

Herbivory Differentially Affects Male and Female Reproductive Traits of *Cucumis sativus*

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Abstract: Herbivory is an important selection pressure in the life history of plants. Most studies use seed or fruit production as an indication of plant fitness, but the impact of herbivory on male reproductive success is usually ignored. It is possible that plants compensate for resources lost to herbivory by shifting the allocation from seed production to pollen production and export, or vice versa. This study examined the impact of herbivory by *Helix aspersa* on both male and female reproductive traits of a monoecious plant, *Cucumis sativus*. The effects of herbivory on the relative allocation to male and female flowers were assessed through measurements of the number and size of flowers of both sexes, and the amount of pollinator visitation. We performed two glasshouse experiments; the first looked at the impact of three levels of pre-flowering herbivory, and the second looked at four levels of herbivory after the plants had started to flower. We found that herbivory during the flowering phase led to a significant increase in the number of plants without male flowers. As a consequence there was significantly less pollen export from this population, as estimated by movement of a pollen analog. The size of female flowers was reduced by severe herbivory, but there was no effect on pollen receipt by the female flowers of damaged plants. The decrease in allocation to male function after severe herbivory may be adaptive when male reproductive success is very unpredictable.

Key words: Pollination, plant-animal interactions, floral characteristics, reproductive allocation.

Introduction

All plants growing in natural environments encounter herbivores at some stage of their life cycle. Herbivory results in direct resource reduction through a loss of nutrients or photosynthetic area, and is often an important selection pressure in the life history of plant species. Herbivory can result in a range of effects on plant fitness, from neutral or even positive effects, to detrimental effects. The response of a plant to herbivory may depend on several factors, including the level of herbivory

suffered (Alward and Joern, 1993), the timing of the herbivory or the conditions under which the plant is growing (Maschinski and Whitham, 1989).

Many studies demonstrate the detrimental effects of herbivory on plants (e.g., Strauss, 1991; Karban and Strauss, 1993; Snyder, 1993; Wise and Sacchi, 1996), however, a number of different measures of plant fitness are used in these studies. As it is difficult to achieve an accurate estimate of fitness, there is much debate about what constitutes the best fitness measurement, and whether different fitness estimates are correlated with each other (Devlin and Ellstrand, 1990). The most common measure of plant fitness is seed or fruit production (female fitness). However, this approach ignores one of the main routes by which genes are transmitted to the next generation – the pollination of flowers on conspecific plants (male fitness; Schlichting and Devlin, 1989; Mutikainen and Delph, 1996; Strauss et al., 1996; Gronemeyer et al., 1997; Lehtila and Strauss, 1999).

In sexual reproduction, an offspring that is produced through male reproduction carries equal amounts of genetic material into the next generation as an offspring produced through female reproduction. Therefore, it is expected that a hermaphroditic plant would allocate an equal amount of resources to male and female reproduction (Horovitz, 1978), leading to the assumption that there is a positive correlation between male and female fitness across plants. Studies that have examined the relationship between male and female fitness have found varying results – from the expected positive correlation (Devlin and Ellstrand, 1990; Gronemeyer et al., 1997), to no detectable relationship (Schlichting and Devlin, 1989) and even a negative correlation (Bertin, 1982). As male and female fitness are not reliably correlated, it is possible that a decrease in allocation to one sexual function could result in an increase in allocation to the other. Whilst the relationship between male and female fitness in plants has been extensively studied (see Campbell, 2000, for a review), the influence of herbivory on relative allocation to male and female reproduction has received less attention. Any herbivory-induced shifts in the expected equal allocation to male and female function may have important implications for plant reproductive strategies (Ashman, 2002).

