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Author(s): Ken N. Paige

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OVERCOMPENSATION IN RESPONSE TO MAMMALIAN HERBIVORY: FROM MUTUALISTIC TO ANTAGONISTIC INTERACTIONS¹

KEN N. PAIGE

*Institute for Environmental Studies, Department of Ecology, Ethology, and Evolution,
University of Illinois, 1101 West Peabody Drive, Urbana, Illinois 61801 USA*

Abstract. Studies of natural and simulated herbivory were conducted to assess the effects of secondary herbivory and plant association on the reproductive success of *Ipomopsis aggregata*. Over the 5-yr period of this study 77% of all plants were browsed by ungulate herbivores at some time during the flowering season. Of these, 33% were subsequently browsed. Removal of the single inflorescence stimulated the production of, on average, five new flowering stalks from dormant lateral buds along the remaining portion of the plant's stem. Although regrowth shoots were initially avoided by ungulates following the removal of scarlet gilia's single inflorescence, plant tips were secondarily browsed following stem elongation and flower bud formation.

Secondary herbivory had no effect on the compensatory outcome. Plants that were naturally browsed produced significantly higher numbers of flowers and fruits than plants that were not eaten, even when plants were secondarily browsed. Because there were no significant differences in numbers of seeds produced per fruit or in seed mass, an increase in total fruits produced by browsed plants resulted in an increase in fitness through seed production.

Observational and experimental results indicate that *I. aggregata* switches from a "mutualistic" to an "antagonistic" interaction with its ungulate herbivores in order to achieve its greatest fitness. Results of experimental clipping showed that high levels of secondary herbivory on *I. aggregata* would be detrimental, decreasing fitness by $\approx 70\%$. An apparent change in plant quality following the initial bout of herbivory, however, deters high levels of subsequent herbivory, restricting tissue removal to the tips of the plant.

When plants were found in close association with either pine or grasses (to add in the potential negative effects of competition), browsed plants still outperformed control plants, producing significantly more flowers and fruits than uneaten control plants. As in a previous study, these results support the contention that mammalian herbivores can benefit plants, enhancing plant fitness.

Key words: *antagonistic interactions; Cervus elaphus; elk; fitness overcompensation; Ipomopsis aggregata; mule deer; mutualistic interactions; Odocoileus hemionus; plant competition; scarlet gilia; secondary herbivory.*

INTRODUCTION

Over the past decade there has been considerable debate regarding the potential beneficial effects of herbivores on plants (Belsky 1986, 1987, McNaughton 1986). The basis of this continuing controversy has centered on whether the direct effects of herbivory can enhance plant fitness. Resolution has, until recently, been hampered by a lack of supportive evidence (see Belsky 1986, Verkaar 1986, Crawley 1987).

A study by Paige and Whitham (1987a) has provided experimental evidence of fitness overcompensation in a natural system. When mule deer and elk browsed the monocarpic biennial *Ipomopsis aggregata*, seed production and subsequent seedling survival averaged 2.4 times that of the uneaten controls (Paige and Whitham 1987a).

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The increase in fitness was largely due to a change in plant architecture; ungulate removal of the single inflorescence resulted in the production of multiple flowering stalks and subsequent increases in flower and fruit production. Because there were no significant differences between browsed and unbrowsed individuals in the number of seeds produced per fruit, seed mass, germination success, or subsequent seedling survival, an increase in total fruits produced by browsed plants resulted in an increase in relative fitness.

These results were particularly surprising when considering the amount of biomass removed. On average, 95% of the aboveground biomass or 72% of the plant's total biomass was removed by mule deer and elk, and yet overcompensation still occurred. Furthermore, aboveground compensation did not come at the expense of belowground biomass. The root systems of natural and experimentally clipped plants were 107% and 72% greater than those of the uneaten controls

(Paige and Whitham 1987a, K. N. Paige, *unpublished data*). Therefore, overcompensation occurred both above- and belowground in response to mammalian herbivory.

These results raised a number of questions. For example, do multistemmed regrowth plants suffer defoliation by the same deer and elk that fed upon the initial shoots? If the attack rates were as high for the regrowth shoots as for the initial shoots, it would be hard to see how fitness could be increased, since repeated stem removal would likely deplete carbohydrate and protein reserves. Therefore, any benefit gained by browsed plants would seemingly depend on differential attack rates between initial and regrowth shoots (Crawley 1987). These issues, however, were not addressed in the initial study. In addition, how might the competitive effects of other plants alter *I. aggregata*'s compensatory response? In recent reviews, Belsky (1986, 1987) suggested that overcompensation would most likely occur where grazing is moderate and where species grow in monoculture, free of interspecific competition. Empirical tests substantiating this supposition, however, are lacking.

