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Regrowth following ungulate herbivory in *Ipomopsis aggregata*: geographic evidence for overcompensation

Received: 15 July 1998 / Accepted: 9 November 1998

Abstract Studies were conducted on eight populations of scarlet gilia, *Ipomopsis aggregata*, across Colorado and in northern Arizona, to assess the fitness consequences of natural and simulated herbivory. To date, geographic studies have failed to incorporate treatment groups that included naturally browsed plants along with clipping treatments. The results presented here clearly demonstrate the importance of assessing, a priori, whether or not clipping experiments accurately reflect natural patterns of herbivory. Although because of the timing of the clip no evidence of overcompensation was found in any of the Colorado populations when ungulate herbivory was simulated in experimental clipping treatments, evidence for overcompensation was found in more than half the populations when plants that were naturally browsed and matched for size using root diameters were included early in the season. Matching plants for size based on root diameter late in the season would be problematic because root diameters significantly increased in size in all eight populations following high levels of ungulate herbivory and/or experimental clipping. Results from this study, and other recent studies on another biennial herb, the field gentian, clearly demonstrate that overcompensation is not only a real phenomenon but also is more widespread, both taxonomically and geographically, than previously thought.

Key words Overcompensation · Ungulate herbivory · Geographic variation · *Ipomopsis aggregata*

Introduction

In 1987, studies showed that when mule deer and elk browsed the monocarpic biennial scarlet gilia, *Ipomopsis aggregata*, seed production and subsequent seedling survival averaged 2.4 times that of the uneaten controls (Paige and Whitham 1987). Subsequent studies (Paige 1992, 1994; Gronemeyer et al. 1997; J. Maschinski and K.N. Paige, unpublished work) confirmed and extended our initial findings. However, studies by Bergelson and Crawley (1992a,b), suggested that overcompensation by scarlet gilia is restricted to a limited portion of its range (i.e., to a few populations in northern Arizona). In a more recent paper, Bergelson et al. (1996) contend that there is no compelling evidence of overcompensation in natural populations of scarlet gilia (due to possible methodological problems associated with matching plants for size), or in any other plant species, and that until such evidence is produced we should revert, for reasons of parsimony, to the conventional view that herbivory is deleterious to the individuals that are grazed.

In this study the effects of experimental clipping and natural herbivory on eight populations of scarlet gilia across much of Colorado and northern Arizona were assessed, including two populations previously studied by Bergelson et al. (1996) and one new hybrid subspecies from three populations. Plants were initially matched for size on the basis of root and shoot diameter in an effort to directly address the concerns of Bergelson et al. (1996) that plants have been consistently mismatched for initial size by using shoot diameter instead of root diameter (see also Gronemeyer et al. 1997). Although arguments have centered primarily upon appropriate methodology, this study shows that arguments have not been fully resolved due in part to the gathering of partial data sets, i.e., Bergelson et al. (1996) omit naturally browsed plants, and perhaps also to the geographical locations in which the studies took place.

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Materials and methods

Study sites and organisms

Field studies on scarlet gilia, *I. aggregata*, were conducted during the summer of 1996 in eight populations located in northern Arizona and throughout much of Colorado. Populations included one located in Kebler Pass near Crested Butte (*I. aggregata aggregata*) in southwestern Colorado, three near Eleven Mile Reservoir (*I. a. collina* × *I. a. candida*) west of Colorado Springs in south central Colorado, one at Minturn (*I. a. aggregata*) in central Colorado, two at Lynx Pass (*I. a. aggregata*) in north central Colorado and one in north central Arizona at Northland Press (*I. a. formosissima*) northwest of Flagstaff, Arizona.