Female reproduction is generally more resource demanding than male reproduction, especially on a cost per gamete basis. Female reproduction involves the production of relatively large fruit and seeds, whereas male reproduction only requires the production of small pollen grains. It is expected that in situations of resource limitation, such as high levels of herbivory, plants will decrease allocation to the more resource demanding female reproduction and increase relative allocation to the less expensive male reproduction (Schlichting and Delesalle, 1997). This expectation has not always been supported by empirical studies. Herbivory reduces male reproductive traits, relative to female, in some species including *Raphanus raphanistrum* (Strauss et al., 1996; Lehtila and Strauss, 1999, but see Strauss et al., 2001), *Taxus canadensis* (Allison, 1990), and *Pastinaca sativa* (Hendrix and Trapp, 1981). In other species, female reproduction is reduced by herbivory more than male reproduction, for example in *Pinus ponderosa* (Snyder, 1993) and *Dactylorhiza maculata* (Vallius and Salonen, 2000). Other studies have found that herbivory affects both male and female reproductive traits similarly, for example, in *Cucurbita texana* (Quesada et al., 1995) and *Ipomopsis aggregata* (Gronemeyer et al., 1997).

Herbivory can affect male gametes directly by reducing the number of pollen grains produced per flower (Quesada et al., 1995; Strauss et al., 1996; Delph et al., 1997; Lehtila and Strauss, 1999), pollen grain size (Lehtila and Strauss, 1999), likelihood of pollen success at siring seeds (Quesada et al., 1995), and pollen tube growth rate (Mutikainen and Delph, 1996). Herbivory can also affect male reproduction indirectly through altering flower characteristics that influence pollinator visitation, and thereby affect pollen transport. For example, herbivory has been shown to reduce flower number (Quesada et al., 1995; Mothershead and Marquis, 2000), flower size (Strauss et al., 1996; Lehtila and Strauss, 1999; Mothershead and Marquis, 2000), nectar production (Strauss et al., 1996), and flowering phenology (Pilson, 2000). All of the above traits may influence pollinators and therefore affect male fitness (Young and Stanton, 1990; Connor et al., 1995; Johnson et al., 1995; Campbell et al., 1996; Connor and Rush, 1996; Strauss and Armbruster, 1997).

Flowers may only require one or two visits to achieve the pollination of all the ovules (i.e., female success), whereas pollen export usually increases with additional visits (i.e., male success, Ashman, 2000). Therefore the number of pollinator visits to a plant is usually assumed to have a larger impact on male rather than female function. In addition, most studies assume that female function is limited by resource availability, rather than pollen availability, even though it is known that this assumption does not hold true for all plants (Burd, 1994; Wilson et al., 1994). Testing the assumption of resource limitation to female function is important for two reasons. First, if we are to make any inferences about the effects of herbivory on male reproductive success (through pollen export) and female reproductive success (through pollen receipt), then reproduction must be limited to some degree by pollen transport. Second, the assumption of resource limitation to female function is embodied in many predictions arising from sex allocation theory.

This paper presents the results of two experiments that consider the effect of herbivory on resource allocation to male and female reproductive traits in *Cucumis sativus* (Cucurbita-

ceae). This species is known to compensate for herbivory by increasing photosynthetic efficiency, but at higher levels of herbivory, growth and fruit production are effected (Thomson et al., 2003). As *C. sativus* plants are monoecious (with separate male and female flowers) we can use the traits of male flowers as indicators of male fitness, and those of female flowers as indicators of female fitness. Although we cannot quantitatively measure allocation to male and female function by examining only flower traits, we can qualitatively assess shifts in allocation due to herbivory. We can also qualitatively assess indirect effects of herbivory on pollen export and receipt by examining pollinator visitation to male and female flowers on damaged and undamaged plants. We predicted that herbivory would reduce plant allocation to female function more than male function, as female reproduction is expected to be the more resource demanding of the two. We also predicted that fruit production would be limited by reduced resources at high levels of herbivory, rather than by pollen receipt. Additionally, we expected that the impact would be less if the herbivory occurred early in the growing season, before the reproductive phase started, as has been demonstrated in other studies (Maschinski and Whitham, 1989; Lehtila and Syränen, 1995; Scarré et al., 1996; Lennartson et al., 1998).

