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Title: Feeding, Colonization and Impact of the Cinnabar Moth, Tyria jacobaeae, on Senecio triangularis, a Novel, Native Host Plant

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Peter B. McEvoy

I conducted field and laboratory studies to determine the impact of the cinnabar moth, Tyria jacobaeae L., on the native perennial herb, Senecio triangularis Hook. The cinnabar moth was introduced into Oregon in 1960 to control the noxious weed Senecio jacobaea L. and is now well established on both the native plant and the weed in Oregon. My objectives were to determine the suitability of S. triangularis as a diet for the cinnabar moth, to estimate the frequency with which the moths colonize the native plant in the field, and to estimate the impact of larval feeding on the plant's survivorship and reproduction.

Larvae successfully completed development on S. triangularis, but development time was longer, growth was slower, and pupae were lighter compared to performance on

S. jacobaea. Cinnabar moth colonization and feeding damage were concentrated at one of the four study sites observed. Cinnabar moth defoliation results in a 3.9% reduction in seed viability and is inversely related to damage to seeds by native insects. I conclude that cinnabar moths commonly discover this native plant in the field, can establish and develop on it, and cause a small reduction in plant reproductive success.

Feeding, Colonization and Impact of the Cinnabar Moth, *Tyria jacobaeae*, on *Senecio triangularis*, a Novel, Native Host Plant

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

FEEDING, COLONIZATION, AND IMPACT OF THE CINNABAR MOTH, *TYRIA JACOBAEAE*, ON *SENECIO TRIANGULARIS*, A NOVEL, NATIVE HOST PLANT

I. INTRODUCTION

Classical biological weed control involves the introduction of an herbivore into a region in order to control a plant pest. Once a weed control agent is introduced, it is difficult to limit its spread, and agents may attack nontarget plants. Literature searches and host specificity tests are conducted prior to introduction to ascertain the host range of the candidate control organism and to provide assurances that agents will not harm nontarget plants. These tests have traditionally focused on economic (crop) plants but recently have been extended to include wild native plants. Several biological control agents have already been recorded on native plants (Turner, 1985), but little is known about their impact on their new host species.

Host specificity tests provide the primary evidence concerning an agent's ability to utilize native plant species. Early tests confined the insect on economic plants to determine whether it would feed and/or lay eggs on them (Harris and Zwolfer, 1968). These tests provided assurances that agents would not attack economic plants but did not provide similar assurances for plants in the native

flora.

The centrifugal phylogenetic method of Wapshere (1974) transcends the testing of economic plants to establish an agent's host range. The agent is exposed to a sequence of plants ranging from close relatives of the target weed to progressively more distantly related plants until the host range has been circumscribed. This leads to the prediction that native plants falling in an agent's host range are likely to be attacked. Such predictions are susceptible to two sources of error: species outside the predicted range may be suitable or species within the predicted range may not be suitable hosts for the insect. The first type of error arises when characteristics that determine a plant's suitability as a host are present in unrelated plant species. For example, in Western Europe, the butterflies Pieris rapae and P. brassicae which feed on plants in the family Brassicaceae also feed on the garden nasturtium, Tropaeolum majus (Tropaeolaceae) which belongs to a family allied to the Geraniaceae (Strong et. al. 1984). Like plants in the Brassicaceae, T. majus contains mustard oils. This illustrates the need to include plants possessing similar secondary chemicals in specificity tests (Wapshere, 1974). A second kind of error arises when individual species within a predicted host range possess characteristics that render them unsuitable. For example, some strains of brussel sprout are resistant to the aphid

Brevicoryne brassicae because their phloem saps have relatively low concentrations of allylisothiocyanate, a secondary chemical that acts as a feeding stimulant (Crawley, 1983).

I used the phylogenetic method to estimate the risk that introduced biological control agents pose to native plants in the Pacific Northwest. Currently, 40 herbivore species have been introduced into this region to control a total of 25 weed species. Six of these herbivores failed to establish , and the status of six species is unknown (Coombs, unpublished data). I predicted the phylogenetic host ranges from host specificity test information and determined the native plant species within this range from the regional flora (Hitchcock and Cronquist, 1973). If the agent's host range included native plant species, I also noted the number of these species that were tested. Of the 11 agents for which I found no host range information, 5 are established, 4 failed to establish and the status of 2 is unknown.

Native plants fell within the host range of 13 agents (12 insects and one nematode) (Table 1). Only 5 genera of native plants were within this range: Euphorbia, Hypericum, Linaria, Cirsium and Senecio. Five of the agents were tested on native northwest plants within their host range prior to introduction. Adult Ceutorhyncus litura fed and oviposited on, and their larvae fed on, Cirsium undulatum,

Table 1. Host range of herbivores introduced into the northwest for the biological control of weeds.

Insect	Weed	Host Range	Northwest Natives	Number Natives Tested	Reference
Family: Chenopodiaceae					
Coleophora klimeschiella	Salsola kali	Salsola kali	None	-	Hawkes and Mayfield (1978)
Family: Fabaceae					
Apion fuscirostre	Cytisus scoparius	Cytisus scoparius	None	-	Andres et. al. (1967)
Leucoptera spartifoliella		Cytisus scoparius Cytisus purgans	None	-	Parker (1964)
Apion ulicis	Ulex europaeus	Ulex europaeus	None	-	Holloway and Huffaker (1957)
Family: Zygophyllaceae					
Microlarinus lareynii	Tribulus terrestris	Tribulus spp., Kallstroemia spp., Zygophyllum spp.	None	-	Andres and Angalet (1963)
Microlarinus lypriformis		Tribulus spp., Kallstroemia spp., Zygophyllum spp.,	None	-	Andres and Angalet (1963)

Table 1: continued

Insect	Weed	Host Range	Northwest Natives	Number Natives Tested	Reference
Family: Euphorbiaceae					
Oberea erythrocephala	Euphorbia esula	Euphorbia spp.	5 Euphorbia species	0	Schroeder (1980)
Family: Hypericaceae					
Agrilus hyperici	Hypericum perforatum	Hypericum spp.	H. anagalloides H. formosum	0	Wilson (1943)
Chrysolina quadrigemina		Hypericum spp.	H. anagalloides H. formosum	0	Wilson (1943) Smith (1958)
Chrysolina hyperici		Hypericum spp.	H. anagalloides H. formosum	0	Wilson (1943) Smith (1958)
Zeuxidiplosis giardi		Hypericum spp.	H. anagalloides H. formosum	0	Wilson (1943)
Family: Umbelliferae					
Agonopterix alstroemeriana	Conium maculatum	C. maculatum	None	0	Berenbaum and Passoa (1983)

Table 1: continued

Insect	Weed	Host Range	Northwest Natives	Number Natives Tested	Reference
Family: Scrophulariaceae					
Calophasia lunula	Linaria dalmatica Linaria vulgaris	Antirhinae	L. canadensis	0	Harris (1963)
Gymnaetron antirrhini	Linaria vulgaris	Linaria spp.	L. canadensis	0	Smith (1959)
Family: Compositae, Tribe Cichorieae					
Aceria chondrillae	Chondrilla juncea	Chondrilla spp.	None	-	Caresche and Wapshere (1974)
Cystiphora schmidti	Chondrilla juncea	Chondrilla spp.	None	-	Caresche and Wapshere (1975)
Puccinia chondrillina	Chondrilla juncea	Chondrilla spp.	None	-	Hasan (1972)
Family: Asteraceae, Tribe Cynareae					
Agapeta zoegana	Centaurea maculosa	Centaurea spp.	None	-	Muller et. al. (1988)
Sphenoptera jugoslavica	Centaurea diffusa	Centaurea spp.	None	-	Zwolfer (1976)
Subanguina picridis	Centaurea repens	Centaureinae Carduinae	16 Cirsium spp.	1	Watson (1986)
Urophora affinis	Centaurea diffusa Centaurea maculosa	Centaurea spp.	None	-	Zwolfer (1970)

Table 1: continued.

Insect	Weed	Host Range	Northwest Natives	Number Natives Tested	Reference
Urophora quadrifasciata	Centaurea diffusa C. jacea C. maculosa C. pratensis	Centaureinae	None	-	Zwolfer (1972)
Urophora siruna-seva	Centaurea solistalis	Centaurea spp.	None	-	Zwolfer (1972)
Ceutorhynchus litura	Cirsium arvense	Cirsium spp. Silybum spp. Carduus spp.	16 Cirsium spp.	3	Zwolfer and Harris (1966)
Rhinocyllus conicus	Carduus nutans Carduus teniflorus Cirsium arvense Onopurdum acanthum Silybum marianum	Carduinae	16 Cirsium spp.	1	Zwolfer and Harris (1984)
Urophora cardui	Cirsium arvense	Cirsium arvense	None	-	Peschken and Harris (1975)
Family Compositae, tribe Senecioneae					
Hylemyia seneciella	Senecio jacobaea	Senecio spp.	30 Senecio spp	3	Frick and Andres (1967)
Longitarsus jacobaeae	Senecio jacobaea	Senecio spp. Emilia spp.	30 Senecio spp	2	Frick (1970)
Tyria jacobaeae	Senecio jacobaea	Senecio spp. Erechites spp.	30 Senecio spp.	0	Bucher and Harris (1961)

C. flodmanii and C. brevistylum in laboratory tests (Zwolfer and Harris, 1966). Adult Rhinocyllus conicus fed on the only native tested, C. undulatum, but did not survive over ten days on this species (Zwolfer and Harris, 1984). Cirsium flodmanii formed galls in response to feeding by the nematode, Subanguina picridis, but these galls had little impact on plant survival (Watson, 1986). Both the ragwort seed fly, Hylemyia seneciella, and the ragwort flea beetle, Longitarsus jacobaeae, oviposited on Senecio triangularis and S. serra. Flea beetle adults fed readily on these plants, but the larvae were unable to mature in the root crowns (Frick, 1970). The ragwort seed fly also oviposited on S. integerrimus (Frick and Andres, 1970); egg transfer tests were inconclusive because the authors failed to get insects to survive on the target plant S. jacobaea let alone on nontarget plants.

Herbivores that are able to feed on a plant species in the laboratory may lack the opportunity to do so in the field. The probability of colonizing a plant in the field depends on herbivore movement, seasonal activity, habitat preference, and tolerance of abiotic conditions. For example, Chrysolina quadrigemina feeds and completes its development on Hypericum anagalloides and H. formosum in the laboratory, but not in the field (Andres, 1985), perhaps because the habitat of the native plants is too wet for the aestivating adults, which die under conditions of

high humidity (Wilson, 1943). At least six agents introduced into the northwest feed on native plants in the field. Chrysolina quadrigemina, Agrilus hyperici and Zeuxidiplosis giardi feed on Hypericum concinnum in California (Andres, 1985). The seed weevil, Rhinocyllus conicus, has been reared from field-collected heads of 12 native Cirsium species in California (Turner et. al., 1987) and one native Cirsium in Montana (Reese, 1977). The cinnabar moth, Tyria jacobaeae, has been observed on three native Senecio species in Washington and Oregon: S. triangularis (pers. observations), S. pseudaureus (Robert Brown, Oregon Department of Agriculture, pers. comm.) and S. cymbalarioides (Mary Friess, Washington Native Plant Society, pers. comm.).

Several weed control agents have been recorded on native plants in the field, but Andres (1985) provides the only experimental evidence of the impact of an agent on a native plant. Hypericum concinnum plants defoliated by C. quadrigemina larvae were smaller than plants protected from herbivory by an insecticide. Andres suggests that H. concinnum's architecture, phenology and ability to reproduce from roots limit the beetle's impact. The limited basal foliage of H. concinnum does not offer the degree of shelter to C. quadrigemina provided by H. perforatum rosettes, and this basal foliage appears later than does the foliage of H. perforatum. The ability of H.

concinnum to reproduce from roots makes it difficult to kill outright. Once a plant has been damaged, daughter plants appear along the roots permitting plant recovery.

Further research is needed to help predict whether an introduced natural enemy will (1) discover a native plant, (2) establish and thrive on it, and (3) decrease its abundance. To meet this need, I investigated the impact of the cinnabar moth Tyria jacobaeae (Lepidoptera: Arctiidae) on the non-target, native plant Senecio triangularis Hook. The cinnabar moth was introduced into Oregon in 1960 to control tansy ragwort S. jacobaea L., a biennial weed that is toxic to livestock and displaces desirable forage in pastures (Isaacson, 1973). The moth is now well established on both the target and nontarget hosts. I addressed the following questions:

1. How suitable is S. triangularis as food for the cinnabar moth?
2. How frequently do cinnabar moths colonize S. triangularis?
3. What effect does cinnabar moth feeding have on survival and reproduction of S. triangularis?

The next chapter will address the first objective, and the third chapter will address the final two objectives.

II. COMPARATIVE GROWTH, DEVELOPMENT AND FEEDING BY *TYRIA JACOBAEAE* ON *SENECIO TRIANGULARIS* AND *SENECIO JACOBAEA*

INTRODUCTION

Biological control workers rely on host specificity tests prior to natural enemy introduction to estimate risk to nontarget plants (Harris and Zwolfer, 1968). It is generally assumed that the more closely related a plant species is to the target host, the more likely the insect will feed on it (Wapshere, 1974). By this criterion, all species with a close taxonomic relation to the host would be considered at risk. This presumes too much since mechanical or chemical traits of a plant species may prevent insect feeding even when closely related plant species are consumed. Plants native to the area of introduction that are within the potential agent's phylogenetic host range need to be included in host specificity tests in order to determine their suitability as food.

Host specificity testing of the cinnabar moth prior to its introduction in to the United States and Canada showed that the caterpillars did not feed on the crop plants tested (Parker, 1960; Bucher and Harris, 1961), and only plants in *Senecio* and closely related genera sustained larval development (Bucher and Harris, 1961). These studies did not test *Senecio triangularis*, however, and,

prior to the current study, only anecdotal evidence (e.g. Stimac, 1978) existed of the ability of cinnabar moth larvae to feed on this plant.

