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Scaptomyza nigrita Wheeler (Diptera: Drosophilidae), a Leaf Miner of the Native Crucifer, *Cardamine cordifolia* A. Gray (Bittercress)

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ABSTRACT: The biology of *Scaptomyza nigrita* on its host plant, a native crucifer (Bittercress) in the Rocky Mountains, is described. Development of each stage in the life history was studied both in the field and in the laboratory. This is the first documentation of a host for *S. nigrita*. We examined the activity of adult flies in two adjacent habitats, sun and adjacent willow shade. Adult flies were more abundant on bittercress plants in sun-exposed versus in shaded areas, and were most active from mid-day to late afternoon. Female flies were significantly larger than male flies, but there were no differences in size of adults between the two habitats. Larval damage to bittercress is generally much greater on plants in sunny areas than on those in the shade, possibly due to the increased activity of ovipositing flies in sun-exposed areas.

Spatial variation in damage by insect herbivores is common, both within host plant patches (Harcourt, 1961; Jones, 1977; Thompson, 1978; Free and Williams, 1978, 1979; Courtney and Courtney, 1982; Collinge and Louda, 1988a) and among patches (Janzen, 1975a, b, c; Stanton, 1975; Whitham, 1978, 1980; Parker and Root, 1981; Faeth et al., 1981; Louda and Rodman, 1983a, b). If this variation is consistent and repeated over time, with certain plants generally suffering higher levels of herbivore damage than others, then there are potentially significant implications for the population dynamics of both the insect herbivore (Janzen, 1975a, b, c) and the host plant (Louda, 1982a, b, 1988).

Larval *Scaptomyza nigrita* Wheeler (Diptera: Drosophilidae) intensively mine the leaves of *Cardamine cordifolia* A. Gray (Bittercress, Cruciferae) at study sites near Rocky Mountain Biological Laboratory in west-central Colorado. In this interaction, and for insect herbivory on bittercress in general, there is a characteristic spatial pattern of feeding damage. Plants in the sun are generally much more heavily damaged by chewing and mining insects than are those in the adjacent willow shade (Louda and Rodman, 1983a, b; Collinge and Louda, 1988a; Louda, 1988).

Since leaf miners are endophagous, the choice of oviposition site by the adult female will largely determine where the larvae feed. Most larvae remain on the same plant throughout development, although some late instar larvae migrate up the stem to mine new leaves (Hering, 1951; Collinge, pers. obs.). Consequently, we examined the patterns of adult fly activity and fly abundance in sun-exposed and shaded habitats. We censused and conducted field observations on each life

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history stage of *Scaptomyza nigrita*. In addition, we reared *S. nigrita* from bittercress leaves in the laboratory from the egg to the adult stage, providing the first definitive evidence on host plant relations for this species. Here we present our field and laboratory observations on the life history of this leaf-mining drosophilid, as well as its distribution on and damage to bittercress within and between habitats.

Materials and Methods

STUDY SITES: Our research was conducted in 1985 and 1986 at Rocky Mountain Biological Laboratory, 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 montane and typical for the region (Langenheim, 1955, 1962). We used two specific study sites: Site 1 is at 3040 m, 1.2 km north of Gothic along Copper Creek ("Main Site" of Louda and Rodman, 1983a, b). Site 2, located at 2985 m, is 3 km west of Gothic on Forest Service Trail 401 ("ABP" of Collinge and Louda, 1988a, b, 1989). Both sites were large (30 × 10 m) snow melt seeps with dense stands of bittercress in and around them. Density at Site 2 was 355 stems/m^2. Plant density was not measured at Site 1, however visually it was similar to Site 2. The laboratory portions of the research were completed at Rocky Mountain Biological Laboratory.

LEAF MINER: *Scaptomyza nigrita* Wheeler was first described in 1952 from "several hundred" specimens caught in Pasadena, California (Wheeler, 1952). The flies were collected from a lawn containing grass and clover, and Wheeler believed that the host plant was clover. However, no larvae or mines were found, and he was unable to successfully rear any flies in the laboratory (Wheeler, 1952). In addition, "a few" specimens of *S. nigrita* were found in Wyoming, and in the mountains near Malad, Idaho (Wheeler, 1952). Later, the known distribution was extended by identification of these flies in collections from Alaska and Canada (Wheeler and Takada, 1966).