Materials and Methods

Study species

Cucumis sativus (Lebanese cucumber) is a climbing annual herb that is widely cultivated for its edible fruit. It is usually monoecious, but gynodioecious, androecious, and hermaphroditic plants are also known (Yin and Quinn, 1995). Insect visitation is necessary for sexual reproduction. Female flowers produce nectar as pollinator reward, but the male flowers do not (personal observation), and individual flowers remain open for one day only. Typically, the reproductive development of *C. sativus* begins with a male flowering phase, moves to a mixed flowering phase and then a female flowering period. Flowering is usually suppressed by the production of large and photosynthetically active fruit (Perl-Treves et al., 1998). The embryonic flower buds contain both stamen and ovary primordia, but later become unisexual (Atsmon and Galun, 1960).

Cucumis sativus encounters a wide range of invertebrate herbivores including generalists as well as specialist herbivores such as diabroticite beetles (Agrawal et al., 1999). We used *Helix aspersa* (brown garden snail) as an experimental herbivore. This species is native to Western Europe and the Mediterranean (Bleakney et al., 1989). Terrestrial gastropods can severely damage cucumber leaves, and some species can consume more than half their body weight in 24 hours (Godan, 1983).

We used the stingless bee, *Trigona carbonaria*, to enhance pollination. *Trigona carbonaria* is a social bee that occurs naturally along the north-east coast of Australia (Dollin et al., 1997). They form large colonies in tree or log hollows, but artificial colonies can be formed in boxes (Heard, 1988). *Trigona carbonaria* forage for both nectar and pollen and are known to remain longer at, and visit more often, flowers with high pollen and nectar concentrations (Heard, 1994). They are known to visit and pollinate a wide variety of plant species, both native and cultivated, including *C. sativus* (Heard, 1999).

Experimental treatments

Plants were grown in sand in 25 cm diameter pots, watered twice per day and fertilised with "Aquasol" (a soluble NPK fertiliser, Hortico Nurseries) twice per week. To establish herbivory treatments, each leaf longer than four centimetres in length was enclosed in a nylon mesh bag with up to five snails. Leaf area was estimated before herbivory and snails were removed when this area was reduced by the appropriate amount (80% or 40%), which took between one and seven days. Leaves in the 0% herbivory treatment were enclosed in mesh bags without any snails to control for possible bag effects. For the continuous herbivory treatment, snails (enclosed in mesh bags) consumed 80% of each new leaf once it had exceeded four centimetres in length. The treatment continued on every leaf until just before harvest. High levels of herbivory (40% and 80%) were chosen because *C. sativus* is known to compensate for at least low levels of leaf loss to herbivory (Thomson et al., 2003).

Effects of pre-flowering herbivory

The effects of pre-flowering herbivory on male and female reproduction were examined in a glasshouse experiment using 36 *C. sativus* plants. Plants were randomly assigned to three treatments: 0%, 40%, and 80% herbivory of each leaf, with 12 plants in each treatment spread evenly over three blocks in the glasshouse. The herbivory treatment was applied when all plants had four leaves but had not yet started flowering. Female flowers on all plants were hand pollinated to ensure maximum fruit set. We stopped recording flowering after 15 days, when many plants had slowed or stopped flowering. After the herbivory treatment had finished, the fruits were allowed to develop for approximately six weeks, and then harvested. This experiment was conducted from September to December 2000.

Effects of during-flowering herbivory

The effects of during-flowering herbivory on male and female reproduction were examined in a glasshouse experiment with plants randomly assigned to four treatments: 0%, 40%, and 80% herbivory (of each leaf at the six-leaf stage), and continuous 80% herbivory of each leaf as produced. Herbivory was applied to each plant after it had produced its first three flowers. Each treatment contained 12 plants which had all of their flowers pollinated by hand. Flowering was recorded until the time of fruit harvest (a total of 28 days) by which time many plants had slowed or stopped flowering. This experiment was conducted between December 2000 and February 2001.

The 0% herbivory and continuous herbivory treatments of the during-flowering herbivory experiment each included an additional 12 plants ($n=24$ for each of these two treatments). Flowers on the extra 12 plants were not hand pollinated, but received only whatever level of insect pollination was occurring in the greenhouse (open pollination). These plants were used to establish a contrast with the hand pollinated plants, and were in every other way treated like plants in the during-flowering herbivory experiment. Including open pollinated and hand pollinated plants, there were 72 *C. sativus* plants in three blocks for the during-flowering herbivory experiment.

