Interaction Between the Cinnabar Moth, Tyria Jacobaeae L. (Lep.:Arctiidae) and Ragwort, Senecio Jacobaea L. (Compositae in Canada

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ABSTRACT

The interaction of the cinnabar moth and tansy ragwort are described for the east and west coasts of Canada. In both regions following the introduction of the moth, for biological control purposes, it increased to defoliate the weed. On the east coast the weed subsequently declined to extremely low densities at release sites followed by a crash in the cinnabar population. In contrast, on the west coast there has been little change in the density of the weed and the moth population appears to be stabilising at below the level needed for complete defoliation.

INTRODUCTION

The cinnabar moth,*Tyria jacobaeae* L. was established in Canada for biological control of ragwort, *Senecio jacobaeae* L., in permanent pasture and waste areas. The importance of this weed and the colonisation of the moth were reported by Harris *et al* (1975). This paper discusses the population interaction between the moth and the weed over a ten year period at the first three locations at which the moth was established. These were at Durham, Nova Scotia; Selkirk, Prince Edward Island; and Nanaimo, British Columbia. The moth increased to defoliate the weed at all three locations but the effect of this on the survival of ragwort and hence the effect on both the weed and moth populations differed in eastern and western Canada. The reasons for this difference were explained by Harris *et al* (1976).

RELEASE SITES AND SAMPLING METHODS

Durham, Nova Scotia

The release field, about 3,500 m², had a dense stand of ragwort since 1955. The infestation was encouraged by over grazing and the uneven ground made ragwort control by cultivation impossible. The surrounding fields were either dense young spruce forest wthout ragwort or were in tame hay with scattered ragwort plants.

The cinnabar population was determined either by a total count of larvae and eggs in the release field or from samples taken at regular intervals across the field. Both the total cinnabar counts and the sample method were used to assess the larval population in 1968 and they were in close agreement (Table 1). In the last years of the study a count was made of the ragwort rosettes. This had been attempted in 1966 but the densities of up to 50 or more rosettes/m² made it difficult to distinguish the individual plants. After 1966, the populations of cinnabar larvae and ragwort were assessed when the first larvae reached the fifth instar, near mid-July; By this time, nearly all the eggs had hatched and the ragwort was in bloom. Very few flowering stems were produced later in the year. Thus it was possible to assess both the moth and the weed with a single annual sample because their development was synchronised and confined to a short period.

Selkirk, Prince Edward Island

The release field consisted of 2.62 ha of abandoned farm land on poorly drained sandy loam. It supported a continuous sward of grass and mouse-eared hawkweed (*Hieracium pilosella* L.) and was not cut or grazed. The flowering stems of ragwort were shorter and the density of the weed considerably less than at Durham; however, heavy stands of ragwort were present in the disturbed soil on the roadsides along two sides of the area. The ragwort and cinnabar populations were sampled a week after those at Durham, because emergence of the moth and larval development were consistently later. All larval densities (Table 2) were based on total counts. The number of ragwort stems per m² was determined at paced inter-

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TABLE 1. Density of cinnabar larvae and ragwort at Durham, Nova Scotia.

Year	Ragwort stems/m²	Rosettes /m²	Larvae/m²	Eggs/m²	Eggs & Larvae/stem
1963)			0.3'		
)	continuous infestation since 1955				
1964)			0.1'		
)					
1965)			0.1'		
1966	5.5 +0.5		0.1'		0.02
1967	8.2 +0.8		0.6'	1.2	0.2
1968	13.6 +0.7		3.2'		0.3
			3.6+0.9		
1969	2.5 +0.2		8.0+1.6		3.2
1970	0.25 +0.07		1.4+0.3	3.1+1.2	18.0
1971	0.06 +0.03		0.6+0.3		10.0
1972	0.001	0.03	0.09+0.04		90.0
1973	0.008	0.06	0.004		0.5
1974	0.008	0.43	0.008		1.0

'Density calculated from total counts (Harris *et al* 1975) all other estimates from 100 - 250m² samples.

vals across the field. The ragwort was sampled only in the year shown in Table 2 but visually the ragwort density remained stable from 1963 to 1970.

Nanaimo, British Columbia

The release site of 7.5 ha was on a gravelly sandy loam slope with an easterly exposure. Much of the field was subject to severe summer drought which usually defoliated the ragwort rosettes, while around a spring and other areas that received enough seepage, defoliation from drought only occurred in 1975, reducing the rosette population to less than 0.05/m². The field was surrounded by a forest of Douglas fir (*Pseudotsuga menziesii*), hemlock (*Tsuga heterophylla*), *Arbutus menziesii* Pursh and western red cedar (*Thuja plicata*) with ragwort wherever there was an opening. The ragwort infestation dated from 1963 when the site was cleared to provide spring grazing. The grazing pressure was light but the sward remained short and thin, and until 1967, it was sprayed once or twice a year with 2,4-D for the control of ragwort. The treatment reduced the amount of ragwort on a temporary basis but did not prevent a substantial number of flowering stems from appearing the following year.

