Influence of plant phenology on the insect herbivore/bittercress interaction

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Summary. We tested the hypothesis that generally higher levels of herbivory on bittercress in sun vs in shade, especially by leaf miners, were related to the earlier phenological development of plants in the sun. Naturally-occurring plants in the sun were taller and had longer leaves than did those in the shade during the first three weeks of the growing season, which corresponded with the timing of adult fly oviposition. We divided individual bittercress plants from the sun into three parts: one part was transplanted into willow shade immediately after snow melt; the other two parts were replanted in the sun and one of these was sprayed with insecticide. The transplant experiment had two primary results. First, bittercress transplanted into the shade suffered significantly higher levels of insect damage than either treatment in the sun. Leaf-mining in the shade also increased and equalled that observed in the sun. These results strongly support the phenology hypothesis; higher damage in the sun is due, at least in part, to the earlier development of plants in sun vs in shade early in the season. Second, the ramets with the greatest damage, e.g. the shade treatment, initiated significantly fewer rosettes than did ramets in the other two treatments. The decrease in vegetative reproduction may have been due to the direct effects of increased insect herbivory on these shade plants. This result is particularly interesting because so little information is available on below-ground, vegetative reproductive response to chronic, above-ground foliage loss to native herbs caused by insect herbivores.

Key words: *Cardamine cordifolia* – Cruciferae – Herbivory – Insect-plant interactions – Phenology

The timing of plant emergence, development and reproduction, both within and between growing seasons may significantly alter the vulnerability of plants to herbivore damage (Feeny 1970; Thompson and Price 1977; Faeth et al. 1981; Solomon 1981; Lowman 1985; Thompson and Moody 1985). For example, small shifts in age and size at sexual reproduction between two populations of umbels resulted in differential probability of lifetime attack by insect herbi-

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vores (Thompson and Moody 1985). Consistent spatial patterns of herbivore damage may reflect habitat-related variation in temporal correspondence between insect and plant development. If these patterns of damage persist over time, significant implications may exist for the distribution and abundance of the plant in subsequent generations (Louda 1982a, b; 1988).

In the relatively harsh, high elevation montane habitat, both plants and insects must respond to the constraints of a short, variable growing season. Emergence, growth, and reproductive development must begin early enough in the season to allow time for completion of the life cycle, but late enough to avoid mortality caused by possible late June snows. In such habitats, snow melt often sets the timing for the season, and at our study site in the Rocky Mountains, snow melts earlier in the growing season in sun-exposed areas than under willow shade. Bittercress plants, *Cardamine cordifolia* A. Gray (Cruciferae), in the sun thus emerge earlier than do those in willow shaded areas (Louda, unpub. data). The early part of the growing season also corresponds to the period in which ovipositing females of a principal herbivore, the leaf miner *Scaptomyza nigrita* Wheeler (Diptera: Drosophilidae) are active and are searching for oviposition sites (Collinge and Louda 1989). Previous studies (Louda and Rodman 1983a, b; Collinge and Louda 1988a) have shown that overall levels of herbivory on bittercress during the growing season are significantly greater on plants in sun-exposed areas than on plants in willow shaded areas. The temporal link between early availability of host plants in sun-exposed areas (as compared to shade) and herbivore activity, especially ovipositing flies, may be a major factor influencing the susceptibility of sun-exposed bittercress plants to attack by herbivores. We conducted this study to assess the contribution of accelerated development of *C. cordifolia* (Bittercress) in sun-exposed versus in adjacent willow-shaded habitats to differentially high levels of herbivory in the sun, especially by the leaf miner *S. nigrita*.

Methods

Study area and study organisms

We conducted the study in 1986 at the Rocky Mountain Biological Laboratory in Gothic, Colorado; 9.6 km northwest of Crested Butte, Gunnison County (38°57′56″ N,

106°59′12″ W). The vegetation in this area is typically montane and has been described in detail (Langenheim 1955, 1962). The specific study site was a large (30 × 10 m), persistent, snow melt seep in the beaver pond area below Avery Peak, located 3 km northwest of Gothic on Forest Service Trail 401, Gunnison National Forest (2985 m; Site 2 of Collinge and Louda 1988a, 1989). This site contains an exceptionally dense (355 stems/m^2) stand of bittercress.

