Depression in Ragwort (*Senecio jacobaea*) Abundance Following Introduction of *Tyria jacobaeae* and *Longitarsus jacobaeae* on the Central Coast of Oregon

Peter B. McEvoy

Department of Entomology, Oregon State University, Corvallis, OR 97331, U.S.A.

Abstract

This study measured the depression in abundance of dormant and actively growing stages of ragwort (*Senecio jacobaea*) following introduction of two phytophagous insects, ragwort flea beetle (*Longitarsus jacobaeae*) and cinnabar moth (*Tyria jacobaeae*) on the central coast of Oregon, U.S.A. Actively growing stages (seedlings, rosettes, flowering plants) declined to 3% and dormant stages (seeds and vegetative buds) declined to 32% of their former abundance following increase in herbivore populations. Based on evidence that the ragwort population was closed to migration, the depression in host abundance was ascribed to a >95% mortality spread over all actively growing stages followed by a 33% decline in per capita birth rate of the surviving reproductive plants. A decrease in ragwort standing crop was balanced by an increase in standing crop of other plant species (88% perennial grasses), leading to no net change in standing crop of the plant community. Two years following the decline, ragwort standing crop has remained at low levels (flowering plants have disappeared altogether), but densities of seedlings and small rosettes have rebounded to previous levels due to recruitment from the dormant seeds in the soil. Further study is required to determine whether ragwort will remain at low levels in the long term.

Réduction de l'Abondance des Séneçons Jacobée (*Senecio jacobaea*) Après l'Introduction du Lépidoptère Tyria (*Tyria jacobaeae*) et de l'Altise du Séneçon (*Longitarsus jacobaeae*)

Cette étude visait à mesurer la réduction de la densité des séneçons *Senecio jacobaea* (parties souterraines et aériennes) après l'introduction de deux insectes phytophages, soit l'altise *Longitarsus jacobaeae* et le lépidoptère *Tyria jacobaeae*, dans la partie centrale de la côte de l'Orégon aux États-Unis. La réduction a été exprimée selon la formule $q = N^*/K$, où K représente l'abondance moyenne de la plante hôte avent l'introduction des herbivores et N* désigne le nombre réduit d'hôtes, cet équilibre étant probablement assuré par les herbivores. La valeur de q pour les parties aériennes (jeunes plants, rosettes, plantes à fleurs) était de 0,03 et de 0,32 pour les parties souterraines (graines et pousses). En se fondant sur des données selon lesquelles il n'y avait aucune migration des séneçons et que leur distribution aux différents stades de croissance était stable, le réduction du nombre d'hôtes a été attribuée à la baisse du taux de reproduction, plutôt qu'aux modifications des taux de survie ou de migration. La réduction du stock existant de séneçon a été équilibrée par une augmentation du stock existant d'autres espèces de plantes (herbes vivaces dans 98% des cas), ce qui n'a provoqué aucun changement net du stock existant de la communauté de plantes.

Introduction

The aim of biological control introductions is to depress host densities below an economic threshold and maintain them there. Hence we are concerned with two dynamic elements: (1) the level of depression in the host caused by the observed level of herbivory; and (2) the stability of the interaction over the long term. I studied depression

and stability in ragwort (*Senecio jacobaea* L.; Compositae) abundance following introduction of cinnabar moth (*Tyria jacobaeae* [L.]; Lepidoptera: Arctiidae) and ragwort flea beetle (*Longitarsus jacobaeae* [Waterhouse]; Coleoptera: Chrysomelidae) on the central coast of Oregon, U.S.A.

The role of herbivores in depressing host abundance was evaluated from observations establishing: (1) an association, evidenced by negative correlation of insect and plant density; (2) a contact, evidenced by herbivore damage to the plants; and (3) a mechanism for population changes, expressed as changes in migration, birth, or death rates. I propose experiments to confirm relations of cause and effect suggested by my observational studies.

Organisms Studied

Ragwort is a biennial or short-lived perennial introduced to North America from Europe. It causes economic losses by poisoning cattle, horses, and swine (Muth 1968) and by displacing desirable forage. Ragwort was first recorded in western North Aermica in 1913 from Vancouver Island (Harris *et al.* 1971) and first recorded in Oregon in 1922 from Portland (Isaacson 1971). The weed now ranges from northwestern California to British Columbia from the coastline to the Cascade Mountains and beyond, with scattered reports having been confirmed from the Blue and Wallowa Mountains (D. Sharratt, OR State Dept. Agric., pers. comm.).

The cinnabar moth 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). Adult moths emerge in late spring from overwintering pupae, and lay eggs in clusters on undersides of basal leaves of the ragwort food plant. 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, regrowth shoots develop in autumn after larvae have entered the overwintering pupal stage.

