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When resources don't rescue: flowering phenology and species interactions affect compensation to herbivory in *Ipomopsis aggregata*

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The ability of plants to tolerate, or compensate for, herbivore damage is highly variable and has been the subject of much research. Although many plants can compensate for herbivore damage, and some even overcompensate, we cannot yet generalize about the conditions that promote a positive response to damage. Here, we asked how abiotic resources (i.e. plant nutrient status) coupled with biotic interactions – i.e. subsequent interactions with pollinators, seed predators and nectar robbing bumble bees – affect the compensatory ability of *Ipomopsis aggregata*, a monocarpic herb that has been the subject of much previous debate. We hypothesized that compensation to herbivore damage in *I. aggregata* (Polemoniaceae) would depend first on plants having an ample supply of resources and, second, on the outcome of subsequent interactions with mutualist pollinators and enemy pre-dispersal seed predators and nectar robbing bumble bees. We used a fully-factorial experiment in which plants were watered, fertilized or left as unmanipulated controls, crossed with clipping to simulate herbivore damage to the apical meristem. Resource addition enhanced both male and female components of fitness, but resource enhancement did not provide the means for plants to fully compensate for simulated herbivory. Clipped plants produced significantly more inflorescences, but at the expense of a delay in flowering and fewer total flowers. Clipping significantly reduced losses to dipteran pre-dispersal seed predators by delaying flowering time, but early flowering plants produced higher numbers of seeds despite incurring higher rates of predation. Clipped plants incurred a higher risk to nectar robbers in one of two years. Overall, clipped plants suffered severe reductions (a nearly 50% reduction in total seed set) in female success, but clipping combined with nutrient addition enhanced male function through increases in per-flower pollen production. However, because clipped plants produced significantly fewer flowers than unclipped plants, whole-plant pollen production was significantly reduced by clipping. Pollinator visitation and nectar robbing were variable between clipping treatments and between years and (nectar robbing) among sites. Our results demonstrate that the variability in plant response to herbivory can, at least in part, be driven by plant interactions with mutualists and enemies. Thus, accounting for such interactions and their variability is important to fully understanding plant compensation for herbivore damage and will likely go far to explain variation in plant response that appears to be independent of resources.

The outcomes of species interactions are inherently variable. Elucidating the mechanisms underlying variation in the direction and strength of species interactions can provide predictive insight and a clearer understanding of the factors that drive both the idiosyncracies and generalities of species' responses. For example, plants vary widely in their ability to compensate for herbivore damage, with outcomes ranging from overcompensation to severe undercompensation (McNaughton 1983, Paige and Whitham 1987, Maschinksi and Whitham 1989, Bergelson et al. 1996, Gruntman et al. 2011). Although over-compensation, and even compensation, was once thought to be an anomaly (Bergelson et al. 1996, Belsky 1987), it has been documented in species with widely different life histories, including annual (e.g. *Arabidopsis thaliana*, Banta et al. 2010 and *Helianthus annuus*, Pilson and Decker 2002) and long-lived perennial forbs (e.g. *Gentianella campestris*, Lennartsson et al. 1997) and long-lived grasses (McNaughton 1983). In addition, the variable responses in compensatory regrowth and reproduction occur among individuals within and among populations as well as within and among years (Bergelson et al. 1996, Paige 1999, Huhta et al. 2003, Freeman et al. 2003, Levine and Paige 2004, Rautio et al. 2005, Banta et al. 2010, Bagchi and Ritchie 2011). The challenge is to understand the mechanisms that drive compensatory responses which may then inform predictions about its ecological and evolutionary consequences (Agrawal 2000).

A suite of factors have been proposed to explain variation in compensation to herbivore damage. These factors can be abiotic or biotic as well as intrinsic or extrinsic to

the two-way interaction between plants and herbivores. For example, pre-existing levels of root carbon storage, nutrient availability and/or drought (Hawkes and Sullivan 2001, Levine and Paige 2004, Wise and Abrahamson 2007), growing season length (Freeman et al. 2003), type of herbivore damage (Boalt and Lehtilä 2007), amount and timing of damage (García and Ehrlén 2002, Muola et al. 2010), and selection or between-generation differences (Lennartsson et al. 1997) may individually or in combination affect variation in compensation. In addition, compensation for herbivory may be affected by plant interactions with mutualists, such as pollinators, and other antagonists (Lehtilä and Strauss 1997, Juenger and Bergelson 1997, 2000). Because plants can plastically and dynamically respond to herbivore damage, physiological, morphological and phenological changes following herbivore damage may affect subsequent plant–animal interactions (Strauss et al. 1996, Mothershead and Marquis 2000, Suárez et al. 2009).

Despite the intense interest in plant compensation, we have yet to fully resolve how resources affect the compensatory response both directly – i.e. by enhancing the opportunity for plants to turn fertilized ovules into seeds or increasing the production of flowers or pollen – and indirectly by increasing pollinator rewards and/or enhancing plant attractiveness to pollinators or other herbivores through signals such as display size and flower morphology. Here, we took a mechanistic approach to understanding variation in plant compensatory response to damage by examining the degree to which resource limitation, and interactions with mutualists (pollinators) and antagonists (seed predators and nectar robbers), affected plant compensatory response across multiple populations and years. In addition, we explored how herbivory and resource availability affected a suite of morphological and phenological traits that may be linked to plant interactions with mutualists and antagonists and their effects on compensatory response. We studied the host plant *Ipomopsis aggregata* (Polemoniaceae) because of its well-known variation in compensatory ability following apical meristem removal by ungulates (Bergelson et al. 1996, Paige 1999, Freeman et al. 2003, Sharaf and Price 2004). Specifically, we asked: how do simulated herbivory, resource addition, and their interaction affect 1) floral and flowering traits, 2) plant interactions with mutualists and antagonists, and 3) subsequent male and female components of plant reproduction? We hypothesized that early-season damage would alter subsequent plant–animal interactions, including reducing pollination and pre-dispersal seed predation while increasing nectar robbing, due to changes in morphological and phenological traits following damage. Thus, we predicted that the outcome of damage would be dependent on the intensity of pollination, seed predation, and robbing, and the degree to which resource availability could rescue plants from the potentially negative effects of biomass removal and delayed flowering. Although our work is focused on compensation to herbivore damage in the wildflower *I. aggregata*, understanding the mechanisms that drive variation in compensation lends predictive insight into how plants in general cope with herbivore damage.

