Effects of Foliar Herbivory by Insects on the Fitness of *Raphanus raphanistrum*: Damage Can Increase Male Fitness

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ABSTRACT: Generally, effects of herbivory on plant fitness have been measured in terms of female reproductive success (seed production). However, male plant fitness, defined as the number of seeds sired by pollen, contributes half of the genes to the next generation and is therefore crucial to the evolution of natural plant populations. This is the first study to examine effects of insect herbivory on both male and female plant reproductive success. Through controlled field and greenhouse experiments and genetic paternity analysis, we found that foliar damage by insects caused a range of responses by plants. In one environment, damaged plants had greater success as male parents than undamaged plants. Neither effects on pollen competitive ability nor pollinator visitation patterns could explain the greater siring success of these damaged plants. Success of damaged plants as male parents appeared to be due primarily to changes in allocation to flowers versus seeds after damage. Damaged plants produced more flowers early in the season, but not more seeds, than undamaged plants. Based on total seed production, male fitness measures from the first third of the season, and flower production, we estimated that damaged and undamaged plants had equal total reproductive success at the end of the season in this environment. In a second, richer environment, damaged and undamaged plants had equal male and female plant fitness, and no traits differed significantly between the treatments. Equal total reproductive success may not be ecologically or evolutionarily equivalent if it is achieved differentially through male versus female fitness. Genes from damaged plants dispersed through pollen may escape attack from herbivores, if such attack is correlated spatially from year to year.

Keywords: Raphanus raphanistrum, male plant fitness, herbivory, tolerance, *Pieris rapae*.

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In natural plant populations, the impact of damage on plant fitness varies greatly among plant species (Van der Meijden et al. 1988) as well as among individuals within species (Rosenthal and Kotanen 1994; Bergelson et al. 1996; Lennartsson et al. 1997; Strauss and Agrawal 1999). Under some circumstances, plants appear to be able to compensate completely for substantial amounts of damage (Gronemeyer et al. 1997). Generally, plant response to herbivory has been measured in terms of female reproductive success (seed production). However, male plant fitness, defined as the number of seeds sired by pollen, contributes half of the genes to the next generation and is an important component of total plant fitness. It therefore plays a crucial role in our understanding of the effects of herbivory on evolution in natural plant populations.

Of interest is whether, in compensating for damage, damaged and undamaged plants have different relative success as male parents versus as female parents. One study has found that mammalian herbivory enhanced both male and female fitness because browsing by elk removed apical dominance and increased total flower production (Gronemeyer et al. 1997). No previous study has examined the impact of leaf damage by insects on both male and female reproductive success. Because foliar damage by insects does not usually alter apical dominance relationships within the plant, it has few, if any, effects through changes in plant architecture. Thus, effects of insect damage to leaves on male versus female fitness are not necessarily expected to follow the same trends as those of mammalian herbivores. Several mechanisms may underlie differences between damaged and undamaged plants in components of fitness, including resource loss and induced defenses that change plant allocation patterns (Agrawal et al. 1999a; Lehtilä and Strauss 1999). Seed and pollen production have different metabolic costs (Saito et al. 1996), and a combination of allocation patterns and ecological interactions with pollinators (Strauss et al. 1996; Juenger and Bergelson 1997; Mothershead and Marquis 2000) may result in dif-

ferential male and female reproductive success for insect-damaged versus undamaged plants. Pollinator foraging behavior on damaged plants may be influenced by changes in the quality or quantity of rewards and/or changes in attraction characters after damage (Frazee and Marquis 1994; Juenger and Bergelson 1997; Lehtilä and Strauss 1997). Male plant fitness may also be affected by differences in pollen competitive ability once pollen has been delivered by pollinators (Quesada et al. 1995; Mutikainen and Delph 1996).

We used the annual wild radish *Raphanus raphanistrum* to examine impacts of foliar herbivory on plant fitness for several reasons: first, previous studies with *R. raphanistrum* showed that foliar damage altered floral traits and visitation patterns by pollinators (Strauss et al. 1996; Lehtilä and Strauss 1997); second, this species has high levels of allozyme heterozygosity that allowed us to determine paternity of seeds sired (male reproductive success) during the experiments (Conner et al. 1996); third, *R. raphanistrum* is generally self-incompatible, so the vast majority of seeds produced are sired by other plants; and finally, many other studies of pollinators and herbivores of *R. raphanistrum* make it a model system for understanding the ecology and evolution of such interactions (Mazer 1987; Stanton et al. 1987; Young and Stanton 1990; Rees and Brown 1992).