The ragwort flea beetle was introduced from Italy and released in California near Fort Bragg in 1969 (Frick 1970*b*; Frick and Johnson 1973; Hawkes and Johnson 1978) and in Oregon near Trask River (Tillamook County) in 1971 and near Salem (Marion County) in 1972 (Isaacson 1978). The life history is described by Newton (1933), Frick (1970*a, b*, 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 tunnel in leaves, petioles, stems and roots during winter and early spring. Pupation occurs in the soil and adults emerge in early summer.

Natural dispersal and deliberate redistribution have resulted in establishment of populations of both insects over nearly all of Oregon west of the Cascades.

Methods and Materials

The study was conducted in an abandoned pasture (Three Rocks Road South, 45°2'2"N., 123°58'42"E.) last grazed by dairy cattle in 1977. The site is part of the 3951 ha Cascade Head Scenic Research Area (CHSRA), which lies in Lincoln and Tillamook counties on the central coast of Oregon.

A total of 6505 flea beetle adults and 7000 cinnabar moth larvae were introduced to CHSRA (Table 1). These totals include local releases at Three Rocks Road Pasture

of 2000 cinnabar moths in 1978, 220 flea beetles in 1979, and 485 flea beetles in 1980. All releases were made by the Oregon State Department of Agriculture and cooperators.

I began monitoring plant and insect populations in 1981. No quantitative estimates were made of insect density in 1981–82 because qualitative surveys revealed very few insects. In 1983, insect density was estimated in late summer from counts of cinnabar moth pupae and flea beetle adults in $\frac{1}{4}$ m^2 quadrats located at random. The percent of generative stems damaged by cinnabar moth and the level of damage to each stem was estimated each year 1981–83. In 1984, generative plants had disappeared so I evaluated cinnabar moth damage to vegetative plants. I made no assessment of damage by the flea beetle.

Table 1. Timing, size, and location of insect releases in Cascade Head Scenic Research Area, Oregon.

Year	Number of Individuals	Location	Ownership
a. *Longitarsus jacobaeae* (Waterhouse) releases.			
1976	750	6S,11W,Sec 14 SW	Nature Conservancy
1979	250	6S,11W,Sec 23 NE	U.S. Forest Service
1979	220	6S,11W,Sec 24 SW[1]	U.S. Forest Service
1980	485	6S,11W,Sec 24 SW[1]	U.S. Forest Service
1980	3000	6S,11W,Sec 23 NE	U.S. Forest Service
1982	2000	6S,11W,Sec 19	Private
b. *Tyria jacobaeae* (L.) releases.			
1978	1000	6S,11W,Sec 14	U.S. Forest Service
1978	2000	6S,11W,Sec 24 SE/SW[1]	U.S. Forest Service
1978	1000	6S,11W,Sec 13 NW/NE	Private
1978	1000	6S,11W,Sec 24 NW	Private
1978	1000	6S,11W,Sec 14 SW/NW	Nature Conservancy
1978	1000	6S,11W,Sec 14	Private

[1]Three Rocks Road Pasture.

Ragwort individuals were classified by stage: dormant seeds and vegetative buds in the soil, small vegetative plants (avg. dia. or $\frac{1}{2}$ [length + width] <7.5 cm), large vegetative plants (avg. dia. >7.5 cm), and generative plants.

Densities of dormant stages in the soil were estimated annually 1982–84 from soil cores 5 cm dia. and 10 cm deep. Soil cores were spread in a thin layer over sterilized potting soil in the greenhouse, watered daily, and the seeds allowed to germinate and vegetative buds allowed to sprout. Plantlets from seed were distinguished by symmetrical cotyledons and fine, fleshy, tapered taproots, while plantlets from vegetative buds on root fragments had asymmetrical leaves and stout, irregular root stocks.

The densities of actively growing stages were estimated each summer 1981–84 from $\frac{1}{4}$ m^2 quadrats. Counts of stems were transformed to counts of individuals by dividing by 3.55, the mean number of stems (ramets)/plant (genet) in a random sample of 64 ragwort plants taken in 1977, assuming that the mean number of ramets/genet did not change in the population from year to year.

Differences in plant density and dry mass among years were tested using the Kruskall-Wallis ANOVA by ranks. Pairwise comparisons between years were made using a non-parametric STP procedure based on the Mann-Whitney U Test (Sokal and Rohlf 1981). The samples sizes were randomly reduced to the minimum for groups compared for purposes of the test, which requires equal sample sizes. Means were estimated from full samples.

