

## PATTERN OF LEAF DAMAGE AFFECTS FITNESS OF THE ANNUAL PLANT *RAPHANUS SATIVUS* (BRASSICACEAE)<sup>1</sup>

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**Abstract.** We investigated how the pattern of leaf damage influences reproduction, growth, and allocation in the wild radish, *Raphanus sativus* (Brassicaceae). We removed an equivalent leaf area from plants with four leaves in five treatments ranging from concentrated to dispersed damage: one entire mature leaf removed, one entire new leaf removed, 50% of two mature leaves removed, 50% of two new leaves removed, and 25% of all four leaves removed. Plants in a control group were undamaged. Reproduction, growth, and allocation were not affected by the age of the damaged leaf. However, the pattern of leaf damage significantly affected our three measures of plant fitness: the number of flowers produced, the reproductive biomass, and the total biomass. Plants in the treatment in which the damage was most dispersed had significantly higher flower number, reproductive biomass, and total biomass than an intermediate damage treatment and significantly more reproductive biomass than the concentrated damage treatment. There were no significant differences between the concentrated and intermediate damage treatments and no differences between the dispersed damage treatment and the undamaged control. Our data indicate that more dispersed damage is less detrimental to the plant than more concentrated damage. Therefore, the pattern of leaf damage must be considered in determining the impact of herbivores on plant performance.

**Key words:** allocation; concentrated herbivory; dispersed herbivory; effects of leaf damage; herbivory; pattern of leaf damage; leaf age; plant fitness; *Raphanus sativus*; simulated herbivory.

### INTRODUCTION

Leaf damage by herbivores has been reported to have no effect (Belsky 1986), a positive effect (McNaughton 1979, Paige and Whitham 1987) or a negative effect (Rausher and Feeny 1980, Marquis 1984) on plant reproduction and growth. These conflicting results have been explained as being due to differences in the availability of resources and to the intensity of competition (Maschinski and Whitham 1989). However, differences in the foraging pattern of different species of herbivores may also be important in contributing to variation in the effects of herbivory on plants (Edwards and Wratten 1983). Different herbivore species may vary in the amount of leaf area they consume, the age of the leaves they damage (Mooney and Gulmon 1982), the timing of their damage (Krischik and Denno 1983), and the pattern of damage they impose (Edwards and Wratten 1983). In this experiment, we examined the

importance of two of these features of herbivore foraging pattern, age of damaged leaves and dispersion of damage, on reproduction and growth of the annual plant *Raphanus sativus* (Brassicaceae).

New leaves have been considered more valuable to the plant because they often have higher photosynthetic rates (Mooney and Gulmon 1982, Bazzaz 1984), higher nitrogen concentrations (Mattson 1980, Field and Mooney 1983), and higher levels of secondary compounds (McKey 1979) than mature leaves. Therefore, a herbivore that feeds preferentially on new leaves may have a more negative impact on the plant than one that feeds on mature leaves (Cranshaw and Radcliffe 1980, Bazzaz et al. 1987).

The spatial pattern of damage may also be critical in determining the impact of herbivory on plant performance (Edwards and Wratten 1983). Studies of patterns of caterpillar foraging have shown that several species forage in a manner that disperses damage (Heinrich 1979, Schultz 1983, Stamp 1984, Dethier 1988), while other species may concentrate their damage on a few individual leaves (Heinrich 1979). Mauricio and Bowers (1990) have shown that a herbivore

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of *R. sativus*, the larva of the cabbage butterfly, *Pieris rapae*, forages in such a way as to produce a pattern of dispersed damage on its host plant. We designed the experiment reported here to examine the fitness consequences for the plant of a dispersed pattern of leaf damage.

