Ecological Mechanisms Underlying Successful Biological Weed Control: Field Experiments with Ragwort *Senecio jacobaea*

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Abstract

We used field experiments to investigate the ecological mechanisms underlying successful biological control of ragwort (*Senecio jacobaea*) by the cinnabar moth (*Tyria jacobaeae*) and ragwort flea beetle (*Longitarsus jacobaeae*) in western Oregon. First, we showed that these herbivores depressed ragwort density to very low levels in experimental plots, reducing the density of vegetative plants by 89% and the number of capitula (flower heads) on generative plants by 93% compared to experimental populations protected from herbivores. Second, the complementary action of the two insects was a key element in successful control in the experimental populations. Each insect had its greatest impact (1) on different host plant stages - flea beetles on vegetative plants and cinnabar moths on reproductive plants; (2) in different seasons - cinnabar moths in summer and flea beetles in fall, winter, and spring; and (3) on different demographic processes - flea beetles on survivorship and cinnabar moths on fecundity. Attack by the flea beetle reduced the capacity of ragwort to recover from attack by the cinnabar moth. Third, localized, temporary disturbances allowed ragwort populations to increase rapidly in density and leaf area, and interspecific plant competition and flea beetle herbivory were the important factors opposing this increase and maintaining ragwort populations at low levels.

Introduction

Biological weed control is a branch of science in which it is usually better to rely on the judgment of an experienced practitioner rather than the predictions of a theorist or the insights of an experimentalist. This paper is written with the twin convictions that biological weed control will not come of age until it has a sound theoretical basis, and that mathematical models and field experiments of a "strategic" kind aimed at understanding the general properties of biological control systems will help carry us toward that goal.

We have used field experiments to investigate the ecological mechanisms underlying successful biological control of ragwort *Senecio jacobaea* L. (Asteraceae) by the cinnabar moth *Tyria jacobaeae* (L.) (Lepidoptera: Arctiidae) and ragwort flea beetle *Longitarsus jacobaeae* (Waterhouse) (Coleoptera: Chrysomelidae) in Western Oregon. We tested the following three hypotheses: (1) natural enemies cause the depression of ragwort populations to very low levels; (2) the complementary action of two natural enemies that use the host in different ways yields better control than either acting alone, (3) interspecific plant competition and herbivory are key elements stabilizing the pest population and improving the reliability of control.

Degree of Depression in Pest Caused by Natural Enemies

Quantitative evaluation of pest density before and after release of natural enemies provides some evidence of their effectiveness in depresssing pest density (e.g., McEvoy 1985). In western Oregon, a survey by the Oregon Department of Agriculture of 42 sites before and after local natural enemy introductions was used to evaluate the effectiveness of biological control of ragwort. The density of ragwort flowering plants declined 93% in the first six years after introduction of the ragwort flea beetle. The flea beetle was introduced after the cinnabar moth was established widely, but presumed to be ineffective. The sites spanned the range of climates, topography, land uses, and timing of local natural enemy introductions in.
western Oregon. However, the validity of ascribing strong and stable depression in host abundance to herbivore activity can be challenged since we do not know what the behavior of the system would have been without herbivores. Successional processes may cause a weedy fugitive species to decline on local sites, even in the absence of natural enemies.

Combining quantitative evaluation of pest density before and after natural enemy introductions and in areas with and without natural enemies provides more reliable evidence of natural enemy effectiveness (Luck et al. 1988). Since sites with and without natural enemies were not compared in the Oregon studies cited above, we undertook small scale experiments after natural enemies were widely established to determine whether the cinnabar moth and ragwort flea beetle caused the depression of ragwort density.

Single vs. Multiple Natural Enemies

A premise of biological weed control programs in North America is that control is likely to be achieved by the cumulative effect of several insect species (Harris 1985). Since phytophagous insects typically consume only parts of individual plants, practitioners have felt that multiple herbivores - attacking different plant parts - would be required for successful biological control. On the other hand, Myers (1985) suggests the record of 26 past successes shows success is more frequently achieved by a single insect, and the strategy for achieving success might resemble a lottery: with every introduction comes the possibility of success.