Overall, both of these measures are important because the history of defoliation (Marquis 1984, Crawley 1987, Olson and Richards 1988) and the competitive effects of other plants (Mueggler 1970, 1972, Harper 1977, Bently and Whittaker 1979, Fowler and Rausher 1985, Belsky 1986, 1987) can influence a plant's physiological state and its ability to compensate (Maschinski and Whitham 1989).

Therefore, the goals of this paper are to extend our previous studies by assessing the effects of secondary herbivory and plant association on the compensatory outcome. In our initial study (Paige and Whitham 1987a), plants were randomized across all habitat types. Thus, the effects of competition on the compensatory outcome were potentially masked (due to an underrepresentation of plants growing in association with pine). In addition, although secondary herbivory is rare at the site where our initial experiments were conducted (Northland Press [Arizona], 2133 m in elevation), high levels of secondary herbivory on *I. aggregata* were found to occur on sites higher in elevation (2500 m) where mule deer and elk migrate during the summer months.

METHODS AND MATERIALS

Organisms and study sites

Studies of the effects of plant association and subsequent herbivory on *I. aggregata* were conducted during the summers of 1986 through 1990 at Northland Press (elevation 2133 m) and on Fern Mountain (elevation 2500 m), near Flagstaff, Arizona. *Ipomopsis aggregata* is a biennial herb of western montane regions that flowers from early-mid July through late September (Paige and Whitham 1985, 1987a,b). Although this

species is usually monocarpic (Hainsworth et al. 1985), limited seed set can induce cloning and repeated bouts of reproduction; herbivory, however, does not induce cloning (Paige and Whitham 1987b, Whitham et al. 1991). In this study all plants were monocarpic and died after flowering.

I. aggregata populations are commonly browsed by vertebrate herbivores, primarily mule deer, *Odocoileus hemionus*, and elk, *Cervus elaphus* (Paige and Whitham 1987a). At the Northland Press site plants were also occasionally grazed by rock and Abert squirrels (*Spermophilus variegatus* and *Sciurus aberti*, respectively). Vertebrate herbivores remove the rapidly dividing meristematic tissue of *I. aggregata*, taking 75–95% of the aboveground biomass (Paige and Whitham 1987a). Removal of the meristem causes a compensatory response by the plant, inducing a single-stalked plant to produce two or more lateral shoots from the remaining portion of the plant's stem (Paige and Whitham 1987a). Because the growth response of browsed plants is so rapid (the plants attaining heights statistically indistinguishable from the uneaten controls within ≈ 4 wk), neither flowering, fruit set, nor fruit dehiscence is delayed (Paige and Whitham 1987a).

Experimental design

Plant association and the compensatory outcome.— To assess how plant association and herbivory interact in affecting plant growth and reproduction, plants were selected from each of two habitat types at Northland Press in the 1986 flowering season: plants growing within a few centimetres (10–20) of brome grass, *Bromus inermis*, and plants growing under ponderosa pine, *Pinus ponderosa*. Approximately 85% of all plants were growing naturally within a few centimetres of grasses (with no tree canopy) and 15% were growing under pine (no other vegetation was found growing with scarlet gilia under pine). Plants from each habitat type were subjected to one of three treatments. Twenty-four plants (13 under pine, 11 intermixed with grass) had previously been browsed by ungulate herbivores (mid-May), 31 plants (16 under pine, 15 intermixed with grass) were experimentally clipped in late May (removing >95% of their aboveground biomass) to simulate natural herbivory, and 29 plants (14 under pine, 15 intermixed with grass) served as unmanipulated controls. Because stem diameter is a relatively accurate measure of plant size (positively correlated with biomass, $R^2 = 0.535$, $N = 25$, $P < .0001$; with height, $R^2 = 0.403$, $N = 25$, $P < .0007$; and with flower production, $R^2 = 0.655$, $N = 25$, $P < .0001$, for example), plants were matched on the basis of basal stem diameter early in the season (late May) during the period of stem elongation prior to flowering (plants intermixed with grass had a mean stem diameter of 4.5 mm; plants growing under pine had a mean stem diameter of 4.0 mm; although stem diameters covered the full range of sizes within the populations, ranging in size from 2–9 mm,

TABLE 1. Effects of plant association and mammalian herbivory on the relative fitness of scarlet gilia, *Ipomopsis aggregata*, in Arizona.*

