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Research article

Effects of herbivory on the reproductive effort of 4 prairie perennials

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Abstract

Background: Herbivory can affect every aspect of a plant's life. Damaged individuals may show decreased survivorship and reproductive output. Additionally, specific plant species (legumes) and tissues (flowers) are often selectively targeted by herbivores, like deer. These types of herbivory influence a plant's growth and abundance. The objective of this study was to identify the effects of leaf and meristem removal (simulated herbivory within an exclosure) on fruit and flower production in four species (*Rhus glabra*, *Rosa arkansana*, *Lathyrus venosus*, and *Phlox pilosa*) which are known targets of deer herbivory.

Results: *Lathyrus* never flowered or went to seed, so we were unable to detect any treatment effects. Leaf removal did not affect flower number in the other three species. However, *Phlox*, *Rosa*, and *Rhus* all showed significant negative correlations between seed mass and leaf removal. Meristem removal had a more negative effect than leaf removal on flower number in *Phlox* and on both flower number and seed mass in *Rosa*.

Conclusions: Meristem removal caused a greater response than defoliation alone in both *Phlox* and *Rosa*, which suggests that meristem loss has a greater effect on reproduction. The combination of leaf and meristem removal as well as recruitment limitation by deer, which selectively browse for these species, is likely to be one factor contributing to their low abundance in prairies.

Background

Herbivory has the potential to impact every stage in a plant's life [1], and thus influences where a plant can grow and its abundance [2]. Different kinds of herbivory have differential impacts on plants. Herbivory can reduce resource availability and subsequently have indirect impacts on plant reproduction [3]. Both meristem damage [4] and leaf damage [3] have been shown to negatively impact components of plant fitness such as survival, flower number, and fruit production [1,4–6].

Herbivores may also feed selectively on specific plant species or tissues, which can lead to increased mortality or slower growth rates of damaged individuals [2]. Insect herbivores can directly limit seed production and lifetime fitness by feeding on inflorescences [7]. Mammalian herbivory has been shown to be strong enough to significantly limit the abundance of a plant species [8–10]. Deer in particular have influenced the composition of plant communities in the northeastern and north-central United States [11,12].

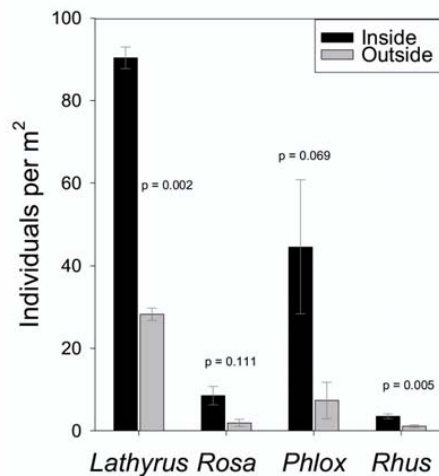


Figure 1

Abundance (mean \pm 1 SE) of *Lathyrus*, *Rosa*, *Phlox*, and *Rhus* inside and outside fenced enclosures. The effect of fencing was compared within each species using oneway ANOVAs (*Lathyrus* $n = 4$, *Rosa* $n = 4$, *Phlox* $n = 8$, *Rhus* $n = 12$). Overall, the abundance of all species was significantly higher inside the fence (Type III GLM $F = 14.7$, $df = 7$, $P < 0.001$, $R^2 = 0.837$; species $F = 21.3$, $df = 3$, $P < 0.001$; enclosure $F = 24.2$, $df = 1$, $P < 0.001$; interaction $F = 6.72$, $df = 3$, $p = 0.003$).

Deer have been shown to reduce the proportional rate of increase in the height of some woody species [13]. It also has been suggested that deer browsing can significantly reduce the growth rate of herbaceous plants [11]. Deer herbivory typically involves the removal of entire leaves and terminal meristems, and reduces the proportion of flowering shoots [11], and has the potential to effect reproductive success of browsed plants. For example, deer browsing reduced the number of flowers and proportion of large fruits produced by the forb, *Lactuca canadensis* [14]. However, there is little known how browsing influences plant fecundity [11].