We tested whether a combination of two herbivores is more effective in depressing host density than either species acting alone. The two herbivore species use the host in different ways. Cinnabar moth larvae strip the shoots in summer, whereas ragwort flea beetle larvae tunnel in petioles, stems, and roots in winter. Moth larvae overlook small vegetative plants whereas beetle larvae and adults attack all plant sizes. McEvoy (1985) hypothesized that this combination of agents would spread herbivore pressure out in space and time, thereby strongly depressing host density by reducing 'escapes' from herbivory.

Joint Effects of Plant Competition and Herbivory

Although natural enemies may cause the depression in host abundance in successful biological weed control, it is not clear that they maintain the host at low levels (Crawley 1983). Successful control may foster a community in which the weed is no longer competitive. Outbreaks of the weed would then be confined to disturbed areas where competition is weak. Where the weed is released from control by disturbance, the herbivores may catch up and check the resurgence.

We examined experimentally the action and interaction of disturbance, colonization, plant competition, and herbivory in maintaining ragwort at low levels following successful biological control at Cascade Head on the central coast of Oregon. Although actively growing ragwort stages have declined to <1% of previous levels, there remains a vast quantity of buried seed (currently 6,000 seeds/m²) which will persist for many years, invulnerable to the natural enemies, buffering the pest from local extinction, and providing the potential for pest resurgence (McEvoy 1985). We have investigated the conditions leading to ragwort outbreaks by varying experimentally levels of disturbance, interspecific competition, and exposure to herbivory.

Methods and Materials

Experiment 1. Cause of Host Depression

To determine whether the cinnabar moth and ragwort flea beetle cause the depression of ragwort density we perturbed the system by: (1) artificial increase in host abundance by transplanting and seed sowing; and (2) artificial decrease in herbivore abundance by exclusion cages and insecticides, with appropriate controls accompanying the latter
manipulation. We established the plants in February 1986 from transplants raised in the greenhouse and from seed sown directly in the field to yield a mixed stage structure (54% seedlings, 35% rosettes, and 11% flowering plants) similar to that of a natural population prior to control (McEvoy 1985). The density of plants in stage classes in herbivore-protected and unprotected plots were then compared at the beginning (April) and end (September) of the 1987 growing season. We also measured reproduction at the end of the season.

The experiment was carried out as a randomized complete blocks design analyzed with a one-way analysis of variance: 4 Blocks x 2 Herbivore Treatments (Protected in Cage, Exposed in Sham Cage) = 8 plots. A 0.90 ha meadow studied earlier (McEvoy 1985) was partitioned into four 0.225 ha blocks, and 2 treatment combinations were allocated at random to 1.83 m x 1.83 m = 3.35 m² plots within each block.

All plants were initially protected from herbivores for the first year (February 1986 - February 1987) by covering plots with cages of woven synthetic fabric (0.08 mm mesh), which reduced photosynthetically active radiation by ca. 38%. Since insect exclusion was not completely successful, on 5 February 1987 we applied the insecticide carbofuran (2,3-Dihydro-2,2-dimethyl-benzofuran-7-yl methylecarbamate) at a rate equivalent to 2.8 kg a.i./ha to remove beetle larvae from protected plots. Thereafter, plots protected from herbivores by cages were compared to plots exposed to herbivores by sham cages (cages with the sides rolled up halfway) to estimate the herbivore effect while ensuring unwanted side effects of caging (e.g., shading or reduction of wind velocity) would be experienced equally by both kinds of plots. Due to low cinnabar moth population levels, we simulated cinnabar moth attack on 19-27 July 1987 by hand defoliation. Henneberger (1986) showed that plant performance was similar following hand-defoliation and cinnabar moth defoliation, suggesting that hand defoliation is a good simulation of feeding damage by the cinnabar moth.