Fitness measure		Natural herbivory	Simulated herbivory	Control (no herbivory)	<i>F</i>	df	<i>P</i>
A. Intermixed with Grass							
Flowers per plant	\bar{X}	211.1 ^A	130.5 ^B	65.3 ^C	17.89	2,38	<.0001
	SE	26.4	19.6	8.1			
	<i>n</i>	11	15	15			
Fruits per plant	\bar{X}	53.1 ^A	48.5 ^A	21.3 ^B	9.25	2,38	<.0005
	SE	8.7	8.6	4.6			
	<i>n</i>	11	15	15			
Seeds per fruit	\bar{X}	13.1 ^A	12.7 ^A	10.3 ^A	1.97	2,31	>.158
	SE	1.5	1.8	1.3			
	<i>n</i>	9	11	12			
Seed dry mass (mg)	\bar{X}	0.74 ^A	0.63 ^A	0.87 ^A	0.75	2,31	>.479
	SE	0.2	0.2	0.2			
	<i>n</i>	9	11	12			
Stem and leaf dry biomass (g)	\bar{X}	27.9 ^A	16.0 ^B	6.1 ^C	19.03	2,38	<.0001
	SE	3.8	2.7	1.3			
	<i>n</i>	11	15	15			
Root dry biomass (g)	\bar{X}	6.9 ^A	3.5 ^B	1.3 ^C	27.72	2,38	<.0001
	SE	1.2	0.5	0.2			
	<i>n</i>	11	15	15			
Stem diameter (mm)	\bar{X}	4.4 ^A	5.0 ^A	4.0 ^A	1.29	2,38	>.287
	SE	.05	0.5	0.3			
	<i>n</i>	11	15	15			
Plant height (cm)	\bar{X}	66.2 ^A	57.5 ^A	65.6 ^A	2.15	2,38	>.130
	SE	4.0	2.8	3.8			
	<i>n</i>	11	15	15			
B. Under Pine							
Flowers per plant	\bar{X}	138.5 ^A	94.9 ^A	52.6 ^B	12.76	2,40	<.0001
	SE	16.1	13.2	5.1			
	<i>n</i>	13	16	14			
Fruits per plant	\bar{X}	48.0 ^A	38.1 ^{A,B}	23.9 ^B	3.41	2,40	<.040
	SE	9.4	5.2	4.1			
	<i>n</i>	13	16	14			
Seeds per fruit	\bar{X}	9.9 ^A	9.0 ^A	11.2 ^A	0.34	2,35	>.716
	SE	1.1	1.0	1.8			
	<i>n</i>	12	14	10			
Seed dry mass (mg)	\bar{X}	0.78 ^A	0.64 ^A	0.85 ^A	0.99	2,35	>.381
	SE	0.1	0.1	0.1			
	<i>n</i>	12	14	10			
Stem and leaf dry biomass (g)	\bar{X}	18.8 ^A	9.4 ^B	6.2 ^B	13.74	2,40	<.0001
	SE	2.8	1.2	0.6			
	<i>n</i>	13	16	14			
Root dry biomass (g)	\bar{X}	3.7 ^A	3.0 ^A	1.5 ^B	10.98	2,40	<.0002
	SE	0.5	0.3	0.2			
	<i>n</i>	13	16	14			
Stem diameter (mm)	\bar{X}	4.0 ^A	4.1 ^A	3.9 ^A	0.01	2,40	>.997
	SE	0.3	0.3	0.2			
	<i>n</i>	13	16	14			
Plant height (cm)	\bar{X}	70.2 ^A	53.8 ^B	64.5 ^{A,B}	9.39	2,40	<.0005
	SE	2.4	3.0	3.0			
	<i>n</i>	13	16	14			

* Some plants experienced natural herbivory by deer and elk, others were clipped to simulate herbivory, and uneaten plants served as controls. Alpha levels were adjusted to .01 for all multiple-range tests to correct for multiple comparisons. Means with the same superscript letters show no significant differences at the .01 level, least significant difference multiple-range test. *n* = number of plants. Tests were run on log-transformed or log(*y* + 1)-transformed data to equalize variances.

there were no significant differences between treatments [Table 1] or among plants in stem diameter between these two habitat types, $F = 1.39$, $df = 5,78$, $P = .24$). Plants were ≈ 10 cm in height at the time of browsing. Plants that were experimentally clipped were chosen from the remaining pool of unbrowsed individuals following herbivory. The clipping treatments occurred ≈ 1 – 2 wk following natural herbivory, and the plants were therefore more advanced phenologically. Previous studies (Paige and Whitham 1987a) failed to show significant differences in relative fitness between naturally browsed and experimentally clipped plants, arguing that plant selectivity by herbivores had no effect on *I. aggregata*'s ability to compensate or, alternatively, that herbivores were not selective. Therefore, plants within a treatment likely represented unbiased samples for comparisons. However, these results represent only a single experiment. Therefore, an experimental clipping treatment was incorporated. At the end of the flowering season plants were harvested and compared in terms of the number of flowers produced, number of fruits produced, number of seeds per fruit, seed dry mass, plant height, root dry mass, and shoot dry mass.

