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Combining the cinnabar moth (*Tyria jacobaeae*) and the ragwort flea beetle (*Longitarsus jacobaeae*) for control of ragwort (*Senecio jacobaea*): an experimental analysis

R.R. JAMES*, P.B. McEVOY and C.S. COX
Department of Entomology, Oregon State University, Corvallis, Oregon 97331-2907, USA

Summary

1. A field experiment tested the independent and combined effects of the cinnabar moth (*Tyria jacobaeae*) and the ragwort flea beetle (*Longitarsus jacobaeae*) on ragwort (*Senecio jacobaea*). These insect herbivores feed on different stages of the host-plant and at different times of the year and were introduced to North America as biological control agents.

2. Flea beetles alone were found to reduce vegetative ragwort densities by 95%, and flower production by 39%, as compared to plants in control plots. Damage by cinnabar moths was simulated by removing all leaves and capitula from generative plants, but plants were able to regenerate some of the foliage and flowers. The treatment ultimately reduced capitulum production by 77% and the number of achenes per capitulum by 15%. Flea beetle damage was found to reduce the ability of flowering plants to compensate for defoliation and defloration to the extent that capitulum production was reduced by 98% and no viable achenes were produced.

3. These findings support the strategy of introducing complementary enemies which attack different stages and at different times, thereby reducing the number of invulnerable life stage and temporal refuges for the host.

Key-words: biological control, weeds, insects, single vs. multiple enemy introductions.

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Introduction

In the practice of biological control, several different agents are often introduced to improve chances of success, be it from the combined effect of all the agents (Harris 1985) or the increased chance of finding one sufficient for control (Myers 1985; Myers, Higgins & Kovacs 1989). However, there has been disagreement over the effectiveness of this practice on the ground that interspecific interference may cause the combined effect of multiple enemy species to be less than the effect of the single most efficient enemy species (Pemberton & Willard 1918; Turnbull & Chant 1961; Turnbull 1967; May & Hassell 1981; Ehler & Hall 1982; Keller 1984; Kakehashi, Suzuki & Iwasa 1984; Myers 1985).

Much of the past evidence for herbivorous insects having a role in reducing host-plant populations has come from observations of weed abundance before and after the introduction of biological control agents (Dodd 1940; Huffaker & Kennett 1959; Hawkes & Johnson 1978; Cullen 1978; McEvoy 1985). More experimental evidence, such as that obtained by Spiller (1986), is needed to determine the relative effectiveness of different natural enemies. An experimental approach was used here to test the independent and combined abilities of the cinnabar moth *Tyria jacobaeae* L. (Lepidoptera: Arctiidae) and the ragwort flea beetle *Longitarsus jacobaeae* (Waterhouse) (Coleoptera: Chrysomelidae), to reduce tansy ragwort (*Senecio jacobaea* L. (Asteraceae)) populations. These two insects differ in feeding behaviour; cinnabar moth larvae feed on flowers and foliage in summer, while flea beetle adults feed on foliage in the autumn, winter and spring. Beetle larvae feed within the roots and leaf petioles of plants during the autumn, winter and spring.

Ragwort is a widespread weed in the Pacific Northwest of the United States, including western Oregon where the experiment was conducted. Plants usually spend their first year as rosettes and bolt and flower the following summer. Flowering

* Present address: NSI Technologies Services Corp., USEPA Environmental Research Laboratory, 200 SW 35th Street, Corvallis, Oregon, 97333, USA.

generally occurs from mid-July to early September in western Oregon, followed by senescence. Ragwort is a biennial but may become a short-lived perennial when damaged by cutting or defoliation. It usually reproduces by seed but can reproduce vegetatively by root and crown buds (Poole & Cairns 1940). These characteristics give it resilience to attack by herbivores.