Few studies have considered the consequences for the plant of the pattern of herbivore damage. Those studies have produced varied conclusions: Lowman (1982) and Marquis (1992) found evidence for tropical trees that dispersed damage is less detrimental than concentrated damage, but Wit (1982) showed that concentrating damage in brussels sprouts caused less of a decrease in yield than dispersing damage. In our experiment we compared the effects of removing an equal area of leaf tissue in different patterns, ranging from a dispersed to a concentrated pattern of herbivory. We also compared the effects of these patterns on new vs. mature leaves. We assessed the response of *R. sativus* to these different damage patterns by comparing reproduction and growth measures among treatments.

#### METHODS

*Raphanus sativus* is a widely distributed annual plant found in such disturbed areas as roadsides and old fields. The early leaves of *R. sativus* form a basal rosette. We germinated *R. sativus* seeds collected from a naturalized population in Yolo County, California, USA, on moist vermiculite in a growth chamber on 1 September 1987 (24°C day [D]; 21°C night [N]; photoperiod, 12D:12N). On 18 September 1987 we transplanted established seedlings into 10-cm diameter clay pots in a 1:1:1 mixture of sand, soil, and Turface (chipped montmorillonite clay) and transferred seedlings to another growth chamber (24°C; photoperiod 10D:14N). We watered the plants daily with quarter-strength Hoagland's solution. We changed growth chamber conditions on 1 October 1987 to 15°C D:13°C N, photoperiod 10D:14N, because some plants had initiated small buds, and on 15 October 1987 we changed conditions to 12°C D:11°C N, photoperiod 9.5D:14.5N to prevent further bolting.

The experiment began when the plants had four completely expanded leaves in their rosettes. We selected 120 plants for the experiment based on uniform size and appearance of leaves. However, 35% of the selected plants had very small flower buds already forming. We noted these plants, but treated them in the same way as the other plants. On 16 October 1987 we transferred the plants to a greenhouse (22°C D, 20°C N, with a photoperiod of 10D:14N) and randomly assigned each to a position on a bench, with  $\approx 15$  cm between adjacent pots. We watered the plants daily and fertilized them every other day with quarter-strength Hoagland's solution.

We randomly assigned 20 plants to each of the following treatments: (1) control, no leaf area removed, (2) one entire mature leaf removed, (3) one entire new

leaf removed, (4) 50% of two mature leaves removed, (5) 50% of two new leaves removed, and (6) 25% of all 4 leaves removed. Therefore, all plants that experienced damage had the same total leaf area removed (25% of the total leaf area available). We placed equal numbers of plants that had initiated small buds in each treatment. Mature leaves were the first two leaves initiated in the rosette and new leaves were the last two leaves fully expanded in the rosette. Mature and new leaves differed in age by  $\approx 2$  wk. We began imposing the damage treatment on 17 October 1987. To mimic the observed rate of defoliation in the field, we removed leaf tissue with a hole puncher in three sessions over 24 h. We avoided damaging the midrib in all treatments except those where the entire leaf was removed. In the first session, in the late afternoon of the first day, we removed one third of the prescribed leaf damage. We removed successive thirds of the prescribed leaf damage area the next day in a morning and a late afternoon session.

We harvested the plants between 22 and 24 November 1987 and separated individual plants into (1) flowers and buds, (2) stem, (3) rosette leaves, (4) stem leaves, and (5) roots. We measured the dry mass of each component, as well as the following parameters for each individual: number of senesced and living flowers, mean flower dry mass, mean flower bud dry mass, area and number of rosette leaves, area and number of stem leaves, number of senesced rosette leaves, and the mean dry mass and area of a mature leaf and a new leaf.

We calculated the dry mass of reproductive structures by adding the dry mass of the buds and flowers present at harvest to an estimated dry mass of senesced flowers, which was calculated by multiplying the average dry mass of a flower ( $N = 100$ ) by the number of pedicels left on the plant. The dry mass of rosette leaves included the estimated dry mass of leaf tissue removed in the defoliation treatment ( $N = 25$ ). The total leaf area reported also included leaf area lost to the herbivory treatment. The total biomass is the sum of all the dry masses, including the estimated dry masses. We calculated the relative allocation for each individual by dividing the mass of the appropriate structures by the total biomass.