Material and methods

Study system

Ipomopsis aggregata (Polemoniaceae) is a monocarpic, perennial herb that grows in dry meadows throughout the intermountain western US. In and around the Rocky Mountain Biological Laboratory (RMBL), Crested Butte, CO, USA where we conducted this study, *I. aggregata* grows for 2–10 years as a vegetative rosette, flowers once, and then dies. Once reproductive, the plant produces a single, flowering stalk that can produce 100 flowers or more (mean = 84 flowers) over 6–8 weeks from mid June to the end of August (Waser 1978). Flowers are protandrous and last ca 5 days. On a given day, a plant will display flowers in both male and female phase. *Ipomopsis aggregata* is self-incompatible and is pollinated primarily by broad-tailed *Selasphorus platycercus* and rufous *S. rufus* hummingbirds (Waser 1978). Fruits mature approximately one month post-fertilization, and seeds are shed passively. There is no seed dormancy, and seeds germinate in early spring of the next year (Price et al. 2005). Both resources and pollination can directly limit fruit and seed production of *I. aggregata*, and there is no evidence for indirect effects of resources on seed set via changes in pollination (Campbell and Halama 1993).

Around the RMBL and elsewhere, *I. aggregata* commonly incurs damage from mule deer *Odocoileus hemionus*, dipteran pre-dispersal seed predators (Anthomyiidae: *Hylemya* sp.; also identified as *Delia* sp. by Juenger et al. 2005), and nectar-robbing bumble bees (Apidae: *Bombus occidentalis*). Plants can experience damage from all of these antagonists within one flowering season, and the extent to which the outcomes of these interactions are independent is not fully known (Juenger and Bergelson 1997, Brody et al. 2008, Irwin and Brody 2011).

Mule deer frequently browse the inflorescences of *I. aggregata*, consuming up to 70% of the bolting stalks per population around the RMBL (Sharaf and Price 2004). Most often, browsing occurs early in the season after the bolting inflorescence has elongated from its basal rosette, but before blooming. Browsed plants, released from apical dominance, subsequently produce multiple flowering stalks but may experience delayed flowering phenology relative to unbrowsed plants (Juenger and Bergelson 1997, Freeman et al. 2003, but see Paige and Whitham 1987). In some cases, *I. aggregata* may fully compensate for browsing – demonstrating equal seed set of their unbrowsed counterparts – however, compensation is variable across studies, sites, and years (Paige 1999, Freeman et al. 2003, Sharaf and Price 2004).

In addition to losses from herbivores, in some years plants can lose up to 90% of their seeds to pre-dispersal seed predation by *Hylemya* (Zimmerman and Brody 1998). Female flies lay eggs singly on flowers and the larva hatches, burrows into the ovary, and eats the developing seeds. Most often, all seeds of a fruit are consumed or destroyed before the larva burrows out of the ovary wall and falls to the ground, where it pupates in the soil and overwinters. *Hylemya* does not pollinate *I. aggregata* flowers and, therefore,

is dependent on pollinator visitation to those flowers on which it lays eggs for its offspring to be provisioned with seeds.

After flowers elongate, they are at risk to nectar-robbing bumble bees. *Bombus occidentalis* steals nectar by chewing a hole in the side of the corolla and extracting the available nectar without pollinating. On average, 66% of flowers are robbed at peak robbing activity, and robbing levels can reach as high as 100% of available flowers. Nectar robbing reduces both male and female fitness by 50% (Irwin and Brody 2000) – primarily due to hummingbird-pollinator avoidance of robbed plants and flowers (Irwin and Brody 1999).

Experimental design

In early June of 2001 and 2002, we selected reproductively mature plants that had begun bolting at each of two sites and randomly assigned them to one of six treatments in a full factorial design of three resource treatments (ambient, water addition, or water plus nutrient addition) by two herbivory treatments (control and clipped). All plants had a single flowering stalk at the start of the experiment. In 2001, we used 23 replicates per treatment per site for a total of 276 plants. In 2002, we used 30 replicates per treatment at one site and 22 replicates per treatment at the other for a total of 312 plants. For all plants, we measured root-stalk diameter at the time of bolting with digital calipers to the nearest 0.01 mm as an estimate of initial plant size. Root stalk diameter can have important effects on the storage and/or uptake of resources and has been implicated as one of the factors affecting the compensatory response of *I. aggregata* to herbivores (Bergelson et al. 1996, Paige 1999). We tested for significant differences in initial root-stalk diameter among our treatments and there were none (clipping: $F_{1,564} = 0.20$, $p = 0.59$; resource addition: $F_{2,564} = 0.32$, $p = 0.73$). We also included root stalk diameter as a covariate in analyzing plant responses to our treatments and, where significant, it was included in final analyses.

To simulate herbivory, after all plants had begun bolting but prior to bud formation, plants assigned to the clipping treatment were clipped to ~2 cm of their base. We clipped plants in early June when we first observed mule deer actively foraging at our sites. Clipping adequately mimics browsing by mule deer in early flowering-stage plants (Paige and Whitham 1987, Juenger and Bergelson 1997). We standardized clipping to examine how resource addition and interactions with other species affected plant response to a level and timing of damage most closely resembling that of natural browsing. All plants were loosely tied to a metal stake to discourage herbivory by deer. Plants tied to stakes were freely visited by pollinators, seed predators and nectar robbers (Brody and Irwin unpubl.).

For the water addition treatment, plants were provided 400 ml of water four times per week. For the water plus fertilizer addition treatment, plants received the same amount of water as in the water addition treatment plus fertilizer once per week using a 20-20-20 NPK fertilizer at a dosage of 4 ml l^{-1} as recommended by the manufacturer and to which plants have responded in previous experiments (Campbell and Halama 1993). Water alone, or water plus fertilizer, was delivered to the root zone of each plant using drip irrigation. Drip irrigators were placed around ambient plants, but these plants were not watered or fertilized.