The cinnabar moth was introduced into Oregon in 1960 as a biological control agent of ragwort (Frick & Holloway 1964). Adult moths are active in May and early June, ovipositing on the undersides of ragwort leaves. Large bolting plants are usually selected for oviposition (Dempster 1982). Larvae often completely defoliate flowering plants, but do not usually feed on rosettes unless flowering plants have all been consumed. Along the Oregon coast, most larval feeding occurs from June to early August and pupation occurs by September. Ragwort plants are often able to recover from defoliation (Cameron 1935; Bornemissza 1966; Harris *et al.* 1978; Cox & McEvoy 1983; Islam & Crawley 1983) and cinnabar moth activity may even result in increased rosette densities in both Europe (Dempster 1971) and North America (Hawkes & Johnson 1978).

The ragwort flea beetle was introduced to California in 1969 to improve ragwort control. Adults emerge in early summer but females undergo a summer aestivation which delays oviposition for 1–5 months; they begin to feed heavily 2–8 weeks before egg-laying (Frick 1970). Adults feed on ragwort by rasping through the leaves, leaving behind small circular holes. Larvae damage ragwort by boring into the roots and petioles where they feed throughout the winter, completing development in the spring.

Hawkes & Johnson (1978) found that the introduction of flea beetles further reduced ragwort populations to levels well below those achieved by the cinnabar moth alone. However, since the cinnabar moth was introduced first it is not clear whether it complements flea beetle activity in controlling ragwort or whether the flea beetle would have been sufficient alone, had it been introduced first. The experiment described here compares the independent and joint effects of these two insects, with different feeding behaviours, on dense ragwort populations in the mild climate of western Oregon.

Materials and methods

STUDY SITE

The study site is a 0·9-ha meadow in the Cascade Head Scenic Research Area on the central coast of Oregon. The Oregon Department of Agriculture introduced both insects into the area between 1978 and 1980. From 1981 to 1983 insect populations increased dramatically and ragwort declined to 3% of its former density (McEvoy 1985; McEvoy, Cox & Coombs 1991).

EXPERIMENTAL DESIGN

An exclusion experiment was conducted using cages and experimental ragwort populations to determine which of the following was most effective in depressing plant populations: the cinnabar moth, the ragwort flea beetle, or the combination of these two agents. The study site was divided into four equal blocks. Fifteen plots ($0{\cdot}5 \times 0{\cdot}5$ m) were placed within a randomly located 3×4 m area in the block. Ragwort was established in the plots by transplanting 2-month-old plants from the glasshouse into tilled plots in February 1986; seeds were sown haphazardly in March and again in November. Planting and seeding was done to create a mixture of age-classes as would typically occur in natural ragwort infestations. All plants other than ragwort were removed from the plots during the summer and autumn of that same year and the ragwort transplants were thinned to eight per plot (32 large plants per m^2) to recreate a stand of flowering plants at least as dense as when the insects were first introduced (i.e. 22 flowering plants per m^2 (McEvoy 1985)). All cages were closed to exclude insects for 1 year while the plants became established. Experimental plots were covered with $61 \times 61 \times 61$ cm frames constructed of 2·5-cm diameter plastic (PVC) tubes covered with bags of 'Leno weave' nylon mesh screens (open spaces in the mesh were $0{\cdot}6 \times 1{\cdot}0$ mm) held down to the ground with sand bags when closed and rolled up partially when open. Each plot was assigned to one of five treatments.

1. Neither insect: cages which were continuously closed to exclude cinnabar moths and flea beetles (control).

2. Moth only: cages which excluded flea beetles but were opened from 6 June to 27 July for cinnabar moths; flowering plants were hand-defoliated in July to simulate cinnabar moth activity.

3. Beetle only: cages which were open for flea beetles but were closed from 6 June until 27 July to exclude cinnabar moths.

4. Both insects: cages were continuously open to both flea beetles and cinnabar moths; flowering plants were hand-defoliated in July.

5. Open controls: open plots with no cages to measure side-effects of caging; flowering plants were hand-defoliated in July.

