

Plant Nitrogen and Fluctuations of Insect Populations: A Test with the Cinnabar Moth – Tansy Ragwort System

Judith H. Myers and Ben J. Post

Institute of Animal Resource Ecology and Department of Plant Science, University of British Columbia, Vancouver Canada V6T 1W5
 Department of Ecology, Zoological Laboratory, University of Leiden, 2300 RA Leiden, The Netherlands

Summary. Nine populations of cinnabar moth, introduced to North America as biological control agents of tansy ragwort, were studied for 4 to 6 years. We tested the hypothesis that good quality of the food plant, measured as percent protein, would destabilize the moth populations. A positive correlation occurred between the percent nitrogen in the plants and the coefficient of variation of moth population density. Moths tended to be larger and produce more eggs in areas with food plants of better quality. Larval survival was also correlated with the quality of the food and the fluctuation of the population density. Food plants with high nitrogen levels increase larval survival and moth fecundity and allow the moth populations to periodically overexploit their food supply, thus accentuating population fluctuations. This finding is discussed in relation to other studies of cinnabar moth.

Introduction

Cinnabar moth (*Tyria jacobaeae* L.) is native to western Europe and Britain but because of its potential as a biological control agent on tansy ragwort (*Senecio jacobaea* L.), a pasture weed, it has been introduced to North America, New Zealand, and Australia. North American cinnabar moth populations were established in the early 1960's and studies of these populations suggest that they have been numerically more stable from year to year (Myers and Campbell 1976, Myers 1978, Stimac and Isaacson 1978) than an intensively studied population in Weeting Heath, England (Dempster 1975). We suggested that the North American populations might be more stable because plants there are more widely spaced (Myers and Campbell 1976). Further studies on these populations showed that areas that support fluctuating populations of moths are characterized by high average densities of small and closely spaced rosette plants. Moth populations fluctuate strongly in areas where the size of rosettes and the distance between clumps of plants have also undergone considerable annual variation.

Thus far only the physical characteristics of the tansy ragwort plants have been considered, but the quality of food plants might also influence the stability of the moth populations. White (1974, 1976, 1978) has related insect outbreaks to conditions which increase the amount of nitrogen available to insects in their food plants. McNeil and Southwood (1978) interpret his hypothesis to indicate that good food quality allows the insects to escape the "natural enemy ravine" and go into outbreak phase. White's ideas suggest that populations of cinnabar moth in areas with good quality food plants (i.e., those with high levels of

nitrogen) will show greater population fluctuations than those where the nitrogen levels of the food plant are low (Rosenzweig 1971). Good food quality can increase larval survival and moth fecundity and cause overexploitation of the food supply, starvation and a population crash. Characteristics which facilitate overexploitation of the food supply cause population instability (Myers 1976). We use data from 9 North American cinnabar moth populations to test if nitrogen level of food plants is one of these characteristics which destabilizes insect populations.

Methods

Field Sites

The main study areas were originally described in Myers and Campbell (1976), and are, with several new areas, enumerated and briefly described by habitat and population characteristics in Table 1. In addition, plant nitrogen, pupal weight, and/or adult wing length data were collected from populations in McKerricker Park and Hare Creek, Ft. Bragg, California, Foster-Cogswell Reserve, near Eugene, Oregon, an old pasture near Summit, Oregon, (OR.-3), and a pasture off Route 104 near Durham, Nova Scotia.

Field Techniques

Moth numbers were estimated by counting the hatched and unhatched eggs on all plants falling on 15 m transects and their nearest neighbour plants (Myers 1980). Moth density was estimated by dividing the total number of eggs counted in all transects taken in an area, by the wet weight of all the plants searched for eggs (eggs per gram food plant). Population fluctuation was indicated by the coefficient of variation (SD/mean) of the annual estimate of moth density for each area over the 4 to 6 years of the study.

Larval survival was also estimated from the transect data. Survival to first and second instars, third and fourth instars, and fifth instar was estimated by dividing the number of each of these larval age groups found on plants on the transect and the nearest neighbour plants, by the total number of hatched eggs observed. The final estimate was made by taking an average of the survival estimates for the 3 age categories. This average survival was used for analysis since it smoothed some of the variation which occurred because not all sites were visited at exactly the same stage of phenological development either within a year or between years.

