

Reports

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COPING WITH MULTIPLE ENEMIES: 10 YEARS OF ATTACK ON *LOMATIUM DISSECTUM* PLANTS

JOHN N. THOMPSON

Departments of Botany and Zoology, Washington State University, Pullman, Washington 99164 USA

Abstract. Most natural plant populations are attacked by a suite of enemy species, but there are differing views on how commonly individuals within populations must confront multiple enemies. I evaluated during 10 years the number of insect and pathogen taxa attacking leaves and flowers on tagged individuals of *Lomatium dissectum* (Apiaceae), a long-lived herbaceous perennial. In addition, I determined the minimum number of established plants killed by pocket gophers. At least 43% of the deaths were attributable directly to feeding on roots by gophers. On average 68% of plants were attacked each year by at least one insect or pathogen species, and plants harbored each year a mean of 1.6 insect/pathogen species. By year 10 all surviving plants had been attacked by at least two enemies. Yearly attack by a small number of enemy species is a pervasive part of the life history of individual plants within this population.

Key words: *Contarinia fly galls; Depressaria leptotaeniae; field experiment; fossorial herbivores; individual plant survival; Lomatium dissectum; long-term plant study; multiple enemies; Phytomyza leaf mines; plants, coping with multiple enemies; Puccinia rust; survival of herbaceous perennials.*

INTRODUCTION

Ecological arguments on the importance of parasites, grazers, and predators in the evolution of host and prey populations range along a continuum between two extremes. At one extreme, most hosts and prey are considered to be confronted almost continually with a diverse array of enemies, thereby decreasing the potential for natural selection imposed by any one enemy species. Some arguments for what is sometimes called “diffuse coevolution” are based in part on this view (review in Thompson [1994]). At the other extreme, enemy species—individually and together—are considered to be generally so rare or erratic that they cannot usually impose selection pressures on host or prey populations. This, for example, is one of the assumptions in Jermy’s (1984) hypothesis on sequential evolution in interactions between plants and insects, although his hypothesis concerns primarily the role of insects in plant diversification rather than adaptation. Between these two extremes are a variety of hypotheses on how the ecology and evolution of interactions proceeds in the midst of multiple enemies and potentially erratic patterns of occurrence (Thompson 1994).

The ecological and evolutionary problem is therefore

to determine where most interactions occur along this continuum of multispecific interactions. Solving the problem requires several kinds of analysis. Some experimental studies have begun to evaluate how selection may proceed on pairwise interactions amid multiple enemies (e.g., Davies and Brooke 1989, Dodson 1988, Thompson and Pellmyr 1992, Iwao and Rausher 1997). Other studies have begun to evaluate genetic correlations, constraints, and trade-offs in adaptation to multiple enemy species (e.g., Simms and Rausher 1993, Kraaijeveld and Van Alphen 1994, Via 1994, Schmitt et al. 1995, Mitchell-Olds et al. 1996, Pilson 1996). Yet other studies are evaluating how the genotypes of individuals can affect predictability and pattern of attack by multiple enemies (Whitham et al. 1994, Root 1996). Still needed are long-term studies of just how pervasive or erratic are particular enemies and groups of enemy taxa during the life histories of individuals within natural populations. In the absence of such data, we have no basis for determining which kinds of ecological experiments most closely match the problems faced by plants within natural populations.

Here I evaluate attack by leaf-feeding, floral-feeding, and root-feeding taxa on tagged individuals of a long-lived perennial plant, *Lomatium dissectum* (Apiaceae) over a 10-yr period. The study was designed specifically to evaluate how often individual plants must contend with enemy species and how often they must con-

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tend with multiple enemies. The study assessed yearly attack on plants by five major enemies representing different feeding guilds that attack leaves and flowers of established *L. dissectum* plants. In addition, the study evaluated how commonly plants die from attack on roots by pocket gophers. The taxa included here encompass the major insects, mammals, and fungi that attack leaves, flowers, and roots. Although the need for studies evaluating simultaneous attack by these taxa has been emphasized repeatedly (e.g., Linhart 1987, Burdon and Leather 1990, Fritz and Simms 1992), there are still few long-term analyses of attack on individual plants in natural populations.