HOST PLANT: *Cardamine cordifolia* A. Gray (Bittercress) is a native, herbaceous perennial crucifer that grows in wet, often shaded areas along streams from Wyoming to Idaho, south to New Mexico and Arizona (Harrington, 1954). Bittercress is very common in moist and shaded areas in our study region. 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* Parry (Chew, 1977; Louda and Rodman, 1983a, b). In this study, sun and adjacent shade represent habitat treatments at each field site.

PROCEDURES: We estimated relative adult fly densities in the field by using ten-minute observations on patches of bittercress (≅50 ramets) at Site 2. Observations were conducted in both sun-exposed and adjacent willow-shaded habitats (≅15 m apart) between 26–28 May 1986 (n = 6/habitat). On 15 June 1986 we followed the daily activity pattern of adult flies in both open sun and willow shade. In this case, 5 minute observations were conducted every 2 hours from 0730–2030 on a patch of bittercress in each habitat. In addition, adults were collected in traps at both sites during the peak oviposition period in early June 1986. Yellow paper rectangles (6.5 × 11.5 cm) were spread with Tangletrap® (Jones et al., 1986) and placed horizontally on a wire stake at 35 cm above the ground. Stakes with sticky traps were placed immediately adjacent to ramets of bittercress and left for 24 hours (n = 5/habitat/date). Habitat densities were sampled twice at Site 1 (4 and

6 June) and three times at Site 2 (3, 5 and 7 June 1986). The sticky traps were returned to the lab and adult drosophilids were counted. Traps were also set out and checked every two hours on 15 June 1986 at Site 2 in conjunction with the observations on the activity pattern.

A subsample (25 females, 7 males) of adult flies collected from the sticky traps in each habitat was examined using a dissecting microscope. We determined the sex of the adults, and for females we measured: thoracic width, as an indication of adult size; number of eggs; and length of eggs. For males we measured only thoracic width. Data from both field sites were pooled for analysis because of small sample sizes.

We collected samples from bittercress plants ($n = 15$ ramets) from both study sites at 3 week intervals throughout both field seasons to quantify larval occurrence and feeding damage. Equal numbers of samples were taken from sun-exposed and adjacent willow-shaded habitats. Ramets were chosen from different plant clones of the same height and reproductive condition in both habitats. Ramets within clones were selected randomly and cut below the lowest leaf. After measuring the leaf area eaten by the leaf miners (see Louda, 1984), we preserved the larvae in 95% ethanol and later measured them using a dissecting microscope.

Bittercress leaves containing leaf miner eggs or larvae were collected from sun-exposed areas at both sites and brought to the laboratory for rearing. Forty leaves were collected in 1985 (between 22 June–9 July) and 79 leaves were collected in 1986 (between 4–18 June). We collected leaves earlier in 1986 to obtain leaves with eggs, but without developed mines. We recorded the number of eggs and larvae on each leaf and the leaf length.

Rearing was accomplished by wrapping cotton around the upper leaf petiole and inserting the petiole and cotton into a two-dram vial filled with water. The vials were placed horizontally in a rack. A rearing chamber was made around the leaf blade by placing a small plastic bag over the leaf, and securing it to the top of the vial with a rubber band. This set-up maintained leaf turgidity and allowed continued larval feeding. As leaves senesced, they were replaced with new leaves and the larvae were transferred manually. Transfer did not harm larvae since soon after being placed on new leaves, the larvae formed new leaf mines.

Upon pupation in the leaf mine, each pupa was moved to a 5 cm diameter covered petri dish containing a piece of moist filter paper and a fresh bittercress leaf. The filter paper was kept moist until the adults emerged (about 9 days later).

