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SUCCESSFUL BIOLOGICAL CONTROL OF RAGWORT, *SENECIO JACOBAEA*, BY INTRODUCED INSECTS IN OREGON[1]

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Abstract. The purpose of our study was to estimate the variability in a biological control process on a regional scale, identify its causes, and quantitatively evaluate overall control success. We present evidence of the success of biological control of *Senecio jacobaea* (ragwort) in western Oregon following introduction of three natural enemies. First, observations from a single site showed that ragwort declined to <1% of its former abundance and has been replaced by a plant community composed predominantly of introduced perennial grasses. Second, a perturbation experiment showed that introduced insects, within one ragwort generation, can depress the density, biomass, and reproduction of ragwort to <1% of populations protected from natural enemies. Third, a 12-yr survey of 42 ragwort populations showed that strong and persistent depression of ragwort recurred at many sites and at different times.

Three features of this case history may be useful in the development of ecological theory as an explanation and guide for biological control: (1) the impact of the natural enemies depends on the distribution of individual sizes and ages in the ragwort population; (2) the long-term dynamics of ragwort may be influenced by the presence of a large persistent seed bank which is invulnerable to the natural enemies; and (3) the success of biological control of ragwort in western Oregon appears to be independent of variation in environmental conditions. Combining local, short-term experiments and regional long-term observations is a powerful method for demonstrating successful biological control.

Key words: biological control; environmental variation; Hylemya seneciella; Longitarsus jacobaeae; *perturbation experiment; population dynamics; regional survey; seed banks;* Senecio jacobaea; *stage structure;* Tyria jacobaeae; *weeds; western Oregon.*

INTRODUCTION

Classical biological weed control involves the introduction of exotic natural enemies (e.g., phytophagous insects, nematodes, and pathogens) to reduce the abundance of a plant that has become a pest when spread outside of its native range without its native herbivores. The practical aims of biological weed control programs are to achieve and maintain low population levels of the weed and to foster replacement of the weed with more desirable vegetation.

Biological weed-control programs are manipulations on a grand scale involving relatively few species. Proper monitoring and detailed evaluation of these programs can benefit both ecology and the practice of biological control. Ecologists gain valuable information on population regulation, the dynamics of interactions within and between trophic levels, and species invasions (Harper 1977, Crawley 1983, May and Hassell 1988). Biological control practitioners gain evidence of the success of their programs, which encourages the implementation of future projects, provides understanding that can increase their success (Andres et al. 1976), and encourages wider use of biological weed control as an alternative to chemical herbicides.

Here we offer evidence of successful biological control of tansy ragwort, *Senecio jacobaea* (Asteraceae), following introduction of three biological control agents: *Tyria jacobaeae* (Lepidoptera: Arctiidae), the cinnabar moth; *Longitarsus jacobaeae* (Coleoptera: Chrysomelidae), the ragwort flea beetle; and *Hylemya seneciella* (Diptera: Anthomiidae), the ragwort seed fly. (The genus *Hylemya* is currently undergoing revision.)

Smith and DeBach (1942) described three types of evidence which, in combination, are adequate to document the success of a biological control program: (1) introduction of the natural enemy in several locations is followed by a reduction in pest populations; (2) pest populations remain at a low level following establishment of the natural enemy; and (3) survivorship of pest populations is higher when protected from attack by the natural enemy than when exposed. Although the importance of obtaining data that satisfy these criteria has been emphasized (for example, DeBach et al. 1976, Harper 1977, McEvoy 1985, Luck et al. 1988), few

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biological weed-control programs have been documented completely. Crawley (1989*a*) reviewed 627 biological weed-control programs and found that few provided an objective measure of the depression of weed abundance. Exceptions are the successful control of *Hypericum perforatum* by two introduced leaf beetles (Huffaker and Kennett 1959) and of *Tribulus terrestris* by two introduced weevils (Huffaker et al. 1983).

We present observations at a single site, data from a perturbation experiment, and the results of a regional survey. Together, these data offer evidence for Smith and DeBach's three criteria that is more detailed, and more closely meets current standards for studies of population dynamics, than that outlined by Smith and DeBach (1942). To demonstrate that the first criterion has been satisfied, we describe the depression of a *Senecio jacobaea* population on the central Oregon coast following introduction of the three biological control agents. We also use an extensive 12-yr survey of 42 ragwort populations in western Oregon to measure the change in weed abundance following introduction of natural enemies. We define a target density, estimate the number of sites reaching the target density, and estimate the time required to reach this density. We also look for correlations between the frequency of achieving the target density, the time required to do so, and some measures of environmental conditions. For the second criterion, we measure the magnitude of fluctuations in weed density after reaching the target density in the regional survey, and we also experimentally test the ability of the system to return to low weed densities following a perturbation that creates high weed densities. In addition, we use the intensive observations at a single site to describe the vegetation that has replaced ragwort. We expand the third criterion and measure biomass, density, and reproduction during one weed generation when populations are protected from and exposed to their natural enemies.

Biology of the organisms

Ragwort is a biennial or short-lived perennial plant whose native range extends from Norway south through Asia Minor, and from Great Britain east to Siberia. It has been introduced to New Zealand, Australia, Tasmania, Argentina, Canada's maritime provinces, and the northwestern coast of North America (Harper 1958). It causes economic loss by displacing desirable forage and poisoning livestock; metabolites of its pyrrolizidine alkaloids are hepatotoxic (Mattocks 1986). 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 1973*a*). In Oregon it is most abundant from the coastline to the crest of the Cascade Mountains; it also occurs in several counties in eastern Oregon. In western Oregon an aerial survey estimated that $>12\,000$ km^2 ($>3 \times 10^6$ acres) were infested in 1976 (Isaacson 1978). By 1988 this area had declined 60–90% (Brown 1989).

The cinnabar moth was introduced as a biological control agent from France and released in northern California by the United States Department of Agriculture (USDA) in 1959. It was first released in Oregon in Linn and Polk Counties in 1960 (Isaacson 1973*b*). Since that time, the Oregon Department of Agriculture (ODA)'s biological control program has made >3500 releases in 17 counties throughout ragwort's range in western Oregon. Dempster (1982) has reviewed cinnabar moth biology. The moth is univoltine. Adults emerge in late spring from overwintering pupae and lay clusters of eggs on the undersides of the basal leaves of large ragwort rosettes or flowering plants. The first instar skeletonizes these leaves. During the next four instars the caterpillars move to the apex of the plant, consume the developing floral parts, and then strip the leaves, leaving bare petioles. Older larvae are commonly forced to emigrate to neighboring ragwort plants following consumption of all leaves and capitula (flower heads) (Isaacson 1973*a*). Although larvae will feed on vegetative ragwort plants, they prefer flowering plants. Following the fifth instar (July–September in coastal Oregon) the caterpillars pupate in litter or soil. Although complete defoliation is common in western Oregon (Isaacson 1973*a*), the plants are rarely killed by larval feeding and often develop secondary flowering shoots from July through October (Cameron 1935). Early assessments were that the cinnabar moth provided "partial control" of ragwort (Hawkes and Johnson 1978). The moth's impact on a native *Senecio* is discussed by Diehl and McEvoy (1989).

