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DISTURBANCE, COMPETITION, AND HERBIVORY EFFECTS ON RAGWORT *SENECIO JACOBAEA* POPULATIONS¹

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Abstract. The balance of forces determining the successful control of ragwort *Senecio jacobaea* by introduced insects was investigated in a field experiment by manipulating the time of disturbance, the level of interspecific plant competition, and the level of herbivory by the cinnabar moth *Tyria jacobaeae* and the ragwort flea beetle *Longitarsus jacobaeae*. We used a factorial design containing 0.25-m² plots arranged as 4 Blocks × 2 Disturbance Times (plots were tilled in Fall 1986 or Spring 1987) × 3 Plant Competition levels (vegetation other than ragwort was Removed, Clipped, or Unaltered) × 2 Cinnabar Moth levels (Exposed, Protected) × 2 Flea Beetle levels (Exposed, Protected). The response of ragwort was measured as colonization, survivorship, and reproduction of the first ragwort generation, establishment of juveniles in the second generation, and changes in ragwort biomass from 1987 through 1990. We also made annual measurements from 1987 through 1990 of the allocation of space (the limiting resource in the Unaltered competition treatment) among the categories ragwort, other species, litter, and open space. Natural enemy responses were characterized by relating variation in the concentration of enemies and the concentration of ragwort among patches.

We found that abundant buried seed and localized disturbances combined to activate incipient ragwort outbreaks, and that interspecific plant competition and herbivory by the ragwort flea beetle combined to inhibit the increase and spread of incipient outbreaks. Time of disturbance had little effect on the outcome of biological control. Under conditions in the Removed and Clipped treatments (where there was sufficient open space for germination and establishment), reduction in seed production in the first generation caused by cinnabar moth larvae led to a reduction in plant numbers in the second generation, but caused only a weak effect on ragwort cover and no detectable effect on ragwort biomass over the longer term from 1986 through 1990. At the spatial scale examined, inhibition by the ragwort flea beetle and plant competition took the extreme form of elimination of all ragwort individuals except the pool of seed buried in the soil.

Our findings lead us to (1) reject the view that successful biological control leads to a stable pest–enemy equilibrium on a local spatial scale, (2) strongly endorse “search and destroy” and weakly endorse “complementary enemies” strategies suggested by Murdoch et al. (1985) as ways to improve control, and (3) emphasize resource limitation in the pest at low density as a key feature distinguishing biological control of weeds from biological control of insects.

Key words: biological control; colonization; competition; disturbance; field experiment; insect herbivory; life cycle; *Longitarsus jacobaeae*; population dynamics; *Senecio jacobaea*; succession; *Tyria jacobaeae*.

INTRODUCTION

Classical biological weed control is achieved by herbivore introductions that reduce and maintain pest populations below an economic threshold resulting in the replacement of the weed by more desirable vegetation. Some spectacular and widely cited cases are control of *Opuntia* in Australia (Dodd 1940) and Klamath weed *Hypericum* in California (Huffaker and Kennett 1959). Despite interest aroused by these successes, there has been comparatively little effort in ensuing years to test assumptions and predictions of ecological theories offered as explanations of biological

control. Do herbivores impose a low, stable pest–enemy equilibrium at a local spatial scale, or does local extinction occur? Is success more likely from a single “best” herbivore species or from the cumulative effects of multiple herbivore species? Is plant competition necessary to augment the impact of natural enemies on the dynamics of weed populations?

The control of ragwort *Senecio jacobaea* L. by cinnabar moth *Tyria jacobaeae* (L.) and ragwort flea beetle *Longitarsus jacobaeae* (Waterhouse) provides an ideal system for investigating questions about successful biological weed control. Ragwort is representative of a large class of weed problems in which an exotic plant, toxic to livestock and capable of displacing desirable forage, infests large areas of nonirrigated pasture and range. Introduced natural enemies are well established

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and have exerted strong and steady depression of ragwort over much of the Pacific Northwest under very diverse conditions (Hawkes and Johnson 1978, McEvoy 1985, 1989, Pemberton and Turner 1990, McEvoy et al. 1991). The population ecology of ragwort has been studied for half a century in native populations in Europe (Cameron 1935, Harper and Wood 1957, Dempster 1971, 1975, 1982, van der Meijden 1971, 1979, Forbes 1977, Dempster and Lakhani 1979, van der Meijden and van der Waals-Kooi 1979, Lakhani and Dempster 1981, Crawley 1983, Crawley and Nachapong 1984, 1985, Crawley and Gillman 1989) and in introduced populations in North America (Harris et al. 1971, Isaacson 1971, 1978, Myers 1976, 1980, Myers and Campbell 1976, Harris et al. 1978, McEvoy and Cox 1987), Australia (Bornemissza 1966, Schmidl 1972*a, b*) and New Zealand (Poole and Cairns 1940, Wardle 1987), and therefore many of the ecological processes affecting ragwort's distribution and abundance have been recorded.

Three issues motivating this study

Local equilibrium vs. local extinction.—Nearly 40 yr ago, referring to successful control of the Klamath weed by the defoliating *Chrysolina* beetle, Huffaker (1953) wrote: "A weed under biological control by its density-dependent, controlling insect would of course undergo the oscillations characteristic of this type of control. The success of this project will be ascertained not on the basis of the number of acres completely freed of the weed but in terms of the average level of weed abundance over a period of years as it is maintained in equilibrium with the insects feeding on it, as contrasted with its proved capabilities in the absence of the beetles. It is expected that if the program is successful, the stands of weed will be greatly reduced in size and will constantly shift from place to place, as in its turn is discovered and gradually weakened or destroyed. New weed patches will of course be coming into being all the while." Since successful control of Klamath weed was primarily responsible for fostering the establishment and expansion of the subdiscipline of biological control of weeds in North America, it is significant that early practitioners characterized the biological control process as leading to a general condition of local instability and stable average concentration of the pest.

By contrast, the standard mathematical theory used to represent and analyze biological control systems has held that enemies control pests by reducing their density to a new low, but nonzero stable equilibrium via density-dependent mechanisms operating on a local spatial scale (Beddington et al. 1978, Hassell 1978, Caughley and Lawton 1981, Crawley 1983, Hassell 1984, May and Hassell 1988, Bergelson and Crawley 1989). In this usage, local is taken to mean the area within which complete mixing is assumed to occur each generation. Successful control then requires that the

negative effects of the enemy on the pest are sufficiently strong to depress pest density to low levels, and sufficiently aggregated to stabilize the interaction over the longer term, thereby preventing wide amplitude fluctuations, outbreaks, or local extinctions. The focus of theoretical research, applied mainly to control of insects rather than weeds, has been to determine what degree of aggregation will yield stability, the relationship between aggregation and organism density, and the various forms of heterogeneity (individual, spatial, and temporal) that yield the desired level of aggregation (Hassell and May 1973, 1974, May 1978, Hassell 1984, Kareiva 1990, Pacala et al. 1990). Several mechanisms that aggregate risk have been found to confer stability on simple mathematical models, and theorists have suggested that screening candidate biological control systems for such stabilizing mechanisms could improve the prospects for successful biological control (Hassell 1978, 1985). There are now both theoretical and empirical grounds for doubting the wisdom of this strategy (Murdoch et al. 1985, Murdoch 1990). Murdoch et al. (1985) claim that many successful control systems are characterized by local extinctions and reinvasions, and many such systems appear to lack the mechanisms that yield stability in models. More unsettling, there is theoretical and experimental evidence that some stabilizing mechanisms operating on a local scale actually interfere with control and lead to higher pest densities (Murdoch and Stewart-Oaten 1989, Murdoch 1992).

Alternative mathematical theories have addressed the question of how local populations that individually exhibit unstable dynamics may collectively persist at a larger spatial scale (Reeve 1988, 1990, Taylor 1990). In theory this requires sufficient asynchrony and sufficient migration among local populations to prevent elimination on more global scales. The challenge is to establish what the sufficient conditions are. By examining biological control systems in this way, we are likely to find new attributes whose importance is obscured by the classical approach.

Field experiments can help discriminate between these alternative theories by answering an important question: To what extent does stability on a local spatial scale contribute to persistence of biological control in the field relative to the contribution of asynchrony and migration between subpopulations? Discrimination may be difficult in the field due to the subjectivity involved in defining the term "local population," inferring population extinction from samples, and selecting scales of spatial heterogeneity and movement to be investigated (Sabelis and Diekmann 1988). Nevertheless, models that differ so radically in their assumptions and predictions should allow a distinction on the basis of experimental observations.

Our experiment asks whether natural enemies regularly eliminate local pest populations that would persist in the absence of natural enemies.

Single vs. multiple enemy species.—A second controversial issue in biological control is whether it is a better strategy to introduce a single “best” enemy species or whether several natural enemy species should be introduced for greatest effect. Some have suggested 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 (Turnbull and Chant 1961, Watt 1965, Kakehashi et al. 1984). This view suggests interference competitors should be avoided in weed biological control (Harris 1992), although in some cases the level of interference appears to be too low to matter (Story et al. 1991). Others have suggested that multiple introductions will often provide the greatest effect, or at least a good way of identifying the best single species or combination of species without any attendant risks of diminished control (Huffaker et al. 1971, van den Bosch and Messenger 1973, May and Hassell 1981, Waage and Hassell 1982). It may be desirable to favor complementary enemies that attack different plant stages (thereby avoiding invulnerable stages), at different times (thereby avoiding temporal pest refuges), or in different spatial locations (thereby avoiding spatial pest refuges), yielding more effective exploitation of the pest (Huffaker et al. 1971, Murdoch et al. 1985, McEvoy et al. 1990, Harris 1992, James et al. 1992). Myers (1985) claims success is more likely to be caused by a single insect, and the strategy for achieving success resembles a lottery: the greater the number of enemy species introduced and established, the greater the possibility of finding the one natural enemy (“the silver bullet”) that brings success.

Our experiment asks whether a combination of enemy species is more effective than a solitary species when treating ragwort infestations.

Plant competition vs. herbivory.—Even when herbivorous insects have caused dramatic depression in host abundance, their role in maintaining the host at low levels is not clear. Many changes, both extrinsic (e.g., land management) and intrinsic (e.g., density and frequency-dependent species interactions), accompany successful weed control. Crawley (1983) suggests that the problem is one of discrimination of alternative causes: while herbivores may cause a crash in weed abundance, it may be interspecific plant competition that maintains weeds at low density (confined to areas of local and temporary soil disturbance where competition is slight). If herbivory and plant competition act sequentially as hypothesized by Crawley, the natural enemies may no longer be needed in a local area after they have done their job. Natural enemies would operate more like a biological pesticide than a regulator of pest populations around a mean density.