Selective exclusion was obtained by varying the timing of opening and closing of cages and was possible because timing of attack by the two insects differs. Each treatment was replicated three times within the block to allow for two destructive samples and a repeated census of plants within the third replicate.

The experiment was a standard randomized block

design analysed by a two-way ANOVA. When the data did not appear to fit an additive, linear model, transformations were used so that the response variables were normally distributed and the variances were homogeneous (based on Hartley's F_{max} test (Sokal & Rohlf 1981)). Open control plots were analysed separately by comparing open plots with the 'both insects' treatment using a one-way ANOVA.

Adult beetles were neither effectively excluded by cages nor effectively removed with an aspirator. Accordingly, the systemic carbamate insecticide carbofuran (presented as 'Furadan': FMC Agricultural Chemical Group, Philadelphia, PA, USA) was sprayed at a rate equal to 2·8 kg active ingredient ha^{-1} in all beetle exclusion treatments on 5 February 1987 (the cinnabar moth was not active at this time). Carbofuran was selected because of its effectiveness against *Longitarsus ferrugineusar* (Foudras) (formerly *Longitarsus waterhousei* Kutschera) larvae in mint (Morris 1989) and it is not phytotoxic (Kuhr & Dorough 1976).

A small test was done to determine any immediate detrimental affects carbofuran might have on ragwort. Eight large rosettes were transplanted from the Corvallis area to 10-inch diameter pots and grown in the glasshouse for 3–4 weeks. Half of the potted plants were sprayed with the field dose and half remained as controls. No damage to treated plants was found in the first month after treatment.

The number of cinnabar moth larvae was insufficient to cause significant damage to experimental plants, so flowering plants in treatments exposed to cinnabar moths were hand-defoliated between 13 and 24 July to simulate larval damage commonly encountered in other populations in North America and Europe (Isaacson 1973, van der Meijden 1979; Dempster 1982, Henneberger 1986; Crawley & Gillman 1989). Flowering plants were hand-defoliated by stripping the laminae from the petioles and removing the capitula, leaving bare stems and petioles. Using this same method at another western Oregon site, Henneberger (1986) found that survivorship, fecundity and leaf of production of plants defoliated and deflorated by cinnabar moth larvae was similar to plants defoliated and deflorated by hand. Rosettes were not defoliated because they are rarely fed on by cinnabar moth larvae. (The degree to which the larvae do feed on rosettes is not well documented, but two of the authors (unpublished) have found in another field study that cinnabar moth larvae had a negligible effect on rosettes and on the transition of rosettes to reproductive plants.)

MEASURES OF PLANT RESPONSE

Cohort censuses

In February 1987, two large rosettes from each treatment in a block were randomly selected and marked with metal tags attached to the base of the plant. Survivorship, number of leaves present, and the number of capitula present was censused monthly during the winter and once every 2 weeks during spring and summer.

Plot harvests

The plants were first harvested in March to ensure that all plots were initially similar in plant age structure, density and biomass, and to determine the effectiveness of the beetle exclusions. All ragwort plants in a plot were dug up and the root crown diameter was measured with callipers. None of the plants had bolted or flowered. Beetles were extracted from the plants as described below.

The second harvest was taken in August to measure the effect of treatments on plant density, biomass and reproduction, and to determine the number of beetle larvae present. Reproductive ability was determined by the number of capitula per flowering stem, the number of seeds per mature capitulum, and seed viability. Subsampling was required to determine seed number and viability. To subsample, three mature seed heads were collected from two randomly selected plants in each plot. The plots exposed to cinnabar moth larvae did not have mature seed heads at the time of the harvest so they were sampled later on 25 September. From each treatment in each block, 100 achenes were tested for germination using the methods described by McEvoy (1984). Thirty days were allowed for germination. Those achenes which failed to germinate were further tested for viability by staining with tetrazolium.