We used three estimates of fitness in this study: total number of flowers, reproductive biomass, and total fitness. Because pollinators were excluded from the greenhouse and because *R. sativus* is insect pollinated and self-incompatible, we could not obtain a more direct estimate of fitness, such as seed number and seed mass. However, in a study of a very closely related species, *Raphanus raphanistrum*, Stanton (1984) found a highly significant ( $P < .001$ ) positive correlation between the total number of flowers initiated and the total number of seeds produced. In addition, flower production is a major determinant of a plant's pollen yield, an important component of male reproductive success (Devlin et al. 1992). Studies of male repro-

TABLE 1. The effect of pattern of leaf damage on the wild radish, *Raphanus sativus*.  $N = 20$  for the control and dispersed treatments and  $N = 40$  for the concentrated and intermediate treatments.  $F$  values and probabilities are reported from a univariate ANOVA performed on each variable.

Variables	Treatment								ANOVA	
	Control		Concentrated		Intermediate		Dispersed		$F$	$P$
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE		
Flower number	107.7	7.6	91.8	6.5	81.0	6.2	115.4	9.4	4.24	.0070**
Reproductive biomass (g)	51.4	4.7	42.7	3.4	38.3	3.7	58.9	5.8	4.29	.0065**
Total biomass (g)	73.2	5.6	62.2	3.9	56.7	3.9	77.5	6.0	3.97	.0098**
Stem biomass (g)	1.3	0.1	1.4	0.1	1.3	0.1	1.5	0.1	0.94	.4222
Rosette leaf biomass (g)	18.9	1.4	16.6	0.8	15.7	1.0	15.7	1.5	1.45	.2315
Stem leaf biomass (g)	0.3	0.04	0.4	0.03	0.3	0.02	0.3	0.02	0.98	.4042
Root biomass (g)	1.3	0.1	1.2	0.1	1.1	0.1	1.1	0.1	1.10	.3520
Rosette leaf area (cm <sup>2</sup> )	221.7	11.9	213.6	7.3	200.4	6.8	190.5	12.1	1.93	.1291
Stem leaf area (cm <sup>2</sup> )	60.4	7.1	65.2	5.4	60.9	4.5	57.0	5.3	0.36	.7808
Stem number	7.8	0.5	7.4	0.5	6.1	0.4	7.6	0.4	2.53	.0604
Flower number/stem	15.0	1.3	12.6	0.7	13.2	0.6	15.8	1.0	2.87	.0394*
Reproductive allocation (%)	68.7	1.9	64.7	2.3	62.7	2.9	73.6	2.7	2.64	.0528
Vegetative allocation (%)	29.4	1.8	32.8	2.0	34.8	2.7	24.8	2.5	2.68	.0504
Root allocation (%)	1.9	0.2	2.5	0.3	2.5	0.3	1.7	0.2	2.44	.0679
Root-to-shoot ratio	0.26	0.01	0.27	0.01	0.29	0.02	0.27	0.02	0.70	.5517

\*  $P < .05$ , \*\*  $P < .01$ .

ductive success in *R. sativus* have shown that a plant's relative success at fathering seed on another plant in the population increases with flower number (Devlin et al. 1992). Total plant dry biomass and reproductive biomass have also been used as measures of plant fitness (Belsky 1986).

Data were analyzed using the GLM procedure in the SAS statistical package (SAS Institute 1989). All variables were tested for normality and homogeneity of variances. The allocation variables were arcsine-transformed in order to conform with statistical assumptions (Sokal and Rohlf 1981). Harvest data were separated into reproductive measures (number of flowers and reproductive biomass) and growth measures (all other variables). Data were analyzed using analyses of variance, followed by both a priori (single-degree of freedom contrasts) and a posteriori (Ryan-Einot-Gabriel-Welsch tests) comparisons in order to identify specific differences among the treatment means (Day and Quinn 1989, SAS Institute 1989). Ryan's  $Q$  test (with Kramer's modification for unequal sample sizes) was recommended by Day and Quinn (1989) as being the most powerful test for all-pairs comparisons while controlling the experimentwise Type I error rate.