We measured flower, fruit, and seed production, as well as number of seeds sired on other plants, for both damaged and undamaged plants in the field. To elucidate possible underlying mechanisms influencing male and female plant fitness in damaged and undamaged plants, we observed pollinator behavior in the field and conducted greenhouse studies on pollen competitive ability.

Methods

Greenhouse-grown *Raphanus raphanistrum* plants were used to create 24 full-sib families. Greenhouse-grown plants control for any differences in parental environment that may have transgenerational effects (Agrawal et al. 1999b), and comparisons of full sibs minimizes variance resulting from heritable traits such as differences in flower number, flower size (Conner and Via 1993), and compatibilities with other genotypes. One offspring from each sibship was randomly assigned to either a damaged (D) or undamaged (U) treatment and was planted as a seedling in a circular array in the field at the Phillips Tract (Main Road site), Urbana, Illinois. In these circular arrays, each of the 24 plants had neighboring plants with the same spatial distribution, an attribute that is important both with respect to pollinator foraging patterns and competitive interactions among plants. Plants were arranged around the circle such that each plant had a D and a U

neighbor (D, D, U, U, D, D, etc.), and families were assigned at random to each position given these order constraints.

A second circular array (Oats site), also at the Phillips Tract, was created identical to the first one (including the order of the families), except that families represented by a damaged plant in the first array had an undamaged member in the second arra and vice versa. Arrays were separated by 500 m and had intervening flowering vegetation that was used by the generalized pollinators of wild radish. Spatial separation of arrays was necessary to minimize siring of seeds between arrays. The surrounding area was searched, and no other known populations of *R. raphanistrum* were within 15 km of the experimental area. All plants completed their growth and reproduction in the field. Arrays were weeded initially to ensure plant establishment, but weeding was then ceased to allow competition from other plants and to measure the responses of plants to damage under natural conditions.

Plants in the damaged (D) treatment were experimentally damaged by larvae of the cabbage white butterfly *Pieris rapae*, a natural herbivore of *R. raphanistrum*. In the field, larvae were placed into clip cages and allowed to consume one-third of the leaf area of each true leaf. Clip cages, made from the bottoms of two small petri plates glued to each side of a hair clip and then to a supporting stake, have been shown to have no effect on wild radish fitness in prior studies (Agrawal et al. 1999a). Cages were placed alongside the midrib of the leaves to allow larvae to feed in a way that resembled natural patterns of larval damage. Field surveys in 1995 of damage levels at three different sites separated by at least 15 km showed that 28%, 26%, and 9% of radish plants received a mean level of damage of at least one-third leaf area removal (averaged over the first four rosette leaves; $n = 35$ plants per site; S. Y. Strauss, unpublished data). Thus, our treatments represent more than the median, but not atypical, damage levels experienced by radish plants in the field. Because most of the leaf area of wild radish plants is present in large rosette leaves produced early in the season prior to flowering, damage to those leaves represents the greatest impact by foliar herbivores. Much smaller, cauline leaves on flowering stems also received this treatment, however. The timing of our experimental treatments is also typical of foliar-feeding herbivores of radish since rosette leaves senesce during flowering and little leaf area is produced on flowering stems.

Twice during the season, in the weeks of June 5 and June 26, 1996, we observed pollinator behaviors in the arrays. The first date was during early seed production, when effects of damage were expected to be large (Lehtilä and Strauss 1999); flowering plants had eight to 85 open flowers by those dates. By the second observation date,

the same plants had 42–273 flowers open. Observations of damaged and undamaged sibling plants were made within 15 min of one another on the same day. Each plant was observed for 12 min, and all pollinators visiting the plant were recorded. Observations of focal pollinators also allowed us to estimate the total number of flowers visited, the total time pollinators spent foraging per plant, and the total time spent per flower (for more detail on these methods, see Conner and Rush 1996).

