

Rachael S. Freeman · Alison K. Brody ·
Christopher D. Neefus

Flowering phenology and compensation for herbivory in *Ipomopsis aggregata*

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Abstract The mechanisms and circumstances that affect a plant's ability to tolerate herbivory are subjects of ongoing interest and investigation. Phenological differences, and the timing of flowering with respect to pollinators and pre-dispersal seed predators, may provide one mechanism underlying variable responses of plants to herbivore damage. The subalpine wildflower, *Ipomopsis aggregata*, grows across a wide range of elevations and, because phenology varies with elevation, phenological delays associated with elevation may affect the ability of *I. aggregata* to compensate for or tolerate browsing. Thus, we examined the response of *I. aggregata* to herbivory across an elevation gradient and addressed the interactions among phenological delays imposed by damage, elevation, pre-dispersal seed predation and pollination, on *I. aggregata*'s compensatory response. Among high and low elevation populations in areas near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, we compared the responses of naturally browsed, artificially browsed (clipped), and unbrowsed (control) plants of *I. aggregata*. We compared responses in the date of initiation of flowering, timing of peak bloom, floral display, nectar production and sugar concentration, oviposition and fruit destruction by the pre-dispersal seed predator *Hylemya* sp. (Anthomyiidae), fruit

production, and aboveground biomass production. Clipping had the greatest effect on reproductive success and clipped plants at high elevation exhibited the lowest tolerance for herbivory. The effects of browsing appear to be mediated by flowering phenology, and both browsing and elevation delayed flowering phenology. Time needed for regrowth delays flowering, and thus affects the overlap with seed predators and pollinators. As a result of delayed flowering, naturally browsed and clipped plants incurred lower rates of seed predation. In the absence of seed predation, plants would exhibit a lower tolerance to herbivory since naturally and artificially browsed plants had fewer fruits destroyed by *Hylemya* larvae. We provide additional evidence that, for populations near the RMBL, clipping and natural browsing do not have the same effect on *I. aggregata* plants. This may be due to the selection of larger plants by herbivores. Although under some conditions plants may tolerate browsing, in areas where the growing season is short a phenological delay imposed by damage is likely to significantly reduce plant fitness. Identifying the mechanisms that allow plants to tolerate herbivore damage will help to develop a general framework for understanding the role of tolerance in plant population and community dynamics, as well as plant-herbivore interactions.

R. S. Freeman (✉) · C. D. Neefus
Department of Plant Biology,
University of New Hampshire,
Durham, NH 03824, USA
e-mail: rachael.freeman@hotmail.com

R. S. Freeman · A. K. Brody
Rocky Mountain Biological Laboratory,
Crested Butte, CO 81224, USA

A. K. Brody
Department of Biology,
University of Vermont,
Burlington, VT 05405, USA

Present address:

R. S. Freeman, 30 Hulbert Ave,
Nantucket, MA 02554, USA

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Introduction

Plants are commonly attacked by herbivores. The ability of plants to compensate for, or tolerate, herbivore damage is highly variable. Although significant reductions in plant fitness due to herbivory are common (e.g. Belsky 1986; Bergelson and Crawley 1992a, 1992b; Herms and Mattson 1992; Marquis 1992; Bergelson et al 1996; Coley and Barone 1996; Lohman et al. 1996), under some circumstances damaged plants demonstrate higher fitness than undamaged plants (Owen and Wiegart 1976;

McNaughton 1979; Owen 1980; Inouye 1982; Paige and Whitham 1987; Paige 1992, 1999; Lennartson et al. 1997, 1998). The underlying mechanisms that control a plant's response to herbivores remain largely unknown (Tiffin 2000).

The fitness effects of herbivory on *Ipomopsis aggregata* (Polemoniaceae) and its ability to tolerate, or compensate for, herbivory has been debated. Near Flagstaff, Arizona, USA, *I. aggregata* plants that were browsed produced 2.4 times as many seeds as unbrowsed control plants (Paige and Whitham 1987). In contrast, there was no evidence of overcompensation in 14 populations of *I. aggregata* measured across the northwestern United States (Bergelson and Crawley 1992a, 1992b). However, differences in protocols between these two studies make a direct comparison problematic (Paige 1994). The variability in the effects of herbivory on *I. aggregata* plants may be explained by Maschinski and Whitham's (1989) "compensatory continuum hypothesis" which suggests that the degree of compensation is dependent on a variety of factors including the competitive environment in which a plant grows, severity and timing of browsing, and nutrient availability. In addition, the ability of *I. aggregata* plants to tolerate browsing can be affected by the degree to which herbivory exacerbates pollen limitation (Juenger and Bergelson 1997). In a recent study, *I. aggregata* growing in northern Arizona overcompensated for herbivory simulated by clipping whereas only equal compensation occurred in six Colorado populations (Paige 1999). What emerges from these studies is that the response of *I. aggregata* to herbivory is highly variable. We propose that much of this variability may be explained by factors affecting phenology which, in turn, affect the time available for regrowth and production of flowers, fruits and seeds. *I. aggregata* grows over a wide range of elevations which, through its effects on phenology, could dramatically affect its response to herbivores. In general, the effects of herbivore-induced delays in phenology are one of the less studied mechanisms that may underlie tolerance (Tiffin 2000).