## RESULTS

Premature initiation of buds did not affect the results of our experiment. An analysis of variance, with a class variable for the presence of initial buds, revealed no significant treatment  $\times$  presence-of-initial-buds interaction for any variable. In addition, removal of those plants with initial buds from the analysis did not qualitatively change our results. Therefore, we pooled plants with and without initial buds for subsequent analysis.

A priori comparisons of the effect of leaf age on all measured response variables revealed that there were

no significant effects of leaf age or significant interactions of age with pattern of damage. Thus, treatments where one entire mature leaf or one entire new leaf was removed were pooled into one treatment (concentrated damage) and treatments where 50% of two mature leaves or 50% of two new leaves were removed were pooled into a second treatment (intermediate damage). We then compared these damage treatments with the treatment where 25% of four leaves were removed (dispersed damage) and the undamaged control. Significant multivariate analyses of variance for the reproductive measures (MANOVA,  $df = 6, 230$ , Wilks'  $\lambda = 0.866$ ,  $P = .0104$ ) and the growth measures (MANOVA,  $df = 27, 316$ , Wilks'  $\lambda = 0.684$ ,  $P = .0288$ ) justified our performing univariate ANOVAs on each of the response variables in the two groups.

Damage treatment had a significant effect on each of our fitness estimates: total number of flowers (ANOVA,  $df = 3, 116$ ,  $F = 4.24$ ,  $P = .0070$ ), reproductive biomass (ANOVA,  $df = 3, 116$ ,  $F = 4.29$ ,  $P = .0065$ ), and total dry biomass (ANOVA,  $df = 3, 116$ ,  $F = 3.97$ ,  $P = .0098$ ) (Table 1). In addition, we found effects of treatment on the number of flowers per stem (ANOVA,  $df = 3, 116$ ,  $F = 2.87$ ,  $P = .0394$ ), reproductive allocation (ANOVA,  $df = 3, 116$ ,  $F = 2.64$ ,  $P = .0528$ ) and vegetative allocation (ANOVA,  $df = 3, 116$ ,  $F = 2.68$ ,  $P = .0504$ ) (Table 1). There were no significant effects of treatment on any of the other variables (Table 1).

Ryan-Einot-Gabriel-Welsch tests ( $\alpha = .05$ ) were performed on means for those ANOVAs with overall significant effects: flower number, reproductive biomass, total biomass, reproductive allocation, and vegetative allocation. There were no differences between the dispersed damage treatment and the undamaged control for any of the variables (Figs. 1 and 2).