Three times during the growing season, we counted and weighed all the seeds produced by each plant (female reproductive success), measured flower size, and counted the number of open flowers and the total number of flowers produced. Previous greenhouse work with this species showed that petal and pollen size and pollen produced per flower were reduced following foliar damage (Strauss et al. 1996; Lehtilä and Strauss 1999). These effects were strongest on flowers produced early in the season (up until about the fiftieth flower), when damage to large rosette leaves was still in the relatively recent past. In addition, work on a closely related species, *Raphanus sativus,* showed that fruit production by the earliest flowers was most important to female fitness (Ashman et al. 1993). Therefore, we sampled flower production, fruit production, and seeds sired from fruits produced prior to June 17, after approximately 3 wk of flowering. Fruit set from this period represented 32% of total lifetime fruit set, on average, and thus encompassed an important portion of total plant reproductive effort. For these fruits, we also estimated seed production and abortion rates. Fruits have a bulge for each seed that begins to develop; we randomly sampled 10 fruits per plant, counted the number of bulges, cracked open the fruit, weighed the seeds, and recorded the number of bulges that were filled (i.e., not aborted).

For each plant, a sample of seeds was selected randomly for paternity analysis from fruits that had been fertilized prior to June 17. Two plants at the Main Road site had not flowered (or produced seed) by June 17 and therefore were excluded from the paternity analysis. These seeds were grown in the greenhouse, and flower buds were collected for electrophoresis. A total of 1,465 offspring were genotyped at eight allozyme loci (Conner et al. 1996) for an average of about 32 offspring per maternal parent. Male fertility, defined as the proportion of offspring of each female that was fathered by each male, was estimated separately for each array using maximum likelihood methods (Roeder et al. 1989). The empirical exclusion probabilities, that is, the average proportion of sires that are absolutely excluded from paternity for any single given offspring, were 0.83 in the Oats array and 0.80 in the Main Road array. Thus, the average number potential sires for each offspring was 3.9 at Oats and 4.6 at Main Road. All possible fathers were excluded for some of the offspring (50, or

6.1%, at Oats; 67, or 10.3%, at Main Road), so these offspring were not included in the fertility estimates. These total exclusions are due to some combination of scoring errors and gene flow between sites and are possibly due to undetected natural wild radish plants in the area. The estimate of each male's fertility on a particular female was multiplied by the number of seeds produced by that female (in the same early sampling period) to calculate the expected number of offspring sired by each male on that female. These numbers were summed over all females to give an estimate of all the seeds sired by each male during the sampling period.

Data from the field experiment were analyzed first with paired multivariate Hotelling's T^2 tests comparing damaged with undamaged sibs in fitness traits. Because the two array sites differed in their suitability for plants (plants in the Oats array produced significantly more seeds than Main Road plants), the multivariate tests were performed on response variables that were standardized to site. Standardization was done by calculating the proportion of seeds produced or seeds sired by each plant at each site. Since the multivariate test was significant, we then conducted univariate tests to explore which response variables were most important in this result. Unknown to us at the establishment of the experiment, site differences between the two arrays were very large; seed production at the Oats site was approximately twice that of the Main Road site. Inspection and further analysis of the data indicated that response of plants at the two sites was not the same; therefore, univariate analyses considered sites separately by comparing damaged and undamaged plants with unpaired *t*-tests within sites. In these comparisons, the sibling structure is lost, but the site effects are evident.

To determine how herbivory affected the competitive ability of pollen in wild radish, a hand-pollination experiment was conducted. Twenty-six pairs of full-sib plants were grown in the greenhouse, and one member of each sib pair was randomly chosen for damage. Damage was imposed using the methods described above. These plants were the pollen donors in the experiment. Another 25 plants were raised undamaged and served as pollen recipients. Sib pair pollen donors (e.g., family A) were each paired with another sib pair (family B) to produce a quartet so that the damaged pollen donor from one sib pair (A) competed against the undamaged donor from the other sib pair (B) and vice versa. Two pollen recipients were assigned to each quartet (one pair of donors was assigned only one recipient) so that the same pairs of competing pollen donors could be tested on two different recipients. These groupings were made based on allozyme genotypes of all six members to maximize our ability to determine paternity of resulting offspring. Pollen from one damaged and one undamaged donor was applied sequen-

tially to saturate one-half of the stigmatic surface for each recipient flower. A total of 12 flowers per recipient plant were pollinated by alternating pollen application from damaged and undamaged donors.

A random sample of 358 offspring from these matings was genotyped at the same eight allozyme loci. Thirty of these offspring were not used because neither pollen donor could be unambiguously excluded as the father. Therefore, the final sample size is 328 offspring for which paternity could be assigned with certainty, or an average of 13 offspring per pollen recipient. Data were analyzed using multiple Latin square ANOVA with the number of seeds sired as the dependent variable. Independent variables were treatment and pollen donor quartet, with pollen donor and the pair of donors competing on the same flower nested within the quartet (Mead 1988). Normality of residuals was tested using the Lilliefors test.