The response of the system to these perturbations was estimated by initial and later comparisons. We initially sampled plants destructively in April 1987 and estimated several plant variables - plant density and biomass in each of four size classes (0-1, 1.1-10, 10.1-20, 20.1-40 mm basal diameter), and several insect variables - beetle density (insects per m²) and beetle intensity (insects/g plant dry mass). Beetle larvae were extracted from plants using 30 cm dia. and 70 cm deep Tulgren funnels equipped with 25 watt light bulbs for small plants and 40 watt light bulbs for large amounts of plant material. To estimate the effect of herbivory over one growing season, we made a final comparison in August 1987 of plant variables. These included the density of plants in three stage classes: small vegetative plants (0-1 mm basal diameter); large vegetative plants (1.1-10 mm basal diameter); and generative (flowering) plants, and reproductive output (number of capitula, or flower heads, per stem).

**Experiment 2. Mechanism of Host Depression**

To test the relative effectiveness of one vs. two herbivore species in depressing host populations we selectively excluded the two herbivore species from high density host populations established by transplanting and seed sowing. We established plants as in Experiment 1 to yield a mixed stage structure (58% seedlings, 30% rosettes, and 12% flowering plants). We used protective cages and spot applications of insecticide to exclude flea beetles. Low cinnabar moth population levels in 1987 made it unnecessary to exclude this insect but forced us to use hand defoliation July 13-24 to simulate cinnabar moth attack.

The experiment was carried out as a randomized complete blocks design analysed in a two-way analysis of variance: 4 Blocks x 2 Levels of exposure to cinnabar moth (Exposed, Protected) x 2 Levels of exposure to flea beetle (Exposed, Protected) x 3 replicates = 48 plots. Four treatment combinations were allocated at random to 0.5 x 0.5 m plots within a 3 x 4 m array located randomly within each of the four blocks described for Experiment 1. The treatments varied exposure of the plots to herbivores as follows: (1) Neither insect - Plots protected from both herbivores were covered with individual 0.5-m-tall cages during the entire course of the experiment after plants were established; (2) Flea beetle - Plots exposed to the flea beetle were covered with closed cages during the active period of the cinnabar moth (July) and sham-caged during the rest of the year; (3) Cinnabar moth - Plots were sham-
caged during the active period of the cinnabar moth (July) and closed the rest of the year; (4) Sham cage with both moth and beetle - Plots exposed to both herbivores were sham-caged during the entire experiment; and (5) Open plot with both moth and beetle - Plots were also exposed to both herbivores in open plots without cages to test for effects of caging.

We sampled destructively plants in March 1987 to estimate plant biomass, stage structure, and beetle intensities; in August 1987, we repeated the sampling and also counted the number of leaves and capitula on each plant.

Experiment 3. Mechanism of Host Regulation

We performed two experiments to examine the action and interaction of disturbance, colonization from the seed bank, interspecific plant competition, and herbivory in maintaining ragwort at low levels. In Experiment 3A, we: (1) artificially disturbed plots by tilling soil and clipping vegetation other than ragwort; (2) artificially protected plants with herbivore-exclusion cages and spot applications of insecticide, with appropriate controls accompanying each manipulation.

The experiment was carried out as a randomized complete blocks design analyzed with a three-way analysis of variance: 4 Blocks x 3 Levels of disturbance intensity (plots undisturbed, clipped, or tilled) x 2 Levels of exposure to cinnabar moth (exposed, protected) x 2 Levels of exposure to flea beetle (exposed, protected) = 48 plots. Twelve treatment combinations were allocated at random to 0.5 x 0.5 m plots within an 11 x 8 m area located randomly within each of the four blocks described for Experiment 1. In disturbance treatments, plots were tilled (simulating soil disturbances by fossorial rodents), species other than ragwort were clipped to a height of 5 cm (simulating grazing), or plots were left unaltered. Disturbances were imposed in a brief episode at the start of the experiment in Spring 1986, then discontinued. They were intended to mimic, in area and intensity, the kinds of natural disturbances currently operating in the meadow, and by extrapolation, the effect of large scale disturbances such as field cultivation and livestock grazing. In herbivore treatments, plots were exposed to neither insect, the moth, the beetle, or both moth and beetle using exclusion techniques described for Experiment 2.