TABLE 2. Density of cinnabar larvae and ragwort at Selkirk, Prince Edward Island.

Year	Ragwort stems/m²	Cinnabar larvae/m²	Larvae/stem
1963	2.6 (6.0 rosettes)	0	
1964	--	—	—
1965	—	0.01§	0.004 '
1966	—	0.002§	0.009 '
1967	2.2+0.4	0.01§	0.005
1968	—	0.05§	0.02 '
1969	—	0.09	0.04 '
1970	—	0.17	0.07 '
1971	0.46	1.2	2.6
1972	0.02	0.1	5.0
1973	0.0	0.0	0

§ Density calculated from total counts 1965 to 1968 (Harris *et al* 1975).

' Based on an assumed density of 2.4 stems/m².

The cinnabar densities from 1964 to 1967 were converted from total counts (Table 3). In subsequent years, 150 to 200 m² samples were taken at 10 pace intervals on 5 transects. As at Durham the samples were taken when the first larvae reached the 5th instar. This was satisfactory in the first years of study but gradually moth emergence extended over a longer period than it did in the Atlantic provinces. For example, moths were observed from 6 June to 10 July 1966 and from late April to late June 1969. This spread of emergence was not important as far as estimating the size of the larval population where there was complete and rapid defoliation of ragwort, since the later emerging moths did not contribute to the population. However, in both 1973 and 1975, there was a slow emergence of the moth over a period of 2.5 months that started in May and continued until mid-July without achieving complete defoliation. In these years the larval population was underestimated by sampling only at one date.

The ragwort flowering stems were counted up to four times through the summer. Stem density did not change through the summer because even those eaten to a short stub could be found in the sparse sward. Thus, for the density of ragwort (Table 3) all the samples taken during a summer were combined. The rosette population varied through the summer and the figures shown in Table 3 were the number present when the larvae

TABLE 3. Density of cinnabar larvae and ragwort at Nanaimo, British Columbia.

Year	Ragwort stems/m²	Rosettes/m²	Larvae/m²	Eggs/m²	Eggs & larvae/stem
1964	—		0.004 '	0	—
1965	—		0.09 '	0	—
1966§	0.9+0.2	—	0.2 '	0	0.2
1967	2.3+0.6	—	.0.2 '	0	0.1
1968	2.7+0.6	—	10.4+2.2	0	3.8
1969	2.0+0.2	—	8.0+1.5	0.3+0.15	4.1
1970	2.5+0.2	—	6.5+1.5	6.5+2.0	5.2
1971	1.4+0.05	—	2.5+0.05	4.9+1.1	5.3
1972	2.1+0.06	10.0	1.2+0.4	3.6+0.3	2.3
1973	0.5+0.07	14.9	0.5+0.2	0	1.0
1974	0.4+0.08	5.0	0.2+0.1	0	0.5
1975	2.0+0.3	4.2	0.1+0.04	0	0.05

' Density calculated from total counts (Harris *et al* 1975), all other estimates from 150 to 200 m² samples.

§ Field treated in the spring with 2,4-D for the control of ragwort.

were sampled, or if necessary in the first sample taken in the subsequent weeks.

NATURAL DISPERSION OF THE MOTH

The annual dispersion limits of the cinnabar moth were followed at Durham,. N.S. by searching the surrounding fields for larvae and noting the distance and direction from the release point. The prevailing wind was from the west and there was a road running SW-NE at the edge of the release field with heavy stands of ragwort in pastures at intervals along it. To the north, there was an area of regenerating spruce forest with no ragwort for 1000 m and to the south there was a river bordered by an area of trees and rank herbacious vegetation but with no ragwort for about 400 m.

The moth population remained within the confines of the 3500 m² release field until 1967 when a small number of larvae were found 270 m NNE. It spread slowly until 1969, the first year of complete defoliation in the release field, when the moth was found 1200 m E and 475 m W. During the next two years, all stands of ragwort within a 1.6 km of the release points had been colonized but spread was greatest along the road and about twice as fast in the direction of the prevailing wind. Subsequent spread could not be followed because farmers were distributing larvae on their land.