Plants were not protected from subsequent herbivory by vertebrates or insects. Repeated bouts of vertebrate herbivory were rare at the lower-elevation site (Northland Press). Insect herbivores (primarily stem-boring and meristem-feeding moths, *Sparganothis belfrageana* and *Heliothis phloxiphaga*, respectively) feed on *I. aggregata* at this site, and can cause a response similar to that caused by vertebrate herbivores (releasing apical dominance; K. N. Paige, *personal observation, unpublished data*). Early-instar larvae, which typically feed on or bore into rapidly dividing meristematic tissue, were likely removed through ingestion by vertebrate herbivores early in the season prior to the production of lateral shoots. Experimental clipping also caused the removal of any early-instar larvae present prior to lateral shoot induction. All plants, including controls, were carefully checked to ensure that there were no moth herbivores present before inclusion in these experiments.

Effects of secondary herbivory on scarlet gilia.—To assess the effects of secondary herbivory on *I. aggregata*, two experiments were conducted at a high-elevation site (Fern Mountain) where insect herbivores are rare and secondary herbivory is common. Plants were browsed by mule deer and elk. All plants in this experiment were growing within a few centimetres (10–20) of the grass *Bromus inermis*.

In the first experiment (1986), 30 plants of similar size (mean basal stem diameter = 4.5 mm, range 3–7 mm, $F = 0.12$, $df = 2,29$, $P > .888$; see Table 3) were selected early in the season prior to flowering (late May). Ten plants had previously been browsed by ungulate herbivores (in mid-May), 10 plants were experimentally clipped (removing $>95\%$ of their aboveground

biomass) to simulate natural herbivory by mule deer and elk (in late May), and the remaining 10 plants served as uneaten controls. As in the previous experiments (see above), experimentally clipped plants were selected from the pool of unbrowsed individuals following the initial bout of herbivory. At the end of the flowering season plants were harvested and compared in terms of number of flowering shoots produced, plant height, number of flowers produced, number of fruits produced, number of seeds per fruit, seed dry mass, root dry mass and shoot dry mass. Because many plants experienced secondary herbivory during the course of the flowering season, a second experiment was conducted in 1987 to determine the effects of differential herbivory on scarlet gilia.

In the second experiment (1987), plants of similar size (mean basal stem diameter = 5.1 mm, range 4–6 mm, $F = 1.95$, $df = 3,39$, $P > .138$; see Table 4) were selected late in the flowering season (late August) following ungulate herbivory. Because the compensatory response resulting from simulated herbivory (for plants selected from the remaining pool of uneaten individuals following herbivory) is similar to that generated by natural herbivory (Paige and Whitham 1987a; see also Table 3), plant selection by herbivores appears random; thus, clipping experiments were unnecessary, and the treatments represent an unbiased sample of all plants (see also Strauss 1988). Four different groups of plants were selected: (1) plants naturally browsed once by ungulate herbivores (in which 95% of the above-ground biomass had initially been removed), (2) plants naturally browsed more than once by ungulate herbivores, (3) single-stemmed plants browsed after plants initiated flowering, and (4) an uneaten control group. 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 and seed dry mass.

Additionally, censuses were conducted to determine the yearly patterns of ungulate herbivory by mule deer and elk on Fern Mountain. Censuses were conducted by randomly selecting 100 plants each year (at the end of the season) and documenting the level of herbivory on each.

Multiple clipping experiments were also conducted to assess the effects of repeated stem removal on the growth and reproductive success of *I. aggregata*. Forty plants of similar size (mean basal stem diameter = 6.3 mm, $F = 2.06$, $df = 3,39$, $P > .124$) were selected in late May (1986) during the period of stem elongation, prior to flowering. Thirty plants were randomly selected and clipped, removing $\approx 95\%$ of the above-ground biomass. In early July, following growth compensation and bud formation, 20 of the previously clipped plants were randomly selected and clipped a second time, again removing $\approx 95\%$ of the above-ground biomass. One month later, again following growth compensation, 10 of the previous 20 plants

were randomly selected and clipped a third time, removing $\approx 95\%$ of the aboveground biomass. Ten plants served as unmanipulated controls. At the end of the flowering season plants were compared in terms of the number of flowers and fruits produced.

Effects of plant architecture on subsequent herbivory.—Observations on the patterns of secondary feeding on *I. aggregata* in 1986 led to follow-up experiments in 1987 and 1989 to determine whether plant architecture or a change(s) in plant quality (e.g., reduced palatability through increased toughness, a change in nutritional quality, or an induced defense) reduced the level of subsequent herbivory. In 1987, 45 “triplets” were selected early in the season during the period of stem elongation. Sets of “triplets” were comprised of two elongating browsed individuals and one elongating unbrowsed individual similar in size and height and all growing within ≈ 1 m of one another. Half of the browsed plants (45) were experimentally clipped, removing all inflorescences except for one (i.e., an experimentally created single-stemmed plant). These plants were checked periodically, and newly developing inflorescences were removed. The remaining 90 plants served as unmanipulated controls (45 uneaten single-stalked and 45 multiple-stalked plants). As mentioned above, because the compensatory response resulting from simulated herbivory (for plants selected from the remaining pool of uneaten individuals following herbivory) is similar to that generated by natural herbivory (Paige and Whitham 1987a; see also Table 3), plants within treatments represent unbiased samples of all plants. Plants were marked and subjected to natural herbivory by mule deer and elk. After ≈ 1 mo plants were checked for the presence and extent of browse damage. This experiment was repeated in 1989 using 31 triplets. In addition, the amount of tissue removed by subsequent browsing (percentage of stem removal) from each plant in 1987 was also estimated by comparing adjacent uneaten individuals of similar size and stature to eaten individuals.