Measurements of male and female reproductive traits

We recorded flowering on each plant on a daily basis. As each new flower was produced, we recorded the sex, diameter (at the widest point, to the nearest mm), and opening date. At the harvest, all fruits were counted and weighed fresh. In the during-flowering experiment, each fruit was dissected lengthways and the number of mature seeds visible on one fruit half was counted. Mature seeds were defined as those similar in size and shape to the seeds germinated for the experiment.

Measurements of pollen movement

A hive of *T. carbonaria* bees was placed in the glasshouse in January 2000 in order to provide pollinators for the plants. Pollen movement between donor male flowers and recipient flowers was estimated using Day-Glo paint powder. Day-Glo powder was placed on all the anthers of the male flowers (donor flowers) and was dispersed to other flowers (recipient flowers) by flower visitors. Day-Glo powder fluoresces when examined under an ultra-violet light so that even tiny amounts on a recipient flower can easily be detected. Although the presence of powder on a recipient flower does not necessarily indicate pollination, it has been found to be an accurate estimate of the amount of visitation (Waser and Price, 1982; Thomson et al., 1986). In this experiment we used it to detect whether there was a difference in pollen export between the treatments.

We estimated pollen movement and pollinator visitation using only the plants in the 0% herbivory and continuous herbivory treatments in the "during-flowering herbivory" experiment (a total of 48 plants). The experiment was carried out over six consecutive days. Powder was applied using a paintbrush to all the anthers of the male flowers of each plant in the two treatments (a different colour for each treatment) in the morning as the flowers opened. We alternated the colours between the treatments each day to account for any pollinator preference for powder colour. The number of donor male flowers (those given powder) was counted for each treatment on each day. At the end of each day, all donor male flowers were removed, and each recipient flower was marked to ensure that each day was a separate experimental replicate using different donor and recipient flowers.

Each evening we examined the unmarked flowers on all plants (including the 40% and 80% herbivory treatments) for the presence or absence of powder of both colours. The total number of flowers receiving powder of each colour was counted for each day to compare pollen donation from the two treatments. We counted both male and female recipient flowers.

Data analysis

We used analysis of variance to compare treatment differences in flower diameter, date of first flower, male and female flowering rate (flowers/day, pre-flowering herbivory experiment), number of female flowers (during-flowering herbivory experiment), anther weight and fruit and seed number. Block was included in the analyses as a random factor, and the interaction between block and herbivory treatment was included when significant. The number of male flowers on each plant (for the during-flowering herbivory experiment) was analysed using

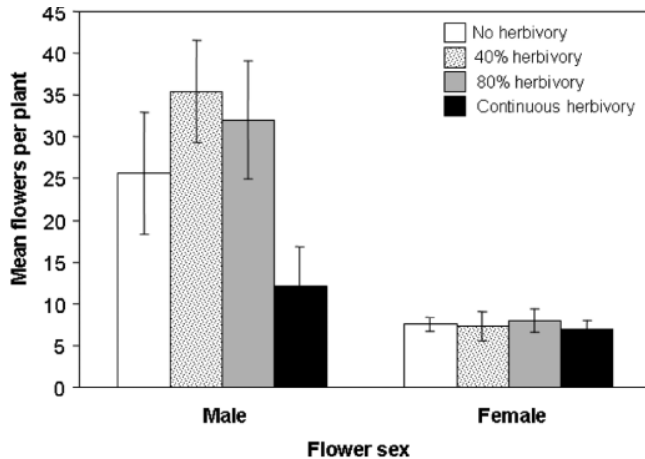


Fig. 1 Mean number of male and female flowers per plant (± 1 SE) in each treatment for the during-flowering herbivory experiment.

analysis of variance with a specific contrast to compare the mean of the continuous herbivory treatment with the mean of the other three treatments. Data were examined for homogeneity of variance and for normality, and transformed to meet assumptions when necessary.

We compared the proportion of plants that produced only female flowers in the continuous herbivory treatment to the proportion in other treatments using Fisher's exact test. The powder transfer data were analysed using g-tests to compare powder movement between treatments, both on individual days and for all days combined.