Beetle extraction

The abundance of beetle larvae was determined in plants from each treatment and size category. Beetles were extracted from the plants using Tullgren funnels (Southwood 1978; James 1989) with 25-watt bulbs for small plants and 40-watt bulbs for large plants. Plants were left in the funnels for 7 days. Once extraction was complete, plants were dried at 60 °C for 3 days and weighed to determine dry biomass.

Results

MARCH HARVEST

In the initial harvest (March 1987), total ragwort density and biomass did not differ among treatments (Table 1). However, when plants were broken into different size-classes, medium-sized vegetative plants had a significantly greater plant density in moth-exposed treatments ($\log_e$ transformation, $F_{1,9} = 19{\cdot}84$, $P \leq 0{\cdot}01$), and the vegetative plant biomass for small and medium-sized plants was

Table 1. Ragwort plant density and biomass and flea beetle larval densities found in March 1987, prior to treatment. Values are means of four 0·25-m^2 plots (with 95% confidence limits). Vegetative plant size was determined by root crown diameter where small are 0–1 mm, medium are 1–10 mm, and large are 10–20 mm. No plants were in the flowering stage. Statistical analysis was 2 × 2 ANOVA. Log_e-transformed data was used on plant density and biomass to equalize the variances

	Treatment			
Measured character	Neither insect	Moth only	Beetle only	Both insects
Small plants per plot	28·5 (5·9–116·9)	12·87 (0·70–112·3)	25·8 (18·5–33·1)	37·5 (31·5–44·6)
Medium plants per plot*	17·25 (7·2–27·3)	30·0 (18·3–41·8)	10·3 (4·5–16·1)	22·0 (15·3–28·7)
Large plants per plot	7·5 (4·9–10·1)	7·5 (6·5–8·5)	7·0 (6·2–7·8)	7·8 (5·9–6·6)
Small & medium plant biomass (g per plot)*	15·3 (7·4–23·1)	25·2 (13·7–36·7)	14·6 (6·7–22·5)	30·3 (18·4–42·3)
Large plant biomass (g per plot)	150·0 (110·2–189·9)	124·5 (91·9–157·0)	192·9 (99·4–286·4)	136·7 (83·0–190·3)
Total plant biomass (g per plot)	165·3 (125·6–204·9)	149·7 (118·9–180·5)	207·5 (107·1–307·8)	167·0 (114·5–219·5)
Beetle larvae per plot†	4·9 (0·01–33·1)	2·9 (−0·2–17·7)	322·8 (161·9–636·8)	251·1 (129·7–481·5)
Beetle larvae g^{-1} dry plant†	0·09 (−0·03–0·21)	0·05 (−0·03–0·15)	1·56 (0·76–3·68)	1·47 (0·77–3·09)

* Significant cinnabar moth effect ($P \leq 0{\cdot}01$).
† Significant beetle effect ($P \leq 0{\cdot}01$).

correspondingly higher in these plots (log_e transformation, $F_{1,9} = 9{\cdot}57$, $P \leq 0{\cdot}01$). The reason for this is unknown.

This harvest also demonstrated the effectiveness of beetle exclusions (Table 1), with beetle-protected plots having significantly fewer total larvae (log transformation, $F_{1,9} = 40{\cdot}9$, $P \leq 0{\cdot}001$) and fewer larvae per gram of plant dry mass ($F_{1,9} = 40{\cdot}8$, $P \leq 0{\cdot}001$) than beetle-exposed plots.

COHORT CENSUS AND AUGUST HARVEST

In August 1987, exposure to beetles had a highly significant effect on vegetative plant density (log transformations, for small plants $F_{1,9} = 34{\cdot}2$, $P \leq 0{\cdot}001$, for medium plants $F_{1,9} = 68{\cdot}4$, $P \leq 0{\cdot}001$) (Fig. 1). There were no large rosettes in any of the harvested plots. Beetles reduced small and medium vegetative plant densities by 95% and 98%, respectively, as compared to control plots. There was no significant moth effect on vegetative plant density; this was expected since none were artificially defoliated. The number of flowering plants at the time of harvest was not affected by either the beetle, the moth, or the combination of the two. Furthermore, all tagged rosettes survived to flower that summer.