Scarlet gilia is a monocarpic, hermaphroditic, biennial/perennial herb that flowers from mid-June through late September. Following germination, scarlet gilia develops into a leafy rosette approximately 12 cm in diameter. After 1–8 years in a vegetative state, it sends up a single stalk that flowers, reproduces once, and then dies. As it is reproductive for only 1 year it is ideal for acquiring measures of lifetime fitness. Scarlet gilia is self-incompatible and pollinated by two species of hummingbird, the rufous hummingbird, *Selasphorus rufus*, and the broad-tailed hummingbird, *S. platycercus*, and a single species of hawkmoth, the white-lined sphinx, *Hyles lineata*.

I. aggregata populations are most commonly browsed by two vertebrate herbivores, mule deer, *Odocoileus hemionus*, and elk, *Cervus elaphus*. These herbivores remove the rapidly dividing meristematic tissue of *I. aggregata*, commonly taking 95% of the aboveground biomass (Paige and Whitham 1987; Paige 1992, 1994; Gronemeyer et al. 1997). Removal of the meristem causes a compensatory response by the plant, inducing a single-stalked plant to produce on average four or five lateral shoots from the remaining portion of the plant's stem. In Arizona, this change in plant architecture has been shown to result in an increase in flower and fruit production. Because no significant differences were found 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 results in an increase in maternal fitness (Paige and Whitham 1987; Paige 1992, 1994). Furthermore, experimental and genetic studies in Arizona have recently shown that ungulate herbivory on scarlet gilia results in an increase not only in maternal, but in paternal fitness as well, through an increase in flower production (Gronemeyer et al. 1997).

Experimental design

To assess the effects of experimental clipping and ungulate herbivory on scarlet gilia, 22–52 plants per population were randomly chosen and divided among three treatment groups (uneaten control, naturally browsed to 1 cm in height, and experimentally clipped to 1 cm in height) in each of six of the eight populations studied. In three (Lynx Pass-Montane, Lynx Pass-Sagebrush, Kebler Pass) of the six populations, naturally browsed treatments were added at the end of the flowering season. These populations had either not been browsed at the time the clipping treatments were employed (on 25 May; Lynx Pass-Montane and Lynx Pass-Sagebrush) or were not naturally browsed in the area where the clipping treatment was conducted [Kebler Pass; the naturally browsed treatment was added at the end of the flowering season but in an area adjacent (approximately 200 m away in similar habitat) to the area in which the clipping treatment was employed]. An additional (fourth) treatment group was added early in the season in the Arizona population (Northland); plants experimentally clipped to a height of 8 cm. Treatments were applied between 22 and 28 May in these six populations during the period of stem elongation prior to bud formation. On the day the treatments were applied, rootstock diameter and stem diameter were measured on each of the plants.

Rootstock diameter and stem diameter are highly correlated early in the flowering season ($R^2 = 0.602$, $P < 0.001$) and both represent accurate measures of plant size and reproduction (e.g., $R^2 = 0.656$, $P < 0.001$ and $R^2 = 0.655$, $P < 0.0001$ for the relationship between flower production and rootstock diameter and flower production and stem diameter, respectively). One-way ANOVAs on rootstock diameters ensured that plants were randomly assigned to treatments ($P > 0.05$ for each comparison at each site, with the exception of experimentally clipped plants at Lynx Pass-Montane, which had significantly larger root diameters at the beginning of the season).

Plants from the remaining two populations (Forest Service Road 90, $n = 113$, and Eleven Mile Reservoir II, $n = 38$) were randomly selected late in the flowering season (late July); plants included two (uneaten control, naturally browsed to 1 cm in height) and three treatment groups (uneaten control, naturally browsed to 1 cm in height, naturally browsed to 8 cm in height), respectively.

At the end of the flowering season in early October, plants were collected and measured. Measurements included the number of flowers and fruits produced, final stem diameter, and final root diameter. Each population was analyzed separately using an ANCOVA treating browsing treatment as a fixed effect and stem diameter as a covariate (for flower and fruit production). Root diameters were analyzed with a repeated-measures ANOVA followed by linear contrasts, with the exception of treatments that were measured only late in the season, i.e., measured only once. In those cases naturally browsed individuals were compared directly to uneaten controls using an ANCOVA with stem diameter as a covariate. When necessary, dependent variables were log-transformed to ensure normality and to homogenize variances.