In contrast to the sequential view of enemies and plant competition, herbivory and plant competition may act concurrently, in which case interactions between the two processes become crucial. For example, an increase in the background vegetation may increase

the negative effect of herbivory if plants weakened by competition are less resistant to herbivory because of changes in plant tolerance, plant defenses, or consumer preference. Alternatively, an increase in the background vegetation could make an herbivore ineffective by decreasing its search efficiency or increasing mortality due to its natural enemies (Root 1973, Kareiva 1983). An increase in selective herbivory may increase the negative effect of competition by placing a grazed plant in a subordinate position within the hierarchy of a crowded population or community (Harper 1977, Lee and Bazzaz 1980, Fowler and Rausher 1985). Alternatively, an increase in herbivory may increase the competitive ability of the attacked plant, a popular idea that has little supporting evidence (see reviews by Belsky 1986, 1987). Thus competition and herbivory may interact in their effects, either to the benefit or detriment of weed control.

Our field experiment asks whether combining natural enemies and plant competition is more effective than either factor alone when treating weed infestations.

The hypotheses

The global hypothesis underlying this research is that persistent biological control results from a balance short-range activation of weed outbreaks by local disturbance and weed colonization, and their long-range inhibition by insect herbivory and plant competition. Activation and inhibition often act on different scales of space and time: activation is largely local and immediate, whereas the source of inhibition is largely nonlocal and delayed. Short-range activation and long-range inhibition are basic features in a wide variety of models of pattern formation in physical and biological systems, ranging from landscape patterns, to animal coat markings, to chemical mixtures (Meinhardt 1982, Levin 1988).

The subsidiary hypotheses of this research are as follows:

- H1) The Activation Hypothesis is that localized disturbance and buried seed (the seed bank) combine to create incipient weed outbreaks.
- H2) The Inhibition Hypothesis is that insect herbivory and interspecific plant competition combine to oppose increase and spread of incipient weed outbreaks.
- H3) The Stability Hypothesis is that the balance in short-range activation and long-range inhibition leads to a general condition of local instability and stable average spatial concentration of the pest.

Natural history of the organisms

Ragwort (*Senecio jacobaea*, Asteraceae) is a biennial or short-lived perennial native to Europe and introduced to North America, Australia, and New Zealand. The plant displaces forage species in pastures, is toxic

to livestock, and is a target of biological, chemical, and cultural control programs. Ragwort was first recorded in western North America in 1913 from Vancouver Island (Harris et al. 1971) and first recorded in Oregon in 1922 from Portland (Isaacson 1971). The weed now ranges in maritime regions of western North America from northwestern California to British Columbia; in Oregon, it is common from the coastline to the Cascade Mountains and less abundant in the more continental regions of eastern Oregon (Dennis Isaacson, Oregon State Department of Agriculture, *personal communication*). The life cycle of ragwort has been reviewed by Cameron (1935), Poole and Cairns (1940), Harper and Wood (1957), and Wardle (1987). Wind dispersal generally places seeds within a few metres of the parent plant, and seed density falls off steeply with distance (Poole and Cairns 1940, McEvoy and Cox 1987), but the few seeds that travel long distances can be crucial for colonizing new areas. Where ragwort is introduced, it tends to leave large reserves of seed in the soil (Thompson and Makepeace 1983, McEvoy 1985, McEvoy et al. 1991) and longevity estimates (time to reach 1% viability in the soil) indicate that ragwort seed persists in the 0–2 cm surface layer at least 4–5 yr and for at least 10–16 yr when buried below 4 cm (Thompson and Makepeace 1983). Seed density declines rapidly with depth (McEvoy et al. 1991), and seeds buried below ≈ 1.5 –2.0 cm do not normally receive the conditions, resources, or stimuli needed for germination but persist in a state of enforced dormancy (Poole and Cairns 1940, Harper and Wood 1957, van der Meijden and van der Waals-Kooi 1979). Growing vegetation and accumulation of litter can suppress germination in the field (Cameron 1935). Thus the recruitment of individuals from the seed bank to the population of actively growing seedlings appears to depend on disturbance that moves buried seed nearer to the soil surface and removes vegetation and litter. Pulses of germination occur in field populations in both fall and spring (Poole and Cairns 1940, van der Meijden and van der Waals-Kooi 1979). The death risk for plants germinating from seed declines with stage; Forbes (1977) estimated 57% die as seedlings, 29% as single rosettes, 6% as multiple rosettes, and the remaining 8% die after flowering. The usual biennial, semelparous life cycle can be converted into a perennial, iteroparous one by the stresses of crowding, cutting, or defoliation (Cameron 1935, Dempster 1982, Cox and McEvoy 1983, Crawley and Gillman 1989). Seed production per individual plant varies greatly with these influences as well; the range in population means among sites is reported to be 68–2489 capitula per plant in Cameron (1935) and 110–392 capitula per plant in Harper and Wood (1957), with an average of 70 seeds per capitulum.

The cinnabar moth (*Tyria jacobaeae*, Arctiidae) was introduced as a biological control agent from France and released near Fort Bragg, California in 1959

(Hawkes 1968) and near Jordan (Linn County) and Valley Junction (Polk County), Oregon in 1960 (Isaacson 1971). The biology of the cinnabar moth has been reviewed by Dempster (1982). The adult moths emerge in May–June from the overwintering pupae and lay eggs in clusters averaging 40 eggs each on the underside of the basal leaves of the ragwort food plant. Mean fecundity in the field ranges from 73 to 295 eggs per female. Some plants are colonized by ovipositing adults, and others are colonized by immigrant larvae leaving defoliated hosts. Larvae can strip the flowering shoot to a bare stem, removing all the leaves and flowering heads. This rarely kills the plant, and in Oregon re-growth shoots develop in the autumn after larvae have entered the overwintering pupal stage.

The flea beetle (*Longitarsus jacobaeae*, Chrysomelidae) was introduced from Italy and released in California near Fort Bragg in 1969 (Frick 1970b, Frick and Johnson 1973, Hawkes and Johnson 1978) and in Oregon near the Trask River (Tillamook County) in 1971 and near Salem (Marion County) in 1972 (Isaacson 1978). The life history is described by Newton (1933), Frick (1970a, 1971), and Frick and Johnson (1972, 1973). Adults of the Italian biotype aestivate in summer, and resume activity in autumn when they mate and feed on foliage. Adults are pit feeders, rasping holes in the leaves of seedlings and rosettes. Eggs are laid singly on the plant or adjacent soil and larvae develop through three instars, tunneling and feeding in leaves, petioles, stems, and roots during winter and early spring. Pupation occurs in the soil and adults emerge in early summer.

An incidental organism in our study was the ragwort seed head fly *Botanophila seneciella* (Meade) (Diptera: Anthomyiidae) (formerly *Hylemia seneciella*). The seed head fly was introduced from Europe and released in California near Fort Bragg and in Oregon near Corvallis in 1966 (Frick 1969). Adults oviposit on unopened and newly opened flower buds, and one larva develops per head regardless of the number of eggs (Cameron 1935). It destroyed only a small fraction of heads (4%) not preempted by the cinnabar moth at our site. Removal experiments and field studies in England (Crawley and Pattasudhi 1988) show that there is strong interspecific competition between the fly and the cinnabar moth, and that competition is highly asymmetric: The cinnabar moth has a substantial effect on the recruitment of the fly, but the fly has no measurable impact on recruitment of the moth.

The plant community is characteristic of coastal pastures and grasslands in the Pacific Northwest, supporting a dense cover dominated by the introduced and widely established perennial grasses *Holcus lanatus* L., *Dactylis glomerata* L., *Anthoxanthum odoratum* L., and *Festuca arundinacea* Schreb. When our experiment began in 1986, ragwort ranked 16th in abundance in the community and represented 0.1% of the aboveground dry mass of the plant community.

METHODS

Experimental design

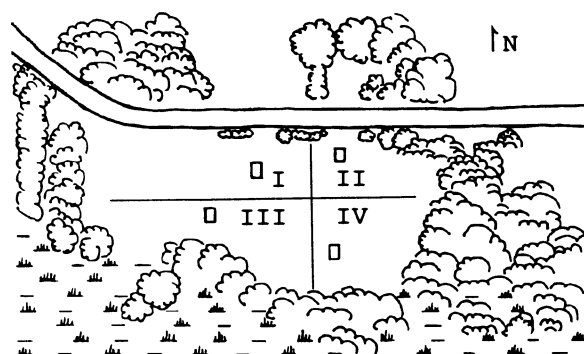
Our experiment concerns the roles of disturbance, plant competition, and insect herbivory in maintaining ragwort at low levels following successful biological control at Cascade Head on the central coast of Oregon. Five years of observational study prior to the start of experiments established the variability in abundance of ragwort, the insect herbivores, and the species in the background vegetation (McEvoy 1985, 1989, McEvoy et al. 1991). Although actively growing ragwort stages had declined to <1% of historical levels by the time we began the experiment in 1986, there remained a vast quantity of buried seed (geometric mean of ≈ 4000 seeds/m²), which may persist for many years (McEvoy 1985, 1989, McEvoy et al. 1991).

Deliberate soil disturbances and a natural abundance of buried seed allowed us to create many incipient ragwort outbreaks in small patches. There were two disturbance times, Fall 1986 and Spring 1987. To measure the ability of biological control to contain or annihilate these outbreaks, we then imposed a manipulative experiment consisting of a factorial arrangement of populations exposed to or protected from each herbivore, compounded with reduced (Clipped or Removed) and Unaltered levels of the background vegetation. The experiment was designed to last for the maximum duration of the life cycle of ragwort. The demography portion of the experiment reported here covers 1986 through 1989, long enough to determine the fate of 97% of the 4217 ragwort individuals recruited during the study period. Population dynamics are represented by annual estimates of percent cover and biomass for 1987 through 1990.

We allowed the abundances of insects to vary in exposed plots through the natural processes of immigration, emigration, survivorship, and mortality, rather than create a single control herbivore density. By letting moth and beetle density vary in exposed plots, we were able to achieve a continuous range of densities and approximate the form of functional relationships between herbivore density and plant biomass.

Experimental design and analysis

A 0.90-ha meadow at Cascade Head studied earlier (McEvoy 1985, McEvoy et al. 1990) was partitioned into four 0.22-ha blocks (Fig. 1), and 24 treatment combinations were allocated at random to 0.5×0.5 m plots within an 8×5 m area located randomly within each block. The experiment used a randomized complete blocks design and was analyzed with a four-way analysis of variance: 4 Blocks \times 2 Disturbance Times (Fall 1986, Spring 1987) \times 3 Levels of Background Vegetation (Removed, Clipped, Unaltered) \times 2 Levels of Exposure to Cinnabar Moth (Exposed, Protected) \times 2 Levels of Exposure to Flea Beetle (Exposed, Protected) = 96 plots.



Scale — 10 m

FIG. 1. Layout of replicate blocks for randomized complete blocks experiment that examined the effects of Time of Disturbance, Interspecific Plant Competition, and Insect Herbivory on ragwort populations. The study area is bounded on the north by a road and on the other sides by woodland, with wetland to the south.

