EFFECT OF SUMMER MOISTURE STRESS ON THE CAPACITY OF TANSY RAGWORT (SENECIO JACOBAEA) TO COMPENSATE FOR DEFOLIATION BY CINNABAR MOTH (TYRIA JACOBAEAE)

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SUMMARY

(1) Tansy ragwort plants were grown under different irrigation regimes to assess the effect of summer moisture stress on their capacity to compensate for defoliation by larvae of the cinnabar moth. Three measures of compensation capacity increased with increasing frequency of irrigation: the amount of growth produced following defoliation, the number of nodes which produced this growth, and the number of flower heads (capitula) produced following defoliation. Thus moisture availability limited plant compensation under these experimental conditions.

(2) Compensation capacity was positively correlated with moisture availability in (a) comparisons of populations at a high summer rainfall site and a low summer rainfall site and (b) comparisons of populations during wet and dry years. Thus moisture availability appeared to limit plant compensation under natural as well as experimental conditions.

(3) These results indicate that the full potential of the cinnabar moth as a biological control agent of tansy ragwort will be apparent in years with below average summer rainfall. In wet areas the introduction of additional biological control agents should be considered. Investigation of the influences of abiotic conditions on the interactions between plants and their herbivores may be necessary in other studies concerned with predicting the outcome of this interaction.

INTRODUCTION

Biological control of weeds should benefit from recent efforts to improve the ability to predict dynamics of plant populations under herbivore attack. This study focuses on improving these predictions by understanding how abiotic factors can interact with plant characteristics that control herbivore damage and thus influence dynamics. Examples of this type of interaction can be found in White (1969, 1974, 1975) and McNaughton (1979b). Here, we report on a study of an environmental control on plant compensation capacity, the ability to maintain homeostasis of growth, development, and reproduction despite disturbance by herbivores. We used experimental manipulation and field correlation to investigate the effect of summer moisture stress on the capacity of tansy ragwort, Senecio jacobaea L. (Compositae) to compensate for defoliation by the cinnabar moth, Tyria jacobaeae (L.) (Lepidoptera: Arctiidae), in western Oregon, U.S.A. This study should allow better predictions to be made about geographical and temporal variation in efficacy of biological control of tansy ragwort.

Tansy ragwort is a biennial weed which has been introduced from its native Eurasia to many coastal areas of the world, including North America from northern California to British Columbia. It is toxic to cattle and horses and is estimated to infest 2 out of every 5 acres in western Oregon (Cheeke 1979). Rosettes generally bolt and flower during the early summer of their second year of growth. The cinnabar moth, a univoltine
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monophagous defoliator, has been widely introduced as a biological control agent of the weed. As the plants bolt, larvae consume the floral parts and the blades of cauline leaves. After the larvae have reached the pupal overwintering stage the plants are able to compensate for this defoliation; new leaves and flowers are produced, drawing on carbohydrates stored in the roots (Otzen 1977). These secondary flowers are less numerous and mature approximately 10 weeks later than flowers on undefoliated plants (Cameron 1935). Stimac (1977) inferred from a model of the system that intermediate levels of compensatory growth were required to stabilize ragwort populations. With high levels of compensatory growth, herbivory ceases to be limiting and an outbreak of the plant occurs. With very low levels of compensatory growth the plant population declines sufficiently that the moth becomes locally extinct. Subsequently, the plant population undergoes a resurgence. Successful control requires stable and low equilibrium densities of both plant and insect.