Results

Results from this study support previous findings of overcompensation in Arizona in terms of flower and fruit production. Plants that were experimentally clipped down to a height of 1 cm or naturally browsed to a height of 1 cm produced 1.2 and 1.7 times as many flowers, respectively, and 1.6 times as many fruits as uneaten controls (Table 1). Plants clipped to heights of 8 cm produced a statistically indistinguishable number of flowers and fruits as uneaten controls, also in accord with previous results (Paige 1994). In addition, these experiments demonstrated that roots significantly increase in size following both natural herbivory and simulated herbivory when initially browsed or clipped down to a height of 1 cm. However, uneaten controls or plants that were clipped to heights of 8 cm showed no significant change in root diameter over the growing season (Table 2A).

Evidence for overcompensation was also found in Colorado. In six of seven Colorado populations, plants that were naturally browsed produced significantly more flowers than uneaten controls. In only one population of the five in which experimental clipping treatments were conducted was there evidence for increased flower production after clipping (Table 1A). In four of these populations plants that were naturally browsed also produced significantly more fruits. None of the plants that were experimentally clipped provided evidence of overcompensation in the five Colorado populations in

Table 2A A comparison of root diameters measured early in the flowering season (late May) with those measured again late in the season (early October) for plants that were experimentally clipped to 1 cm and 8 cm, plants that were naturally browsed by ungulate herbivores to 1 cm, and uneaten controls, across six populations in Colorado and Arizona. **B** In three populations (Lynx Pass-Sagebrush, Lynx Pass-Montane, and Kebler Pass) naturally browsed plants were only measured late in the season, so these were compared to late season uneaten controls. In two additional populations (Eleven Mile Reservoir II and Forest Service Road 90) measurements were acquired only at the end of the flowering season, so comparisons were made between naturally browsed plants and uneaten controls. Means with the same letters show no significant differences at the 0.05 level

Site and subspecies	Control						Clipped to 1 cm		Naturally browsed to 1 cm		Clipped to 8 cm		Repeated-measures ANOVA Root Treatment <i>F</i>	<i>df</i>	<i>P</i>
	Early season		Late season		Early season		Late season		Early season		Late season				
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE			
Northland Press, Ariz.	5.82 ± 0.41a	6.46 ± 0.41a	6.53 ± 0.38a	7.77 ± 0.41bc	6.94 ± 0.48a	8.63 ± 0.53c	6.18 ± 0.41a	7.18 ± 0.45ab	33.83	1,39	0.000				
<i>I. a. formosissima</i>	4.43 ± 0.26a	5.93 ± 0.40b	4.39 ± 0.26a	6.71 ± 0.40b	5.07 ± 0.37a	9.86 ± 0.56c	—	—	2.86	3,39	0.049				
Eleven Mile Reservoir I, Colo.	4.80 ± 0.32a	5.10 ± 0.32ab	4.75 ± 0.29a	5.67 ± 0.29b	—	—	—	—	162.00	1,32	0.000				
<i>I. a. collina</i> × <i>I. a. candida</i>	4.06 ± 0.32a	4.53 ± 0.28ab	4.65 ± 0.20b	5.50 ± 0.27c	—	—	—	—	10.80	2,32	0.000				
Lynx Pass, Colo.-Sagebrush	4.17 ± 0.29a	4.67 ± 0.36ab	4.40 ± 0.27a	5.20 ± 0.34b	—	—	—	—	12.08	1,9	0.007				
<i>I. a. aggregata</i>	5.34 ± 0.25ab	5.84 ± 0.33b	4.88 ± 0.24a	5.68 ± 0.32b	4.96 ± 0.31a	7.54 ± 0.41c	—	—	0.42	1,9	0.531				
Lynx Pass, Colo.-Montane	4.77 ± 0.32a	4.59 ± 0.19a	—	—	—	—	—	—	21.14	1,31	0.000				
<i>I. a. aggregata</i>	4.35 ± 0.22a	4.73 ± 0.28a	—	—	—	—	—	—	6.42	1,31	0.017				
Kebler Pass, Colo.	4.24 ± 0.43a	5.85 ± 0.33b	—	—	—	—	—	—	8.20	1,17	0.011				
<i>I. a. aggregata</i>	4.16 ± 0.24a	5.00 ± 0.23b	4.57 ± 0.35a,b	3.82	2,34	0.032	—	—	0.99	1,17	0.332				
Eleven Mile Reservoir II, Colo.	3.54 ± 0.17a	5.57 ± 0.18b	—	—	—	—	—	—	31.62	1,48	0.000				
<i>I. a. collina</i> × <i>I. a. candida</i>	—	—	—	—	—	—	—	—	3.84	2,48	0.028				

