

FOLIAR HERBIVORY AFFECTS FLORAL CHARACTERS AND PLANT ATTRACTIVENESS TO POLLINATORS: IMPLICATIONS FOR MALE AND FEMALE PLANT FITNESS

Plants are subject to selection exerted by both herbivores and pollinators simultaneously. Despite this fact, no previous study has directly linked foliar herbivory and pollination. A few studies have addressed how floral displays that attract pollinators may subsequently attract seed predators, when flowers mature to fruits (Campbell 1991; Brody 1992), but no one has examined how folivore-caused changes in floral characters, particularly corolla characters, affect pollinators. In the past, it has been assumed that floral characters, and particularly corolla characters, are relatively invariant because of the fitness consequences that reduced attractiveness to pollinators may have for self-incompatible plants (e.g., Harper 1977, p. 195). However, it is well known that natural variation in flower size, flower number, nectar production, and pollen production affects the attractiveness of plants to pollinators (e.g., Schemske 1980; Roubick and Buchmann 1984; Willmer 1986; Stanton and Preston 1988; Galen 1989). Effects of foliar herbivory on floral traits other than flower number are not well known (but see McKone 1989; Frazee and Marquis 1994; Quesada et al. 1995). Herbivore damage directly to corollas reduced the attractiveness of flowers to pollinators (Karban and Strauss 1993). The effects of *foliar* damage by herbivores on floral traits and, in turn, on the attractiveness of plants to pollinators have been generally ignored (Crawley 1989; Marquis 1992).

The significance of floral responses to foliar herbivory is twofold. First, estimates of the effects of herbivory on plant fitness based on female fitness (seed production) may be misleading if plants suffer a reduction in male fitness (number of seeds sired on other plants through pollen). Herbivory affecting attractiveness to pollinators has the potential to strongly influence plant fitness through male function, since visitation rates can often affect male fitness (number of seeds sired by pollen) more strongly than female plant fitness (numbers of seeds set) (Bell 1985). Only a handful of studies have documented male and female plant fitness simultaneously, and at least three have shown that male and female plant fitness are either negatively or only weakly correlated (Bertin 1982; Ennos and Dodson 1987; Schlichting and Devlin 1989; Broyles and Wyatt 1990; Devlin and Ellstrand 1990). Thus, the impact of herbivory on the fitness of hermaphroditic plants requires knowledge of both male and female reproductive success. Second, how plants have evolved to respond to damage from herbivores in allocation patterns to floral resources may be influenced or constrained by floral adaptations

to animal pollinators. Here, we show that early leaf damage reduces several floral attraction and reward characters and that these reductions decrease pollinator visitation. Our data are meant to illustrate some less considered ways in which herbivory may influence both male and female plant fitness.

METHODS

To examine the effects of foliar herbivory on floral morphology and pollinator visitation, we used wild radish, *Raphanus raphanistrum*, a self-incompatible annual that depends on pollinator visitation for reproduction (Sampson 1964). In east-central Illinois, these plants are visited by a diverse assemblage of pollinators, including cabbage white butterflies, honey bees, small native bees, and syrphid flies. Members of all these taxa have been shown to be effective pollinators (Stanton et al. 1991; Conner et al. 1995).

We selected pairs of equal-sized, equal-aged sibling (either full or half) seedlings from 18 families of wild radish and chose one at random to be damaged by cabbage white butterfly larvae (*Pieris rapae*). All experiments were designed as paired tests comparing floral characters or attractiveness to pollinators between pairs of damaged and undamaged siblings. We compared siblings to control partially for maternal effects and for genetic variation in floral morphology (Conner and Via 1993). Plants were grown in a pollinator-free greenhouse. Seeds were planted in 4-inch pots of Metro-mix 360 and fertilized on planting and every third week thereafter. Under this regimen, plants produced about 250 flowers, a size that is small but not atypical of plants in wild populations (M. L. Stanton and A. A. Snow, personal communication). For each pair, half of each of the first four true leaves of one randomly selected sibling was consumed by cabbage white butterfly larvae, and the other sibling served as an undamaged control. Any leaves subsequently produced by plants were left undamaged, so the herbivory treatment removed 50% of leaf area in early life and translated to approximately 25% total leaf area removal over the plant's lifetime. This level of leaf area removal was within the range of that exhibited by both seedling and mature plants in the field (S. Y. Strauss and J. K. Conner, unpublished data). Our main purpose here is to use *R. raphanistrum* as a model system to inquire about the *potential* effects of herbivory on pollination and not to address specifically effects on *R. raphanistrum*.