I. aggregata plants that flowered early were more tolerant of browsing than those that flowered late (Juenger and Bergelson 2000). These plants were studied at relatively low elevations, and the effects of phenological delays on *I. aggregata* living at high elevations have not been reported. Air temperature falls 10°C with every 1,000 m of altitude in dry air (Birkenheuer 1992). Accompanying this drop in air temperature are delayed snowmelt, early snowfall, and frequent summer frosts that combine to produce a truncated growing season. Phenological delays imposed by browsing combined with phenological delays imposed by late snowmelt, and truncated growing seasons due to early snowfall may impact a plant's ability to compensate for herbivory.

A plant's ability to tolerate herbivory may also be mediated by its biotic interactions with pollinators and seed predators. If flowering is delayed as a result of elevation and herbivory, migratory pollinators, such as

hummingbirds, may no longer be present when plants come into full bloom. There may also be an effect of phenology on a plant's risk to pre-dispersal seed predators (Brody 1997) and florivores (Pilson 2000). For *Helianthus annuus*, early flowering plants incurred a significantly greater loss of seeds to the sunflower moth (*Homeosoma electellum*) and sunflower bud moth (*Suleima helianthana*) than those that flowered later, and thus selection favored early-flowering plants (Pilson 2000). If elevation and browsing delay flowering, the temporal overlap between pollinators, pre-dispersal seed predators, and their host plants may be reduced (Juenger and Bergelson 1997). Phenological delays may shift overlap with both seed predators and pollinators such that plants are at less risk of having their seeds damaged but are also more likely to be pollen limited.

Here, we examined how plant compensatory response is influenced by the effects of phenological delays imposed by elevation and mediated by interactions with pre-dispersal seed predators and pollinators. We asked:

1. To what degree do *I. aggregata* plants compensate for herbivory?
2. Does the ability of *I. aggregata* to tolerate herbivory vary with elevation?
3. Does herbivory, simulated and natural, and/or elevation affect a plant's risk to ovipositing pre-dispersal and loss of seeds to such predators?
4. Does simulated and natural herbivory affect floral traits (flowering phenology, floral display, and nectar quantity and quality) known to influence pollinator choice and thus the likelihood that a plant is pollinated?
5. Do floral traits vary with elevation as well?

Materials and methods

Study system

Ipomopsis aggregata ssp. *aggregata* (Polemoniaceae) grows in a variety of habitats at alpine and sub-alpine elevations in the western United States (Grant and Wilken 1986). In the area surrounding the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado where this study was performed, *I. aggregata* grows between 2,500 m and 3,700 m (personal observation). It is semelparous and grows as a vegetative rosette for 2–8 years before it bolts and flowers in a single season (Waser 1978). Plants most often produce a single inflorescence with multiple red, trumpet-shaped flowers. Although the flowers are protandrous, geitonogamy (the transfer of self pollen among flowers within a plant) does occur (Waser 1978), but *I. aggregata* is self-incompatible (Waser and Price 1983). Nectar is produced at a rate of 1–5 µl of nectar per flower per day with a sugar concentration of 20–25% sucrose equivalents (Pleasants 1983). Nectar is produced throughout the life of the flower at a constant rate, independent of removal by pollinators (Pleasants 1983). *I. aggregata* is primarily pollinated by Rufus (*Selasphorus rufus*) and Broad-tailed (*Selasphorus platycercus*) hummingbirds (Waser 1978).

The principal herbivores are mule deer (*Odocoileus hemionus*). Mule deer frequently browse bolting stalks of *I. aggregata*, damaging the apical meristem and resulting in the production of multiple, lateral flowering stalks. *I. aggregata* is also the host of a

common, pre-dispersal seed predator (Diptera: Anthomyiidae: *Hylemya* sp.; Zimmerman 1980). *Hylemya* females lay their eggs beneath the sepals of *I. aggregata*. After hatching, the larvae burrow into the fruit and feed on the developing seeds after which they chew an exit hole through the carpal wall and drop to the ground to pupate (Zimmerman 1979b, 1980; Brody 1992a, 1992b; Brody and Waser 1995). Adult flies feed on the pollen of *I. aggregata* flowers, but they do not affect pollination (Brody, unpublished data).