The objective of this study was to identify the effects of leaf and meristem damage on fruit and flower production in four species of prairie plants that are known targets of deer herbivory. We simulated herbivory with four unrelated species and asked three questions: (1) Does leaf removal influence plant reproduction? (2) If so, is there a threshold level of leaf removal that must be reached before plant reproduction is influenced? (3) Does a combination of leaf removal and meristem removal have a greater impact on a plant than random leaf removal? We report on our findings for each of these questions.

Results

There was a significant influence of the exclosures on the abundance of three out of the four species, *Phlox*, *Rhus*, and *Lathyrus* (Figure 1). Flower number strongly correlated with leaf biomass for *Phlox*, *Rosa*, and *Rhus* (Figure 2). The number of flowers produced by *Phlox* ($P = 0.6$), *Rosa* ($P = 0.13$), and *Rhus* ($P = 0.3$) was not significantly affected by the leaf removal treatment when accounting for plant size. We did not detect an effect in *Lathyrus* because the few flowers produced were all aborted. Seed mass positively correlated with both flower number (Figure 3a) and leaf biomass. The strong, collinear relationship between flower number and leaf biomass (Figure 2) prevented us from using both variables in the seed mass analyses. We chose to use flower number as a covariate since it has a more direct impact on seed set and the number of seeds produced by an individual plant.

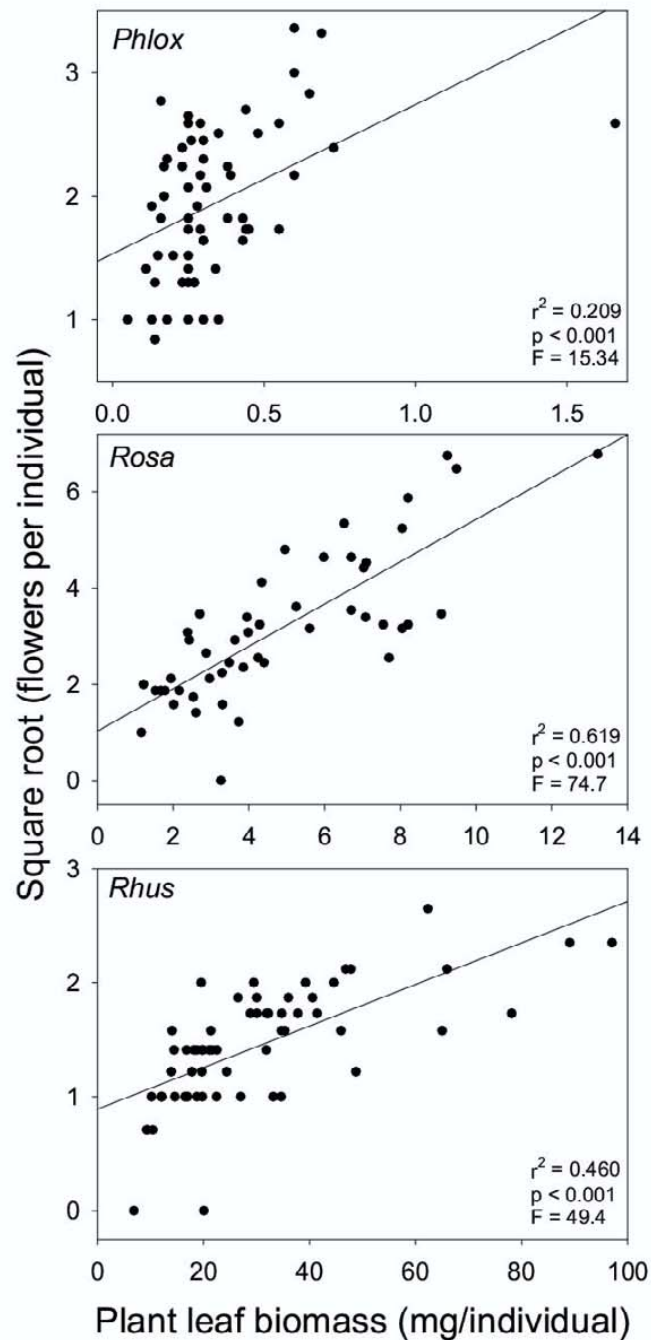
Phlox, *Rosa*, and *Rhus* all showed a significant, negative correlation between leaf removal and seed weight when accounting for flower number (Figure 3b). The more biomass that was removed, the smaller the overall seed mass per individual. There was not a leaf removal frequency threshold that influenced flower or seed production when all the species were examined together ($P = 0.1$) or when *Rhus* ($P = 0.3$), *Phlox* ($P = 0.1$) and *Rosa* ($P = 0.3$) were examined individually. We were unable to detect an effect in *Lathyrus*, which flowered a little, but no single plant went to seed. None of the plants in the study produced fruits and only three fruits were found when the field inside and outside the fence was surveyed.