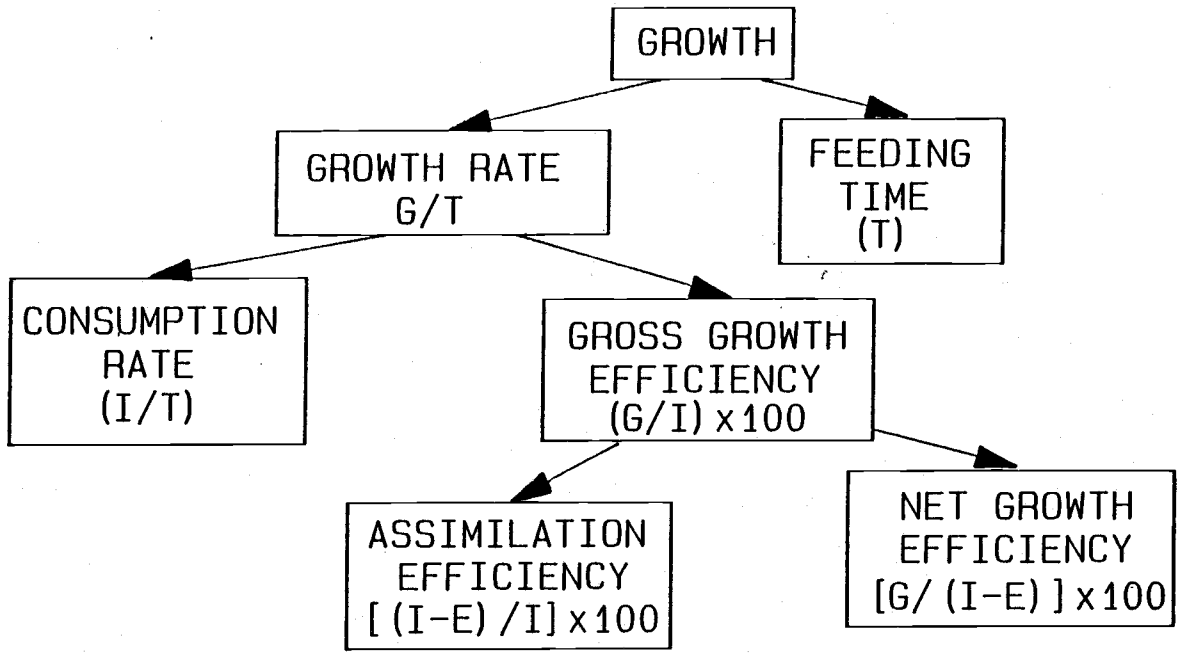
Host specificity testing rarely provides the quantitative measurements needed to establish the suitability of a nontarget species relative to the target weed. Even if a native plant sustains larval development in the lab, the species is unlikely to become established on the native plant in the field if fecundity and survival are poor relative to their performance on the target weed.

One objective of this study was to determine whether cinnabar moths were able to complete larval development on S. triangularis. I had earlier observed larvae feeding on S. triangularis on Marys Peak and wished to quantify their ability to grow and develop on this species.

A second objective was to compare the suitability of S. triangularis and S. jacobaea as food for larvae of T. jacobaeae. I compared (1) survival; (2) development time from egg to pupa; and (3) pupal mass for larvae fed on the two plant species. I then projected how these factors combine to affect the rates of population growth. A slow development time resulting from a poor diet may increase exposure to mortality factors including predation, parasitism, disease and starvation; smaller pupal size is correlated with reduced cinnabar moth fecundity (Dempster, 1971; van der Meijden, 1976; Rose, 1978).

I further studied how variation in growth was related to variation in the speed and efficiency of food utilization (Waldbauer,1968; Scriber and Slansky, 1981; Slansky and Scriber, 1985). Caterpillars may compensate for reduced growth rates on a low quality diet by feeding longer (Figure 1). An insect may also maintain its growth rate in spite of reduced food quality by consuming food faster (increasing consumption rate) or converting ingested food into biomass more efficiently (increasing gross growth efficiency). Gross growth efficiency in turn is a product of the efficiency with which ingested food is assimilated (assimilation efficiency) and the efficiency with which this assimilated food is converted into insect biomass (net growth efficiency).

Several studies have compared caterpillar growth and development when fed different parts of S. jacobaea, but none has compared caterpillar performance of different host species. Van der Meijden (1976), Rose (1978), and Dempster (1982) all obtained larger pupae when larvae were reared on ragwort flowers than when they were fed ragwort leaves although this result was only statistically significant in van der Meijden's study. Van der Meijden (1976) found that a diet of flowers yielded faster development than did a diet of leaves, but Rose (1978) found no effect of diet on development time. The faster development rate and larger pupae obtained on a floral diet is correlated with higher



G = Growth (biomass gained during feeding period) (mg.)

T = Feeding time (days)

I = Ingested food (mg.)

E = Egested food

A = Assimilated food (mg.) = I - E

G = G/T X T

G/T = I/T X G/I

G/I = A/I X G/A

Figure 1. Model of food consumption and utilization.

nitrogen content (Pajutee, 1980; Dempster, 1982). Pajutee (1980) compared indices of nutritional performance for cinnabar larvae fed low leaves, high leaves, and flowers; growth rate did not differ significantly between larvae fed on high leaves and flowers but was greater for larvae fed both of these diets than for larvae fed low leaves. McEvoy (1984) found no significant variation in respiration rates of larvae fed different S. jacobaea diets, but respiratory rates increased linearly with ingestion rate.

The relative suitability of S. triangularis and S. jacobaea as food for the cinnabar moth might be related to differences in physical traits, nutrient content, or the quantity and quality of allelochemicals (Tabashnik and Slansky, 1987). Only allelochemical (pyrrolizidine alkaloid) differences have been studied for S. triangularis and S. jacobaea. Senecionine is the dominant alkaloid in S. triangularis, and integerrimine, platyphylline, rosmarinine, retrorsine triangularine and neotriangularine are present in small amounts (Roitman, 1983). In S. jacobaea, jacobine, jacozine, and jacoline make up 40 - 60% of the total alkaloid concentration while senecionine, seneciphylline and integerrimine are present in lower concentrations (Aplin and Rothschild, 1972). The dominant alkaloids in S. triangularis are those most concentrated by cinnabar moths. Senecionine, seneciphylline, and integerrimine compose 60-70% of the alkaloids present in

cinnabar moth pupae while jacobine, jacozine, and jacoline make up only 10-15% (Aplin and Rothschild, 1972).

The cinnabar moth might be expected to perform better on S. jacobaea on which it has a long history of association than on S. triangularis with which it has been associated for less than 30 years. Over time insects may become better adapted to host plant attributes including physical defenses, chemical defenses, and nutritional quality; cases of such adaptations abound (Strong et. al. 1984). However, insect species may perform well in the laboratory on plant species with which they have had little association in the field. For example, Pieris rapae larvae grew faster on Dentaria diphylla than on other plants tested although D. diphylla is rarely attacked in nature because it occurs in woodlands where P. rapae rarely fly (Slansky and Feeny, 1977).

METHODS

The experimental design for my 1985 feeding study was a randomized block with two blocks (block 1: S. triangularis egg mass and block 2: S. jacobaea egg mass) and two treatments (S. triangularis diet and S. jacobaea diet).

I reared larvae used in laboratory feeding studies in 1985 from two egg masses collected on Marys Peak. One egg mass had been laid on S. triangularis, and the other had been laid on S. jacobaea. I chose egg masses of approximately equal large size (64 and 57 eggs per mass), avoiding smaller mass sizes because eggs and first instar larvae from smaller egg masses have low survival (Dempster, 1971, van der Meijden, 1976, Rose, 1978). Individual female cinnabar moths lay their largest egg masses at the onset of oviposition with the majority of eggs being laid in a few large masses early in the oviposition period (Rose, 1978). Egg masses which I observed on plants on Marys Peak in 1986 varied in size from 1 to 115 eggs per mass.

When the eggs hatched, I randomly assigned ten larvae from each egg mass to a S. triangularis diet and ten larvae from each egg mass to a S. jacobaea diet. Larvae were reared individually in 8 oz. wax-paper cups placed in a growth chamber with a 16 hour light, 8 hour dark

photoperiod and a temperature setting of 25 C:10 C. I placed water-filled pans in the bottom of the chamber to maintain humidity as recommended by Rose (1978). Plant material was collected every 2-3 days from Marys Peak. Larvae were fed leaves from the top third of the plants and this food was replaced daily. I restricted larval diet to leaves because larvae do not feed on S. triangularis flowers.

I weighed each larva and its food daily from the time the larva molted into the fourth instar until it had pupated. Fecal material and uneaten food were also collected daily, dried to a constant mass at 70 C, and weighed. I continued these procedures until all larvae had pupated. Dry mass of pupae was determined three days after pupation. Food consumption was estimated by standard gravimetric methods (Waldbauer, 1968).

Fourth and fifth instar larvae were chosen for these experiments because they account for 95% of food consumed (15% in the fourth instar and 80% in the fifth instar, Isaacson, 1973). It is convenient to use penultimate instar larvae in experiments measuring food consumption and utilization because they consume much larger quantities of food than do earlier instars and the weight loss at premolt is less than for final instar larvae, which tend to be very active prior to the pupal molt (Waldbauer, 1968). I included the final instar larvae because they account for a

large percentage of total food consumption and probably have the greatest impact on their host plant.

Dry mass of leaf material fed to each larva was estimated by dividing leaves along the midrib, feeding half to the larva, and drying the other half to determine percent dry weight. The conversion factor from fresh mass to dry mass for larvae was 0.173 (s.e. = .0043, n=23).

I calculated the following parameters of larval food consumption and utilization (Waldbauer, 1968):

Growth rate (GR) = biomass gained / day

Consumption rate (CR) = biomass ingested / day

Gross growth efficiency (ECI) = larval mass gain / mass food ingested

Net growth efficiency (ECD) = [insect biomass gained / (mass of food ingested - mass of feces)] x 100

Assimilation efficiency (AE) = [(mass of food ingested - feces)/ mass of food ingested] x 100

Feeding time (T) = number of days during which feeding occurred

All biomass measurements used in the calculation of these parameters were in mg. dry mass. Mean larval masses were estimated for each feeding period by the weighted averages method (Waldbauer, 1964) and are included in the tables so that relative rates may be calculated to facilitate comparison with other studies.

To compare water loss by the two plant species during the feeding experiments, I weighed 10 leaf halves of each

species each day and placed them in wax paper cups in the growth chamber without an insect. These leaves were weighed again after 24 hours and the percent mass loss during the feeding period was then calculated.

In 1986, I again reared cinnabar moth larvae on each of the two Senecio species. I replicated egg masses collected from each plant species (4 replications) because there were significant block x treatment interactions in 1985. The mean egg mass size used was 44.38 eggs (standard error = 4.45). From each of the eight egg masses (four from each plant species) I randomly selected 10 newly hatched larvae and reared five on S. triangularis and five on S. jacobaea. These larvae were reared under the same conditions as the larvae from the previous year, but they were not weighed until they pupated. Fresh masses, dry masses, and pupal diameters were measured three days after pupation. Development time from egg to pupa was also recorded for each insect.

Data Analysis

Feeding parameters for each caterpillar were estimated from the beginning of their penultimate instar through the cessation of feeding in the final instar and individually for the feeding periods of the penultimate and final instars. Means for pupal masses, development times and feeding parameters of insects fed on the two Senecio species were compared using a two way analysis of variance

(ANOVA). Homogeneity of variances was determined using a F max test, and data were transformed when necessary to homogenize variances (Sokal and Rohlf, 1981).

RESULTS

Survival

In the 1985 experiment all insects survived from egg to pupa. I accidentally damaged two pupae before weighing and did not include their masses in Table 2.

In the 1986 experiment, four larvae from the same egg mass died in the late fifth instar; three had fed on S. triangularis, and one had fed on S. jacobaea. The surviving larvae from this egg mass developed into pupae which were smaller than the pupae from all the other egg masses.

Development Time

Insects fed S. triangularis developed more slowly from egg to pupa than did caterpillars fed S. jacobaea (Table 2, Table 3). This result was statistically significant only in the 1986 experiment in which larvae fed S. triangularis required 9.6% more time to complete development than did larvae fed S. jacobaea (Table 3).

Development time also differed significantly between larvae from egg masses laid on the two plant species; however, the direction of this difference was inconsistent between years. In 1985, individuals from egg masses laid on S. triangularis (block 1) completed their development faster than larvae from eggs laid on S. jacobaea (block 2) (Table 2). In 1986, the reverse was true: individuals from

Table 2. Pupal mass and development time from egg to pupa for larvae in 1985 feeding experiment. Degrees of freedom = 1, 34. Pupal masses were transformed using an inverse transformation in order to homogenize variances. Back-transformed means are presented for pupal masses with 95% confidence limits placed in parentheses. Values in the upper table for development time are means with standard errors in parentheses.

BLOCK	FEEDING HOST	PUPAL MASS (dry mass mg.)		DEVELOPMENT TIME (days)	
		$\bar{X}$	C.I.	$\bar{X}$	S.E.
1	S. tri.	45.18	(42.96 - 47.64)	27.70	(0.42)
	S. jac.	48.15	(45.51 - 51.14)	26.56	(0.24)
2	S. tri.	42.91	(40.80 - 45.25)	29.89	(0.31)
	S. jac.	65.85	(60.51 - 70.22)	29.70	(0.40)

ANALYSIS OF VARIANCE RESULTS

	PUPAL WEIGHT		DEVELOPMENT TIME	
	F	P	F	P
BLOCKS	16.61	0.0003	54.15	0.0001
DIETS	64.65	0.0001	3.47	0.07
BLOCK X DIET INTERACTIONS	32.24	0.0001	1.78	0.19

Table 3: Comparison of pupal masses, pupal widths and development time for larvae reared from eggs laid on S. triangularis or S. jacobaea and fed leaves from one of the two plant species in 1986. Values in the upper table are means with standard errors in parentheses.

EGG MASS HOST	FEEDING HOST	N	DRY MASS (MG)	FRESH MASS (MG)	WIDTH (CM)	DEVELOPMENT TIME (DAYS)
S. tri.	S. tri.	20	51.96 (1.72)	155.79 (4.32)	.49 (.008)	28.1 (.49)
	S. jac.	19	58.77 (2.52)	170.24 (5.45)	.50 (.006)	26.05 (.42)
S. jac.	S. tri.	15	51.97 (1.52)	158.79 (4.42)	.49 (.008)	26.87 (.45)
	S. jac.	18	57.43 (2.76)	167.46 (5.40)	.49 (.006)	24.22 (.38)
AVERAGE	S. tri.	35	51.97 (1.16)	157.07 (3.08)	.49 (.005)	27.57 (.35)
	S. jac.	37	58.12 (1.84)	168.89 (3.79)	.50 (.004)	25.16 (.32)

ANALYSIS OF VARIANCE RESULTS

EGG HOST EFFECTS				
F	.04	.03	.21	23.51
P	.85	.86	.65	.0001
DIET EFFECTS				
F	12.54	8.39	1.57	45.05
P	.0008	.005	.22	.0001
MASS EFFECTS				
F	8.23	6.68	1.86	8.43
P	.0001	.0001	.10	.0001
EGG HOST X DIET INTERACTIONS				
F	.42	.04	.74	.06
P	.52	.84	.39	.81

Degrees of freedom = 1,62 for Egg Host, Diet and Egg Host x Diet Interactions
Degrees of freedom = 6,62 for Mass effects

eggs laid on S. jacobaea completed their development two days earlier than larvae from eggs laid on S. triangularis (Table 3). These inconsistent results suggest that variation in development time among individuals from different egg masses may be unrelated to host species on which eggs were laid.

Two of the caterpillars fed S. triangularis leaves in 1985 molted into an extra, sixth instar four to five days after molting into fifth-instar larvae. Although these larvae were lighter than the other larvae in the same block at the onset of the fifth instar, by feeding longer they developed into heavier pupae than the other caterpillars from the same block fed on the same diet.

Male and female pupae did not differ in development time or mass.

Pupal Size

Larvae fed S. triangularis developed into smaller pupae than did larvae fed S. jacobaea, but the magnitude of the difference differed between the two years and among egg masses (Table 2, Table 3). In the 1985 experiment there was a significant block x treatment interaction. Pupae from block 1 weighed 5.7% less when fed S. triangularis than when fed S. jacobaea while pupae from block 2 weighed 34.4% less when fed S. triangularis than when fed S. jacobaea (Table 2). In 1986, larvae fed S. triangularis developed into pupae which were 11% lighter than pupae

which fed on S. jacobaea as larvae (Table 3). Pupal weight varied for cinnabar moths from different egg masses (Table 3) and was strongly correlated with pupal width (Figure 2).