(1) How do simulated herbivory, resource addition, and their interaction affect floral and flowering traits?

For all plants, we measured flowering phenology (bloom start and end dates), the number of flowering stalks produced, total flower production, and flower morphological traits, including corolla width and length and sepal width (to the nearest 0.01 mm using digital calipers). We measured corolla width and length and sepal width on up to three flowers per plant and calculated the average per plant for each measure. Measures of flower morphology are highly repeatable across flowers within *I. aggregata* plants (Campbell et al. 1991). Corolla width and length are important to pollinator effectiveness – flowers with wider corollas both export and import more pollen, and there is a positive correlation between corolla width and length and between corolla width and nectar production (Campbell et al. 1991, 1996). In addition, sepal width is positively correlated with *Hylemya* survivorship from egg to larva (Zimmerman and Brody 1998). To the extent that pollinators and/or seed predators limit compensation, these morphological traits could play an important role.

We included bloom date, number of flowering stalks produced, total flower production (square-root transformed), and bloom duration as response variables in a MANOVA with clipping, resource addition, year, site, and their interactions as main effects. Finding the MANOVA significant, we followed with univariate ANOVAs for each response variable (here and below, Scheiner 1993). Estimates of flowering phenology as bloom date and duration provided results that were qualitatively similar to more complicated estimates using percentiles of the frequency distribution of open flowers and were therefore used for simplicity. We tested for all two-way interactions; those that were not significant were removed from the final models. Throughout our analysis, Tukey's HSD post hoc tests allowed us to determine which resource treatments differed significantly from one another. We used similar MANOVA and ANOVA as above to ask if herbivory and resource addition affected flower morphological traits. All analyses were performed in JMP 8.02 (SAS Inst).

(2) How do simulated herbivory, resource addition, and their interaction affect plant interactions with mutualists and antagonists?

Herbivory can have both direct (consumptive) effects on plant reproduction as well as indirect effects through changes in a plant's subsequent interactions with other organisms (Strauss and Irwin 2004). Adequate resources may or may not rescue plants from the negative impacts of herbivore damage, depending at least in part on plant interactions with mutualist pollinators and enemies such as seed predators and nectar robbers (Juenger and Bergelson 1997, Sharaf and Price 2004, Juenger et al. 2005).

To examine if resource availability and herbivory affected plant interactions with pollinators, we used pollen receipt as a proxy for visitation by pollinators (Engel and Irwin 2003). Each week, we emasculated 20% of elongated buds

(up to three) on each plant. We collected the stigmas of these flowers after the corollas had abscised. Stigma collection at this stage does not affect subsequent fruit or seed set (Waser and Price 1991). We stained the stigmas in basic fuchsin dye (Kearns and Inouye 1993) and counted all pollen under a compound microscope at 40×. Over 94% of all pollen was from *I. aggregata*, and there were no significant differences among treatments in the percentage of con- versus hetero-specific pollen (data not shown). Therefore, only conspecific pollen load was used as the response variable in an ANCOVA with clipping, resource addition, year, and site as main effects and bloom date and corolla length and width as covariates. We included the covariates because floral morphological traits can influence pollination in some years (Campbell et al. 1996, Juenger and Bergelson 2000) as can flowering phenology (Brody and Mitchell 1997).

To examine how herbivory and resource addition affected susceptibility to seed predators and robbers, we censused all flowers every 3–5 days for the presence of *Hylemya* eggs and evidence of nectar robbing. Because *I. aggregata* flowers last only 3–5 days, we were unlikely to count the same eggs or the same robbed flowers more than once. For each census date, we calculated the mean proportion of buds and flowers oviposited on by *Hylemya* as well as the mean percentage of flowers that experienced robbing. We analyzed the percentage of flowers oviposited on or robbed (both arcsine square-root transformed) using ANCOVAs with clipping, resources, year, and site as main effects and bloom date as covariates. We included sepal width as an additional covariate in examining the percentage of flowers oviposited on as *Hylemya* prefers flowers with wider sepals (Zimmerman and Brody 1998). We did not include floral traits as covariates in examining robbing because they do not significantly affect robbing rates (Irwin 2006).

(3) How do simulated herbivory, resource addition, and plant interactions with mutualists and antagonists affect male and female components of plant reproduction?

We quantified components of both male and female reproduction to examine plant compensatory response. To estimate the effects of clipping and resource addition on male function, we measured pollen production and pollen removal (in 2002 only). Each week, we took one anther prior to flower opening and one from the same flower 48 h after opening, for 20% of the flowers (up to three) on each plant. Anthers collected prior to the flower opening were used to calculate pollen production, and those collected after the flower had been open and exposed to floral visitors were used to calculate pollen removal. We placed all anthers in microcentrifuge tubes and allowed them to air dry. After drying, we added 1500 µl of 90% ethanol, sonicated the anthers for 5 min to release the pollen, and counted subsamples of pollen from this solution using a hemacytometer under a dissecting microscope (Kearns and Inouye 1993). For each plant we calculated pollen production per flower (averaged across the flowering season) and average pollen removal per flower (by subtracting the amount of pollen remaining after ca 48 h from the amount of pollen on anthers collected prior to opening, averaged within flowers per plant per week). In addition, we calculated whole-plant measures of pollen production by multiplying the average amount of pollen produced per flower by the total number of flowers for each plant. We used pollen production per flower and per plant as response variables in ANCOVAs with clipping, resource addition, and site as main effects, and bloom date as a covariate. Pollen removal was analyzed using the same ANCOVA model, but each week was analyzed separately because the subset of plants for which we had both pre-flowering and post-flowering pollen data to calculate pollen removal differed each week.