Results

Effects of pre-flowering herbivory on flower traits

After pre-flowering herbivory, the 40% herbivory treatment resulted in a non-significant increase in the number of male flowers produced per day (ANOVA, $p = 0.08$, $F = 2.74$, $df = 2$), but female flower production was unaltered by any herbivory treatment (ANOVA, $p = 0.77$, $F = 0.27$, $df = 2$). There were no treatment effects on the diameter of either male or female flowers, the opening date of the first flower, or on anther weight (results not presented). There was also no effect of herbivory treatment on the total fruit weight per plant (ANOVA, $p = 0.32$, $F = 1.19$, $df = 2$). Variation between plants in flower sex ratio was great, but was not affected by herbivory treatment. Individual plants did not follow the flowering phases reported in previous studies of *C. sativus*, and the production of male and female flowers over time did not appear to be affected by the herbivory treatment.

Effects of during-flowering herbivory on flower and fruit traits

Following during-flowering herbivory, plants in the 40% and 80% treatments had more male flowers, on average, than plants in the 0% herbivory treatment, while plants in the continuous herbivory treatment produced fewer male flowers. This effect was not significant (specific contrast, continuous

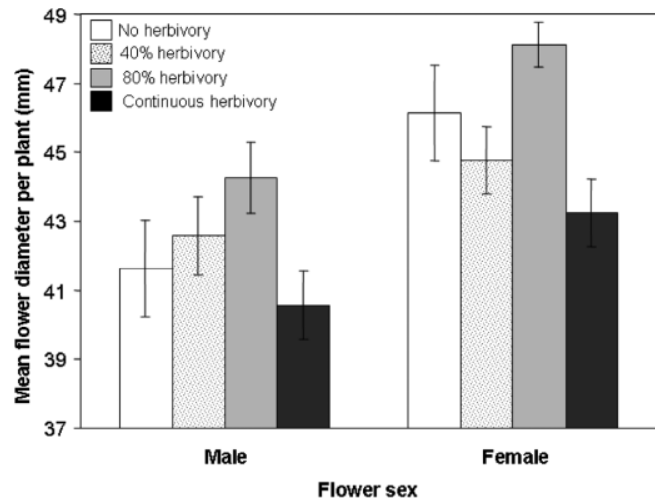


Fig. 2 Mean diameter of male and female flowers per plant (± 1 SE) in each treatment for the during-flowering herbivory experiment.

vs. other three treatments: $p = 0.075$; Fig. 1) but because of the high levels of variance and relatively small sample sizes, this test was found to have low power (0.54). However, there was no effect of treatment on the number of female flowers (ANOVA, $p = 0.64$, $F = 0.57$, $df = 3$; Fig. 1). The variation between plants in flower sex ratio was large – eight plants were functionally female (with no male flowers), and one plant was functionally male. Interestingly, the proportion of functionally female plants was significantly higher in the continuous herbivory treatment (55%) than in the other three treatments combined (6%) (Fisher's exact test $p < 0.005$).

The diameter of the male flowers was slightly larger in the 40% and 80% herbivory treatments (compared to the 0% herbivory treatment), but smaller in the continuous herbivory treatment (Fig. 2), but the variance was high and these effects were not significant (ANOVA, $p = 0.33$, $F = 1.18$, $df = 3$). Continuous herbivory plants had significantly smaller female flowers than the plants in the 80% herbivory treatment (Fig. 2, Scheffe post hoc $p = 0.03$).

The production of male and female flowers over time was examined, but did not appear to be affected by the herbivory treatment. There were also no treatment differences in the opening date of the flowers, or in the estimated number of seeds per fruit (ANOVA, $p = 0.7$, $F = 0.12$, $df = 1$).