The ragwort flea beetle was introduced from Italy to northern California by USDA in 1969 (Frick 1970) and was first released in Oregon in Tillamook County in 1971 (Isaacson 1976). Like the cinnabar moth, it has since been distributed widely throughout western Oregon. Frick and Johnson (1973) described the life cycle of the strain introduced in California, and James (1989) studied its biology at our coastal study site. The adults are pit feeders and chew holes in ragwort leaves. Mating occurs in October and November, while egg laying begins in October and continues throughout the winter and early spring. Eggs are laid singly on the plant, and larvae tunnel into leaf petioles and roots. Following the third instar the larvae pupate in the soil and adults emerge in early summer. They begin feeding immediately, but remain in reproductive diapause until egg-laying begins.

Early assessments are that the combined action of the flea beetle and the cinnabar moth has led to improved control; persistence of moth, beetle, and ragwort populations at very low density; and replacement of ragwort with a more desirable vegetation (Hawkes and Johnson 1978, McEvoy 1985, Pemberton and Turner 1990). The interactions between the cinnabar moth and the flea beetle and the impact of these interactions on the biological control of ragwort and are reported elsewhere (James 1989 and McEvoy et al. 1989).

The ragwort seedfly was first introduced from France in 1965 by USDA and released in northern California and Oregon's Willamette Valley in 1966 (Frick 1969), and was re-released in 1976. Its biology has been described by Cameron (1935). The seedfly is univoltine, and adult eclosion coincides with the expansion of ragwort capitula in late spring. Eggs (usually one per capitulum) are laid between the bases of the florets in the capitula. Eggs hatch 3–4 d after oviposition. The larvae consume immature seeds and the base of the involucre and create a frothy exudate on the disc florets during their three larval instars. Mature larvae drop with the flowers and overwinter as pupae in the soil. The seedfly has been found in nearly all infestations of ragwort throughout the state, including infestations >200 km from the closest known release. ODA has made >300 releases of the seedfly throughout Oregon.

SINGLE-SITE OBSERVATIONS

Methods

We observed ragwort population dynamics on a 0.9-ha abandoned pasture in the Cascade Head Scenic Research Area (CHSRA), Siuslaw National Forest, which lies on the border of Lincoln and Tillamook counties on the central Oregon coast. The pasture was last grazed by cattle in 1977. The cinnabar moth was introduced in 1978 and the flea beetle was introduced into the site in 1979 and 1980 (McEvoy 1985). The seed fly was not introduced in the area, but spread to the site following introduction into other areas of the state.

From 1981 through 1988 we made annual estimates of the standing crop of ragwort and associated plant species in the pasture. Once each year, between July and October, we harvested aboveground portions of all vascular plant species from 10 0.25-m^2 circular quadrats randomly located in the northwest quarter (Block 1 of the experiment described below: see *Perturbation experiment: Methods*) of the pasture. All of the plant material was then dried (for 72 h at 60°C) and weighed. During the first 2 yr all material other than ragwort was weighed together; since 1983 we have separated other species into (1) grasses and sedges and (2) forbs other than ragwort. We used Spearman's rank correlation coefficient to measure the significance and the sign of the association between years and the standing crop of both ragwort and other species.

We estimated natural enemy damage and abundance in each of the years when ragwort flowered on the site (1981–1983, 1985, and 1987). Cinnabar moth damage (percentage of flowering plants with any damage and percentage of flowering plants completely defoliated) was estimated in all five years. Beginning in 1983 we also estimated adult flea beetle densities, and in 1987 we estimated seedfly densities. The sampling scheme differed among years due to the variation in the population of the flowering plants and the amount of time available for data collection. In 1981 and 1982 we estimated natural enemy damage and abundance on the same plants used in the estimate of standing crop. In 1983 natural enemy damage and abundance estimates were done on randomly located quadrats in the southern two-thirds of the site. In 1985 we surveyed all flowering plants on the site (53 individuals), and in 1987 we surveyed a random sample of 50 of the 266 flowering plants present.

We estimated densities of ragwort seeds in the soil annually in spring or early summer from 1984 through 1988. We collected 29 soil cores 5 cm in diameter and 10.5 cm deep from the northwest quadrant of the pasture. The cores were sliced into five layers (0–1.5 cm, 1.5–3.0 cm, 3.0–5.5 cm, 5.5–8.0 cm, and 8.0–10 or 10.5 cm), spread in a thin layer over sterilized potting soil in the greenhouse, and watered daily, and ragwort seedlings were counted as they germinated. Ragwort achenes have no innate or acquired long-term dormancy and germinate readily when presented with these conditions (McEvoy 1984). To analyze the changes in seed density over time we first used a logarithmic transformation to stabilize the variances and make the relationship linear. We then used the test for heterogeneity of regression slopes among treatment groups within an analysis of covariance to test whether changes in seed-bank density over time were different at different depths. Because the data involve repeated sampling of the same area, we tested for autocorrelated errors using the Durbin-Watson test (Bowerman et al. 1986, Freund et al. 1986).

Results

The ragwort population at our CHSRA site decreased dramatically between 1981 and 1983 (Fig. 1). Ragwort standing crop in 1981 was >700 g/m^2 and represented 90% of the total plant standing crop. The vegetation on the site appeared to be almost exclusively ragwort. By 1983 the ragwort standing crop had declined to 0.25 g/m^2, only 2.4% of the total plant standing crop. On the site as a whole, ragwort appeared to be reduced to a few, scattered flowering plants. Ragwort standing crop remained low, <1 g/m^2, through 1988.

The rank correlation between ragwort standing crop and year is negative ($r_s = -0.38$, $P < .01$; Fig. 1), and species other than ragwort increased as ragwort declined ($r_s = 0.39$, $P < .01$). The result is that the total plant biomass has remained relatively constant. Since 1983, a large fraction of the standing crop has been grasses, ranging from 96% in 1983 to 53% in 1988 (Fig. 1). The four most abundant grass species are *Holcus lanatus* L., *Festuca arundinacea* Schreb., *Dactylis glomerata* L., and *Anthoxanthum odoratum* L. All four are introduced perennial grasses.