Plants were scored as rosettes or stems, cut at the base and immediately weighed to the nearest gram with a spring balance. Distance (cm) to the nearest neighbour plant was measured for each plant touching the tape, and the position on the 15 m tape recorded. In analyzing the data, plants which were separated by 30 cm or more along the tape were considered to be in separate "clumps". The average distance between clumps of plants gave another measure of plant spacing.

Nitrogen Analysis

In 1977, 7 to 10 stem plants were cut in each of the study sites at the time of bud formation and oven dried until brittle (overnight). The leaves and buds were then removed from the stems and a well mixed sample taken for nitrogen analysis, which was done by the staff of the Animal Science Department laboratory at the University of British Columbia.

In 1978, samples were taken by selecting 4 leaves along the vertical axis of the stem plant, avoiding the basal leaves, and combining samples of 5 to 10 plants. These samples were analysed with the Kjeldahl technique by Ben J. Post. Total percent protein (%N times 6.25) for each area was used in analyses (Table 2).

All the nitrogen measurements in 1978 were lower than in 1977. This is probably because the samples were taken in different ways in the two years. For comparisons to the long term population fluctuations, we have used an average of the values for the two years. In other comparisons of characteristics measured in one year only, we have used the estimate of food plant nitrogen made for that year. Variation of nitrogen levels within and among plants will be reported in another paper (Post and Myers, Ms.).

Moth Characteristics

The relation of the quality of the food plant to moth characteristics was investigated in several ways. Pupal weight was estimated by collecting late fifth instar larvae in the field and rearing them to pupation in milkshake containers, with an overabundance of food plants from that field site. Most larvae stopped feeding within a day or two and began pupation. Pupal collections were also made in the spring from 4 of the populations for 1 to 6 years. The wing length of moths (cm) was measured in the field with calipers. The number of eggs in egg batches on plants collected in the field transects was counted. Averages of these moth size and fecundity characteristics were considered as they related to the amount of nitrogen in plants.

In addition, the effects of the quality of food plants on pupal size was measured directly by feeding larvae on plants which had been fertilized with urea in the field, transplanted to pots and brought to the laboratory. Pupal weights were compared for larvae reared on these fertilized and unfertilized plants in a screened insectary. In 1979, the pupal weights of larvae collected from shaded and open field plants were compared as were the protein levels of these two types of plants.

Results

Relation of Plant Nitrogen to Fluctuations in Moth Populations

The coefficient of variation of moth density (eggs/gram) was significantly correlated to the average nitrogen levels of tansy ragwort for the 9 populations studied for 4 to 6 years (Table 2), (Fig. 1). These data support the hypothesis that good food quality, measured as percent nitrogen, is associated with greater fluctuation in the density of moth populations. We now explore the details of this association by considering the relation of food plant quality to specific moth characteristics and other population attributes.

Relation of Plant Nitrogen to Moth Size

The size of moths will be influenced by crowding and genetic potential (Richards and Myers 1980) but it is worthwhile to ask if it is also related to the quality of the food plant. The direct test of this came from comparing larvae raised on plants which had been fertilized with urea to those reared on unfertilized plants. Larvae reared on fertilized plants produced significantly larger pupae than those reared on unfertilized plants (Table 3).

In the field, variation in the % protein was found to occur

Table 1. Description of the habitat and population characteristics of 9 North American and 2 intensively studied European populations. * Meijden (pers. comm.).

Area	C.V. population and characteristic	(eggs/g) av. density	Type of habitat	Years studied
Weeting Heath	1.73 Strongly fluctuating	4.9	Heavily grazed by rabbits	10
Meijendel Netherlands	1.08* Fluctuating	10.9*	Patchy distribution of plants and larvae	6
Oregon-1 Silbernagel	0.34	1.75	Formerly heavily grazed by cattle. Rapid decline with fertilization and no cattle	6
Oregon-2 Neal Ck.	0.68	2.67	Old road cut. Increasingly overgrown, little flowering	6
B.C.	0.95 Fluctuating	0.43	Lightly grazed, rapid shrub invasion	6
N.S.-1 Cow Field	0.69 Plant decline	0.67	Heavily grazed pasture well drained	5
N.S.-2 Sylvester	0.56 Some plant decline	0.42	Lightly grazed, well drained	5
N.S.-3 MacKinnon-1	0.80 Fluctuating	0.16	Heavily grazed, moist	5
N.S.-4 MacKinnon-2	1.11 Fluctuating	0.40	Heavily grazed, moist	4
CA.-1 Ft. Bragg	0.32 Decline	1.14	Coastal weed area. Successful control by <i>Longitarsus jacobaeae</i> in 1978	4
CA.-2 Comptche	0.60 Little change	0.73	Dry interior, heavily grazed	5