To create the experimental disturbances, we initially tilled all plots by digging to a depth of 25–30 cm with a shovel, breaking up the sod and sieving out roots and rhizomes through wire mesh with 1.3×1.3 cm openings. To exclude fossorial rodents, we encircled each plot with wire mesh (1.3×1.3 cm openings), buried to a depth of 46 cm and overlapping the walls of the cage near the ground surface. Ragwort seedlings appeared soon after tilling with a Fall 1986 cohort established by tilling 5–16 September 1986 (plots in each block were tilled on the same day), and a Spring 1987 cohort established by tilling another set of plots 13–20 April 1987. The natural abundance of buried ragwort seed allowed us to achieve high initial seedling densities. We mapped the location of seedlings by placing a 25×25 cm (0.06 m²) sheet of acetate over a permanent subplot at the center of each plot and circling the position of each seedling on the map. We visited the plots at weekly intervals during the first 6–8 wk when seedlings were becoming established and changes in ragwort population size were fast, and at 1-wk to 3-mo intervals thereafter, when changes in population size were slow. In this way we followed the fate of each individual from the Fall 1986 and Spring 1987 cohorts, beginning with emergence and establishment, through growth and reproduction, to death.

We manipulated the background vegetation and insect herbivores to test their role in inhibiting the increase and spread of incipient ragwort outbreaks. The background vegetation colonizing each plot was either manually removed (Removed), clipped to a height of 5 cm (Clipped), or left unaltered (Unaltered). We excluded herbivores from Protected plots with cages (BioQuip, El Segundo, California). A cubic framework of 2.5 cm polyvinyl chloride plastic pipe, 60 cm on a side was placed over each plot to support nylon "Leno weave" netting cage covers (open spaces in the mesh

TABLE 1. Regression equations used to predict ragwort plant dry mass and its components.

Y	X	n	Intercept		Slope		r ²
			a	SE	b	SE	
log Y = a + b log X							
Number of capitula per adult	Basal diameter	122	-0.163	0.111	2.239	0.118	0.75
Dry mass of capitula per adult	Basal diameter	39	-2.299	0.188	2.655	0.204	0.82
Dry mass of foliage per adult	Basal diameter	39	-2.090	0.169	2.402	0.183	0.82
Total dry mass per adult	Basal diameter	39	-1.136	0.093	2.318	0.101	0.93
log Y = a + bX							
Dry mass of foliage per juvenile	Length of longest leaf	84	-1.998	0.066	0.066	0.003	0.88
Total dry mass per juvenile	Length of longest leaf	84	-1.726	0.057	0.061	0.002	0.90
Total dry mass per juvenile	Rosette diameter	84	-1.613	0.049	0.053	0.002	0.91

were 0.6 × 1.0 mm) used to exclude herbivores. Plots exposed to insects were covered with sham cages (on which the netting covered the top of the cages but was rolled half-way up the sides to allow access to herbivores, while ensuring that unwanted side effects of caging would be experienced equally by all plots). The herbivores were excluded from protected plots by securing the netting covering the cages firmly to the ground on all sides to prevent any access by herbivores and spot applications of insecticide (Rotenone dust, 1% active ingredient). Rotenone (which contains only C, H, and O) was chosen to avoid potential stimulation of plant growth by nitrogen-containing insecticides; it deteriorates rapidly in sun, air, and water (Anonymous 1990). On each visit to the plot, we renewed treatments as needed.

A convenience of the study system is that the beetle and the moth attack the host at different times of year. With the exceptions noted below, plots exposed to (1) neither insect were caged throughout the experiment, (2) cinnabar moth alone had cage covers removed during oviposition (May and early June), were sham caged during caterpillar feeding periods (late June and July), and were protected the rest of the year, (3) flea beetle alone were protected during the active period of cinnabar moth (late June and July) and sham caged the rest of the year when the beetle was active, (4) both insects were sham caged throughout the experiment. We temporarily removed sham cages on cinnabar-moth-alone plots to allow oviposition by the moth, and we removed sham cages and the tops of full cages to allow pollinator visits during the flowering season. During this period, barriers of adhesive (Stikem Special, Seabright Enterprises, Emeryville, California) were placed around the rim of the topless cages to exclude wandering cinnabar moth larvae, and the walls of the cage and spot applications of rotenone excluded flea beetle adults. We increased the height of cages (by stacking modular frames on top of one another) as needed when the height of plants increased during the growing season. As plants died back, we decreased the height of cages to reduce the risk of damage by fall and winter storms.

The distribution of flea beetle larvae among patches

of hosts was characterized by correlating beetle concentration and ragwort concentration per subplot in samples taken in March 1988. We estimated the number of flea beetle larvae in our experimental subplots by extracting larvae from plants growing in plot margins (the area outside of the subplot containing the experimental cohort), calculating the mean number of larvae per plant, and multiplying by the number of plants in our cohort. We harvested five marginal plants (or all survivors if less than five were available) from each plot. We then placed the plant material in Tullgren funnels (Southwood 1978), extracted the larvae for 7 d using a 25-W light bulb as a heat source (James 1989), and counted the number of larvae extracted. We estimated the dry mass of ragwort available to the larvae by drying (for 72 h at 60°C) and weighing the plant sample following beetle extraction. We then calculated the mean plant dry mass for each plot and multiplied by the number of plants in the cohort.

Similarly, the distribution of cinnabar moth larvae among host patches was described by correlating cinnabar moth concentration and ragwort concentration per subplot in samples taken in July 1988. We counted the number of cinnabar moth larvae on each ragwort plant in our experimental cohorts. We estimated the dry mass of food resources (ragwort foliage and capitula) using regression equations that predict the dry mass of plant parts in the absence of the cinnabar moth from nondestructive measurements of each plant in our cohort (Table 1). The dry masses of foliage and capitula of adult plants, as well as the total number of capitula produced, were estimated from a measurement of the diameter of the stem at the base of the plant made in July 1988. The dry mass of foliage of juvenile plants was estimated from measurements of the length of the longest leaf of each plant taken at the same time.

The parameters of the regression equations in Table 1 were determined by sampling plants spanning the range of sizes present in experimental cohorts from several sites in three different years (1986, 1987, and 1988). For this sample, we measured the length of the longest leaf of the juvenile plants, measured the stem diameter and counted capitula of adult plants, and divided both juvenile and adult plants into dry mass

components. We then dried (for 72 h at 60°C) and weighed the plant material. We carried out the regression analysis after we first transformed our data as necessary to make the relationships linear, and we pooled data taken across sites and years after analysis of covariance revealed no significant differences among sites and years.

We evaluated our control over the treatment variables in our experiment as follows. First, we estimated the percent cover of ragwort, the background vegetation, litter, and open space each year in July from 1987 to 1990. An observer estimated the proportion of ground occupied by a perpendicular projection of each component. Total cover for a single component could not exceed 100%, but total cover for all components in the plot could exceed 100% and normally did so. We compared cover estimates among competition treatments to determine whether our manipulation of background vegetation successfully created differences in mean background vegetation cover among competition treatments. Second, we compared insect densities in exposed and protected plots to test whether we had successfully manipulated the abundance of the cinnabar moth and the ragwort flea beetle. Third, we evaluated the unplanned intrusion by the seed head fly by comparing the number of heads infested by the seed fly in cinnabar-moth-Exposed and -Protected plots.

Our experiment allowed variation in abiotic (temperature and precipitation) and biotic (ragwort, background vegetation, beetle, moth, seed head fly) variables. This variability must be evaluated in light of the trade-off between including a wide range of conditions, so as to make any conclusions general, and a restricted set of conditions, thereby avoiding so much variability that analysis of the results yields no conclusions, or at best weak conclusions (Hairston 1989).

Ragwort responses were categorized as colonization, survival, reproduction, and population dynamics. Colonization included number of emerging seedlings and timing of emergence. The frequent monitoring of experimental plots allowed us to construct ragwort survivorship curves and estimate mean length of life per plot. Reproduction was measured and analyzed as number of adults in 1988 (the first ragwort generation after disturbance), seeds produced by these adults in 1988, and new juveniles established in 1989 (the second ragwort generation after disturbance) from seed produced in previous years. We also estimated ratios of these variables including seeds/adult (fecundity), juveniles/seed (establishment rate), and juveniles/adult (fertility). Following the usage of human demographers, we use "fertility" to describe actual reproductive performance and "fecundity" to denote the physiological maximum reproductive output (Caswell 1989). Population dynamics was described by outbreak development curves, in which annual estimates of biomass and cover were plotted against time for 1987 through 1990. We estimated total ragwort biomass

(above and below ground) indirectly from linear measurements using the regressions in Table 1 for 1987–1989 and directly by measuring dry mass of ragwort harvested from the plots in 1990. The area under the curve (biomass duration) defined by plotting annual estimates of ragwort biomass against time was used as integrative measures of ragwort abundance over time for testing of treatment effects. Biomass duration can be used to describe the extent and duration of the weed outbreak, from activation by disturbance, through maximum development, to eventual extinction. Similar measures are the area under the disease progress curve used by plant pathologists (Shaner and Finney 1977) and leaf area duration used by plant ecologists (Harper 1977). We used mean ragwort cover (instead of cover duration) to allow us to apply the arcsine transformation appropriate for percentages in the original data and thereby better meet the assumptions of the ANOVA. We also examined correlations among the suite of treatment variables (cover of other plant species, litter, and open space) manipulated by the Competition treatments.

Analysis of variance was carried out on the ragwort response variables representing colonization (number of emerging seedlings), survival (mean length of life), reproduction (numbers of adults, seeds, and next-generation juveniles), and population dynamics (biomass duration, mean cover). We used orthogonal contrasts to test if responses differed depending on (1) whether background vegetation was Present or Absent, (2) whether background vegetation was Clipped or Unaltered. Testing of reproductive responses was problematic because some treatment combinations (Unaltered competition treatment and Exposed beetle treatment) yielded all zero values for the response variables (number of adults and number of next-generation juveniles) or had high concentrations of missing values (number of seeds). In such cases our approach was to examine the data for adherence to assumptions (variances are homogeneous and missing values are randomly distributed among treatment combinations) and carry out statistical analysis on a subset of treatment combinations for which statistical assumptions were approximately met.