Results and Discussion

Herbivore Dynamics

The herbivores multiplied slowly at first. The cinnabar moth population remained at low levels through 1981–82, causing minor damage to 2% of 211 flowering stems sampled in the two years. In 1983, four years after release of the moth, the population erupted, causing major damage to 98% of the 92 flowering stems sampled, stripping them of their leaves and flower heads. In September 1983, cinnabar moth density averaged 2.4 (0–12) pupae/m^2. The flea beetle population erupted after summer 1982, reaching an average density of 5.6 (0–16) adults/m^2 in September 1983.
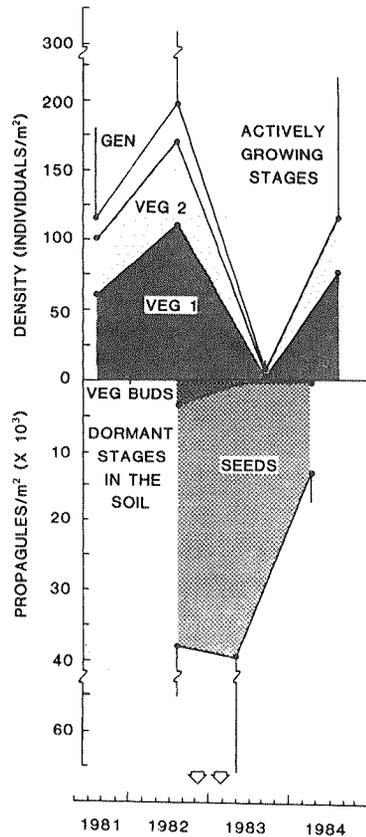

Fig. 1. Annual estimates of mean density (individuals/m^2) for dormant (vegetative buds and seeds) and actively growing stages (gen = generative plants, veg 2 = large vegetative plants, veg 1 = small vegetative plants) of ragwort population at Three Rocks Road pasture. Bars represent standard deviations. Sample sizes from left to right: actively growing stages (10, 10, 20, 10), dormant stages in soil (7, 13, 20). Arrows along time axis indicate approximate dates of insect outbreaks.

Host Dynamics

During 1981–82, ragwort's absolute and relative abundances were unchanging and extremely high. The combined density of actively growing stages averaged 157.2 plants/m^2 (Fig. 1). The distribution of density among stages was pyramidal; the percent of individuals in each actively growing stage declined in the series: small vegetative plants (54%), large vegetative plants (32%), generative plants (14%). Over 99% of

individuals in the population were dormant propagules in the soil. In greenhouse experiments, 91–99% of the recruits were from seed, the remainder from vegetative buds. The combined dry mass of actively growing ragwort stages averaged 580.6 g/m^2 (Fig. 2); ragwort accounted for 72% of the above-ground dry mass of the plant community. The distribution of dry mass among stages was inversely pyramidal; the percent of total dry mass in each stage increased in the series: small vegetative plants (<1%), large vegetative plants (4%), and generative plants (95%).
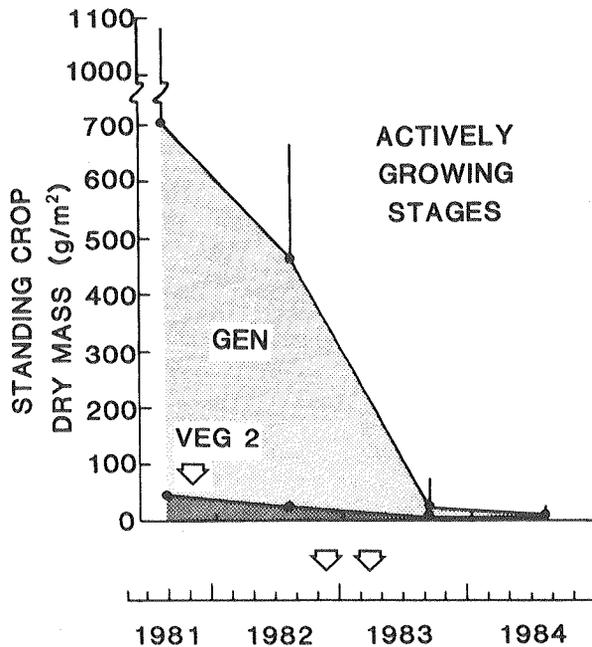

Fig. 2. Annual estimates of standing crop (dry g/m^2) for actively growing ragwort stages at Three Rocks Road Pasture. Means for the dry mass of small vegetative plants (2.3, 1.6, 0.04, 0.63 g/m^2 for 1981–84) were too small to graph. Bars represent standard deviations. Samples sizes listed in Fig. 1.

