SHORT COMMUNICATION

APHIDS LIMIT FECUNDITY OF A WEEDY ANNUAL (RAPHANUS SATIVUS)[1]

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ABSTRACT

Few previous studies document effects of herbivores on the reproduction of wild plants in situ. We examined the impact of aphids on seed production in wild radish (*Raphanus sativus* L.), an annual herb. Aphid infestation increased during the three-month flowering period. Flower and fruit production declined during the season, in part due to aphids. Inflorescences of late-blooming plants more than doubled their fruit production when aphids were removed. Thus, aphids curtailed the blooming period of wild radish, perhaps conferring a selective advantage on early-flowering plants. A few individuals were not susceptible to aphid colonization.

HERBIVORES cause dramatic reductions in the yield of agricultural species, yet few previous studies concern their effects on the fecundity of wild plants. Plant reproductive success is obviously affected when severe damage results in mortality (e.g., Fedde, 1973; Schmitt and Antonovics, 1986). More often, herbivores merely reduce plant growth, usually leading to a decrease in fecundity (Rausher and Feeny, 1980; Louda, 1984; Marquis, 1984; Whitham and Mopper, 1985; but see Hendrix, 1979; Paige and Whitham, 1987). The detrimental effects of sucking insects, such as aphids, are generally less visible than the damage caused by leaf-chewing herbivores. However, these sap-feeders can severely reduce plant growth and reproduction (in agricultural systems: Kennedy and Stroyan, 1959; Harper, 1963; Banks and Macaulay, 1967; Dixon, 1971a, b; Vereijken, 1979).

Further ecological studies are needed to understand how herbivory affects lifetime reproduction in wild plants, thereby promoting evolutionary change. Relatively little is known about the impact of sap-feeding insects on wild species. Here we describe the effects of aphid feeding and variation in flowering time on some fitness components of *Raphanus sativus*.

MATERIALS AND METHODS—Wild radish is a cosmopolitan annual that became naturalized in California in the late 1800's (Panetsos and Baker, 1967). This economically important weed is largely self-incompatible, relying on insect vectors for pollen transfer and seed set. Flowers open sequentially on indeterminately growing branches. Local pollinators include honeybees, lepidoptera, syrphid flies, and other insects (Stanton, 1987a). In this and several previously studied California populations, seed production was not limited by pollinator service (Stanton, 1987b).

We studied patterns of flowering and fruit set during the 1983 growing season (March–May). Field work was conducted at a population of several thousand wild radish plants growing in an abandoned field at the University of California at Davis, CA. (See Stanton, 1987a, for description of "Arboretum" site.) The 1–1.5 m tall plants each had several hundred inflorescences (also referred to as flowering branches) that began producing fruits in mid-March. Aphids did not appear until later in the season, so their effects on plant reproduction were determined using plants that reached peak flowering in late April. These plants will be referred to as late-flowering plants.

Prior to the arrival of aphids, we measured fruit set on 18 haphazardly chosen plants that flowered early in the season. Starting on 19 March and 20 April we labelled all open flowers on each of 3 randomly selected flowering branches per plant. This procedure was repeated 3 times over a period of 10 days. Flowers were marked by attaching a small adhesive label to the stem section below each pedicel. Fruit set from these flowers was recorded ap-

proximately 1 month later. The frequency of naturally occurring aphid colonies on these inflorescences was noted on 12 April and 20 April.