The ANOVA for reproductive responses was carried out on a subset of the experiment: two levels of competition (Clipped and Removed), two levels of the Moth (Exposed and Protected), and from one (Protected) to two (Exposed and Protected) levels of the Beetle, depending on the response variable. In interpreting reproduction, we adopted more stringent criteria for rejection of the null hypothesis of no effect to allow for the lack of independence in separate tests on three correlated reproductive responses (adults, seeds, next-generation juveniles). We estimated ratios of variables including seeds/adults (fecundity), juveniles/seed (establishment rate), and juveniles/adult (fertility), but did not test for treatment effects because further testing

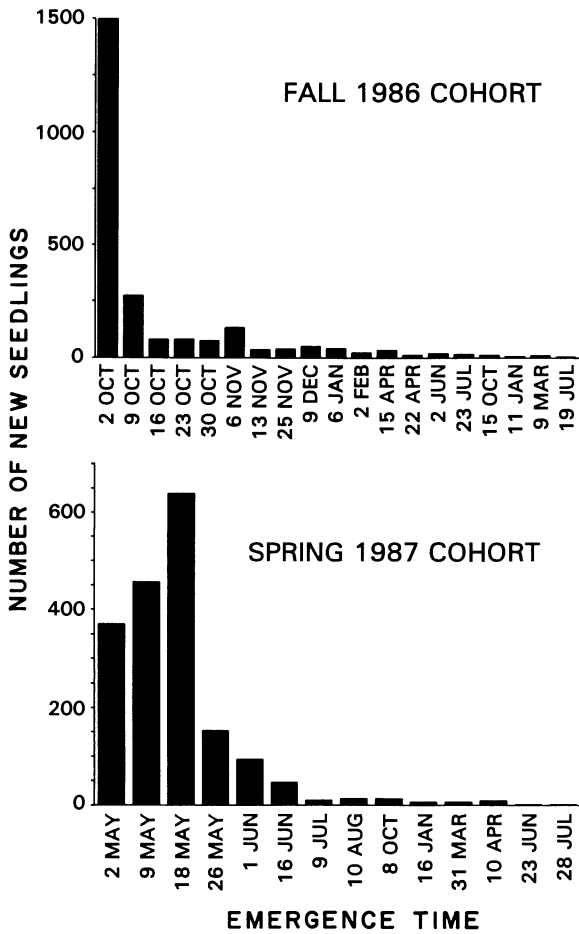


FIG. 2. Distributions of seedling emergence times for Fall 1986 and Spring 1987 ragwort cohorts. Cohorts were established by tilling 5–16 September 1986 (Fall 1986) and 13–20 April 1987 (Spring 1987).

TABLE 2. Effects of timing of disturbance, competition, and herbivory treatments on total number of emerging ragwort seedlings per 0.06-m² subplot. ANOVA performed on untransformed data.

Source of variation	df	MS	F	P
Block	3	2883	6.25	.0008
Time (T)	1	3553	7.70	.0071
Beetle (B)	1	301	0.65	.4221
Competition (C)				
Removed vs. other	1	4	0.01	.9227
Unaltered vs. clipped	1	2174	4.71	.0334
Moth (M)	1	210	0.46	.5022
B × T	1	726	1.57	.2140
B × M	1	876	1.90	.1728
M × T	1	561	1.21	.2743
C × B × M	2	291	0.63	.5354
C × T	2	165	0.36	.7007
C × B	2	154	0.33	.7173
C × M	2	801	1.73	.1841
C × T × B	2	116	0.25	.7790
C × T × M	2	376	0.81	.4473
T × B × M	1	67	0.14	.7051
C × T × B × M	2	263	0.57	.5688
Error	69	462		

of nonindependent samples would increase the risk of a Type I error (wrongly rejecting a null hypothesis that is in fact true), and because of the many problems associated with ratio data (Green 1979).

All statistical procedures were performed with PC-SAS (SAS 1987). The General Linear Models procedure was used for ANOVA; Type III sums of squares were used for tests where missing data created an unbalanced design.

RESULTS

Ragwort responses

Ragwort colonization.—Disturbance renewed open space, the limiting resource in our system, and set the stage for colonization and occupancy. The number of emerging seedlings rose sharply after disturbance, then slowed to a trickle (Fig. 2). The time period required after first tilling to accumulate 95% of the new seedlings (defined as the colonization period) was twice as long for the Fall 1986 cohort (96 d) as for the Spring 1987 cohort (48 d). The number of emerging ragwort seedlings varied with Time of Disturbance ($P = .0071$)

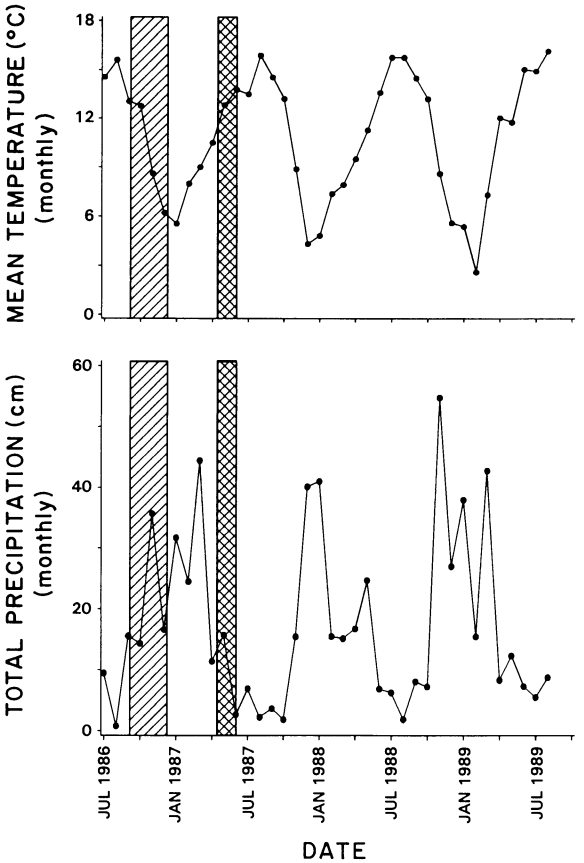


FIG. 3. Mean monthly temperature and precipitation during the study period 1986–1989 at Otis, Oregon. Shaded intervals represent for each cohort (Fall 1986 diagonal shading and Spring 1987 cross-hatched shading) the interval from the date of disturbance to the date at which 95% of seedlings were established.

TABLE 3. Effects of timing of disturbance, competition, and herbivory treatments on mean length of life of ragwort per subplot. ANOVA performed on untransformed data.

Source of variation	df	MS	F	P
Block	3	37267	2.00	.1222
Time (T)	1	149462	8.02	.0061
Beetle (B)	1	382029	20.49	.0001
Competition (C)				
Removed vs. Other	1	243069	13.04	.0006
Unaltered vs. Clipped	1	176055	9.44	.0030
Moth (M)	1	2890	0.16	.6950
B × T	1	228	0.01	.9123
B × M	1	399	0.02	.8841
M × T	1	12	0.00	.9797
C × B × M	2	20547	1.10	.3380
C × T	2	32796	1.76	.1799
C × B	2	22051	1.18	.3126
C × M	2	9024	0.48	.6184
C × T × B	2	35650	1.91	.1555
C × T × M	2	15510	0.83	.4395
T × B × M	1	17934	0.96	.3301
C × T × B × M	2	6475	0.35	.7078
Error	69	18645		

(Table 2): ragwort seedling densities were 32% higher in plots disturbed in Fall 1986 (50 ± 3.3 seedlings/0.06-m² subplot [mean ± 1 SE]) compared to plots disturbed in Spring 1987 (38 ± 3.3 seedling/0.06 m²). Time of Disturbance was the only treatment that affected number of established seedlings per subplot.

Initial abiotic conditions varied considerably with Time of Disturbance, reflecting the pronounced seasonal variation in temperature and precipitation (Fig. 3). Conditions became progressively cooler and wetter in Fall 1986 and progressively warmer and drier in Spring 1987. It was cooler and wetter during the colonization period in Fall 1986 (mean daily temperature 10.6°C, mean daily precipitation 6.88 mm) than in Spring 1987 (mean daily temperature 12.1°C, mean daily precipitation 4.41 mm). Thus a longer colonization period was associated with cooler and wetter conditions.

Ragwort survivorship.—Ragwort survivorship represented by mean length of life varied with Time of Disturbance ($P = .0061$), Beetle ($P = .0001$), and Competition treatments, however the Cinnabar Moth ($P = .6950$) had no detectable effect (Table 3). Survivorship curves suggest populations in the Fall 1986 cohort suffered higher rates of mortality compared to populations in the Spring 1987 cohort in the early stages, but after day 500 the curves were more similar (Fig. 4a): mean length of life averaged 24% (79 d) longer in populations created in Spring 1987 than in populations created in Fall 1986. Mean length of life averaged 41% (126 d) longer in populations Protected from the flea beetle compared to Exposed populations (Fig. 4b). The presence of the background vegetation reduced mean length of life ($P = .0006$); the reduction was less if the background vegetation was Clipped than if it was Unaltered ($P = .003$) (Table 3). The mean length of life in the Unaltered treatment was 159 d less than under the

Removed treatment; the mean length of life under the Clipped treatment was 54 d less than under the Removed treatment (Fig. 4c).

Ragwort reproduction.—Treatment effects on ragwort reproduction were represented by effects on stages in the path from adults, to seeds, to juveniles established from seeds (Fig. 5A–C, respectively). Inspection of the figures suggests that the treatments affected ragwort reproduction in different ways. First (Fig. 5A), the number of adults varied with the Competition treatment: the number of adult ragwort plants was reduced by the presence of the background vegetation; the reduction was less when the background vegetation was Clipped than when it was Unaltered. The number of

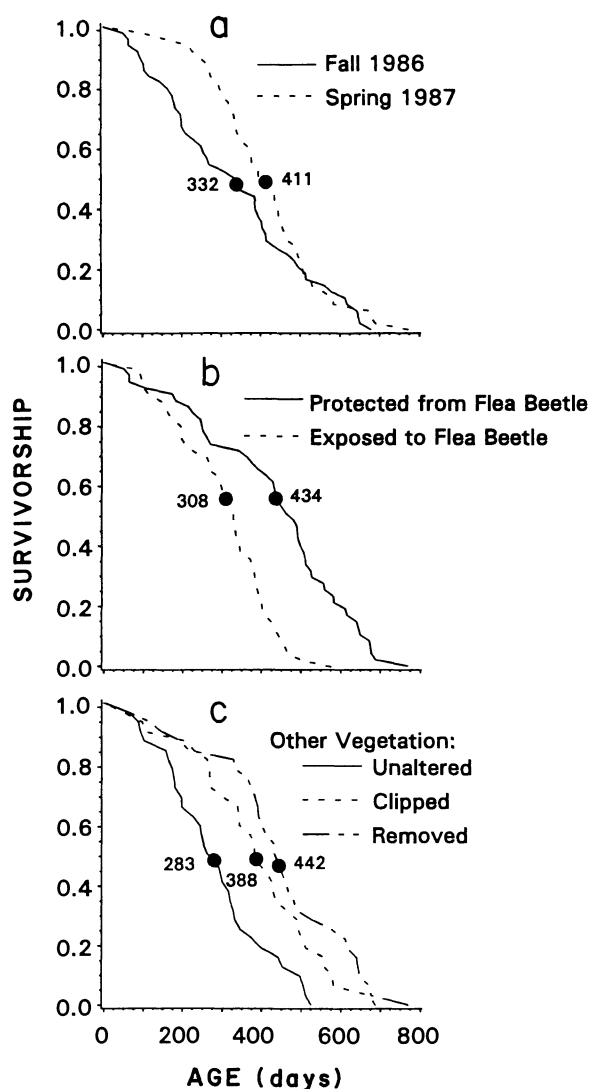


FIG. 4. Survivorship curves comparing (a) Time of Disturbance treatments, (b) Flea Beetle treatments, (c) Competition treatments. Solid symbols and adjacent numbers represent the mean length of life for each level of a given treatment, averaged over all levels of the other treatments.