Results

From the paired multivariate Hotelling's T^2 test, herbivory significantly affected early plant fitness, which represented 32% of total seed production in the arrays (fig. 1). This effect was mainly due to a difference in male reproductive success (the proportion of seeds fertilized on other plants), which was significantly greater for damaged plants than for undamaged plants over this period. This result still held when we excluded seeds produced by the father plant from the total seeds produced as being unavailable for siring (because of self-incompatibility; average D−U = 0.01817, paired $t = 2.34$, $P = .028$). In contrast, the proportion of seeds produced was less for damaged plants than for undamaged plants, but this difference was not statistically significant (fig. 1). Neither total early fitness, defined as the sum of male and female plant fitness, nor seed mass was significantly affected by treatment (fig. 1).

Univariate *t*-tests comparing damaged and undamaged plants within sites showed that the response to damage was site dependent and that the significant effect of damage was driven by plants at the Main Road site (table 1). Damaged plants at this site had greater siring success and had greater seed abortion rates than undamaged plants at the same site. Total seed production, however, was not statistically different between damaged and undamaged plants (table 1). The end result is that the proportion of early fitness due to male function was significantly greater for damaged plants at the Main Road site (table 1).

Greater male fitness in these damaged plants could have resulted from a number of mechanisms. Differences in allocation patterns to reproduction may have been responsible for some of the differences between the two treatments. While there was no difference in the date when plants began flowering between treatments, damaged
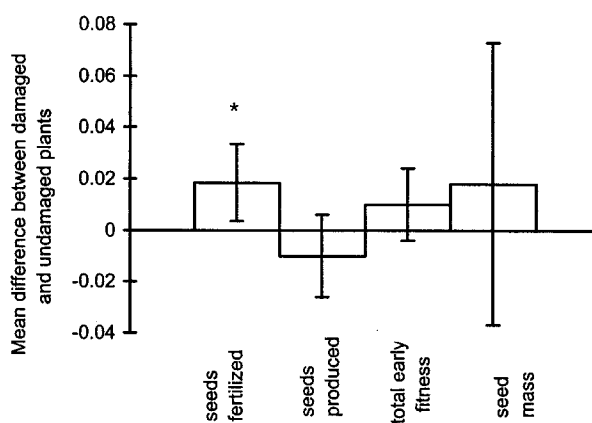
Figure 1: Difference between damaged and undamaged full-sib plants in components of reproductive success. A nonzero difference indicates an effect of damage on that trait. The multivariate Hotelling's T^2 test on the three fitness components is significant at $P = .0035$ (Hotelling's $T^2 = 20.40$, df = 3,21); univariate paired tests show that this significance is due primarily to differences in male fitness measures (paired $t = 2.54$, df = 23, $P = .02$) and not to differences in seed production (paired $t = -0.81$, df = 23, $P = .43$) or the combined estimate (paired $t = 0.72$, df = 23, $P = .48$). Seed mass, which was not included in the multivariate analysis owing to a smaller sample size, did not differ between treatments (mean difference = −0.018, $t = -0.33$, df = 19, $P = .73$). With inclusion of seed data in the multivariate Hotelling's T^2 test, effects of damage were still significant at $P = .03$ with the reduced sample size.

plants produced the first 50 flowers at a marginally greater rate than undamaged plants early in the season (paired *t*-test, standardized by site, D = 1.095, U = 0.91, $t = 1.9$, df = 23, $P = .067$; this represents a mean difference of 19% more flowers per day produced by damaged plants). This result was not site dependent and not significant at either site when sample sizes were halved in the within-site comparisons (see power analysis; table 1).

Resource availability may also play a role in the relative success of male versus female parents in damaged plants at this site; abortion rate of seeds was greater in damaged plants (table 1) and thus indicates an allocation switch from female to male in damaged plants.

At the Oats site, plants produced many more seeds overall and appeared to compensate completely for damage in every measured trait; there were no effects of damage on any of the measured fitness components (table 1) nor in relative success as a male versus female parent.