Buried ragwort seed densities decreased at the same time as the actively growing population declined, although the seeds have persisted longer than the aboveground population. The geometric mean number of ragwort seeds in the upper 10.5 cm of the soil declined

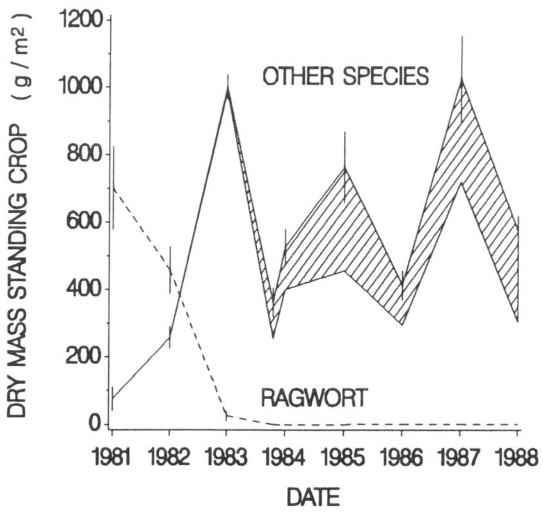

FIG. 1. Ragwort (*Senecio jacobaea*) standing crop at the Cascade Head Scenic Recreation Area (Oregon) site decreased following release of the ragwort flea beetle. Other species increased so that the total standing crop remained relatively constant. Other species are divided into two bands representing forbs (shaded area) and grasses (unshaded area below it).

exponentially, from 14 500 seeds/m^2 in 1982 to 4800 seeds/m^2 in 1988 (Table 1).

The rate of decline of the seed bank varied with depth beneath the soil surface ($F_{4,490} = 4.58$ for the depth × years interaction of an ANCOVA, $P = .0012$). The regression coefficients decrease with increasing depth, indicating that the persistence of the seed bank is longer at greater depths. The residuals of the regression of density on time at the shallowest depth are significantly autocorrelated (Table 2); this means the standard errors calculated at this depth may be underestimated (Bowerman et al. 1986).

Natural-enemy damage estimates are less complete than the ragwort abundance data. However, they show that all three introduced herbivores were present on ragwort plants at our site (Table 3). Damage from cinnabar moth larvae was <2% in 1981 and 1982; defoliation was widespread in 1983 and 1985 and moderate in 1987. In years when the proportion of plants damaged by the moth was high, complete defoliation was frequent. Both the flea beetle and the seed fly were present at moderate levels in the years when counts of those insects were made.

TABLE 1. The density of ragwort seeds in the soil at the Cascade Head Scenic Recreation Area (Oregon) site from 1984 through 1988.

Year	Seed densities (no./m^2)*	
	Mean	95% CI
1984	14 500	12 010–17 530
1985	6500	4940–8560
1986	5300	4000–7070
1987	4300	2600–7090
1988	4800	3710–6200

* Back transformed.

TABLE 2. Decline in the density of buried ragwort (*Senecio jacobaea*) seeds at the Cascade Head Scenic Research Area (Oregon) site between 1984 and 1988; the rate of decline decreased with increasing depth.†

Depth (cm)	b	T	P	Durbin-Watson D
0–1.5	−0.33	−7.00	.0001	1.41*
1.5–3.0	−0.21	−4.32	.0001	2.09
3.0–5.5	−0.20	−4.10	.0001	1.86
5.5–8.0	−0.13	−2.67	.0078	1.94
8.0–10.5	−0.06	−1.26	.2079	1.89

* Significant autocorrelation ($P < .01$).

† The model $y = a \cdot 10^{bx}$ was used, where y = seed density and x = time in years. The t statistic and its associated probability test whether the slopes are significantly different from zero. The standard error of b for all depths is 0.048.

PERTURBATION EXPERIMENT

Methods

The objective of the perturbation experiment was to create high-density ragwort populations and then to compare ragwort density, biomass, and reproduction after populations of the plant were exposed to and protected from introduced biological control agents. We used a single-factor randomized-block design with two treatments (exposed to and protected from herbivores), four blocks, and one replicate per block. We divided the CHSRA study site into four equally sized blocks with one dividing line running north-south and one east-west through the center of the study site. Two plots were located at random locations in each block and one plot randomly assigned to each treatment.

Our goal was to create density and stage structure of ragwort plants in the experimental plots similar to what we had observed in the area prior to introduction of the biological control agents. We prepared eight square 2.25-m^2 plots during the fall of 1985 by removing sod and tilling the soil. We then created high-density stands of ragwort by transplanting small ragwort rosettes in February 1986. The plants had been raised for 2 mo in the greenhouse free of the natural enemies. To protect the plots from herbivory, we covered them with cages (1.83 × 1.83 m) supported by galvanized pipe frames (1.27 cm diameter) and covered with Lumite saran mesh (Chicopee, Gainesville, Georgia) with 0.8 × 0.8 mm openings. The bottoms of the cages were buried 15 cm in the soil to prevent insects from entering.

We then removed all beetles found inside the cages with aspirators and removed all vegetation other than ragwort. Removals continued monthly during the following spring and summer.

In April, and again in November, we sowed seeds in each plot to create populations each with three stage

TABLE 3. Cinnabar moth damage, flea beetle presence, and seed fly presence on ragwort (*Senecio jacobaea*) at the Cascade Head Scenic Recreation Area (Oregon) site, 1981–1987.

Condition of ragwort plants	1981	1982	1983	1985	1987
	Proportion of plants				
1) Damaged by the cinnabar moth	.01	.02	.99	.94	.76
2) Completely defoliated by cinnabar moth	0	0	.82	.94	.14
3) With flea beetle adults	NA*	NA	NA	.45	.88
4) With seed fly larvae	NA	NA	NA	NA	.26
Number of ragwort plants sampled	145	187	102	53	50

* NA = data not available.

classes (small vegetative plants, large vegetative plants, and flowering plants) in the summer of 1987.

After high-density populations were well established and the beetles had begun to oviposit (November 1986), we opened the cages covering plots that were to be exposed to herbivory by rolling up the sides of the cage to expose the bottom half of the cage frame. We used this "sham cage" so that all plots were equally exposed to the unwanted side effects of caging.