By late April, when most early-flowering plants had stopped producing flowers, aphids were common on many later flowering individuals. Ten such plants were haphazardly chosen for an aphid removal experiment. It was not possible to exclude aphids from entire plants without also affecting pollinators, so aphids were continually removed from a subset of branches on each plant. The late plants had just begun setting fruit and each flowering branch had many remaining buds. All naturally occurring aphids were manually removed from 8 branches per plant on 26 April. On a random sample of 4 of these branches, any aphids that appeared were removed daily. Aphids were reintroduced to each of the remaining 4 branches by cutting off an aphid-infested inflorescence (usually from the same plant) and attaching it to the experimental inflorescence with a wire twist-tie. If aphids failed to move onto the new branch, this procedure was repeated. By 4 May, colonies of at least 20 aphids had been established on all 4 aphid-treatment branches of 7 plants. Three plants had few aphids on any branches, even after repeated introductions, and data from these plants were not included in analyses of treatment effects. Beginning 1 May, the youngest flower on each experimental branch was labelled weekly until flower production ceased. Fruit set from flowers that opened during these intervals was recorded on 25 May, when most fruits had reached their final size. Branches were then collected for counts of seed number per fruit. A portion of the fruits fell off before their seeds were counted, so sample sizes for seed counts are less than those for fruit set measurements. (A total of 158 fruits were collected.)

Data were analyzed using nonparametric statistical tests because variances were not homogeneous and distributions were not normal. To test for effects of aphids on plant reproduction, we averaged data from 4 inflorescences per treatment on each plant. For flower, fruit, and seed counts, the paired means from 7 plants were compared using Wilcoxon's signed ranks test, which is analogous to a paired t test (Sokal and Rohlf, 1981). Percent fruit set of individual plants was analyzed using log-linear frequency analysis (CATMOD procedure in SAS; Freund and Little, 1981).

RESULTS—*Seasonal changes in flowering and fruit set*—Flowering of individual plants was staggered over the blooming period, and early

plants were not heavily colonized by aphids (see below). The 18 early study plants ceased flowering by late April, when individuals in the later study group had reached their peak. Phenological differences among co-occurring wild radish plants have also been noted in other years (personal observation).

Fruit set from early- and late-blooming plants reached over 70%, but on the late-blooming plants fruit set declined rapidly over time. On the early plants, 75% of 361 flowers that opened on 19–29 March set fruit. One month later, fruit set on these plants was still 64% ($N = 437$, April 20–29). On uninfested branches of late-blooming plants, fruit set declined from 71% ($N = 222$) on May 1–4 to 20% ($N = 236$) on May 13–19. This decrease in fruit set corresponded to increasingly dry soil conditions (personal observation). Stanton (1987b) observed a similar decrease in fruit set in 1984, and showed that this was not due to insufficient visitation by pollinators.

Effects of aphids—As in other years, aphids were not observed at the beginning of the flowering season. By late March, they were seen feeding on the buds of a few inflorescences. Common aphid species were turnip, cabbage, and potato aphids (*Hyadaphis erysimi, Brevicoryne brassicae,* and *Macrosiphum euphorbiae*). The frequency of aphids on branches of early plants increased from 50% on 12 April to 78% on 20 April ($N = 54$ branches on 18 plants; most parasitized branches had 5–10 aphids). By May, much larger colonies of >30 aphids were common, often feeding on both buds and young fruits of late-flowering plants. Daily inspections were necessary to maintain branches free of aphids. Even at the height of aphid abundance, however, 3 of the 10 late study plants were not colonized.

