneaten control plants. For example, by combining our most direct measures of plant fitness (i.e., number of seeds per fruit times the number of fruits per plant times percent germination times percent seedling survival after 4.5 mo), we can obtain a cumulative estimate of plant performance with various treatments (data from tables 1, 2). These calculations show that plants experiencing natural or simulated herbivory could both expect to produce an average of 87 surviving seedlings, whereas uneaten control plants could expect to produce only 37 surviving seedlings. When estimates of relative fitness were replicated (e.g., percent germination), average values were used for calculations.

MECHANISMS OF OVERCOMPENSATION

The mechanisms that potentially lead to overcompensation following herbivore impact probably include complex and interrelated physiological responses. Growth compensation, for example, could result from assimilate reallocation from storage organs such as roots (Kende 1965; Gifford and Marshall 1973; McNaughton 1983; McNaughton and Chapin 1985), hormones present in animal saliva that are thought to promote plant growth (Dyer 1980; McNaughton 1983), and/or the activation of dormant buds followed by increased photosynthetic rates (Overbeek 1966; McNaughton 1983).

Although we do not know the mechanism(s) involved in overcompensation by *Ipomopsis aggregata*, two prominent hypotheses can be eliminated. For example, aboveground compensation may come at the expense of belowground biomass when energy from the roots is simply reallocated to aboveground tissue (Overbeek 1966). If such were the case, one would expect a decrease in root biomass following herbivory. To examine this hypothesis, root biomass was compared for

15 uneaten control plants, 14 experimentally clipped plants (in which over 95% of aboveground biomass had been removed), and 10 naturally browsed plants (table 1). Plants were initially similar in size and height. The root biomass of naturally browsed plants was 107% (±25%) greater than that of the uneaten controls. Similarly, the root biomass of experimentally clipped plants was 71% (±15%) greater than that of the uneaten controls (Student-Newman-Keuls multiple-range test, $P < 0.05$, table 1). Because both natural and simulated herbivory result in plants with larger roots, clearly compensation by aboveground tissues does not come at the expense of the roots. It appears that root enlargement enables an increase in nutrient uptake promoting growth compensation (Overbeek 1966).

Similarly, stimulation of plant growth by hormones potentially present in herbivore saliva did not lead to growth compensation by scarlet gilia. In 10 of 11 traits measured, no significant differences between simulated and natural herbivory were observed (Student-Newman-Keuls multiple-range test, $P > 0.05$; tables 1, 2). Only for the numbers of flowers per plant did we find a significant difference (table 1).

Most importantly, when we examined the traits directly associated with fitness (i.e., fruit production, seeds per fruit, percent germination, and subsequent survival), we observed no significant differences between simulated and natural herbivory. Furthermore, when we combined these measures to produce a cumulative estimate of the number of surviving seedlings per plant (i.e., number of seeds per fruit times fruits per plant times percent germination times percent seedling survival after 4.5 mo), plants experiencing natural or simulated herbivory can expect to produce 87 surviving seedlings. Thus, our experiments and cumulative estimates of relative fitness detect no significant differences between natural and simulated herbivory, strongly suggesting that hormone transfer by herbivores is not important in this system.

CONCLUSIONS

Our experiments support the contention that mammalian herbivores can benefit plants and enhance their fitness. Scarlet gilia that are browsed overcompensate in terms of the numbers of inflorescences, flowers, and fruits produced and of total plant biomass. Because there are no differences in the number of seeds produced per fruit, seed weight, or subsequent germination success and survival, the advantage of being eaten is an average 2.4-fold increase in relative fitness over uneaten individuals.

Our results are unique in studies of overcompensation because they represent a closer approximation of true plant fitness in that seed quality and subsequent survival were examined. Because other studies have shown that herbivory can result in smaller seeds with lower germination probabilities, findings of overcompensation based on increased numbers of inflorescences or rosettes (e.g., Peschken 1971; van der Meijden and van der Waals-Kooi 1979; Inouye 1982) lack a crucial part of the plant life cycle. For example, Fedde (1973) showed that when Fraser fir (*Abies fraseri*) experienced herbivory by the balsam wooly aphid (*Adelges piceae*), seed weight dropped 39%, germination dropped 43%, and loss to seed parasites increased 10-fold (for a similar example with *Rumex crispus*, see Maun and Cavers 1971). Such dramatic declines in seed survival could easily offset observed increases in relative fitness at an earlier stage. Even studies that have experimentally demonstrated negative effects of herbivory on growth and reproduction (e.g., Morrow and LaMarche 1978; Whitham and Mopper 1985) usually lack data on seed quality and survival. It is important that future studies of plant-herbivore interactions examine this stage of plant development.

From an evolutionary perspective it is not clear why some plants should benefit from being eaten. That plants should evolve to negate the deleterious effects of herbivory is obvious; that they should evolve to depend on herbivores to achieve their greatest fitness through overcompensation is less clear. In our study 95% of the aboveground biomass was removed, yet these plants experienced the greatest success. Because these results are unexpected, it is important that future studies address the precise mechanisms of this interaction. It would also appear that the negative effects of herbivory cannot simply be assumed; they must be experimentally demonstrated. Furthermore, if the mechanisms of overcompensation are genetically based, such responses to herbivory should be of great interest to agriculturists who, through selective breeding, might incorporate these desirable traits into crop plants.

SUMMARY

Plants of scarlet gilia, *Ipomopsis aggregata*, are exposed to high levels of mammalian herbivory (by mule deer, *Odocoileus hemionus*, and elk, *Cervus elaphus*) early in the season, before flowering. During this period of our study, up to 56% of all individuals experienced a 95% reduction in aboveground biomass. Browsed plants rapidly responded by producing new inflorescences and flowering within 3 wk. Unbrowsed plants produced only single inflorescences, whereas browsed plants produced multiple inflorescences. Field observations and experimental manipulations showed that plants with multiple inflorescences produced significantly greater numbers of flowers and fruits than unbrowsed individuals. Because there were no differences between browsed and unbrowsed individuals in the number of seeds produced per fruit, seed weight, subsequent germination success, and survival, browsed plants enjoyed a 2.4-fold increase in relative fitness. Consequently, there is an immediate reproductive advantage to being eaten. Under the natural field conditions of this study, mammalian herbivores played a beneficial role in the survival and reproductive success of scarlet gilia.

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