Beetle treatments had a highly significant effect on small vegetative plant biomass (inverse transformation, $F_{1,9} = 24{\cdot}82$, $P \leq 0{\cdot}001$); beetle-exposed plots had only 19% of the small plant biomass found in control plots. The cinnabar moth had no significant effect on small vegetative biomass at the 5% level (Fig. 2), but there was a significant interaction between cinnabar and beetle effects for large vegetative plant biomass (interaction $F_{1,9} = 5{\cdot}73$,

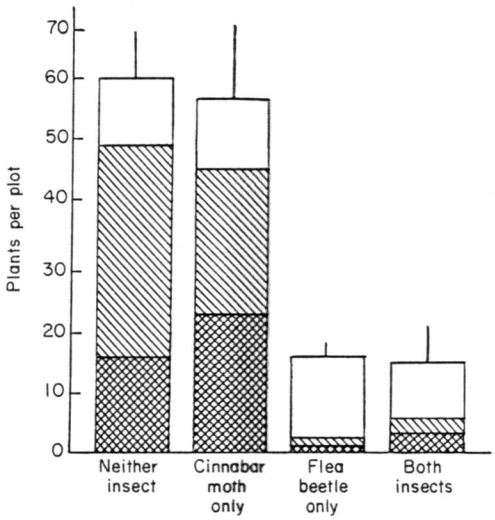

Fig. 1. The effect of herbivore treatment on plant density, by stage, in August (bars: +ve SE). Cinnabar moth damage was simulated with hand-defoliation of flowering plants. There were no large vegetative plants (root crown diameter >10 mm) present. □, flowering plants; ▨, medium vegetative plants (root crown diameter 1–10 mm); ▩, small vegetative plants (root crown diameter 0–1 mm).

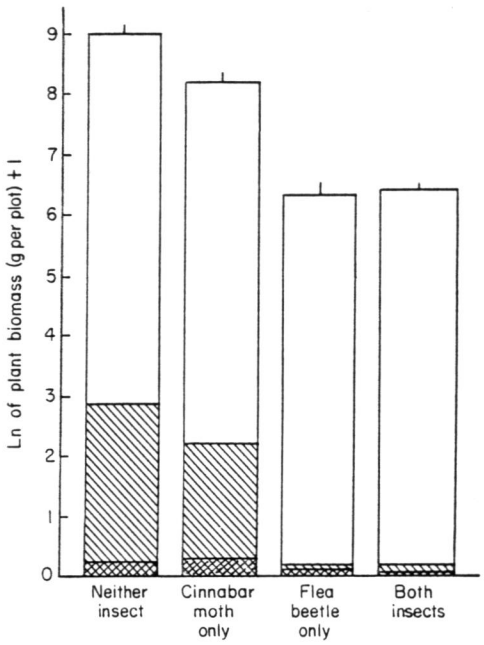

Fig. 2. The effect of herbivore treatment on plant biomass, by stage, in August (bars: +ve SE). Cinnabar moth damage was simulated with hand-defoliation of flowering plants. □, flowering plants; ▨, medium vegetative plants (root crown diameter 1–10 mm); ▩, small vegetative plants (root crown diameter 0–1 mm).

$P \leq 0{\cdot}05$). When acting in the absence of the cinnabar moth, the beetle effectively reduced large plant biomass by 99% (as compared to controls). In the absence of the beetle, the cinnabar moth reduced large vegetative plants by 60% (Fig. 2). This effect must have been indirect because hand defoliation was applied only to flowering plants. Neither insect, nor the combination of the two, had any significant effect on flowering plant biomass.