The meristem removal treatment had a significantly negative effect on flower number in both *Phlox* and *Rosa* (Figure 4a). The individuals in the meristem removal treatment produced very few flowers when compared to those individuals in the control and leaf removal treatments. Meristem removal also caused the seed mass to be significantly lower in *Rosa*, though the seed masses of both *Phlox* and *Rhus* remained unaffected (Figure 4b).

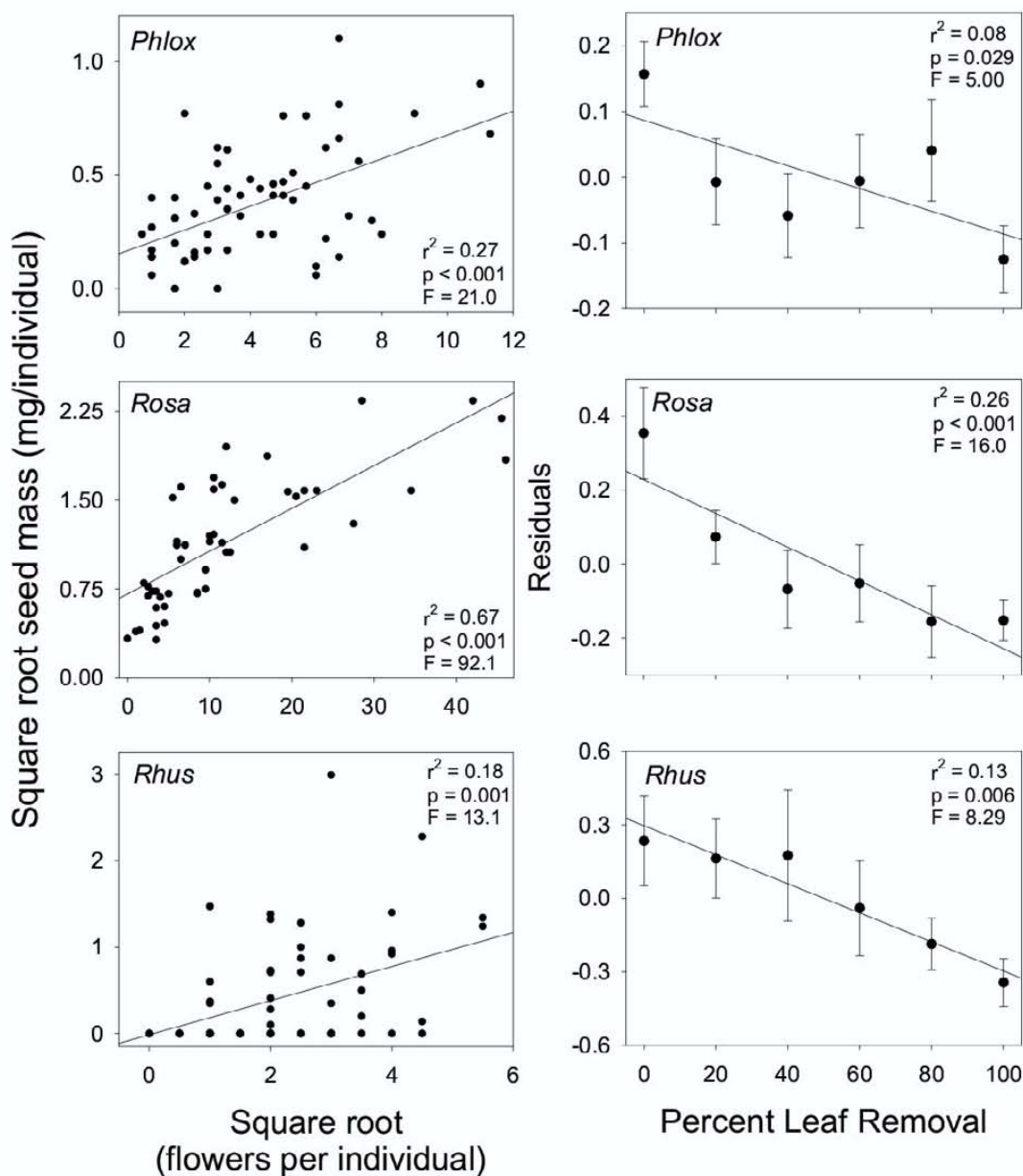
Discussion

Three of the four species studied were significantly more abundant within the exclosures than outside of them. This pattern is consistent with other results found for herbaceous species at this [6,15] and other sites [8–10] where mammalian herbivory has been shown to limit overall plant abundance in some species. It is therefore not surprising that deer browsing should effect the overall abundance of species known to be preferred by deer. Less clear is which aspect of herbivory is most important.

Leaf removal did not affect flower production in any of the species, which is consistent with other studies [7,16,17]. Ehrlén demonstrated that flower numbers were

**Figure 2**

The relationship between flower number and leaf biomass for *Phlox* ($n = 60$), *Rosa* ($n = 48$) and *Rhus* ($n = 60$) respectively. Flower number per individual was square root transformed.

**Figure 3**

a) The relationship between seed mass and flower number for *Phlox* ($n = 60$), *Rosa* ($n = 48$) and *Rhus* ($n = 60$) respectively. Both seed mass and flower number were square root transformed, b) The relationship between the residuals (mean \pm 1 SE) of seed mass versus flower number and the percent leaf removal for *Phlox* ($n = 60$), *Rosa* ($n = 48$) and *Rhus* ($n = 60$) respectively.