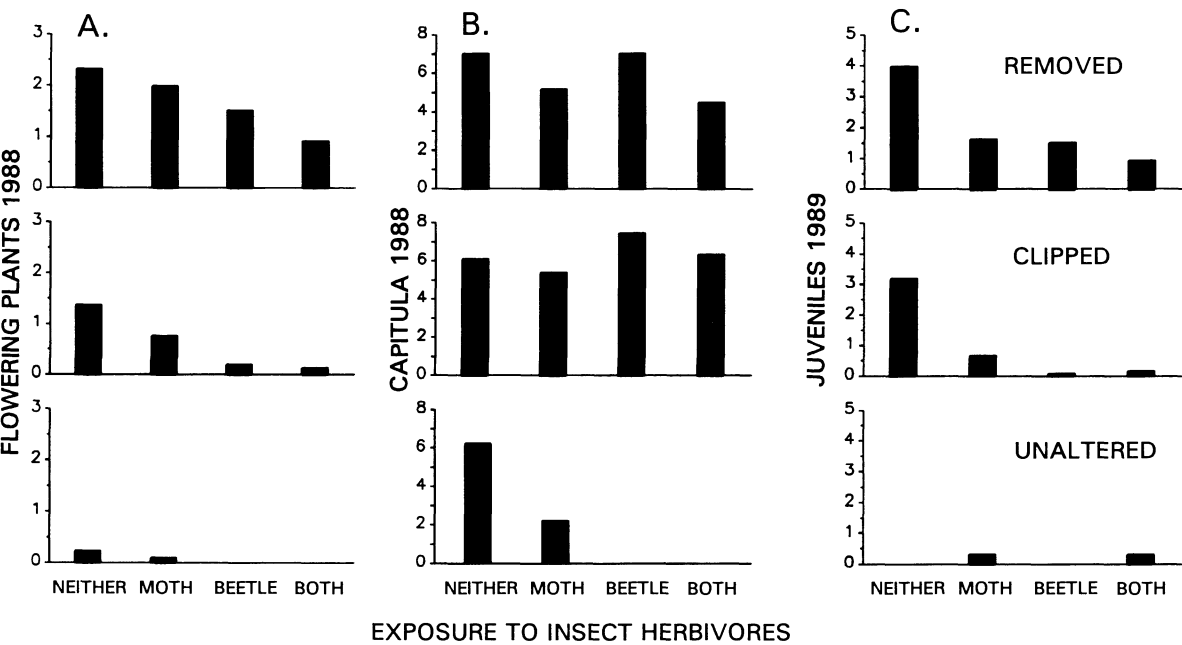


FIG. 5. Ragwort reproduction represented by numbers of (A) adults, (B) capitula (proportional to no. seeds), and (C) juveniles per 0.06-m² subplot for each combination of Competition, Beetle, and Moth treatments averaged over all levels of the Time of Disturbance treatment.

adults also varied with the Beetle treatment: the number was less in Exposed compared to Protected plots. Second (Fig. 5B), the number of seeds produced varied with the Moth treatment. The combination of the Unaltered competition treatment and the Exposed beetle treatment eliminated seed production through the elimination of all adult plants. There appears to be little evidence in the other 10 treatment combinations of an effect of the Competition treatment or the Beetle treatment on seed production. Third (Fig. 5C), the number of juveniles recruited to the second generation varied with Moth, Beetle, and Competition treatments. The cinnabar moth reduced the number of recruits (Fig. 5C) through reduction in the number of seeds produced (Fig. 5B). The flea beetle reduced the number of recruits (Fig. 5C) through reduction of the number of adults (Fig. 5A). Unaltered competition treatment reduced the number of recruits (Fig. 5C) through reduction in the number of adults (Fig. 5A).

Further support for these inferences was obtained from statistical tests. We excluded the observations from the Unaltered competition treatment for all measures of reproduction, and, in addition, the observations from the Exposed beetle treatment for the special case of seed production, to better meet the assumptions of the ANOVA. The number of adults varied with Beetle ($P = .0001$) and Removed vs. Clipped Competition ($P = .0001$) treatments (with weak evidence of a Moth effect judged by criteria explained in *Methods*) (Table 4); the number of seeds varied with the Moth ($P = .0002$) treatment (Table 5); and the number of juveniles varied with Moth ($P = .0001$), Beetle ($P = .0001$), and Removed vs. Clipped Competition

($P = .0002$) treatments (Table 6). There was an interaction of Beetle and Moth effects ($P = .0001$) on juveniles in the ANOVA (Table 6). This is not surprising since each individual effect tended to eliminate juveniles (Fig. 5C) and their combined effect could therefore not be strictly additive. It should be noted that the response at one ragwort life history stage in our experiment depends on effects operating at the present stage and effects operating at previous stages; estimates for each stage of development in our cohort are serially

TABLE 4. Effects of time of disturbance, plant competition, and insect herbivory on number of ragwort adults per plot. Data were \log_{10} transformed to homogenize variance. Analysis was carried out on only a subset of the data set, i.e., Clipped and Removed competition treatments.

Source of variation	df	ms	F	P
Block	3	6.0761	10.77	.0001
Time (T)	1	0.0120	0.04	.8516
Beetle (B)	1	21.9564	38.91	.0001
Competition (C)	1	30.3194	53.73	.0001
Moth (M)	1	4.0210	7.13	.0105
B \times T	1	0.9514	1.69	.2007
B \times M	1	0.1076	0.19	.6644
M \times T	1	0.0107	0.02	.8912
C \times B \times M	1	1.3417	2.38	.1301
C \times T	1	0.3074	0.54	.4643
C \times B	1	0.0145	0.03	.8733
C \times M	1	0.0506	0.09	.7659
C \times T \times B	1	0.2651	0.47	.4966
C \times T \times M	1	0.0313	0.06	.8148
T \times B \times M	1	0.3974	0.70	.4058
C \times T \times B \times M	1	0.0691	0.12	.7281
Error	45	0.5643		

TABLE 5. Effects of time of disturbance, plant competition, and insect herbivory on number of ragwort seeds per plot. Data were \log_{10} transformed to homogenize variance. Analysis was carried out on only a subset of the data set, i.e., Clipped and Removed competition treatments and Beetle Protected herbivory treatments. Five of 32 observations were missing.

Source of variation	df	MS	F	P
Block	3	2.6574	4.84	.0139
Time (T)	1	0.5164	0.94	.3467
Moth (M)	1	12.6222	22.98	.0002
Comp (C)	1	2.3664	4.31	.0544
M \times T	1	0.2857	0.52	.4812
C \times T	1	0.0576	0.10	.7503
C \times M	1	0.8128	1.48	.2414
C \times T \times M	1	0.7148	1.30	.2707
Error	16	0.5492		

dependent. Independent samples and tests would be required to more clearly distinguish present and prior effects.

Ragwort biomass.—The biomass of the experimental ragwort populations showed damped oscillations over time, particularly in the Removed competition treatment (Fig. 6). The 2-yr period in the oscillations reflects the biennial life cycle, with peaks and valleys associated with years with high and low frequencies of flowering plants, respectively. The second peak (1990) was consistently lower than the first peak (1987), suggesting that populations were declining. Over the course of the experiment, all 8 of 8 populations exposed to biotic interactions (Unaltered competition treatment and Exposed moth and beetle treatments) declined to zero biomass, while all 8 of 8 populations protected from biotic interactions (Removed competition treatment and Protected moth and beetle treatments) persisted.

The biomass duration varied with Competition and Beetle ($P = .0001$) treatments, while the Moth ($P = .1840$) had no detectable effect (Table 7). The failure to establish a cinnabar moth effect is noteworthy because it shows that a reduction in ragwort density (seeds in one generation and juveniles in the next) caused by the moth did not lead to an overall reduction in ragwort biomass. The Time of Disturbance had no effect, suggesting that the outcome of biological control was not sensitive to variation in the initial conditions. However, the Competition \times Time of Disturbance interaction ($P = .0099$) in the ANOVA indicates that the effect of one factor depended on the level of the other. The crossed lines in the interaction plot (obtained by plotting biomass duration against competition treatment separately for each level of the Time of Disturbance treatment) indicate that the effect of competition depended on the time of disturbance: the magnitude of the competition effect was greater for Fall 1986 treatment than for Spring 1987 treatment (Fig. 7). Such results suggest there was temporal variation in the strength and importance of plant competition.

Allocation of space

There was strong evidence that mean ragwort cover averaged over 4 yr varied with the Competition and Beetle ($P = .0001$) treatments, weaker evidence of a moth effect ($P = .0001$, but see below), while Time of Disturbance ($P = .2220$) had no detectable effect (Table 8). By inspection of the variance ratios (Table 8), most of the variation in mean ragwort cover was explained by the main effects of the Beetle and Competition treatments, whereas a relatively small portion was accounted for by the Moth treatment and the various interactions ($B \times M$, $C \times B \times M$, $C \times M$). The presence of a background vegetation reduced ragwort cover ($P = .0001$); the effect was less when the vegetation was Clipped than when it was Unaltered ($P = .0001$) (Table 8). The mean ragwort cover over 4 yr was 58% for Removed plots, 32% for Clipped plots, and 6% for Unaltered plots. The effects of herbivores on mean ragwort cover were not consistent among Competition levels (evidenced by $C \times B$ and $C \times M$ interactions in Table 8), but were consistent between Times of Disturbance. The effects of moth and beetle were additive in plots in which competing vegetation was removed, whereas in Clipped and Unaltered plots the effects of both herbivores together was never greater than the effect of the beetle alone (Fig. 8).

The cover of other plant species, litter, and open space are strongly correlated, suggesting each could be regarded as a contributor to the Competition effect on ragwort abundance. As is shown by inspection of Fig. 8, the manipulation of the background vegetation clearly reduced the space occupied by other species as planned, and correlated with the reduction in other species was a reduction in space occupied by litter (Spearman's coefficient of rank correlation, $r_s = 0.75$, $P = .0001$, n

TABLE 6. Effects of time of disturbance, plant competition, and insect herbivory on number of ragwort juveniles per plot. Data were \log_{10} transformed to homogenize variance. Analysis was carried out on only a subset of the data set, i.e., Clipped and Removed competition treatments.