To assess female reproduction, we collected all fruits at the end of the season when mature but just prior to dehiscing. We calculated three estimates of female reproduction: percent fruit set (number of expanded fruits divided by the total number of flowers produced), seeds per successful fruit (averaged across the season), and total seed set per plant. Fruit set provides an index of visitation rates by pollinators (*I. aggregata* is self-incompatible and flowers not visited do not set fruit), while seeds per fruit provides an index of the quality of the pollen or the ability of the plant to utilize the pollen delivered (Waser and Price 1989). Finally, total seed set accounts for pollen and resource limitation that could simultaneously affect a plant's investment in seeds.

We analyzed components of female reproduction using MANCOVA with clipping, resource addition, year, site, and their interactions as main effects, and bloom date as a covariate. We included bloom date as covariate in the analysis because we wanted to examine if clipping and/or resource addition had any additional explanatory power after we accounted for differences in flowering date. To assess how important seed predation and nectar robbing were to female plant reproduction, we included the percentage of fruits fully and partially destroyed by *Hylemya* and the percentage of flowers robbed by *B. occidentalis* as covariates as well. If compensation is strongly influenced by biotic interactions – e.g. plants' ability to attract pollinators and avoid seed predators and robbers – then the effects of ample resources and will depend on subsequent species interactions. Thus, we would expect the interaction term between resource addition and clipping to be non-significant, but we would find significant effects of pollination, seed predation and nectar robbing. For these analyses, percent fruit set (arcsine square-root transformed), seeds per fruit (square-root transformed), and total seed set (square-root transformed) were included as response variables. We followed the significant MANCOVA with univariate ANCOVAs, deleting those interactions that were not statistically significant.

Results

(1) How do simulated herbivory, resource addition, and their interaction affect floral and flowering traits?

Clipping significantly affected flowering phenology, duration of blooming, flowering stalk production, and floral traits. Clipped plants took an average of 18 days longer to bloom than those not clipped ($F_{1,562} = 1401.7$, $p < 0.0001$; Fig. 1), and plants responded more strongly to clipping at one site (OH) than at the other site (VF) (clipping by

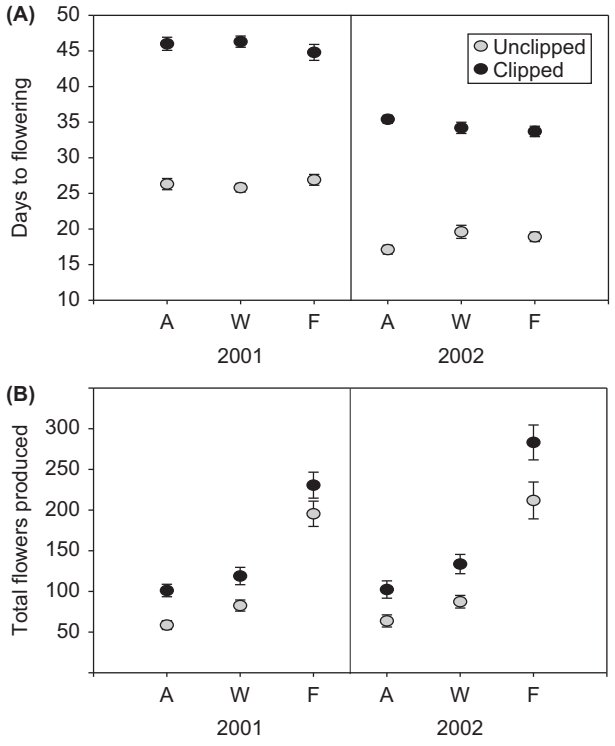

Figure 1. (A) Flowering date (days to flowering from June 1) and (B) total flower production as a function of clipping (clipped plants in closed circles) and resource availability. Means and standard errors are shown.

site: $F_{1,562} = 5.5$, $p = 0.02$) and responded more strongly in 2001 than in 2002 (clipping by year: $F_{1,562} = 16.31$, $p < 0.0001$). Plants in 2001 took significantly longer to bloom than those in 2002 and clipping exacerbated this effect (Fig. 1A). Clipping also shortened the duration of blooming by 12 days on average ($F_{1,560} = 48.87$, $p < 0.0001$), while fertilizer lengthened bloom duration by 13 days ($F_{2,560} = 44.11$, $p < 0.0001$). The effect of fertilizer on bloom duration was stronger for clipped compared to unclipped plants (clipping × resources interaction: $F_{2,560} = 3.06$, $p = 0.048$), and resource addition had a stronger effect at one site (VF) than at the other (OH) (site × resources: $F_{2,560} = 5.03$, $p = 0.007$). However, resource addition did not affect flowering onset ($F_{2,562} = 0.21$, $p = 0.81$), and there was no significant interaction between resources and clipping on onset of flowering.

Clipping released apical dominance. Clipped plants receiving only ambient resources produced, on average, five flowering stalks to the single stalk produced by non-clipped plants ($F_{1,555} = 3808.86$, $p < 0.0001$). Fertilization enhanced stalk production of clipped plants by 1.5 times ($F_{2,555} = 18.56$, $p < 0.0001$), but the number of stalks produced by unclipped plants was unchanged by adding water or water plus fertilizer (clipping by resources: $F_{2,555} = 27.42$, $p < 0.0001$).

Despite the production of additional flowering stalks, clipped plants produced fewer flowers than unclipped plants ($F_{1,562} = 52.94$, $p < 0.0001$; Fig. 1B). Resources enhanced flower production overall ($F_{2,562} = 119.18$, $p < 0.0001$), but we found no interaction between clipping and resource addition for flower production. We did find a significant interaction between resource addition and site ($F_{2,562} = 4.53$, $p = 0.01$), again with VF responding more strongly to resources than OH.