Acting independently, neither the cinnabar moth nor the beetle had much impact on the mean number of leaves per flowering plant (Table 2). At the time of the harvest, one month after the defoliation treatment, flowering plants in the cinnabar moth only treatment had regenerated nearly all of their leaves. Beetles appear to have had some impact on the number of leaves but their effect was greatly magnified by the presence of the cinnabar moth, as there was a significant interaction between the two main effects ($\log_e$ transformation, $F_{1,9} = 7{\cdot}06$, $P \leq 0{\cdot}05$).

The interaction between cinnabar moth and flea beetle effects arises because the beetle reduces the plant's ability to regenerate leaves after defoliation. Evidence for this was also seen when changes in foliage production (Fig. 3) were followed over a period of time. There was little difference between treatments in foliage production before defoliation. In early July, the number of leaves per plant in the control began to decline as plants matured. Simulated moth defoliation caused an abrupt decline in leaf number and then regrowth occurred and senescence was delayed. When exposed to both insects, the plant's ability to regenerate defoliated leaves was greatly reduced. In plots exposed to beetles only, senescence occurred slightly earlier than in controls.

The success of plant reproduction is a function of both the number of capitula produced and the number and viability of the achenes produced per capitulum (realized fecundity, Table 2). At the time of harvest, the cinnabar moth and the beetle each caused a significant reduction in capitulum production: cinnabar moths reduced capitulum number by 77% and beetles reduced it by 39%

Table 2. The relationship between treatments and ragwort achene number, mass, and viability in August 1987. Values are means of four 0·25-m^2 plots (with 95% confidence intervals). Cinnabar moth damage was simulated with artificial defoliation. Statistical analysis was a 2 × 2 ANOVA, $\log_e$-transformed data were used for leaf number, square-root transformed data were used for capitulum number to equalize the variances

	Treatment			
Measured character	Neither insect	Moth only	Beetle only	Both insects
Leaves per stem*	37·9 (21·2–64·4)	37·0 (23·3–58·7)	31·5 (21·4–46·0)	8·8 (4·9–9·4)
Capitula per stem*†‡	240·6 (111·4–415·4)	53·9 (28·9–86·4)	144·0 (75·9–233·4)	2·4 (−0·7–9·1)
Achenes per head*†	65·5 (60·0–71·0)	55·0 (51·4–58·6)	66·5 (59·6–73·4)	53·5 (37·1–69·9)
% Viable achenes*	34·9 (21·4–48·4)	25·7 (17·2–34·2)	54·3 (34·0–74·6)	0·0 (0·0`
Realized fecundity§	5 500	762	5 200	0

* Significant interaction between cinnabar moth and beetle effects ($P \leq 0{\cdot}05$).
† Significant cinnabar moth effect ($P \leq 0{\cdot}01$).
‡ Significant beetle effect ($P \leq 0{\cdot}05$).
§ The product of capitula per stem, achenes per head, and the fraction of viable achenes.