STATISTICAL ANALYSES: Relative densities of adults in sun and shade habitats, as well as adult sizes and numbers of eggs in females, were analyzed using Student's t-test. The diurnal pattern of adult fly activity in sun and shade was compared using the non-parametric Sign Test (Campbell, 1974). The relationship between the number of individuals per leaf and leaf length was determined using Pearson's product-moment correlation.

Results and Discussion

ADULTS: Adult flies were at least twice as frequent on plants sampled in sun-exposed areas than on plants in willow shade (Table 1A). This pattern was consistent between sites (Table 1A). Adults were most active from midday to late afternoon in mid-June (Table 1B). The observations can be divided into three periods: early morning (0730–1130), midday (1130–1530) and late afternoon

Table 1. Number of adult *Scaptomyza nigrita* observed in timed observations on bittercress and caught in sticky traps in the sunny habitat and in the adjacent shaded habitat.

	A. Habitat activity pattern (1986)					
	Observation[a]		Traps[b]			
	Site 2 (26–28 May)		Site 1 (2–7 June)		Site 2 (2–7 June)	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Sun	4.2	1.23	5.4	1.32	1.4	0.31
Shade	0.7	0.21	2.4	0.53	0.1	0.06
	*		*		*	

	B. Diurnal activity pattern (Site 2: 15 June 1986)[c]			
	Observation		Traps	
	Sun	Shade	Sun	Shade
Time (hr)				
0730	3	1	—	—
0930	2	7	0	0
1130	6	5	1	1
1330	10	4	5	0
1530	5	2	0	0
1730	10	6	0	2
1930	9	6	1	0
2030	6	2	0	0
Totals	51	33**	7	3

[a] Ten minute observations, $n = 6$/habitat.
[b] $n = 10$/habitat at Site 1; $n = 15$/habitat at Site 2.
[c] Five minute observations: $n = 1$/habitat, traps: $n = 5$/habitat.
* $P < 0.05$, t-test with unequal variances.
** $R = 1.0$, $P < 0.05$, sign test.

(1730–2030). The total number of active flies of both sexes increased from early morning to late afternoon: 24, 32 and 39, respectively (25.0%, 33.7%, 41.1%).

The adults were usually seen on the top half of bittercress stems, crawling on both the upper and lower leaf surfaces and often pausing on the edges. Females often stopped to puncture the leaf surface with their ovipositor, and then turned around and appeared to sample the punctured area with their proboscis. Dissected adults had green plant material in their digestive tracts, suggesting that they were feeding, assessing plant quality for oviposition sites, or both. During the course of these observations, we observed both mating and oviposition.

In early season, adult females were carrying eggs and were observed ovipositing on the adaxial surfaces of lower to mid-stem leaves (Collinge and Louda, 1988a). *Scaptomyza nigrita* eggs were found on bittercress leaves in the field only during the early part of the short growing season. Females trapped in the sun contained slightly more eggs than did those in shade (Table 2; $t = 1.71$, d.f. = 23, $P > 0.05$), but these data were highly variable. The mean number of eggs per female decreased from June 3 to June 7 at both study sites: from 11.8 to 3.0 at Site 1, and from 11.6 to 4.0 at Site 2, suggesting that eggs were being deposited and that the primary oviposition period is very early in June.

Adult females averaged 26% larger than males (Table 2; $t = 2.03$, d.f. = 19, P

Table 2. Adult size and number of eggs per female dissected from field-captured *Scaptomyza nigrita*. Adults were obtained from sticky traps set at both study sites between 2–7 June 1986; (*n*) = number of specimens dissected.

	Females				Males			
	Sun		Shade		Sun		Shade	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Thoracic width (mm)*	0.89	0.07 (11)	0.80	0.17 (3)	0.66	0.17 (3)	0.65	0.05 (4)
Number of eggs**	7.9	1.21 (17)	4.6	0.94 (8)	—	—	—	—

* $P < 0.05$, *t*-test with unequal variances, females vs. males.
** $P < 0.05$, *t*-test with unequal variances, sun vs. shade.