Similarly, at Selkirk, P.E.I., there was a slow spread along the roadside but the moth did not appear in the fields separated from the release field by about 400 m of forest until the ragwort in the release field had been defoliated.

CHANGES IN THE DENSITY OF RAGWORT AND CINNABAR LARVAE

The density of cinnabar larvae at the Durham site was so low up to 1968 (Table 1) that only scattered ragwort stems were defoliated. Counts of larvae during this establishment phase (Harris *et al* 1975) showed that initially their number declined, then the total population increased by 5 times in 1968 and finally increased to completely defoliate the tansy ragwort. During the period the moth was becoming established, the number of flowering stems fluctuated, but always remained high. In 1968, the weed peaked at 13.6/m² and the larvae at sampling time had defoliated only 8.8% of the stems and damaged a further 2.9%. The eventual level of defoliation may have been about 11% which was far too low to be the cause of the reduction of stems in 1969. Instead of an expected resurgence of the weed during the subsequent years, there was a decline to 0.001/m² in 1972 to about 1/10,000 of its former density. During this decline there was a complete defoliation of ragwort in the release field. The decrease in number of flowering stems followed as an inevitable result of a decrease in the number of rosettes. Originally the rosettes, clumps of up to 50/m², were too dense to count individual plants but following defoliation they declined to 0.03/m² in 1972 and 0.06/m² in 1973.

Ragwort plants normally die after flowering and this seem to be the basis for classifying ragwort as a biennial. However, in a closed sward recruitment of new rosettes is almost entirely by vegetative propagation and not by seed (Harris *et al* 1976). Thus, death of the rosettes following defoliation by the cinnabar larvae or from any other cause will reduce both the source of flowering plants in the following year and of vegetatively propagated rosettes.

At Selkirk (Table 2) the cinnabar moth population remained low from 1965 to 1970 inclusively. During this establishment phase there was no visible change in the density of the ragwort. In 1971 the cinnabar population increased to 2.5 larvae/stem and completely defoliated the ragwort. Many of the flowering stems were eaten down to ground level making it difficult to find the stems and the larvae in the unmown grass. Consequently both the weed and the larval populations were probably higher than recorded. The much reduced ragwort population was again completely defoliated in 1972. No ragwort was found in the release field from 1973 to 1975 although both it and the moth persisted on the disturbed ground along the edge of the road. Thus, the ragwort and the moth followed the same trend as at Durham: the weed declined rapidly following defoliation by cinnabar larvae and did not return to its former density in the succeeding years even though the moth popultion was relatively low.

At Nanaimo (Table 3) the ragwort was first defoliated in 1968 by a population of 4.0 larvae/stem. The ragwort was defoliated again in each of the following three years but this did not affect the density. The first major decline of the weed occurred in 1973 after only partial defoliation by the moth. Hence, from 1972 to 1975 there was considerable fluctuation in the density of stems and rosettes. The larvae/stem ratio decreased between 1968 and 1975 but showed much less change than at Durham.

It appears from Tables 1-3 that the cinnabar moth has a strong and immediate controlling effect on ragwort in the Canadian Maritimes whereas on the west coast in most years it has little effect on ragwort density. At Nanaimo the moth declined steadily from a high of 10.4 larvae/m² in 1968 to 0.1 in 1975. Thus, the moth has declined and is apparently remaining below the level necessary for complete defoliation.

RAGWORT BIOMASS AND CINNABAR CARRYING CAPACITY

Meijden (1970) used the dry weight of ragwort foliage to determine the number of cinnabar larvae that can be matured in an area. This equation was No. larvae/ 20 m²=163 log X – 194, where X is the dry weight of ragwort foliage on 20 m². The weight of ragwort foliage was measured at the Nanaimo release site from 1971 to 1973 when the fifth instar larvae were present. Flowering plants cut at ground level from a 150 m² plots across the field were oven dried and weighed. The foliage from 300 rosettes was treated similarly for the latter two years. For the calculation of the cinnabar carrying capacity in the previous years, an average flowering plant was assumed to weigh 1.8 g and the rosettes to weigh 12.4 g/m². The latter weight was the average value for 1972 and 1973.

The results (Table 4) show that after the initial build up, the observed larval population was slightly over the carrying capacity of the area from 1968 to 1971. Similarly in 1972, when the defoliation index was 42% (Table 5) the observed larval population was just over half the carrying capacity. Some of the observed larvae were small and probably died before they matured, so Meijden's equation gives a close estimate of the carrying capacity of the Nanaimo site. If so, it follows that a population of 6.8 larvae/m² would be to achieve the 1973 defoliation index of 89% rather than the observed density of 1.1 larvae/m². The fact that the cinnabar population was near the carrying capacity of the Nanaimo site implies that the population was limited by available food and

TABLE 4. Cinnabar carrying capacity of the release site at Nanaimo, British Columbia.