^a Stem diameter was used as a covariate

which clipping experiments were conducted (Table 1). Thus, evidence of overcompensation from clipping experiments was found only in Arizona, not in Colorado.

Evidence for a significant increase in root diameter was found in all five Colorado populations in which clipping experiments were performed (Table 2A). In all five populations plants that were experimentally clipped showed a significant increase in root diameter, and in three of the five populations plants that were naturally browsed showed a significant increase in root diameter [two populations, Eleven Mile Reservoir I and Minturn, in which naturally browsed plants were matched for size (root and stem diameter) early in the flowering season (Table 2A) and one, Kebler Pass, in which naturally browsed plants were matched for size (stem diameter) late in the flowering season (Table 2B)]. Evidence for increased root diameter was also found in two additional Colorado populations (Eleven Mile Reservoir II and Forest Service Road 90) in which naturally browsed plants were matched for stem diameter late in the season (Table 2B). Only plants that were naturally browsed or experimentally clipped down to 1 cm showed significant increases in root diameter. No significant increase in root diameter was found for plants that were experimentally clipped or naturally browsed to a height of 8 cm or more, consistent with previous results (see Paige 1994). At only one site (Eleven Mile Reservoir I) was there any evidence for uneaten control plants to show any significant change (in this case an increase) in root diameter (Table 2A).

In two of the six populations in which clipping experiments were conducted stem diameters of uneaten control plants increased significantly (Minturn and Northland Press) and stem diameter significantly decreased in one population (Lynx Pass-Sagebrush) for plants that were experimentally clipped down to a height of 1 cm ($P < 0.05$). No significant changes in stem diameter were found for plants that were naturally browsed in the three populations in which naturally browsed plants were matched for size early in the flowering season (Northland Press, Eleven Mile Reservoir I, and Minturn; $P > 0.05$). Thus, significant changes occurred in 3 of 16 stem diameter comparisons in which plants were measured for size early and again late in the season.

Discussion

Overcompensation: simulated versus natural herbivory

Results show that overcompensation in scarlet gilia is not only a real phenomenon, but is more widespread than previously thought. As in previous studies, overcompensation was found in northern Arizona for plants that were either experimentally clipped or naturally browsed down to a height of 1 cm. In addition, evidence for overcompensation was found in four of seven pop-

ulations in Colorado for plants that were naturally browsed. Experimental clipping, however, did not reflect natural herbivory in all Colorado populations (Fig. 1). Evidence of overcompensation from clipping experiments was only found in Arizona, not in Colorado. These results point out the importance of ensuring, a priori, that experimental clipping treatments accurately reflect natural patterns of herbivory, to avoid interpretational problems. Bergelson et al. (1996) concluded from clipping experiments alone that there is no evidence for overcompensation throughout most of scarlet gilia's geographic range. When natural herbivory is taken into account, however, half of the populations show evidence for overcompensation.