Table 2. Percent protein in tansy ragwort plants in 10 Cinnabar moth populations. The Oregon-3 (Summit) site was only studied for 2 years so it wasn't included in the analysis of population variation. * This value is based on samples from a small unfertilized portion of the field. The corresponding value was 20.7% protein for the fertilized plants. Areas as in Table 1

	% protein 1977	% protein 1978	N	S.D.	Av. % protein
B.C.	18.3	15.3	5	1.31	16.8
N.S.-1	19.6	20.2	2	2.04	19.9
N.S.-2	19.9	19.3	4	0.85	19.6
N.S.-3	22.9	17.3	2	2.36	20.1
N.S.-4	22.3	17.6	2	1.18	20.2
Oregon-2	-	19.5	3	4.17	19.5
Oregon-1	13.4	13.4*	4	0.06	13.4
Oregon-3	20.2	16.7	5	1.22	18.4
C.A.-1	13.7	8.6	2	0.57	11.2
C.A.-2	17.2	15.8	6	3.1	16.5

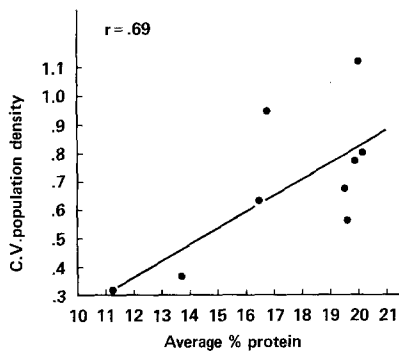


Fig. 1. The relationship between the percent protein in tansy ragwort foliage and the coefficient of variation of cinnabar moth populations

Table 3. Difference in pupal size of larvae reared on high and low nitrogen level plants

Treatment	% N	Pupal wt. (mg)	S.E.	N
Urea ^a	27.6	209	6.1	22
Unfertilized	16.2	191	4.7	17
Sun ^b	16.8	160	4.3	31
Shade	20.7	167	6.0	24

^a $t=4.46$, $p<0.01$ for fertilized and unfertilized plants

^b $t=1.03$, NS. for sun and shade plants

between plants growing in the open sun and in shaded areas, the latter being considerably higher in nitrogen (Table 3). In 1978, larvae collected from exposed plants produced significantly smaller pupae than those collected from shaded plants (Post and Myers Ms.). Samples collected in 1979 showed similar trends but the difference was not significant (Table 3).

In 1978, late fifth instar larvae were collected from field sites and fed with food plants cut from these sites. The size of pupae obtained in this way was not correlated with the percent of total protein measured in the plant samples taken from those sites in that year. This lack of association may have resulted from variable conditions before and after the larvae were collected.

Pupae were collected from 4 field sites in the winter or spring in several years and we can use these weights to determine if there is any association between the quality of food plants in those areas, estimated from the 1977 and 1978 plants, and the average weight of the field collected pupae. These data indicate an association between food quality and pupal size (Table 4).

Wing length of adults was measured in 1978. These animals would have fed on the tansy ragwort in 1977, so another measure of the influence of the quality of the food plant on the moths was to determine if wing length of the 1978 generation was correlated to the % protein in plants measured in 1977. Data for wing length and nitrogen content of the food plants in 1977 were available for only 7 populations, but male wing length was significantly correlated with food plant quality and female wing length almost significantly so (Table 5). Therefore, this direct measure of moth size showed an association between quality of the food and the size of animals produced.