Changes in pollinator attraction and foraging behavior could have played a role in the differences in male or female fitness between damaged and undamaged plants at Main Road. However, there were no significant differences in the total number of pollinators visiting damaged and undamaged plants at either site nor were there differences in the number of flowers visited per pollinator or the time

Table 1: Results of *t*-tests with means (SE) for damaged and undamaged plants at the Main Road and Oats sites

Trait	Damaged	Undamaged	*t*	df[a]	*P*	NR[b]
Main Road:						
Seeds fertilized	649.74 (129.38)	248.26 (72.33)	2.71	22	.02	
Flowering rate[c]	4.05 (.33)	3.14 (.52)	1.73	19	.15	26–62
Seeds produced early	405.08 (78.86)	492.92 (212.33)	−.39	14	.70	158–932
Total seeds	1,305.76 (211.29)	1,727.58 (273.59)	−.98	17	.33	48–81
Proportion early fitness that is male[d]	.59 (.05)	.40 (.07)	2.22	18	.04	
Seed mass	5.10 (.33)	5.57 (.36)	−1.00	18	.33	84
Seed abortion rate per silique	.10 (.026)	.03 (.014)	2.27	15	.04	
Estimated total fitness	1,955.49 (267.63)	1,975.84 (436.51)	−.04	18	.52	≫10,000
Oats:						
Seeds fertilized	1,014.52 (184.75)	1,021.65 (214.11)	−.02	22	.98	≫10,000
Flowering rate[c]	4.93 (.27)	4.33 (.31)	1.42	22	.16	41–53
Seeds produced early	913.67 (179.37)	1,122.5 (278.88)	−.63	19	.54	142–285
Total seeds	3,317.56 (598.06)	4,057.11 (951.89)	−.66	19	.52	125–317
Proportion early fitness that is male[d]	.53 (.03)	.51 (.06)	.37	16	.72	260–1,017
Seed mass	5.05 (.19)	4.95 (.20)	.37	22	.71	693
Seed abortion rate per silique	.04 (.020)	.04 (.013)	.33	12	.75	≫10,000
Estimated total fitness	4,332.08 (692)	5,078.76 (962)	−.63	20	.70	165–320

[a] Based on Satterthwaite's approximation for unequal variances; $n = 12$ per treatment at the Oats site; $n = 11$ (damaged) and 10 (undamaged) for the Main Road site for seed mass and abortion rate comparisons.

[b] Values represent the sample size required to detect the observed difference, given the observed SD (power $= 0.80$, $\beta = 0.20$; Lehr 1992). Range represents sample size required for high and low observed SD values.

[c] Flowers per day.

[d] Seeds sired early/(seeds sired early + seeds produced early).

spent per flower (paired multivariate Hotelling's $T^2 = 1.97$, df $= 3, 21$, $P = .74$; table 2). Pollinator attraction characters of petal area and number of open flowers measured during the pollinator observation period also did not differ significantly between treatments at either site (table 2).

The increased number of seeds fertilized by damaged plants at Main Road was not likely a result of superior siring ability by pollen produced by these plants. In controlled greenhouse trials, there was no significant difference in the number of seeds sired by damaged versus undamaged fathers (multiple Latin square ANOVA: $F = 0.151$, df $= 1, 12$, $P = .70$; mean number of seeds sired by damaged fathers $= 6.80$ [6.32 for undamaged fathers]). This result is supported by indirect evidence from the field experiment as well; the slopes relating male fitness and flower production did not differ between treatments (slopes were 1.09 and 0.86 for damaged and undamaged plants, respectively; *t* [comparing slopes] $= 1.13$, df $= 44$, $P = .21$) nor was the proportion of seeds sired by damaged plants statistically different from the proportion of flowers produced by these plants (paired *t* $= −1.36$, df $= 23$, $P = .19$). If superior pollen competitive ability was the cause of greater seed siring, then we might have expected greater siring success on a per flower basis by damaged plants.

When we combined lifetime female reproductive success (seed production) with early male reproductive success (based on 32% of seeds) to estimate total reproductive success and accounted for site effects, we found that there was no significant overall difference between damaged and undamaged plants (paired tests by sibling standardizing across sites, $t = 0.86$, df $= 23$, $P = .40$). The same result was obtained using separate *t*-tests by site (table 1), so damaged plants compensated completely for 33% leaf area removal.