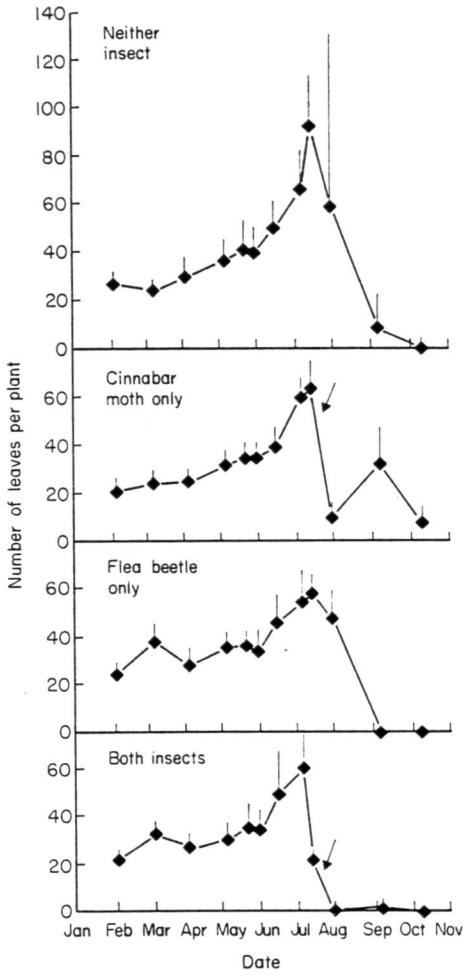

Fig. 3. Ragwort foliage production throughout 1987 for each herbivore treatment. Points represent mean (bars: +ve SE) number of live leaves from a marked cohort of second year plants. Arrows indicate timing of hand-defoliation used to simulate cinnabar moth feeding.

of control levels (square root transformation, for moths $F_{1,9} = 42{\cdot}4$, $P \leq 0{\cdot}001$, for beetles $F_{1,9} = 10{\cdot}4$, $P \leq 0{\cdot}05$, interaction NS). Together, the two insects reduced the number of capitula by 98%.

Only cinnabar moth treatments had a significant effect on the number of achenes per head ($F_{1,7} = 10{\cdot}30$, $P \leq 0{\cdot}01$), reducing achene production by 15% (Table 2). Achenes in the treatments exposed to the cinnabar moth were collected 1 month later than the other treatments since they matured later. A dramatic effect was seen in seed viability where there was a significant interaction between moth and beetle effects ($F_{1,9} = 13{\cdot}41$, $P \leq 0{\cdot}01$). In plots exposed to both insects, none of the seeds sampled were viable (Table 2). Cages may have reduced pollinators' access to flowers. Pollinators were observed visiting flowers that were near the cage screens.

The census determined the effect of treatments on capitula production and development over the flowering season and further illustrated the interaction that occurred between beetle and cinnabar moth effects. The earliest stage of flower development (buds) was little affected by any treatment, yet the survivorship of the buds to maturity was strongly reduced by herbivory (Fig. 4). Simulated cinnabar damage reduced and delayed flower production while beetles alone caused only a small reduction in flowers and fruits. When both insect treatments occurred together, flower and fruit production was negligible.

SIDE-EFFECTS OF CAGING

The side-effects of caging were minimal for most parameters measured (Table 3), except that caging increased flowering plant biomass by 37%. Numbers of capitula per stem were not significantly different, but did appear to be higher in open plots and may account for some of the difference in biomass of flowering plants. For this reason, use of sham cages was prudent but did not have a strong effect on the final results. The effect of cages on pollination was not measured. However, plants in cages that were continuously closed were given less of an opportunity for pollination than plants in sham cages, and this may explain the low levels of viability in the caged control plots. Had we provided for uniform pollination, the effects of the beetle with and without the moth would have been magnified.