Floral traits responded to clipping, resources, year, and site (Wilk's $\lambda = 0.837$, $F_{30,1615} = 3.39$, $p < 0.0001$). Sepals from flowers on clipped plants were ca 5% narrower than sepals on unclipped plants ($F_{1,557} = 12.19$, $p < 0.0005$), but clipping did not significantly alter corolla length ($F_{1,557} = 2.56$, $p = 0.11$) or width ($F_{1,557} = 0.67$, $p = 0.41$). Nutrient addition had a positive effect on all three floral traits measured. Plants that received water or water plus fertilizer produced 3% longer corollas ($F_{2,557} = 3.14$, $p = 0.044$), 4% wider corollas ($F_{2,557} = 5.41$, $p = 0.005$), and 4% wider sepals ($F_{2,557} = 3.26$, $p = 0.039$). The effect of year was significant for corolla width and sepal width ($p = 0.0006$ and $p < 0.0001$, respectively), with plants producing larger flowers in 2001 than in 2002. The responses of corolla width and sepal width to clipping and resources were consistent across both sites, while plants produced flowers with longer corollas at one site (OH) than at the other site (VF; $F_{2,557} = 10.01$, $p = 0.002$).

(2) How do simulated herbivory, resource addition, and their interaction affect plant interactions with mutualists and antagonists?

Pollination

Clipped plants received less pollen per flower, a proxy for pollinator visitation, over all sites and years by ca 6% relative to unclipped plants (Table 1). However, the main effect of clipping was not statistically significant (Table 2) due to the degree of variance across years and resource treatments – the reduction in pollen receipt experienced by clipped plants was ca 4% in 2001 compared to 18% in 2002 ($F_{1,539} = 5.92$, $p = 0.009$). Resources enhanced pollen receipt per flower, with fertilized plants receiving ca 10% more pollen per flower than watered plants, which received ca 9% more pollen per flower than plants in the ambient treatment ($F_{2,539} = 11.58$, $p < 0.0001$; Table 2), but we found no significant interaction between resources and clipping. We did, however, find that fertilized plants in 2001 received the most pollen and ambient plants in 2002 receiving the least (resources by year: $F_{2,539} = 5.17$, $p = 0.006$). Bloom date had no significant effect on pollen receipt ($F_{2,539} = 0.040$, $p = 0.53$). Pollen receipt was, however, positively correlated with longer corollas ($F_{2,539} = 6.98$, $p = 0.015$).

Seed predation

There was no direct effect of clipping on *Hylemya* oviposition rates ($F_{1,555} = 0.73$, $p = 0.39$) and no interaction between clipping and resource addition on oviposition rates. The main effect of resources was significant, however – plants that were watered suffered 10% higher rates of oviposition than those in the water plus fertilizer or ambient treatments ($F_{2,555} = 8.49$, $p = 0.0002$; Table 1). We also found a significant effect of bloom date on *Hylemya* oviposition ($F_{1,555} = 7.60$, $p = 0.006$); later-blooming plants experienced lower risk to *Hylemya* oviposition (Fig. 2). Furthermore, we found a significant interaction between

Table 1. Effects of clipping and resource addition on pollen receipt (a proxy for pollinator visitation), oviposition rates and fruit destruction by *Hylemya*, and nectar robbing by *B. occidentalis*. The percent destroyed is calculated as the number of fruits destroyed by *Hyleyma* larvae divided by the total number of filled fruits produced per plant. Percent eggs and percent robbed are the total percentage of flowers oviposited on by *Hylemya* and nectar robbed by *B. occidentalis*, respectively, over the season. Values are means ± 1 SE.

Response variable	Year	Clip treatment	Ambient	Water (W)	W + Fertilizer
Pollen receipt	2001	clipped	108.5 ± 6.9	115.2 ± 5.4	135.2 ± 7.6
		control	116.3 ± 6.9	104.8 ± 6.5	127.8 ± 5.6
	2002	clipped	71.3 ± 5.5	87.4 ± 4.4	93.1 ± 5.5
		control	83.0 ± 5.0	109.4 ± 5.4	106.4 ± 5.4
Percent eggs	2001	clipped	21.1 ± 2.2	23.1 ± 1.6	18.7 ± 1.7
		control	30.4 ± 2.0	33.9 ± 1.7	31.8 ± 1.1
	2002	clipped	34.9 ± 3.0	40.9 ± 2.8	34.2 ± 2.2
		control	35.5 ± 2.2	44.5 ± 2.1	40.0 ± 2.0
Percent destroyed	2001	clipped	14.9 ± 1.8	15.1 ± 1.5	13.9 ± 1.1
		control	18.5 ± 1.5	20.1 ± 1.0	19.8 ± 1.2
	2002	clipped	11.9 ± 1.4	19.6 ± 1.7	16.5 ± 1.4
		control	14.6 ± 1.5	20.6 ± 1.5	20.2 ± 1.2
Percent robbed	2001	clipped	5.7 ± 1.3	6.6 ± 1.5	6.2 ± 1.2
		control	1.5 ± 0.4	1.8 ± 0.4	3.9 ± 0.6
	2002	clipped	0.05 ± 0.04	0.20 ± 0.11	0.08 ± 0.03
		control	0.37 ± 0.14	0.47 ± 0.02	0.17 ± 0.001

clipping and bloom date on *Hylemya* oviposition ($F_{1,555} = 25.74$, $p < 0.0001$) with unclipped, early-blooming plants receiving significantly more eggs than clipped, early-blooming plants. Although sepals of clipped plants were significantly narrower than those on unclipped plants, sepal width did not explain a significant amount of the variance in oviposition ($F_{1,555} = 1.13$, $p = 0.29$).

Nectar robbing

Robbing rates differed between clipping treatments, and were variable between years and sites as well. Clipped plants experienced a three-fold higher rate of nectar robbing than unclipped plants ($F_{1,557} = 4.28$, $p = 0.039$; Table 1). These differences were driven by the effects of clipping on nectar robbing in 2001; there was no difference between clipping treatments in 2002 (clipping by year: $F_{1,557} = 21.68$, $p < 0.0001$; Fig. 3). We should note that the percentage of robbed flowers was low in 2001 and extraordinarily low in 2002 (Table 1, Fig. 3). The significant difference in robbing between clipped and unclipped plants in 2001 was driven by a difference at one site (VF), while there were no differences in robbing at the other site (OH) (significant interaction between clipping and site, $F_{1,557} = 6.54$, $p = 0.01$). Resources also affected nectar robbing, with fertilized plants incurring 14% higher rates of robbing than those experiencing ambient conditions ($F_{2,557} = 3.05$, $p = 0.048$). And, fertilized plants in 2001 experienced higher levels of robbing than those receiving only water or ambient conditions, while in 2002 that was not the case (resources by year: $F_{2,557} = 4.66$, $p = 0.0098$). We found no significant interactions between resources and clipping on robbing rates. In contrast to the results of seed predation, bloom date alone had no significant effect on nectar robbing ($F_{1,557} = 0.47$, $p = 0.49$). However, late-blooming plants at OH in 2001 incurred significantly higher rates of robbing than early plants, but not at VF (thus we found a significant bloom date by site interaction: $F_{1,557} = 32.66$, $p < 0.0001$).