Experimental design

In the area surrounding RMBL, we selected three drainage basins where *I. aggregata* populations were present from below 2,800 m to approximately 3,400 m. Within each of the three drainage basins, study sites were established at "high" (~3,200 m) and "low" elevations (~2,800 m). The elevations represented high and intermediate elevation populations within the elevational range of *I. aggregata* in the area surrounding the RMBL. The three drainages used, from east to west, were Gothic, Washington Gulch, and Slate River. These drainages converge at their apex in the area of Paradise Divide and are geographically isolated by two ridgelines.

High and low elevation sites were paired within each drainage basin based on similarity of slope and aspect. Within the Gothic drainage, both sites were west facing. The high elevation site was at 3,125 m and the low elevation site was at 2,900 m. High and low elevation sites within the Washington Gulch drainage were at 3,334 and 2,891 m respectively and these sites faced directly south. In the Slate River drainage, the high and low elevation sites were at 2,738 and 3,125 m respectively and, similar to those in the Gothic drainage, these sites faced west.

At each site, 10 naturally browsed and 30 unbrowsed plants were selected at random. The 30 unbrowsed plants were then randomly assigned to one of two treatments: 10 to a simulated browsing treatment and 20 to serve as unbrowsed controls. Before assigning treatments, we measured the initial height of the bolting stalk and rootstock diameter of all plants. We selected 20 (rather than 10) as controls to allow us to discard control plants that were naturally browsed by deer during the course of the summer. We clipped bolting plants in the simulated browsing group to a height of 5 cm as that reflected of the average degree at which plants were naturally browsed. Plants in the high elevation populations were clipped 10–12 days after plants in the low elevation populations, thus maintaining equality in phenological stage at clipping across elevations. Although the exact timing of browsing was unknown, plants were recently browsed based on the appearance of damage and lack of secondary branching at the time of selection. Peak browsing occurred early in the season during the time we clipped plants.

We recorded the date of first bloom for all plants and counted flowers each week on all plants at all sites. Flower counts were used to assess floral display size and to determine when plants reached peak bloom. Peak bloom was characterized for each plant as the week during which the greatest number of flowers were open.

Once all plants in all grazing treatments commenced blooming at a particular site, we measured 24-h nectar production and sugar concentrations weekly. Nectar measurements were made on the same day at high and low elevations sites within each drainage basin to control for abiotic factors (e.g. rainfall, sunlight, temperature) that might affect nectar production and sugar concentrations. To measure nectar production, we covered three elongated buds on five plants in each treatment group with straws with the ends stapled shut. After 24 h, we removed nectar from these now-open flowers using a calibrated microcapillary tube and calculated the quantity produced. At the same time, we measured sugar concentration using a refractometer. Weekly nectar quantities and sugar concentrations were averaged by plant before statistical analysis.

Oviposition behavior of *Hylemya* was assessed by egg censuses conducted once elongated buds were present on a plant. Every 5–8 days, 10 plants from each of the three grazing treatment groups

were randomly selected to be censused. Censusing involved checking beneath the sepals of all flowers and elongated buds for *Hylemya* eggs. When an egg was found, we marked the outside of the calyx with a small spot of permanent ink to prevent recounting. Because buds elongate over a period of 1–3 days, and corollas abscise after 3–5 days, our censuses included virtually all buds and flowers on each plant. We averaged individual censuses by plant for the season and used the average percentage of buds and flowers with eggs as a response variable in analyzing the effects of elevation and browsing on the oviposition behavior of *Hylemya* females.

We collected all fruits throughout production. The number of fruits containing viable seeds, aborted fruits, damaged fruits and seeds were scored. Fruits damaged by *Hylemya* larvae were identified by the presence of an exit hole on the outside of the fruit wall or evidence of seed destruction accompanied by frass in the interior of the fruit. We also collected all plants and dried and weighed them to assess aboveground biomass. Our study was concluded at the end of 10 weeks because the majority of plants had completed flowering. By then, there were frequent frosts and occasional snow at the high elevation sites. Although some plants were still flowering, flowers produced so late in the season were unlikely to be pollinated and set seed. Therefore the few remaining flowers were counted as unsuccessful (per Brody and Morita 2000).