Food Consumption and Utilization

On average, larvae consumed 64% of the food offered to them. Water loss may have decreased food quality but did not differ with plant species. Initial mean water content in both species was an average of 84% (s.e. = .001). S. triangularis leaves experienced an average of 64% (s.e. = 7%) weight loss while S. jacobaea lost 65% (s.e. = 6%) of their weight over 24 hours.

I discuss the food consumption and utilization results separately for the two 1985 egg masses because I found significant block x diet interactions (Table 2).

Block 1

Larvae from block 1 grew 14% more slowly during the final two instars when fed S. triangularis than when fed S. jacobaea (Table 4). Larvae consumed S. triangularis slightly faster than they consumed S. jacobaea (2.5%), but grew more slowly due to a 19.8% lower gross growth efficiency. A decrease in the proportion of ingested food assimilated (18%) offset an increase in the proportion of assimilated food converted to caterpillar biomass (2.4%). The number of days spent feeding did not differ significantly between the two diet treatments (Table 4).

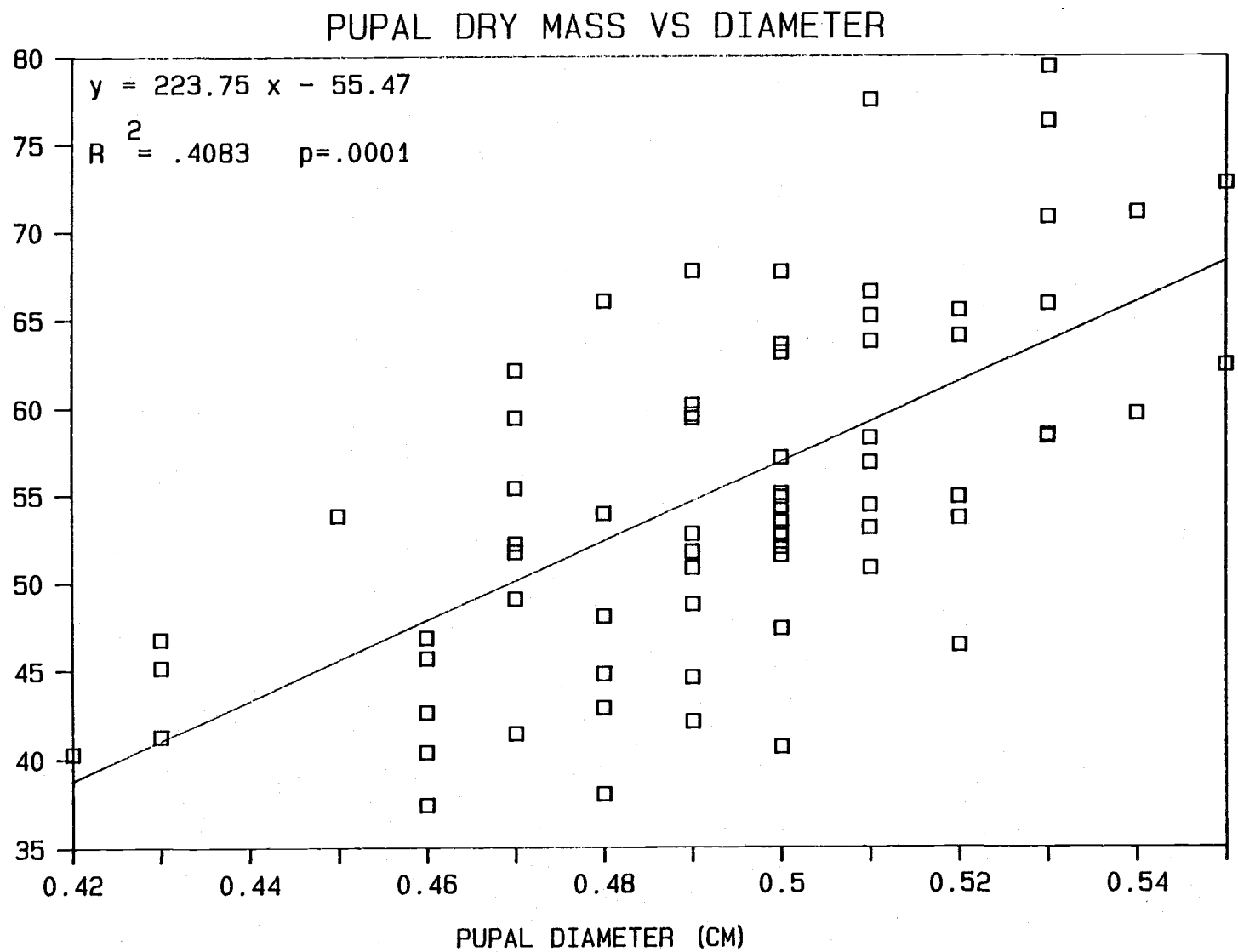


Figure 2. Correlation between pupal dry mass and pupal diameter.

Patterns of food consumption and utilization in the final instar were similar to the patterns from penultimate through final instars. The growth rate of larvae fed S. triangularis was 12% slower than that of larvae fed S. jacobaea, but consumption rates did not differ between the two diets. A decrease in assimilation efficiency was balanced by an increase in net growth efficiency leading to no significant difference in gross growth efficiency. Feeding time also did not differ significantly. Larvae feeding on S. triangularis averaged 7% lighter than larvae feeding on S. jacobaea during the final instar (Table 5).

Food consumption and utilization trends differed between the penultimate instar and the final instar. Growth rate was significantly slower on S. triangularis than on S. jacobaea (21%) but there were no significant differences in consumption rate, assimilation efficiency or net growth efficiency. The combined trends of lower assimilation and net growth efficiencies resulted in a 20% lower gross growth efficiency for larvae fed S. triangularis compared to larvae fed S. jacobaea. There was no significant difference in feeding time (Table 6).

Block 2

During the final two instars larvae from block 2 grew 27% more slowly when fed S. triangularis than when fed S. jacobaea. This decreased growth rate was due both to a 25% slower ingestion rate and a 23% lower assimilation

efficiency for larvae fed S. triangularis than larvae fed S. jacobaea. The lower assimilation efficiency for larvae fed S. triangularis offset a 28% increase in proportion of assimilated food converted into biomass resulting in a 3% decrease in the proportion of ingested food converted into larval biomass. Feeding time did not differ significantly between larvae reared on the two diets (Table 4).

In the final instar, larvae grew 25% more slowly when fed S. triangularis than when fed S. jacobaea (Table 5). This reduced growth rate for larvae fed S. triangularis is primarily a result of a 22% reduction in ingestion rate. Larvae fed S. triangularis compensated for a 25% lower assimilation efficiency by converting assimilated food into growth 28% more efficiently than S. jacobaea fed larvae, and the difference in gross growth efficiency was not significant. Gross growth efficiency and feeding time did not differ between the two diets (Table 5).

During the penultimate instar, larvae fed S. triangularis grew 30% faster than larvae fed S. jacobaea. Consumption rate did not vary significantly with diet. Although the 23% lower assimilation efficiency for larvae fed S. triangularis was not statistically significant, ingested S. triangularis was utilized for growth significantly less efficiently (14%) than ingested S. jacobaea. Feeding time did not differ significantly

Table 4. Food consumption and utilization parameters for larvae from penultimate through final instars. Values in the upper table are means with standard errors in parentheses.

BLOCK	DIET	N	GR (Mg dry mass/day)	CR (Mg dry mass/day)	AE	ECD*	ECD**	ECI	MEAN LARVAL MASS (Mg)	FEEDING TIME (DAYS)
1	S. tri.	10	2.16	33.73	20.01	32.29	32.90	6.43	19.67	12.2
			(.09)	(1.2)	(1.00)	(1.07)	(2.04)	(.25)	(.79)	(.20)
	S. jac.	9	2.52	32.90	24.50	31.53	32.14	7.64	20.36	11.6
			(.12)	(.52)	(1.62)	(1.07)	(2.13)	(.28)	(.46)	(.24)
2	S. tri.	10	1.82	27.76	18.42	36.54	37.69	6.56	18.03	14.7
			(.09)	(.95)	(1.38	(1.08)	(3.32)	(.13)	(.62)	(.33).
	S. jac.	10	2.50	36.96	23.90	28.46	28.60	6.79	24.24	14.5
			(.06)	(.96)	(0.65)	(1.03)	(0.92)	(.11)	(.85)	(.40)
	Block									
	F		3.21	1.03	0.66	0.02		2.71	2.60	76.98
	P		0.08	0.32	0.42	0.87		0.11	0.12	0.0001
	Diet									
	F		32.83	20.26	17.43	4.67		12.38	24.72	1.82
	P		0.0001	0.0001	0.0002	0.04		0.001	0.0001	0.19
	Block X Diet Interactions									
	F		3.02	27.30	0.17	3.04		5.94	15.21	0.52
	P		.09	0.0001	0.68	0.09		0.02	0.0004	0.48

* Back transformed from log ECD.

** Untransformed data.

Table 5. Food consumption and utilization for final instar larvae. Degrees freedom are 1,35 for food and egg mass effects. Values in the upper table are means with standard errors in parentheses.

BLOCK	DIET	N	GR (Mg dry mass/day)	CR (Mg dry mass/day)	AE	ECD*	ECD**	ECI	MEAN LARVAL MASS (Mg)	FEEDING TIME (DAYS)
1	S. tri.	10	2.33	46.1	19.56	25.90	26.55	5.09	25.67	7.8
			(.13)	(1.87)	(.99)	(1.08)	(1.79)	(.30)	(1.00)	(.20)
	S. jac.	9	2.64	46.2	23.61	24.23	24.74	5.69	27.53	7.0
			(.18)	(1.15)	(1.57)	(1.08)	(1.67)	(.31)	(.51)	(.24)
2	S. tri.	10	2.06	37.6	17.23	32.42	33.47	5.46	23.78	9.5
			(.10)	(1.30)	(1.27)	(1.08)	(3.03)	(.16)	(.78)	(.22)
	S. jac.	10	2.74	48.3	23.09	24.62	24.81	5.67	31.06	10.0
			(.07)	(1.02)	(0.79)	(1.04)	(1.00)	(.14)	(1.01)	(.33)
	Block									
	F		0.39	5.23	1.27	2.81		.66	1.01	83.70
	P		0.54	0.03	0.27	0.10		0.42	0.32	0.0001
	Diet									
	F		15.88	16.06	18.10	6.08		2.89	28.69	0.27
	P		0.0003	0.0003	0.0001	0.02		0.10	0.0001	0.61
	Block X Diet Interaction									
	F		2.15	14.50	0.60	2.19		0.67	9.77	6.51
	P		.15	0.0005	0.44	0.15		0.42	0.004	0.02

* Back transformed from log ECD.

** Untransformed data.

Table 6. Food consumption and utilization for penultimate instar larvae. Degrees freedom are 1,35 for food and egg mass effects. Values in the upper table are means with standard errors in parentheses.

BLOCK	DIET	N	GR (Mg dry mass/day)	CR (Mg dry mass/day)	AE*	AE**	ECD	ECI	MEAN LARVAL MASS (Mg)	FEEDING TIME (DAYS)
1	S. tri.	10	1.86	12.01	22.02	22.67	74.68	15.58	9.09	4.4
			(.09)	(0.64)	(1.08)	(1.77)	(8.98)	(0.58)	(0.63)	(0.16)
	S. jac.	9	2.38	12.66	25.99	27.75	84.98	19.43	9.37	4.6
			(.13)	(1.03)	(1.14)	(3.57)	(16.87)	(1.36)	(0.24)	(0.24)
2	S. tri.	10	1.41	9.79	22.88	25.37	74.47	14.73	6.79	5.2
			(.10)	(0.63)	(1.15)	(4.46)	(13.30)	(1.09)	(0.31)	(0.13)
	S. jac.	10	2.00	11.80	29.50	31.42	62.07	17.10	9.24	4.5
			(.09)	(0.66)	(1.12)	(3.88)	(7.40)	(0.62)	(0.35)	(0.17)
	Block									
	F		15.93	4.20	0.53		0.89	2.47	8.29	4.50
	P		0.0003	0.05	0.47		0.35	0.12	0.007	0.04
	Diet									
	F		30.62	3.27	3.12		0.01	10.66	11.08	2.56
	P		0.0001	0.08	0.09		0.91	0.002	0.002	0.12
	Block X Diet Interactions									
	F		0.12	0.84	0.14		0.90	0.60	6.79	5.81
	P		.72	0.37	0.71		0.35	0.44	0.01	0.02

* Back transformed from log AD.

** Untransformed data.

between the two diets (Table 6).

Correlation Between Consumption Rate and Other Parameters of Food Utilization

Consumption rate was not significantly correlated with any of the other parameters of food utilization for larvae from block 1 during the penultimate through the final instar or during the final instar alone (Figure 3, Figure 4). In the penultimate instar, consumption rate was positively correlated with assimilation efficiency and gross growth efficiency and negatively correlated with net growth efficiency (Figure 5). When the two outlying data points were removed, however, these correlations were not statistically significant.

In contrast, for larvae from the S. jacobaea egg mass during all three time periods, consumption rate was positively correlated with growth rate and assimilation efficiency, and negatively correlated with the efficiency of conversion of digested food to biomass (Figure 3-5).

Figure 3. Correlations of growth rate, assimilation efficiency, net growth efficiency, and gross growth efficiency with consumption rate for larvae from the final through penultimate instars. □'s represent values for larvae fed S. triangularis, and +'s represent values for larvae fed S. jacobaea.