As Baldwin (1990) points out we need to proceed with caution when using mechanical damage to simulate natural patterns of herbivory, given that more often than not mechanical damage fails to adequately simulate true herbivory. There are several reasons as to why there might be differences in response when comparing mechanically and naturally damaged plants: (1) mechanical damage may not match the natural timing, amounts, types or ages of tissues eaten, (2) mechanical damage

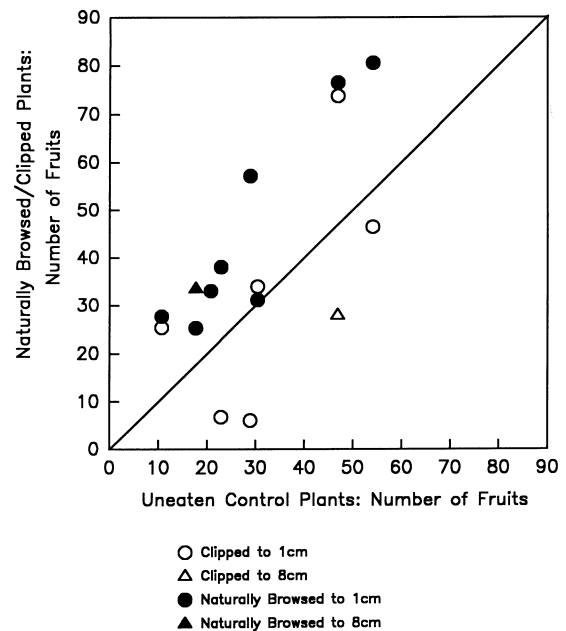


Fig. 1 Average number of mature fruits produced by experimentally clipped, naturally browsed, and uneaten control plants in the biennial herb scarlet gilia, *Ipomopsis aggregata*, for a total of 16 browsing/clipping treatments across eight populations in Colorado and Arizona. At the *diagonal compensation line*, clipped and naturally browsed plants produce equal numbers of fruits to uneaten controls. Clipped and naturally browsed plants overcompensate in treatments/populations located *above* the compensation line. Those located *below* the compensation line undercompensate. The majority of plants that were naturally browsed overcompensated, whereas the majority of plants that were experimentally clipped either equally compensated or undercompensated (with the exception of the Arizona population in which plants that were experimentally clipped to a height of 1 cm overcompensated)

may differ from herbivore damage in some physical attribute such as the amount of cellular tearing, which could cause qualitative or quantitative differences in damage cues and consequent defensive responses, and/or (3) herbivores may manipulate a plant's physiology through hormones present in saliva that could affect plant growth (Baldwin 1990).

The most parsimonious explanation for the differences in response between naturally browsed and experimentally clipped plants is that clipping experiments took place later than natural herbivory in some of the Colorado populations, limiting the amount of time available for growth compensation. In four of the six populations in which clipping experiments were conducted (Northland Press, Minturn, Eleven Mile Reservoir I, and Kebler Pass), a large proportion of the plants were definitely or probably already browsed by mammalian herbivores prior to the clipping treatments. (In the case of Kebler Pass no early direct observations were made on the adjacent area where the natural browsing data were collected, but the magnitude of overcompensation by naturally browsed plants nonetheless suggests that this was the case.) Observations suggested that plants in Colorado were browsed at least 3 weeks prior to the clipping experiments (which were designed to simulate the experimental clipping regime reported by Bergelson et al. 1996), and approximately 1 week earlier in Arizona, based on the amount of regrowth already achieved. Naturally browsed plants were approximately two-thirds the height of the uneaten controls at the time of clipping in Colorado and just beginning to send out shoots in Arizona. In three of the four populations, including Kebler Pass, Northland Press, and Minturn, naturally browsed plants overcompensated in terms of flower and fruit production. In the fourth population (Eleven Mile Reservoir I), naturally browsed plants produced significantly more flowers and a nonsignificant trend toward increased fruit production. In three of these populations, however, experimentally clipped plants only equally compensated or undercompensated (Eleven Mile Reservoir I, Kebler Pass and Minturn). Only in Arizona (Northland Press) did experimentally clipped plants overcompensate. However, even in Arizona, plants that were experimentally clipped to 1 cm produced flowers intermediate in number between naturally browsed and uneaten control plants. These results suggest that naturally browsed plants had a significant time advantage over those that were experimentally clipped, particularly in Colorado; timing is known to be important in maximizing growth compensation (Oosterheld and McNaughton 1988, 1991; Paige 1994; Bergelson et al. 1996; Lennartsson et al. 1998). Previous experimental studies in Arizona, for example, have shown that as little as a 2-week difference in the timing of damage can cause as much as a two-fold difference in plant reproductive success (see Table 3 in Paige 1994).