Because ragwort’s compensatory growth in Oregon occurs under much drier conditions than does the bolting and flowering of undefoliated plants, an obvious possibility is that compensation capacity is constrained by summer moisture stress. This relationship was suggested by three types of evidence. First, a relationship between the availability of water and compensatory growth has been documented in studies of ragwort in its native range. Van der Meijden (1971) showed that compensatory growth of dune populations of tansy ragwort in the Netherlands would not begin until mean relative humidity had exceeded 70% for a 2-week period. Dempster & Lakhani (1979) found a positive correlation between the numbers of regenerative rosettes produced in an English population of ragwort and the rainfall from July to September. Second, water relations have influenced the success of other biological control agents of ragwort. In northern California, Hawkes & Johnson (1976) observed that mortality of plants attacked during winter by *Longitarsus jacobaeae* (Coleoptera: Chrysomelidae) occurred during the drought of the following summer. Third, water relations have been important in determining the success of several other attempts at biological control of weeds. Control of *Lantana camara* (Verbenaceae) in Hawaii was most successful in areas with an annual rainfall less than 40 inches (Andres & Goeden 1971). Control of *Tribulus terrestris* (Zygophyllaceae) in California was more successful if plants were not irrigated (Kirkland & Goeden 1978).

To investigate the relationship between summer moisture stress and compensation capacity, we used three types of variation in summer moisture stress: (i) variation manipulated artificially by irrigation, (ii) variation due to geographical variation in climate, and (iii) variation due to temporal variation in weather patterns. We asked the following questions:

(i) When ragwort plants are grown under controlled conditions so that other factors that can influence compensation capacity are held constant, is there a positive relationship between frequency of irrigation, water potentials, and compensation capacity?

(ii) When adjustments are made to account for other differences in natural populations that can influence compensation capacity, is there (a) a positive relationship between summer rainfall, xylem potentials, and compensation capacity in wet and dry areas? (b) a positive relationship between summer rainfall and compensation capacity in wet and dry years?

MATERIALS AND METHODS

To isolate the effect of summer moisture stress on compensation capacity, an attempt was made to eliminate two confounding factors—timing of attack and plant size. First, Stimac
C. S. Cox and P. B. McEvoy (1977), in field experiments, demonstrated that compensation capacity declines with delay in the defoliation date. Second, it seemed likely that plant size could be important. Since large plants have larger reserves of stored carbohydrates, compensation capacity may be expected to increase with plant size. In experimental plots the measurements of these factors were not critical since random assignment of plants to treatments will remove effects of uncontrolled variation. These measurements were of critical importance in the second and third parts of this study involving field correlations of moisture stress and compensation capacity.

In all three sections of this study comparisons were made with parametric statistics whenever possible. If variances were heterogeneous according to the $F_{max}$ test (Sokal & Rohlf 1969), transformations or non-parametric tests were used. Detail of tests used are reported with the results.

Artificial manipulation of moisture stress

This experiment measured the relationship between the frequency of irrigation, water potentials and the capacity of ragwort to compensate for defoliation by the cinnabar moth. The experiment was done during the summer of 1980 at the Oregon State University Entomology Farm, Corvallis, Oregon using plants transplanted during April and May from a wild population 16 km north. The study site was a $15 \times 25$ m uncultivated field surrounded by roads and small outbuildings. Other species present were *Cirsium vulgare* (Savi) Tenore, *Daucus carota* L., *Festuca rubra* L., *Phleum pratense* L., and *Poa pratensis* L. Plants interfering with access to ragwort individuals were removed. In June and July the local population of cinnabar moths defoliated the plants. If insect densities were less than three per plant, individuals from a neighbouring population were added. Insects were excluded from control plants by plastic barriers topped with Tanglefoot®. Weekly observations during this period were made of plant height, and the progress of defoliation. Following defoliation, 160 plants were distributed equally among four experimental treatments in a randomized block design: Treatment 1—plants which received no irrigation; Treatment 2—plants which received one irrigation on 17–18 August; Treatment 3—plants which received two irrigations on 22–23 July and 8–9 September; Treatment 4—plants which received ten weekly irrigations between 11 July and 15 September. Twenty-four plants were left undefoliated and non-irrigated as controls. Sample size in all treatments decreased because 12% of the plants failed to bolt and were excluded.

The only natural rainfall was 1 cm which fell on 12 September. Each irrigation, and the one event of natural rainfall during the period, supplied enough water to bring the soil in the root zone of the plant (a depth of 10 cm) to field capacity.

Soil water potential was measured by recording the resistance of gypsum blocks (Delmhorst Instrument Company, Boonton, New Jersey) with a model KS-1 resistance meter. Blocks were buried 10 cm below the soil surface and readings made twice weekly from 6 August until 22 September.