If single-stemmed plants (both natural and experimental) showed significantly higher levels of browse damage than multiple-stemmed plants, then results would suggest that plant architecture alone can affect subsequent herbivory. However, if natural single-stalked plants showed higher browse damage than either experimentally created single-stemmed or multiple-stemmed plants, one would conclude that there was some associated change in plant quality that reduced subsequent herbivory and that plant architecture would make little difference.

RESULTS

Plant association and the compensatory outcome

When plants were found in close association with pine or grasses (to add in the potential negative effects

of competition), browsed plants still outperformed control plants. Plants that were naturally browsed or experimentally clipped produced significantly more flowers and fruits than uneaten control plants (Tables 1A and B; least significant difference multiple-range test, $P < .01$). For example, when growing in association with grasses, browsed individuals produced 3.2 times as many flowers and 2.5 times as many fruits as plants that were not browsed. Similarly, experimentally clipped plants produced 2.0 times as many flowers and 2.3 times as many fruits as control plants.

Browsed plants growing in close association with pine produced 2.6 times as many flowers and 2.0 times as many fruits as plants that were not browsed. Furthermore, experimentally clipped plants produced 1.8 times as many flowers and 1.6 times as many fruits on the average as uneaten controls (fruit-set was, however, not statistically different from either naturally browsed or uneaten control plants). Because there were no significant differences in the numbers of seeds produced per fruit or seed mass among the three treatment groups (Tables 1A and B), fruit-set reflects relative plant fitness (as in Paige and Whitham 1987a). Although there were no significant differences in those measures most closely associated with true fitness (i.e., fruits per plant, seeds per fruit, or seed mass) between naturally browsed and experimentally clipped plants, the significantly lower means in other plant attributes reflect the delay in the timing of the experimental clip, which was performed 1–2 wk following natural herbivory (Table 1). Because sample sizes were relatively low, post hoc power analyses were conducted for each nonsignificant result for each experiment to assess the power of the *F* test (Cohen 1988: 359). In every case sample sizes were adequate to conclude that the null hypothesis is true at an alpha level of 5% with a 99% probability.

As in earlier studies (Paige and Whitham 1987a, K. N. Paige, unpublished data), both above- and belowground biomass was significantly greater for naturally browsed plants following regrowth (Tables 1A and B; least significant difference multiple-range test, $P < .01$), even though plants were initially of the same size (as measured by stem diameter). Therefore, aboveground compensation did not come at the expense of belowground biomass.

Secondary herbivory and the compensatory outcome

Over the 5-yr period of this study, on the average, 77% of all plants were browsed by ungulate herbivores sometime during the flowering season. Of these, 33% were subsequently browsed (Table 2).

The removal of *I. aggregata*'s single inflorescence stimulated the production of, on average, five new flowering stalks from dormant lateral buds along the remaining portion of the plant's stem (Table 3; Paige and Whitham 1987a, K. N. Paige, unpublished data). Although regrowth shoots were avoided by ungulates

TABLE 2. Percentage of plants browsed by ungulate herbivores on Fern Mountain (Arizona) over a 5-yr period from 1986 through 1990.

Year	Percentage of plants browsed	Percentage of plants secondarily browsed	Percentage uneaten
1986	80	23	20
1987	66	36	34
1988	64	31	36
1989	83	36	17
1990	91	39	9
5-year average	77	33	23

following the removal of scarlet gilia's single inflorescence, plant tips were secondarily browsed following stem elongation and flower bud formation (with ungulates removing, on average, ≈ 7 cm of plant material per inflorescence). Plants responded by producing additional lateral shoots and flowers.

As in previous studies (Paige and Whitham 1987a, K. N. Paige, unpublished data), plants that were naturally browsed produced significantly higher numbers

of flowers and fruits than plants that were not eaten, even when plants were secondarily browsed (results below and Table 4). In the 1986 experiment plants that were naturally browsed or experimentally clipped produced 2.3 times as many flowers and 1.5 and 1.7 times as many fruits, respectively, as plants that were not browsed (Table 3; least significant difference multiple-range test, $P < .01$). No significant differences in the numbers of seeds produced per fruit or seed mass among the three treatment groups were found (Table 3; least significant difference multiple range test, $P < .01$).