Statistical analysis

To examine whether the overall distribution of flowering differed between damage treatments or elevations, we compared the cumulative frequency of browsing using two-sample Kolmogorov-Smirnoff tests (Sokal and Rohlf 1995). To examine the effects of elevation, artificial clipping and natural browsing on bloom date, peak bloom, weekly flower production, nectar production, nectar sugar concentration, *Hylemya* oviposition rates and fruit set, we performed Randomized Complete Block, Split Plot Two-way ANOVAs with elevation as the main plots, browsing as the subplots and drainage basin as the blocking factor. To assess the effects of elevation and browsing on aboveground biomass production, we performed an ANCOVA using rootstock diameter as the continuous variable. For all analyses we used SYSTAT v.10, SPSS, Chicago, Ill. Analyses and error terms were performed as per Little and Hill (1978). Drainage × browsing treatment and drainage × elevation × browsing treatment interactions were tested and in all cases insignificance justified dropping these terms from the model.

Interactions between drainage basins and elevation could not be evaluated statistically because there is no appropriate error term. In addition, it was not possible to test for the effect of block as it could not be determined whether there was a significant interaction between the blocking factor (drainage basin) and the main plots (elevation) (Sokal and Rohlf 1995).

Hylemya oviposition rates were transformed using an Arcsine arcsine square root transformation (Zar 1999) and the number of seeds produced was transformed by natural log prior to analysis. When appropriate, Tukey-Kramer HD multiple comparison tests were used to compare means within treatments or between treatment combinations (Zar 1999, SYSTAT v.10, SPSS, Chicago, Ill.).

Results

Flowering phenology

Two-sample Kolmogorov-Smirnoff tests on the cumulative distribution of flowering showed significant differences between elevations and damage treatments (Fig. 1). Plants at high elevation bloomed an average of 6 days later than plants at low elevation ($F_{1, 2}=51.25$; $P=0.02$)

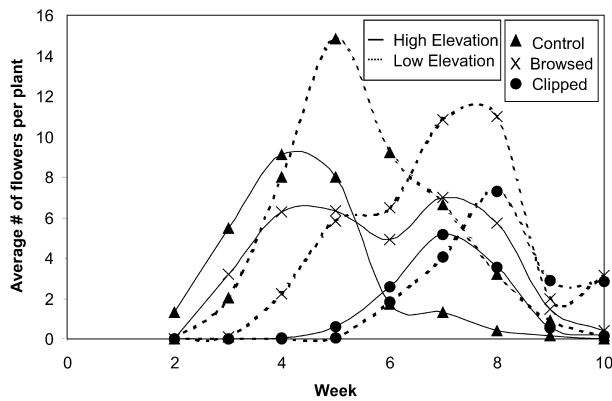


Fig. 1 Seasonal course of flowering depicted as the average number of flowers produced weekly by plants in the three grazing treatments at high and low elevations. Kolmogorov-Smirnov maximum differences (D): high vs low elevation $D=0.194$, $P<0.0001$; browsed vs control plants $D=0.3882$, $P<0.0001$; clipped versus control plants $D=0.779$, $P<0.0001$

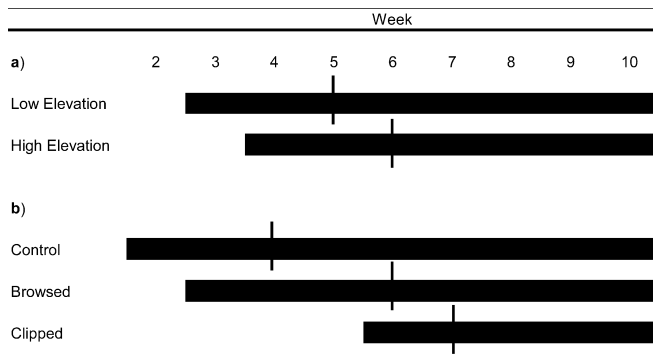


Fig. 2 Flowering phenology for **a** bloom date and peak bloom of plants at high and low elevations and **b** bloom date and peak bloom of control, browsed and clipped plants

(Fig. 2a) and, averaged across all populations, clipped plants bloomed 26 days later than control and 22 days later than browsed plants ($F_{2, 117}=183.26$; $P<0.001$) (Fig. 2b). There was no significant difference in the bloom date of browsed and control plants. Control plants reached peak flower production significantly earlier than browsed or clipped plants (week 4 vs 6 vs 7, respectively; $F_{2, 224}=219.04$; $P<0.001$). Using week 10 as the cessation of flowering, plants in high elevation populations bloomed for an average of 6 weeks while plants in low elevation populations bloomed for an average of 7 weeks. Unclipped plants bloomed for an average of 8 weeks, browsed plants for 7 weeks and clipped plants for only 4 weeks (Fig. 2a, b).

