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EFFECTS OF ARTIFICIAL DEFOLIATION ON REPRODUCTIVE ALLOCATION IN THE COMMON VETCH, *VICIA SATIVA* (FABACEAE: PAPILIONOIDEAE)[1]

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Previous field experiments have shown that, for the annual herb *Vicia sativa,* leaf area lost to herbivory results in reduced number of fruit (pods) produced per plant as well as fewer seeds per pod. We conducted a controlled garden experiment to determine the precise relationship between level of defoliation and various measures of maternal fitness through fruit and seed. We employed manual clipping of individual leaflets of newly produced leaves to 25% increments of damage (from 0% to 100%) over the entire period of development and flowering of these annual herbs, harvesting pods when filled but not dehisced. We found significant reduction in number of pods, number of seeds, total seed mass, and individual seed mass with leaf area lost. Even with the highest levels of defoliation over the life of the individual, plants still produced a substantial number of pods and seeds. Seeds produced by plants in all treatment groups showed similar percentages of germination and time to germination.

Key words: allocation; defoliation; Fabaceae; herbivory; legumes; reproduction; *Vicia sativa.*

Leaf-chewing herbivores remove leaf area that is potentially able to photosynthesize and to provide energy for plant growth, flowering, and fruiting. The effects of herbivores might be expected to differ among plants with different life history strategies.

Perennial plants are polycarpic, and their reproductive output can vary from year to year, in general increasing with plant size. In many studies, defoliation of perennial species has been shown to decrease significantly growth (Nunez-Farfan and Dirzo, 1991), fruit set (Rockwood, 1973; Niesenbaum, 1993; Obeso, 1993) or fruit mass (Marquis, 1991); in others, no effect of defoliation has been found (Obeso and Grubb, 1993). Perennials may respond to severe damage with increased vegetative growth and reduced sexual reproduction (Archer and Tieszen, 1983; Jonsdottir, 1991). Severe defoliation of trees can decrease ring size (Hoogesteger and Karlsson, 1992). Defoliation of proleptic species such as temperate spring-flowering perennials (Lyrene, 1992; Rockwood and Lobstein, 1994) or tropical deciduous species (Dominguez and Dirzo, 1994) in one year may not affect reproduction in that same year if flower buds were initiated during the previous year, but will affect the subsequent year's flowering and fruiting. Leaf area lost to herbivores has been found to affect subsequent reproductive effort for more than one year following the damage in tropical shrubs (Marquis, 1984). All these responses are possible in plants with options for future reproduction.

In annual plants, however, there is only one opportunity to reproduce, and any damage sustained from leaf-chewing herbivores can only affect that year's reproductive effort. Defoliation at certain times during flowering decreases fruit maturation from flowers produced (Pate, Atkins, and Perry, 1980; Gedge and Maun, 1992; Sharma and Ghildiyal, 1992). We cultivated the herbaceous annual *Vicia sativa* L. (native to our study area) to investigate how much damage was required to affect significantly overall fruit production and also viability of seeds produced.

Vetches have been the focus of a variety of field studies of plant/herbivore interactions. The common vetch bears stipular nectaries that attract ants who provide generalized antiherbivore defense, especially in nonnative habitats (Koptur, 1979). Experimental exclusion of ants via removal of nectaries increased damage to leaves, and this difference was coupled with reduced fruit and seed set in individuals with excised nectaries vs. those with nectaries intact (Koptur, 1979). Infestation by leaf-chewing adult weevils of *Sitona lineatus* resulted in substantial reduction in pods per plant *Vicia faba* (Nielsen, 1990), though seeds per pod and seed mass were unaffected. Aphids tended by ants on *V. faba* reduce fruit set (Banks and Macaulay, 1967). In experiments where insect herbivory was reduced via insecticide spraying of fields (Brown et al., 1987), *Vicia sativa* produced more pods and more seeds per pod (but no effect on individual seed mass was found).

MATERIALS AND METHODS

We started with seeds collected in bulk samples from the meadow areas on the University of York campus in late summer 1983 by J. H. Lawton. In March 1984 seeds were scarified and soaked overnight, then planted on 30 March 1984 in vermiculite where they germinated and grew for 1 mo in a greenhouse.

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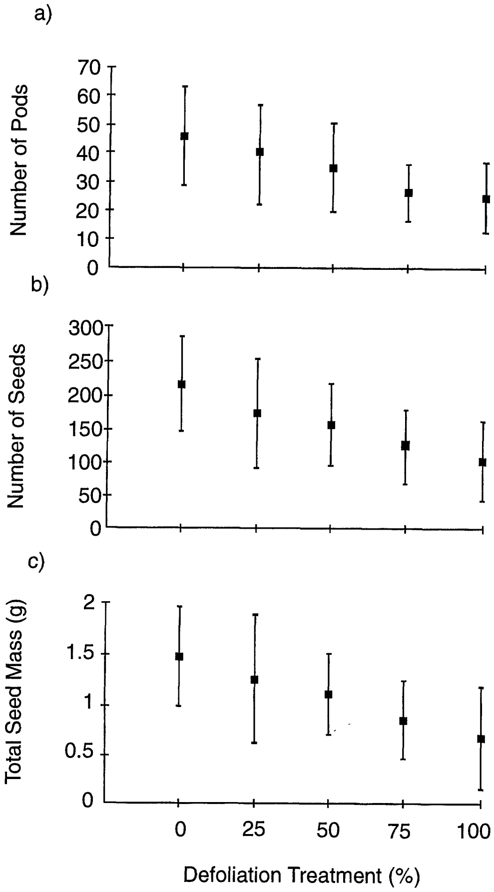