Source of variation	df	MS	F	P
Block	3	6.7708	4.56	.0072
Time (T)	1	0.0697	0.05	.8295
Beetle (B)	1	60.3050	40.59	.0001
Competition (C)	1	24.2949	16.35	.0002
Moth (M)	1	36.9117	24.84	.0001
B \times T	1	0.6491	0.44	.5120
B \times M	1	25.4969	17.16	.0001
M \times T	1	5.5221	3.72	.0602
C \times B \times M	1	1.3353	0.90	.3482
C \times T	1	1.6661	1.12	.2953
C \times B	1	0.3860	0.26	.6128
C \times M	1	0.1762	0.12	.7321
C \times T \times B	1	5.7456	3.87	.0554
C \times T \times M	1	1.0634	0.72	.4020
T \times B \times M	1	1.2409	0.84	.3656
C \times T \times B \times M	1	0.1187	0.08	.7787
Error	45	1.4858		

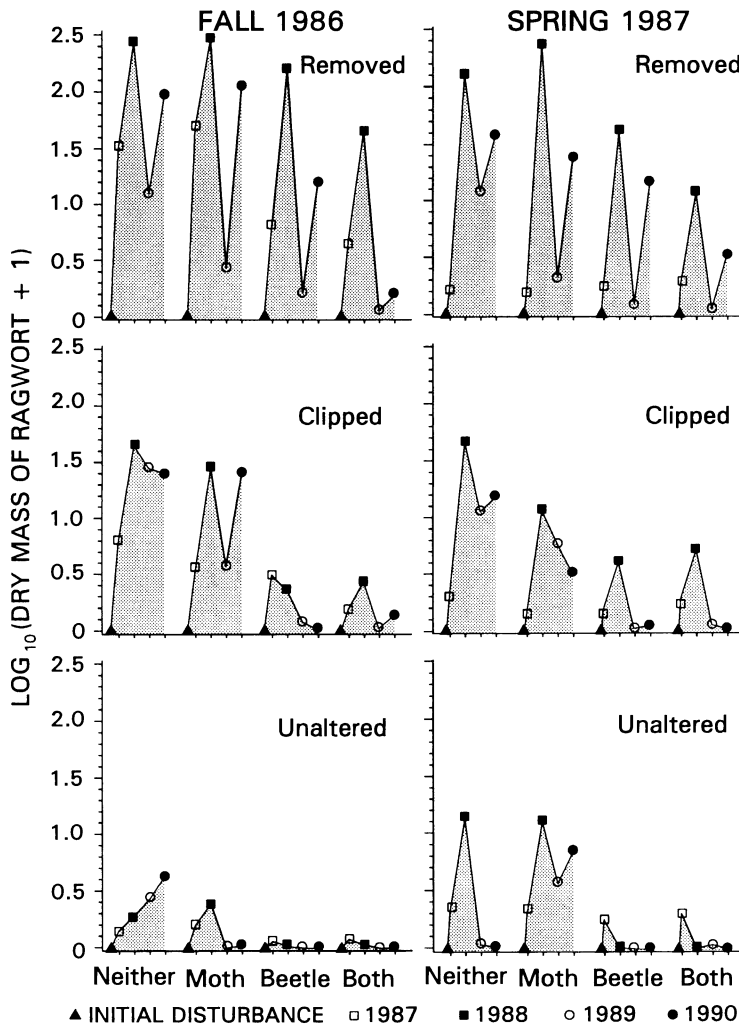


FIG. 6. Ragwort biomass plotted over time for each combination of Time of Disturbance, Beetle, Moth, and Competition treatments. Biomass was measured in grams.

= 95) and an increase in the amount of open space (Spearman's coefficient, $r_s = -0.50$, $P = .0001$, $n = 95$). The effects of manipulation were less when the background vegetation was Clipped than when it was Removed. The mean cover in each category (other: litter:open) was 4:11:46% for Removed, 79:45:22% for Clipped, and 127:64:15% for Unaltered. The allocation of space to these categories varied with time after disturbance as gradually the available space became occupied. In the Unaltered treatment, the supply of open space declined to zero some time between 1988 and 1989, leaving little open space available for colonization by the second ragwort generation. In Clipped and Removed competition treatments, the supply of open space decreased over time, but open space was generally present from one ragwort generation to the next, throughout the period of observation from 1987 through 1990, creating opportunities for ragwort colonization and establishment.

Natural enemy responses

The ragwort flea beetle attacked all Exposed ragwort populations and was satisfactorily excluded from Protected populations. Protected populations revealed some small contamination by beetle larvae (median of 0 and range of 0–134 individuals per subplot). In exposed populations, there was considerable variation in number of beetle larvae (0–5031 individuals) and host food resources (0–122 g) per 0.06-m² subplot, and a strong positive correlation between flea beetle larvae and dry mass of food resources per subplot (Fig. 9a).

The cinnabar moth attacked all Exposed populations and was satisfactorily excluded from Protected populations. Protected populations revealed virtually no larvae (one subplot contained only one larva). Exposed populations revealed considerable variation in number of cinnabar moth larvae (0–122 individuals) and host food resources (0–161 g) per 0.06-m² subplot, and a

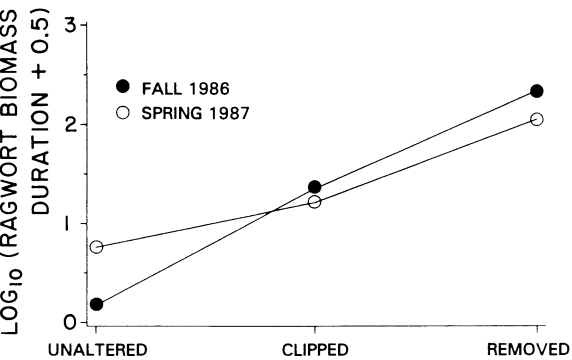


FIG. 7. Interaction plot showing the ragwort biomass duration for each level of the Competition treatment, plotted separately for each Time of Disturbance Treatment. Biomass was measured as grams of dry mass.

positive correlation between cinnabar moth larvae and dry mass of food resources per subplot that was weaker than the analogous relationship for the flea beetle (Fig. 9b).

Most of the variation in herbivore abundance could be explained by the strong, positive correlation of herbivore abundance with ragwort abundance (Fig. 9a, b). Each enemy species increased when and where the pest did, but there were important differences in their response to an increase in host concentration. The log number of flea beetle larvae in relation to dry mass of ragwort per patch accelerates rapidly from the origin and then reaches an asymptote that has a positive slope of $\approx \frac{1}{3}$ (Fig. 9a). The number of cinnabar moth larvae in relation to dry mass of ragwort per patch increases not directly from the origin as in the flea beetle relationship but from a minimum threshold value of ≈ 25 g. There is considerably more scatter in the cinnabar

TABLE 7. Effects of timing of disturbance, competition, and herbivory treatments on ragwort biomass duration per subplot. ANOVA performed on \log_{10} transformed data.

Source of variation	df	MS	F	P
Block	3	3.307	9.22	.0001
Time (T)	1	0.103	0.29	.5941
Beetle (B)	1	22.500	62.72	.0001
Competition (C)				
Removed vs. other	1	37.346	104.10	.0001
Unaltered vs. clipped	1	10.664	29.73	.0001
Moth (M)	1	0.646	1.80	.1840
B \times T	1	0.001	0.00	.9675
B \times M	1	0.004	0.01	.9156
M \times T	1	0.114	0.32	.5744
C \times B \times M	2	0.712	1.98	.1452
C \times T	2	1.773	4.94	.0099
C \times B	2	0.764	2.13	.1266
C \times M	2	0.179	0.50	.6095
C \times T \times B	2	0.568	1.58	.2124
C \times T \times M	2	0.148	0.41	.6627
T \times B \times M	1	0.006	0.02	.8996
C \times T \times B \times M	2	0.206	0.58	.5653
Error	69	0.3588		

TABLE 8. Effects of timing of disturbance, competition, and herbivory treatments on mean cover of ragwort averaged over 1987 through 1990. ANOVA performed on arcsine transformed data. One of 96 observations was missing.

Source of variation	df	MS	F	P
Block	3	0.2239	10.98	.0001
Time (T)	1	0.0310	1.52	.2220
Beetle (B)	1	3.4479	169.06	.0001
Competition (C)				
Removed vs. other	1	3.9384	193.11	.0001
Unaltered vs. clipped	1	2.1502	105.43	.0001
Moth (M)	1	0.4334	21.25	.0001
B \times T	1	0.0020	0.10	.7567
B \times M	1	0.1234	6.05	.0165
M \times T	1	0.0317	1.56	.2165
C \times B \times M	2	0.0822	4.03	.0222
C \times T	2	0.4047	19.84	.0001
C \times B	2	0.2369	11.62	.0001
C \times M	2	0.1565	7.68	.0010
C \times T \times B	2	0.0322	1.58	.2138
C \times T \times M	2	0.0439	2.15	.1240
T \times B \times M	1	0.0021	0.10	.7521
C \times T \times B \times M	2	0.0380	1.86	.1628
Error	68	0.0204		

moth relation (Fig. 9b) than in the flea beetle one (Fig. 9a).

The uncontrolled intrusion by the seed fly was evaluated as follows. Plots protected from the moth revealed small numbers of seed fly larvae (0–7 larvae), while plots exposed to the moth sometimes had large numbers of seed fly larvae (median 22.5, range 1–815 individuals per subplot). This establishes that plots exposed to or protected from the moth were necessarily likewise exposed to or protected from the seed head fly. How did intrusion by the seed head fly affect the magnitude of the difference in seed production between moth exposed and moth protected plots? The average effect was calculated as the difference in geometric means for the number of capitula in moth-Exposed and moth-Protected plots with and without seed head fly infested heads. Including capitula infested by the seed head fly increased the average difference between exposed and protected plots by 4% from 33.27 to 34.72 capitula per subplot. We conclude that the unplanned intrusion of the seed head fly in our experiment led to negligible bias in estimates of cinnabar moth effects.

DISCUSSION

We have demonstrated that abundant buried seed and localized disturbances combined to activate incipient weed outbreaks (consistent with the Activation Hypothesis), and that interspecific competition and herbivory by the ragwort flea beetle combined to inhibit the increase and spread of incipient outbreaks (consistent with the Inhibition Hypothesis). The balance between activation and inhibition was insensitive to variation in initial conditions represented by Time of Disturbance in our experiment. In competition treatments with open space (Removed and Clipped