We mapped, measured, and counted at intervals plants surviving from a Spring 1986 cohort to determine emergence and establishment, survivorship, growth, and reproduction. To map seedlings, we placed a 25 cm x 25 cm (0.0625 m²) sheet of acetate over a permanent subplot at the center of each plot and the position of each seedling was circled on the map and color-coded to denote damage by herbivores. Seedling emergence was estimated by weekly census during establishment, and at census intervals of 1 week to 3 months thereafter. Survivorship to reproduction in subplots was estimated by noting the fraction of emerging plants that survived to produce capitula. Reproduction was estimated by multiplying counts of capitula times the number of seeds per capitulum, assuming a mean of 70 seeds/capitulum (McEvooy 1984).

We estimated the density of seed buried in the soil (seed bank size) in August 1987 from soil cores 5 cm dia. and 10.5 cm deep. We took only one core from the S.W. corner of each plot, placed to minimize interference with the plant cohort being monitored in the subplot at the center of each plot. Soil cores were spread in a thin layer over sterilized potting soil in the greenhouse, watered daily, and the seeds were allowed to germinate.

Our continuing account of the demography now spans two growing seasons following emergence of the cohort in Spring 1986.

In Experiment 3B, we initially tilled all plots, then: (1) artificially reduced interspecific competition by continuously clipping or removing other species; and (2) artificially protected plants with herbivore-exclusion cages and spot applications of insecticide, with appropriate controls accompanying each manipulation. Treatments were imposed in early Fall 1986 and maintained continuously thereafter.

The experiment was carried out as a randomized complete blocks design analyzed with a
three-way analysis of variance: 4 Blocks x 3 Levels of interspecific plant competition (other species removed, clipped, unaltered) x 2 Levels of exposure to flea beetle (exposed, protected) = 48 plots. Twelve treatment combinations were allocated at random to 0.5 x 0.5 m plots within a 8 x 5 m area located randomly within each of the four blocks described for Experiment 1. In Competition treatments, species other than ragwort were continuously removed, continuously clipped to a height of 5 cm, or left unaltered. The herbivore treatments were as described for Experiment 3A.

We estimated emergence, establishment, and survivorship as in Experiment 3A. Plant size was measured as the length of longest leaf (cm) and converted to leaf area (cm²) using a regression of leaf area (LA) on length of longest leaf (LL) derived from earlier destructive samples (ln LA = -2.3 + 2.24 ln LL; R² = 0.91). We now have demographic information spanning a full growing season following emergence of the cohort in Autumn 1986.

Results and Discussion

Experiment 1. Herbivores Cause Depression in Host Populations

We first compared exposed and protected plots in April 1987, two months after insecticide removed flea beetles from protected plots and prior to natural and simulated cinnabar moth attack. Distributions of plant numbers and biomass among four size classes were similar between treatments, indicating that no effect of beetles on plant performance was yet apparent. Beetle density was far greater in exposed plots, averaging 906 beetle larvae per plot compared to near zero in protected plots, indicating that we had successfully implemented different herbivore levels. In exposed plots, beetle intensity (beetles per g dry mass of plant) declined as plant size increased, alerting us to the possibility that the effect of beetle herbivory is more severe on small plants (Fig. 1A).

We next compared exposed and protected plots in September 1987, seven months after beetles were removed from protected plots, and two months after simulated cinnabar moth feeding. Exposure to herbivory reduced the density of vegetative plants by 89%, had no effect on the density of generative plants, but reduced the number of capitula on generative plants by 93% (Fig. 1B,C). We predict that this level of herbivory, if sustained over several years, would rapidly depress ragwort populations due to very low fecundity and juvenile survivorship.