Overall, it is unlikely that clipping experiments inherently fail to reflect natural patterns of herbivory. Studies in Arizona have consistently shown that exper-

imental clipping accurately simulates natural herbivory if the timing of the clip is closely matched to natural patterns of herbivory (Paige and Whitham 1987; Paige 1992, 1994). The same appears to be true in Colorado populations. In the two Lynx Pass populations in which natural herbivory occurred following the experimental clip, clipping reflected natural herbivory, indicating that timing was not a significant factor at these sites. In addition, none of the above results can be explained by size selection differences because plants were matched for size in these experiments. It is also unlikely that herbivores selectively choose genotypes with more vigorous regrowth capabilities. Experimentally clipped plants in Arizona consistently simulate natural herbivory even though these plants are chosen from the remaining pool of uneaten individuals immediately following natural herbivory (see Strauss 1988). Results from the Lynx Pass populations, where the responses of experimental clipping treatments and natural herbivory were similar, and the timing of the treatments was close, also support this notion. In sum, the above results indicate a variety of responses across the geographic range of this species and illustrate the importance of including natural herbivory in the experiment.

Potential for overcompensation

Evidence for increased flower production was found in seven of the eight populations following natural herbivory and/or experimental clipping. These results suggest that some of the observed variation in fitness compensation may be environmentally induced (e.g., due to pollen limitation and/or nutrient availability), not due to an innate inability to overcompensate, although the magnitude of floral production and compensation following herbivory is greater in some populations/subspecies than in others. Juenger and Bergelson (1997) recently showed that growth compensation in Colorado populations of *I. a. candida* increased seed production following the combined treatments of clipping, hand pollination, and nutrient addition. Some of the individuals in this treatment combination overcompensated, although at the population level the response was primarily one of equal compensation (Juenger and Bergelson 1997, see their Fig. 1 for 1995). Thus, there is the potential for overcompensation in terms of maternal fitness to occur in the majority of populations, but the potential may not be reached due to environmental constraints. There is also the possibility that when the paternal contribution to fitness is included, given increased flower production by browsed plants, overcompensation might be the norm for *Ipomopsis*. Using a combination of experimental and genetic approaches we have recently shown in an Arizona population that ungulate herbivory on scarlet gilia results in an increase in paternal, as well as maternal, fitness through an increase in flower production (Gronemeyer et al. 1997).

Matching plants for size

Results also show that matching plants for size based on root diameter late in the season (as in Bergelson and Crawley 1992a) would be problematical, because root diameters increased significantly in six of eight populations as a result of high levels of ungulate herbivory (i.e., where 95% of the above ground biomass is removed leaving approximately 1 cm of the main shoot) and in all six populations in which plants were experimentally clipped (again leaving approximately 1 cm of the main shoot) (Fig. 2). These results suggest that browsed and unbrowsed plants were mismatched for size in the 14 populations previously studied by Bergelson and Crawley (1992a), biasing their results toward finding evidence for equal or undercompensation rather than overcompensation.