Cardamine cordifolia is a herbaceous perennial crucifer found throughout the Rocky Mountains, from Wyoming to Idaho, south to New Mexico and Arizona (Harrington 1954). It is very common in moist and shaded areas in our study region (pers. obs.). If the soil is wet enough, bittercress can grow in the sun as well as in the shade of willows, *Salix* spp., or spruce, *Picea engelmanni* (Chew 1977; Louda and Rodman 1983a, b). These plants typically begin flowering in late June and set seed in August or early September (Louda and Rodman 1983a). Bittercress plants also reproduce vegetatively by rosettes of basal leaves that develop from rhizomes. Large clones average about 50 ramets (pers. obs.).

In our study region, over 25 invertebrate herbivores utilize the leaves of bittercress to some extent (Louda 1988, unpub. data). The dominant insects at our site were the leaf miner *S. nigrita*, *Phaedon* sp. nr. *oviformis* (Chrysomelidae), and *Aphalara* sp. nov. (Psyllidae). The leaf miner, *S. nigrita* is one of the most abundant insect herbivores on bittercress (Louda, unpub. data). The life history of this species (Collinge and Louda 1989) can be summarized as follows. Adult female flies oviposit on bittercress leaves in late May to early June, immediately after snow melt. The larvae begin feeding in early to mid-June, forming a linear mine. After 3–4 weeks, pupation occurs, usually within the leaf mine. Adults generally emerge nine days later ($\bar{x} = 9.2$, range = 6–15).

Phenology

In order to document seasonal development of bittercress plants in sun and in shade, we measured several plant growth parameters of naturally occurring (unmanipulated) bittercress plants ($N = 15$/habitat/date) in sun and in willow shade at approximately three-week intervals throughout the growing season (5 and 23 June, 15 July, and 4 August 1986). Variables recorded were stem height; length of the mid-stem leaf; and number of buds, flowers and pods (sum = sexual reproductive output). We also recorded the number of leaves per stem which had been attacked by leaf miners (Collinge and Louda 1988a).

Experimental procedures

In order to test the hypothesis that the use of bittercress plants by herbivorous insects, especially by *S. nigrita*, depends significantly upon the early season development of the plant, we transplanted clonal material of bittercress from the sun-exposed area into the shaded area immediately after snow melt, 26–28 May 1986. At this time, the plants in the sun were small (5–10 cm tall) and free of insect damage. Bittercress plants in the shade were less developed than those in the sun ($\cong 1$–3 cm tall). Our experimental design was a randomized complete block with location at the site as the blocking criterion.

Single clones from the sun-exposed area were divided into thirds. Each third was planted into a four-inch peat pot filled with soil from the site. Each pot was assigned randomly to one of three treatments: (I) transplanted under adjacent willows, (II) replanted in the sun-exposed area and sprayed weekly with insecticide, and (III) replanted into the same area (control). Four clones were used for each block, and there were eight blocks. The plants were watered initially to encourage establishment. Plants remained in pots throughout the course of the experiment.

The insecticide treatment was included as a control to evaluate the impact of insect feeding on growth and reproduction of bittercress. Plants in the insecticide treatment were sprayed with Lindane ("leaf miner killer": Ortho®) dissolved in 1.5 L water (recommended rate) at weekly intervals from 31 May–6 August. Lindane is a non-systemic insecticide which does not contain nitrogen, and so should not act as a fertilizer to accelerate plant growth. Plants in the willow shade and sun control treatment were sprayed with water at the same intervals.

To determine the light intensities in sun-exposed and willow shaded areas, measurements of photosynthetically active radiation (PAR) were taken at mid-stem of bittercress plants in each treatment (5 June, 23 June) using a PAR sensor (Li-Cor 190S).