Fig. 1. Means ± 1 SD of (a) Fruit production, (b) seed production, and (c) seed mass of plants subjected to different defoliation treatments. Sample sizes for the treatment groups increasing from 0% to 100% defoliation are: 22, 22, 21, 21, and 22, respectively. All measures show significant differences among treatments: (a) for number of pods per plant, ANOVA between treatments df = 4, total df = 107, $F = 9.43$, $P < 0.0001$; (b) for number of seeds per plant, $F = 11.39$, $P < 0.0001$; and (c) for total seed mass per plant, $F = 11.79$, $P < 0.0001$.

Young plants ($N = 110$) were planted on 5 May 84 in six rows 1 m apart with 0.5 m between each plant in an allotment garden (walled, outdoors, and relatively free of herbivores) in bare soil that was kept free of other plants during the course of the experiment. Plants grew unshaded throughout the course of the experiment. All plants were watered when necessary to avoid water stress. Treatments were assigned with ascending levels of defoliation in repeating order (22 individuals in each group). Plants of the same treatment were not in the same position of each row to control for position effects on productivity. On 5 June 84, 1 mo after transplanting and prior to flowering, we began defoliation treatments, which were maintained by twice-weekly clipping of all new leaves to the level assigned to that plant. Each individual leaflet of the odd-pinnately compound leaves was trimmed using fine surgical scissors to remove the distal portion with a blunt cut to levels of 25, 50, 75, and 100% removed. Two plants were lost to hoeing (so $N = 21$ for the 50 and 75% defoliation treatments).

We continued the defoliation treatments until the end of the experiment in mid-August. When fruit began maturing, we collected fruit from each plant into paper envelopes for later seed counts and weighings (pods were harvested from early July through mid-August). We dried the seeds for 48 h at 40°C prior to obtaining dry masses of the total number of seeds produced; seeds were dried again prior to weighing 30 (a few plants had only 20 +) individual seeds per plant. A sample of 100 seeds produced by each treatment group was chosen from the bulk samples, soaked overnight, and then planted individually in tray sections filled with vermiculite and watered. Germination was monitored for 28 d.

TABLE 1. Effects of defoliation treatments on average seed mass. Superscripts denote statistically significant differences between means (if letters differ, Tukey $P < 0.05$).

Treatment	N	Mean seed mass	Variance
0% defoliation	22	0.0088[a]	0.0015
25% defoliation	21	0.0083[b]	0.0021
50% defoliation	22	0.0081[b]	0.0015
75% defoliation	21	0.0076[b]	0.0017
100% defoliation	22	0.0072[c]	0.0016

Data from defoliation experiments were tested for normality. We used a square-root transformation to normalize data prior to analysis. Data were analyzed using analysis of variance and contingency table procedures in GLIM and SYSTAT.

RESULTS

The sunny, warm summer of 1984 provided ideal growing conditions for our plantation of wild vetches. Growing as they were in the midst of other vegetable gardens full of edible species (including the commonly cultivated vetch species, broad bean, *Vicia faba*) left the *Vicia sativa* remarkably free from damage from insects or other herbivores.

Individual control plants produced an average of nearly 50 pods (ranging from 23 to 105 pods) (Fig. 1a), and defoliation had a statistically significant effect on pod production (ANOVA between treatment df = 4, total df = 107, $F = 9.43$, $P < .0001$). Even at 100% defoliation, plants still produced on average >20 pods each, though many of these pods were shorter and contained fewer seeds than normal (the proportion of small pods did not, however, differ significantly among treatments). This observation was borne out in the precise seed counts, done in bulk rather than on a per-pod basis: control plants produced >200 seeds per plant (on average), whereas plants with the most extreme defoliation produced on average 50% fewer seeds (Fig. 1b). Fewer seeds were produced with increasing levels of defoliation ($F = 11.39$, $P < 0.001$).

Total seed mass varied with treatment (Fig. 1c) even more significantly ($F = 11.79$, $P < 0.0001$), perhaps because we also found that plants subject to greater levels of defoliation had lower individual seed masses on average (Table 1), a difference that was statistically significant ($F = 3.24$, $P = 0.015$).

The proportion of seeds germinating within 1 mo was not significantly different (Pearson chi-square = 9.003, df = 4, $P = 0.61$) among defoliation treatment groups (Table 2). Mean time to germination for the seeds that did germinate (Table 3) did not differ significantly among groups either (ANOVA $F = 0.695$, $P = 0.597$).