Year	Stems/m²	Dry wt/stem	Dry Wt. stem/20 m²	Rosettes/m²	Dry wt/rosette	Dry wt. rosettes/ 20 m²	Total dry wt/ 20 m²	Larval population/m² calculated§	obs
1966	0.9	1.8 g	32.4 g	12.4	0.3 g	76.4 g	108.8 g	6.9	0.2
1967	2.3	1.8	82.8	12.4	0.3	76.4	159.2	8.3	0.2
1968	2.6	1.8	93.6	12.4	0.3	76.4	170.0	8.5	10.3
1969	2.0	1.8	72.0	12.4	0.3	76.4	148.4	8.0	8.3
1970	2.5	1.8	90.0	12.4	0.3	76.4	166.4	8.4	13.0
1971	1.5	1.5	45.0	12.4	0.3	76.4	121.4	7.3	7.4
1972	2.1	1.1	46.2	9.8	0.3	58.8	105.0	6.8	4.8
1973	0.5	1.8	18.0	14.9	0.3	89.4	107.4	6.9	1.0

§ No. larvae/m²=163 log dry ragwort biomass per 20 m² – 194.

not by the microsporidian and the cyptoplasmic virus which were present (Harris *et al* 1975).

It follows from Meijden's (1970) equation that areas with less than 15.5 g/20 m^2 of ragwort foliage are unsuitable for cinnabar larval development. If an equal division of foliage between ragwort stems and rosettes is assumed, cinnabar larvae are unable to complete development in stands with less than 0.21 stems/m^2. This density seems to be related to the ability of the larvae to transfer between plants. According to Green (1974) the probability of a 5th instar larva finding another plant was $Y=1.095\ X/2.202+X$, where X is the density of ragwort stems/m^2. In a subsequent study, Campbell (1975) reported that the larvae were more successful at transferring between plants at medium densities than found by Green. According to her, the probability of transfer was $Y=-0.80229 \log X+0.3572$, where X is the proportion of plants spaced more than 1 m apart. This equation allows for differences in the distribution pattern of the ragwort which vary from strongly to moderately clumped. Also, Campbell's equation has a cut-off below which no further transfer can occur whereas Green's equation allows successful larval transfer, although at a diminishing rate, regardless of the distance between plants. Clearly, the latter is untenable as the larvae must have a finite dispersion range. Unfortunately, Campbell's equation cannot be applied to the present data as no measure of plant dispersion was recorded; therefore Green's equation was applied (Table 5) to both the Nanaimo, and the Durham sites. The probability of larval transfer was multiplied by observed larvae per stem to obtain an effective cinnabar density. The effect of this is to reduce the influence of plant spacing on the ability of the cinnabar moth to defoliate ragwort.

The results (Table 5) show that at Durham between 1966 and 1969 the probability of larva transfer was high and the cinnabar population increased rapidly. In contrast between 1970 and 1973, almost all the larvae perished in attempting to transfer and their density decreased rapidly (Table 1). It did not achieve an equilibrium because the ragwort declined even faster. Presumably this reduction reflected the small number of rosettes that escaped defoliation to survive to the following year. The moth should become locally extinct unless there is a disturbed site, such as the roadside at Selkirk, where both the moth and the weed can persist. At Durham, it may be necessary to reintroduce the moth if the ragwort reappears in large numbers as a result of overgrazing or the decline of pasture vigour.

TABLE 5. Observed and "effective" cinnabar density/ragwort stem.

NANAIMO

Year	Probability of larval transfer	Observed cinnabar/stem	"Effective" stem cinnabar/	Defoliation index§
1966	0.3177	0.2	0.06	
1967	0.5594	0.1	0.06	
1968	0.6031	4.0	2.4	100
1969	0.5212	4.1	2.1	100
1970	0.5822	5.2	3.0	100
1971	0.4256	5.3	2.3	93
1972	0.5345	2.2	1.2	42
1973	0.2026	1.1	0.2	89
1974	0.1683	0.5	0.1	—
1975	0.5212	0.1	0.05	—

DURHAM

Year	Probability of larval transfer	Observed cinnabar/stem	"Effective" stem cinnabar/	Defoliation index§
1966	0.7819	0.03	0.02	
1967	0.8632	0.2	0.2	
1968	0.9424	0.3	0.3	11
1969	0.5822	3.2	1.9	100
1970	0.1116	18.0	2.0	100
1971	0.0290	10.0	0.3	100
1972	0.005	90.0	0.04	100
1973	0.004	0.5	0.002	
1974	0.004	1.0	0.004	—

§ Defoliation index=percentage of stem defoliated+half of those damaged.