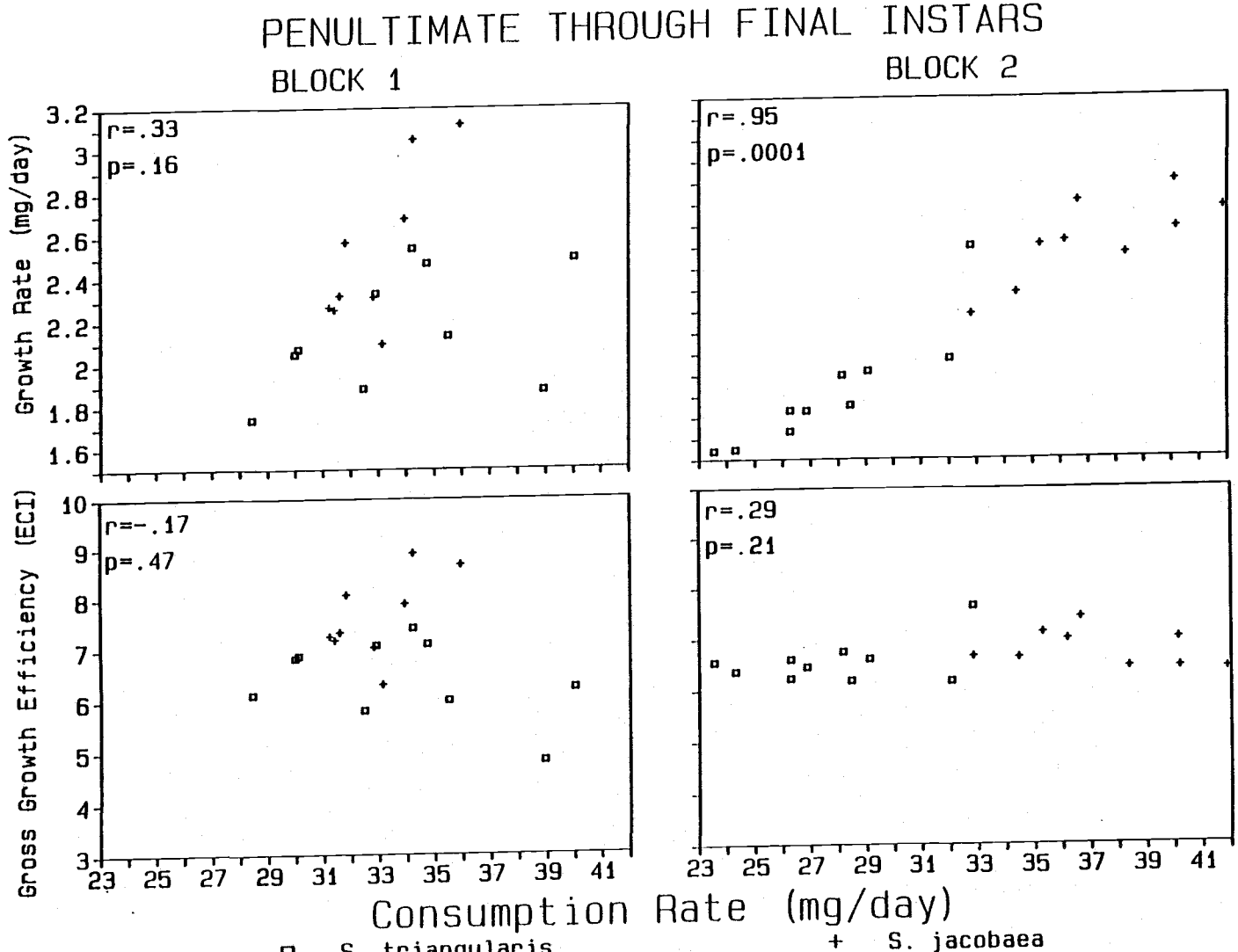

PENULTIMATE THROUGH FINAL INSTARS
BLOCK 1
BLOCK 2
Growth Rate (mg/day)
Gross Growth Efficiency (ECI)
r=.33
p=.16
r=.95
p=.0001
r=-.17
p=.47
r=.29
p=.21
Consumption Rate (mg/day)
S. triangularis
S. jacobaea

Figure 3.

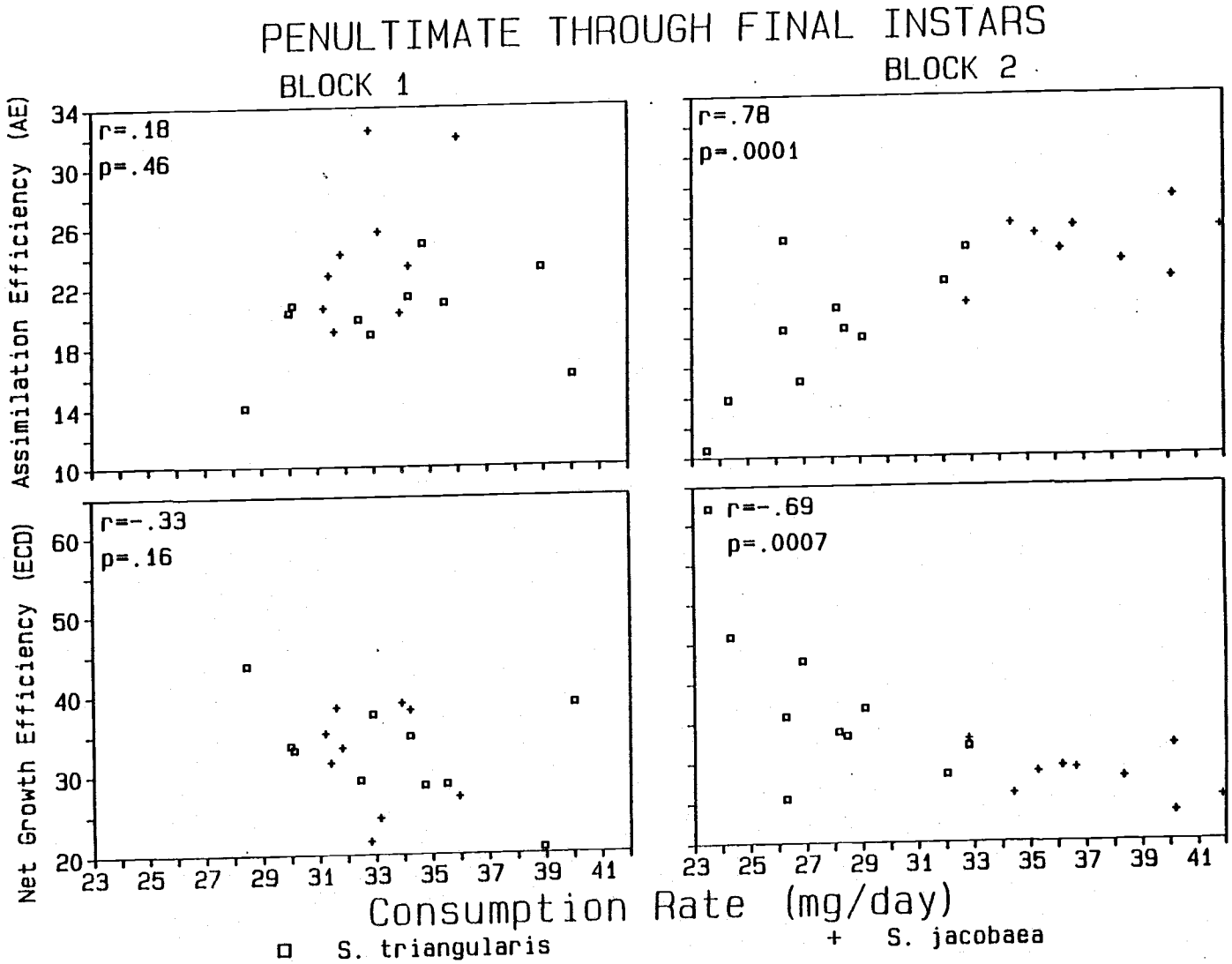


Figure 3. Continued.

Figure 4. Correlations of growth rate, assimilation efficiency, net growth efficiency, and gross growth efficiency with consumption rate for final instar larvae. □'s represent values for larvae fed S. triangularis, and +'s represent values for larvae fed S. jacobaea.

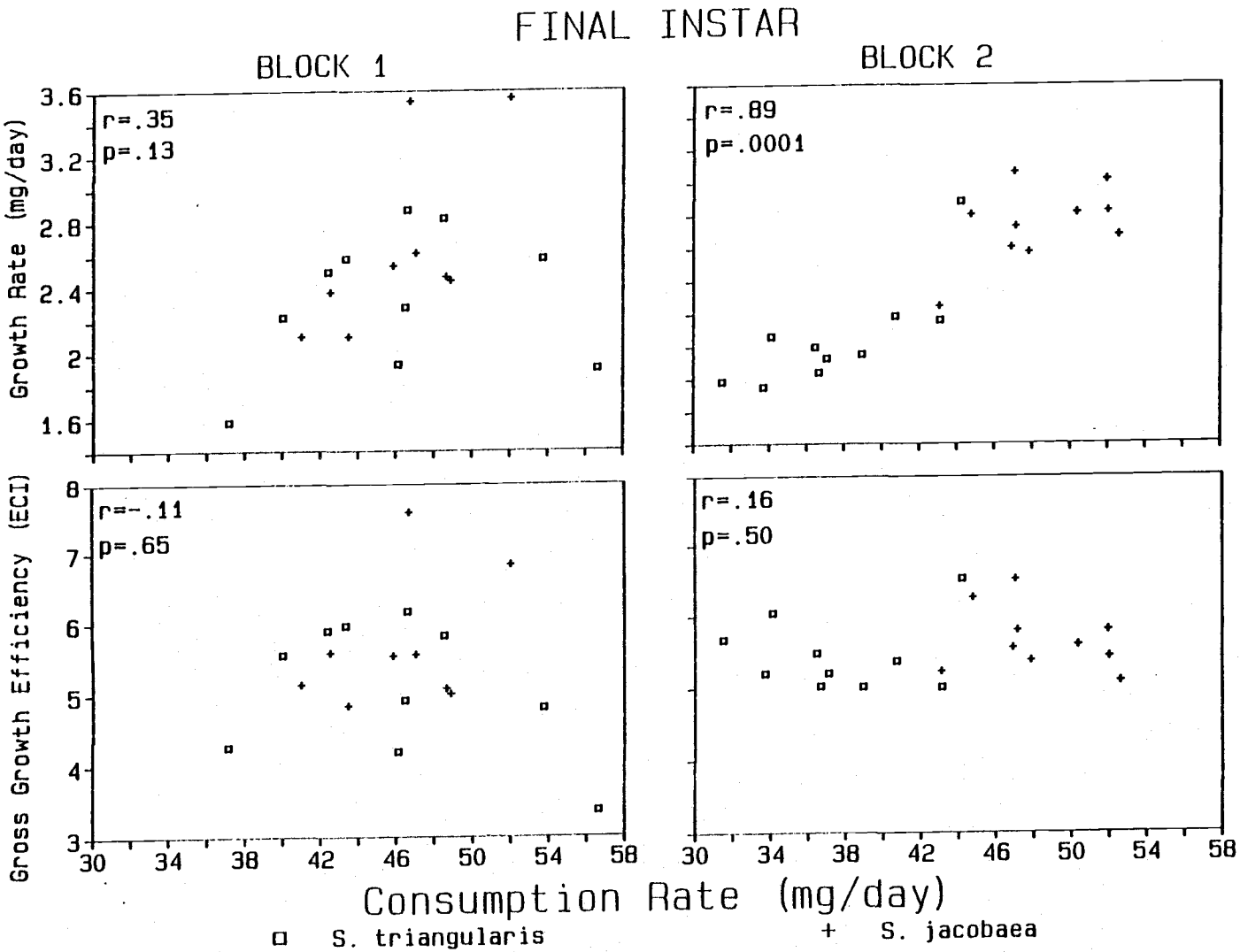

FINAL INSTAR
BLOCK 1
BLOCK 2
r=.35
p=.13
r=.89
p=.0001
r=-.11
p=.65
r=.16
p=.50
Growth Rate (mg/day)
Gross Growth Efficiency (ECI)
Consumption Rate (mg/day)
S. triangularis
S. jacobaea

Figure 4.

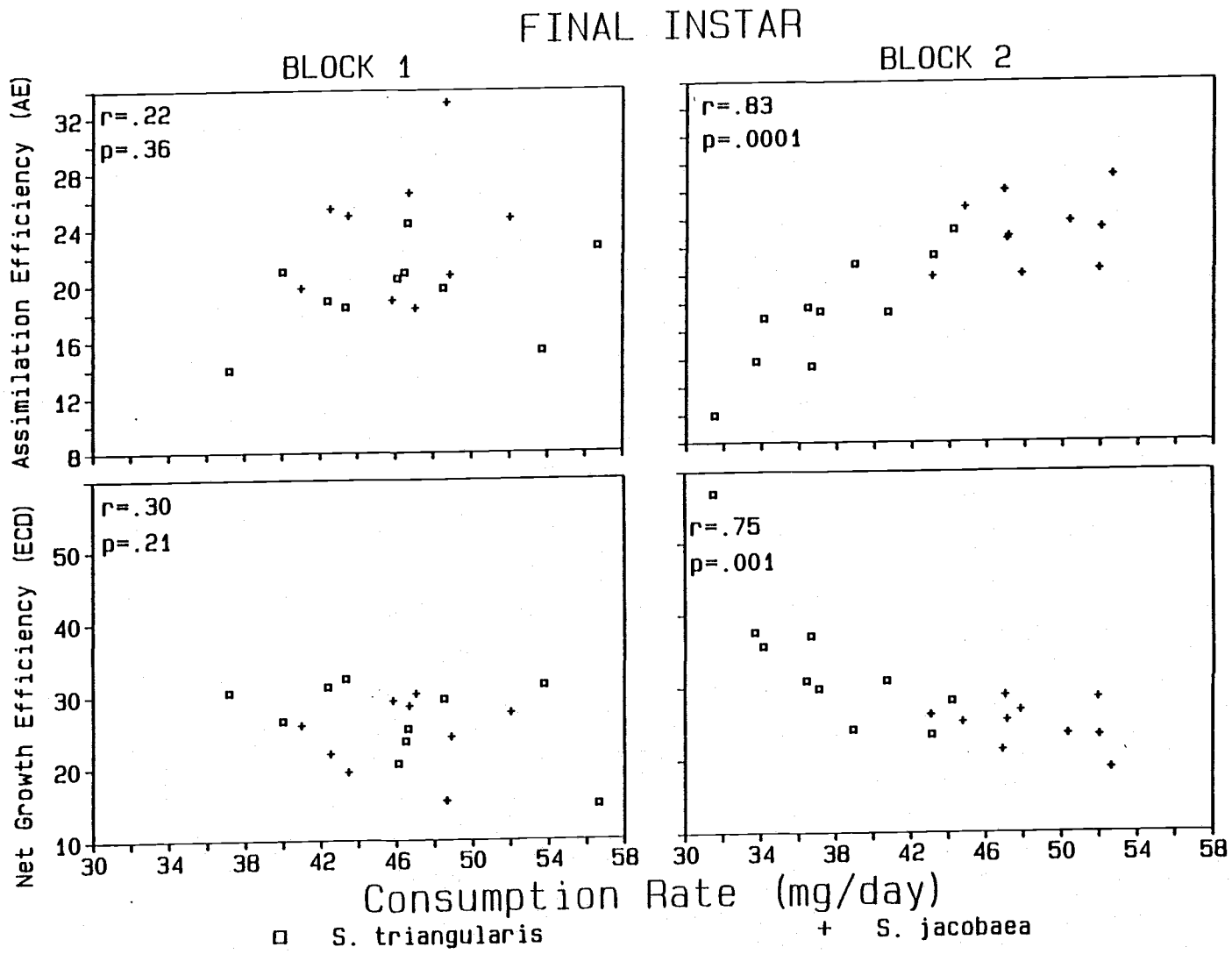


Figure 4. Continued.

Figure 5. Correlations of growth rate, assimilation efficiency, net growth efficiency, and gross growth efficiency with consumption rate for penultimate instar larvae. □'s represent values for larvae fed S. triangularis, and +'s represent values for larvae fed S. jacobaea.