METHODS

Lomatium dissectum (Nutt.) Math. & Const. is a long-lived perennial herb, common in steppe communities in the northern Intermountain West of North America. Plants grow each year from a large taproot, producing up to 10 highly dissected leaves often >40 cm in length. In the Palouse region of eastern Washington, plants flower in April and May, each individual developing up to several flowering stalks 0.5–1.5 m in height. Flowers are grouped into compound umbels composed of a combination of 50–200 male and hermaphroditic flowers. After flowering and seed set, all aboveground plant parts senesce.

The study area was the Smoot Hill Biological Research Area of Washington State University, located 18 km north of Pullman, Washington, USA. The study site was at the top of Smoot Hill in steppe dominated by native and alien grasses (*Agropyron spicatum*, *Festuca idahoensis*, and *Bromus* spp.) and perennial herbs, especially *Lomatium* spp. and *Balsamorhiza sagittata*. One hundred and three plants were chosen on 12 May 1979 by tagging all established plants intersecting three 30-m transect lines within the study area. Each transect line was separated from the other two by 15–20 m. All tagged plants were established individuals in at least their 2nd yr of growth.

Each plant was checked for attack every May during the following 10 yr for attack by five enemy taxa. For some taxa, the taxonomy at the species level is in flux and hence only a genus name is given. *Depressaria leptotaeniae* Clark is an oecophorid moth restricted to *L. dissectum*. Female moths that have overwintered as adults oviposit onto the expanded leaf petioles surrounding unopened umbels or sometimes onto the expanded leaf petioles on vegetative plants, and larvae move among plant parts during development (Thompson 1983). *Contarinia* sp. (Diptera: Cecidomyiidae) flies oviposit into male and hermaphroditic floral buds, causing the flowers to develop into galls. Females lay batches of eggs into each umbel, and 1–6 larvae develop within each gall. *Phytomyza* sp. (Diptera: Agromyzi-

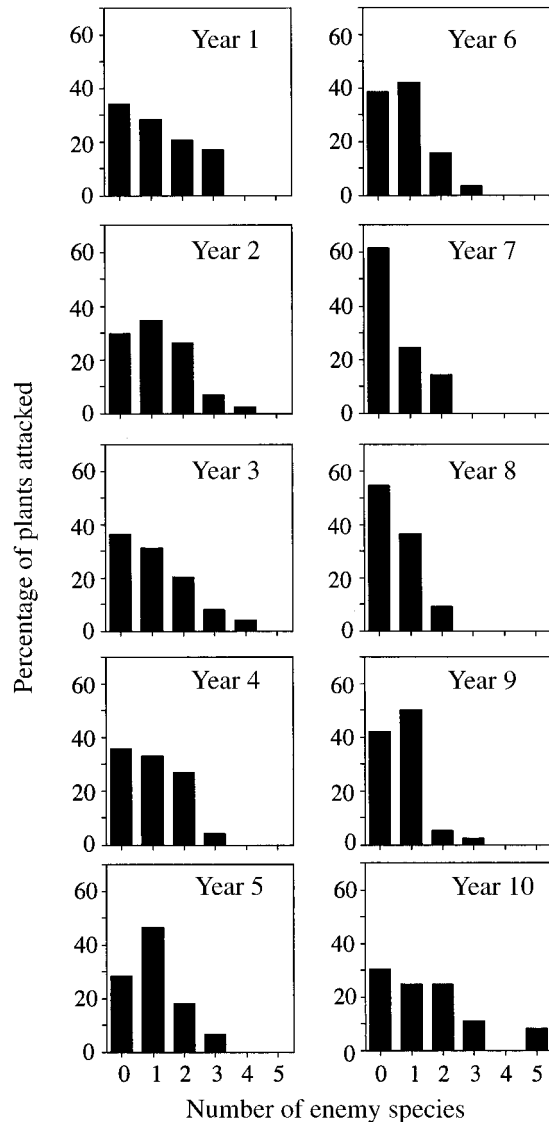


FIG. 1. Percentage of *Lomatium dissectum* plants attacked by 0–5 of the major leaf-feeding and flower-feeding taxa during each of the 10 yr of the study.