Floral display

Control plants produced significantly more flowers per week at high elevation than at low elevation ($P<0.001$), but browsed and clipped plants produced similar numbers

of flowers at high and low elevations ($P=0.263$ and $P=0.986$ respectively), thus there was a significant interaction between the effects of elevation and browsing on the average number of flowers produced per week ($F_{2, 228}=6.56$; $P=0.002$). At both low and high elevation, control and browsed plants produced significantly more flowers per week than clipped plants ($P=0.003$ and $P<0.001$ respectively) (Fig. 2).

Nectar measurements: quantity

Nectar production was slightly greater at low elevation ($\bar{x}=4.0\pm 0.34 \mu\text{l flower}^{-1} \text{day}^{-1}$) than at high elevation ($\bar{x}=2.6\pm 0.32 \mu\text{l flower}^{-1} \text{day}^{-1}$), but the difference was not statistically significant ($F_{1, 2}=2.06$; $P=0.288$). Neither natural browsing nor artificial clipping affected the amount of nectar produced by flowers ($\bar{x}_{\text{browsed}}=3.6\pm 0.3$, $\bar{x}_{\text{clipped}}=3.2\pm 0.5$, $\bar{x}_{\text{control}}=3.1\pm 0.4 \mu\text{l flower}^{-1} \text{day}^{-1}$).

Nectar measurements: quality

There was no significant effect of elevation on the sugar content of nectar produced. At high and low elevations the average sugar content of nectar was $24.9\%\pm 0.9$ and $25.0\%\pm 0.9$ respectively. There was no effect of browsing on the sugar content of nectar produced. Nectar from flowers on browsed plants averaged $25.2\%\pm 0.9$ sucrose equivalents, nectar from flowers on clipped plants averaged $24.9\%\pm 1.3$ sucrose equivalents and nectar from flowers on control plants averaged $24.9\%\pm 1.0$.

Oviposition behavior

Elevation did not affect the percentage of buds or flowers oviposited on by *Hylemya* (Table 1). However, browsing affected both the percentage of buds with eggs and the percentage of flowers with eggs (Table 1). Control plants had a significantly greater percent of buds with eggs ($\bar{x}=25\%\pm 1.9$) than either browsed ($\bar{x}=17\%\pm 2.1$) or clipped ($\bar{x}=13\%\pm 2.0$) plants. Flowers on control ($\bar{x}=38\%\pm 2.2$) and browsed plants ($\bar{x}=35\%\pm 3.2$), on the other hand, were significantly more likely to have been oviposited on than flowers on clipped plants ($\bar{x}=20\%\pm 2.7$).

Fruit production

There was a significant effect of browsing treatment on the total number of fruits produced by plants ($F_{2, 219}=10.06$; $P=0.0002$). Control and browsed plants produced a significantly higher number of total fruits than clipped plants ($P=0.0001$ and $P=0.005$ respectively). There was no significant difference between control and browsed plants ($P=0.171$) and there was no effect of elevation ($F_{1, 2}=0.134$; $P=0.749$) on the total number of fruits produced (Table 2).

Table 1 Results of ANOVAs for treatment effects on the proportion of buds and flowers with *Hylemya* eggs. Proportions were Anscombe arcsine squareroot transformed prior to analysis. Grazing treatment significantly affected both the proportion of buds with eggs and flowers with eggs. Drainage by elevation interactions could not be analyzed because elevations were not replicated within drainages

Source	Buds			Flowers		
	df	F-ratio	P-value	df	F-ratio	P-value
Main plot						
Drainage (D)	2	–	–	2	–	–
Elevation (E)	1	8.059	0.105	1	9.395	0.092
Main plot error, D×E	2	–	–	2	–	–
Sub plot						
Grazing (G)	2	8.757	<0.0001	2	12.729	<0.0001
G×E	2	1.354	0.261	2	0.815	0.444
Sub plot error	199			219		

Table 2 The effects of elevation and grazing on fitness components. Values represent averages of individual plant totals ± standard errors. Standard errors were calculated using the least squares

means generated in SYSTAT. Within columns, letters indicate significant differences ($P<0.05$) between plant means compared using Tukey-Kramer HD multiple comparisons tests