The results of these experiments confirm relations of cause and effect suggested by earlier observational studies. McEvoy (1985) evaluated the role of these herbivores in depressing ragwort abundance at Cascade Head, Oregon from observations establishing: (1) an association, evidenced by negative correlation of insect and plant density; (2) a contact, evidenced by herbivore damage to the plants; and (3) a mechanism for population changes, expressed as changes in migration, birth, or death rates. The combination of cinnabar moth and ragwort flea beetle depressed ragwort to <=1% of its former abundance at that site. A similar strong depression in the ragwort abundance occurred near Fort Bragg, California, where ragwort flea beetle combined with the cinnabar moth reduced plant density from 71 rosettes/m² to 0.6 rosettes/m² in a period of 4 yrs (Hawkes and Johnson 1978).

Experiment 2. Two herbivores which Differ in the Ways They Exploit the Host cause Stronger Depression in Host Populations than Either Acting Alone

We first compared plots exposed to different herbivore treatments in March 1987, one month after insecticide removed flea beetles from protected plots and prior to natural and simulated cinnabar moth attack. We found that: (1) plant density, size structure, and biomass did not differ among herbivore treatments, indicating no effect of beetles on plant performance was yet apparent; and (2) larval beetle density varied significantly among flea beetle treatments in both small (0-10 mm basal dia.) and large (10.1-20 mm basal dia.) plants, indicating that we had successfully implemented differences in the level of flea beetle herbivory among treatments.
Figure 1. Variation in flea beetle larval intensity, plant survivorship, and plant reproduction in relation to herbivore treatment in Experiment 1 (mean ± SE, n = 4). (a) Exposure to the flea beetle significantly increased larval intensity in the three smallest plant size classes, but not in the largest size class (Wilcoxon 2-sample test for basal diameter classes from smallest to largest, Z = 2.31, P = 0.021; Z = 2.18, P = 0.029; Z = 3.18, P = 0.029; Z = 1.48, P = 0.139 NS). (b) Exposure to herbivory reduced survivorship of both small and large vegetative plants (small plants, ANOVA on log-transformed data, F_{1,3} = 11.15, P = 0.044; large plants, Wilcoxon 2-sample test, Z = 2.17, P = 0.030) but did not affect survivorship of flowering stems (ANOVA, F_{1,3} = 0.06, P = 0.820 NS). (c) Exposure to herbivory significantly reduced the numbers of capitula per stem (ANOVA, F_{1,3} = 19.47, P = 0.022).
In August 1987, six months after beetles were removed and one month after simulated cinnabar moth feeding, the effects of herbivore treatments on density and biomass of vegetative plants, and number of leaves and capitula on reproductive plants were apparent. Exposure to flea beetles sharply reduced the density and biomass of small and large vegetative plants, but the density and biomass of generative plants was unaffected (Fig. 2A,B). Vegetative plants accounted for most of the individuals (81%) in the ragwort populations protected from insects, while generative plants accounted for nearly all of the biomass (97%).

Simulated cinnabar moth defoliation of flowering plants had no effect on their density (e.g., by increasing mortality); their biomass at harvest time 37 d after defoliation was also unaffected (Fig. 2A,B), apparently because regrowth of defoliated plants allowed them to catch up to undefoliated plants. Simulated defoliation of flowering plants had no significant effect (e.g., by increasing sunlight) on density or biomass of vegetative plants in the understory.

The flea beetle reduced the ability of reproductive plants to compensate for attack by the cinnabar moth. At the August 1987 harvest, plants exposed to both herbivores had at most 27% of the number of leaves on plants exposed to one or no herbivores (Fig. 2C). Plants exposed to cinnabar moth alone yielded 23% as many capitula as did undefoliated plants; plants exposed to both herbivores yielded 1% as many (Fig. 2D).

The response of ragwort density, biomass, leaf production, and flower production to herbivore treatment was similar for sham cage and open plots (Fig. 2), suggesting that unwanted side effects of caging did not affect the outcome of these experiments.