We recorded plant growth and insect damage in each pot on four dates during the summer (30 May, 19 June, 15 July, 6 August). Plant variables measured were: stem height; inflorescence height; number of buds, flowers and pods (sum = sexual reproductive output); and number of basal and cauline leaves. We counted the number of rosettes in each pot as an estimate of vegetative reproduction. We also estimated leaf senescence by recording any yellow or dead leaves present. Total insect damage (including leaf-mining) and specific damage by leaf miners were recorded as the area damaged (or mined) per leaf, estimated by comparison with a mm^2 grid (e.g. Louda 1984).

Statistical analyses

PAR measurements in the three treatments were compared using one-way ANOVA. Plant growth and insect damage were analyzed on each sampling date using one-way ANOVA. In addition, repeated measures ANOVA was used to analyze the treatment*date interactions (Winer 1971). Orthogonal contrasts compared the mean PAR, mean total area damaged and the mean area mined of the two sun treatments to the shade treatment, and tested for any differences between the sun treatments.

Results

Unmanipulated plants

Naturally-occurring bittercress plants in the sun were taller and had longer leaves than those in the shade for approximately the first three weeks of the growing season (Fig. 1A, B). However, by late June, plants in the willow-shaded areas had surpassed the sun plants in both height and mid-stem leaf length (Fig. 1A, B). Bittercress plants in the sun had a greater than ten-fold increase in the number of mined leaves per stem than did those in the willow shade on 23 June ($[\bar{x} + SE]$ 6.2 ± 0.34 leaves vs 0.3 ± 0.21 leaves, Collinge and Louda 1988a).
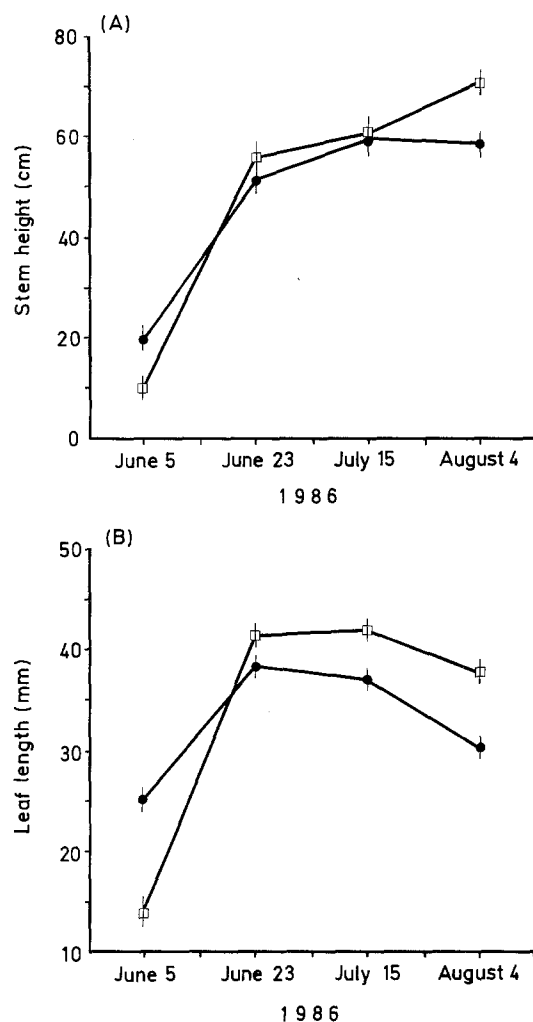
Fig. 1. A Stem height (cm) of unmanipulated bittercress plants in sun and in willow shade over the course of the 1986 growing season. The means were significantly different at the beginning of the growing season (5 June, $F_{1,28} = 29.85$, $P < 0.001$) and near the end of the growing season (4 August, $F_{1,28} = 27.80$, $P < 0.001$). Stem height increased at different rates in sun and shade (repeated measures ANOVA, trt*date interaction, $F_{3,112} = 8.372$, $P < 0.001$). Vertical lines represent standard errors. B Length of mid-stem leaf (mm) of unmanipulated bittercress plants in sun and in willow shade over the course of the 1986 growing season. The means were significantly different at the beginning of the growing season (5 June, $F_{1,27} = 28.92$, $P < 0.001$) and approached statistical significance near the end of the growing season (4 August, $F_{1,20} = 4.041$, $P = 0.058$). Leaf length increased at different rates in sun and shade (repeated measures ANOVA, trt*date interaction, $F_{3,101} = 9.552$, $P < 0.001$). Vertical lines represent standard errors. ● sun; □ shade