Elevation	Grazing treatment	Total fruits	% Fruit set	% Destroyed	Total seeds
High	Control	53.7±4.1 ^a	87.3±2.3 ^a	19.1±2.1 ^{a,d}	78.8±28.9 ^a
High	Browsed	59.5±7.4 ^a	75.4±4.0 ^{a,d}	15.0±3.6 ^c	-42.4±26.4 ^{a,c}
High	Clipped	30.6±6.1 ^b	51.4±3.3 ^b	8.5±3.0 ^{a,c}	10.8±6.5 ^b
Low	Control	40.5±4.4 ^{a,b}	81.2±2.4 ^{a,d}	30.0±2.1 ^b	39.0±14.5 ^{a,c}
Low	Browsed	55.3±6.4 ^{a,b}	73.0±3.4 ^{c,d}	29.0±3.1 ^{a,b}	45.5±25.4 ^{a,c}
Low	Clipped	31.3±6.0 ^b	59.5±3.3 ^{b,c}	22.0±3.0 ^{d,b}	21.4±12.3 ^{b,c}

There was an elevation by browsing effect on the percentage of flowers that set seed ($F_{2, 213}=3.091$; $P=0.047$). At high elevation, control and browsed plants had a significantly higher percentage of flowers set seed than clipped plants ($P<0.0001$ and $P<0.0001$). At low elevation, control plants had a significantly higher percent fruit set than clipped plants ($P<0.0001$) however percentage fruit set for browsed plants did not differ significantly from either control or clipped plants ($P=0.359$ and $P=0.056$). Within a damage treatment, percentage fruit set did not differ between the two elevations (Fig. 3, Table 2).

Control and browsed plants had an equal percentage of fruits destroyed by *Hylemya* larvae, as did browsed and clipped plants ($P=0.633$ and $P=0.085$). However, control plants had significantly more fruits destroyed than clipped plants ($P=0.0009$). Although the mean percentage of fruits destroyed by *Hylemya* larvae was greater at low elevation, analysis by ANOVA showed no significant difference in the percentage of fruits destroyed by *Hylemya* larvae at high and low elevations ($F_{1, 2}=4.207$; $P=0.177$) (Fig. 4). However, Tukey-Kramer HD multiple comparisons of means indicated that all three browsing treatments had a significantly higher percentage of destroyed fruits at low elevation than at high elevation (Table 2).

Seed production between control and browsed plants was equivalent at high elevation and these plants produced significantly more seeds than clipped plants ($P=0.016$ and $P<0.0001$ respectively). At low elevation, plants in all three treatments produced similar numbers of seeds (Table 2). Within a damage treatment, the number of seeds produced did not differ between elevations. Thus,

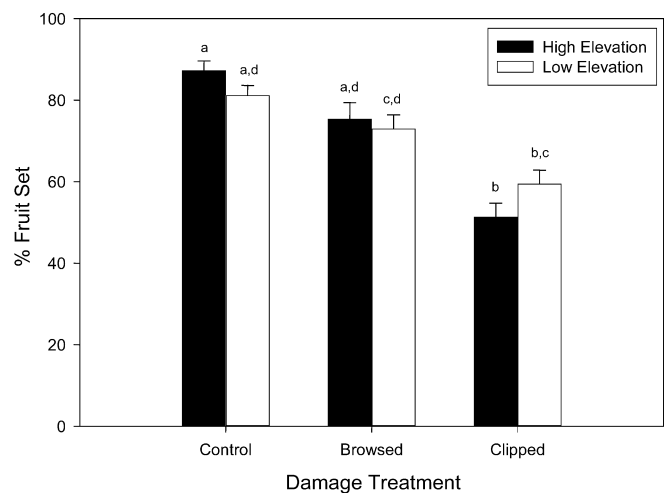


Fig. 3 Average percentage of fruit set for plants in the three grazing treatments at high and low elevations. Error bars represent standard errors calculated using the least squares means generated in SYSTAT. Letters indicate significant differences ($P<0.05$) between means compared using a Tukey-Kramer HD multiple comparisons test

there was an elevation by browsing effect on the total number of seeds produced ($F_{2, 203}=4.66$; $P=0.010$).