Accompanying the outbreak of herbivores in 1982–83 the plant community underwent dramatic changes. All stages of ragwort declined significantly. Above ground, the total density and total dry mass of stages declined to 3% of 1981–82 levels (Figs. 1 and 2). Comparing 1981 and 1984 populations, a 110-fold, 696 dry g/m^2 decline in ragwort standing crop was balanced by a 10-fold, 707 dry g/m^2 increase in standing crop of other species, leading to no net change in mean standing crop of the plant community. Perennial grasses accounted for 88% of the standing dry mass of other species in the new community. Below ground, the total density of ragwort propagules declined to 32% of 1982–83 levels (Fig. 2). Composition of the propagule bank changed as vegetative buds from root fragments declined to undetectable levels, suggesting they have a far shorter longevity in the soil than seeds.

To determine the mechanism for ragwort population decline, I evaluated the relative contribution of changes in rates of birth, death, and migration to changes in ragwort abundance. Here I summarize these findings, as they are to be reported in full detail elsewhere. Migration contributed very little to changes in local abundance. In mark-recapture experiments on wind-dispersed achenes, my co-worker Caroline Cox, and I have found dispersal distances are very short. For example, of 280,000 achenes marked,

31% travelled only 1 m, 89% travelled <5 m, and none travelled >14 m from the source plant. These findings suggest the population is effectively closed to migration, and we can look to changes in birth or death rates to explain local dynamics in the host population. The decline in the ragwort population was caused by >95% mortality spread evenly over actively growing stages followed by a 33% decline in the per capita birth rate of the surviving reproductive plants.

Long-term Stability

Further study is required to determine whether the ragwort population will remain at low levels. Ragwort relative abundance expressed as a percent of community standing crop remained at very low levels in 1983 (2.3%) and 1984 (0.8%). There were no generative plants in 1984, but very small vegetative plants rebounded to former levels due to recruitment from seed lying dormant in soil (Fig. 1). If herbivore pressure remains high, these small plants may grow to a size at which they become attacked by the insects and control will be maintained. On the other hand, reduction in herbivore populations by mortality or emigration may release the plant from control.

A Strategy for Biological Control

Findings in Oregon suggest a combination of agents which differ in the ways they exploit the host can be more effective in depressing host abundance than a single agent acting alone. Liberated from restraining mortalities in Oregon, the cinnabar moth has the capacity to locate all or nearly all the generative plants in a population and strip them to bare stems. The moth is strictly univoltine, and the inedible stems and roots left behind regenerate foliage and flowers in autumn after the moth has pupated. Thus damage is reduced by a portion of the plant being inedible, and compensatory growth and reproduction when the probability of encounter is low. The flea beetle consumes parts which are inedible to the cinnabar moth (petioles, stems, and roots) during seasons (autumn, winter) when the feeding stages of the cinnabar moth do not encounter the plant. Spreading herbivore pressure out in space and time may depress equilibrium levels of the host by reducing 'escapes' from herbivory.

Observational vs. Experimental Studies

Biological control introductions, including those made in this study, are rarely conducted as experimental tests of a herbivore treatment effect to which inferential statistics can be applied. Yet the effects of herbivores in depressing the host and maintaining it at low levels have been convincingly demonstrated by successful cases of biological control. In cases of marginal control, results could be made clearer and the conclusions firmer by experiments incorporating controls (designating treated and untreated systems), replication (using several systems for control and several for treatment), randomization (separating the subject systems into two groups by a random process), and interspersion of treated and untreated systems. I envision two kinds of experiments. First, the experiment could be imposed at the time agents are released. One difficulty with this approach is that migration of the insects will tend to compromise the independence of experimental units. Another difficulty is that establishment, in the present state of the art of biological control, is unpredictable. To enhance chances of success, it is perhaps a better expenditure of limited resources to make releases and follow up on those that become established, rather than conduct experiments at the establishment phase. A second kind of experiment could be performed after agents are

established and appear to be affecting the host by: (1) deliberate increase in weed density; and (2) deliberate decrease or removal of herbivore populations. This would be an ideal follow-up to my observational study of population changes at Three Rocks Road pasture.

Conclusions

1. Acting alone, the cinnabar moth has not yielded strong depression in ragwort density in Oregon. In contrast, a combination of the cinnabar moth larvae attacking shoots in summer and flea beetle larvae attacking petioles, stems and roots in winter has yielded a 110-fold depression in ragwort standing crop at Cascade Head, Oregon. A similar strong depression in the ragwort abundance occurred near Fort Bragg, California, where ragwort flea beetle combined with the cinnabar moth reduced plant density from 71 rosettes/m^2 to 0.6 rosettes/m^2 in a period of four years (Hawkes and Johnson 1976).