Once plants started flowering (about 2 wk after damage to leaves), we measured petal length, petal width, volume of standing nectar crop, and number of pollen grains produced by the third flower of each plant. Measurements of the petal length and width were made with digital calipers. Nectar droplets produced by the two nectaries were collected with a 2- μ L microcapillary tube. Height of the column was then measured with digital calipers and converted into nectar volume. Number of pollen grains was estimated by collecting anthers from newly opened flowers and counting pollen grains with a Coulter counter.

We subsequently measured petal length and width on the fiftieth flower (approximately) to determine whether we could still detect differences between damaged and undamaged sibs. At the end of the experiment, we weighed total plant

biomass and counted numbers of flowers produced by siblings in both treatments. Univariate paired *t*-tests were used to compare traits on damaged versus undamaged siblings; in addition, a multivariate analogue of the paired *t*-test, Hotelling's T^2 (Harris 1985), was used to compare sets of floral characters simultaneously.

To determine the impact of this early leaf herbivory on attractiveness to pollinators, we placed pairs from 11 of the 18 families in the field in May 1993 and observed pollinator visitation patterns. Each plant was observed continuously over a 15-min interval, and damaged and undamaged sibs were observed simultaneously (or within 12 min) to control for changing weather conditions and pollinator activity patterns. For each plant, we recorded numbers of pollinators, pollinator type, duration of visit, and number of flowers visited.

In May, the predominant pollinators were small, native bees. Because the pollinator community varies seasonally, we made similar observations in September, when syrphid flies, rather than native bees, dominated the pollinator assemblage. For this second experiment, pairs of siblings from seven new families (all different from the original 18) were used. One member of each pair of sibling seedlings was selected at random to be damaged manually. Manual damage was done in a manner similar in timing and pattern to that of larval damage. Half of the leaf area of the first four true leaves was removed over a 2-wk period by cutting along the midrib of each leaf. After the plants flowered, they were placed in the field for pollinator observations as before, except that observation periods were 10 min. Patterns of pollinator visitation were similar in the two trials. Fewer pollinators visited damaged plants in both trials (paired *t*-test for first trial, $t = -2.025$, $P = .07$; *t*-test for second trial, $t = -2.857$, $P = .03$). Since pollinators behaved similarly in both trials, and the paired *t*-test compares only damaged and undamaged sibling plants within trials, we pooled data into a single analysis to allow us to examine attributes of visitation (such as duration of time spent foraging per flower) with increased power.

In retrospect, it was also interesting to consider the rate of visitation per flower on damaged and undamaged plants. Since we observed pollinators during observations and not individual flowers, we could only estimate this parameter. We took the average number of flowers visited per pollinator during the observation period multiplied by the total number of pollinators observed foraging during that period as an estimate of the total number of flowers visited per plant per observation period. We then used (total number of flowers visited)/(total number of open flowers) to determine whether flowers on damaged plants were being visited at the same rate as those on undamaged plants. This technique can result in ratios greater than one, when pollinators visit flowers on the same plant more than once. Because these proportions were highly nonnormal, as well as being outside the range of the angular transformation, we used a sign test to compare rate of flower visitation on damaged and undamaged plants.