One could argue that undamaged plants may have sired more seeds later in the season in the unmeasured portion of male fitness (male contributions to the remaining 68% of seeds produced). The number of seeds sired was significantly positively correlated with the number of flowers produced in our study (fig. 2) and in other studies of male fitness of *Raphanus sativus* and *Raphanus raphanistrum* at the same site (Devlin and Ellstrand 1990; Devlin et al. 1992; Conner et al. 1996). The total number of flowers produced was not significantly different between damaged and undamaged plants 2–3 wk after flowering began (mean difference in proportion flowers produced by damaged vs. undamaged $= 0.0015$, $t = 0.23$, df $= 23$, $P = .82$); the mean number of flowers produced per plant at that time was 293 for the Oats site and 200 for the Main Road site. At 4–5 wk after flowering began (mean number of flowers produced was 870 at Oats and 440 at Main Road), damaged and undamaged plants still did not differ

Table 2: Floral traits and pollinator responses to damaged and undamaged plants

Trait	Damaged	Undamaged	t	df[a]	P	NR[b]
Main Road:						
Petal area early	61.16 (4.39)	66.18 (5.95)	−.68	17	.51	147–224
Number flowers open	23.4 (3.43)	27 (7.84)	−.42	15	.67	175–759
Number flowers visited	26.59 (10.95)	20.89 (8.6)	.34	19	.69	328–708
Total number pollinators	7.5 (1.12)	8.22 (2.79)	−.23	11	.81	465–2,405
Time spent per flower	15.68 (3.07)	9.52 (2.19)	1.63	18	.12	18–48
Oats:						
Petal area early	66.60 (4.39)	68.02 (4.14)	−.23	22	.82	1,835
Number flowers open	31 (5.86)	30.25 (6.04)	.089	22	.93	10,377
Number flowers visited	22.31 (7.81)	15.48 (3.94)	.78	15	.45	64–230
Total number pollinators	9.36 (2.67)	7.25 (1.73)	.66	11	.51	129–307
Time spent per flower	35.05 (6.91)	29.85 (8.48)	.48	18	.64	339–511

[a] Based on Satterthwaite's approximation for unequal variances; sample sizes ranged from nine to 12 at the Main Road site and from 11 to 12 at the Oats site; sample sizes for pollinator visitation measures only on plants with pollinators.

[b] Values represent the sample size required to detect the observed difference, given the observed SD (power = 0.80, $\beta = 0.20$). Range represents sample size required for high and low observed SD values.

significantly in flower production, although U plants for the first time produced more flowers than D plants ($t = -0.81$, df = 23, $P = .42$). One and one-half weeks after that, or 6 wk after flowering began, 13 out of 24 plants had completely ceased flowering at the Main Road site, and these plants were split evenly between D and U treatments; the Oats site was not sampled completely, but of nine plants sampled, a similar percentage (three out of nine: two U and one D) had also ceased flowering. Thus, there was only a small period of time in which undamaged plants could have exceeded damaged plants in flower production. This time was also at the very end of the season, when flower and fruit production were both declining. For these reasons, we feel it is unlikely that undamaged plants ever significantly exceeded damaged plants in the number of seeds sired.
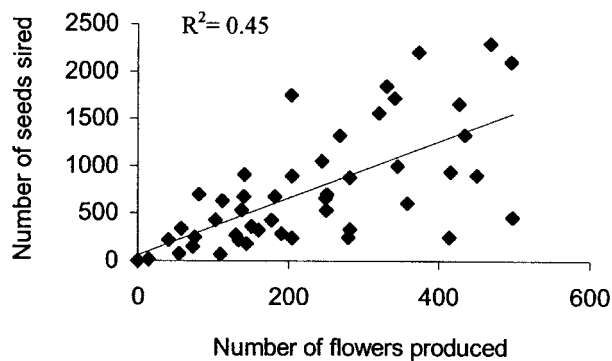

Figure 2: Relationship between number of seeds sired and number of flowers produced. Number of seeds fertilized = 2.99 (number of flowers produced) + 0.58; $R^2 = 0.44$, $P < .001$.

Discussion

Damage to leaves by herbivores caused shifts in allocation patterns in the period following damage at the lower-quality Main Road site but did not affect any measured trait significantly at the higher-quality Oats site. At the Main Road site, damaged plants had greater success as male parents than did undamaged plants. Damaged plants initially allocated relatively more resources to male function through increased flower production, without the concomitant increase in seed production. Recall that no differences were present in the number of seeds produced by damaged and undamaged plants (undamaged plants produced slightly more seeds) and that seed abortion was significantly greater in damaged plants at the Main Road site. These results are consistent with a shift away from carbon-intensive female reproduction when photosynthetic tissue is lost (Agrawal et al. 1999*a*).