Aboveground biomass

Browsing treatment had no effect on plant dry weight at high elevation. Average dry weight of aboveground biomass for control, browsed and clipped plants at high elevation was 1.54 g±0.14, 1.49 g±0.24, and 1.32 g±0.17

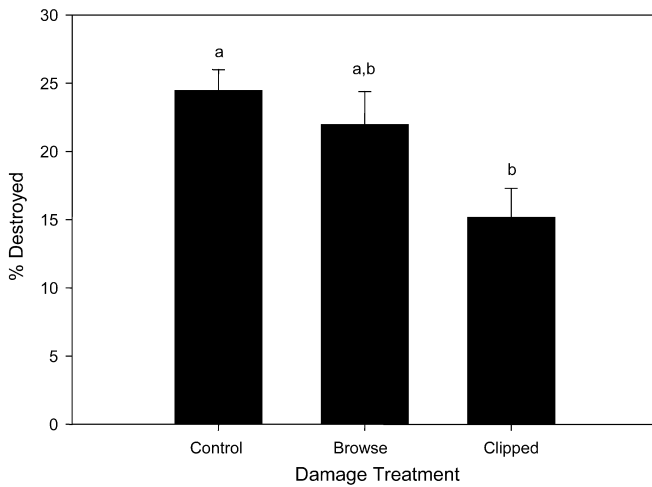


Fig. 4 Average percentage of destroyed fruits produced by plants in the three grazing treatments at high and low elevations. Error bars represent standard errors calculated using the least squares means generated in SYSTAT. Letters indicate significant differences ($P < 0.05$) between means compared using a Tukey-Kramer HD multiple comparisons test

Table 3 Results of the ANCOVA for treatment effects on the dry weight of aboveground biomass produced by plants. There was a significant interaction between grazing treatment and elevation. The covariate, rootstock diameter, was also significant. Drainage by elevation interactions could not be analyzed because elevations were not replicated within drainages

Source	df	F-ratio	P-value
Main plot			
Drainage (D)	2	–	–
Elevation (E)	1	0.128	0.754
Main plot error, D×E	2	–	–
Sub plot			
Rootstock diameter (RD)	1	21.142	<0.0001
Grazing treatment (GT)	2	5.96	0.003
GT×E	2	3.37	0.037
Sub plot error	153		

respectively. At low elevation control plants ($\bar{x}=1.32 \pm 0.14$) produced similar amounts of aboveground biomass as browsed ($\bar{x}=2.01 \pm 0.21$ g) and clipped plants ($\bar{x}=0.83 \pm 0.18$ g). However, at low elevation, naturally browsed plants produced significantly more above ground biomass than clipped plants ($F_{2,153}=3.38$; $P=0.037$) (Table 3). There was not a significant difference in biomass between elevations. When used as a covariate, rootstock diameter was significant ($F_{1,153}=21.14$; $P < 0.0001$)

Discussion

Flowering phenology can have a strong effect on plant reproductive success (Augsburger 1981; Rathcke and Lacey 1985; English-Loeb and Karban 1992; Pilson 2000) and the effects of foliar damage on reproduction may be influenced by the amount of time available for

recovery (Oosterheld and McNaughton 1988, 1991). Here, clipping had a strong negative effect on plant reproductive success, and clipped plants in high elevation populations displayed the largest reduction in seed set (Table 2). The flowering distributions of plants differed significantly among treatments (Fig. 1) as did initial date and peak bloom (Fig. 2). Thus, the negative effects of clipping were most likely a product of the phenological delay resulting from the time needed to regenerate lost tissue (Fig. 2b). At high elevation, the clipping-induced phenological delay was compounded by a delay in initial bloom date (Fig. 2a). In *I. aggregata*, vertebrate herbivores most often browse the entire bolting stalk which must be regrown before the plant can initiate flowering.

In plant species inhabiting alpine habitats in Japan, flowering and seed set were reduced by late snowmelt and early snowfall that lead to a shortened growing season (Kudo 1991). Here, the onset of flowering was delayed by elevation. But even among plants growing at similar elevations, the degree to which artificial and natural browsing delays phenology is largely responsible for determining a plant's ability to compensate for damage.

Comparisons of the effects of phenology and length of growing season between high and low elevation populations may be extrapolated to explain some of the differences seen in the tolerance of *I. aggregata* to browsing in different geographic regions. Here, clipped plants in low elevation populations compensated in some measures of reproductive fitness (Table 2) whereas clipped plants at high elevation were unable to compensate. In a comparison of eight populations of *I. aggregata* growing in northern Arizona and Colorado, clipped or browsed plants in Arizona were able to fully compensate and, even, overcompensate for damage, while the Colorado populations at best compensated and showed no overcompensation (Paige 1999). Although elevation and timing of clipping with respect to the length of growing season are not compared, these are two factors which may help explain the different responses to herbivory among populations.