Plant water potential was estimated by measuring xylem sap pressure potential with a pressure chamber manufactured by PMS Instrument Company (Corvallis, Oregon). The technique is described in Scholander et al. (1965). Measurements were made at dawn and shortly after noon on 14 August, 28 August and 17 September.

Compensation capacity was assessed by using three measures of plant performance: (i) the number of nodes on each plant with compensatory growth counted at five weekly
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intervals between 31 July and 28 August; (ii) the dry weight of compensatory growth (dried at 70 °C for 72 hours) on plants harvested from 9 to 22 September, (iii) the total number of mature capitula produced by each plant before 8 December, after which date no new fruits matured.

Geographical variation of moisture stress

In order to determine the range of water potentials which ragwort exhibits in western Oregon, and to correlate water potential with compensation capacity, a series of observations were made at two sites chosen to represent the extremes of summer moisture stress in western Oregon. To select sites, we used an index of stress called the summer water deficit, calculated by subtracting estimates of potential evapotranspiration from average precipitation. Summer water deficits throughout western Oregon range from 14.0 cm to 40.6 cm (Johnsgard 1963). A population at Cascade Head Natural Area (near Otis, Tillamook County, Oregon) on the northern Oregon coast was used to represent populations that grow under conditions of minimal moisture stress. The average summer water deficit in this area is 14.0 cm. A population at Camp Adair (near Corvallis, Benton County, Oregon) in the central Willamette Valley was chosen to represent populations that grow under conditions of maximal moisture stress. The average summer water deficit in this area is 36.1 cm.

At each site two sets of measurements were made: the first on 26 July 1980 at the coastal site and 29 July at the valley site, and the second on 25 August at the valley site and 2 September at the coastal site. During each visit three measurements (on twenty plants) were made: (i) xylem sap pressure potentials at dawn and early afternoon; (ii) plant heights; (iii) the number of capitula, classified by developmental stage as primordia, buds, flowers, fruits and dispersed heads (Cox 1981). Each capitulum was assigned a value from one to five depending on its developmental stage and the mean per plant was used as an index of the maturity of the plant.

At each site there were plants that had been defoliated by cinnabar moths shortly before the date of the first measurements. The number of secondary capitula produced by the date of the second measurement was used to represent compensation capacity.

Temporal variation of moisture stress

In order to estimate the effect of year-to-year variation in summer rainfall on compensation capacity, records of the production of secondary capitula in ragwort populations at Camp Adair (Corvallis, Benton County, Oregon) were used. Data were collected in 1977, 1978 and 1980 from plants which were defoliated by hand to simulate cinnabar moth feeding. The population studied in 1980 was 2 km south of the population studied in 1977 and 1978. Records from each year included (for a sample of twenty plants): (i) plant heights on 15 July; (ii) the number and developmental stages of capitula produced prior to defoliation on 15 July; (iii) the number of secondary capitula produced before 11 October 1977, 5 October 1978 and 24 September 1980. Rainfall was estimated from measurements taken at Oregon State University, 16 km south of the study site.

RESULTS

Artificial manipulation of moisture stress

Measurements of plant size and defoliation history assured us, as expected, that plants in each treatment were similar prior to irrigation. Maximum plant height before defoliation
and the dates on which defoliation began and ended did not significantly differ among treatments.

Xylem sap pressure potentials measured in early afternoon differed significantly among treatments ($H_1 = 21, P < 0.001$, Kruskal-Wallis test). Potentials were lowest in Treatment 4 (ten irrigations), highest in Treatment 1 (no irrigation) and intermediate in Treatments 2 and 3 (Fig. 1). Dawn potentials followed the same pattern, as did seasonal averages of soil water potential. Biweekly measurements of soil water potentials in this experiment are given in Cox (1981).