Many of the protected plots contained flea beetles by the end of the 1986, so all protected plots on 5 February 1987 were sprayed with a systemic carbamate insecticide (2,3-dihydro-2,2-dimethyl-7-benzofuranyl-N-methylcarbamate or carbofuran; Furadan 4F) at a rate of 2.8 kilograms of active ingredient per hectare. We applied 320 mL of a water-based formulation to each protected plot and added an equal amount of water to all exposed plots. A short-term greenhouse test indicated carbofuran applied at this rate is not toxic to ragwort (James 1989). Since carbofuran is 6% nitrogen by mass (Anonymous 1990), our application added 0.17 kg/ha of nitrogen. This small amount should not be a significant source of nutrients for the plant. Nitrogen is the only plant nutrient in carbofuran.

Next, we collected data to verify that the initial ragwort densities and sizes in the experimental plots were similar to those observed at the site when ragwort had been at its highest density (1981–1982). To do this we counted ragwort plants, and measured their basal diameter, in a randomly placed 0.25-m^2 quadrat in each plot during April 1987.

At the same time, we verified that the plots exposed to herbivores contained more flea beetle larvae than those which had been protected. We harvested the above- and belowground parts of all ragwort plants in the quadrats described above and divided them into size classes based on their basal diameters (<1 mm, 1.1–10 mm, 11–100 mm, and >100 mm; these classes were chosen to correspond to the small vegetative, large vegetative, and flowering plant classes used by McEvoy [1985]). Plants, together with the soil adjacent to their roots, were stored in plastic bags inside an ice chest. After returning to the laboratory, we put the plant material in Tullgren funnels (Southwood 1978), with a 25-W incandescent bulb as a light and heat source. The funnels required 7 d to completely extract the beetle larvae. The larvae were then stored in jars of 70% ethyl alcohol. We had earlier measured extraction efficiency and discovered that more larvae were extracted with Tullgren funnels than by dissection of the petioles and root crowns. After the extraction, we counted the number of larvae, then dried (for 72 h at 60°C) and weighed the plant material.

We simulated cinnabar moth feeding on flowering plants in July 1987, because moth densities at our site, and throughout western Oregon, were low during the 1987 season. The simulation consisted of stripping the leaf blades from their petioles by hand and removing all floral parts. It was designed to mimic feeding when larval densities are high enough to completely defoliate ragwort and remove all floral parts, as had occurred in 1983 and 1985. This artificial defoliation of flowering ragwort plants has been compared experimentally with insect defoliation and shown to yield similar biomass and capitulum production (Henneberger 1986).

We estimated the effect of the herbivore treatments on the survivorship and reproduction of the experimental plants on three dates between August 1987 and October 1988. In August 1987 we counted ragwort plants from a second randomly placed 0.25-m^2 circular quadrat, dividing the plants into the same size classes we had used earlier. We also counted the number of capitula. In April 1988 we harvested a third quadrat, following the procedures we had used the previous spring. We made a final harvest in October 1988, drying and weighing the plant material in the quadrat censused the previous fall.

We did not measure seedfly abundance in any of the harvests because hand defoliation removed all the capitula before larvae were large enough to count.

The experiment was analyzed with standard analyses of variance for randomized-block designs. We used transformations to achieve homogeneous variances when the F-max test indicated variances were heterogeneous (Sokal and Rohlf 1981). We used a univariate repeated-measures analysis of variance to analyze repeated harvests over time, after verifying that the assumption of the sphericity of the orthogonal compo-

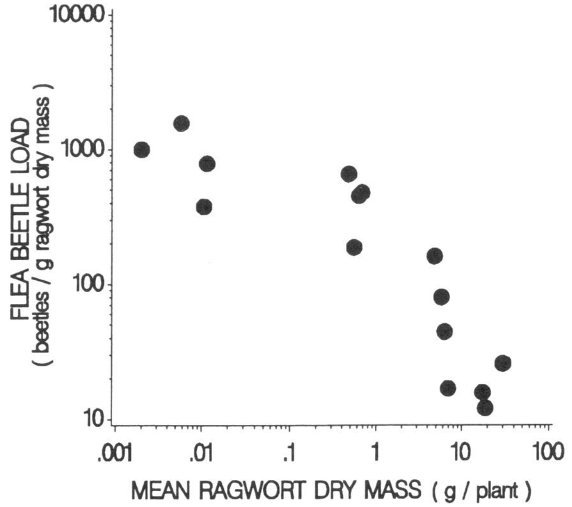

FIG. 2. Flea beetle load in the April 1987 harvest of the perturbation experiment was negatively correlated with plant biomass ($r^2 = 0.86$).

nents of the ANOVA was met. This assumption is satisfied when the differences between all pairs of measurements within harvest dates have homogeneous variances (Gurevitch and Chester 1986).

Data from the first year of the perturbation experiment have been reported in McEvoy et al. (1989).

Results

Initial conditions.—Initial estimates (April 1987) of ragwort density, ragwort stage structure, and beetle density showed that three assumptions about the implementation of the experiment had been satisfied.

First, initial levels of ragwort biomass and density were similar in plots protected from and exposed to herbivory. Ragwort density (mean ± 1 SE) was 274 ± 94.4 plants/m² in protected plots and 308 ± 63.2 plants/m² in exposed plots. There was no significant difference between plots exposed to or protected from herbivores (ANOVA, $F_{1,3} = 0.06$, $P = .82$). Ragwort dry mass was 477 ± 73 g/m² in exposed plots and 328 ± 33 g/m² in protected plots. There was no significant difference in mean biomass between treatments (ANOVA, $F_{1,3} = 8.02$, $P = .07$). Since the test approaches significance, it should be noted that if plants in exposed plots were actually larger than those in protected plots, the experiment will be a conservative test of the effects of herbivores.

Second, the size structure of ragwort populations in our experimental plots was similar to that previously observed in the wild ragwort population at the site: 45% of the plants had a basal diameter <1 mm, 42% had a basal diameter between 1 and 10 mm, and 13% had a basal diameter >10 mm. This distribution roughly corresponded to the size structure of the natural population of the site when high densities of ragwort occurred (1981–1982): 54% small vegetative, 32% large vegetative, and 14% generative plants (McEvoy 1985). Total density was higher in the experimental plots (mean ± 1 SE = 308 ± 63 plants/m²) than in the natural population (157 ± 24 plants/m²).

TABLE 4. Repeated-measures analysis of variance of ragwort (*Senecio jacobaea*) density in harvests 2, 3, and 4 of the perturbation experiment following a logarithmic transformation.*

Source of variation	df	MS	*F*	*P*
Block	3	0.13	1.86	.1902
Treatment	1	18.13	156.87	.0011
Block × Treatment (error term for treatment)	3	0.12	1.59	.2428
Harvest date	2	1.66	22.99	.0001
Treatment × Harvest date	2	1.91	26.30	.0001
Error	12	0.07		

* The sphericity assumption is satisfied (Mauchly's criterion = 0.76, $\chi^2_2 = 0.51$, $P = .76$).