DISCUSSION

Linum, Vicia, and *Agrostemma* all display constancy in numbers of stems per plant, seeds per fruit, and in mean fruit mass over a range of densities, but their fecundity changes are due to a change in the number of

TABLE 2. Germination of seeds from defoliation treatments. Contingency table analysis shows no significant effect of defoliation (Pearson chi-square = 9.003, df = 4, P = 0.061).

Treatment	Germination	No germination	Total
0% defoliation	32 seeds	68	100
25% defoliation	25	75	100
50% defoliation	36	64	100
75% defoliation	22	78	100
100% defoliation	38	62	100

TABLE 3. Mean days to germination (Days to germin.) of seeds from defoliation treatments. Abbreviations: SE = standard error; N = sample size. Analysis of variance shows no effect of defoliation (F = 0.695, P = 0.597).

Treatment	Days to germin.	SE	N
0% defoliation	15.97	1.26	32
25% defoliation	16.84	1.42	25
50% defoliation	14.28	1.19	36
75% defoliation	16.54	1.52	22
100% defoliation	14.95	1.16	38

fruit per stem (Harper, 1977). In general, weeds and annuals show a linear relationship between seed production and size (Watkinson, 1978; Weaver and Cavers, 1980). One might therefore expect a linear relationship between defoliation level and seed production, as we see in our results.

Negative effects of high levels of herbivory may be highly conditional (Lee and Bazzaz, 1980; Primack, Miao, and Becker, 1994); these effects may be greater at higher plant densities where competition for light is more severe, or in shade, where light is limiting. In our garden experiment, however, the plants had space between them and grew in full sun, so these additional stresses were not present.

Reduction in leaf area reduces the resources available for fruit development; fruit abortion can be correlated with levels of herbivore damage (Stephenson, 1981). Legumes regularly initiate pods and develop them to nearly full size before "filling" them (maturing the seeds). Seed production is limited by resources and seed predators (Lee and Bazzaz, 1982); in *Cassia fasciculata* the removal of rapidly growing fruit resulted in the growth and maturation of other fruit that normally would not mature. Experiments with a variety of legume species have shown that defoliation negatively affects reproductive output (Bastrenta and Belhassen, 1992; Bossard and Rejmanek, 1992; Shibairo and Nyabundi, 1993; Hunt, Higley, and Witkowski, 1994; Schaafsma and Ablett, 1994). Defoliation during pod filling results in smaller seeds in *Phaseolus vulgaris* (Schaafsma and Ablett, 1994). Mature plants are more resistant to damage than seedlings (Dirzo, 1984) and are more likely to survive severe damage, though often with diminished fitness, perhaps because the same amount of leaf area lost is proportionately great in young plants (Koptur, 1991).

Our experiment exaggerated the effects that the common vetch might experience in nature from surface-feeding insect herbivores. Natural levels of leaf damage on mature plants range from <10% to rarely >25% leaf area lost (Koptur, 1979; Brown et al., 1987; Koptur and Lawton, 1988), the lowest level of damage in our garden experiment. This may explain why some other, more natural, studies have not found effects on individual seed mass (Brown et al., 1987) or number of seeds per pod (Nielsen, 1990). Additionally, the pattern in which damage is distributed on a plant can influence the magnitude of the negative impact of that damage on the plant (Marquis, 1992). In our experiment, damage was distributed evenly over all the leaves of the plants.

The performance of individual vetches that have 100% of their leaflets removed over the course of their development was impressive; pod and seed production were not reduced >50% over controls. This phenomenon may be due to the fact that leaf rachises, tendrils, stipules, stems, sepals, and developing fruit are all green and photosynthetic, so that even when all leaflets were removed there was still a significant amount of photosynthetic tissue remaining. Stems have been shown to make significant contributions to growth and biomass of other legumes, such as *Cytisus scoparius* (Bossard and Rejmanek, 1992), as have photosynthetic fruit (Sharma and Ghildiyal, 1992). In fact, certain varieties of cultivated legumes have tendrils in place of leaflets; these are homologous structures determined from leaf base to tip within plastochrons of the initiation of the leaf (Gould, Cutter, and Young, 1994). There may be compensatory responses to herbivory, such as increased photosynthesis in undamaged leaves or photosynthetic parts, but this possibility has not been well tested (Whitham et al., 1991).

While many studies have concluded that seed mass is the least plastic of all the reproductive components (e.g., Horton and Lacey, 1994), in our study, higher levels of defoliation produced significantly smaller seeds. Smaller seeds produce smaller seedlings that may be inferior competitors; an interspecific comparison (Armstrong and Westoby, 1993) revealed that seedlings of large-seeded species tolerate defoliation better than those of small-seeded species. In the case of the common vetch, initial survival is apparently dependent upon a number of random factors encountered before the need to compete arises (e.g., the seed landing in a moist spot, the seedling being encountered by a vole, slug, or other herbivore that clips the stem or devours the entire plant). Thus, seed size may not be quite as important as in some other species.

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