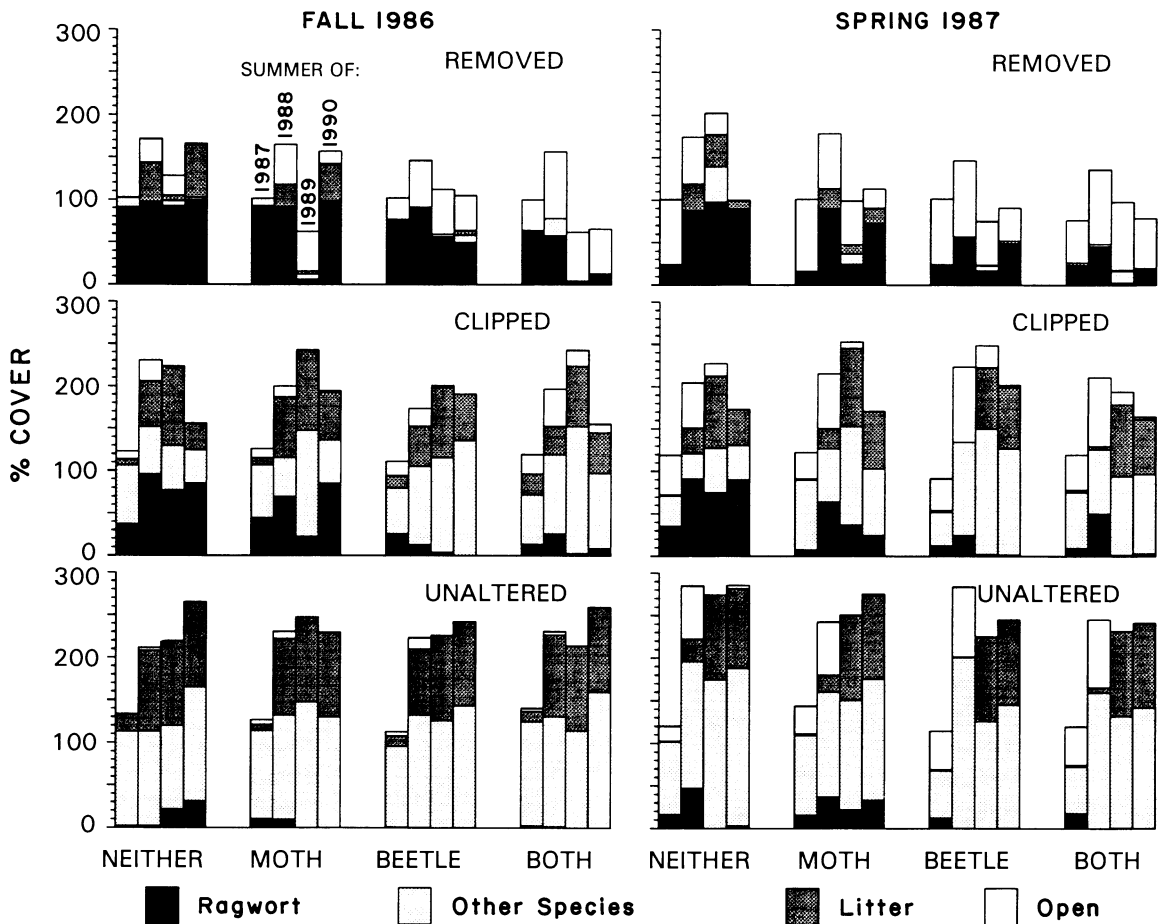


FIG. 8. Ragwort cover plotted over time for each combination of Time of Disturbance, Beetle, Moth, and Competition treatments. Within each bar is shown the portion of total cover allocated to ragwort, other species, litter, and open space.

treatments), the cinnabar moth reduced seed production in the first generation, and the number of juveniles in the next, but this had no detectable effect on ragwort population dynamics represented by variation in annual estimates of ragwort cover and biomass from 1987 through 1990. At the spatial scale examined, inhibition took the extreme form of elimination of all ragwort individuals except seed buried in soil: ragwort tended to be displaced by its competitors and eliminated by the ragwort flea beetle. In the absence of these factors, however, it persisted. This suggests that species interactions in a local area may be unstable (consistent with the first half of the Stability Hypothesis). Natural enemies readily colonized incipient ragwort outbreaks and inhibited their growth in our experiment, suggesting that if a large pool of dormant seeds is present, enemy and pest species can persist on more global spatial scales despite interactions that doom these species on local scales (consistent with the second half of the Stability Hypothesis). Taken together, our results suggest that the outcome of biological control depends on the balance in the forces of disturbance, colonization, and successional development of plants and herbivores.

Disturbance

Our experimental disturbances recycled open space, the primary limiting resource in the Unaltered competition treatment, and created opportunities for colonization and occupancy. In our experiment, localized disturbance combined with a natural abundance of buried seed was sufficient to trigger incipient ragwort outbreaks. A companion experiment comparing different types of disturbances establishes that this level of disturbance is both necessary and sufficient to trigger an upsurge in ragwort abundance from the seed bank (P. B. McEvoy and N. T. Rudd, *unpublished manuscript*). Based on prior knowledge of ragwort recruitment reviewed in the *Introduction*, our disturbances probably (1) promoted germination by moving seed vertically short distances to the activation site, and (2) promoted emergence and establishment by loosening soil and removing competing vegetation and litter. Seasonal differences in Time of Disturbance (Fall 1986, Spring 1987) in our experiment were sufficient to cause differences in ragwort recruitment among local populations, but these timing differences did not cause sufficient asynchrony in local population fluctuations to

prevent extinction of the entire subset exposed to interspecific competition and flea beetle herbivory. In theory, when disturbances are localized and regionally asynchronous, they can cause local populations to fluctuate independently, and thereby contribute to stability of the ensemble.

Prior studies suggest that the vulnerability of a habitat to ragwort invasion is increased by many kinds of natural and anthropogenic disturbances, including tilling, clipping or mowing (Cameron 1935), disturbance of turf by rabbits (Harper and Wood 1957), grazing and other activities of livestock (Harper and Wood 1957), and logging (Isaacson and Schrumph 1979). One problem in interpreting effects is that our experimental "crop grazing" and disturbance regimes are different from the ones the system usually experiences. Our clipping treatment grazed the crop selectively, intermittently with periods of rest, and to a fixed height. This is a limited representation of natural grazing with the numerous and variable effects of real livestock teeth, hooves, dung, and urine. Our experimental disturbances were of a standard shape, size, intensity, timing, and spatial arrangement, whereas real disturbances come in many shapes, sizes, and intensities, with complex patterns of spatial and temporal correlation. Since we have shown that pest-enemy-crop interactions are unlikely to persist in the absence of external disturbance or selective grazing on the crop, the actual disturbance regimes affecting biological control systems may now be examined more carefully.

It is important to know whether results from small spatial scales can be extrapolated to larger spatial scales. Levin (1989) has emphasized the general need in ecology for studies that look across scales to see how system description changes with scales of observation. We have shown the ragwort biological control system is able to recover from small area disturbances. How much longer would the system take to recover from larger area disturbances? The ragwort biological control system required 1–3 yr to control metre-scale infestations in a companion experiment involving different disturbance types (plots were Tilled, Clipped, or Unaltered) (P. B. McEvoy, *unpublished manuscript*), and 5–6 yr to control hectare-scale infestations in previous observational studies (McEvoy et al. 1991). Thus a 10 000-fold change in spatial scale of the ragwort infestation yields less than a 10-fold change in the speed of the control process. This encourages the view that our results are not sensitively dependent on spatial scale of the disturbance.

Colonization

After our experimental disturbances created gaps in the vegetation, space was available for recolonization. Colonization by ragwort and its competitors and enemies occurred on different scales of space and time. Ragwort colonized our experimental disturbances promptly from a local source. Some of ragwort's competitors (particularly the perennial grasses) colonized

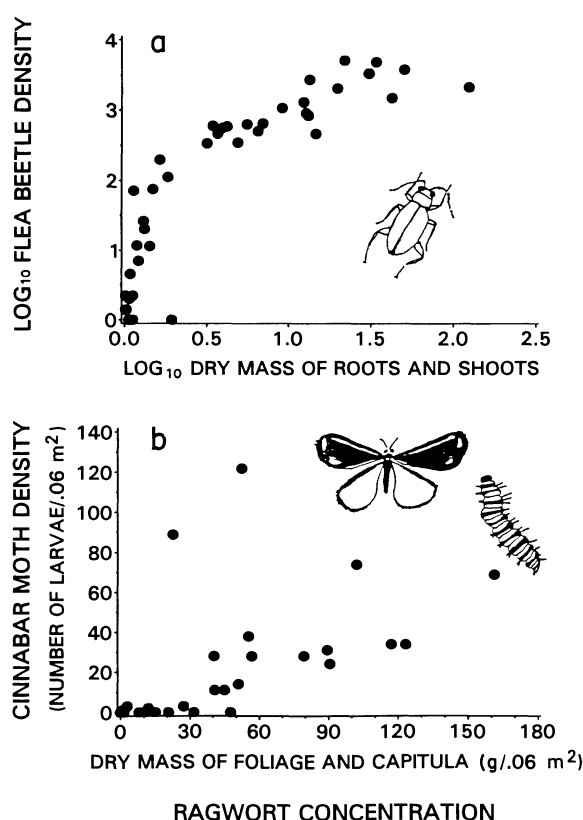


FIG. 9. Density of insect larvae per subplot (measured as number per 0.06 m²) against dry mass of ragwort per subplot (measured in grams per 0.06 m²): (a) flea beetle larval density vs. combined dry mass of ragwort roots and shoots in Spring 1988 (Spearman's coefficient of rank correlation $r_s = 0.93$, $P = .0001$ for exposed plots). The log metric was used on both variables to magnify what is happening near the origin (0,0), to accommodate on a single graph changes of several orders of magnitude in beetle and host abundance, and to linearize the relationship over most of the range in x . (b) Density of cinnabar moth larvae vs. combined dry mass of ragwort roots and shoots in Summer 1988 (Spearman's coefficient of rank correlation $r_s = 0.79$, $P = .0001$ for exposed plots). The untransformed variables were adequate to yield a linear relationship and reveal behavior of $f(x)$ near the origin.

from longer range by both lateral encroachment from the perimeter and local emergence from buried seeds and buds. The natural enemies colonized from a still longer range, moving to the activation site from unknown locations in the world outside our experiment.

The superior searching and colonizing ability of the beetle may have contributed to its superiority as a regulator of ragwort abundance. The seasons for colonization by ragwort (fall and spring) were more effectively overlapped by those of the flea beetle (fall, winter, spring) than by those of the cinnabar moth (late spring–early summer). Evidence from this study established that the threshold ragwort concentration that must be exceeded in a patch for successful insect colonization and establishment was lower for the flea beetle than for the cinnabar moth, and the positive spatial correlation between enemy and pest concentration was

stronger for the beetle than for the moth. These attributes of the beetle's colonizing and searching behavior likely improve its efficiency as a control agent by helping to reduce the delay and uncertainty in the arrival of natural enemies at the site of an incipient ragwort outbreak.

There are other important differences in the biology of the enemy species associated with differences in their colonizing and searching behavior. Flea beetle larvae reach a small maximum size (third [final] instar larvae average 0.1 mg dry mass), are mostly confined to the host on which they are laid as eggs, and feed in roots and shoots of individual hosts. Cinnabar moth larvae reach a larger maximum size (fifth instar averages ≈ 30 mg dry mass), can leave defoliated plants as fourth and fifth instar larvae and wander distances of many metres in search of hosts (van der Meijden 1971, Dempster 1982), and feed mostly on foliage and flowers, which comprise $\approx 33\%$ of total host dry mass.

Insect herbivory and plant competition

The local interactions that followed species colonization and occupancy led to a process of successional development that eliminated ragwort and favored other plant species. The speed of ragwort elimination represents one measure of the speed of the successional process, and it is inversely related to our measures of cover and biomass duration. By manipulating the interactions within and between adjacent trophic levels, our experiment established how changes in the system's structure affected its dynamics. While the ragwort system bears little resemblance to the theoretician's delight of a tightly coupled, two-species interaction, we can build on such simple, two-species systems by asking to what degree interactions between two species were altered by presence or absence of a third species (Fowler and Rausher 1985).