The 1987 experiment, designed to separate the effects of a single bout of herbivory from the effects of multiple bouts of herbivory, showed that plants that were secondarily browsed fully compensated, producing more, though not significantly more, flowers and fruits than plants experiencing only a single bout of herbivory (Table 4). Plants browsed once or more than once also produced significantly more flowers (producing 1.9 and 2.4 times as many flowers, respectively) and fruit (producing 2.0 and 2.4 times as many fruits, respectively) than control plants that were not browsed (Table 4; least significant difference multiple-range test, $P < .01$). Because there were no significant differences

TABLE 3. Comparisons of nine measures of relative fitness for scarlet gilia, *Ipomopsis aggregata*, on Fern Mountain (Arizona).*

Fitness measure		Natural herbivory	Simulated herbivory	Control (no herbivory)	F	df	P
Flowers per plant	\bar{X}	261.8 ^A	259.0 ^A	114.3 ^B	11.04	2,29	<.0003
	SE	50.6	26.6	14.6			
	n	10	10	10			
Fruits per plant	\bar{X}	82.7 ^{A,B}	91.2 ^A	54.7 ^B	3.35	2,29	<.050
	SE	11.9	14.1	7.7			
	n	10	10	10			
Seeds per fruit	\bar{X}	7.4 ^A	7.6 ^A	9.9 ^A	1.89	2,26	>.174
	SE	0.8	0.7	1.2			
	n	10	9	8			
Seed dry mass (mg)	\bar{X}	1.4 ^A	1.3 ^A	1.3 ^A	0.11	2,26	>.898
	SE	0.2	0.2	0.2			
	n	10	9	8			
Stem and leaf dry biomass (g)	\bar{X}	16.9 ^A	17.7 ^A	11.9 ^A	2.16	2,29	>.134
	SE	3.8	1.9	2.2			
	n	10	10	10			
Root dry biomass (g)	\bar{X}	4.0 ^{A,B}	5.2 ^A	2.6 ^B	5.96	2,29	<.007
	SE	0.5	0.7	0.4			
	n	10	10	10			
Stem diameter (mm)	\bar{X}	4.4 ^A	4.6 ^A	4.5 ^A	0.12	2,29	>.888
	SE	0.3	0.3	0.4			
	n	10	10	10			
Plant height (cm)	\bar{X}	53.7 ^A	53.0 ^A	58.4 ^A	0.81	2,29	>.456
	SE	2.5	3.0	3.3			
	n	10	10	10			
Stem number	\bar{X}	5.1 ^A	5.8 ^A	1.0 ^B	140.08	2,29	<.0001
	SE	0.6	0.3	0.0			
	n	10	10	10			

* Some plants experienced natural herbivory by deer and elk, others were clipped to simulate herbivory, and uneaten plants served as controls. Alpha levels were adjusted to the .01 level for all multiple-range tests to correct for multiple comparisons. Means with the same letters show no significant differences at the .01 level, least significant difference multiple-range test. n = number of plants. Tests were run on log-transformed or log(y + 1)-transformed data to equalize variances.

TABLE 4. Effects of timing and secondary herbivory on the compensatory outcome in scarlet gilia, *Ipomopsis aggregata*, in Arizona.*

Fitness measure		Initial herbivory, early season (on single-stemmed plant)	Secondary herbivory (on multiple-stemmed plant)	Initial herbivory, late season (on single-stemmed plant)	Control (no herbivory)	<i>F</i>	df	<i>P</i>
Flowers per plant	\bar{X}	280.80 ^A	347.90 ^A	132.90 ^B	146.80 ^B	13.73	3,39	<.0001
	SE	28.7	47.0	17.3	20.6			
	<i>n</i>	10	10	10	10			
Fruits per plant	\bar{X}	53.4 ^A	64.3 ^A	28.3 ^B	27.1 ^B	4.99	3,39	<.005
	SE	9.2	12.4	5.7	4.6			
	<i>n</i>	10	10	10	10			
Seeds per fruit	\bar{X}	10.3 ^A	10.5 ^A	13.7 ^A	7.2 ^A	1.71	3,26	>.193
	SE	1.6	1.1	2.2	1.8			
	<i>n</i>	10	7	5	5			
Seed dry mass (mg)	\bar{X}	1.5 ^A	1.7 ^A	1.6 ^A	1.5 ^A	0.55	3,26	>.654
	SE	0.1	0.2	0.2	0.3			
	<i>n</i>	10	7	5	5			
Stem diameter (mm)	\bar{X}	5.0 ^A	5.3 ^A	5.2 ^A	4.8 ^A	1.95	3,39	>.138
	SE	0.2	0.2	0.2	0.1			
	<i>n</i>	10	10	10	10			
Plant height (cm)	\bar{X}	54.1 ^A	55.6 ^A	59.7 ^A	59.0 ^A	0.51	3,39	>.680
	SE	2.6	3.0	3.6	3.7			
	<i>n</i>	10	10	10	10			
Stem number	\bar{X}	4.7 ^A	6.0 ^A	1.0 ^B	1.0 ^B	115.83	3,39	<.0001
	SE	0.4	0.6	0.0	0.0			
	<i>n</i>	10	10	10	10			

* Some plants experienced natural herbivory by deer and elk; other plants served as uneaten controls. Alpha levels were adjusted to .01 for all multiple-range tests to correct for multiple comparisons. Means with the same letters show no significant differences at the .01 level, least significant difference multiple-range test. *n* = number of plants. Tests were run on log-transformed or log(*y* + 1)-transformed data to equalize variances.

in the numbers of seeds produced per fruit or seed mass among the four treatment groups (Table 4; least significant difference multiple-range test, *P* < .01), an increase in the total number of fruits produced by browsed plants resulted in an increase in relative plant fitness.