To examine the relationship between corolla size and flower number on attractiveness to pollinators, we made observations of pollinators in an experimental field population of 50 undamaged plants in July and August 1992, when both bees and flies were abundant. We observed each plant for 60 min and recorded numbers and kinds of pollinators, petal length of one flower, and number of open

TABLE 1
EFFECTS OF DAMAGE TO LEAVES ON FLORAL CHARACTERS AND FINAL BIOMASS OF WILD RADISH

| Trait | Damaged | Undamaged | <i>t</i> | df | <i>P</i> |
|---|---------|-----------|----------|----|----------|
| Days to first flower | 17.28 | 14.44 | 3.338 | 17 | .004 |
| Third flower attributes:* | | | | | |
| Univariate tests: | | | | | |
| Petal length (mm) | 8.26 | 9.96 | -4.020 | 17 | .001 |
| Petal width (mm) | 6.63 | 8.22 | -5.665 | 17 | .001 |
| Nectar (mL) | .14 | .18 | -1.762 | 16 | .09 |
| Pollen grains | 69,866 | 81,505 | -2.214 | 16 | .04 |
| Fiftieth flower attributes:† | | | | | |
| Univariate tests: | | | | | |
| Petal length | 8.29 | 8.75 | -1.745 | 14 | .10 |
| Petal width | 6.63 | 7.16 | -2.308 | 14 | .04 |
| Final plant biomass and flower production: | | | | | |
| Total biomass (g) | 3.80 | 3.95 | -1.425 | 17 | .17 |
| Total flowers | 261.00 | 246.00 | 1.056 | 17 | .31 |

NOTE.—Comparisons of floral characters and plant size were made between caterpillar-damaged and undamaged sibling plants.

* Multivariate test, Hotelling's T^2 (all four traits) = 29.21, $F = 5.93$, $P = .006$.

† Multivariate test, Hotelling's T^2 (both traits) = 5.46, $F = 2.54$, $P = .12$.

flowers on the plant. To relate pollinator visitation rates to flower size and flower number, two multiple regressions were performed, one with the number of small bees as the dependent variable and the other with the number of syrphid flies. Independent variables were petal length, number of open flowers on the plant, amount of pollen produced, time, and date. We corrected for nonlinear effects of time and date by including quadratic (squared) terms for these variables in initial models. In all but one case (time in the small bee regression), the quadratic terms were not significant and were therefore dropped from the final models.

To test directly whether syrphid flies and bees differed in their responses to flower size and number, we compared the slopes of the regressions of visitation rates on the plant traits across the two taxa. To do this, we calculated the difference between the number of syrphid flies and the number of small bees visiting each plant, and we regressed this on the variables listed above (C. McCulloch, personal communication). This approach takes advantage of the paired nature of the data, since the data for both taxa were taken in the same hour observation periods from the same plant. A significant slope for either flower size or number indicates that the two pollinator taxa respond differently to that plant trait; that is, their individual slopes are different.

RESULTS

We found that early damage to young leaves significantly delayed flowering, reduced petal size (both length and width), and lowered pollen production (table 1). Potted plants in the herbivory experiment had petal lengths that were typical of plants in the field population. Mean petal lengths of experimentally damaged

TABLE 2
PATTERNS OF POLLINATOR VISITATION TO DAMAGED AND UNDATED PLANT SIBLINGS

| Response | Damaged | Undamaged | <i>t</i> | df | <i>P</i> |
|---|---------|-----------|----------|----|----------|
| No. of pollinators per observation period | 1.2 | 2.4 | -3.06 | 17 | .01 |
| Duration on plant per pollinator (s) | 36.9 | 138.2 | -3.55 | 9 | .006 |
| No. of flowers probed per visit | 3.5 | 9.5 | -2.85 | 9 | .019 |
| Time spent per flower (s) | 10.2 | 19.60 | -1.39 | 9 | .21 |
| No. of flowers open during trials | 10.3 | 17.7 | -4.09 | 17 | .001 |
| Mean petal length | 8.61 | 9.57 | -1.92 | 10 | .04 |
| Mean petal width | 6.96 | 7.67 | -1.74 | 10 | .10 |
| Mean no. of flowers open during first trial | 14 | 25 | -4.52 | 10 | .001 |
| Mean no. of flowers open second trial | 3.86 | 6.29 | -1.451 | 6 | .20 |