Fig. 2. A Leaf area damaged (LAD) (mm^2) per leaf on bittercress sun clones transplanted under adjacent willows (shade), replanted in the sun and sprayed weekly with insecticide (sun/ins.), and replanted in the sun as a control (sun), over the course of the 1986 growing season. The means were significantly different at the conclusion of the experiment (6 August, orthogonal contrasts: both sun treatments vs shade, $F_{1,1577} = 34.63$, $P < 0.001$, sun/insecticide vs sun control, $F_{1,1577} = 5.29$, $P < 0.05$. Damage accumulated significantly more rapidly on the shade transplants (repeated measures ANOVA, trt*date interaction, $F_{6,5447} = 14.92$, $P < 0.001$). Vertical lines are standard error bars. B Leaf area mined (LAM) (mm^2) per leaf on bittercress sun clones transplanted under adjacent willows (shade), replanted in the sun and sprayed weekly with insecticide (sun/ins.), and replanted in the sun as a control (sun), over the course of the 1986 growing season. The sun treatments were not statistically different from the shade treatment at the conclusion of the experiment (6 August, orthogonal contrasts: both sun treatments vs shade, $F_{1,1577} = 1.77$, $P > 0.15$); the sun treatment was slightly higher than the sun/insecticide treatment (orthogonal contrast sun/insecticide vs sun control, $F_{1,1577} = 3.02$, $P = 0.08$). Leaf-mining damage accumulated similarly over the growing season for the three treatments (repeated measures ANOVA, trt*date interaction, $F_{6,5447} = 1.51$, $P > 0.15$). Vertical lines are standard error bars. ● sun/ins; ▲ sun; □ shade

Manipulated plants

Insect damage was significantly higher in the shade transplants than in either of the sun treatments by the end of the experiment (Fig. 2 A, B). Plants sprayed with insecticide had the least amount of damage, as expected. Damage was approximately equal in the three areas until late June, when it accumulated much more rapidly on the shaded leaves (Fig. 2). Leaf area mined was not significantly different for the three treatments, although the insecticide-treated plants had the least amount of damage, as expected (Fig. 2B).

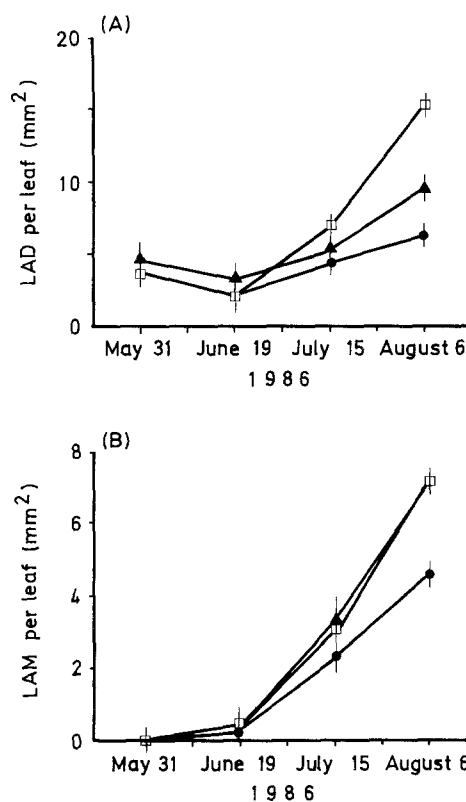PAR intensities were approximately equal in the two