Approximately 13.5% of all plants were browsed after flowering. These single-stemmed plants equally compensated, producing as many flowers and fruits as uneaten control plants (Table 4). These plants, however, produced significantly fewer flowers and fruits than plants that were browsed once early in the season or individuals browsed more than once. These plants typically produced short lateral shoots and additional flowers along the length of the remaining stem.

Plant architecture and subsequent herbivory

Although *I. aggregata* initially benefits from high levels of mammalian herbivory, high levels of secondary herbivory on these same individuals would be detrimental. For example, when regrowth shoots (the new multiple inflorescences that are produced following removal of the plant's single inflorescence) were experimentally clipped (removing 95% of the aboveground biomass) to simulate high levels of secondary herbivory, plant fitness decreased by ≈70% (Table 5). Field

results, however, showed that compensatory growth by *I. aggregata* was accompanied by an apparent change in either plant quality or plant architecture that reduced the amount of tissue subsequently removed.

Experimental results designed to test the effects of plant architecture on plant herbivory did not support the idea that a change in plant architecture deterred high levels of secondary herbivory on *I. aggregata*. In 1987, 30% of the single-stemmed plants were browsed, 20% of the multiple-stemmed plants were browsed, and 12% of the experimental single-stemmed plants were browsed ($\chi^2 = 3.95$, *df* = 2, *P* > .15). In the 1989 experiment, 67% of the single-stemmed plants were browsed, 54% of the multiple-stemmed plants were browsed, and 46% of the experimental single-stemmed plants were browsed ($\chi^2 = 2.33$, *df* = 2, *P* > .30).

Although no significant differences in plant selection by ungulate herbivores were found among the three treatment groups in either year, there was a trend toward the selection of natural single-stemmed plants by ungulate herbivores. More importantly, there was a significantly greater amount of tissue removed from natural single-stemmed plants (66.2% of the stem, on average) than from either multiple-stemmed plants (14.1%) or experimental single-stemmed plants (24.8%) in these experiments (least significant difference mul-

TABLE 5. Effects of repeated stem removal on the reproductive success of scarlet gilia, *Ipomopsis aggregata* in Arizona. Approximately 95% of the aboveground biomass was experimentally clipped following stem elongation and flower bud formation.*

Date	Treatment		Flowers per plant	Fruits per plant
30 May	Unmanipulated control	\bar{X}	254.3 ^A	106.8 ^A
		SE	27.0	22.1
		<i>n</i>	10	10
30 May	1st clip	\bar{X}	490.1 ^A	248.7 ^B
		SE	83.4	45.8
		<i>n</i>	10	10
1 July	2nd clip	\bar{X}	258.8 ^A	78.2 ^A
		SE	38.2	9.5
		<i>n</i>	10	10
3 August	3rd clip	\bar{X}	34.2 ^B	2.1 ^C
		SE	5.7	0.8
		<i>n</i>	10	10
			$F = 37.31;$	$F = 61.98;$
			$df = 3,39;$	$df = 3,39;$
			$P < .0001$	$P < .0001$

* Alpha levels were adjusted to the .01 level for all multiple-range tests to correct for multiple comparisons. Means with the same letters show no significant differences at the .01 level, least significant difference multiple-range test. *n* = number of plants. Tests were run on log-transformed or log(*y* + 1)-transformed data to equalize variances.

multiple-range test, $P < .05$). Thus, there appears to be some change in plant quality that deters high levels of subsequent herbivory on plants that had been previously browsed.

DISCUSSION

Plant association and the compensatory outcome

In recent reviews Belsky (1986, 1987) suggested that overcompensation would most likely occur where grazing is moderate and where species grow in monoculture, free of interspecific competition. Results here, however, demonstrate that plant association and exceptionally high levels of mammalian herbivory (in which 95% of the aboveground biomass was removed) did not alter the compensatory outcome, thus failing to lend support to Belsky's premise. Although the two habitat types provide differing environmental regimes (varying in terms of light, nutrients, water, soil pH, and plant competitors), browsed plants clearly outperformed uneaten control plants irrespective of association. Browsed plants growing in close association with either grasses or pines, for example, produced significantly greater numbers of seeds than uneaten control plants. Furthermore, no significant differences in seed quality, as measured by mass, were found. Thus, as in an earlier study (Paige and Whitham 1987a), there is an immediate reproductive advantage to being eaten.