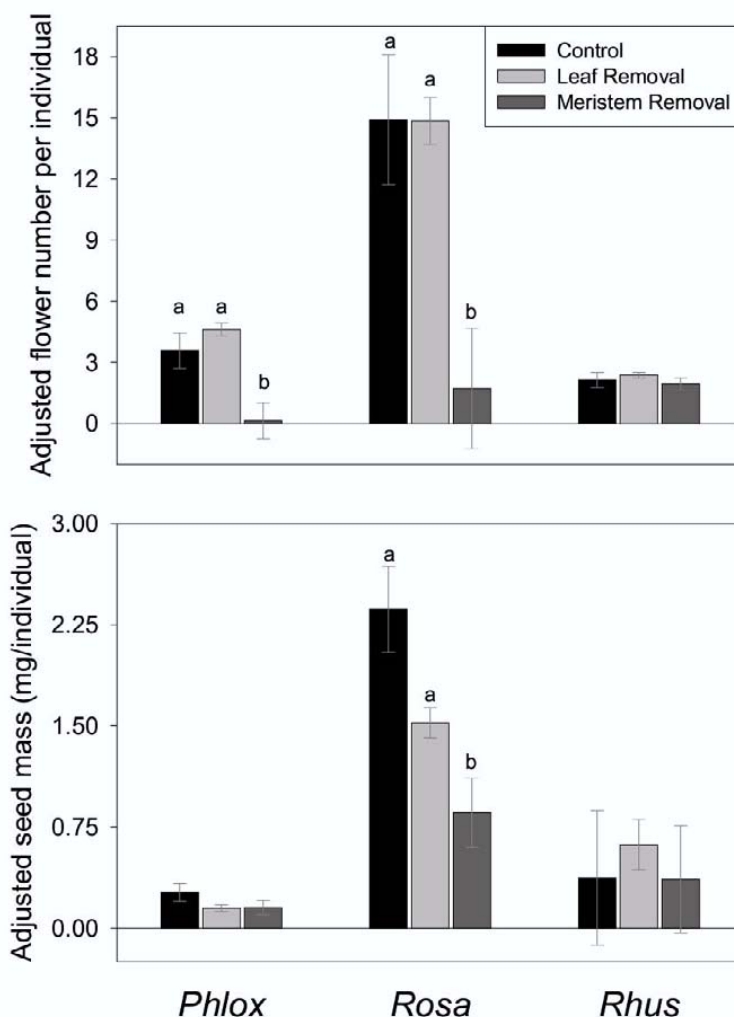


Figure 4

a) Flower number for *Phlox*, *Rosa* and *Rhus* under three different simulated herbivory treatments (control, leaf removal only, or meristem removal). Values are shown as adjusted means \pm 1 SE from Type III GLMs with treatment as the main effect and plant size and leaf removal as covariates. Overall, the treatment effect was significant for *Phlox* ($F = 14.2$, $P < 0.001$) and *Rosa* ($F = 6.80$, $P < 0.001$) but not for *Rhus* ($P = 0.8$). Flower values are based on the average of multiple counts on individual plants (*Phlox*-June 15, 17 and 21; *Rosa*-June 15 & 21; *Rhus*-June 1 & July 1). Flower number was square root transformed for analysis, b) Seed mass for *Phlox*, *Rosa* and *Rhus* under three different simulated herbivory treatments. Values are shown as adjusted means \pm 1 SE from Type III GLMs with treatment as the main effect and square root flower number and leaf removal as covariates. Treatment had a significant effect for *Rosa* ($F = 6.80$, $P < 0.001$) but not for *Phlox* ($P = 0.2$) or *Rhus* ($P = 0.6$). Different letters denote significant effects at $P < 0.05$ following Bonferroni correction for multiple comparisons.

predetermined the previous fall by budding in *Lathyrus vernus* [18]. The same may be true in all of our species because removing leaves did not impact their flower numbers. Nonetheless, high levels of leaf removal did negatively impact the seed weight in all of the study species which produced seeds (Figure 3b). These results suggest that stored resources are available for flowers and seeds before the onset of flowering [19,20] and changes in current year resources have a negligible effect on flower number. However, leaf removal appears to reduce the amount of carbon available for allocation to developing seeds in *Phlox*, *Rosa*, and *Rhus*, which causes a decrease in the overall seed mass produced by an individual plant.

Though we found a negative relationship between seed mass and percent leaf damage in *Phlox*, *Rosa*, and *Rhus*, we did not detect a threshold level of leaf removal that had to be reached before seed mass was impacted. Other studies, which have attempted to quantify the point where defoliation begins to impact reproduction, have yielded widely variable results [1,4–6], though these studies all found significant results at 50% or lower levels of defoliation.