dae) leaf miners oviposit into the leaflets and produce small blotch mines both on vegetative and flowering plants. *Puccinia* sp. rust develops a bright-orange infection on the leaves and sometimes the floral stems. The fifth enemy group includes mammals that graze on *L. dissectum*. These were primarily white-tailed deer (*Odocoileus virginianus* (Boddaert)) but also occasionally rabbits (*Sylvilagus floridanus* (Allen)). Because damage by these two mammalian herbivores could not always be reliably separated, they are grouped here as one category.

A plant was recorded as attacked by an enemy if it

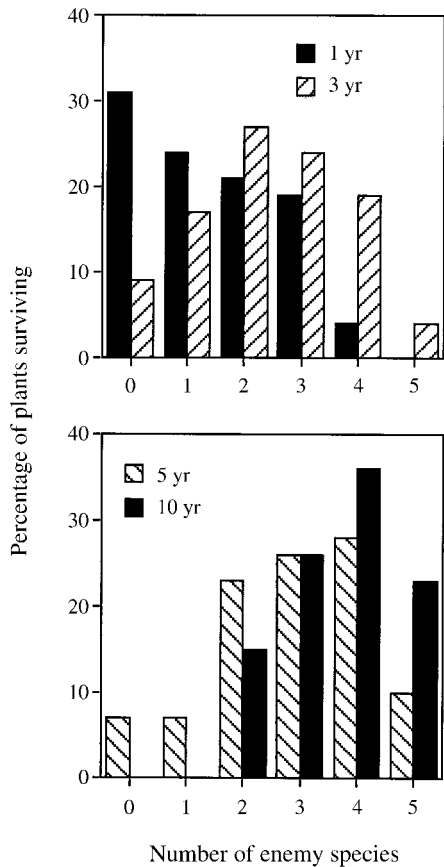


FIG. 2. Percentage of plants surviving 1 yr, 3 yr, 5 yr, or 10 yr that had remained unattacked for that time span, or had been attacked by 1–5 leaf-feeding and flower-feeding taxa.

showed clear evidence of attack: webs and associated missing plant tissue resulting from *Depressaria* feeding, *Contarinia* galls, *Phytomyza* blotch mines, bright-orange *Puccinia* rust infection sites, or mammalian-grazed plant tissue. In all cases, categorization of the agent of attack was unambiguous.

In addition to yearly attack by these species, deaths directly attributable to feeding on roots by pocket gophers (*Thomomys talpoides* (Richardson)) were recorded throughout the study. For gophers, unlike the other enemy taxa, sublethal feeding on roots during each year could not be evaluated, but death caused directly by feeding could be readily assessed. I attributed a death to pocket gopher feeding if I found a mound of freshly tilled earth at the precise spot where a lived tagged plant had been.

RESULTS

There was a linear and slow decrease in the number of plants surviving each year over the 10 yr. Survivor-

ship between years was $90.1 \pm 4.3\%$ (mean ± 1 SD, $N = 10$ yr) and was consistently high among all years (range: 85.4–95.5%). By the end of the decade, 35% of the initially tagged plants were still alive. The additional life-span of plants once tagged was 6.3 ± 2.6 yr (mean ± 1 SD), as estimated using the actual values for the decade and estimated values for subsequent years obtained from a linear regression of the data ($y = 103 - 6.5x$, where y = number of plants alive and x = year of the study; $r^2 = 0.98$, $F_{1,9} = 437.9$, $P < 0.0001$). Hence, the average individual *L. dissectum* plant, once established, has the opportunity to interact repeatedly with a number of enemy species over its lifetime.

At least 43% of the deaths observed throughout the study could be attributed unambiguously to feeding on the roots of live plants by pocket gophers. In other cases, plants died between years without readily discernible causes.

Most plants did not flower every year, and the proportion of plants flowering ranged among years from 4% to 34%. Hence, plants varied among years in their chance of being attacked by the two flower-feeding herbivores (*Contarinia* sp. gall flies and *D. leptotaeniae* caterpillars).