Third, beetle densities were high in exposed plots and negligible in protected plots. Geometric mean densities of beetle larvae were 906 (back-transformed 95% confidence limits: 520–1577) larvae per plot in exposed plots and only 1 (back-transformed 95% confidence limits 0.1–3) larvae per plot in protected plots, a highly significant difference (ANOVA of log-transformed data, $F_{1,3} = 178$, $P = .0009$). Following a logarithmic transformation, beetle load (number of larvae per gram of host plant dry mass) in exposed plots was negatively correlated with plant biomass (Fig. 2).

Responses to experimental treatments.—Ragwort density in exposed plots declined sharply during the experiment (Fig. 3A). In August 1987 the mean densities in exposed plots were 12.32 plants/plot, 24% of those in protected plots; mean density in October 1988 was 0.19 plants/plot, only 0.5% of protected plots. In protected plots, mean density increased to 1800 plants/plot in in the April 1988 harvest following the germination of a large number of new seedlings. A repeated-measures analysis of variance indicated that exposure to herbivores significantly decreased ragwort density (Table 4). The effect of harvest date was significant, indicating that plant density changed over time. The interaction between treatment and harvest date was also significant; density increased over time in the protected treatment and decreased in the exposed treatment. The result was that magnitude of the difference between treatments increased over time.

Ragwort biomass showed a trend similar to the density measurements (Fig. 3B), although heterogeneous variances (not correctable by transformation) did not allow us to use the repeated-measures ANOVA.

Ragwort reproduction (number of capitula/0.25 m²) in exposed plots was 1.8% of that in protected plots in 1987. In 1988 no plants flowered in exposed plots (Fig. 3C). A repeated-measures ANOVA indicated that exposure to herbivores significantly decreased ragwort

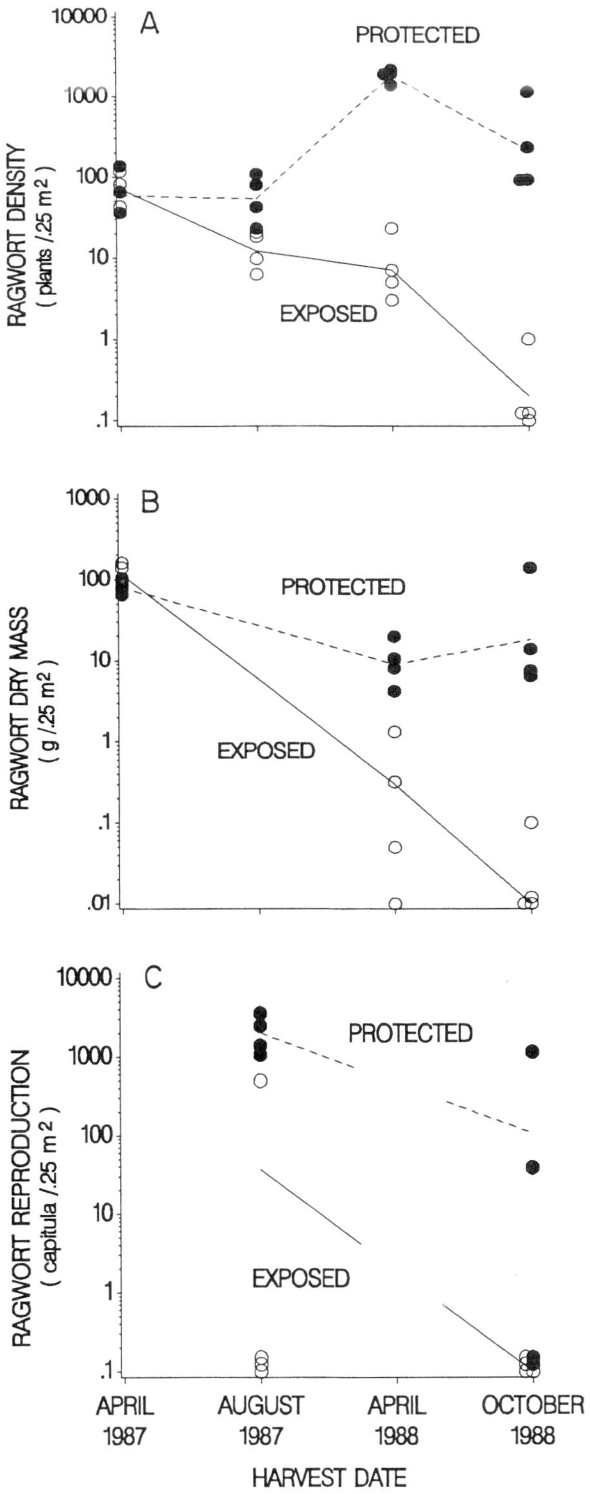

FIG. 3. Ragwort density (A) and biomass (B) in the perturbation experiment declined when plants were exposed to herbivores (○) and remained high when plants were protected from herbivores (●). Ragwort reproduction (C) was lower when plants were exposed to herbivores (○) than when plants were protected from herbivores (●). Lines connect back-transformed treatment means.

TABLE 5. Repeated-measures analysis of variance of ragwort (*Senecio jacobaea*) reproduction in harvests 2 and 4 of the perturbation experiment. We applied a square-root transformation before analysis.*

Source of variation	df	Mean square	*F*	*P*
Block	3	59	0.32	.8109
Treatment	1	2357	25.22	.0152
Block × Treatment (error term for treatment)	3	93	0.51	.6923
Harvest date	1	1596	8.64	.0260
Treatment × Harvest date	1	847	4.59	.0759
Error	6	185		

* The test for sphericity could not be applied because data from only two harvests were analyzed.

reproduction (Table 5). The effect of harvest date was also significant; 1988 reproduction was less than 1987 reproduction in both protected and exposed treatments. The interaction was not significant.

The decrease of ragwort density that occurred during 1987 in exposed plots occurred mostly in the smallest size classes. In August the density of small vegetative plants (basal diameter <1 mm) in exposed plots was 2.4% of that in protected plots. Density of large vegetative plants (basal diameter between 1 and 10 mm) in exposed plots was 22.2% of that in exposed plots, while densities of flowering plants (the largest size class) did not differ between treatments (Fig. 4).