Removal of aphids led to a dramatic increase in fecundity. Aphids inhibited flower production as well as the proportion of flowers setting fruit (Fig. 1, Table 1). During the first 3 days of aphid establishment, flower production on branches with aphids was not significantly different from that on aphid-free branches (Fig. 1). Initial fruit production (prior to abortion) was also similar (6.5 vs. 6.8 fruits per inflorescence). After 4 May, aphid removal caused a 46% increase in the number of flowers produced (Fig. 1), and an 80% increase in percent fruit set. Combining these effects, we see that removing aphids resulted in 2.4× more fruits per branch after 4 May (Fig. 2). Individual plants showed significant variation in overall fruit set, and the interaction term from log-linear frequency analysis was almost significant
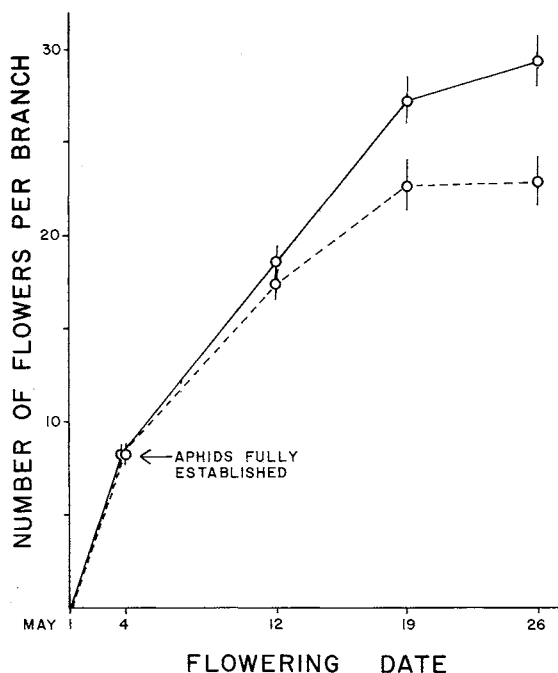
Fig. 1. Effects of aphids on the total number of flowers per inflorescence. Branches without aphids (solid line) had significantly more flowers and fruits than those with aphids (dashed line; $P < 0.005$; $N = 7$). Means $\pm$SE are shown for 7 plants, using the mean of 4 inflorescences for each plant.
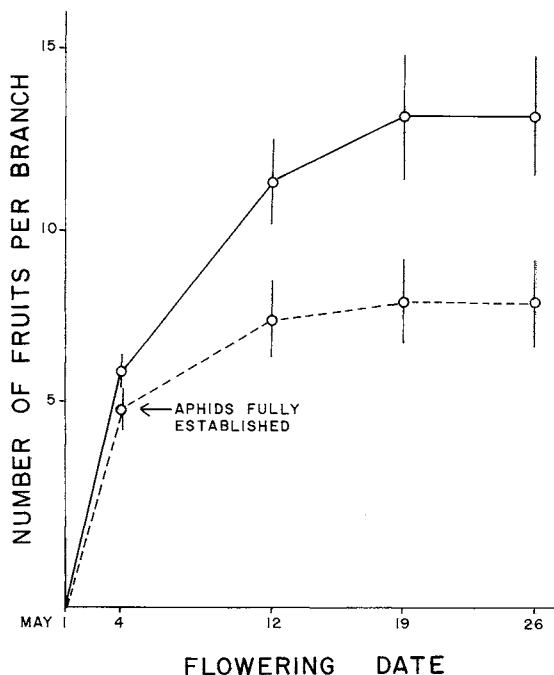
Fig. 2. Effects of aphids on the total number of fruits. Branches without aphids (solid line) had significantly more flowers and fruits than those with aphids (dashed line; $P < 0.005$; $N = 7$). Means $\pm$SE are shown for 7 plants, using the mean of 4 inflorescences for each plant.

(Table 1). Individuals were statistically homogeneous in their response to aphid herbivory ($P < 0.08$).

Aphid feeding had no effect on the number of seeds per fruit (Wilcoxon's signed rank test; both treatments averaged about 3 seeds per fruit). Seed set data were also analyzed using the General Linear Model procedure of SAS (Freund and Little, 1981), but even when variation due to maternal plant and flowering date was accounted for, aphid effects were not significant.

DISCUSSION—Naturally occurring aphid herbivores can significantly reduce the fecundity of wild radish. Aphid feeding limited female reproductive success by reducing flower and fruit production. Male-based reproduction probably suffered also because few flowers were available to act as pollen-donating organs, and pollen from these flowers was less likely to sire seeds. Models of sexual reproduction in plants often assume that paternal success will increase with pollen and/or flower production (Lloyd, 1984). There are few data to support this seemingly reasonable assumption, but Schoen and Stewart (1986) showed that paternal success in white spruce increased with production of male cones. Because wild radish is an outcrossing annual, we expect that decreases in flower production strongly influence both male and female fitness of plants subjected to different levels of infestation.