At Nanaimo, the probability of larval transfer remained more stable than it did at Durham but the cinnabar population has shown a steady decline since 1971 (Table 3). Some of the fluctuation may have arisen because the effect of defoliation is in part dependent on the climatic conditions. For example, Dempster (1971) found that in a wet summer foliation increased vegetative propagation of ragwort from root buds. This did not occur in dry summers and presumably the detrimental effects of defoliation increase with the severity of a drought.

At moderate cinnabar densities (Table 5) complete defoliation was achieved with 'effective' populations of 2.1 - 3.0 larvae/stem at Nanaimo and 1.9 - 2.0 larvae/stem at Durham. The equivalent observed densities were 4.0 - 5.2 larvae/stem and 3.2 - 18.0 larvae/stem respectively. Thus, the correction for successful larval transfer removed much of the variation both within and between sites. On the other hand, the degree of defoliation did not relate to plant density when there were many moths and a few widely spaced ragwort plants, as at Durham in 1972. Under these circumstances, not only does the moth deposit larger egg masses (Myers 1976, *in litt.*) but most of the plants received one or more egg masses, so the stand was defoliated with larval transfer and the cinnabar population destroyed itself. The effective larval population indicates that complete rather than 93% defoliation would be expected at Nanaimo in 1971.

GENERAL DISCUSSION

The cinnabar moth and dense stands of ragwort can remain in equilibrium for many years. This has occurred at Dempster's (1971) study site in England and at Meijden's (1970) study site in Holland. In most years each of these stands was severely or completely defoliated by the cinnabar moth and yet ragwort continued as a common and dominant plant. At Nanaimo, B.C. the cinnabar moth population has shown a steady decline after peaking in 1968 but the number of ragwort stems per m^2, although much reduced for 2 years, remained between 2 and 3 per m^2 most years. Myers (1976) pointed out that selection in an insect will be for maximum resource utilisation if this does not prejudice the next generation. This seems to describe the cinnabar moth at these three sites. Some insect populations provided with a constant resource over expand and then crash or oscillate violently. One of the classical examples of this is provided by Nicholson's (1954) studies wtih the sheep blow-fly. Myers (1976) showed with a simulation model, that the cinnabar moth had achieved a high degree of stability by clumping its progeny in larger groups than could be sustained on a single plant and requiring some of the larvae to transfer to other plants to complete development. This characteristics seems to be genetically determined as many of the larvae transferred regardless of available food. This clumping and dispersal provides food refuges that assure that some individuals survive if the ragwort plants are not too far apart. The cinnabar moth is able to adjust some fluctuations in the density of a ragwort because the mortality of the larvae increases with the distances between the plants (Green 1974, Campbell 1975) and this mortality is further increased because the moths lay larger and more egg clusters on widely spaced plants (Myers 1976, *in litt.*). According to Meijden's (1970) data the cinnabar moth cannot persist if there is less than 15.5 g/20 m^2 dry weight of ragwort foliage. At the Nanaimo site, this represents about 0.2 stems/m^2, plus the same amount of foliage provided by rosettes. At plant populations below this density, the moth population presumably destroys itself because it deposits large egg masses on plants too far apart for successful transfer. This may account for the absence of the cinnabar moth on the scattered pockets of ragwort plants in the Swiss Jura around Delémont, although the moth is common on the larger stands in the nearby Rhine Valley at Mulhouse.

The cinnabar moth is adapted to attacking dense stands of ragwort growing where there is a relatively long growing season, good summer moisture supply and good winter drainage. Under these conditions the moth does not affect the abundance of its host and it has behavioural controls that regulate itsown density to achieve maximum long term utilisation of its host (Myers 1976). The moth is of some value for biological control under these conditions because it reduces the amount of ragwort foliage in pastures over much of the growing season. It also provides a stress on the plant that can be supplemented by the addition of other biocontrol agents. The moth is of most use for biological control where the stress of cinnabar defoliation is reinforced by a climatic stress (Harris *et al* 1976). Under these conditions dense stands of ragwort are eliminated altogether. The moth appears to have some adaption to this situation as local defoliation or absence of ragwort increases adult dispersal and hence the possibility of colonising other ragwort stands within a radius of several miles. The moth is of least use for biological control on sparse stands of ragwort or on ragwort growing on soils that are wet in winter, such as river flood plains because it cannot survive in either situation.

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