NOTE.—Pollinator visitation results were pooled over both trials (see text). Pairs of plants in which one member of the pair received no pollinators during observations were removed from comparisons of number of flowers visited, duration on plant per pollinator, and time spent per flower.

and undamaged plants were 8.61 and 9.57 mm, respectively (table 2), while field plants had a mean petal length of 8.10 mm (SD = 1.19), with a range of 6.06–10.70 mm. Nectar production was also lower in damaged plants, but this trait was extremely variable, and differences were only marginally significant (table 1). Later flowers produced by damaged plants (i.e., after about 20% of lifetime flower production had occurred) were still smaller than those of undamaged siblings, but marginally so (table 1). Because flowering was delayed in damaged plants, these plants generally had fewer flowers open at any one time than undamaged plants (table 2). Despite this delay, there was no effect of herbivory on final plant biomass or lifetime flower production (table 1). Thus, plants were able to compensate for early foliar damage in terms of total numbers of flowers produced. Had effects of herbivory been measured strictly by plant size or flower number, one would miss these other potentially important effects of herbivory on total plant fitness, primarily through male function.

Pollinators discriminated against damaged plants by visiting such plants less frequently and by spending less time on them (table 2). The proportion of open flowers visited was marginally less on damaged plants than on undamaged plants (mean proportions were 0.45 and 0.76, respectively; $P = .08$; $n = 18$ pairs). Pollinators also spent half as much time per flower, but this difference was not significant (table 2).

Pollinators used different cues to discriminate among plants. Syrphid fly visitation increased strongly with increasing petal length (fig. 1A) but was unrelated to the number of open flowers on the plant (fig. 1B). In contrast, solitary bee visitation was unrelated to petal size (fig. 1C) but strongly increased with increasing numbers of open flowers on a plant (fig. 1D). The slopes of the regressions between bees and flies are significantly different for flower number (slope of difference = 8.6 ± 2.7 , $P = .002$) but not significantly different with respect to petal size (slope = -4 ± 2.8 , $P = .17$). Because different pollinator groups are differentially affected by changes in floral characters (see also data in Clements and Long 1923; Thomson et al. 1982; Conner and Rush, in press; Johnson et al., in