Our data show that intermediate damage causes the

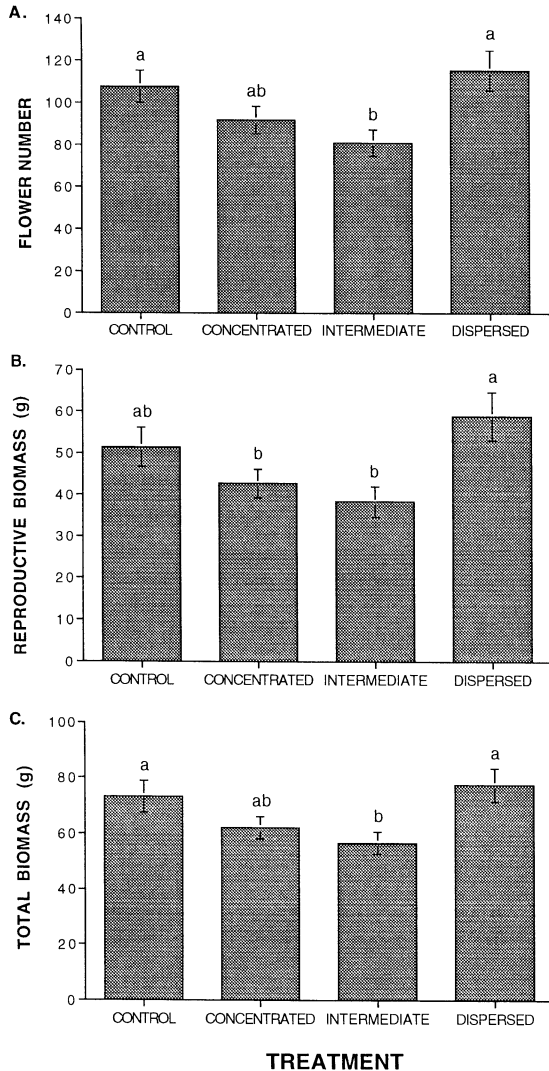


FIG. 1. The effect of pattern of leaf damage on (A) flower number, (B) reproductive biomass, and (C) total biomass of the wild radish, *Raphanus sativus*. Total  $N = 120$  for each variable. Within a variable,  $N = 20$  for the control and dispersed damage treatments and  $N = 40$  for the intermediate and concentrated damage treatments. Means with the same letter are not significantly different by Ryan-Einot-Gabriel-Welsch tests ( $\alpha = .05$ ,  $df = 116$ ).

most significant reduction in fitness to the plant, with concentrated damage being intermediate in terms of fitness between dispersed damage and intermediate damage (Fig. 1A, B, and C). Both concentrated and intermediate damage treatments showed significant decreases in reproductive biomass compared to the dispersed damage treatment and lower means compared to the undamaged control (Fig. 1B). For flower number and total biomass, the concentrated damage treatment was not significantly different from the control (Fig. 1A and C), although the means for the concentrated damage treatment were always lower than the control and higher than the intermediate damage treatment.

The means for flower number, reproductive biomass, and total biomass in the intermediate damage treatment were consistently and significantly lower than the means for these variables in the dispersed damage treatment and significantly lower than the control for flower number and total biomass (Fig. 1A, B, and C).

The dispersed damage treatment had significantly higher reproductive allocation than the intermediate damage treatment (Fig. 2). Conversely, the intermediate damage treatment had a significantly higher mean vegetative allocation compared to the dispersed damage treatment (Fig. 2), although the vegetative allocation was not different from the control or the concentrated damage treatment. There were no significant differences among treatments in root-to-shoot ratio (Table 1).

DISCUSSION

Our results showed that under conditions of a constant level of defoliation (25%), the pattern of leaf removal (dispersed, intermediate, or concentrated) influenced the effect of damage on the performance of *Raphanus sativus*. The dispersed pattern of leaf damage resulted in no negative effect on any of our measures of plant fitness when compared to an undamaged control, while the other damage patterns resulted in reductions in at least one of our measures of plant fitness. These data suggest that a dispersed pattern of herbivory is less detrimental than a more concentrated pattern for *R. sativus*.

There are several ways in which the pattern of damage can be important in determining the effect of damage (Edwards and Wratten 1983, McNaughton 1983, Gold and Caldwell 1989, Marquis 1992). For example, certain patterns of damage may reduce senescence rates of remaining tissue (Nowak and Caldwell 1984) or increase the longevity of remaining foliage (McNaughton 1983). Damage of active meristems may also be im-