Fruit production was influenced by both pollination and herbivory level. In both the 0% and continuous herbivory treatments, pollen-supplemented plants produced more fruit per female flower than open-pollinated plants (ANOVA, $p = 0.009$, $F = 7.64$, $df = 1$; Fig. 3), suggesting that pollination was limiting fruit production. Also, plants in the continuous herbivory treatment produced fewer fruit than the plants in the no herbivory treatment, regardless of pollination level (ANOVA, $p = 0.009$, $F = 7.54$, $df = 1$; Fig. 3). There was no interaction effect between herbivory and pollination (ANOVA, $p = 0.2$, $F = 1.62$, $df = 1$).

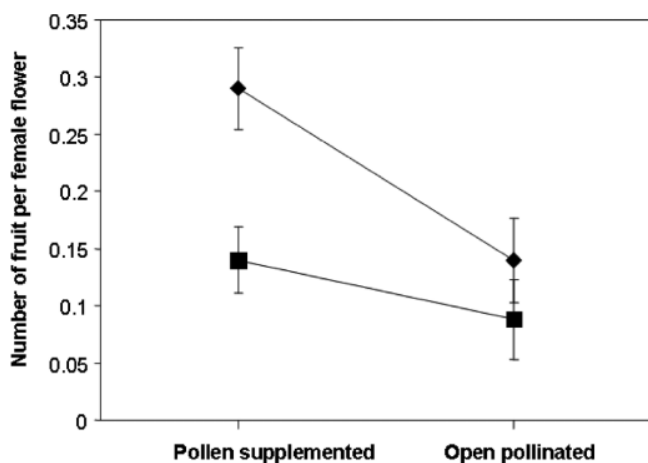


Fig. 3 Mean number of fruit per female flower (± 1 SE) comparing pollen supplemented plants (left) to open pollinated plants (right) with two herbivory treatments: 0% herbivory (diamonds) and continuous herbivory (squares) in the during-flowering herbivory experiment.

Effect on pollen export and receipt

Continuous herbivory reduced the estimated pollen export by male flowers. Day-Glo powder was transferred from male flowers of the plants in the 0% herbivory treatment to more recipient flowers than from the male flowers of the plants in the continuous herbivory treatment (Fig. 4A). This effect was significant on most individual days, and when the data for all days were pooled (Table 1). The difference was in the same di-

rection whether all recipient flowers (male and female) were counted, or only the female recipients (Figs. 4A,B). When only female recipients were counted, the difference was significant on half of the individual days, and when the data for all days were pooled (Table 1).

When the number of recipient flowers was divided by the number of donor males for each treatment (to account for the difference in the number of donor male flowers), pollen donation effects were not significant (Table 1), although the direction of difference was similar, with no herbivory treatment plants exporting more (Figs. 4C,D). This was the case whether the total number of recipient flowers, or just the female recipient flowers were used in the analysis.

When female function was assessed by examining female powder receipt (regardless of donor), there was no significant difference between the treatments in the estimated amount of pollen receipt (pooled G test, Table 1).

In summary, estimated pollen export was significantly reduced from plants exposed to continuous herbivory. Herbivory did not significantly effect the estimated amount of pollen export on a per male flower basis, nor did it effect receipt by female flowers.

Discussion

This study looked at the effects of the severity and timing of herbivory by *Helix aspersa* on both male and female reproductive traits of a monoecious plant, *Cucumis sativus*. Pre-flowering herbivory had no significant impacts on plant reproduc-