= 0.06; sun and shade combined). Females caught in sun-exposed areas appeared slightly, but not significantly, larger than those in shade (Table 2; $t = 0.56$, d.f. = 12, $P > 0.50$). There were no differences in male size between the two habitats (Table 2; $t = 0.10$, d.f. = 5, $P > 0.90$).

EGGS: *Scaptomyza nigrita* eggs were creamy white, ovoid, and were slightly embedded in the tissue of adaxial leaf surfaces. Eggs found in dissected females were very similar in appearance, and averaged 0.24 mm long (SE = 0.01, n = 23). Eggs were concentrated on leaves in the lower half of bittercress ramets (Collinge and Louda, 1988a). Leaves on plants in the sun had more eggs than did those in the shade at Site 1 on the first sampling date (4 June 1986 = 4.1 vs. 1.3 eggs per leaf, ANOVA $P < 0.05$, n = 42, 8) and equal or slightly more eggs than shaded leaves on the second sampling date (17 June 1986 = 2.9 vs. 2.5 eggs per leaf, ANOVA $P > 0.10$, n = 59, 65). At Site 2, sun leaves had equal or slightly more eggs than shade leaves on 5 June 1986 (1.3 vs. 1.0, ANOVA $P > 0.50$, n = 3, 1). No eggs were observed on leaves at later sampling dates at either site. We conclude that egg deposition at Site 2 occurred somewhat later than at Site 1.

The number of eggs per leaf on leaves collected specifically for larval rearing was highly variable ($\bar{x} = 7.7$, SE = 1.14 at Site 1, $\bar{x} = 10.2$, SE = 2.08 at Site 2, range = 1–42). At Site 2 egg number was directly correlated with leaf length (Table 3) but not at Site 1 (Table 3). Since egg deposition appears later at Site 2 and leaf senescence is earlier at Site 2 than at Site 1, there may be significant selective pressure for adults to oviposit first on larger leaves. Presumably, larger leaves will

Table 3. Correlation between number of individuals per leaf and leaf length (mm) at each life history stage on leaves selected for presence of eggs in the first week of June 1986. r = Pearson product-moment correlation, * = $P < 0.05$.

	Leaf length			
	Site 1		Site 2	
	r	P	r	P
Eggs/leaf	−0.11	0.59	0.70	0.002*
Larvae/leaf	−0.05	0.81	0.70	0.002*
Pupae/leaf	0.49	0.02*	0.75	0.001*
Adults/leaf	0.38	0.02*	0.75	0.001*

have a higher probability of having sufficient leaf biomass to support larval development. Of the eggs collected on these leaves, 74% hatched (Table 4).

LARVAE: *Scaptomyza nigrita* larvae form characteristic linear leaf mines soon after hatching. The mine commences from the site of egg deposition as a very thin line, increasing in width as the larva develops and increases in size. Larvae freely cross the veins of bittercress leaves, and eventually their mines merge into large areas containing as many as eight larvae. When the leaf interior has been consumed, larvae often migrate up the stem to intact leaves and form new mines. These "secondary" mines are easily identified and distinguishable from earlier mines because of their large initial size.

As expected, the size distribution of larvae and pupae shifted over the course of the 1986 growing season (Fig. 1). The size distributions over the season suggest that this leaf miner is univoltine at these locations. The frequency of the small size classes of larvae decreased to zero by the end of the season. Because it was not possible to determine the instar of larvae, we estimated larval instar lengths by identifying the modal length frequencies in the measurements. We estimate that three larval instars in this species have the following average larval lengths: 0.95 mm (range = 0.6–1.60), 2.60 mm (range = 1.61–2.70), and 3.25 mm (range = 2.71–4.05).

Larvae reared in the laboratory under ambient conditions completed development in 16 days (Table 4). Larval survivorship in the laboratory was low. This may be due in part to larval "starvation" on crowded leaves, to nutritional changes induced in the leaves by cutting them (Scriber and Slansky, 1981), or to changes in water content in the cut leaves. In the field, either increased movement from crowded leaves or higher mortality on the crowded leaves may help to explain the correlation between the number of larvae per leaf and leaf length, at least for Site 2 (Table 3).