Whereas Maschinski and Whitham (1989) showed that *I. arizonica* required nutrient supplements for overcompensation to occur on the nutrient-poor soils of Sunset Crater (near Flagstaff, Arizona), *I. aggregata* naturally overcompensated (increased the number of flowers as well as fruits produced). Perhaps this was due to the fact that soil nutrients are as much as 10

times as high on the sites where these studies were conducted as on the Sunset Crater site (Maschinski and Whitham 1989), suggesting that nutrients are not limiting.

Plant architecture, secondary herbivory, and the compensatory outcome

Although ecologists have recognized some of the evolutionary responses by plants to herbivory, such as the production of antiherbivore chemicals and mechanical defenses, other responses, such as compensatory plant growth and alteration of growth form, have not been as well studied (Janzen 1979, Inouye 1982). Even less is known about defensive plasticity (i.e., the use of alternative defenses in response to changing conditions). Typically we view plants as having only a single response (or line of defense) to herbivory, ignoring the potential for alternative avenues in response to changing conditions.

Although *I. aggregata* initially benefits from high levels of mammalian herbivory, high levels of secondary herbivory on these same individuals would be detrimental. For example, when regrowth shoots (the new multiple inflorescences that are produced following removal of the plants single inflorescence) were experimentally clipped (removing $\approx 95\%$ of the aboveground biomass), to simulate high levels of secondary herbivory by mule deer and elk, plant fitness decreased by $\approx 70\%$.

In regrowth shoots, however, only tips of the newly formed inflorescences were naturally browsed following stem elongation and flower bud formation. This secondary bout of herbivory, in which only a small portion of the plant's stem was removed, had no effect on the compensatory outcome (Table 4); i.e., plants that were secondarily browsed fully compensated, pro-

ducing as many flowers, fruits, and seeds as plants experiencing only a single bout of herbivory, and significantly more flowers, fruits, and seeds than uneaten control plants. There was, however, a small percentage (13.5%) of plants that were initially browsed only after the onset of flowering (Table 4). These single-stemmed plants equally compensated, producing as many flowers and fruits as uneaten control plants. Thus, early-season herbivory or multiple bouts of herbivory resulted in overcompensation by *I. aggregata*, while late-season herbivory on single-stemmed plants that had already flowered resulted in equal compensation. Therefore, the timing of herbivory is an important factor influencing the degree to which a plant can compensate (see also Maschinski and Whitham 1989). Nonetheless, at the population level the most common response was still one of overcompensation.

Mutualistic to antagonistic interactions: mechanisms

The mechanisms involved in *I. aggregata*'s switch from a "mutualistic" interaction to an "antagonistic" interaction likely includes a change(s) in plant quality (e.g., reduced palatability through increased toughness, a change in nutritional quality, or an induced defense). Although changes in plant architecture alone could alter ungulate feeding behavior, experiments designed to test the effects of plant architecture on subsequent herbivory did not support the idea that a change in plant architecture deterred high levels of secondary herbivory on *I. aggregata*.

Although the phytochemistry of *I. aggregata* has not been extensively investigated, it is known to contain a number of phenolic compounds, including hydroquinone, scopoletin, related coumarin derivatives, and cucurbitacins, primarily cucurbitacin B (Arisawa et al. 1984a, b, c). Cucurbitacins, in particular, are bitter triterpenes that are highly toxic to vertebrate herbivores (David and Vallance 1955, Guha and Sen 1975, Metcalf 1985); these compounds are induced in other systems by herbivore feeding (Tallamy and Krischik 1989). Studies are presently under way to assess the potential role of cucurbitacins in deterring ungulate feeding in *I. aggregata*.

Evolutionary implications

Before we can begin to understand the evolutionary interactions between plants and herbivores, it is necessary to ascertain the past and present selective pressure(s) involved in generating the observed plant-response patterns. Apical damage, for example, could be caused by a number of factors other than herbivory, including frost damage, desiccation, fire, pathogen attack, trampling, and breakage by wind (Benner 1988). The most likely selective agents involved in the destruction of apical dominance in this system, other than herbivory, include fire (which was a historical component of the system) and freeze damage (K. N. Paige,

personal observation). Recent experimental results (Paige 1992), however, have shown that neither fire nor freeze damage generate the observed response patterns. From an evolutionary perspective, given that herbivory is predictably high each year (77% of all plants are eaten, on average; Table 2), herbivory likely represents the major selection pressure favoring overcompensation. Furthermore, these results are consistent with the theoretical results of Van Der Meijden (1990), which indicate that if the probability of an individual being eaten is >50%, an evolutionary advantage will accrue to genotypes capable of vigorous multistemmed regrowth following attack.

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