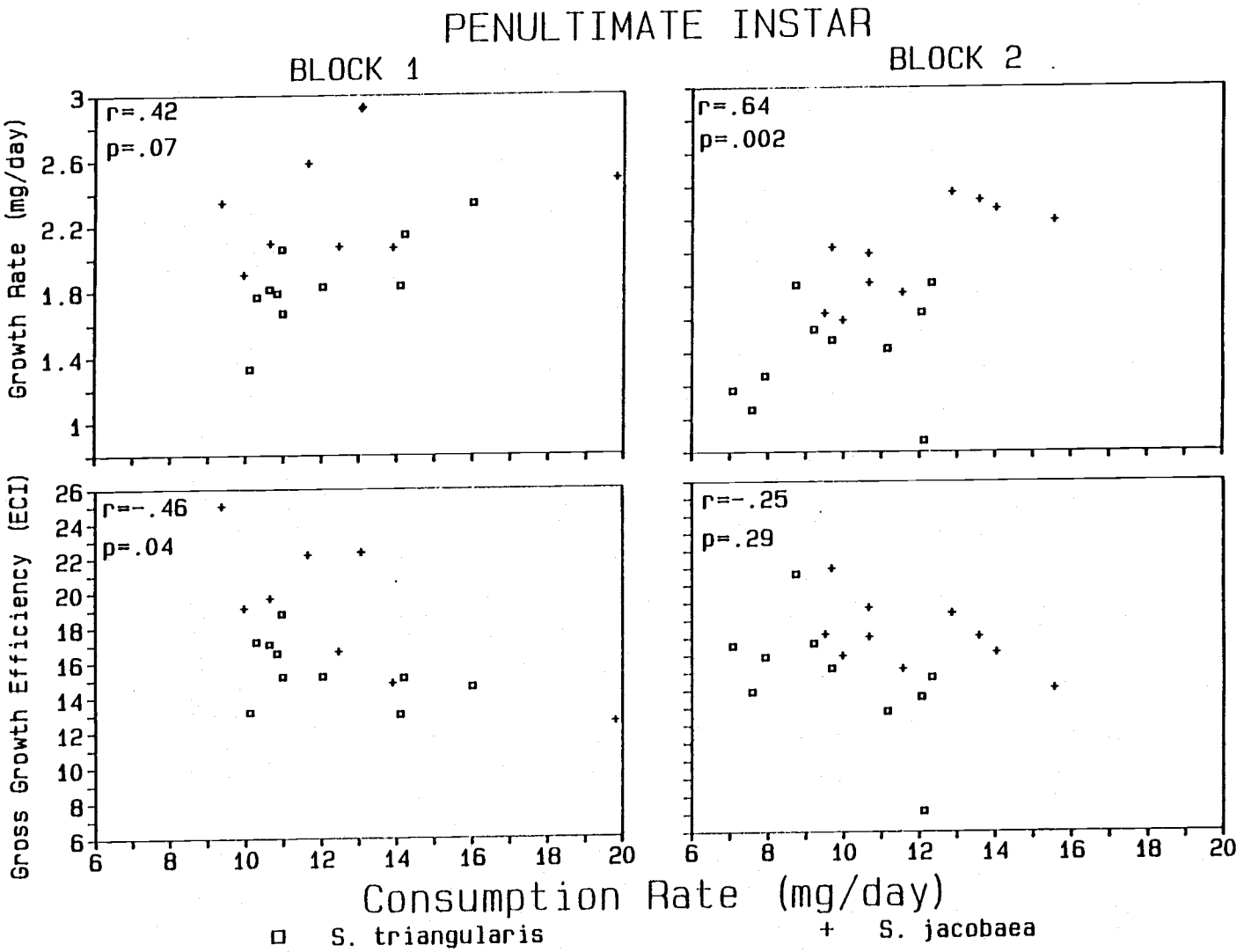

PENULTIMATE INSTAR
BLOCK 1
BLOCK 2
r=.42
p=.07
r=.64
p=.002
r=-.46
p=.04
r=-.25
p=.29
Growth Rate (mg/day)
Gross Growth Efficiency (ECI)
Consumption Rate (mg/day)
S. triangularis
S. jacobaea

Figure 5.

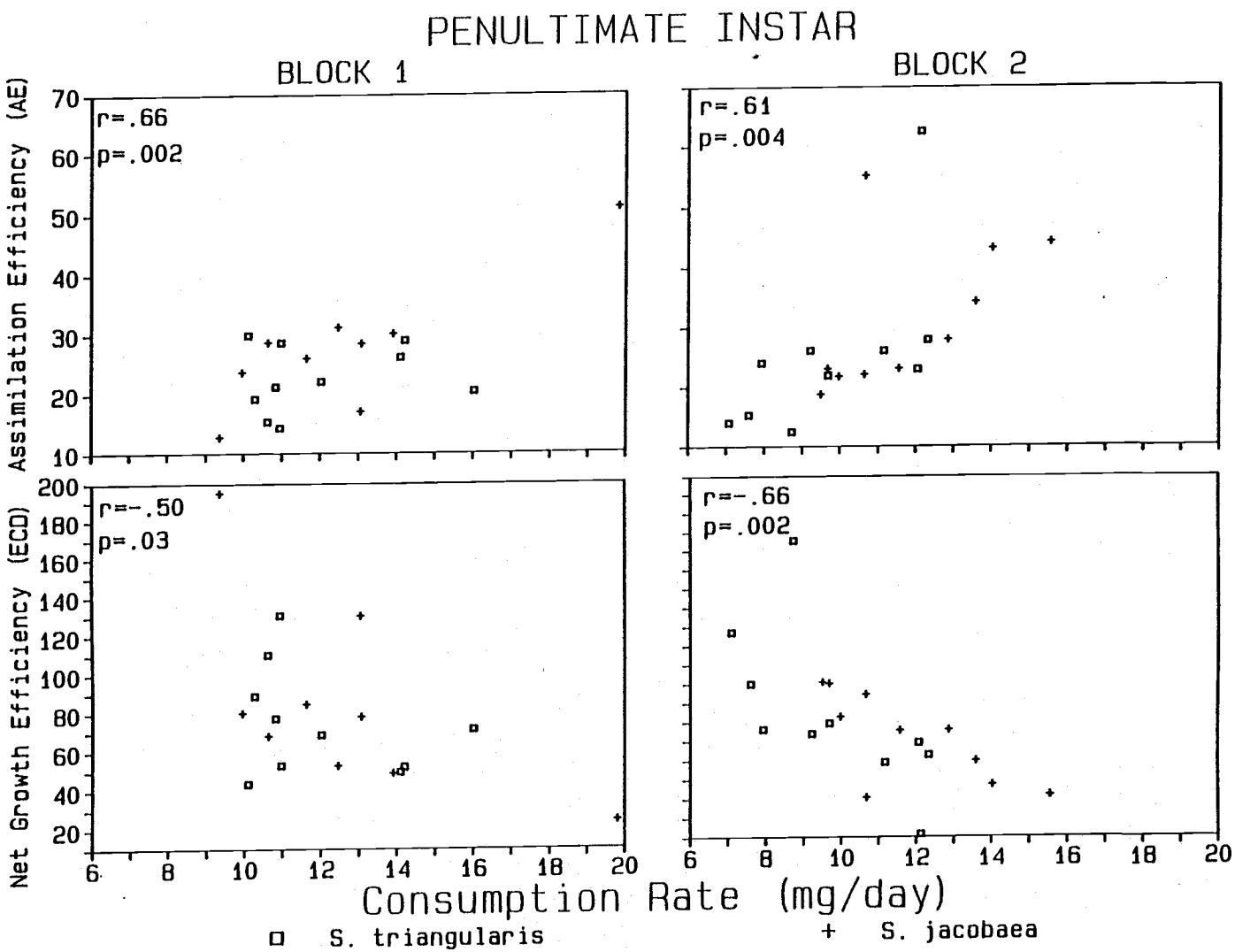


Figure 5. continued.

DISCUSSION

The cinnabar moth can develop from egg to pupa on S. triangularis, but S. triangularis is less suitable for growth and development than the insect's traditional host, S. jacobaea. A S. triangularis diet yields smaller pupae, longer development times, and slower growth rates than a S. jacobaea diet.

Growth ($G = G/T \times T$)

Differences in pupal size arise from differences in growth. Growth rate was reduced on a S. triangularis diet, but differences in feeding time were not significant (Tables 4-6).

For two exceptional larvae fed S. triangularis, feeding time was prolonged by undergoing a sixth instar. The extra time spent feeding by these larvae compensated for their slow growth rate and yielded pupal sizes comparable to those yielded by a S. jacobaea diet. Extra instars have been recorded for other insects, but have not been previously reported for the cinnabar moth. Taylor (1984) found that larvae of Samea multiplicalis (Lepidoptera: Pyralidae) increase their weight in spite of a low nitrogen diet by undergoing an extra instar and feeding longer.

An extra instar can allow larvae to maintain growth in spite of a decline in food quality, but an extra instar

occurs infrequently. Further research is needed to determine the constraints to prolonged development time and extra instars in the cinnabar moth. It would also be interesting to know if extra instars in the cinnabar moth are genetically determined and if the frequency can be increased by natural selection.

Growth rate (G/T = I/T x A/I x G/A)

Differences in growth rate between larvae fed on the two diets may be explained by differences in both consumption rate and assimilation efficiency. The relative importance of these two parameters varied between the two blocks in my 1985 experiment. It remains unclear whether consumption rate or assimilation efficiency best explains differences in growth rate because I lack the replication required to estimate variability among egg masses.

For larvae from block 2, reduced growth rate on S. triangularis is best explained by a slower consumption rate. These larvae fed slower on S. triangularis than on S. jacobaea (Tables 4-6). In addition, growth rate was tightly correlated with feeding rate (Figures 4-6). Gross growth efficiency, in contrast, was independent of feeding rate due to the manner in which its components, assimilation efficiency and net growth efficiency varied with feeding rate. As consumption rate increased, an increase in assimilation efficiency was offset by a decrease in net growth efficiency resulting in a constant

gross growth efficiency (Figures 4-6). The increase in assimilation efficiency with consumption rate is contrary to the expectation that digestive efficiency should decrease with increase in consumption rate due to faster throughput (Slansky and Feeny, 1977) but is consistent with previous findings for the cinnabar moth (Pajutee, 1980). The decreased net growth efficiency with increased feeding rate is consistent with the findings of Pajutee (1980) for the cinnabar moth. An inverse relationship between assimilation efficiency and net growth efficiency has been observed often in other insects and may be a manifestation of homeostatic regulation (Slansky and Scriber, 1985). The increased net growth efficiency for cinnabar moth larvae reared on a S. triangularis diet may be a compensatory response to the decreased assimilation efficiency.

For larvae from block 1, decreased growth rate on S. triangularis is best explained by decreased gross growth efficiency resulting from a decrease in assimilation efficiency. Feeding rates differed only slightly on the two diets (Tables 3-5), but differences in growth rate persisted. Correlations between consumption rate and the other parameters were not significant for larvae in the final and penultimate through final instars (Figure 4-5).

Factors influencing insect consumption rate and assimilation efficiency appear to be responsible for the inferiority of S. triangularis as a diet for the cinnabar

moth relative to S. jacobaea. Among insects in general, an absence of phagostimulants (Waldbauer, 1968), an increase in leaf toughness (Tanton, 1962), and the presence of feeding deterrents (Tabashnik and Slansky, 1987) may all reduce consumption rate. I have little evidence concerning these factors for S. triangularis. A reduced assimilation efficiency may result from an increase in food attributes such as indigestible fibers which decrease digestibility. In the field, cinnabar moths skeletonize S. triangularis leaves leaving behind the epidermis. This epidermal tissue may be difficult for the larvae to digest. In contrast, larvae completely consume S. jacobaea leaf laminae leaving only the petiole.

Environmental factors, particularly temperature, may modify the cinnabar moth's feeding performance. My values for food consumption and utilization indices were well within the range of values found by other authors for forb feeding Lepidoptera (Slansky and Scriber, 1985) but differ from those of Pajutee (1980) for the cinnabar moth. Pajutee's (1980) mean estimate of growth rate for penultimate instar larvae fed high leaves of S. jacobaea was 53% larger than my estimate, and her estimates of consumption rate, assimilation efficiency, gross growth efficiency and net growth efficiency were all higher than mine. She may have obtained higher values because her growth chamber was kept at a constant temperature of 25C

while I kept my growth chamber at a temperature of 10C for 8 hours a day in order to simulate night temperatures. Performance rates in other insects tend to increase with temperature (Slansky and Scriber, 1985). Pajutee (1980) also maintained the water content of leaves by placing the petioles in water-filled vials. I did not use vials because I cut leaves in half before feeding them to larvae. Consequently, leaves lost a large amount of water. Water content has been found to effect the growth efficiency of some Lepidoptera (Scriber, 1977). This water loss should not affect the validity of my comparison of the two diets because the average and variance of the water loss were similar for the two plant species.

I may have underestimated differences in the suitability of the two host species by comparing feeding on leaves. Larvae commonly feed on S. jacobaea flowers, but I observed little feeding on S. triangularis flowers in the field (chapter 3). Larvae fed on a diet of S. jacobaea leaves and flowers grow faster and become bigger pupae than larvae fed only leaves (van der Meijden, 1976). A diet of S. jacobae leaves and flowers would have more closely simulated the natural diet and might have yielded higher values for larval growth rate and pupal mass.

Effects of Population Growth

Differences in feeding performance may lead to

differences in population growth in the field by influencing fecundity and mortality. The smaller pupae resulting from larval feeding on S. triangularis rather than S. jacobaea may be expected to result in less fecund females. I estimated this reduction in fecundity using my data relating pupal diameter to pupal weight and van der Meijden's (1976) data relating fecundity to pupal diameter. The 34% reduction in pupal weight experienced by larvae from block 2 in 1985 would result in a 21% decrease in adult fecundity, and the 5.7% reduction in pupal weight experienced by larvae from block 1 would result in a 3.5% decrease in fecundity. In 1986, I measured pupal width directly, but width did not differ significantly between insects fed on the two plant species although the pupal weights did differ (Table 3). Pupal weight may be a better predictor of adult fecundity than pupal width, but there are no data available relating fecundity to pupal weight for the cinnabar moth. The prolonged development of larvae feeding on S. triangularis will increase the time these larvae are exposed to mortality factors in the field. Larval mortality may be substantial. Under field conditions studied by Dempster and Lakhani (1979) larval mortality was between 50% and 99.5%.

Phenotypic variation in larval performance on S. triangularis is well documented by this study. If abilities to increase adult fecundity by undergoing a

supernumerary instar are heritable, then a race of cinnabar moths better adapted to S. triangularis may evolve. If a race of cinnabar moths able to grow larger on S. triangularis did evolve, these moths would be more fecund, and their potential for population increase on this host would be enhanced. Thus I close on the cautionary note that the impact on S. triangularis might increase with time.

III. COLONIZATION AND IMPACT OF THE CINNABAR MOTH ON *SENECIO TRIANGULARIS*

INTRODUCTION

Evidence that the cinnabar moth feeds and completes its development on *S. triangularis* leaves in the laboratory (Chapter II) is necessary but not sufficient grounds for predicting the insect's impact on its new host plant. An insect that utilizes a plant species in the laboratory may fail to do so in the field. For example, the butterfly *Pieris rapae* feeds on *Dentaria diphylla* in the laboratory but not in nature because *P. rapae* seldom fly in woodlands where this plant species occurs (Slansky and Feeny, 1977). To estimate the probability that a cinnabar moth will colonize a *S. triangularis* plant in the field, we would like to know the degree to which the distributions of the plant and insect overlap spatially and temporally, the habitat preferences of the organisms, and the herbivore's searching range and behavior. Once cinnabar moths have been shown to colonize and feed on *S. triangularis* plants in the field, there remains the question of how this feeding affects plant population dynamics. The insect's impact on the plant's dynamics will depend on the nature of feeding damage, the timing of attack and the plant's life history.