Two measures of compensation capacity, the dry weight of compensatory growth and secondary capitula production, increased as the frequency of irrigation increased, although there was considerable variation within treatments (Fig. 2). The dry weight of compensatory growth was significantly different among treatments ($\chi^2 = 20.3, P < 0.01$, Friedman's method for randomized blocks). A non-parametric simultaneous test of multiple comparisons (Sokal & Rohlf 1969) showed Treatment 4 (ten irrigations) significantly greater than Treatment 1 (no irrigation). Production of mature capitula was also significantly different among treatments ($H_3 = 20.7, P < 0.001$, Kruskal-Wallis test). The test of multiple comparisons showed Treatments 3 and 4 (two and ten irrigations) had

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**Fig. 1.** The relationship between mid-day xylem sap pressure potential and the frequency of irrigation. Curve was fitted by eye to treatment means.

**Fig. 2.** The relationship between compensation capacity and the frequency of irrigation. The graphs show two measures of compensation capacity, the dry weight of compensatory growth (gm/plant) and the reproductive output (capitula/plant) of plants following defoliation. Both are expressed as percent of control (undefoliated and non-irrigated) plants and graphed as log $(y + 1)$ to facilitate plotting. Curves were fitted by eye to treatment means.
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Fig. 3. Mean number of nodes/plant with compensatory growth. Values are means/plant with 95% confidence limits for a sample size of thirty-two. • = Treatment 1 (no irrigation); ■ = Treatment 2 (one irrigation). ▲ = Treatment 3 (two irrigations). ○ = Treatment 4 (ten irrigations). A = first irrigation of Treatment 3. B = irrigation of Treatment 2. Within each treatment, significant ($P > 0.05$ according to an LSD procedure) increases between dates are indicated by dashed lines.

Greater capitula production than did Treatment 1 (no irrigations). Capitula production of control plants was about half of that found in undisturbed (untransplanted) populations.

Further evidence that irrigation influences the response of ragwort to defoliation is shown in Fig. 3. Following the first irrigation of Treatment 3 and the only irrigation of Treatment 2, the mean number of nodes per plant with compensatory growth increased significantly. The second irrigation of Treatment 3 occurred late in the season, and no such effect was visible. Plants in Treatments 1 and 4, in which water availability was relatively constant throughout the season, did not show similar mid-season increases in the amount of compensatory growth. By the end of the season, plants in all three irrigated treatments had significantly more nodes with compensatory growth than did unirrigated plants ($F_{3,124} = 24.5$, $P < 0.001$, ANOVA and LSD procedure). Changes through time of some other plant performance variables are given in Cox (1981).

Geographical variation of moisture stress

In this section we give the results of measurements made to test the prediction that the capacity of ragwort to compensate for defoliation by the cinnabar moth is greater in areas of western Oregon that typically have relatively high amounts of summer rainfall than in areas with little summer rainfall. Our results are summarized in Table 1.

Summer rainfall at the coastal site was over four times that at the valley site. As expected, xylem sap pressure potentials reflected this difference. At the wet coastal site potentials were 2 bars less negative than those at the dry valley site. These differences were significant for all four sets of measurements (July dawn: $F_{1,38} = 7.3$, $P < 0.05$, ANOVA; July noon: $F_{1,38} = 6.5$, $P < 0.05$, ANOVA; August dawn: $F_{1,38} = 7.0$, $P < 0.05$, ANOVA; August noon: $U_{20,20} = 438$, $P < 0.001$, Mann-Whitney U-test).

To isolate the effect of a difference in rainfall at the two sites, it was necessary to eliminate the effects of other factors that could influence compensation capacity. In particular, we were concerned about the effects of differences in plant size and development at the time of defoliation. We measured plant height and the production of capitula prior to defoliation as indices of plant size. Plants at the valley site were 1.4 times as tall as plants at the coastal site ($F_{1,38} = 65.5$, $P < 0.001$, ANOVA) and produced 1.4
TABLE 1. Geographical variation of moisture stress and plant characteristics