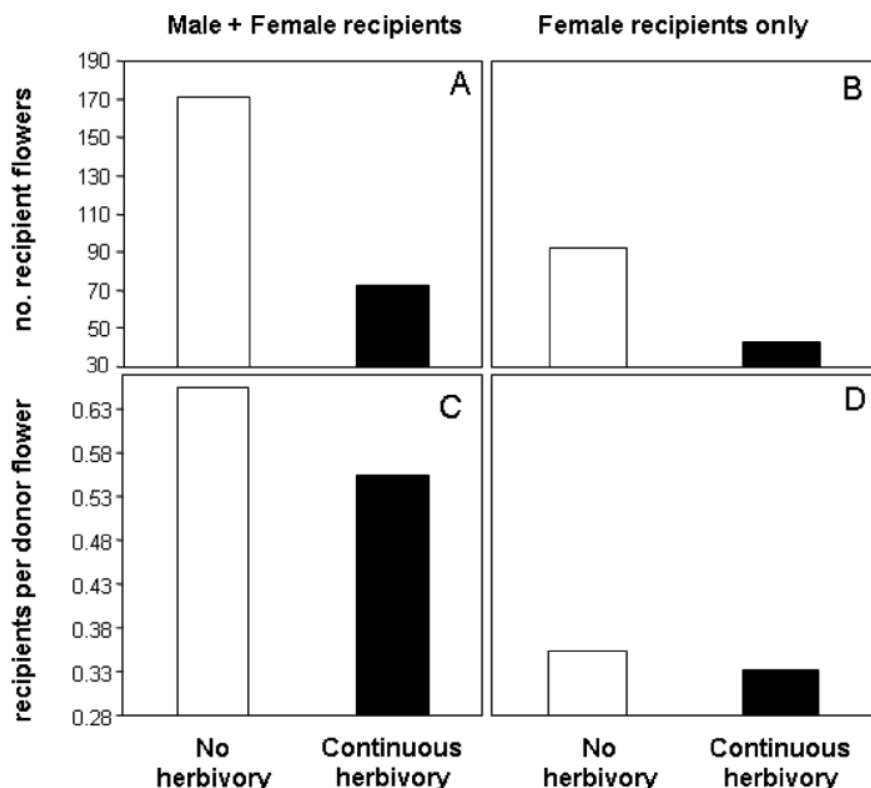


Fig. 4 Pollen export from two different pollen donor treatments (0% herbivory vs. continuous) determined by the number of flowers receiving Day-Glo powder (a pollen analog) from each donor treatment group. Each panel contrasts the result for plants with 0% herbivory (open) to those with continuous herbivory (black) in the “during-flowering herbivory” experiment. Left panels (A,C) present the total number of recipient flowers (male plus female). Right panels (B,D) present recipient female flowers only. Upper panels (A,B) present the number of flowers. Lower panels (C,D) present the number of recipients/number of donors.

Table 1 Significance of herbivory treatment on donor plants (contrasting 0% herbivory to continuous herbivory) on pollen export, analysed using G-test of frequency. Pollen export was estimated by the number of flowers receiving Day-Glo powder (a pollen analog) from each donor treatment group. For all significant values the number of flowers receiving powder from male flowers of the continuous herbivory treatment was lower than expected

| Day | d.f. | All recipient flowers | | Recipient female flowers only | | All recipients/ number of donors | |
|---------------|------|-----------------------|-----|-------------------------------|-----|----------------------------------|----|
| | | G | P | G | P | G | P |
| 1 | 1 | 6.2 | * | 2.9 | NS | 4.5 | * |
| 2 | 1 | 4.6 | * | 4.2 | * | 0.5 | NS |
| 3 | 1 | 6.5 | * | 4.9 | * | 0 | NS |
| 4 | 1 | 20.2 | *** | 6.5 | * | 5.9 | * |
| 5 | 1 | 3.7 | NS | 0.9 | NS | 0.3 | NS |
| 6 | 1 | 7.1 | * | 2.8 | NS | 0.1 | NS |
| Heterogeneity | 5 | -6.9 | NS | -4 | NS | -9.8 | NS |
| Pooled | 1 | 41.5 | *** | 18.2 | *** | 1.6 | NS |

* $p < 0.05$; *** $p < 0.001$; NS: $p > 0.05$

tion, and herbivory during-flowering only affected plant reproduction in the most severe treatment (which was not applied in the pre-flowering experiment). As the most significant and interesting outcomes were found in response to continuous, during-flowering herbivory, the following discussion will focus on these results.

We predicted that herbivory would have a greater negative impact on female flower production than on male flower production, as female reproduction is usually more resource demanding (Schlichting and Delesalle, 1997). The most striking result of these experiments was, however, quite contrary to this prediction. We found that high levels of herbivory reduced male function, leading to a significant increase in the proportion of plants that had no male flowers. This decline in male flowers across the herbivore-damaged population (which was most apparent in the number of plants with no male flowers) led to a significant decrease in export of the pollen analog when compared to the undamaged plant population. This result suggests that the herbivore induced decline in male flower production is likely to translate into a decline in the number of offspring sired by pollen export from affected plants. Herbivore damage led to non-significant decreases in male flower diameter and pollen export on a per flower basis, but the dominant effect was linked to the amount of male flowering.