The distribution of the cinnabar moth, its conventional host, *S. jacobaea*, and its novel host *S.*

triangularis all overlap in western Oregon. The cinnabar moth is native to Europe where it is distributed throughout the continent with the exception of the far north (Dempster, 1982) and is now widespread in Oregon west of the Cascade Mountains. S. jacobaea is also native to Europe, and is now found throughout western Oregon, and in some places in eastern Oregon in pastures and other disturbed habitats. The cinnabar moth's novel host, S. triangularis, is distributed throughout North America west of the Rocky Mountains from Alaska to Southern California and occurs primarily along streambanks and other moist places at moderate and high elevations in the mountains (Hitchcock et. al. 1955). In western Oregon, S. triangularis grows in the Cascade Mountains and the higher mountains of the Coast Range.

The ability of the cinnabar moth to colonize S. triangularis will depend on the searching range and behavior of the insect. The probability of colonization will increase with searching range and efficiency. Cinnabar moths colonize their host plant as either ovipositing adults or late-instar larvae. This two-phase colonization increases overall search efficiency. Adult dispersal distances tend to be short (Dempster, 1982). Cinnabar moth larvae have been recorded traveling several hundred yards in open habitats (Dempster, 1982), but Islam and Crawley (1983) found that the average distance traveled by larvae

was only 1.57 m. in closed meadow vegetation. Larval movement may account for a major portion of host finding in ragwort populations. In Henneberger's (1986) study, only 40% of the ragwort plants received egg masses while 89% of the plants contained larvae. Plants growing in the shade are more likely to be colonized by larvae than by ovipositing adults because adults rarely lay eggs on shade plants (Frick and Holloway, 1964).

Given that the cinnabar moth is able to colonize S. triangularis, the ability of the insect to become established on the plant may be limited by environmental conditions in which this plant species is found. In particular, moist areas such as streambanks where S. triangularis is common may not be suitable for pupal survival, but the evidence is inconclusive. Wet soils have been noted in some regions where cinnabar moth introductions have failed to establish (Frick and Holloway, 1964; Hawkes, 1973; Bornemissza, 1966), possibly due to increased pupal mortality due to disease (Hawkes, 1973). However, in experiments in which soil moisture was varied, Bornemissza (1966) noted no significant difference in pupal mortality among treatments. Low temperatures characteristic of high elevations where S. triangularis is found may also affect cinnabar moth survival. Philogene (1975) found that both larval development rate and mortality increase with temperature. Harman et. al. (in

press) observed optimum temperature for survival of cinnabar moths from eggs to pupae to be between 20 C and 25 C.

I compared cinnabar moth colonization in S. triangularis in habitats by comparing levels of feeding damage. Although I did not measure environmental parameters in the different habitats or replicate habitats, I hoped to determine if some S. triangularis sites were more suitable for cinnabar moth colonization than others. I also was interested to see if some sites provided S. triangularis refuges from cinnabar moth attack.

Other biota may hinder cinnabar moth colonization on S. triangularis. Such influence by other organisms on the success of an invading species has been termed biotic resistance (Simberloff, 1986) and may be divided into two models: the niche saturation model and the enemy free space model (Strong et. al., 1984). Under the niche saturation hypothesis, colonization by an herbivorous insect is deterred by the presence of other phytophages which may compete with the insect for resources. To determine possible competitors of the cinnabar moth, I recorded the phytophagous insect species which I found on S. triangularis and the plant parts they exploited. I expected that leaf defoliators would give the cinnabar moth the greatest competition for resources. Under the enemy free space hypothesis, natural enemies, not herbivores

limit establishment of an invading species. For example, Bornemissza (1966) believed that the combination of predation by a scorpion fly (Harpobittacus nigriceps Selys) and viral disease may have been responsible for the failure of the cinnabar moth to become established in Australia; larval mortality caused by these natural enemies was high.

The impact of cinnabar moth feeding on a host plant depends on both the level and distribution of the feeding damage and the plant's life history. The cinnabar moth feeds on both the leaves and the flower heads of S. jacobaea, often completely stripping the plant. The primary effect of the cinnabar moth on S. jacobaea is a reduction in seed number due to a reduction in capitula (McEvoy et. al., in press, Islam and Crawley, 1983). McEvoy et. al. (in press) found a 73% decrease in number of capitula, Cameron (1935) recorded a 65% reduction in seed production, and Bornemissza (1966) recorded a 98% reduction in seed production by tansy ragwort plants after cinnabar moth defoliation.

Ragwort compensates for defoliation by producing secondary capitula and foliage. In Oregon, secondary flower shoots may be produced within two weeks of defoliation (Stimac and Isaacson, 1978), and the dry weight of regrowth increases with the frequency of irrigation (Cox and McEvoy, 1983). Ragwort rosettes which are regrowing after defoliation are more susceptible to frost than

undefoliated rosettes (Harris et. al., 1978).

Due to life history differences in the two species, S. triangularis may be better buffered than is S. jacobaea against a given level and distribution of herbivory. S. jacobaea is usually a biennial that dies after seed production although some plants may also reproduce vegetatively from rootstocks. In contrast, S. triangularis is a perennial which reproduces vegetatively from rhizomes in addition to reproducing from seeds. Prolonged life (perenniality), repeated reproduction (iteroparity) and clonal spread may allow S. triangularis to reduce the impact of an episode of herbivory by averaging losses over time and space.

Feeding damage by the cinnabar moth may not translate into changes in plant population dynamics. Crawley (1983) stated that cinnabar moth feeding did not determine the numbers of S. jacobaea in southern England, where weather conditions affecting seedling establishment appear to be more important in determining plant population dynamics.

To determine the impact of cinnabar moth feeding on S. triangularis, I manipulated the intensity of cinnabar defoliation in the field and measured the resulting effect on plant survivorship, seed production, and seed viability. These parameters are crucial to estimating the cinnabar moth's potential to affect its new host plant's rate of increase.

METHODS

Study Sites

Most of my observations and measurements of cinnabar moth colonization and impact took place at four sites on Marys Peak, a 1,248 m. mountain in the Oregon Coast Range, 24 km. west of Corvallis. Merkle (1951) and Snow (1984) classified the vegetation near the summit area of Marys Peak. On this peak, S. triangularis is most abundant in a meadow community on the north slope. S. triangularis is also found in small openings in the conifer woodlands and along roadsides near the summit.

My four study sites were representative of S. triangularis habitat on Marys Peak:

1. Roadside: This is a 50m. long, 5m. wide strip of grassland (Snow's, 1984, Festuca rubra-Agrostis diegoensis-Carex californica community, disturbed phase) at 1,085 m. bordered by noble fir (Abies procera Rehder) on one side and a road on the other.

2. Forest I: This opening in the noble fir stand at 1,067 m. on an east-facing slope was dominated by forbs including S. triangularis, Scrophularia californica, Pteridium aquilinum, and Smilacina racemosa.

3. Forest II: This plot was adjacent to a small creek on a north-facing slope at 1,112 m. It was also an opening in the noble fir stand and had similar vegetation to Forest I.

4. Meadow: At 1,158 m., this north-facing meadow was the highest of the four sites. S. triangularis and grasses were the most prominent species, and Snow (1984) named it the Senecio triangularis community.

Colonization Studies

I surveyed cinnabar moth damage in September 1986 and August 1987. Most of the feeding damage had already taken place by mid-August, when most of the cinnabar moths had pupated or were in their final instar. At each site I randomly chose 30-50 plants and recorded cinnabar moth damage and the presence of native insects. In 1986, I also placed a 45 cm. x 42 cm. plastic bag over each sampled plant, cut the plant at ground level, and took it back to the laboratory to assess the number of damaged leaves and the presence of native insects within stems and seed heads.

Impact Studies

I regulated the intensity of defoliation by the cinnabar moth on individual stems of S. triangularis at the Forest I site. I tied metal identification tags around the base of the stems to allow location of the genet the following year. Larvae were enclosed on plants using 4 mm.-mesh hardware cloth barriers covered with stickum on the top edge to prevent escape. These cylindrical, open-ended barriers were 50 cm. tall and 30 cm. in diameter. I placed 0, 5, or 10 larvae in each enclosure. Caterpillars

were removed from the cages with 5 larvae after 50% of the leaves had been defoliated and from the cages with 10 larvae after 100% of the leaves had been defoliated. A leaf was considered defoliated if 50% or more of its leaf area had been removed. Each treatment had 20 replicates. Larvae were first placed on the plants 2 August 1986, and by 27 August, all larvae had been removed.

I collected the mature seed heads from the caged plants. For a random subsample of 187 seed heads, I counted the number of seeds and noted whether seeds were intact or damaged by insects. The percent germination was estimated from 276 undamaged seeds that were individually weighed on a Cahn microbalance to the nearest .001 mg and incubated at 20 C and a 12:12 photoperiod on moist filter paper in 11 cm. x 11cm. x 3 cm. plastic boxes. Seeds that did not germinate after one month were pierced with a needle and placed in tetrazolium dye for 48 hours at 20 C. These seeds were then dissected and judged to be viable if they turned red in reaction to the dye (AOSA, 1970).

RESULTS

Colonization Studies: Cinnabar Moth Colonization

Cinnabar moths laid eggs on S. triangularis on Marys Peak, and the larvae defoliated up to 100% of the leaves on some stems. Feeding behavior on S. triangularis differs from that on S. jacobaea. On S. jacobaea, larvae consume flowers and entire leaves. On S. triangularis, larvae did not consume flowers, apparently because most of the seed heads were mature by the time the caterpillars reached the later instars; they did not consume the entire leaf but often left epidermal tissue.

The highest level of attack by cinnabar moths occurred in both years at the roadside population (Table 7). In 1986, 77% of the roadside stems were attacked by larvae; in 1987, 23.3% of the stems had cinnabar moth damage. In 1986, 10% of the stems in Forest I were attacked and 6.7% of the stems in Forest II were colonized, but none of the plants sampled in either of these sites was colonized in 1987. The meadow study site had low levels of cinnabar moths in both years (Table 7). The lower percentage of stems attacked in 1986 compared to 1987 is consistent with the low number of cinnabar moths observed throughout western Oregon that year (personal observation).

Ramets damaged by cinnabar moths were often 100% defoliated. To take an extreme case, 27% of the ramets

Table 7. Colonization of S. triangularis by the cinnabar moth.

STUDY SITE	ELEVATION (m)	PLANT DENSITY ($stems/m^2$) 1986	% STEMS ATTACKED 1986		% STEMS ATTACKED 1987		PLANT MASS (g dry mass/stem)
		$\bar{X} \pm$ S.E.	%	n	%	n	$\bar{X} \pm$ S.E.
Roadside	1,085	6.8 ± 1.7	77	30	23.3	30	1.7 ± 0.2
Forest I	1,067	8.4 ± 1.4	10	29	0	30	2.2 ± 0.2
Forest II	1,112	2.4 ± 0.7	7	31	0	30	1.4 ± 0.2
Meadow	1,158	37.2 ± 4.7	0	50	6	50	2.0 ± 0.2

Figure 6. Damage by cinnabar moth to roadside plants in a) 1986 and b) 1987. Frequency of different levels of leaf damage is only presented for the roadside population because cinnabar moth colonization was so low at the other sites.

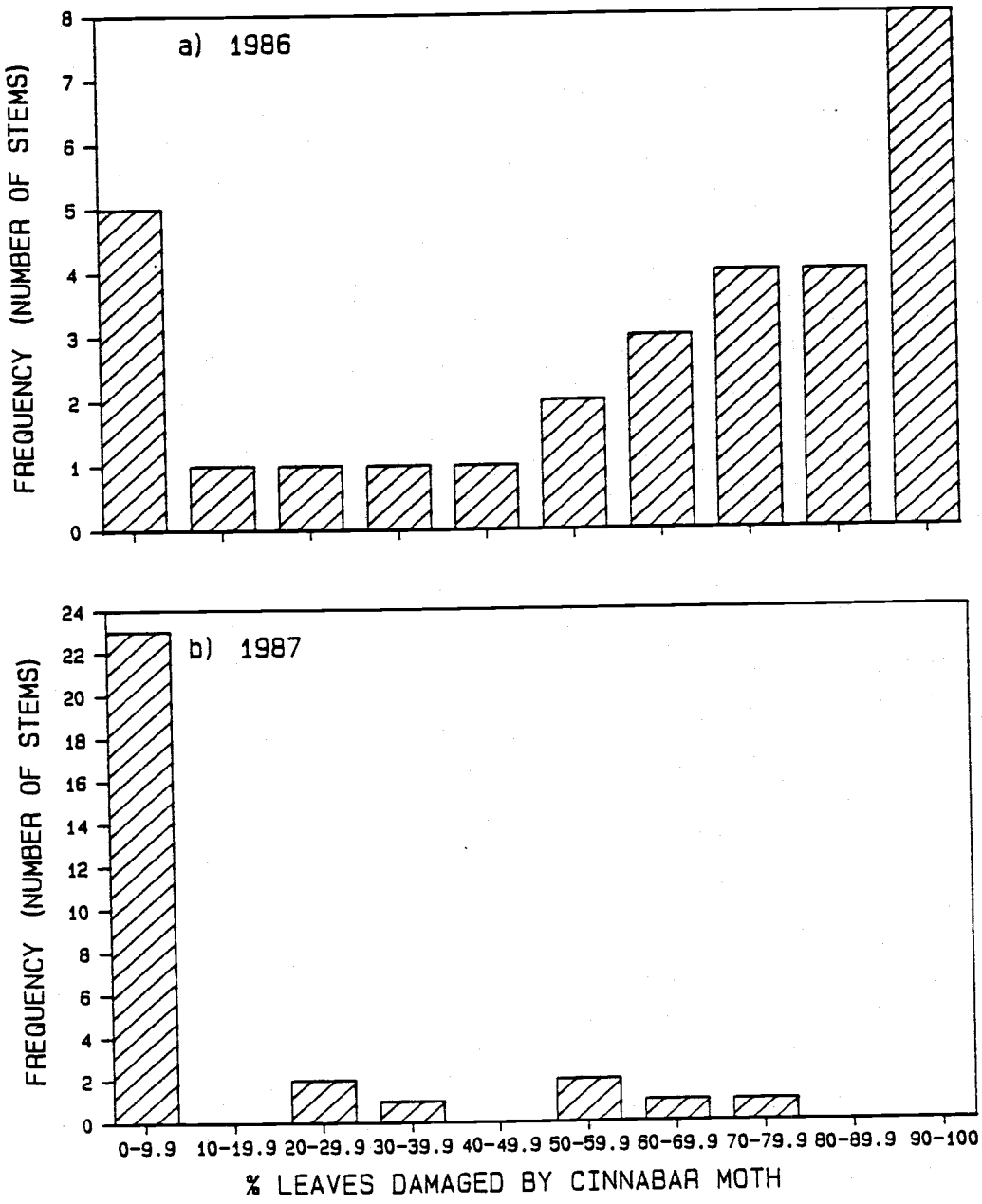

a) 1986
FREQUENCY (NUMBER OF STEMS)
0
1
2
3
4
5
6
7
8
b) 1987
FREQUENCY (NUMBER OF STEMS)
0
2
4
6
8
10
12
14
16
18
20
22
24
0-9.9
10-19.9
20-29.9
30-39.9
40-49.9
50-59.9
60-69.9
70-79.9
80-89.9
90-100
% LEAVES DAMAGED BY CINNABAR MOTH

Figure 6.

were 100% defoliated at the roadside in 1986 (Figure 6a). None of the roadside plants was more than 80% defoliated in 1987 (Figure 6b). The frequency and intensity of damage for the other sites were uniformly low in both years.