<table>
<thead>
<tr>
<th>Site</th>
<th>Rainfall (cm)</th>
<th>Plant xylem sap pressure potentials (bars)</th>
<th>Plant size before defoliation height (cm)</th>
<th>Developmental stage (n = 20)</th>
<th>Secondary capitula production</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(1 July–15 Sept.)</td>
<td>( \bar{x} \pm S.E. (n = 20) )</td>
<td>( \bar{x} \pm S.E. (n = 20) )</td>
<td>( \bar{x} \pm S.E. (n = 20) )</td>
<td>( \bar{x} \pm S.E. (n = 20) )</td>
</tr>
<tr>
<td>Coast</td>
<td>10.01</td>
<td>(-8.3 \pm 0.6) \quad (-8.3 \pm 0.6)</td>
<td>(-9.6 \pm 0.2) \quad (-12.5 \pm 0.3)</td>
<td>70 \pm 3 \quad 109 \pm 11</td>
<td>1.71 \quad 1.27–2.60</td>
</tr>
<tr>
<td>Valley</td>
<td>2.18</td>
<td>(-10.8 \pm 0.6) \quad (-14.7 \pm 0.4)</td>
<td>(-10.7 \pm 0.4) \quad (-15.8 \pm 0.6)</td>
<td>98 \pm 3 \quad 158 \pm 14</td>
<td>2.35 \quad 1.63–2.98</td>
</tr>
</tbody>
</table>

All differences between sites are significantly different \((P < 0.05)\).
times as many capitula ($F_{1,39} = 5.9, P < 0.05$, ANOVA). Together these measurements indicate that the population at the coastal site consisted of smaller plants and should have less compensation capacity.

The mean developmental stage of plants at the coastal site was significantly younger than that at the valley site at the time of defoliation ($U_{20,20} = 354, P < 0.001$; Mann-Whitney U-test). Forty-five per cent of the capitula at the coastal site were in the youngest class (primordia) compared to 23% at the valley site. This difference represents a phase difference of about one week. Since plants that are defoliated early in the season have a greater compensation capacity than those that are defoliated late in the season, this difference indicates that plants at the coastal site should have greater compensation capacity than those at the valley site.

To compare compensation capacity at the two sites, secondary capitula production was compared. Next, the effect of differences in plant size and the timing of defoliation were considered. If these differences could lead to differences in compensation capacity similar to those hypothesized due to the difference in moisture stress, the results were adjusted to remove the effect of plant size or timing of attack.

Plants at the coastal site produced 2.2 times as many secondary capitula as plants at the valley site ($U_{10,18} = 128, P < 0.05$, Mann-Whitney U-test). If these results were adjusted to account for the differences in plant size between the two sites, the magnitude of the difference in compensation capacity between the two sites would increase. The difference in plant size and development, on the other hand, would reduce the difference in compensation capacity. In order to account for the difference in plant size and development, we compared compensation capacity of the coastal population with that of plants from the valley population defoliated 2 weeks earlier (15 July 1980). At this date plants at the valley site were at a significantly younger developmental stage ($U_{20,20} = 367, P < 0.001$, Mann-Whitney U-test) than plants at the coastal site on 26 July ($\bar{x} = 1.71$, range: 1.00–1.91) than plants at the coastal site on 26 July ($\bar{x} = 1.71$, range: 1.27–2.60). Plants at the coastal site produced more secondary capitula ($\bar{x} \pm S.E. = 69 \pm 14$) than plants defoliated earlier at the valley site ($\bar{x} \pm S.E. = 41 \pm 6$). This difference was significant ($U_{10,19} = 132, P < 0.05$, Mann-Whitney U-test). It therefore seems possible to conclude that some of the greater compensation capacity at the coastal site is due to the lower levels of moisture stress.

**Temporal variation of moisture stress**

In this section we compare the amount of compensatory growth in neighbouring populations of tansy ragwort during 3 years. During the first 2 years for which data are available, rainfall from 1 July to 15 September was considerably above average (160 cm above average in 1977 and 556 cm above average in 1978). During the summer of 1980, rainfall was 173 cm below average. A summary of the comparisons of compensation capacity in wet and dry years is given in Table 2.