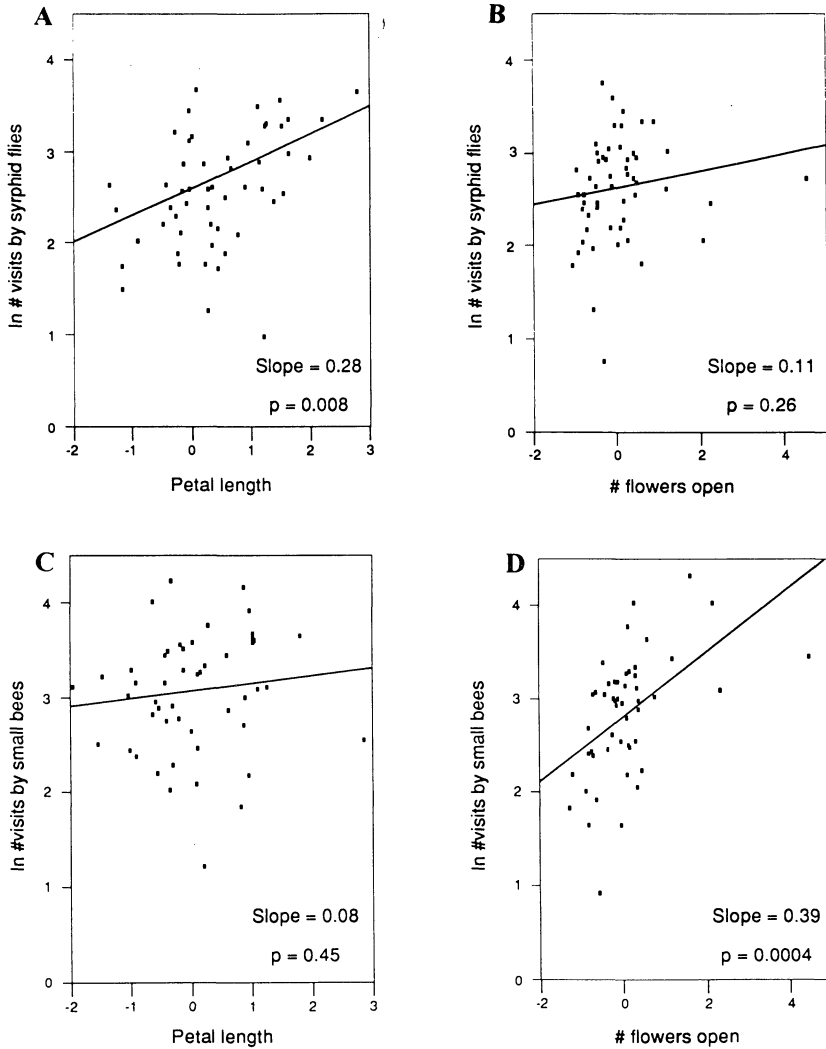


FIG. 1.—Observations of pollinators made on 50 undamaged plants in an experimental field population. Standardized partial regression leverage plots (Sall 1990) show the relationship between attractive traits of wild radish plants and visitation rates by the two main groups of pollinators, native bees and syrphid flies, after correcting for other variables in the model (see Methods). Dependent variables (visitation) were ln-transformed to improve model fit; independent variables were standardized to mean = 0, variance = 1.

press), herbivory has the potential to change the species composition of the pollinator community visiting a plant.

It might be argued that differences in flowering phenology alone between damaged and undamaged plants could explain our results. Flowering is delayed in damaged plants, but later in the season, damaged plants could actually have more flowers than undamaged plants (as the latter senesce) and thus recoup their early disadvantage. Since we only have data over a single window in that flowering period, our results may simply be an artifact of our limited sampling. We have several lines of evidence that suggest that flower number is not the only effect contributing to reduced pollinator visitation on damaged plants. First, our observations of pollinators in the field population showed that flower size, *independent of flower number*, had significant effects on syrphid fly visitation. In addition, in other experiments we have conducted, we have found that trimmed flowers received significantly fewer visits than control flowers located on the same plants (Conner and Rush, in press). Also, in our second pollinator trial, flower number was not significantly different between damaged and undamaged plants (though the trend for damaged plants to have fewer flowers was still there; table 2), and pollinators (mainly syrphid flies) still visited undamaged plants significantly more than damaged ones ($P = .03$; see Methods). Since we find clear effects of herbivory on flower size and clear effects of flower size on attractiveness to pollinators, we feel our results show that pollinators discriminate against damaged plants based on both flower size and flower number.

Given that herbivory reduces plant attractiveness to pollinators, the preferences of pollinators may act as selective pressures that shape how plants allocate resources to floral characters after damage. In particular, plants may face a trade-off between individual flower quality and total flower number produced by a plant. For *Chamaecrista fasciculata*, a prairie legume, damage caused no changes in flower size but decreased lifetime flower production (Frazee and Marquis 1994). In contrast, after damage, wild radish altered investment to individual flowers but preserved lifetime flower production (table 1). Plants like wild radish that have a diverse array of effective pollinators may have more flexibility in their response to herbivory, since different pollinator species vary in the floral cues they use. In contrast, plant species that depend on fewer pollinator species with specific preferences for floral cues or energetic rewards might be forced to maintain individual floral traits at the cost of flower number.