We conclude that two herbivores which differ in the ways they exploit the host can cause stronger depression in host populations than either acting alone. To the extent that we have adequately mimicked cinnabar moth attack, the action of the two insects is complementary, spreading herbivore attack out in space and time and thereby reducing the probability that some plants or their parts would escape herbivory. Each insect has its greatest impact: (1) on different host plant stages (flea beetles on vegetative plants and cinnabar moths on reproductive plants); (2) in different seasons (cinnabar moths in summer and flea beetles in fall, winter, and spring); and (3) on different demographic processes (flea beetles on survivorship and cinnabar moths on fecundity). Attack by the flea beetle reduces the capacity of ragwort to recover from attack by the cinnabar moth.

Our results are not sufficient to declare that the two natural enemies yield better control than one. We have demonstrated the effect the two natural enemies have on their host, not the effect the two natural enemies have on each other. Do they compete with each other? Is competition bad for control? Cinnabar moth numbers have declined in Oregon following introduction of the ragwort flea beetle and decline in ragwort abundance. Can both natural enemies stably coexist on the same low density host population? Are rates of local extinction of one species conditioned by presence or absence of the other? What is the minimum host population size required to maintain viable and effective populations of each natural enemy species? Is control by multiple herbivores inherently unstable over the long term? To resolve these issues we should move beyond the search for patterns of association in documented case histories (e.g., Hall and Ehler 1979, Ehler and Hall 1982, 1984, Myers 1985, Simberloff 1986) to design mathematical models (e.g., Kakehashi, et al. 1984) and field experiments (e.g., Spiller 1986) that incorporate measures of niche overlap and interspecific competition (both exploitative and interference competition) among natural enemies.

Experiment 3. The Compensatory Action of Interspecific Plant Competition and Herbivory are Key Elements Stabilizing the Pest Population and Improving the Reliability of Control

Control can be viewed as a balance between stabilizing and destabilizing forces. By varying the intensity of disturbance, we varied the magnitude of displacement of the host population away from its current low level. By varying the levels of interspecific plant competition and
herbivory, we isolated and quantified the effects of these factors in causing the host population to return to low levels.

Experiment 3A: Effects of disturbance and herbivory. The response of the system to disturbance and herbivory treatments was measured both within and between ragwort

Figure 2. Effect of herbivore treatments on density and biomass of plants in each stage and number of leaves and flowers on August 1987 in Experiment 2 (mean \(\pm\) SE, \(n = 4\)). (A) Exposure to the flea beetle significantly increased the density of small and large vegetative plants (ANOVA after log-transformation, small plants, \(F_{1,9} = 34.20, P = 0.0002\); large plants, \(F_{1,9} = 68.38, P = 0.0001\)). There was no significant effect of exposure to cinnabar moth (small plants, \(F_{1,9} = 0.51, P = 0.494\) NS; large plants, \(F_{1,9} = 0.15, P = 0.704\) NS) and no significant cinnabar moth x flea beetle interaction. There was no significant effect of the moth (\(F_{1,9} = 3.28, P = 0.104\) NS) or the beetle (\(F_{1,9} = 0.05, P = 0.834\) NS) on flowering plant density (ANOVA on log-transformed data). (B) Exposure to flea beetles significantly reduced the biomass of small and large vegetative plants (small plants, ANOVA after inverse transformation, \(F_{1,9} = 24.82, P = 0.0008\); large plants, ANOVA after log-transformation \(F_{1,9} = 144.56, P = 0.0001\)). Exposure to the cinnabar moth did not significantly affect small plants (\(F_{1,9} = 0.29, P = 0.605\) NS) but did affect large plants (\(F_{1,9} = 5.22, P = 0.048\)). The moth x beetle interaction was not significant for small plants but was significant for large plants (\(F_{1,9} = 5.73, P = 0.040\)). Neither herbivore significantly reduced flowering plant biomass (ANOVA after log-transformation, beetle, \(F_{1,9} = 1.07, P = 0.329\); moth, \(F_{1,9} = 0.002, P = 0.965\) NS). (C) Exposure to flea beetles significantly reduced the number of leaves on flowering stems in August (ANOVA after square root transformation, \(F_{1,9} = 8.40, P = 0.018\); there was no significant effect of exposure to cinnabar moth (\(F_{1,9} = 4.33, P = 0.067\)) and no significant moth x beetle interaction (\(F_{1,9} = 3.67, P = 0.088\)). (D) Exposure to flea beetles significantly reduced the number of flower heads per stem (ANOVA after square root transformation, \(F_{1,9} = 10.57, P = 0.011\)). The cinnabar moth effect was also significant (\(F_{1,9} = 42.41, P = 0.001\)); the cinnabar moth x beetle interaction was not significant (\(F_{1,9} = 0.54, P = 0.482\)).
generations, and the results will be reported in full detail elsewhere. For the present paper, we summarize the changes in abundance between generations of a single stage, the seeds lying on or in the soil. We estimated rates of change in population size by comparing the number of seeds produced in the current generation with the number carried over from previous years in the seed bank.