In order to eliminate factors other than summer rainfall that might affect compensation capacity, plant size and development at the time of defoliation during the 3 years were compared and results were adjusted as described in the previous section. We used plant height and capitula production (both of undefoliated plants) as indices of plant size. Capitula production in undefoliated plants in 1977 and 1978 was not significantly different than that in 1980 ($U_{20,31} = 403, P > 0.05$, Mann-Whitney U-test). Neither were there significant differences among heights ($F_{1,58} = 0.001, P > 0.05$, ANOVA). In the wet years plants were defoliated at a significantly more mature stage than were plants in 1980 ($U_{20,31} = 565, P < 0.001$, Mann-Whitney U-test). This difference in development represents about one week and is probably due to the cool, wet June in 1980 which slowed plant development.
TABLE 2. Temporal variation of moisture stress and plant characteristics

<table>
<thead>
<tr>
<th>Rainfall (cm)</th>
<th>Plant size before defoliation</th>
<th>Developmental stage</th>
<th>Secondary capitula production</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1 July–15 Sept.)</td>
<td>$\bar{x} \pm$ S.E. ($n = 20$)</td>
<td>$\bar{x}$</td>
<td>range</td>
</tr>
<tr>
<td>Wet years (1977 &amp; 1978)</td>
<td>7.49</td>
<td>79 ± 2</td>
<td>167 ± 22</td>
</tr>
<tr>
<td>Dry year (1980)</td>
<td>2.18</td>
<td>79 ± 2</td>
<td>109 ± 12</td>
</tr>
</tbody>
</table>

All differences between years are significant ($P < 0.05$), except that capitula production and plant height before defoliation did not differ between years. Values for wet years are means of data collected in 1977 and 1978.

Ignoring differences in phenology, defoliated plants in the two wet years produced 1.8 times as many secondary capitula as did defoliated plants in the dry year ($U_{20.38} = 429$, $P < 0.01$, Mann-Whitney U-test). If these results were adjusted to account for the differences in phenology among years, the magnitude of the difference in compensation capacity would increase. Therefore, it is likely that some of the greater compensation capacity during wet years is due to decreased levels of moisture stress.

DISCUSSION

The results of this study show that the capacity of tansy ragwort to compensate for defoliation by the cinnabar moth is positively correlated with the amount of moisture available to plants following defoliation. One irrigation during the season of compensatory growth was sufficient to increase one of the measures of compensation capacity, the mean number of nodes per plant with compensatory growth. Field correlations indicate that the same relationship exists in natural populations. The wide variation in compensation capacity within each of the treatments used in the experimental part of this study points to interesting possibilities for further research. The causes of this variation, whether environmental or genetic, will be important to further understanding of this plant-herbivore interaction.

The final applied results of this study ideally would be to define, based on weather records, areas and years in which cinnabar moth will be an unsuccessful control agent of tansy ragwort. Because of the limited scope of our field correlation, and because our experimental work may have been biased by the use of transplanted individuals, we do not feel we can make detailed predictions about the efficacy of biological control. In general, we predict that the full potential of the cinnabar moth to control ragwort populations will be visible in years with below average rainfall. In regions of Oregon with high summer rainfall, introduction of other control agents may be necessary to achieve satisfactory control. Other agents present in Oregon include the ragwort flea beetle, *Longitarsus jacobaeae* (Waterhouse) and the ragwort seed fly, *Hylemya seneciella* (Meade). Additional control measures may also be necessary on irrigated land.

These results also suggest that environmental controls of compensation capacity are important to the interaction between tansy ragwort and the cinnabar moth. The influence of abiotic factors on the population dynamics of herbivores (Andrewartha & Birch 1954) or plants (Harper 1977) has been well documented for many species. Documentation of these influences on the interaction of the two trophic levels is less common, but is well studied in managed ecosystems of domestic ungulates and forages (McNaughton 1979a, b).
This type of investigation may be necessary in other studies concerned with predicting the outcome of interactions between plants and their herbivores.

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REFERENCES


Cox, C. S. (1981). Environmental controls on the capacity of tansy ragwort (Senecio jacobaea L.) to compensate for defoliation by cinnabar moth (Tyria jacobaeae [L.]). MS thesis, Oregon State University.


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