In contrast to the significant negative effect on male flowering and pollen export, female flowering was relatively higher at the high level of herbivory. The only negatively affected female flowering trait was flower diameter (which was lower in the 80% herbivory treatment) but this did not translate into reduced pollen receipt by female flowers on damaged plants. This absence of effect is in contrast to several other studies, which have demonstrated that even small changes in flower size can affect pollinator behaviour (Rodríguez-Roules et al., 1992; Connor and Rush, 1996; Ashman, 2000; Mothershead and Marquis, 2000).

The high level of herbivory did, however, have a negative impact on fruit set, which is the most expensive component of female reproduction. Hand-pollinated plants exposed to continuous herbivory produced significantly fewer fruits than hand-pollinated plants in the no herbivory treatment. In spite of this apparently resource-mediated effect on fruit set, fruit set efficiency was nevertheless sensitive to pollen supply even in the continuous herbivory treatment. Importantly, this sensitivity to pollen supply indicates that the reduced pollen export from high herbivory plants is likely to translate into differences in effectiveness in siring offspring in this system.

Studies of other plant species also support the finding that seed production is not always limited only by resources alone (Campbell and Halama, 1993; Cunningham, 1996; Juenger and Bergelson, 1997; McCall and Primack, 1985; Lawrence, 1993). That both pollen supply and resources limit fruit production is consistent with predictions that selection should balance a plant's allocation to pollinator attraction and seed provisioning to the point where both effects are limiting (Haig and Westoby, 1988).

The observation that herbivore damage led to a more negative effect on male flowering than on female flowering, seems at odds with the observation that the resource cost of reproduction through female reproduction is greater than male costs, especially for a large fruited species such as this. By comparison, a study on a related species, *Cucurbita texana*, found that both male and female flower production suffered after high levels of herbivory, although flower production was only measured on a single defoliated branch, not over the whole plant (Quesada et al., 1995). Surely if herbivory reduces available resources then reducing investment in the resource-hungry female reproductive route seems the obvious strategy? We suggest that this apparent conundrum might be resolved by application of the Trivers-Willard (1973) hypothesis for sex ratio allocation.

In species where parental investment by males is negligible, variance among individuals in male reproductive success exceeds variation among individuals in female reproductive success (Bateman, 1948). A successful male has the potential to father thousands of offspring, but a successful female produces many fewer offspring. On the other hand, a poor-condition male is expected to produce no offspring, but even poor-condition females are likely to produce some offspring. Trivers and Willard (1973) predicted that in mammals where the mother is able to determine the sex-ratio of her offspring, a mother in poor condition will tend to produce female offspring because they are reliable. If we extend the Trivers-Willard hypothesis to hermaphroditic plants, the decision would not be the sex of the offspring, but rather whether the offspring is produced through the male or female reproductive pathway. The hypothesis predicts that plants growing in poor conditions (such as intense herbivory) should decrease allocation to the relatively risky male function, and produce offspring mainly through the more secure female function.

Other studies have also found changes in male success due to herbivory, including reduced competitive ability of pollen in some species, including cucurbits (Delph et al., 1997; Mutikainen and Delph, 1996; Quesada et al., 1995) and reduced male flower production (Allison, 1990; Frazee and Marquis, 1994;

Hendrix and Trapp, 1981), but they have not explored the Trivers-Willard explanation. In contrast, Lehtila and Strauss (1999) do attempt to explain a pattern of reduced male success (pollen production) in herbivore-damaged wild radish plants. They suggest that a reduction in pollen production occurs because there are many steps between pollen production and offspring produced by pollen. Because the link between pollen traits and male fitness is weaker than the link between ovule production and female fitness, a decrease in pollen production may not result in a corresponding decrease in male fitness. The weak causal link between male traits and male fitness is part of the reason male success is more unpredictable than female success and in this sense is consistent with our application of the Trivers-Willard hypothesis.

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