PUPAE: Pupae collected from leaves in the field averaged 3.5 mm in length. In the field, pupation usually occurred in the leaf mines. However, very early in the 1986 season, two pupae were found at the base of a bittercress stem, suggesting that they had overwintered there, possibly in decaying leaves. Interestingly, when these two pupae were reared, two parasitoid wasps (Hymenoptera: Chalcidoidea) emerged instead of adults of *Scaptomyza nigrita.* In late July to early August 1985, four chalcidoid wasps also emerged from pupae of *S. nigrita* in the laboratory. This represents 16% of the pupae reared in 1985.

The number of larvae that pupated per leaf was positively correlated with initial leaf size from both study sites (Table 3), with more larvae pupating on larger leaves. The pupal stage lasted 9 days in the laboratory; 40% of the pupae reared successfully emerged as adults (Table 4). Pupae in petri dishes that became dry did not emerge, suggesting that a moist environment is necessary for pupae to remain viable. Lab survivorship from the egg to the adult stage was twice as high on leaves collected from Site 2 than Site 1 (25.6% versus 13.2%, Table 4). This was not related to any difference in rates of parasitism between the two sites. The number of individuals reaching adulthood was positively correlated with the length of the leaf on which they were collected, with more adults emerging from larger leaves (Table 3).

HOST RELATIONS: *Scaptomyza nigrita* is one of the dominant phytophagous insects on bittercress in the study region. Leaf miner damage to leaves of plants

Table 4. Vital statistics under laboratory-rearing conditions for *Scaptomyza nigrita* eggs on leaves selected for initial presence of eggs in early June 1986: mean number of individuals per leaf, duration, and survivorship (n = 28, 25 at Sites 1 and 2, respectively).

	Number[a]				Proportion surviving (l_x)[a]				Duration of stage (days)			
Source site:	Site 1		Site 2		Site 1		Site 2		Site 1		Site 2	
Trait	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Eggs/leaf	7.7	1.14	10.2	2.08	1.00	0.00	1.00	0.00	5.1	0.36	4.3	0.35
Larvae/leaf	5.3	0.85	6.6	1.09	0.75	0.06	0.74	0.05	16.2	0.95	16.2	0.56
Pupae/leaf	1.9	0.42	3.5	0.64	0.33	0.06	0.47	0.06	9.6	0.75	9.0	1.22
Adults/leaf	0.8	0.27	1.8	0.38	0.13	0.05	0.26	0.05	16.5	0.25	13.6	1.27[b]

[a] l_x was calculated for each leaf individually; then these values were averaged to obtain the mean proportions surviving from the egg stage to each subsequent stage.

[b] Duration of the adult stage is approximate, since adult "breeding chambers" were checked only once a week.