(3) How do simulated herbivory, resource addition, and plant interactions with mutualists and antagonists affect male and female components of plant reproduction?

Investment of plants in male reproduction, measured as the amount of pollen produced, differed among treatments. Clipping enhanced pollen production per flower by ca 6% (Table 2, Fig. 4A). Resources also enhanced per-flower

Table 2. ANCOVA testing the effects of clipping and resource addition on pollen production (measured one year) and pollen receipt (measured in both years). Cells that are blank are factors or interactions that were removed from the final analyses because they were not statistically significant ($p > 0.05$).

	Pollen produced per flower			Pollen produced per plant			Pollen received per flower		
Source	DF	F	p	DF	F	p	DF	F	p
Clipping	1	5.96	0.015	1	11.20	0.0009	1	2.52	0.11
Resources	2	3.97	0.02	2	54.97	< 0.0001	2	11.58	< 0.0001
Year							1	27.45	< 0.0001
Site	1	2.51	0.11	2	1.61	0.21	1	1.43	0.23
Year × Clipping							1	6.98	0.009
Year × Resources							1	5.17	0.006
Clipping × Resources	2	3.54	0.0302						
Corolla length							1	5.92	0.015
Error	273			273			539		

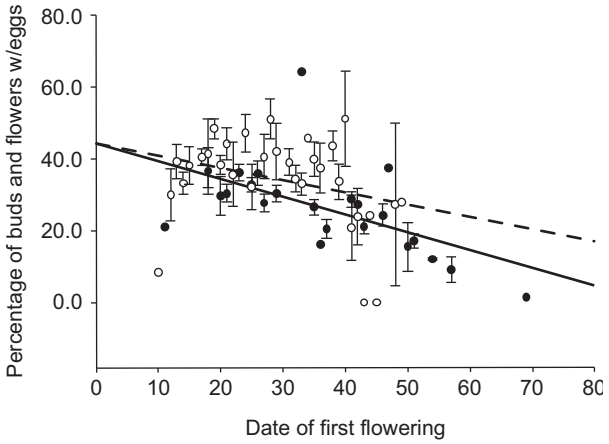

Figure 2. *Hylemya* oviposition (percentage of buds and flowers with eggs) as a function of first date in flower (from 1 June in each year) for plants in 2001 (closed circles) and 2002 (open circles).

pollen production, with fertilized plants producing more pollen per flower than those receiving ambient resources (Table 2, Fig. 4A), and there was a significant interaction between clipping and resource addition on pollen per flower (Table 2) driven by the result that flowers on clipped plants produced more pollen when plants were watered or fertilized, but these resources did not enhance per-flower pollen production for unclipped plants. However, because clipped plants produced significantly fewer flowers over their lifetime (Fig. 1B), whole-plant pollen production was significantly lower for clipped versus unclipped plants (Table 2). Despite differences in pollen production, neither clipping nor resource enhancement significantly altered pollen removal for any of the five weeks in which it was measured in 2002 ($p > 0.05$ in all cases).

Clipping reduced some components of female reproduction ($\lambda = 0.06$, $F_{3,538} = 11.41$, $p < 0.0001$) while resource addition enhanced other components of female reproduction ($\lambda = 0.78$, $F_{6,1076} = 23.46$, $p < 0.0001$). Clipped plants produced 24% fewer (an average of 4.2 ± 0.10 vs 5.5 ± 0.11) seeds per fruit and 50% fewer total seeds (124.1 ± 8.1 vs 260.6 ± 13.9) than unclipped plants (Table 3). Clipping reduced percent fruit set by ca 10% ($40.8\% \pm 1.2$ vs $50.2\% \pm 1.1$) averaged over the two years. However, these effects were driven by the delay in flowering and, with bloom date in the model, the only significant effect of clipping was on total seed set. Early-flowering plants experienced higher reproduction overall – the date of flowering was positively correlated with fruit set, seeds per fruit and total seeds (Table 3). In addition, root stalk diameter (RSD) had a significantly positive effect on total seed set, and we found a significant RSD by clipping treatment interaction. Thus, initial size (RSD) significantly affected seed set for unclipped plants but not as greatly for clipped plants (Table 3).

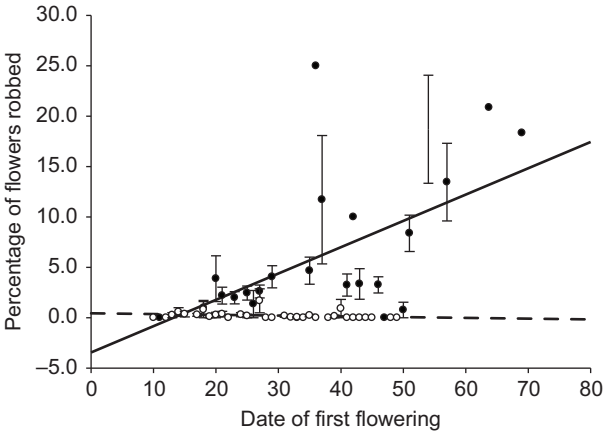

Figure 3. Nectar robbing by *B. occidentalis* (percentage of flowers robbed) as a function of first date in flower (from 1 June in each year) for plants in 2001 (closed circles) and 2002 (open circles). Symbols and abbreviations as in Fig. 2.