Generally the size of female insects influences their fecundity and we expected that the number of eggs in egg batches might also be influenced by food plant quality. While the wing length of female moths from 8 populations measured in 1978 was corre-

Table 4. Average weight for pupae collected for 1 to 6 years from four field sites and average % protein measured in 1977 and 1978 from these sites

Area	Av. % protein	Av. pupal wt. (mg)	S.D.	No. years
CA-1	11.2	108.1	—	1 (1977)
OR-1	13.4	131.0	10.2	5 (1974–1978)
BC	16.8	152.5	18.5	6 (1974–1979)
OR-3	18.4	152.8	10.5	2 (1977–1978)

Table 5. Relation of cinnabar moth size and egg batch to % protein in food plants. The correlation coefficients between 1978 winglength and 1977% plant protein were $r=0.78$, $p<0.05$ for males; and $r=0.72$, $p<0.07$ for females. The correlation coefficient for female winglength and average egg batch size in 1978 was $r=0.70$, $p<0.05$. The correlation coefficient for % plant protein in 1977 and average egg batch size that year was $r=0.78$, $p<0.02$

Area	Wing length (cms)				\bar{x} number eggs/batch	
	1977		1978		1977	1978
	♂	♀	♂	♀		
N.S.-3+4	2.00	1.78	2.10	1.81	3 – 52.1 4 – 46.8	44.4
N.S.-2	1.97	1.79	2.00	1.79	40.8	51.5
McKerricker CA.	—	—	1.95	1.77	—	42.7
OR.-2	—	—	2.05	1.74	32.4	36.6
OR.-3	1.94	1.75	1.98	1.82	40.4	43.3
OR.-1	1.93	1.81	1.92	1.73	32.6	38.9
CA.-2	1.98	1.77	1.96	1.78	33.1	38.9
CA.-1	1.86	1.62	1.86	1.59	31.3	—
B.C.	2.02	1.82	1.99	1.83	34.4	49.7
N.S.-1	—	—	—	—	29.8	40.1
Foster-OR.	—	—	2.01	1.81	—	—
Mt. Thom-N.S.	—	—	—	—	—	41.0

lated to the average egg batch size for those populations (Table 5), egg batch sizes in 1978 were not directly correlated with the quality of food plants the year before, or in 1978. In 1977, the average number of eggs per mass was correlated with plant protein measured that same year (Table 5). These relationships support the proposal that good food quality is associated with larger moths and with greater egg production measured as the average number of eggs per batch.

Larval Survival and Plant Protein

The basis of White's hypothesis is that the survival of developing insects is usually low because of a relative shortage of nitrogen in their food. We have tested the relationship between larval survival and plant nitrogen in field populations. Average larval survival (Table 6) is significantly correlated with the average percent protein in the plants (Fig. 2). Average larval survival is also correlated with the degree of population fluctuation

Table 6. Proportion of larvae surviving from egg to indicated instar in 10 areas measured for 2 to 6 years (S.E.). Areas as in Table 1

Area	Larval survival			
	1st and 2nd	3rd and 4th	5th	Mean
CA.-1	0.08 (0.05)	0.014 (0.012)	0.011 (0.009)	0.035
CA.-2	0.21 (0.11)	0.02 (0.01)	0.002 (0.001)	0.080
OR.-1	0.19 (0.10)	0.04 (0.01)	0.033 (0.01)	0.09
OR.-2	0.42 (0.10)	0.05 (0.02)	0.00 -	0.16
OR.-3	0.21 (0.11)	0.06 (0.06)	0.00 -	0.09
N.S.-1	0.12 (0.05)	0.26 (0.10)	0.18 (0.11)	0.19
N.S.-2	0.11 (0.06)	0.16 (0.07)	0.31 (0.23)	0.19
N.S.-3	0.09 (0.04)	0.21 (0.07)	0.29 (0.12)	0.20
N.S.-4	0.03 (0.01)	0.42 (0.29)	0.34 (0.23)	0.26
B.C.	0.15 (0.04)	0.09 (0.01)	0.23 (0.16)	0.16

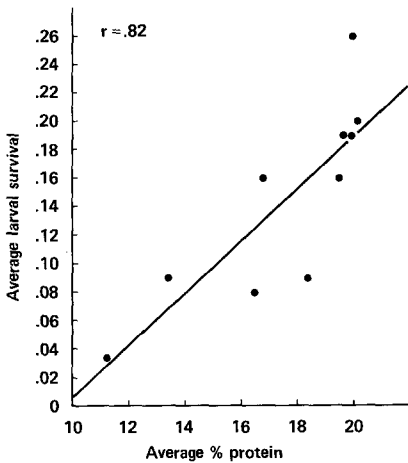


Fig. 2. The relationship between the average percent tansy ragwort protein and the average cinnabar moth larval survival

(Fig. 3). Therefore, the connection between good food quality, good larval survival and population fluctuations seems to be supported.