In one of two populations also studied by Bergelson et al. (1996) evidence was found for an increase in root diameter from clipping experiments conducted in Lynx Pass-Sagebrush, contrary to their findings. There was, however, no evidence for an increase in root diameter for naturally browsed plants when compared to uneaten controls, although at this site early-season measures

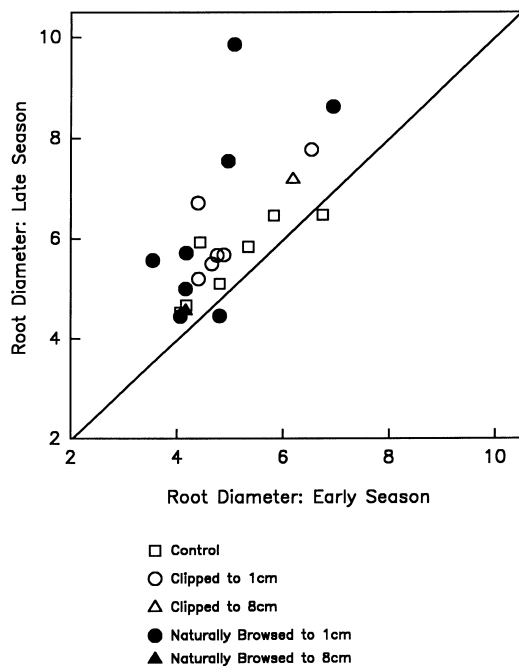


Fig. 2 Root diameter measured early in the season and late in the season in *I. aggregata* across eight populations in Colorado and Arizona. At the *diagonal line*, root diameters show no change throughout the growing season. *Above* the diagonal line root diameters increased throughout the growing season. *Below* the diagonal line root diameters decreased. Results show that in the majority of cases of plants that were either experimentally clipped or naturally browsed to a height of 1 cm, root diameters increased throughout the growing season, while uneaten control plants or plants that were either naturally browsed or experimentally clipped to a height of 8 cm did not change significantly over the course of the growing season

were not taken on naturally browsed plants, only on uneaten controls and plants that were experimentally clipped, because browsing occurred after the experimental clipping treatment. In the Minturn population, also studied by Bergelson et al. (1996), evidence was found for an increase in root diameter in both clipping experiments and naturally browsed plants, contrary to their findings (early-season measures were taken on naturally browsed plants as well as on those that were experimentally clipped in this case). These results may be due to an effect of year, because the summer of 1996 was exceptionally wet. Overall, using root diameter as an a posteriori measure of size should be avoided unless experiments demonstrate that root diameters do or do not change through time.

For the most part, stem diameters did not change significantly over the course of the growing season. Significant changes were found in only 3 ($P < 0.05$) of 16 stem diameter comparisons across six populations. In two populations (Northland Press and Minturn) significant increases in stem diameters were found for uneaten control plants and in one population (Lynx Pass-Sagebrush habitat) plants that were experimentally clipped showed a significant decrease in stem diameter. Such changes, where they occurred, would bias estimates against finding evidence of overcompensation if plants were matched for size late in the season rather than early in the season.

Summary and concluding remarks

Bergelson et al. (1996) stated that there is no compelling evidence of overcompensation in natural populations of *I. aggregata* or in any other plant species. Results from this study and recent studies by Lennartsson et al. (1997) on another biennial herb, the field gentian, *Gentianella campestris*, clearly demonstrate that overcompensation is not only a real phenomenon but is also more widespread than previously thought, both taxonomically (with evidence from two disparate families) and geographically.