sun treatments on 5 June, before the willows had leafed out, while the shade treatment was similar but somewhat lower ([$\bar{x} \pm SE$] sun/insecticide = 1068.9 ± 54.77, sun = 1049.4 ± 67.40, shade = 966.5 ± 75.01 $\mu E/m^2/sec$, $N = 16/$ treatment. By 23 June, the willow leaves had developed, significantly reducing the light reaching bittercress plants ([$\bar{x} + SE$] sun/insecticide = 1748.7 ± 63.81, sun = 1711.1 ± 105.14, shade = 525.2 ± 147.98 $\mu E/m^2/sec$; both sun vs shade $F_{1,38} = 76.8$, $p < 0.01$, $N = 16/$treatment). The large increase in PAR in the sun between 5 and 23 June reflected the fact that 5 June was overcast, whereas 23 June was clear.

Table 1. Growth and reproductive characteristics of clonal ramets of bittercress in sun + insecticide, sun control, and shade treatments at the conclusion of the transplant experiment (6 August 1986)

	Sun +Insecticide			Sun Control			Shade		
	$\bar{x}$	SE	(N)	$\bar{x}$	SE	(N)	$\bar{x}$	SE	(N)
Morphological Traits									
Stem Height (cm)	20.2	1.57	(28)	21.9	1.97	(25)	22.8	2.07	(30)
Cauline Leaves (no)	11.0	0.81	(30)	10.4	0.70	(25)	10.1	0.74	(32)
Leaf Length	14.4	0.29	(580)	13.4	0.30	(590)	18.6	0.38	(417)*
Reproductive Traits									
Repro. output[a]	2.3	0.90	(24)	3.6	1.35	(14)	3.8	1.23	(21)
Rosettes (no/plant)	2.9	0.40	(31)	3.4	0.49	(29)	1.5	0.37	(34)*

$* = P < 0.05$, orthogonal contrast, both sun treatments vs shade
[a] Sexual reproductive output = number of flower buds + flowers initiated + siliques (fruits) matured per ramet

Bittercress transplanted from sun into shaded areas had significantly longer leaves, but had initiated fewer rosettes than the two sun treatments by the conclusion of the experiment (Table 1). All other growth characteristics measured were not significantly different for the three treatments (Table 1). Leaf senescence was highest in the shade plants (% of leaves senesced [total N]: sun/insecticide [676] = 13.9, sun [678] = 12.8, shade [497] = 15.4). Transplanting slowed growth in all three treatments. Plants were approximately half as tall, and had leaves half as long, as adjacent naturally-occurring bittercress plants (Table 1 vs. Fig. 1 A, B).

Discussion

Unmanipulated bittercress plants in the sun-exposed areas clearly initiated development earlier than plants in adjacent willow-shaded areas (Fig. 1A, B). Sun plants maintained this size differential for about three weeks into the growing season, after which willow-shaded plants were taller and had slightly larger leaves (Fig. 1A, B). Unmanipulated sun plants also suffered significantly higher levels of leaf-mining damage than did those in adjacent willow shade (Collinge and Louda 1988a). These patterns suggest that under natural conditions, shade plants are able to temporally "escape" oviposition by adult flies and thus suffer much less leaf-mining damage.

The transplant experiment had two primary results. First, clonal material from sun plants, when transplanted into the willow shade, had significantly increased levels of damage by all insect herbivores, compared to the sun control treatment (Fig. 2A). In addition, leaf-mining damage was augmented in the shade and, consequently, it equalled that on the control sun leaves (Fig. 2B). This is in direct contrast to the usually observed pattern in this system of significantly higher levels of overall damage and leaf-mining in the sun (Louda and Rodman 1983a, b; Louda 1988; Collinge and Louda 1988a, b, 1989). These results, equal leaf miner damage and higher overall levels of herbivory in the shade, thus support the hypothesis that early season

plant phenology is one of the critical factors affecting the natural pattern of higher insect damage, especially leaf mining damage, in sun-exposed versus willow-shaded bittercress.