Colonization Studies: Native Insect Colonization

I observed 14 insect species other than the cinnabar moth feeding on S. triangularis (Table 8). The list includes the most abundant phytophages on S. triangularis on Marys Peak but could doubtless be extended as I did not sample extensively or sample for root feeders.

Hemiptera

Melanocoryphus bicrucis Say. This lygaeid seed feeder occurs from Brazil to Canada and feeds primarily on members of the tribe Senecioneae (Solbreck and Pehrson, 1979). It has also been recorded from S. jacobaea (Frick 1972). On Marys Peak I saw M. bicrucis most frequently at the meadow site where it was present on 30% of the S. triangularis stems in 1986. I saw both nymphs and adults on these plants.

Lygus convexicollis Reuter and Lygus shulli Knight. Specimens of both of these mirids have been taken previously from Marys Peak by other collectors (O.S.U. Entomology Museum). L. shulli has also been collected on S. jacobaea on Marys Peak (P. McEvoy, personal collection). Both of these insects appear to be feeding on leaf tissue.

Homoptera

Aphis lugentis Williams. This aphid has been collected previously from both S. triangularis (Palmer, 1952; Leonard, 1974) and S. jacobaea (Frick, 1964). On Marys Peak, these aphids were most abundant at the Forest I site where they colonized 73% of the S. triangularis stems in 1987 (Table 9). These aphids feed on the phloem of both the stem and the leaves of their host and are often tended by ants.

Philaenus spumarius L. This spittlebug has a holarctic distribution and feeds on a wide variety of plants (Weaver and King, 1954). Frick (1964) has recorded P. spumarius on S. jacobaea. Nymphs feed on the xylem of their host plant.

Sonronius maculipes Zett. This leafhopper species has a holarctic distribution and has been collected on a variety of host plants (Ossiannilsson, 1983). I saw this species only in the meadow site at Marys Peak where I collected both nymphs and adults. These insects feed on leaves where they tap into the phloem.

Coleoptera

Phyllotrox nubifer Lec. This weevil was abundant at all my study sites on Marys Peak except the Forest II site (Table 9). The adult weevils began feeding on the upper leaves and meristems of the plants in late May and appear to kill many of the meristems. The association between weevil presence and lack of capitula is weak, however,

suggesting that other factors are also responsible for the low percent of stems with capitula (Table 9). Larvae feed on seeds.

Lepidoptera

I observed three caterpillar species other than T. jacobaeae on S. triangularis but I did not rear any of them through to adults. All three species fed on leaves.

Diptera

Paroxyna snowi Hering. This tephritid seed fly was present in all four study sites (Table 9). The larvae often consume all of the seeds in a head. P. snowi is distributed from Washington to California and is recorded only from S. triangularis (Novak, 1974).

Cylindrotoma sp. I collected larvae of this crane fly species in late April and early May in 1985. I did not rear the larvae through to adults. The larvae feed on the leaves of S. triangularis.

Unknown leaf miner. This leaf miner was particularly abundant in the forest II site where it colonized 70% of the stems in 1986 and 20% of the stems in 1987. I did not succeed in rearing the larvae through to adults because the leaves dried up before the larvae pupated and the larvae would not switch leaves. Perhaps some substrate such as sand should be included in rearing containers for the larvae to pupate in.

Unknown stem borer. I found larvae of this species in

Table 8. Native insects observed feeding on S. triangularis. Voucher specimens when available are housed in the Oregon State University Systematic Entomology Laboratory.

HEMIPTERA

Lygaeidae
Melanocoryphus bicrucis Say[1]

Miridae
Lygus convexicollis Reuter[1]
Lygus shulli Knight[1]

HOMOPTERA

Aphididae
Aphis lugentis Williams[3]

Cercopidae
Philaenus spumarius L.[2]

Cicadellidae
Sonronius maculipes Zett.[1]

COLEOPTERA

Curculionidae
Phyllotrox nubifer Lec.[1]

LEPIDOPTERA

Noctuidae
Unknown species[3]

Pterophoridae
Unknown species[2]

Tortricidae
Unknown species[2]

Table 8. continued.

DIPTERA

Tephritidae
Paroxyna snowi Hering[1]

Tipulidae
Cylindrotoma sp.[2]

Unknown leaf miner[3]

Unknown stem borer[2]

[1] Voucher specimen(s) of adult insect

[2] Voucher specimen(s) of nymph or larva only

[3] No voucher specimen

Table 9. Colonization of S. triangularis by herbivores other than the cinnabar moth: colonization by Phyllotrox nubifer, Paroxyna snowi, Aphis lugentis, and the percent of stems with meristems damaged before capitula could be produced.

		Phyllotrox nubifer (% stems)	Paroxyna snowi (% stems)	Aphis lugentis (% stems)	No Capitula Produced (% stems)
Road	1986	17	10	3	47
	1987	10	20	0	60
Forest I	1986	27	3	-	43
	1987	-	10	73	80
Forest II	1986	0	17	0	73
	1987	0	40	0	60
Meadow	1986	36	10	7	33
	1987	-	-	0	22

all four study sites in 1986. These maggots tunnel into the stem of the plant. In 1986, 3.3% of the stems at the roadside, 30% of the stems at forest I, and 27% of the stems at forest II were colonized by this species.

Impact Studies

Cinnabar moth feeding on S triangularis ramets did not increase mortality of genets in the short term. In 1987, 27 of 60 ramets tagged in 1986 were recovered; all ramets were dead and attached to live genets. The recovered ramets were distributed equally among the three defoliation treatments.

Cinnabar moth herbivory also did not affect seed production. No new capitula were produced after the initiation of the experiment, and the total number of seeds/stem did not differ significantly among treatments (Figure 7).

Although the number of seeds produced by S. triangularis was not affected by defoliation, cinnabar moth feeding did influence the fate of the seeds produced. Caterpillar feeding caused the seed heads to fall off the plant. I do not know whether any of the seeds in these fallen capitula remained viable. As defoliation increased from 0% to 100%, the number of capitula falling off the plant increased from 6% to 50%, seed damage by native insects decreased from 70% to 33%, and viable seeds declined from 4% to .4% of total seed production (Figure

7). The percentage of nondropped seed heads attacked by the seed fly P. snowi decreased from 38% to 28% when defoliation increased from 0% to 100% (Chi-square, $Chi^2=6.2$, d.f.=2, p=.05). Furthermore, the ratio of viable seeds to nonviable seeds (seeds which were not damaged or dropped from the plant but were inviable) declined from 18% in the no cinnabar moth defoliation treatment to 2% in the 100% defoliation treatment (Figure 7). All seeds weighing greater than 0.8 mg. were viable, while all seeds weighing less than 0.6mg. were nonviable and, perhaps, undeveloped.

Figure 7. Fate of S. triangularis seeds in relation to cinnabar moth defoliation. Histograms are mean values; error bars represent the standard error of the mean number of seeds/stem. The mean number of seeds/stem did not differ significantly among treatments ($F_{2,56}$=1.08, p=.3). The mean number of seeds that fell from the pedicel increased (ANOVA, $F_{2,56}$=12.4, p=.0001), the mean number of seeds damaged by native insects decreased (ANOVA, $F_{2,56}$=7.4, p=.001), and the mean number of viable seeds (Kruskal-Wallis test, Chi^2=27.1, p=.0001) decreased significantly with increased cinnabar moth defoliation. The ratio of viable to nonviable seeds also decreased significantly (chi-square, Chi^2=13.5, p=.001) with increased defoliation. The mean number of viable seeds in the 100% defoliation treatment (.9) was too small to graph.

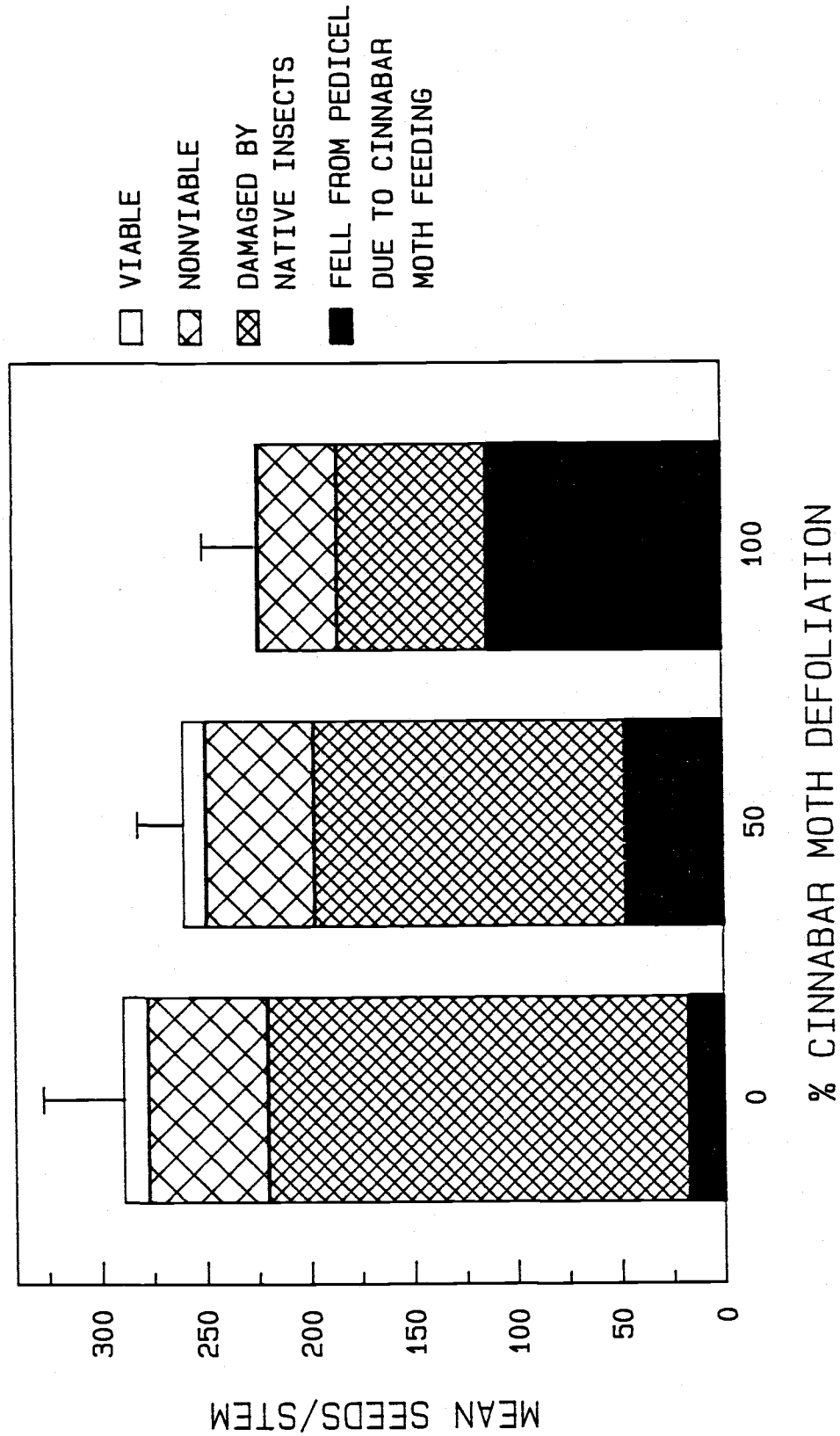

VIABLE
NONVIABLE
DAMAGED BY NATIVE INSECTS
FELL FROM PEDICEL DUE TO CINNABAR MOTH FEEDING
MEAN SEEDS/STEM
300
250
200
150
100
50
0
0
50
100
% CINNABAR MOTH DEFOLIATION

Figure 7.

DISCUSSION

The cinnabar moth readily colonized S. triangularis plants on Marys Peak and reduced the number of viable seeds when 100% of the leaves were defoliated. Colonization was concentrated at the roadside site, damage by the cinnabar moth and other insects were inversely related, and differences in S. triangularis and S. jacobaea life histories may indicate that S. triangularis is better buffered against cinnabar moth damage.

There was no consistent pattern of association between level of attack and variations in habitat characteristics such as altitude, shading, host plant density, average plant size or the presence of potential competitors. Attack varied greatly between sites of similar altitude (roadside and Forest I) (Table 7). Both shaded (Forest I and Forest II) and open sites (meadow) had low percentages of attack (Table 7). Attack did not vary consistently with plant density; the densest S. triangularis population (meadow) was not attacked at all in 1986 (Table 7). Average plant size in the roadside site was intermediate between sizes in the other habitats (Table 7). Phytophagous insects appeared to be as abundant in the roadside site as in the other sites (Table 9).

Adult searching behavior may explain the high level of colonization at the roadside. The forest may present a

barrier to flight resulting in a concentration of moths on the adjacent roadside. Alternatively, as S. jacobaea is most prevalent at Marys Peak along the roadside, it may be that search is restricted to habitats where the traditional host species exists.

Once cinnabar moths colonized a S. triangularis plant, their feeding pattern differed from that typical on S. jacobaea. The larvae did not feed on the seed heads which were mostly in later stages of development. Cinnabar moths do not feed on mature ragwort capitula either (Henneberger, 1986), and it appears that they prefer capitula in which the seeds are not well developed. The stage at which capitula become invulnerable to cinnabar moth consumption has not been studied. An experiment offering S. triangularis capitula to cinnabar moth larvae would clarify whether young capitula are unsuitable food or simply unavailable.

Cinnabar moths influenced the viability rather than the number of seeds produced because feeding on S. triangularis began relatively late in its growing season. Seed loss in the 100% defoliation treatment was caused mostly by capitula falling from their pedicels due to cinnabar moth feeding (Figure 7). I did not test the viability of these seeds, but the percentage of viability was probably less than for those seeds that remained on the plant. The ratio of viable to nonviable seeds declined

with increased defoliation, suggesting that seeds continued to develop after caterpillar feeding began. Capitula fell from the plant shortly after the commencement of feeding, and the seeds may not have had time to complete their development.

The increasing number of seeds that fell off the plant in response to cinnabar moth defoliation was largely offset by a decrease in damage by native insects (Figure 7). In the absence of larvae, 74% of the seeds remaining on the plant were damaged compared to 64% with high cinnabar moth defoliation (Figure 7). It is not clear why native herbivore damage should decline as cinnabar moth damage increased. Cinnabar moths may have interfered directly with the other insects or indirectly by influencing seed development. The decrease in seed fly damage was probably not due to direct interference. Caterpillars did not have the opportunity to interfere with oviposition by adult flies since I initiated the experiments after oviposition had occurred. Cinnabar moth defoliation may have reduced the quality of the seed maggot's food by reducing carbohydrate allocated to seeds, resulting in a decrease in fly survival.