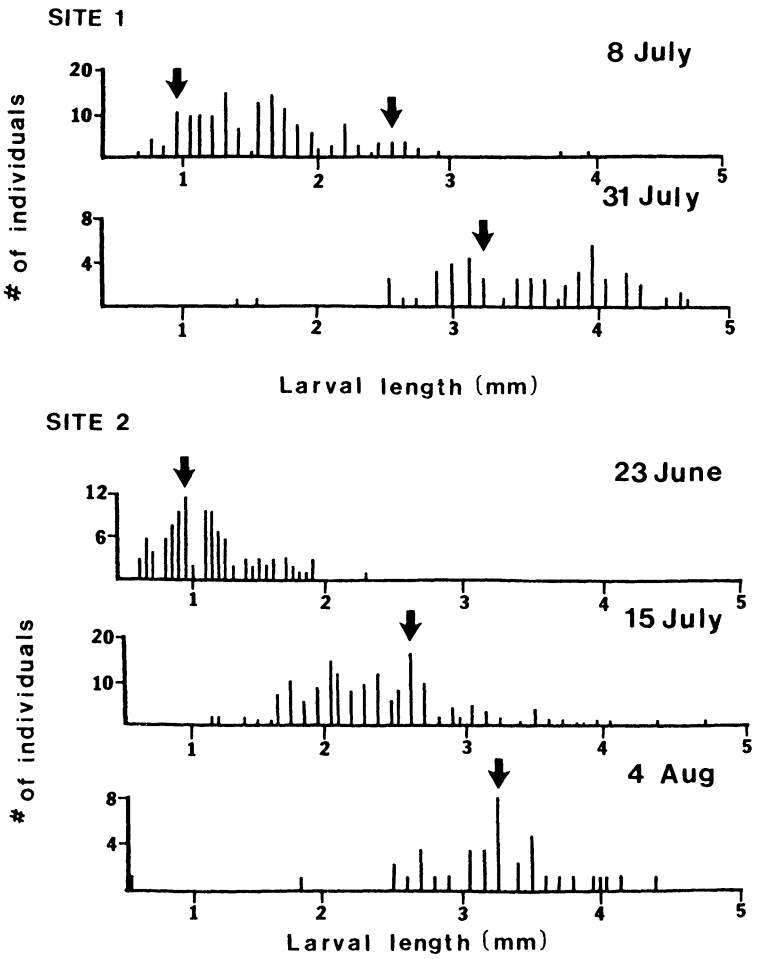

Fig. 1. Frequency distributions of *Scaptomyza nigrita* larval sizes from sun and shade leaves combined at two study sites in 1986. The arrows denote the mean larval length for each of the three estimated larval instars: first instar (length = 0.95 mm), second instar (length = 2.60 mm), third instar (length = 3.25 mm).

in the sun is generally high, on the order of 75% of leaf area removed (Collinge and Louda, 1988a). Large-scale removal of leaf biomass causes early leaf senescence (Louda, 1984) and contributes to reduced vegetative growth of bittercress plants (Louda, 1984; Collinge and Louda, 1989). The available data suggest that adult oviposition choice reflects assessment of leaf quality. Eggs are most abundant on the lowest leaves, and larval damage is distributed primarily on the lower-central leaves of bittercress stems (Collinge and Louda, 1988a). These are the most mature leaves and they contain the lowest above-ground concentrations of mustard oils (Louda and Rodman, 1983a). Use of these leaves enables the larvae to avoid the higher mustard oil concentrations in the young, upper leaves. In a parallel study, leaf-mining damage was also correlated with higher leaf nitrogen concentrations (Collinge and Louda, 1988b). Plant phenology may also be im-

portant (Collinge and Louda, 1989), as the lower leaves are the first available and are present at the time of oviposition.

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Literature Cited

Campbell, R. C. 1974. Statistics for Biologists, 2nd ed. Cambridge University Press, London. 300 pp.

Chew, F. S. 1977. Coevolution of pierid butterflies and their cruciferous food plants. II. The distribution of eggs on potential foodplants. Evolution 31:568–579.

Collinge, S. K., and S. M. Louda. 1988a. Patterns of resource use by a drosophilid (dipteran) leaf miner on a native crucifer. Ann. Entomol. Soc. Am. 81:733–741.

Collinge, S. K., and S. M. Louda. 1988b. Herbivory by leaf miners in response to experimental shading of a native crucifer. Oecologia (Berlin) 75:559–566.

Collinge, S. K., and S. M. Louda. 1989. Influence of plant phenology on the insect herbivore/bittercress interaction. Oecologia. In press.

Courtney, S. P., and S. Courtney. 1982. The "edge effect" in butterfly oviposition: causality in *Anthocharis cardamines*. Ecol. Entomol. 7:131–137.

Faeth, S. H., S. Mopper, and D. Simberloff. 1981. Abundances and diversity of leaf-mining insects on three oak host species: effects of host plant phenology and nitrogen content of leaves. Oikos 37:238–251.

Free, J. B., and I. Williams. 1978. The response of the pollen beetle *Meligethes aeneus*, and the seed weevil *Centhorhyncus assinilis*, to oil seed rape *B. napus* and other plants. Journ. Appl. Ecol. 15:761–774.

Free, J. B., and I. Williams. 1979. The distribution of insect pests on crops oil seed rape (*Brassica napus*) and the damage they cause. Journ. Agri. Science 92:139–149.