2. In most weed populations, the number of individuals present as dormant propagules vastly exceeds the numbers present as growing plants. My findings suggest dormant seeds in the soil may allow regeneration of the plant population decimated by herbivores.

3. The role of biological agents in the control of host plant populations could be effectively demonstrated by showing: (a) host maintains high densities in absence of herbivores; (b) herbivores depress host density to low levels; (c) host is maintained at low densities by herbivores; and (d) host returns to high densities when released from herbivores. Observations made before and after introduction of the agents can provide evidence bearing on these propositions by establishing: (1) an association, evidenced by negative correlation of herbivore and plant density; (2) contact, evidenced by herbivore damage to the plants; and (3) a mechanism for population changes, expressed as changes in migration, birth, or death rates. My findings illustrate high ragwort levels in the absence of herbivores and a depression to low levels following herbivore increase due to >95% mortality spread over all actively growing ragwort stages. It remains to evaluate the long-term stability of the interaction between host and insects.

4. The validity of ascribing strong and stable depression in host abundance to changes in the activity of herbivores can be challenged since rarely do we know what the behaviour of the system would have been without herbivores. Experiments imposed on established populations by artificially increasing plant density and artificially decreasing herbivore density appear to be the most promising ways to answer this challenge.

Acknowledgments

References

Dempster, J.P. 1982. The ecology of the cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera, Arctiidae). *Adv. Ecol. Res.* 12: 1–36.

Frick, K.E. 1970a. *Longitarsus jacobaeae* (Coleoptera: Chrysomelidae), a flea beetle for the biological control of tansy ragwort. 1. Host specificity studies. *Ann. Ent. Soc. Am.* **63**: 284–96.

————. 1970b. Ragwort flea beetle established for biological control of tansy ragwort in northern California. *Calif. Agric.* **24**: 12–3.

————. 1971. *Longitarsus jacobaeae* (Coleoptera: Chrysomelidae), a flea beetle for the biological control of tansy ragwort. II. Life history of a Swiss biotype. *Ann. Ent. Soc. Am.* **64**: 834–40.

Frick, K.E., and Johnson, G.R. 1972. *Longitarsus jacobaeae* (Coleoptera: Chrysomelidae), a flea beetle for the biological control of tansy ragwort. 3. Comparison of the biologies of the egg stage of Swiss and Italian biotypes. *Ann. Ent. Soc. Am.* **65**: 406–10.

————. 1973. *Longitarsus jacobaeae* (Coleoptera: Chrysomelidae), a flea beetle for biological control of tansy ragwort. 4. Life history and adult aestivation of an Italian biotype. *Ann. Ent. Soc. Am.* **66**: 358–67.

Harris, P., Wilkinson, A.T.S., Neary, M.E., and Thompson, L.S. 1971. *Senecio jacobaea* L., tansy ragwort (Compositae) 1959–1968. Biological control programmes against insects and weeds in Canada. *Commonw. Inst. Biol. Contr. Techn. Comm.* **4**: 97–104.

Hawkes, R.B. 1968. The cinnabar moth, *Tyria jacobaeae*, for control of tansy ragwort. *J. Econ. Ent.* **61**: 499–501.

Hawkes, R.B., and Johnson, G.R. 1978. *Longitarsus jacobaeae* aid moth in the biological control of tansy ragwort. Proc. IV Int. Symp. Biol. Contr. Weeds, August 30–September 2 1976, Gainesville, Florida. Freeman, T.E. (ed.). Cent. Env. Prog., Inst. Food Agric. Sci., Univ. Fl., pp. 193–6.

Isaacson, D.L. 1971. Population dynamics of the cinnabar moth, *Tyria jacobaeae* (Lepidoptera: Arctiidae). M.S. Thesis, Oregon State University.

————. 1978. The role of biological agents in integrated control of tansy ragwort. Proc. IV Int. Symp. Biol. Contr. Weeds, August 30–September 2 1976, Gainesville, Florida. Freeman, T.E. (ed.). Cent. Env. Prog., Inst. Food Agric. Sci., Univ. Fl., pp. 189–92.

Muth, O.H. 1968. Tansy ragwort (*Senecio jacobaea*), a potential menace to livestock. *J. Am. Vet. Med. Assoc.* **153**: 310–2.

Newton, H.C.F. 1933. On the biology of some species of *Longitarsus* living on ragwort. *Bull. Ent. Res.* **24(4)**: 511–20.

Sokal, R.R., and Rohlf, F.J. 1981. *Biometry.* W.H. Freeman and Company, San Francisco, CA, 859 p.