The mechanisms underlying increased male fitness for undamaged plants are still unclear; however, both early flower production (particularly in the paired analysis) and time spent foraging per flower by pollinators show trends in the right direction, and these would have been significant with modest increases in sample size (see power analysis; table 2).

Our estimates suggest that at both sites, damaged and undamaged plants had similar total fitness by the end of the season. One problem with that deduction is that undamaged plants might have produced more flowers than damaged plants after our sampling period. While we could not rule this possibility out completely, we feel several lines of argument make this scenario unlikely. First, flower production was followed until the last few weeks of plant lifetimes, and at no time did undamaged plants have sig-

nificantly greater flower numbers than damaged plants; in fact, for most of the season, they had fewer flowers. Second, in some years with early drought, all plant reproduction would have occurred over the measured time period of this study (Lehtilä and Strauss 1997), and thus we would have measured total plant reproductive success. Third, Ashman et al. (1993) showed that early flowers accounted for most reproduction in closely related *Raphanus sativus.* Thus, under many natural conditions, it appears that damaged and undamaged plants would have achieved equal total reproductive success.

Even when total reproductive success is equal, changes in allocation to male and female fitness will not have identical outcomes for damaged and undamaged plants. Pollen is dispersed three to 124 times farther from the parent than are seeds (McCauley 1997; Tarayre et al. 1997; Streiff et al. 1998; Levy and Neal 1999), and gene flow is greater through pollen in every study that has compared pollen and seed dispersal. Therefore, investment in male function may result in a more widespread spatial distribution of genes from damaged plants than from undamaged plants. This spread could aid in spatial escape of susceptible genes/genotypes from herbivores in the next generation if attack from herbivores is spatially correlated from year to year (e.g., Wool and Bogen 1999).

Plant response to damage is strongly related to resource levels as well as damage levels (Maschinski and Whitham 1989; see Strauss and Agrawal 1999 for review). This may be one explanation for why the Oats site experimental plants did not show obvious effects of damage. In some of our earlier studies in which plants were grown in pots and were smaller, floral traits were reduced and pollinators were less abundant on damaged plants relative to undamaged sibs (Lehtilä and Strauss 1999). In fact, our sampling scheme was motivated by our prior observations, and we expected damaged plants to sire fewer seeds in the arrays. In contrast, in this field experiment where plants were grown on rich, prairie-derived soils, we did not see these effects.

It appears that plants are extremely plastic in both the nature and the extent of their responses to herbivory, and these responses may be in large part mediated by resource availability (if we can judge resource levels by total seed and flower production produced in an annual plant). We have observed several qualitatively distinct responses by *Raphanus raphanistrum* to the same type of damage under different environmental conditions. In the greenhouse, under a regime of fewer resources and slightly more damage (50% leaf area removal), plants exhibited reduced floral display, with smaller flowers and less pollen produced per flower (Strauss et al. 1996; Lehtilä and Strauss 1997, 1999). Field trials with these plants showed that pollinators discriminated against these damaged plants both in terms of the number of pollinators visiting plants and the time per flower (Strauss et al. 1996; Lehtilä and Strauss 1997); we expect that these changes would result in decreased male fitness for plants. At the Main Road site, which was of intermediate quality (and had plants with slightly lower amounts of leaf area damaged than in our previous study), flower size decreases were again present in damaged plants, but these differences were not statistically different (see power analyses; tables 1, 2). Pollinators did not distinguish between damaged and undamaged plants. At this site, damaged plants sired more seeds (did better as males) but had the same overall fitness as undamaged plants; they aborted more seeds early on and therefore had a greater proportion of their total early fitness as males. Finally, at Oats, the richest site, plants completely compensated for damage in every measured character, and damaged and undamaged plants did not differ in their success as male versus female parents.

In conclusion, environmental quality affected not only total plant fitness but also the relative success and investment in male versus female plant fitness when plants were damaged by insect folivores. Greater allocation to male versus female fitness on the part of damaged plants was observed early in the season at a lower-quality site but not at a higher-quality site. Overall, wild radish is extremely tolerant of foliar damage; differences in fitness between damaged and undamaged plants came in the form of differential success of male versus female parents but not in the total number of genes contributed to the next generation. This result may be important in altering the spatial distribution of genes responsible for susceptibility to herbivores. Examination of other less tolerant plant species, under a range of environmental conditions, will allow a deeper understanding of the impact of herbivory on male versus female components of total plant fitness.

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