Arguments to date have appropriately centered upon the use of sound methodologies. In this study I have addressed the concerns of Bergelson et al. (1996) by matching plants for size early in the flowering season and assessing compensatory outcomes. The results of these comparisons not only provide evidence for overcompensation, but also clearly indicate that in the majority of the populations studied, root diameters increase following ungulate and simulated herbivory. Thus, matching plants for size late in the season using rootstock diameter is problematical if it is not known whether rootstock diameters change through time or not, as in the 14 populations studied by Bergelson and Crawley (1992a). Furthermore, arguing that the results from one population directly apply to other populations is a risky proposition. For instance, Bergelson et al. (1996) use the results from their northeastern Colorado

experiments to argue that rootstock diameters universally do not change following ungulate herbivory, which is clearly not the case.

In addition, results here clearly show that it is important to demonstrate that clipping experiments accurately simulate natural patterns (in this case timing) of herbivory. In this study, as in that of Bergelson et al. (1996), no evidence for overcompensation was found in any of the Colorado populations when ungulate herbivory was simulated. However, in four of the seven Colorado populations evidence for overcompensation was found when naturally browsed plants were included. To date, none of the studies have incorporated treatment groups that have included both simulated and naturally browsed plants, which helps to explain much of the controversy surrounding the existence of overcompensation in scarlet gilia (Bergelson and Crawley 1992a,b; Bergelson et al. 1996).

Acknowledgements I thank B.J. Dilger, T.Lugo, K.D. Paige, and J.R. Paige for field and/or laboratory assistance and J.L. Bouzat, L. Carlstrom, L. Fischer, and B. Williams for comments on the manuscript. This work was supported in part by Army Research Office grant no DACA88-95-C-0019 to K.N. Paige.

References

- Baldwin IT (1990) Herbivory simulations in ecological research. *Trends Ecol Evol* 5:91-93
- Bergelson J, Crawley MJ (1992a) The effects of grazers on the performance of individuals and populations of scarlet gilia, *Ipomopsis aggregata*. *Oecologia* 90:435-444
- Bergelson J, Crawley MJ (1992b) Herbivory and *Ipomopsis aggregata*: the disadvantages of being eaten. *Am Nat* 139:870-882
- Bergelson J, Juenger T, Crawley MJ (1996) Regrowth following herbivory in *Ipomopsis aggregata*: compensation but not overcompensation. *Am Nat* 148:744-755
- Gronemeyer PA, Dilger BJ, Bouzat JL, Paige KN (1997) The effects of herbivory on paternal fitness in scarlet gilia: better moms also make better pops. *Am Nat* 150:592-602
- Juenger T, Bergelson J (1997) Pollen and resource limitation of compensation to herbivory in scarlet gilia, *Ipomopsis aggregata*. *Ecology* 78:1684-1695
- Lennartsson T, Tuomi J, Nilsson P (1997) Evidence for an evolutionary history of overcompensation in the grassland biennial *Gentianella campestris* (Gentianaceae). *Am Nat* 149:1147-1155
- Lennartsson T, Nilsson P, Tuomi J (1998) Induction of overcompensation in the field gentian, *Gentianella campestris*. *Ecology* 79:1061-1072
- Oosterheld M, McNaughton SJ (1988) Intraspecific variation in the response of *Themeda triandra* to defoliation: the effect of time of recovery and growth rates on compensatory growth. *Oecologia* 77:181-186
- Oosterheld M, McNaughton SJ (1991) Effect of stress and time for recovery on the amount of compensatory growth after grazing. *Oecologia* 85:305-313
- Paige KN (1992) Overcompensation in response to mammalian herbivory: from mutualistic to antagonistic interactions. *Ecology* 73:2076-2085
- Paige KN (1994) Herbivory and *Ipomopsis aggregata*: differences in response, differences in experimental protocol, a reply to Bergelson and Crawley. *Am Nat* 143:739-749
- Paige KN, Whitham TG (1987) Overcompensation in response to mammalian herbivory: the advantage of being eaten. *Am Nat* 129:407-416
- Strauss SY (1988) Determining the effects of herbivory using naturally damaged plants. *Ecology* 69:1628-1630