On average, $68\% \pm 26$ (mean ± 1 SD, range: 40–73%, $N = 10$ yr) of plants were attacked by at least one of the five aboveground herbivore and pathogen species each year, and in all but two years the values were $>50\%$. The number of enemy taxa on attacked plants varied between 1.4 and 2.2 among all years (10-yr mean = 1.6 ± 0.8 enemy taxa). Few individuals were attacked by >2 taxa in any year (Fig. 1). Consequently, most plants were attacked by a small subset of the enemy taxa each year.

Plants surviving until the end of the study had been attacked by most of the enemy species (Fig. 2). During the 1st yr most plants were attacked by 0–1 enemy taxa, and by the 3rd yr most surviving plants had been attacked by 2–3 taxa. By year 5 more than 80% of the plants had been attacked by two or more enemy taxa, and by year 10 all plants had been attacked by at least 2 enemies. Nevertheless, even by year 10 less than one quarter of the plants had been attacked by all five enemy taxa.

The percentage of plants attacked by each enemy species varied among years, thereby subjecting plants to different combinations of enemies in different years (Fig. 3). *Puccinia* rust and *Phytomyza* leaf miners were the most consistent enemies among years, attacking one third or more of the plants in at least half the years. There were no significant correlations among insect/pathogen taxa in the percentage of plants attacked across years (all Pearson correlations with Bonferroni corrections, $P > 0.05$).

DISCUSSION

Most plants in this *Lomatium dissectum* population are attacked by at least one enemy species almost every year. Although each plant must contend with only a