REGIONAL SURVEY

Methods

Oregon Department of Agriculture (ODA) personnel have surveyed ragwort densities on sites throughout western Oregon since 1976 (Fig. 5). A total of 42 sites (9–31 sites each year) have been surveyed. Sites were first surveyed between 1976 and 1986 at the time that beetles were released as part of ODA's biological control program to collect and redistribute beetles throughout the ragwort-infested areas of Oregon. Surveys continued (not always annually) until forest succession or a change in land use made it unfeasible to continue observing the site. Six sites were surveyed for ≥10 yr, 16 sites between 5 and 10 yr and 20 sites for <5 yr (see Appendix).

Survey personnel counted flowering ragwort plants in 50 0.25-m^2 plots (10 plots in 1976 and 1977) uniformly spaced 2 m apart along two transects located arbitrarily in the survey site. The survey was conducted between August and October each year. As measures of the environmental variation encompassed by the survey, we classified each site according to land use, estimated elevation from topographic maps, and estimated precipitation from a map of rainfall isoclines.

In addition to the survey of actively growing ragwort populations, we used the procedure followed in our intensive seed-bank study to estimate the size of the seed banks at 10 of the survey sites. We collected 10

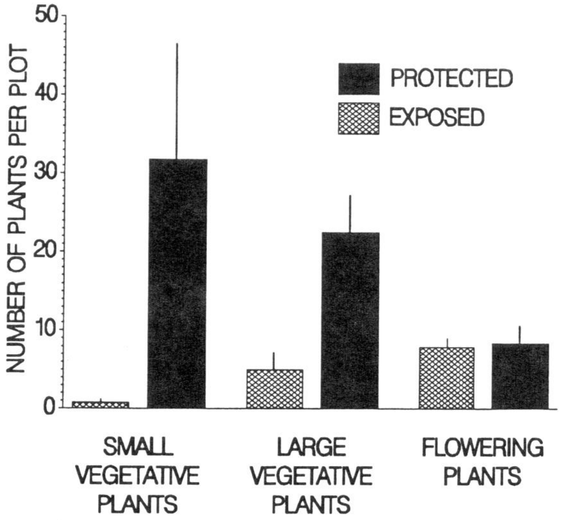

FIG. 4. Mean densities of small and large vegetative ragwort plants (graphed with their back-transformed standard errors) were higher in protected plots than in exposed plots. There was no difference in densities of flowering plants. Densities were measured in October 1987. These data were first reported in McEvoy et al. (1989).

soil cores (5.5 cm diameter × 10.5 cm deep) from Sites 1, 2, 3, 20, 24, 33, 37, 38, and 40 in 1986. We then correlated the density of the seeds in the soil with the maximum recorded flowering-plant density.

Plot locations in the survey were not randomly selected, and we lack assurance that they are representative of ragwort densities on the entire site. Therefore we decided not to use a parametric multivariate analysis to evaluate the significance of the trends following beetle introduction and the relationships with our measures of environmental variability. Instead, we report the qualitative results of this survey, together with nonparametric tests of some summary response variables.

We summarized the survey data by calculating the length of time (in years) between the introduction of flea beetles at a given site and the first survey on that site in which no flowering ragwort was recorded. We call this interval the "time to reach the target density." We use zero ragwort density as a target density since an economic threshold has not been established for ragwort. A density of zero mature plants in the sample transect most likely represents a small, but nonzero, ragwort density on the site as a whole. Using zero as a target density also is consistent with recent reviews that suggest many successful biological control systems are characterized by local extinctions and reinvasions (Murdoch et al. 1985).

We then tested whether this summary variable was associated with our measures of environmental variability. We used a Kruskal-Wallis nonparametric analysis of variance to test whether the time to reach target density varied among land-use types or among years of beetle release. We compared time to reach the target density for the releases made in years (1976, 1980, and 1984) when beetles were introduced at ≥5 sites. We also used Spearman's rank correlation coefficients to measure the associations among elevation, precipitation, and time to reach target density.

In addition, we calculated the maximum ragwort density in any survey subsequent to the first observed zero ragwort density as a measure of the magnitude of fluctuations following achievement of the target density. Only the 14 sites with ≥ three surveys subsequent to the first survey recording zero flowering plants were included in this analysis.

The abundance of the cinnabar moth and the seed fly was not recorded in these surveys. However, it is likely that both insects were present throughout the survey area since the moth had been extensively distributed by ODA in Oregon prior to the introductions of the flea beetle and the seed fly had dispersed throughout the state.

Results

The 42 sites surveyed by ODA (see Appendix) are located throughout the area of western Oregon in which ragwort occurs (Fig. 5), and they appear to be representative of the habitats and conditions that exist where control of ragwort is desired. They span a range of elevation from sea level to 1000 m. Twelve are below 150 m elevation, 25 are between 150 and 750 m, and 5 are above 750 m. The sites span the range of annual precipitation (1000–2500 mm) in western Oregon's ragwort habitat; 24 of the sites have an annual precipitation between 1500 and 2100 mm. They represent a variety of land uses; 37 of the 42 sites can be classified as either timber land (early forest succession following

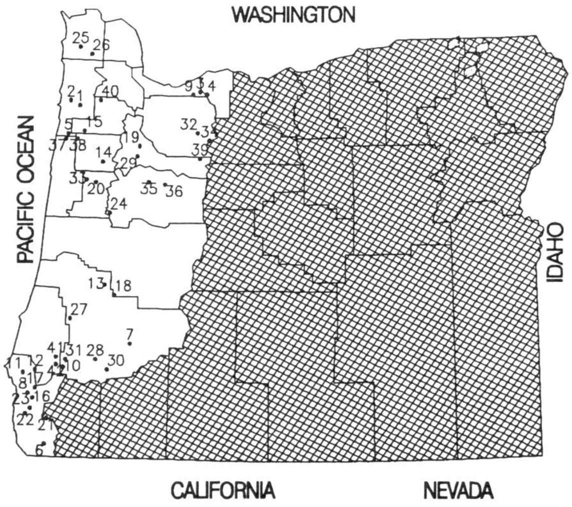

FIG. 5. Location of the 42 ragwort sites surveyed by the Oregon Department of Agriculture. White areas indicate ragwort's distribution in Oregon. The eastern edge of ragwort's distribution generally follows the crest of the Cascade Range.