Harcourt, D. G. 1961. Spatial pattern of the imported cabbage worm *Pieris rapae* L. on cultivated crucifers. Can. Entomol. 93:945–952.

Harrington, H. D. 1954. Manual of the Plants of Colorado. Sage Books, Denver, CO. 666 pp.

Hering, E. M. 1951. Biology of the Leaf Miners. Dr. W. Junk, The Hague. 420 pp.

Janzen, D. H. 1975a. Intra- and interhabitat variations in *Guazuma ulmifolia* (Sterculiaceae) seed predation by *Amblycerus cistelinus* in Costa Rica. Ecology 56:1009–1013.

Janzen, D. H. 1975b. Behavior of *Hymenaea courbaril* when its predispersal seed predator is absent. Science 189:145–147.

Janzen, D. H. 1975c. Interactions of seeds and their insect predators/parasitoids in a tropical deciduous forest. *In* P. W. Price (ed.), Evolutionary Strategies of Parasitic Insects and Mites, pp. 154–186. Plenum Press, New York, NY. 224 pp.

Jones, R. E. 1977. Movement patterns and egg distributions in cabbage butterflies. J. Animal Ecol. 46:195–212.

Jones, V. P., M. P. Parella, and D. R. Hodel. 1986. Biological control of leaf miners in greenhouse chrysanthemums. Calif. Agric. 40:10–12.

Langenheim, J. H. 1955. Flora of the Crested Butte Quadrangle, Colorado. Madroño 13:64–78.

Langenheim, J. H. 1962. Vegetation and environmental patterns in the Crested Butte Area, Gunnison County, Colorado. Ecol. Monogr. 32:249–285.

Louda, S. M. 1982a. Limitation of the recruitment of the shrub *Haplopappus squarrosus* (Asteraceae) by flower- and seed-feeding insects. J. Ecol. 70:43–53.

Louda, S. M. 1982b. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. Ecol. Monogr. 52:25–41.

Louda, S. M. 1984. Herbivore effect on stature, fruiting, and leaf dynamics of a native crucifer. Ecology 65:1379–1386.

Louda, S. M. 1988. Insect pests and plant stress as considerations for revegetation of disturbed ecosystems. *In* J. Cairns (ed.), Rehabilitating Damaged Ecosystems, Vol. II, pp. 51–67. CRC Press, Boca Raton, FL.

Louda, S. M., and J. E. Rodman. 1983a. Ecological patterns in the glucosinolate content of a native mustard, *Cardamine cordifolia,* in the Rocky Mountains. J. Chem. Ecol. 9:397–421.

Louda, S. M., and J. E. Rodman. 1983b. Concentration of glucosinolates in relation to habitat and insect herbivory for the native crucifer *Cardamine cordifolia.* Biochem. Syst. Ecol. 11:199–207.

Parker, M. A., and R. B. Root. 1981. Insect herbivores limit habitat distribution of a native composite, *Machaeranthera canescens.* Ecology 62:1390–1392.

Scriber, J. M., and F. Slansky, Jr. 1981. The nutritional ecology of immature insects. Ann. Rev. Entomol. 26:183–211.

Stanton, N. 1975. Herbivore pressure of two types of tropical forest. Biotropica 7:8–11.

Thompson, J. N. 1978. Within-patch structure and dynamics in *Pastinaca sativa* and resource availability to a specialized herbivore. Ecology 59:443–448.

Wheeler, M. R. 1952. The Drosophilidae of the Neartic region, exclusive of the genus *Drosophila.* Univ. Texas Publ. 5204:162–218.

Wheeler, M. R., and H. Takada. 1966. The Nearctic and Neotropical species of *Scaptomyza* Hardy (Diptera: Drosophilidae). Univ. Texas Publ. 6615:37–78.

Whitham, T. G. 1978. Habitat selection by *Pemphigus* aphids in response to resource limitation and competition. Ecology 59:1164–1176.

Whitham, T. G. 1980. The theory of habitat selection: examined and extended using *Pemphigus* aphids. Amer. Nat. 115:449–466.