We found no significant differences among disturbance treatments in the density of buried seed carried over from previous years (ANOVA on ln-transformed data, $F_{2,33} = 0.57$, $P = 0.57$ NS; Fig. 3). The back-transformed mean (and 95% confidence limits) was 4,230 (3,539 - 5,044) seeds/m².

![Graph showing mean number of seeds per m² with disturbance treatments: Tilled, Clipped, Undisturbed, Neither Insect, Moth, Beetle, Moth & Beetle.]

**Figure 3.** Effect of disturbance, cinnabar moth, and flea beetle treatments on new seed production in Experiment 3A (mean + SE, $n = 4$). Disturbances were imposed in a brief episode at the start of the experiment, then discontinued. Buried seed carried over from previous years, shown in the lower portion of the graph, did not differ among treatments (see text). The results of the 3-way ANOVA on log-transformed data indicate that new seed production was significantly affected by disturbance ($F_{2,33} = 5.89$, $P = 0.0065$) and flea beetles ($F_{1,33} = 54.54$, $P = 0.0001$), but the significant disturbance x beetle interaction ($F_{2,33} = 5.89$, $P = 0.0065$) qualifies our conclusions (see text).

A total of 52% of the variation in new seed production among our experimental plots was due to disturbance (9%) and flea beetle (43%) treatments, but the presence of a significant interaction makes us qualify our statements. The nature of the interaction is revealed by inspection of the data (Fig. 3). No seed was produced in plots exposed to the flea beetle. In plots protected from the flea beetle, the presence of other plant species reduced seed production, but the effect was removed when other species were clipped. In disturbed plots (other species clipped or removed) protected from the flea beetle, new seed production (16,991 seeds per m²) was four times greater than the quantity of buried seed carried over from previous years listed above. These results show that a single episode of reproduction brought on by a temporary lapse in control can quickly restore a seed bank that has been slowly depleted by seed germination and mortality. Thompson and Makepeace (1983) estimated the time for 99% decline in viability of buried ragwort seed in New Zealand to be at least 4-5 years in the 0-2 cm surface layer and 10-16 years below 4 cm soil depth.
Figure 4. Effect of interspecific plant competition, cinnabar moth, and flea beetle treatments on plant leaf area and density in Experiment 3b (mean ± SE, n = 4). All plots were initially tilled, and clipping and removing other species were continuous throughout the experiment. (a) Leaf area. The results of the 3-way ANOVA on log-transformed data on leaf area indicate significant effects of competition ($F_{2,33} = 35.54, P = 0.0001$) and flea beetle ($F_{1,31} = 11.96, P = 0.0015$) treatments. The orthogonal contrasts "other species present vs. absent" ($F_{3,31} = 46.19, P = 0.0001$) and "other species clipped vs. not clipped" ($F_{3,31} = 24.89, P = 0.0001$) indicated that the effect of other species was highly significant and that this effect was less when other species were clipped than when they were not clipped. (b) Plant density. The results of the corresponding ANOVA on plant density indicate significant effects of competition ($F_{2,33} = 10.59, P = 0.0003$) and flea beetle ($F_{1,31} = 8.85, P = 0.006$) treatments. The orthogonal contrasts "other species present vs. absent" ($F_{1,33} = 16.02, P = 0.0003$) and "other species clipped vs. not clipped" ($F_{1,33} = 5.17, P = 0.030$) were both significant.
The probability of ragwort establishment has been now been studied experimentally under a range of competitive conditions. Previous studies have found virtually no establishment of sown seed in dense grass, while cut grass and cultivated soil yield high seedling establishment (Cameron 1935, Crawley and Nachapong 1985). Our experiment - starting with recruitment from buried seed and culminating in production of new seed two years later - indicates the growth rate of the buried seed population is negligible in dense grass, and high in clipped grass and cultivated soil. The experimental findings confirm field observations that overgrazing and disturbances that expose and loosen soil tended to promote ragwort establishment.