Plant Characteristics and Percent Protein

Analysis of the characteristics of tansy ragwort plants which are associated with fluctuations of the number of cinnabar moths show that fluctuating populations tend to live in areas where rosettes are small, closely spaced and numerous compared to flowering stem plants (Myers 1980). However, average levels of plant protein were not correlated with average size of plants or average distances between plants based on the 4 to 6 years sampling of the 9 populations. In 1978, 14 plant populations were sampled and again neither plant size nor spacing characteristics were correlated with levels of plant nitrogen. We have not been able to show an association between the physical characteristics of tansy ragwort plants, their quality as measured as plant protein levels, and the dynamics of the moth populations. This may be because the sample size is insufficient to show weak relationships.

An Attempted Field Experiment

The obvious field experiment is to increase the nitrogen level in the plants in a population and see if this switches the popula-

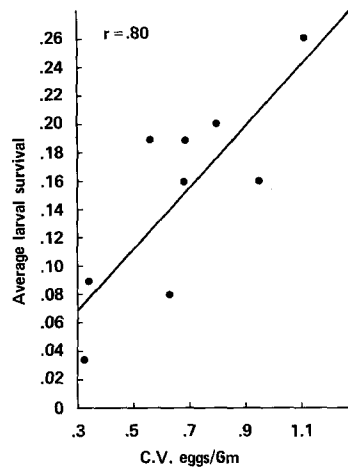


Fig. 3. The relationship between the average cinnabar moth larval survival and the coefficient of variation of moth population density (eggs/gm)

Table 7. Effect of urea fertilization and removal of cattle on Oregon-1 population (S.E.)

Year	% protein	Biomass stems (g)	Distance between plants (cm)	Density moths (eggs/g)
1977	13.4	15.9 (4.3)	15.0 (1.3)	2.3
1978	20.7	41.1 (3.9)	21.9 (1.9)	0.3
	13.4 ^a			

^a Unfertilized control area

tion from a stable one to a fluctuating one. The Silbernegel site (Oregon-1) was fertilized with urea in April 1978, and this was associated with a dramatic increase in the size of the plants and a decrease in the density of plants (Table 7). Unfortunately, in the autumn prior to this perturbation, the farmer removed the cattle from the field, and this, with the fertilization, led to a major increase in the undergrowth vegetation. The density of moths declined sharply, even though the nitrogen levels in the plants increased. This is probably because predation of eggs, larvae and pupae intensified with increases of invertebrate predators in the undergrowth. Competition between the tansy ragwort and other vegetation in the absence of cattle grazing most likely caused the reduction in density of the tansy ragwort.

Plant Protein Levels and Frequency of Attack of Subpopulations

Dr. Eddy van der Meijden has been studying 102 clusters of tansy ragwort plants in the coastal dunes of Meijdenel, near The Hague in The Netherlands (Meijden 1979). He provided us with plant samples from four types of areas: those which had been attacked by insects in 4 of 6 years study, those attacked for 3 of 5 years, those attacked in 1 of 6 years, and those in which larval attack had not been observed in 6 years. For comparison, these areas were lumped into those with frequent larval

attack (3 to 4 times in 5 or 6 years) and those with rare larval attack. The nitrogen levels of plants subject to frequent attack were significantly higher than those in which attack was rare (attacked = 16.73% plant protein, unattacked 14.82%, $t=4.93$, $df=3$, $p<0.05$). These data suggest that moths may choose plant patches of higher quality for oviposition, but more work on this interesting situation is necessary.

Discussion

Insect size is generally influenced by the density at which they occur or are reared (Bryant 1977; Danthanarayana 1977; Lorimer 1979). The phenotypic adjustments insects are capable of making, can help stabilize or at least promote the persistence of populations. Many studies have implicated a relationship between the quality of plants and attack by and survival of insect herbivores (examples in Beck and Reese 1976; Dixon 1970; Kimmins 1971; McClure 1979; McNeill and Southwood 1978; Onuf et al. 1977; White 1974). Other studies have shown direct relationships between the quality of the food plant and the growth rate, size and survival of insects (examples in Fox and Macauley 1977; McNeill and Southwood 1978; Scriber and Feeny 1979). Amalgamating these two lines of study allows the prediction that improved food quality could disrupt the normal density-related feed-back systems and cause insect outbreaks which magnify population fluctuations. The insects fall into the "paradox of enrichment" in which increasing the supply of limiting nutrients destroys the steady state (Rosenzweig, 1971). Cinnabar moth in North America and possibly also in Europe seems to fit this description; populations are less stable when living in areas where the food plants have a high nitrogen content.