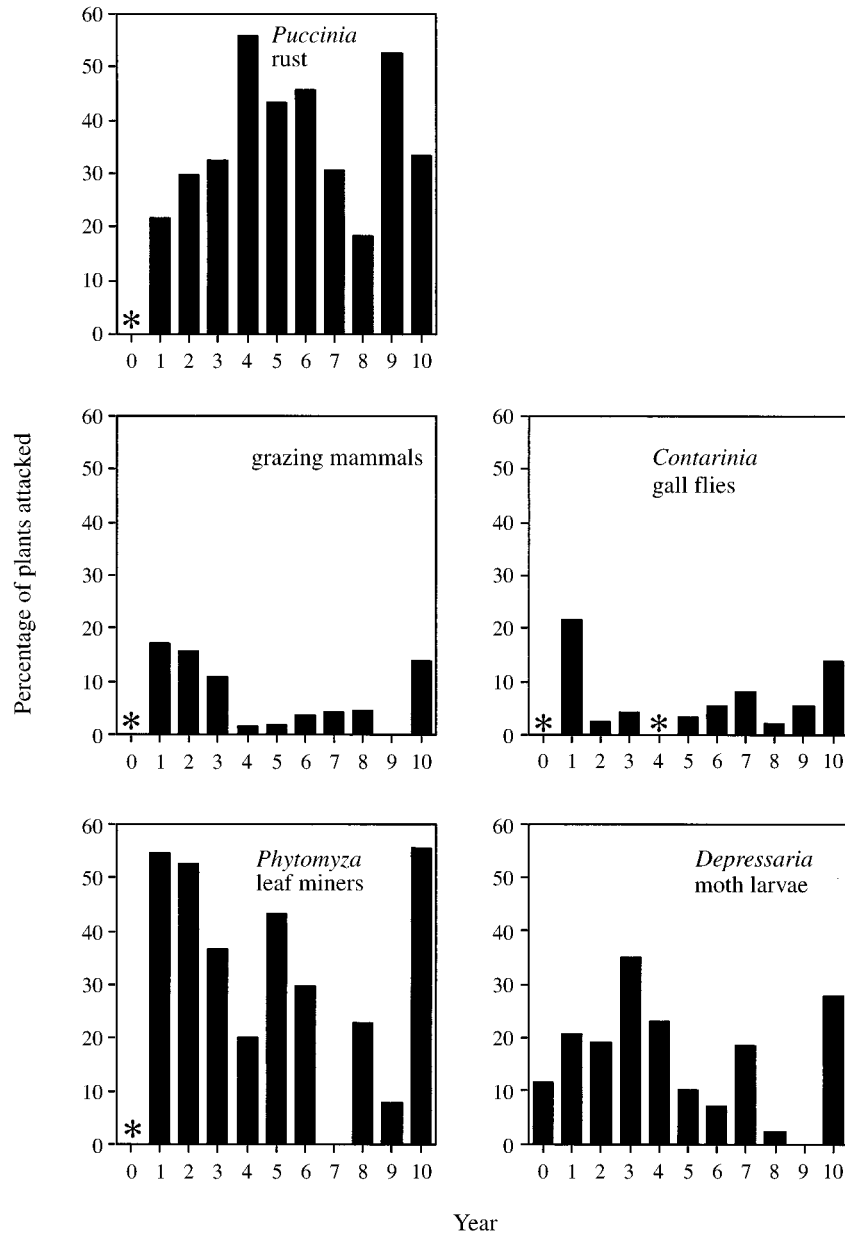


FIG. 3. Percentage of *Lomatium dissectum* plants attacked by each of the leaf-feeding and flower-feeding taxa during each of the 10 yr of the study. Asterisks (*) indicate that the data were not collected in that year.

small subset of enemies during any particular year, most individuals are attacked by multiple enemy taxa during their lifetimes. In addition to aboveground parasitism and grazing of leaves and flowers, the plants have a high probability of ultimately being killed outright through predation by pocket gophers. Hence, the defenses of *L. dissectum* plants must be capable of coping with attack by a small number of enemy taxa in most years throughout their lives.

Moreover, the combination of taxa attacking plants varies among years. Too few taxa regularly attack *L. dissectum* year after year to evaluate the results for evidence of herbivore suites, as found by Maddox and Root (1990) in their analysis of 17 insect herbivores attacking goldenrod (*Solidago altissima*). The 10-yr results, however, indicate that most plants surviving for >5 yr will have been attacked by most of the enemy taxa at least once during their lifetimes.

Besides the taxa included in this study, *L. dissectum* plants must also cope with more erratic attack on its leaves or flowers by several other insects: anise swallowtail butterflies (*Papilio zelicaon*) and tortricid moths (*Sparganothis* near *inconditana*) that attack the leaves and flowers, and aphids that cluster on the flowering stalks just below the inflorescence. Attack by these insects was rare during the study (<1% of observations), but they add to the problem of coping with multiple enemies.

Seeds are attacked by yet another group of enemy taxa analyzed in earlier studies. *Greya subalba* (Prodoxidae) moths oviposit into the developing seeds and distribute their eggs broadly among plants throughout the population (Thompson 1986, 1987). Once dispersed, as many as 99% of *L. dissectum* seeds are consumed by mammalian and coleopteran (e.g., *Eleodes*) seed predators (Thompson 1985). Consequently, every stage of the life history of *L. dissectum* is subject to a high probability of attack by enemies.

The original plan for this long-term study was to evaluate attack not only on the marked plants, but also on the plants that replaced them when they died in order to evaluate inter-generational patterns of herbivory. But plants turned out to be longer lived than expected, and few of the sites made available by deaths of marked *L. dissectum* plants during the 1980s and early 1990s were colonized by new *L. dissectum* plants. There have been at least three causes for this lack of replacement at the same local site: high levels of seed predation (Thompson 1985), colonization by other species, and highly erratic germination and survival success of *L. dissectum* among years (J. N. Thompson, *personal observation*).

The results of this study and the previous studies on other life-history stages of this population fall between the view that attack by enemies is rare and the alternative view that it is both common and regularly diffused over many enemy species. Attack by enemies is a pervasive component of the life history of this population, but individual plants have neither the luxury of coping with only one major enemy nor the problem of confronting dozens of enemies. Rather, plants must confront a few enemy species each year. We will need a number of studies like this one to determine where most plants fall along this continuum of attack by multiple enemies together with related studies on how plants respond to ongoing attack by small suites of herbivore species.

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