We conclude from our experiment that even small, temporary disturbances in spring can have a dramatic effect in increasing ragwort density. Buried seed, rapid growth, and high fecundity create the potential for explosive increase in ragwort populations. Herbivory by the ragwort flea beetle in the presence of interspecific plant competition is capable of offsetting this increase and maintaining ragwort populations at low levels. The contribution of the cinnabar moth is small and undetectable.

**Experiment 3B. Effects of interspecific plant competition and herbivory.** We next directly compared the role of herbivory and interspecific plant competition in regulating the pest population at low levels. We perturbed the ragwort population in Fall 1986 by tilling soil, then varied the levels of interspecific plant competition, cinnabar moth, and flea beetle to measure the role of these factors in returning the perturbed population to low levels. The initial number of emerging seedlings in each plot, analyzed by three-way ANOVA, did not vary significantly among competition ($F_{1,33} = 0.69$, $P = 0.51$ NS), moth ($F_{1,33} = 1.82$, $P = 0.21$ NS), or beetle treatments ($F_{1,33} = 2.13$, $P = 0.15$ NS).

For the present paper, we measure the response of the population in terms of leaf area on 23 July 1987 and plant density on 11 January 1988, 10 and 16 months respectively after plots were perturbed in September 1986. A substantial and significant portion of the variation in leaf area and plant density among plots was explained by the interspecific plant competition (55% for leaf area and 27% for density) and flea beetle (9% for leaf area and 11% for density) treatments (Fig. 4). As expected, the presence of competing species decreased ragwort leaf area and density, and the effect of competing species on ragwort was less if they were clipped than if they were not clipped. The beetles contributed a significant, additive effect, but once again, we could detect no effect of the cinnabar moth.

We conclude that localized disturbances allow ragwort populations to rapidly increase in leaf area and density, and that interspecific plant competition and herbivory by the ragwort flea beetle are the important factors opposing this increase and maintaining ragwort populations at low levels. Cinnabar moth had no detectable effect on plant density or leaf area within the first 10-16 months following disturbance, when ragwort plants are in the vegetative stage. They may yet have a significant effect on the generative stage, which they prefer to attack.

**Conclusions**

1. Ragwort has declined to <1% of its former abundance following introduction of the cinnabar moth and the ragwort flea beetle at our study site on the central coast of Oregon. Experiments imposed by increasing artificially plant density and decreasing artificially herbivore density confirm that the herbivores were the cause of host decline.

2. The complementary action of two natural enemies that use the host in different ways was a key element in the strong depression of our experimental ragwort populations. Our findings demonstrate the additive effects that the cinnabar moth and ragwort flea beetle have on ragwort, but we need to evaluate the effect these two natural enemy species have on each other.

3. Mechanisms of interaction that stabilize pest populations are important to biological control. Buried seed and other invulnerable stages can permit the pest to rapidly rise to epidemic levels when controls are disrupted. In our experiments, most of the stability in the pest population appears to be generated by interactions between the pest and its competing...
species rather than by the interaction between the pest and its natural enemies. Since the
minimum time period for judging stability is one complete turnover of all individuals in a
cohort (Connell and Sousa 1983), we will extend the time period of our observations to
clarify this point.

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