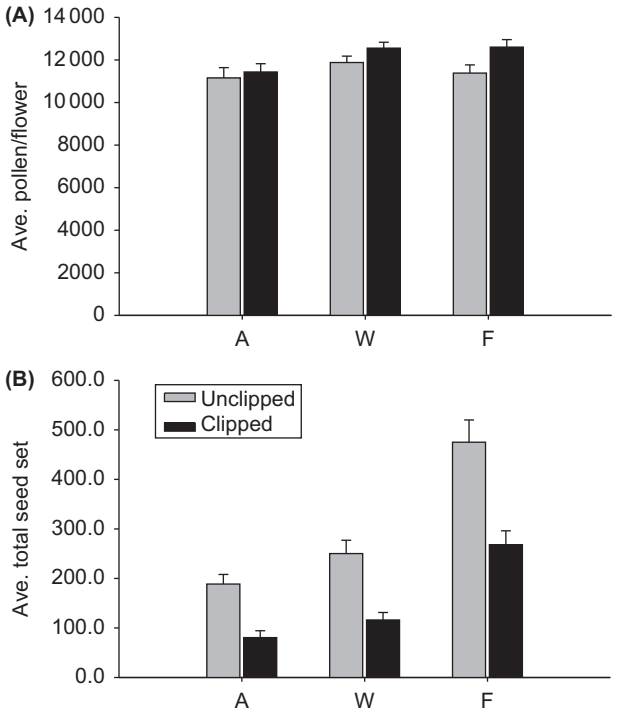

Figure 4. (A) Average pollen production per flower as a function of clipping and resource addition for plants in 2002. Abbreviations are as follows: A refers to ambient resources, W to added water, and F to added water plus fertilizer. (B) Average total seed set per plant as a function of clipping and resource addition, 2001 and 2002 combined.

Resources, too, affected female reproduction. On average, fertilized plants produced ca 2% more seeds per fruit than watered plants and almost 10% more seeds per fruit than plants garnering only ambient resources. In 2002, fruit set for watered plants was 5% higher than for fertilized plants and 7% higher than those not watered or fertilized (Table 3). Overall, fertilized plants produced 51% more total seeds over ambient plants and 38% more than those that were watered (Table 3, Fig. 4B). However, we found no significant interactions between clipping and resource addition for the three components of female reproduction. Thus, plants that received higher levels of resources produced more seeds, but resource addition was unable to fully rescue these plants from the negative effects of clipping.

Table 3. ANCOVA testing the effects of clipping and resource addition on female reproduction with seed predation (% destroyed) and nectar robbing (% rob) included as covariates. Cells that are blank are interactions that were removed from the final analyses because they were not statistically significant ($p > 0.05$).

	Percent fruit set			Seeds per fruit			Total seeds		
Source	DF	F	p	DF	F	p	DF	F	p
Clipping	1	0.22	0.64	1	2.62	0.11	1	5.19	0.023
Resources	2	0.28	0.75	2	3.23	0.04	2	68.84	<0.0001
Year	1	85.51	<0.0001	1	33.32	<0.0001	1	57.01	<0.0001
Site	1	0.29	0.59	1	2.09	0.15	1	7.85	0.005
Julian bloom date	1	8.07	0.005	1	7.80	0.005	1	13.70	0.0002
Root stalk diam (RSD)							1	43.77	<0.0001
% destroyed	1	637.40	<0.0001	1	58.84	<0.0001	1	90.50	<0.0001
% rob	1	0.56	0.46	1	1.53	0.22	1	4.95	0.026
Clipping × RSD							1	6.15	0.013
Resources × % destr	2	2.46	0.09						
Resources × % rob	2	7.58	0.0006						
Clipping × % rob							1	5.373	0.021
Clipping × % destr				1	4.08	0.04	1	5.65	0.018
Error	556			524			553		

Effects of species interactions on female fitness components

Seed predators and nectar robbers had significant effects on female reproduction. In the full ANCOVA model with the percentage of fruits destroyed by *Hylemya* and the percentage of flowers robbed as covariates, clipping alone had no effect on percent fruit set or the numbers of seeds per fruit, and only a marginal effect on total seed production (Table 3). However, the percentage of flowers destroyed by *Hylemya* and the percentage of flowers robbed had significant effects on all female fitness measures (Table 3), although not in the direction initially predicted. The percentage of fruits destroyed by *Hylemya* was positively correlated with female reproduction – i.e. plants with higher levels of damage also had higher rates of fruit set, seeds per fruit, and total seed set (Table 3). However, the slope of the relationship between total seed set and *Hylemya* damage was greater in unclipped plants than in clipped plants (significant interaction between clipping and percent of fruits destroyed, Table 3). Similarly, the relationship between robbing and total seed set was positive, but only so for unclipped plants (significant interaction between clipping and percent of flowers robbed, Table 3). We found a significant interaction between the effects of resource addition and percentage of flowers robbed on percent fruit set, and a marginally significant interaction between resources and percentage of fruits destroyed by *Hylemya* (Table 3).

Discussion

Plants exhibit wide variation in their responses to herbivory. The challenge remains to understand the mechanisms driving that variation (Parra-Tabla and Herrera 2010, Bagchi and Ritchie 2011). Compensatory response to damage can be predicated on stored nutrients (Wise and Abrahamson 2007) or more immediate availability of resources (Juenger and Bergelson 1997, Sharaf and Price 2004), pollen limitation (Mothershead and Marquis 2000), the timing of damage (Maschinski and Whitham 1989) and/or subsequent interactions with other floral enemies (Strauss and Irwin 2004). Although each of these mechanisms may, in some cases, fully account for compensation, plant compensatory response is notoriously variable. We predicted that plants receiving ample resources would fully tolerate clipping and be able to take advantage of the release of apical dominance as long as pollination was sufficient and plants delayed by clipping did not incur high rates of nectar robbing. We also expected that phenological delays would result in lower rates of pre-dispersal seed predation. Thus the outcome of damage would depend on the intensity of seed predation and nectar robbing, coupled with the strength of resource limitation. Our results partially supported these predictions. Clipping released apical dominance and induced the production of multiple flowering stalks, but at significant costs due to phenological delays and, in some cases, higher risk to enemies. Fertilization enhanced reproduction over non-fertilized plants within clipping treatments, but fertilization did not rescue female reproductive success from the negative effects of clipping. In addition, plants responded differently among sites and among years, due – at least in part – to temporal and spatial variability in flowering phenology. Phenology is likely to be strong driver of plants' ability to capture resources (Banta et al. 2010), as well as affect interactions with mutualists and antagonists that, in turn, significantly affect plant fitness (Strauss and Irwin 2004).