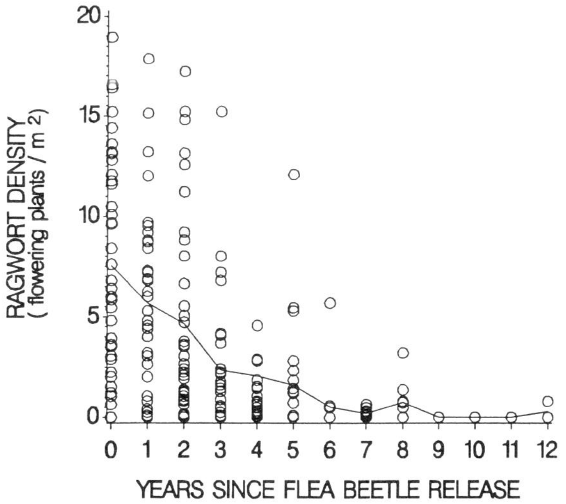

FIG. 6. Ragwort flowering-plant density decreased following release of the ragwort flea beetle at the 42 sites surveyed by the Oregon Department of Agriculture. Two high values of ragwort density (Site 28, year 1: density 21.8 plants/m^2; Site 24, year 4: density 31.3 plants/m^2) have been omitted from the graph to improve resolution, but are included in the mean.

timber harvest; 19 sites), grazed pasture (10 sites), or ungrazed meadow (8 sites).

Ragwort densities throughout western Oregon declined to low levels following ODA's flea beetle introduction and redistribution program (Fig. 6). At the time of beetle release, the density of flowering ragwort plants was 7.52 ± 0.80 plants/m^2 ($\bar{X} \pm 1$ SE, $n = 42$). At the 14 sites surveyed 6 yr after release, mean flowering-plant density had declined 93% to 0.52 ± 0.40 plants/m^2. At the six sites surveyed 10 yr after beetle release, the mean density of flowering plants in the survey plots was zero, although occasional plants were observed in the nearby area.

Densities of flowering ragwort plants declined to the target density, zero flowering plants, during at least one survey at 30 of the 42 sites. Eight of the remaining sites (Sites 4, 9, 10, 15, 16, 30, 34, and 41) were surveyed only for 2 or 3 yr after beetle release, and therefore we do not have enough information to judge whether or not the target density was reached. At Site 28, ragwort density, while never zero, was 0.08 plants/m^2 six years following beetle release, a decrease of 99% from the original density of 13.12 plants/m^2. Ragwort density 6 yr after beetle release at Sites 14, 22, and 39 had declined only 33% (to 8.61 plants/m^2), leading us to question whether the target density has been achieved on those three sites.

Time to reach the target density on the 30 sites for which it could be measured (all sites on which no flowering ragwort had occurred in samples on at least one census) was not correlated with either precipitation ($r_s = -0.04$, $P > .05$) or elevation ($r_s = -0.27$, $P > .05$). Time to reach the target density did not differ among land-use types (Kruskal-Wallis nonparametric analysis of variance, $H = .966$, df = 3, $P = .809$). Also there were no significant differences (Kruskal-Wallis ANOVA, $H = 4.48$, df = 2, $P = .106$) in the time to reach target density among the release years that could be tested (1976, 1980, and 1984). Median time to reach target density was 5 yr for releases made in 1976 ($n = 13$, range: 1–9 yr), 5 yr for releases made in 1980 ($n = 7$, range: 1–7 yr), and 3 yr ($n = 3$, all values equal) for releases made in 1984. The three sites at which target density has not yet been achieved do not share a common elevation, annual precipitation, land use, or release year.

Ragwort densities appear to be maintained at a relatively low level following decline to the target density in the 14 sites surveyed for ≥3 yr after zero flowering ragwort was first recorded. Subsequent ragwort density in the survey plots remained zero at 5 (37%) of the 14 sites. In the remaining nine sites, the maximum ranged from 0.5 to 3.2 flowering plants/m^2. The maximum was <35% of the original ragwort density at eight of the sites; at the remaining site (Site 32) ragwort density following an initial decline to zero, increased to 64% of the original density, but then declined again to zero.

We found ragwort seed in the soil of 9 of the 10 sites sampled. The median seed density at the 10 sites was 387 seeds/m^2 with a range of 0 (Site 32) to 3145 (Site 37) seeds/m^2. Following a logarithmic transformation, seed-bank density was correlated ($r^2 = 0.61$) with that of the maximum density of flowering plants that had been recorded (Fig. 7). Since the maximum flowering-plant density density occurred 5–10 years prior to the measurement of the seed bank, this correlation highlights the persistence of the seed bank after aboveground populations have declined.

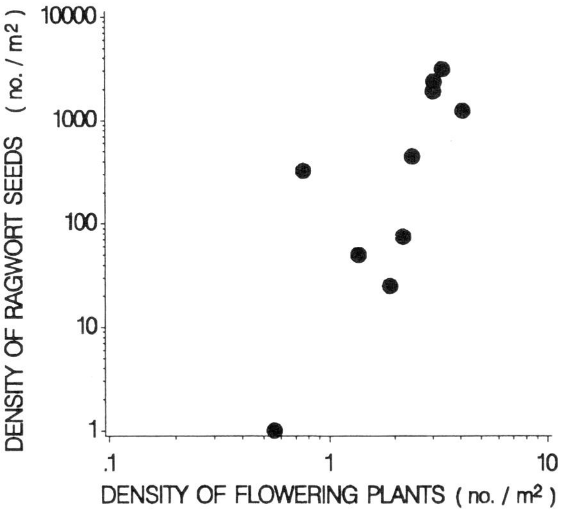

FIG. 7. The mean number of ragwort seeds in soil at 10 of the sites in the Oregon Department of Agriculture survey was positively correlated ($r^2 = 0.61$) with the maximum density of flowering plants observed at the site prior to 1986.

DISCUSSION

We observed a 99.9% reduction in ragwort standing crop during an 8-yr period following introduction of insect natural enemies at a site on the central Oregon coast. A regional survey of 42 sites throughout western Oregon recorded a decline of similar magnitude (93%) in 6 yr. These data satisfy the first criterion established by Smith and DeBach (1942) for evaluating biological control and are similar to data obtained from other successful biological weed-control case histories (*Opuntia sp.*, Dodd 1940; *Hypericum perforatum,* Huffaker and Kennett 1959; *Tribulus terrestris,* Huffaker et al 1983; *Salvinia molesta,* Room et al. 1984; *Carduus nutans,* Kok and Pienkowski 1985). Decline of ragwort populations has also been recorded in California and Canada, two other areas where the natural enemies have been introduced (Harris et al. 1978, Hawkes and Johnson 1978).

Our observations from a single site and the regional survey also demonstrate that Smith and DeBach's second criterion has been satisfied. Following establishment of natural enemies and decline of ragwort populations, densities of the plant remained depressed for the durations of our observations and our survey. These data are similar to data obtained from the case histories mentioned previously. In addition, our perturbation experiment provides experimental verification that insects cause ragwort populations to remain at low levels following biological control. A return of a population to predisturbance levels following experimental perturbation (convergence experiments; Murdoch 1970) is a generally acceptable method of detecting population regulation. We performed this kind of experiment after ragwort populations had declined to zero flowering plants by creating high-density ragwort populations. Subsequently, populations exposed to herbivory returned (within one ragwort generation) to pre-perturbation levels while populations protected from herbivory continued at high density; this is one measure of the biological control system's tendency to maintain pests at low levels following successful control.