In the transplant experiment, ramets from sun plants transplanted early in the season into adjacent shade and those replanted into the sun were equally damaged by the leaf-mining fly (Fig. 2B). Since the leaf miners are endophagous, the larval feeding site is determined by the ovipositing female, and females normally prefer to oviposit on plants in the sun (Collinge and Louda 1988a). The results of this transplant experiment suggest that *S. nigrita* female preference for plants in the sun is due, at least in part, to their advanced phenological stage.

Damage by the rest of the herbivore guild was highest on sun plants transplanted into shade. In fact, finding the highest levels in the shade was quite unexpected. This outcome suggests three hypotheses. The first hypothesis is that phenology contributes to plant vulnerability. The leaf miner data lend support to this hypothesis. The second hypothesis is that sun genotypes are more susceptible to damage by insects than are shade genotypes. Third, insect herbivores feeding on shade-transplanted bittercress may have had accelerated development relative to those feeding on sun plants because of higher leaf quality, and thus produced more feeding damage. Naturally-occurring bittercress in the shade had higher leaf total nitrogen concentrations than did sun plants at this study site (see Collinge and Louda 1988a). Sun plants transplanted into shade may have responded physiologically to the low light conditions, resembling typical shade plants. Leaf length of the shade transplants was significantly higher than the sun plants by the conclusion of the experiment (Table 1), which parallels the pattern found in naturally-occurring plants.

Feeny (1970) found that the timing of winter moth emergence and feeding was closely related to oak leaf phenology and quality. MacGarvin et al. (1987) also demonstrated that plant phenology played a role in the occurrence of a subset of insects on bracken. In contrast, Faeth et al. (1981) suggested that plant phenology was "inconsequential" compared to other factors affecting the distribution of leaf miners on oaks.

Our results have major implications for the interpretation of plant-insect herbivore dynamics under naturally-occurring conditions. Specifically, they provide clearcut experimental evidence for a major mechanism distributing insect consumption consistently and differentially among plants in adjacent microhabitats. The selective impact of such a pattern within a population is clear, especially if genetic differences exist between sun and shade plants (Louda 1988; Vescio and Louda, in prep.). In addition, such sun-shade differences in oviposition and damage by insect herbivores are extremely common (e.g. Burgess 1977, Rausher 1979, Faeth et al. 1981, Maiorana 1981, Risch 1981, Coley 1983, Williams 1983, Louda and Rodman 1983a, b, Lincoln and Mooney 1984, Lowman 1985, Louda 1988, Louda et al. 1987a, b). For example, losses differed significantly between sun and shade for 7 of 13 native species examined across the natural sun-shade meadow-to-aspen woodland transition in our study region (Louda et al. 1987a). We also propose that phenological differences among plants may be generally important (e.g. Feeny 1970, Thompson and Price 1977, MacGarvin et al. 1987, but see Faeth et al. 1981), and thus merit further examination in

the analysis of plant-herbivore interactions within native plant communities.

Our second primary result was that increased damage by insects on bittercress in the shade was accompanied by a negative effect on vegetative reproduction. Fewer rosette shoots were initiated from rhizomes by the more heavily damaged ramets of the clone, i.e. those transplanted into the shade (Table 1). The reduced vegetative growth may have been due to the direct effects of shade on rosette production, the direct effects of increased herbivore damage on rosette production, or an interaction of these two factors. The relative contribution of these two factors could be evaluated by an additional experimental treatment: sun plants transplanted into the shade and sprayed with insecticide. The result is particularly interesting since so little information is available on below-ground, vegetative reproductive response by native perennial forbs to chronic, above-ground foliage loss by adapted insects.

Our data on the impact of herbivory on plant below-ground growth complement and contrast with the information available from crops. Comparable data exist for several crucifers that are cultivated as root crops. Root tuber yields of both radish and turnips, for example, were decreased by insect herbivory (Taylor and Bardner 1968). Data also exist for a noncruciferous root crop, potatoes; in this case, severe levels of defoliation led to decreases in tuber weight (Cranshaw and Radcliff 1980). Thus, our data for a native plant are consistent with those from related crop plants. However, since contradictory data exist, further work on the effect of insect foliage consumption on plant allocation patterns is warranted, especially for native plants under natural conditions.

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