Additionally, defoliation may have differential effects on seeds depending on when it occurs. In this study, all treatments were administered within a few weeks of flowering. One study [5,20] found that when leaves were removed several months before the time of flowering, the plant suffered a large loss in reproductive output. When the same treatment was administered just before flowering, there was no response [5,20]. Timing, then, may be a key in determining how well a plant copes with herbivory [11].

Meristem removal was more harmful to the reproductive output of *Phlox* and *Rosa* than leaf removal alone (Figures 4a & 4b). With meristem removal, *Phlox* had fewer flowers than in the control and leaf removal treatments, but its seed mass was not affected. Meristem removal more strongly impacted *Rosa*, which had fewer flowers and a lower seed mass than either the leaf removal or control groups.

Because *Phlox* is a small herbaceous plant with terminal flowers, it often suffered complete flower loss and substantial leaf removal under the meristem removal treatment. The individuals in this treatment that did produce seeds sent up a side shoot after the meristem was nipped off. In contrast, *Rosa* produced many flowers and never suffered a complete flower loss with meristem removal. The flower loss may have allowed the *Phlox* to compensate by increasing seed set, which has shown to be resource limited in other species [21], in the remaining flowers. The relationship between seed mass and flower number is much stronger in *Rosa* than in *Phlox* (Figure 3a), and *Rosa*, possibly because of its woody nature, was unable to com-

pensate for the flower loss by generating new shoots and flowers or by increasing seed set in the remaining flowers. Therefore, the significance of this treatment is most likely due to a combination of how many buds remained after meristem removal as well as the allocation of remaining resources for reproduction.

Conclusions

High levels of defoliation reduced total seed weight in *Phlox*, *Rosa*, and *Rhus*, all of which are found in Minnesota prairies. The removal of meristems along with defoliation caused a greater response than defoliation alone in both *Phlox* and *Rosa*. This suggests that loss of meristems is more important than defoliation alone in its influence on the reproductive success of these species. All three species studied are preferred by large mammal herbivores (primarily white tailed deer). These results suggest that both defoliation, which limits the resources available for reproduction, and meristem removal may be partly responsible for the comparative rarity of the study species outside fenced enclosures.