For example, our results help us interpret how the basic weed-crop interaction is likely to be altered by (a) livestock grazing on the crop or background vegetation and (b) insect feeding on the weed. In the absence of herbivory, competition between ragwort and the crop led to elimination of ragwort. Grazing of ragwort's competitors (represented by our clipping treatment) reduced the competitor's abundance and delayed ragwort elimination. Grazing on ragwort (represented by beetle herbivory treatments) had the opposite effect, speeding ragwort's elimination and replacement by its competitors. It is noteworthy that both living and dead components of vegetation were reduced by our competition treatments. Recent work with other species has shown that the impact of one plant species on another does not stop after the death of individuals: litter can impede the performance of seeds, seedlings, and even adult plants (Bergelson 1991, Facelli and Pickett 1991). The speed of successional process increased in series for ragwort populations exposed to neither insect, the moth, the beetle, and both the moth

and beetle. In this case, the coexistence of competitors, and the speed and possibly the direction of plant succession, depended on the relative competitive abilities of the plants and the diversity and selectivity of the herbivores. Similar findings in terrestrial and intertidal landscapes show that when herbivory is added to the interaction between two plant species, the outcome depends on the relative competitive ability of the plants and the intensity and selectivity of the herbivory (Harper 1969, Lubchenco 1978). Most models of succession neglect herbivory as a driving force (see reviews by Edwards and Gillman 1987 and Brown 1990), and few investigators have used field experiments to examine the role of insects in plant succession (McBrien et al. 1983, Brown 1990). Other examples of enhanced weed control from the combined forces of plant competition and natural enemies in biological control systems include prickly-pear cacti in California (Goeden et al. 1967), skeleton weed in Australia (Groves and Williams 1975), and musk thistle in Virginia (Kok et al. 1986).

Our results also indicate how the basic pest-enemy interaction is likely to be altered by the presence or absence of (a) a second natural enemy species and (b) crop or background vegetation. Adding a secondary enemy, the ragwort flea beetle, to an existing ragwort-cinnabar moth interaction accelerated ragwort elimination, but the same could not be said for adding the cinnabar moth to a ragwort-flea beetle interaction. In either case, we found no evidence to suggest that adding a second enemy to an existing pest-enemy interaction leads to reduced success due to interspecific interference. In this case, interspecific interference may be minimal because the flea beetle and the cinnabar moth are complementary, i.e., attacking different host stages, at different seasons, and at different stages in development of an outbreak. Adding a crop or a background vegetation to an existing weed-enemy interaction also accelerated ragwort elimination. We found no evidence that the presence of the crop or background vegetation interferes with regulation of the weed by the enemy. Apparently the presence of the crop did not reduce insect rates of increase, for example, by decreasing host finding success; by increasing herbivore mortality due to predators, parasitoids, or parasites; by creating an unfavorable microclimate; or by decreasing food quality as reported in other systems (see review by Kareiva 1983).

Cinnabar moth

The effectiveness of the cinnabar moth in ragwort control in the Pacific Northwest has not been definitively established. In observational studies in northern California (Hawkes 1973, Hawkes and Johnson 1978, Pemberton and Turner 1990), and Oregon (McEvoy 1985, McEvoy et al. 1991), an increase in the cinnabar moth abundance was associated with a decline in rag-

wort abundance. In experiments using natural levels of the ragwort flea beetle and a single level of artificial defoliation and defloration to mimic cinnabar moth attack, complete removal of foliage and seed heads in July caused a reduction in seed production despite regrowth of foliage and flower heads within the same year (James et al. 1992). There was a synergistic interaction between the cinnabar moth and the flea beetle treatments: the combination of two types of damage had a greater effect on seed production than the sum or product of their independent effects (James et al. 1992). In experiments using natural variation in real cinnabar moth larvae, slightly different results have been obtained (this experiment and a companion experiment by P. B. McEvoy and N. T. Rudd, *unpublished manuscript*). Under conditions of the companion study by P. B. McEvoy and N. T. Rudd (*unpublished manuscript*) where open space for ragwort germination and establishment was limiting, reduction in seed production caused by the moth did not change ragwort cover or biomass over the longer term from 1986 through 1990. In the present experiment, where open space was available in the Clipped and Removed competition treatments, reduction in seed production in the first generation caused by moth larvae led to a reduction in plant numbers in the second generation, a small reduction in ragwort cover contingent on the levels of the other factors, and no change in ragwort biomass over the longer term from 1987 through 1990. The conclusion from these studies, consistent with the views of Crawley (1983) and Crawley and Gillman (1989), is that the effect of the cinnabar moth on ragwort population dynamics depends on attributes of the disturbance regime. In undisturbed, mesic grassland, ragwort's population growth rate will be insensitive to change in fecundity, but highly sensitive to change in the quality and quantity of open space and the speed with which it is colonized. Only when recruitment is seed limited will herbivores that reduce seed production regulate the plant population (Crawley 1983).

The moth effect on ragwort cover and biomass was smaller than the competition and beetle effects. The weaker effect of the moth can be attributed to time delays in (1) moth increase relative to ragwort increase, (2) ragwort decrease relative to moth increase. With regard to insect increase, moth colonization did not peak until the number of flowering plants peaked in 1988, 2 yr after disturbance. With regard to ragwort decrease, reduction in ragwort seed in one ragwort generation (seed in 1988) did not lead to reduction in ragwort abundance until the next generation (juveniles in 1989). Ragwort cover was more sensitive to moth effects than ragwort biomass. This is expected because cinnabar moth larvae remove foliage and flowers, which are the major components of aboveground cover, while leaving behind stems and roots, which are the major components of combined above- and belowground biomass.

For other situations that have been studied, it is debatable whether significant cinnabar moth effects are absent, or whether significant effects are present but not detected by the conventional, nonexperimental methods (such as *k*-factor analysis of field data) used to detect host regulation by natural enemies in the field (Hassell 1985). Most interpreters contend that the cinnabar moth abundance is limited by availability of ragwort, but ragwort abundance is not limited by the cinnabar moth (van der Meijden 1979, Myers 1980, Crawley 1983, Crawley and Gillman 1989). Such would be the case if larvae reduce seed production, but ragwort is not limited by seed. Local ragwort populations may not be seed limited because (1) individual plants can produce a secondary seed crop during an herbivore-free period after the primary seed crop is destroyed (Cameron 1935, Poole and Cairns 1940, Green 1974, Cox and McEvoy 1983, Islam and Crawley 1983), (2) the population is maintained by colonization in space or time from outside sources, i.e., seed produced elsewhere (seed rain) or earlier (seed bank) (van der Meijden 1979, McEvoy et al. 1991), (3) recruitment is limited by other factors, such as safe sites for germination and establishment (Crawley and Gillman 1989). It would be inappropriate to presume that the cinnabar moth is ineffective under all conditions. Even where a reduction in seed by the cinnabar moth does not immediately reduce local abundance, it may reduce the risk of outbreaks elsewhere (by reducing the number of dispersing seeds) or in the future (by reducing the number of dormant seed buried in the soil).

Stability

If interactions doom these species on local scales, what mechanisms ensure coexistence of the species on more global scales? Regional surveys of 42 sites in western Oregon (McEvoy et al. 1991) and 4 sites in northern California (Pemberton and Turner 1990) show that ragwort has persisted at low and steady average densities once the initial, vigorous stages of biological control are played out. Can local rules developed around the basic ingredients of short-range activation (seed source, localized disturbance) and longer range inhibition (plant competition, natural enemies) give rise to stability on more global scales? In theory, asynchronized local disturbance, colonization, and extinction can create populations that are quasi-discrete in both space and time. Communication among populations is provided by the life history mechanisms that link populations in space (dispersal) and time (dormancy, a perennial life style, iteroparity). By averaging over many local patches, these mechanisms reduce the variability associated with a single patch. An apparent general feature of insect-plant interactions is that the insect (the inhibitor) averages primarily in space, while the plant (the activator) averages primarily in time. In this case, the insects are temporally limited (due to seasonal dormancy, annual life cycles, and seasonal reproduc-

tion), while ragwort is temporally extended (due to long-term seed dormancy, a flexible life cycle ranging from a semelparous, biennial to an iteroparous, perennial). Plant diffusion is spatially limited (due to short distances traveled by wind-dispersed seed) (McEvoy and Cox 1987), while insect diffusion is more extended (Dempster 1982, McEvoy and Cox 1987, Crawley and Gillman 1989, Harrison and Thomas 1991).

With these ideas as background, it is instructive to ask why our collection of patches failed to persist when exposed to interspecific competition (Unaltered competition treatment) and natural enemies (Exposed moth and beetle treatments). Differences in Time of Disturbance were too short, and the spatial mixing among enemy populations was too strong, to enhance differences among local patches created by our initial disturbances and create the asynchrony required for persistence. Further, the temporal communication among ragwort patches was limited due to (1) the low frequency of populations shifting from a biennial, semelparous life cycle to a perennial and iteroparous one, and (2) the absence of recurrent disturbance, which effectively uncoupled the seed bank from the rest of the ragwort population. Having shown that disturbance, colonization, and successional development are essential ingredients in our experimental model, we can focus future research on the precise adjustment of parameters required to generate persistence.

General features

Our research parallels recent reexaminations of pattern and process underlying theory and practice of biological control of insects by parasitoids (Murdoch et al. 1984, 1985, Murdoch 1990) and predators (Kareiva and Odell 1986). It is useful to try to abstract those features that are common to situations involving different kinds of natural enemies. In agreement with Murdoch et al. (1985), our findings lead us to reject the conventional wisdom that successful biological control leads to a stable pest-enemy equilibrium on a local spatial scale, and they provide strong support for "search and destroy" and weak support for "complementary enemies" as alternative strategies for improving control. The ragwort flea beetle epitomizes the search and destroy strategy, in which the enemy is monophagous on the pest, or nearly so, and highly capable of finding and destroying it. The cinnabar moth and the ragwort flea beetle represent complementary enemies that attack different stages (thereby avoiding invulnerable pest stages) at different times (thereby avoiding temporal pest refuges). However, the value of the cinnabar moth, acting alone or in combination with the flea beetle, has yet to be demonstrated: it can't hurt weed control, but will it help? In agreement with the Kareiva and Odell (Kareiva and Odell 1986) model of ladybird beetles searching for aphid prey, our results suggest that successful natural enemies must rapidly congregate at incipient pest outbreaks and contain or

annihilate them. In departing from these investigations, we emphasize resource limitation in low-density pest populations as a key feature distinguishing biological control of weeds from biological control of insects. In cases of insect biological control, it can be assumed that the pest is limited by the natural enemy, and complex issues of density-dependent effects of resources on prey vital rates seldom arise. In cases of biological weed control, decline in the pest is often accompanied by increase in a background vegetation, and we have shown that pest increase in low-density populations is inhibited by both natural enemies and competition for resources. We emphasize, as special features of biological weed control, the mechanisms that renew the supply of open space (a limiting resource in our system), the rules by which it is apportioned among plant species, and the modification in these rules imposed by natural enemies.

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