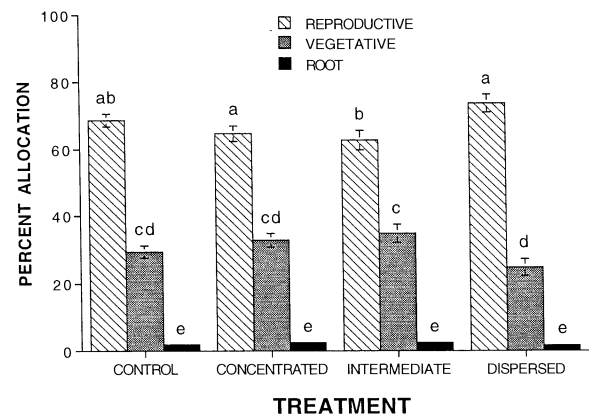


FIG. 2. The effect of pattern of leaf damage on reproductive, vegetative, and root allocation.  $N = 120$  for each variable. Means with the same letter are not significantly different by Ryan-Einot-Gabriel-Welsch tests ( $\alpha = .05$ ,  $df = 116$ ).

portant in the ability of a plant to recover from damage, and in the length of time it takes to recover (Gold and Caldwell 1989). There was no meristem damage and little leaf senescence in our experiment as most of the growth of this annual plant subsequent to the damage was in the reproductive portions of the plant.

Different patterns of tissue loss may also affect plant performance because leaves of different age, and perhaps of different value to the plant, may be damaged (McKey 1979, Mooney and Gulmon 1982). The results of our experiment showed no difference in the effects of tissue removal from leaves that differed in age by  $\approx 2$  wk. This suggests that the contribution of these leaves to the carbon budget of the plant did not significantly differ during the time course of our experiment.

There may also be effects of damage pattern that operate by affecting the herbivores doing the damage. For example, induction of defensive chemicals in response to damage may cause herbivores to move after eating only a fraction of a leaf (Carroll and Hoffman 1980, Edwards and Wratten 1983, Schultz 1983), and there may be increased predation on moving herbivores (Edwards and Wratten 1983, Bergelson and Lawton 1988). Because we simulated herbivory, effects on herbivores could not be important in our experiment.

The individuals in the dispersed damage treatment did not differ from the undamaged control for any of our three fitness measures. Therefore, the damaged plants with the most dispersed pattern of damage were able to compensate for damage while plants with a more concentrated pattern of damage were less able to compensate. Although the mean fitnesses of the concentrated damage treatment were always lower than the control and higher than the intermediate damage treatment, the impacts of the intermediate and the concentrated damage treatments on fitness were statistically indistinguishable.

However, our data suggest that there may be a threshold effect of damage in individual *R. sativus* leaves. This threshold may lie between 25% and 50% damage to a leaf. Leaves with 25% of their area removed may be able to compensate for damage by elevated photosynthetic rates in the remaining tissue (Heichel and Turner 1983, von Caemmerer and Farquhar 1984). As a result, those plants with 25% damage to all four leaves did not differ from the control plants with no damage. Damaged leaves on plants with 50% of two leaves removed may have been damaged to such an extent that there was no compensation, and leaves with half of their tissue removed may have had lower photosynthetic rates (on a unit area basis) than intact leaves or leaves with only 25% of their tissue removed. As a consequence, those plants with a single entire leaf removed were able to perform better than those plants with 50% of two leaves damaged and only two intact leaves, but less well than the controls with four intact leaves.

Our results have important implications for the interaction of *R. sativus* and its herbivores. Patterns of insect herbivory may vary substantially, depending on the insect species involved, the growth form of the host plant, the presence or absence of natural enemies, and abiotic conditions (Heinrich 1979, Mauricio and Bowers 1990, Stamp and Bowers 1990). A herbivore species that disperses damage over many leaves may have a less negative impact on plant fitness than a herbivore that concentrates its damage. A localized induction of secondary chemicals may cause herbivores to move to another part of the plant, resulting in a dispersed pattern of damage, and minimizing the negative impact of herbivory on the plant. Therefore, consideration of not only the amount of damage to a plant, but also the pattern of damage to the plant, is important in determining the ultimate impact of herbivory on plant fitness.

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