Materials and Methods

Study site and study species

The study was conducted at Cedar Creek Natural History Area (CCNHA) in central Minnesota. For a detailed description of the study site, see Tilman [22]. The four species studied include smooth sumac (*Rhus glabra*), wild rose (*Rosa arkansana*), bushy vetch (*Lathyrus venosus*), and phlox (*Phlox pilosa*). Smooth sumac is a perennial shrub (1–4 m tall). Wild rose is a short woody perennial shrub (1 m or shorter). *Lathyrus venosus* is a perennial legume (1.5 m or shorter). *Phlox* is an herbaceous perennial (30 cm or shorter). These species were chosen because they were abundant inside the fenced area and absent or rare outside the fence (see methods below). There is also evidence that *Rhus* [23], *Lathyrus* [15], *Phlox* (Haarstad, personal communication), and *Rosa* [24] are all browsed by deer. The density of deer in this area has been minimally estimated to be 0.16 deer per ha [25]. This density is similar to other protected areas, where deer herbivory has caused changes in plant composition [25]. Target species were located inside exclosures which kept out large herbivores.

Experimental design

To compare abundance of the study species inside and outside the fenced enclosures, temporary transects (0.5 × 8 m) were established within and outside of each fenced area. For each species, the total number of individuals along the transects were counted. For *Rosa* and *Lathyrus*, two transects on either side of the fence were counted. *Phlox* was counted in four transects inside the fence and four outside. *Rhus* transects were established at fenced ar-

eas in 2 different fields. Two transects on either side of the fences were counted in each field.

To measure the effects of different levels of defoliation, individuals of each species within the enclosures were randomly selected and tagged. Initial height and number of leaves were recorded. Ten individuals of each species (except *Rosa*, which only had enough for 8 individuals for each treatment level) were randomly assigned to one of the following treatments: 1) control, no simulated herbivory, 2) 20 % of all leaves removed, 3) 40 % of all leaves removed, 4) 60 % of all leaves removed, 5) 80 % of all leaves removed, 6) 100 % of all leaves removed, or 7) meristem + natural leaf removal (called the meristem removal hereafter). This treatment was designed to simulate deer and rabbit browsing in which the entire top of a plant is often removed. Meristems, leaves and flower buds were all removed from the top of the plant and left at the bottom of the plant. The mass of the leaves removed by the meristem removal was determined and converted to the percent of the plant's total leaf biomass.

Removed leaves were dried at 55 degrees C for one week and then weighed. Following the initial damage treatment, the sites were visited twice a week. Flowers were counted on multiple visits. Seeds were collected and dried, and then weighed to give the total mass of all the seeds collected per individual plant. Mesh bags were placed over *Phlox* flowers because seeds are small and fall off when they ripen. No such bags were needed for *Rosa* or *Rhus*, both of which have large seeds, which are retained on the parent plant.

Statistics

All statistical analysis was performed on SPSS 10.0 for Windows. One-way ANOVAs were used to determine the effect of the enclosures on the abundance of the individual species. Type III GLM analysis was used to test for differences between areas within and outside the enclosure, with abundance as the dependent variable and species, enclosure, and their interaction as the independent variables.

Total leaf biomass was calculated for each plant since larger plants generally produce more biomass and larger and/or more seeds than smaller plants. Using the weight of the leaves collected, the following formula was used to calculate the total leaf biomass per individual:

$$(\text{dried leaf weight/number of leaves collected}) \times (\text{total number of leaves on the plant})$$

This leaf biomass was used to account for plant size in statistical analysis.

Multiple regression was used to examine the relationship between percent leaf removal and flower number with plant size as the covariate. Multiple regression was also used to examine the relationship between percent leaf removal and seed mass with flower number as the covariate. Type III GLMs were run to examine the effect of the different treatments (leaf removal, meristem removal, and controls) on both flower number and seed mass. Plant size was run as a covariate for flower number, and flower number was used as a covariate for seed mass. We also corrected for the actual biomass of the leaves removed since the meristem removal often removed leaves. The level of Type III GLM analysis was also used to test for effects of different levels of leaf removal on flower number and seed mass. Bonferroni tests were performed for multiple comparisons. For all these analyses, seed mass and flower number were square root transformed.

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