In sum, damage to foliage by herbivores caused changes in floral characters that may influence the male and female fitness of damaged plants. We found that damaged plants produce less pollen than undamaged plants and thus may have fewer opportunities to sire seeds. A recent study of *Cucurbita texana* also found that damaged plants produced less pollen than undamaged plants; in addition, this pollen was of poorer quality, and it lost in the race to fertilize ovules when competing with pollen from undamaged plants (Quesada et al. 1995). So foliar herbivory could affect male fitness through both reduced pollen production and reduced pollen viability. Other more subtle effects of leaf herbivory could also affect plant fitness. For example, increased levels of secondary chemicals in

leaves induced by herbivory may find their way to floral parts and affect pollinator visitation. This is an understudied aspect of herbivory we are currently pursuing.

Our results are the first to show that damaged plants may be less attractive to pollinators as a result of changes in floral characters. This result has a number of implications. First, in a self-incompatible plant such as *R. raphanistrum*, effects of herbivory on pollinator visitation are likely to affect primarily male plant fitness (number of seeds sired), if pollen is not limiting. Decreased attractiveness to pollinators has been shown to result in decreased opportunities to sire seeds in *R. raphanistrum* but not in decreased numbers of seeds set (Stanton et al. 1989). In other, pollen-limited species, reduced pollinator visitation affected male and/or female fitness (e.g., Galen 1992; Johnson et al. 1995). Taken in toto, our results suggest that estimates of the effects of herbivory on plant fitness based on female plant fitness may be misleading if plants suffer a reduction in male fitness because of decreased pollen production and attractiveness to pollinators. Since the vast majority of studies of herbivory have measured only female fitness, researchers are likely to have underestimated effects of herbivory on total plant fitness.

Second, the effects of herbivory may differ for plants with different mating systems. For species that are self-compatible and/or have mixed mating systems, changes in pollinator behavior or species composition as a result of herbivory could affect the ratio of selfed versus outcrossed progeny produced. Such changes in degree of outcrossing could have profound effects on the population structure of plants, the incidence of inbreeding depression, and the relationship between plants and their herbivores and pathogens (e.g., Schmitt and Antonovics 1986; Parker 1991; Strauss and Karban 1994).

In conclusion, recent work by several authors has shown that the effects of herbivory on plant fitness through male function (pollen performance) may be quite large. We have expanded on this possibility to show how herbivory may affect the relationships of plants with their pollinators through changes in floral characters. This potential influence of herbivory on pollination raises new questions. For example, has the way in which plants have evolved to respond to damage from herbivores been influenced or constrained by the energetic needs or required cues of pollinators? Such constraints may be particularly marked in self-incompatible species for which visitation by pollinators is critical for sexual reproduction. The work presented here is a first step to illustrate how selection by leaf-feeding herbivores and pollinators in concert may shape the ecology and evolutionary biology of plants and their associates.

ACKNOWLEDGMENTS

We thank C. Augspurger, M. D. Bowers, C. Galen, R. Karban, D. Pfennig, M. Rausher, B. Silverman, M. L. Stanton, M. W. Schwartz, A. Zangerl, and an anonymous reviewer for their comments on earlier drafts of this note. This work was supported by National Science Foundation grants HRD-9103471 to S.Y.S., DEB-9318388 to J.K.C., and DEB-9407362 to S.Y.S. and J.K.C.

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SHARON Y. STRAUSS*

SECTION OF EVOLUTION AND ECOLOGY
UNIVERSITY OF CALIFORNIA
DAVIS, CALIFORNIA 95616

JEFFREY K. CONNER
SCOTT L. RUSH

DEPARTMENT OF ECOLOGY, ETHOLOGY, AND EVOLUTION
UNIVERSITY OF ILLINOIS
URBANA, ILLINOIS 61801

Submitted May 22, 1995; Revised November 18, 1995; Accepted November 21, 1995

* To whom correspondence should be addressed; E-mail: systrauss@ucdavis.edu.