We predicted that a delay in flowering from clipping would reduce risk to seed predators while increasing plant risk to nectar robbers. Although clipped plants experienced a reduced risk to pre-dispersal seed predators and, in one year, an increased risk to nectar robbers, both predation and robbing rates were positively correlated with total seed set. Plants with larger floral displays (those not clipped and provided supplemental resources) experienced higher rates of predation and robbing and outperformed their clipped counterparts. A positive link between seed predation and flowering success, although counter-intuitive, is not unprecedented (Brody and Mitchell 1997, Brody and Morita 2000). High rates of attack in plants with large floral displays

have been demonstrated for *Primula veris* (Kolb and Ehrlén 2010), *Lathyrus vernus* (Ehrlén and Münzbergová 2009) and several species in the Asteraceae (Fenner et al. 2002). Thus, large floral displays appear to often represent a bet-hedging strategy whereby plants maximize pollinator visits while incurring some loss to enemies. The negative effects of seed predation are likely to be realized only under conditions of substantial pollen and/or resource limitation.

Unexpectedly, the effects of clipping and resulting changes in flowering phenology had no direct effect on pollinator visitation rates as measured by pollen receipt (Engel and Irwin 2003). However, pollen receipt was significantly higher in plant provided with ample resources – an effect which was likely due to higher nectar production rates in fertilized plants ($F_{2,527} = 9.17$, $p = 0.011$). In addition, the variability in pollen receipt across years and resource treatments suggests that pollen availability is affected by a variety of factors including plant nutrient status, floral display size, timing of flowering and attractiveness to pollinators. In contrast to our results, herbivory significantly affected plant interactions with pollinators through damage-induced changes floral traits (Strauss et al. 1996, Mothershead and Marquis 2000, Goméz 2003), flowering phenology (Huhta et al. 2003) and floral chemistry (Kessler et al. 2011).

Pollinator abundance, and the importance of pollen limitation, is notoriously variable in this system (Campbell and Halama 1993, Juenger and Bergelson 1997, Price et al. 2005) and in others as well (Knight et al. 2005). Indeed, in one study of *Ipomopsis aggregata*, clipped plants provided ample pollen fully compensated for damage (Juenger and Bergelson 1997) while in another, despite being hand-pollinated, clipped plants still severely undercompensated (Sharaf and Price 2004), a result likely driven by resource limitation. Likewise, variation in plant compensatory response has been directly linked to resource availability for both *I. arizonica* (Maschinski and Whitham 1989) and *I. aggregata* (Levine and Paige 2004). Taken together, our results along with these others suggest that compensatory response in *Ipomopsis* is driven by a combination of resource and pollen limitation and both of these factors are spatially and temporally variable.

Although a wealth of studies has examined compensation through female fitness, few other studies have examined compensation to herbivory through male fitness components. For those that have, results have been mixed. Previous studies with *I. aggregata* demonstrated equal or higher compensation to herbivory through male- than through female-fitness components (Gronemeyer et al. 1997) due to equal pollen production from a greater number of flowers. Nectar robbing, too, induced greater flower production and greater pollen export in some *I. aggregata* plants as well (Irwin 2009); however, on average, high levels of nectar robbing reduce seed siring in *I. aggregata* (Irwin and Brody 2000). In the gynodioecious wild strawberry, *Fragaria virginiana*, male fitness estimates suffered more than those of female fitness as a result of florivore damage (Ashman et al. 2004). Moreover, in studies of tolerance and the costs of induction in wild radish, *Raphanus raphanistrum*, leaf damage by lepidopteran herbivores lowered per-flower pollen production as well as pollen grain size (Lehtilä and Strauss 1997, Agrawal et al. 1999), but per-flower pollen production did not differ significantly between experimentally clipped plants and controls (Agrawal et al. 1999). Thus, the response of male fitness can differ depending on the type and degree of damage and depending on the accounting – i.e. whether measurements are done per flower or per plant.

However, none of these studies examined the interaction between resource addition and herbivore damage for estimates of male plant function. When examined, again in wild radish, tolerance to herbivore damage through male fitness (estimated as flower production) was higher than tolerance through female fitness in one environment, but in a richer environment, estimates of tolerance through male and female function were indistinguishable (Strauss et al. 2001). The ability of plants to take advantage of added resources and shunt those resources into higher pollen production per flower has, to our knowledge, rarely been examined or found (but see Lau et al. 1995). Whether or not an increase in pollen production per flower translates into an increase in realized paternity for damaged plants in some weeks in natural populations remains to be determined. It would be interesting to examine if, in general, male fitness is more tolerant to damage and/or more responsive to resource conditions than female fitness. If so, that would suggest that many prior studies, by not measuring male function, have underestimated compensation to herbivory and future studies need to account for both male and female fitness components (Agrawal et al. 1999). In addition, the realized effects of flower and pollen production will depend on phenology and the availability of pollinators to insure adequate pollination.

The picture emerging from these studies is that plant response to herbivore damage depends not simply on ample abiotic resources, but on interactions with multiple mutualists and antagonists, and these interactions are highly variable (Kolb and Ehrlén 2010, Parra-Tabla and Herrera 2010). The overall benefit, or cost of herbivory, will ultimately depend on a combination of the direct negative effects of damage on plant reproduction, the positive effects of releasing apical dominance, and the indirect effects of damage on mutualist pollinators and floral enemies. Examining the full suite of these direct and indirect effects moves us toward a greater understanding of herbivore–plant interactions and closer to general predictions about when herbivory might be tolerated and when not.

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