When studying the population dynamics of any organism, one is usually confronted by a number of influences on the population. Differences of opinion about the relative importance of these often causes heated debate in the literature. However, progress toward understanding will occur only when an attempt is made to integrate the various interpretations and determine the underlying generalities.

For the cinnabar moth, there is general agreement that the population dynamics are controlled by interactions between the insects and their food plants. The reproduction, growth and possibly quality of the food plants are influenced by rain or soil moisture (Dempster and Lakhani 1979; Meijden 1979; Myers 1980) and the heterogeneity of the spatial and temporal patterns of their food plants promotes the persistence of populations (Birch 1971; Meijden 1979; Myers 1980). High moth density is associated with (1) the production of smaller moths, (2) increased moth dispersal, (3) reduced moth fecundity, and (4) reduced larval and perhaps pupal survival. Plant populations provide food refuges in the following ways: (1) flowering stems are preferred for oviposition over rosettes, (2) some plants receive more eggs than others, and (3) some plant patches may be overlooked or avoided by moths for several years. In addition, cinnabar moths have been observed to frequently defoliate most of their food plants and the response of the plants to this attack will depend on rain and soil moisture (Dempster and Lakhani 1979) and/or the lag between defoliation and the first winter frost (Harris et al. 1978).

Moth populations living in areas characterized by high year to year variation in rosette size and in spacing between clumps of plants, are less stable than those in more constant plant environments (Myers 1980). This indicates that the plants may be driving the dynamics of the insects.

Perhaps the greatest disagreement in the description and in-

terpretations of the dynamics of cinnabar moth populations has to do with the nature of the density-size relationship shown by the moths. Moths will be smaller when they are crowded, when food is limited and when the quality of the food plants is poor (Dempster 1971; Myers 1979; Roze 1978). But there is also a maternal influence on the size of moths which can be demonstrated under controlled laboratory conditions; small females tend to have small offspring (Richards and Myers 1980). Although minor in its effect, this heritability may delay the response of the insect to environmental conditions. In both Dempster's (Dempster and Lakhani 1979) and our own studies (unpublished), two years were required after a population peak for the size of the pupae to recover completely. This delay may be caused by a shift in the genetic composition of the population, a change in the physiology of the female moths which takes several generations of sufficient quantity and quality of food to overcome, or a reduction in the quality of food plants in the year following extensive defoliation. This lag in the readjustment of moth size following a year of high density and defoliation of the food plants can influence the stability of the population, and deserves further research.

The continued monitoring of plant nitrogen levels is crucial for future work. After two years' sampling, populations tended to fall into either high or low nitrogen categories. Continued measurements will be necessary to know how rainfall and herbivore pressure influence the plant nitrogen levels.

Implications for Biological Control

The cinnabar moth in general hasn't reduced populations of tansy ragwort sufficiently to allow it to be considered a very successful control agent. Part of the problem seems to be that the fluctuations in moth density and the resilience of plants to attack result in "equilibrium" densities which are too high. In some areas of Australia, prickly pear was controlled by *Cactoblastis* only after it had been fertilized with nitrogen (Dodd 1940). In this situation, moth survival was boosted by improving the quality of food plants and therefore larval attack was sufficient to cause suppression of plants. For cinnabar moth, the problem is the reverse, plants recover too well in most areas to allow continued suppression.

In this study, a fertilization experiment was attempted and resulted in a dramatic decline in tansy ragwort density. Unfortunately, the removal of cattle several months prior to the experiment prevents our interpreting the results as being caused by fertilization or by increased competition from other vegetation released from grazing pressure. The quality of the pasture did not improve, however, since most of the new vegetation was other weeds.

The Californian tansy ragwort population which had low levels of plant nitrogen was attacked during the study by increasing densities of flea beetles (*Longitarsus jacobaeae*, Waterhouse). The flea beetle attack may have been responsible for the poor plant quality at that site and flea beetles and cinnabar moths did cause suppression of the tansy ragwort (Hawkes and Johnson 1978). The combined attack of cinnabar moth and flea beetle might achieve successful control of tansy ragwort in other areas where cinnabar moth alone has not been successful. It will be interesting to see if one of the effects of flea beetles is to decrease the nitrogen levels in the plants and stabilize the cinnabar moth populations.

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