Smith and DeBach's third criterion required experimental demonstration that pest survival is higher when protected from its natural enemies than when exposed. This criterion is satisfied by our perturbation experiment; after two growing seasons, ragwort densities in plots exposed to herbivores were 0.5% of those in protected plots, and reproduction was zero. Of the case histories mentioned previously, only the evaluation of biological control of *H. perforatum* (Huffaker 1951), *Opuntia aurantiaca* (Zimmerman and Moran 1982), and *T. terrestris* (Huffaker et al. 1983) included such an exclusion experiment.

There has recently been considerable interest in examining case histories in order to develop theory that can be used as an explanation and guide for biological control, to test predictions of models, and to describe characteristics of successful biological control (Murdoch et al. 1985, Crawley 1986, 1987, 1989*a, b*; Bergelson and Crawley 1989). There are three features of this ragwort case history that appear to be worth considering in such reviews.

First, the impact of its natural enemies varies with the size and stage structures of the ragwort population. The enemies caused heavy mortality of the smaller, younger plants in the population; these plants also had the highest loads of flea beetle larvae. The pattern appears similar to the heavy mortality of small plants that was observed following introduction of *Cactoblastis cactorum* to control *Opuntia ficus-indica* in South Africa (Zimmerman and Moran 1982). In addition, the herbivores caused a sharp decline in the amount of successful reproduction by the large, adult plants in the population. Although the generalization that mortality is size dependent forms part of the core of plant demographic theory (Crawley 1983), this has rarely been documented for biological weed-control programs. We plan further research to study whether large plants are more tolerant of flea beetle herbivory, if higher densities of beetles can cause mortality of large plants, and how the competitive interactions with other neighboring plants might affect this relationship.

Ragwort's large, persistent seed bank is invulnerable to the natural enemies and may soften their impact when environmental conditions allow recruitment. Ragwort's seed bank at our site was >14 000 seeds/m^2 at the beginning of this study, and seeds have persisted longer than actively growing plants. Persistence of the seed bank increased with the depth at which the seeds were buried; at a depth below 8 cm we could not measure a decline in seed-bank density during an interval of 5 yr. The regional seed-bank survey showed that moderate to high numbers of ragwort seeds in the soil were widespread in western Oregon. Ragwort seed banks of similar magnitude have been found in New Zealand pastures (300–4800 seeds/m^2; Thompson 1980, 1985) and in an abandoned pasture (>2000 seeds/m^2) in England, part of ragwort's native range (Chippindale and Milton 1934). Although seed banks of weeds of cultivated land have often been measured (Cavers and Benoit 1989), and models of biological insect control have shown that the presence of an invulnerable stage can have important effects on the dynamics of biological insect control systems (Murdoch et al. 1987, Murdoch 1990), seed banks have rarely been studied in conjunction with biological control programs. One exception is *T. terrestris,* where densities of seeds following control ranged from 45 to >9000 seeds/m^2 in the soils at four southern California sites (Goeden and Ricker 1973).

Third, the success of biological control of ragwort in western Oregon appears to be independent of variation in the environmental conditions we measured: precipitation, elevation, land use, and year of flea beetle releases. Neither the frequency nor the speed of successful control was associated with variation in any of these four environmental conditions. Previous studies have shown that ragwort's interactions with the cinnabar moth (Cox and McEvoy 1983) or the flea beetle (Hawkes and Johnson 1978) can be strongly influenced by summer moisture stress, but this study suggests that the variation in precipitation that occurs in western Oregon does not lead to any reduction in the ability of this combination of herbivores to depress their host-plant populations.

The combination of experimental and observational studies is a powerful method of demonstrating successful biological weed control. Experiments are essential for a determination of cause and effect, but are usually too expensive to be replicated spatially or temporally. Observational studies can provide information on the variability of the biological control process from multiple sites over multiple years. The combination provides the evidence needed to satisfactorily document successful biological weed control and justify its wider use.

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APPENDIX

Dates of ragwort (*Senecio jacobaea*) censuses and some environmental details at the 42 sites surveyed in western Oregon by the Oregon Department of Agriculture.

Site	Beetle release year	Last year surveyed	Number of surveys	Precipitation (mm/year)	Elevation (m)	Land use
1	1976	1988	12	2500	200	Meadow
2	1978	1988	10	2000	60	Grazed, cultivated
3	1980	1987	7	2500	700	Timber
4	1986	1988	3	2500	900	Timber
5	1976	1981	6	1500	100	Meadow
6	1984	1987	4	2000	300	Grazed
7	1984	1988	5	1250	1200	Timber
8	1980	1988	9	2000	45	Grassy bluff
9	1980	1981	2	2500	450	Timber
10	1986	1988	3	1500	850	Timber
11	1980	1988	9	1500	200	Grazed
12	1980	1981	2	2000	400	Timber
13	1976	1987	11	1250	300	Timber
14	1976	1981	6	1250	100	Meadow
15	1980	1982	3	2000	300	Meadow
16	1984	1986	3	2000	300	Timber
17	1984	1988	5	2000	300	Swampy meadow
18	1976	1981	6	1250	700	Timber
19	1976	1981	6	1250	60	Grazed
20	1976	1987	10	2500	60	Timber
21	1980	1981	2	2000	700	Meadow
22	1976	1981	6	2000	60	Grazed
23	1986	1988	3	2000	100	Power line
24	1976	1986	10	1000	100	Cultivated
25	1976	1981	6	2500	500	Skid road
26	1979	1981	3	2000	300	Timber
27	1985	1988	4	2000	430	Timber
28	1983	1988	6	1000	500	Timber
29	1976	1981	6	1250	100	Grazed
30	1984	1985	2	1000	800	Abandoned orchard
31	1976	1981	6	1500	300	Timber
32	1981	1987	6	2000	700	Timber
33	1976	1988	13	2500	300	Grazed
34	1986	1988	3	2000	800	Timber
35	1976	1981	6	1750	300	Grazed
36	1976	1982	7	1750	700	Timber
37	1980	1988	9	2000	60	Grazed
38	1980	1988	8	2000	60	Meadow
39	1978	1981	4	2500	1000	Timber, grazed
40	1976	1982	7	2500	300	Timber
41	1980	1981	2	1500	150	Grazed
42	1978	1981	3	1500	150	Grazed