The plant-to-plant variation in aphid attack seen in this study can be attributed to several factors. First, individuals flowering before aphid populations reached their peak escaped the brunt of feeding that occurred later. Second, susceptibility to aphid colonization varied among synchronously blooming neighbors, as we could not establish colonies on three out of ten late-blooming plants. Resistance to aphids could be due to environmental and/or genetic factors (Maddox and Cappucino, 1986). To the extent that variation in flowering time and resistance have a genetic basis (e.g., Harper, 1964; Murfet, 1977; McIntyre and Best, 1978), and if these traits are additively controlled (Eenink, Dieleman, and Groenwold; 1982), herbivores could act as a strong selective agent in natural populations. For example, in wild parsnip early-flowering genotypes experienced less herbivory than did late-flowering genotypes (Berenbaum, Zangeri, and Nitao, 1986). Schemske (1984) showed that seed predation within for-

TABLE 1. *Effect of aphids on fruit set of individual plants*[a]

Plant number	Aphids removed		Aphids present	
	Proportion set	(Number of flowers)	Proportion set	(Number of flowers)
1	0.33	(70)	0.02	(43)
2	0.23	(88)	0.07	(59)
4	0.60	(105)	0.41	(68)
5	0.36	(77)	0.19	(64)
7	0.28	(74)	0.13	(66)
8	0.26	(86)	0.24	(41)
9	0.20	(89)	0.19	(70)
Total	0.33	(589)	0.19	(411)

Source	df	χ square	P
Individual plant	6	65.24	0.0001
Aphid treatment	1	23.19	0.0001
Plant × treatment	6	11.26	0.081

[a] Frequencies of fruit set after 4 May were analyzed using the log-linear method in the CATMOD procedure of SAS in a 7 × 2 × 2 design. Plants #3, 6, and 10 were not included in this analysis because aphids could not be established on them.

est habitats selected for earlier flowering ecotypes of *Impatiens pallida.* Flowering time has been shown to be under additive genetic control in another radish species, *Raphanus raphanistrum* (Mazer, 1987), which is closely related to *R. sativus* (Panetsos and Baker, 1967). Genetically distinct families of *R. sativus,* also vary in phenology (M. Stanton and H. Young, unpublished). We suggest that selective pressures due to both climatic constraints and herbivores may influence the optimum flowering time for wild radish.

In this study, effects of aphids were demonstrated experimentally by removing aphids from a random subset of branches on infested plants. One problem with having two different herbivory treatments on the same plant is that resource-sharing among branches could confound our results. (As described earlier, it was impossible to apply treatments to separate plants.) If branches with aphids used more energy and nutrients than uninfested branches, we may have *under*estimated the impact of aphids. We suspect that even greater effects might be seen if aphids were removed from entire plants, which would presumably be healthier as a result. On the other hand, if aphid feeding caused unused resources to be allocated to uninfested shoots, the effect of aphids was *over*estimated. This could occur if aphids did not constitute a strong metabolic sink, or if feeding impaired normal meristem development through hormonal or other effects. Unfortunately, the relative amount of resources used by aphids and uninfested shoots is not known. In many species, however, aphid feed-

ing represents a major sink, depriving other parts of the plant of resources (Kennedy and Stroyan, 1959). We saw no evidence of mechanical damage (e.g., necrosis) at aphid feeding sites, but possible effects on morphogenesis cannot be ruled out. In summary, we think it is unlikely that resources were redirected from branches attacked by aphids to those without them.

Morrow and LaMarche (1978) used a similar experimental design to show that chronic herbivory depressed growth in subalpine *Eucalyptus* trees. They compared growth of branches that were sprayed with insecticide with the growth of unsprayed branches on the same trees. Sprayed branches grew faster than unsprayed ones, and both showed much better growth than branches of untreated trees. Two conclusions were drawn. First, sprayed branches exported photosynthate to other parts of the tree, improving subsequent growth of branches that were exposed to herbivores. Second, since the average growth of sprayed and unsprayed branches combined was significantly greater than growth of untreated trees, the damaging effect of herbivores was not simply an artifact of using branches rather than individuals as experimental units. Within-plant comparisons *under*estimated the impact of phytophagous insects. Whenever possible, future investigators should assign different treatments to different individuals to avoid uncertainty about the role of resource-sharing among branches.

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