The degree to which flowering phenology affects interactions among a host plant and its suite of visitors has been examined in several recent studies (e.g. Brody 1997; Juenger and Bergelson 2000; Pilson 2000; Mahoro 2002). For *I. aggregata*, phenological delays can lead to pollen limitation (Juenger and Bergelson 1997). Juenger and Bergelson (1997) suggest that the phenological delay caused by clipping begets pollen limitation in *I. aggregata*, and that lack of adequate pollination may be the strongest factor affecting the ability of plants to tolerate herbivory. In *Petrocoptis grandiflora*, temporal synchrony with pollinators had the greatest effect on reproductive success, while floral characteristics such as flowering intensity, duration of flowering, number of flowers, flowering order and flowering overlap were inconsequential to fruit set (Gutian and Sanchez 1992). Similarly, in our study, the combined phenological delays caused by clipping and elevation most likely decreased overlap with pollinators and contributed to the signifi-

cantly larger number of aborted fruits (Table 2) observed for artificially browsed plants at high elevation.

The effects of herbivory on phenology may not always be negative, however. Pre-dispersal seed predation is most severe on *I. aggregata* flowers produced early in the season and then declines (Brody and Morita 2000, Campbell et al. 2002). Thus, the costs incurred by a reduced overlap with pollinators and a shortened growing season may be partially or fully ameliorated by benefits of a reduction in pre-dispersal seed predation. For *Vaccinium hirtum* Thunb (Ericaceae), early-flowering individuals were provided some escape from weevil and fly pre-dispersal seed predators, but incurred a cost in terms of pollinator availability (Mahoro 2002). Here, control plants were preferred by *Hylemya* and had the greatest percentage of fruits destroyed. If *Hylemya* were absent or rare, clipped and naturally browsed plants would be less likely to show an ability to tolerate herbivory as the reproductive measures of control plants would increase and damaged plants would reap no benefit from a phenological delay. For *Silene alba*, the benefits of reduced seed predation accrued by late flowering individuals outweighed the costs of higher rates of fruit abortion (Biere and Honders 1996). In our study, although clipped plants experienced the lowest levels of seed predation at high elevation, this did not offset the cost of reduced fruit set due to a decreased overlap with pollinators and a shorter growing season. The lack of a large fitness benefit from a reduction in the risk of seed predation, along with more severe pollen limitation, provides further support for the idea that selective pressures may drive the evolution of early flowering in *I. aggregata* as a mechanism underlying tolerance (Juenger and Bergelson 2000).

In low elevation populations, naturally browsed plants produced more aboveground tissue than unbrowsed controls or clipped plants. However, these plants were larger to begin with as demonstrated by a significant difference in root stock diameter (Table 3). Deer and elk are selective in choosing which individuals they consume (here, and see Strauss 1988). The difference in plant response to natural browsing and clipping has underscored several studies (Paige 1999; Juenger and Bergelson 2000). Aboveground biomass production is an important part of plant compensation, but can enhance or limit a plant's ability to compensate for damage. The timing of reproduction in monocarpic perennials is generally based on the relationship between plant size and reproductive effort (Reekie 1997). Clipped plants produced similar amounts of aboveground biomass as did unclipped controls. Thus, clipped and browsed plants may allocate resources that might otherwise be used for flowering and fruit production towards replacing aboveground biomass. However, because the root stock diameter, and thus the stored photosynthate in roots and rosette leaves, is greater for naturally browsed plants, recovery of lost tissue may be easier for those plants. There is a trade-off between allocating resources to growth or reproduction (Biere 1995; Lesica and Shelly 1995; Reekie 1997) and our results indicate that clipped and naturally browsed

plants are allocating resources towards the production of biomass in lieu of seeds. Despite their larger size, fruit and seed production of naturally browsed plants seed did not exceed that of control plants.

Monocarpic herbs seem to tolerate herbivory and demonstrate a surprisingly high capacity to replace lost tissue (Huhta et al 2000). Sometimes, such replacement exacts a cost in fitness measures (Hendrix and Trapp 1989; Bergelson and Crawley 1992a, 1992b; Bergelson et al 1996; Escarré et al 1996) and sometimes it does not (Paige and Whitham 1987; Gronemeyer et al 1997; Lennartsson et al 1997; Paige 1999). One of the least studied mechanisms underlying plant tolerance to herbivore damage is the degree to which flowering phenology is affected and the degree to which this, in turn, disrupts a plant's interactions with other organisms that influence fitness. For the monocarpic herb *I. aggregata*, the highly variable response to herbivory is, at least in part, driven by the phenological effects of damage. If a plant flowers out of synchrony with the rest of the population, or too late in the season to capture many visits by hummingbird pollinators, its reproduction will suffer as a result of pollen- or pollinator-limitation. Thus, our results provide additional evidence and explanation for the variable response of scarlet gilia to herbivore damage, and may be generalizable to other systems as well.

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