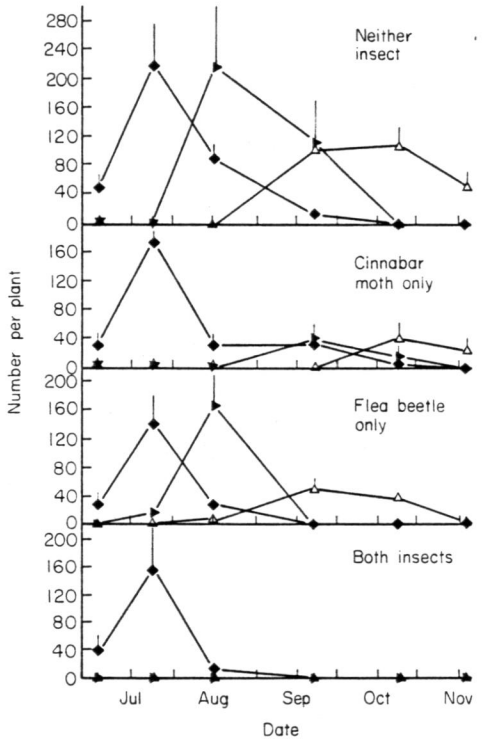

Fig. 4. Ragwort capitulum production throughout the 1987 flowering season for each herbivore treatment. Points are means (bars: +ve SE) from a marked cohort of plants. Three stages of development are represented: ◆, buds; ►, flowers; △, fruits (capitula whose achenes have a well-developed pappus). Arrows indicate timing of hand-defoliation used to simulate cinnabar moth feeding.

Table 3. A comparison of the side-effects of cages on various ragwort characteristics in August 1987. *F* ratios are from ANOVAS. Square-root transformed data were used for capitula number to equalize the variances

Measured character	Means (SE) Sham plots*	Open plots†	*F* ratio (df = 1, 9)
Small vegetative plants per plot	3·25 (2·36)	1·50 (1·19)	1·62‡
Large vegetative plants per plot	2·25 (2·25)	2·25 (1·93)	<0·005‡
Flowering plants per plot	9·50 (1·44)	11·25 (1·18)	0·95‡
Small vegetative plant biomass (g)	0·03 (0·02)	0·04 (0·02)	0·40‡
Large vegetative plant biomass (g)	0·20 (0·20)	0·83 (0·72)	1·47‡
Flowering plant biomass (g)	484·83 (53·13)	291·92 (49·78)	72·69§
Leaves per stem on flowering plants	9·75 (2·59)	11·00 (3·49)	0·10‡
Capitula per stem on flowering plants	2·99 (1·35)	16·38 (14·17)	1·35‡

* Plots with cages that are open year round and exposed to both insects.
† Plots with no cages.
‡ Not significant.
§ $P \leq 0{\cdot}01$.

Discussion

The results of our experiment support the hypothesis that two insects together, feeding on different plant parts and at different times of the year, can have a greater impact on host-plants than either insect acting alone. Alone, beetles decreased vegetative plant biomass and density and the cinnabar moth treatment reduced fecundity. There was a statistically significant interaction in the effects of the two types of insect damage on flowering plants, which was interpreted to mean that there was a synergistic effect resulting from the plant's inability to recover from defoliation and defloration when the beetle was present. The combination of both herbivore treatments reduced achene production and viability to the extent that fecundity was negligible.

Even though the two insects were more effective together, the beetle was quite effective alone. The high mortality of young plants (80–99%) caused by beetle activity undermined the pyramidal structure of the plant population, leaving fewer individuals to be recruited into the reproductive stage. The beetle also reduced flower production and caused early senescence of plants. However, simulated cinnabar moth defoliation of flowering plants had a greater impact on plant reproduction.

A decrease in vegetative plants was seen in the simulated cinnabar moth treatment, despite the initially higher densities in these plots before the treatments were initiated. This result was unexpected and must be a result of indirect effects, such as increased sunlight to the plots. We speculate that increased sunlight may have increased competition for other resources or caused unfavourable environmental conditions (such as desiccation). We exclude the possibility that the number of rosettes decreased due to an increase in their transition to the flowering stage, because there was no increase in the number of flowering plants and there was no observed mortality of flowering plants.

Myers *et al.* (1989) suggest that the success of biocontrol could be improved by selecting those species of agents which are likely to be successful rather than by selecting several different agents. They suggest that agents which kill later life stages of the host tend to be more successful. However, Murdoch (1990) suggests that temporal and physical refuges for the pest can lead to incomplete control and such a situation is more likely to occur if only one life stage of the host is attacked. We suggest a combination of the two approaches: each agent should be carefully selected based on its likelihood to succeed, but also combinations should be selected of agents that attack different plant parts, different life stages, and/or in different seasons to reduce the number of invulnerable stages and spatial or temporal refuges.

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