The importance of the added reduction in seed viability caused by the cinnabar moth is difficult to interpret due to the already low seed viability caused by native insect feeding. The percent of viable seeds dropped

only 3.9%, but this represents 91% of the viable seeds. Further research on the importance of reproduction by seed in sustaining S. triangularis populations and maintaining genetic diversity are needed to assess the significance of the reduction in viable seeds caused by cinnabar moth defoliation.

The perennial habit of S. triangularis may buffer plants from the effect of cinnabar moth damage. This perenniality contrasts with the biennial habit of S. jacobaea. Tansy ragwort compensates for cinnabar moth defoliation by producing regrowth the same season, and plants may fail to produce new growth if moisture is low (Cox and McEvoy, 1983) or if there is a killing frost (Harris et. al., 1978). If a S triangularis ramet is defoliated, it does not produce regrowth, but the genet may survive to grow and produce seeds the next year. Because of the temporal variation in cinnabar moth colonization (Table 7), it is likely that a plant that is defoliated one year will escape defoliation the next.

FURTHER RESEARCH

From my study I have found that cinnabar moths colonize S. triangularis plants on Marys Peak, the frequency and intensity of attack vary among sites, and cinnabar moth defoliation reduces the seed viability. Many questions remain concerning cinnabar moth colonization and impact on S. triangularis, and I have listed further research needs below.

1. Long term studies are needed to elucidate the effects of feeding by caterpillars on the growth and survival of S. triangularis genets.
2. Long term observations are needed to determine how cinnabar moth colonization on S. triangularis fluctuates with time.
3. The fate of seeds in capitula which fall from plants due to cinnabar moth feeding needs to be determined.
4. The filling of seed over time in attacked versus nonattacked plants should be compared to determine if the cinnabar moth is reducing seed viability by reducing seed fill.
5. The interaction between the cinnabar moth and the other herbivores needs further study. In particular, it would be interesting to know why the number of damaged seeds decreases with increased cinnabar moth damage.
6. Further study is also needed to determine the stage at

which both S. triangularis capitula and S. jacobaea capitula become invulnerable to cinnabar moth attack.

REFERENCES

Andres, L.A. 1985. Interaction of Chrysolina quadrigemina and Hypericum spp. in California. Proc. VI Int. Symp. Biol. Contr. Weeds, 19-25 August 1984, Vancouver, Canada. Delfosse, E.S. (ed.). Agric. Can., pp. 235-39.

Andres, L.A. and G.W. Angalet 1963. Notes on the ecology and host specificity of Microlarinus lareynii and M. lypriformis (Coleoptera: Curculionidae) and the biological control of puncture vine, Tribulus terrestris. J. Econ. Entomol. 56: 333-340.

Andres, L.A., R.B. Hawkes, and A. Rizza 1967. Apion seed weevil introduced for biological control of Scotch broom. Calif. Agric. 21: 13.

Aplin, R.T. and M. Rothschild 1972. Poisonous alkaloids in the tissues of the garden moth (Arctia caja L.) and the cinnabar moth (Tyria (=Callimorpha) jacobaeae L.) (Lepidoptera). In Toxins of Animal and Plant Origin A. de Vries and K. Kochva eds. Gordon and Breach, London. pp. 579-595.

Association of Official Seed Analysts (AOSA). 1970. Tetrazolium Testing Handbook for Agricultural Seeds: Contribution No. 29 to the handbook on Seed Testing. D. F. Grabe (ed.). AOSA.

Berenbaum, M. and S. Passoa 1983. Notes on the biology of Agonopterix alstroemeriana (Clerck), with descriptions of the immature stages (Oecophoridae) J. Lepid. Soc. 37(1): 38-45.

Bornemissza, G.F. 1966. An attempt to control ragwort in Australia with the cinnabar moth Callimorpha jacobaeae (L.) (Arctiidae: Lepidoptera). Aust. J. Zool. 14: 201-243.

Bucher, G.E. and P. Harris 1961. Food plant spectrum and elimination of disease of cinnabar moth larvae, Hypocrita jacobaeae (L.) (Lepidoptera: Arctiidae). Can. Entomol. 93: 931-936.

Cameron, E. 1935. A study of the natural control of ragwort (Senecio jacobaea L.). J. Ecol. 23: 266-322.

Caresche, L.A. and A.J. Wapshere 1974. Biology and host specificity of the Chondrilla gall mite Aceria chondrillae (G. can.) [Acarina, Eriophyidae]. Bull. Entomol. Res. 64: 183-192.

Caresche, L.A. and A.J. Wapshere 1975. The Chondrilla gall

midge, Cystiphora schmidti (Rubsaamen) [Diptera, Cecidomyidae]. Biology and host specificity . Bull. Entomol. Res. 65: 55-64.

Cox, C.S. and P.B. McEvoy, 1983. Effect of summer moisture stress on the capacity of tansy ragwort (Senecio jacobaea) to compensate for defoliation by cinnabar moth (Tyria jacobaeae). J. Appl. Ecol. 20: 225-234.

Crawley, M.J. 1983. Herbivory. The Dynamics of Animal-Plant Interactions. University of California Press. Berkeley and Los Angeles.

Dempster, J.P. 1971. The population ecology of the cinnabar moth, Tyria jacobaeae L. (Lepidoptera: Arctiidae). Oecologia (Berl.) 7: 26-67.

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

Dempster, J.P. and K.H. Lakhani 1979. A population model for cinnabar moth and its food plant, ragwort. J. Anim. Ecol. 48: 143-163.

Frick, K.E. 1964. Some endemic insects that feed upon tansy ragwort (Senecio jacobaea) in western United States. Ann. Entomol. Soc. Am. 57:707-710.

Frick, K.E. 1970. Longitarsus jacobaeae (Coleoptera: Chrysomelidae), a flea beetle for the biological control of tansy ragwort, I. Host plant specificity studies. Ann. Entomol. Soc. Am. 63: 284-296.

Frick, K.E. 1972. Third list of insects that feed upon tansy ragwort, Senecio jacobaea in the western United States. Ann. Entomol. Soc. Am. 65: 629-631.

Frick, K.E. and L.A. Andres 1967. Host specificity of the ragwort seed fly. J. Econ. Entomol. 60(2): 457-463.

Frick, K.E. and J.K. Holloway 1964. Establishment of the cinnabar moth, Tyria jacobaeae L. on tansy ragwort in the western United States. J. Econ. Entomol. 57: 152-154.

Harman, H.M., J.J. Dymock and P. Syrett. In Press. Temperature and development of cinnabar moth, Tyria jacobaeae (L.) (Lepidoptera: Arctiidae), in New Zealand. Proc. VII Int. Symp. Biol. Contr. Weeds, 6-11 March 1988, Rome Italy. Delfosse, E.S. (ed.).

Harris, P. 1963. Host specificity of Calophasia lunula

(Hufn.) (Lepidoptera: Noctuidae). Can. Entomol. 95: 101-105.

Harris, P., L.S. Thompson, A.T.S. Wilkinson, and M.E. Neary 1978. Reproductive biology of tansy ragwort, climate and biological control by the cinnabar moth in Canada. Proc. IV Int. Symp. Biol. Contr. Weeds, 30 August-2 September 1976, Gainesville, Florida. Freeman, T.E. (ed.). Univ. Florida, pp. 163-173.

Harris, P. and H. Zwolfer 1968. Screening of phytophagous insects for biological control of weeds. Can. Entomol. 100: 295-303.

Hasan, S. 1972. Specificity and host specialization of Puccinia chondrillina. Ann. Appl. Biol. 72: 257-263.

Hawkes, R.B. 1973. Natural mortality of cinnabar moth in California. Ann. Entomol. Soc. Am. 66: 137-146.

Hawkes, R.B. and A. Mayfield 1978. Coleophora klimeschiella, biological control agent for Russian thistle, host specificity testing. Environ. Entomol. 7: 257-261.

Henneberger, D. 1986. Adequacy of hand-defoliation of tansy ragwort (Senecio jacobaea L.) as a simulation of defoliation by Cinnabar Moth (Tyria jacobaeae (L.)). M.S. Thesis, Oregon State University.

Hitchcock, C.L., and A. Cronquist 1973. Flora of the Pacific Northwest. Univ. of Wash. Press. Seattle.

Hitchcock, C.L., A. Cronquist, M. Ownbey, and J.W. Thompson 1955. Vascular Plants of the Pacific Northwest. Part 5: Compositae. Univ. of Wash. Press, Seattle.

Holloway, J.K. and C.B. Huffaker 1957. Establishment of the seed weevil, Apion ulicis Forst., for suppression of gorse in California. J. Econ. Entomol. 50: 498-499.

Isaacson, D.L. 1973. Population dynamics of the cinnabar moth, Tyria jacobaeae L. (Lepidoptera: Arctiidae). M.S. Thesis, Oregon State University.

Islam, Z. and M.J. Crawley 1983. Compensation and regrowth in ragwort (Senecio jacobaea) attacked by cinnabar moth (Tyria jacobaeae). J. Ecol. 71: 829-843.

Leonard, 1974. A list of the aphids of Oregon (Homoptera: Aphididae). Agicultural Research Service. U.S.D.A.

McEvoy, P.B. 1984. Increase in respiratory rate during feeding in larvae of the cinnabar moth Tyria jacobaeae. Physiol. Entomol. 9: 191-195.

McEvoy, P.B, C.S. Cox, R.R. James, and N.T. Rudd (in Press) Ecological mechanisms underlying successful biological weed control: field experiments with ragwort Senecio jacobaea. Proc. VII Int. Symp. Biol. Contr. Weeds, 6-11 March 1988, Rome Italy. Delfosse, E.S. (ed.).

Meijden, E. van der 1976. Changes in the distribution pattern of Tyria jacobaeae during the larval period. Neth. J. of Zool. 26: 136-161.

Merkle, J. 1951. An analysis of the plant communities of Marys Peak, western Oregon. Ecology 32: 618-640.

Muller, H., D. Schroeder and A. Gassmann 1988. Agapeta zoegana (L.) (Lepidoptera: Cochylidae), a suitable prospect for biological control of spotted and diffuse knapweed, Centaurea maculosa Monnet de la March and Centaurea diffusa Monnet de la March (Compositae) in North America. Can. Entomol. 120 (2): 109-124.

Novak, J. A. 1974. A taxonomic revision of Dioxyna and Paroxyna (Diptera: Tephritidae) for America north of Mexico. Melanderia 16: 1-53.

Ossiannilsson, F. 1983. The Auchenorrhyncha (Homoptera) of Fennoscandia and Denmark. Part 3: The Family Cicadellidae: Deltocephalinae, Catalogue, Literature and Index. Scandinavian Science Press Ltd. Copenhagen.

Pajutee, M.S. 1980. Food utilization by cinnabar moth larvae, Tyria jacobaeae L. (Lepidoptera: Arctiidae) in relation to feeding site on the host plant, Senecio jacobaea L., (Compositae). M.S. Thesis, Oregon State University.

Palmer, M.A. 1952. Aphids of the Rocky Mountain Region. Thomas Say Foundation. Vol. 5. A.B. Hirschfeld Press. Denver.

Parker, H.L. 1960. Starvation tests with larvae of the cinnabar moth. J. Econ. Entomol. 53: 472-473.

Parker, H.L. 1964. Life history of Leucoptera spartifoliella with results of host transfer tests conducted in France. J. Econ. Entomol. 57: 566-569.

Peschken, D.P. and P. Harris 1975. Host specificity and biology of Urophora cardui (Diptera: tephritidae) a

biocontrol agent for Canada thistle (Cirsium arvense). Can. Entomol. 107: 1101-1110.

Philogene, B.J.R. 1975. Responses of the cinnabar moth Hypocrita jacobaeae to various temperature/photoperiod regimes. J. Insect Physiol. 21: 1415-1417.

Reese, N.E. 1977. Impact of Rhinocyllus conicus on thistles in southwest Montana. Environ. Entomol. 6(6): 839-842.

Roitman, J.N. 1983. The pyrrolizidine alkaloids of S. triangularis. Aust. J. Chem. 36: 1203-1213.

Rose, S.D. 1978. Effect of diet on larval development, adult emergence and fecundity of the cinnabar moth, Tyria jacobaeae (L.) (Lepidoptera: Arctiidae). M.S. Thesis, Oregon State University Corvallis.

Schroeder, D. 1980. Investigations on Oberea erythrocephala (Schrank) (Col: Cerambicidae) a possible biocontrol agent of leafy spurge, Euphorbia spp. (Euphorbiaceae) in Canada. Z. Angew. Entomol. 90: 237-254.

Scriber, J.M. 1977. Limiting effects of low leaf-water content on the nitrogen utilization, energy budget, and larval growth of Hylaphora ceropia (Lepidoptera: Saturniidae). Oecologia (Berl.) 28: 269-287.

Scriber, J.M. and F. Slansky, Jr. 1981. The nutritional ecology of immature insects. Annu. Rev. Entomol. 26: 183-211.

Simberloff, D. 1986. Introduced insects: a biogeographic and systematic perspective. In Ecology of Biological Invasions of N. America and Hawaii. ed. H.A. Mooney and J.A. Drake. Springer Verlag. pp. 3-26.

Slansky, F. Jr. and P. Feeny. 1977. Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. Ecol. Monogr. 47: 209-228.

Slansky, F. Jr. and J.M. Scriber. 1985. Food consumption and utilization. Inf G.A. Kerkut and L.I. Gilbert, eds. Comprehensive Insect Physiology, Biochemistry and Pharmacology, Vol. 4. Pergamon, Oxford. pp. 87-163.

Smith, J.M., 1958. Biological control of Klamath weed, Hypericum perforatum L., in British Columbia. Proc. 10th Int. Congr. Entomol. 4: 561-565.

Smith, M.J. 1959. Notes on insects, especially Gymnaetron spp. (Coleoptera: Curculionidae) associated with toadflax, Linaria vulgaris Mill. (Scrophulariaceae), in North America. Can. Entomol. 91: 116-121.

Snow, B.D. 1984. Plant communities of the grassy balds of Marys Peak, Oregon. M.S. thesis, Oregon State University, Corvallis.

Solbreck, C. and I. Pehrson, 1979. Relations between environment, migration, and reproduction in a seed bug, Neacoryphus bicrucis (Say) (Heteroptera: Lygaeidae). Oecologia (Berl.) 43: 51-62.

Sokal, R.R. and F. James Rohlf. 1981. Biometry. Second Edition. W. H. Freeman and Company. San Francisco.

Stimac, J.L. 1978. A model of a plant-herbivore system. PhD. thesis, Oregon State University Corvallis.

Stimac, J.L. and D.L. Isaacson 1978. Cinnabar moth as a biological control of tansy ragwort: comparison of population dynamics in England and Oregon. Proc. IV Int. Symp. Biol. Contr. Weeds, 30 August-2 September 1976, Gainesville, Florida. Freeman, T.E. (ed.). Univ. Florida, pp. 155-158.

Strong, D.R., J.H. Lawton, and T.R.E. Southwood. 1984. Insects on Plants Community Patterns and Mechanisms. Harvard. Boston.

Tabashnik, B.E. and F. Slansky Jr. 1987. Nutritional ecology of forb-chewing insects. In F. Slansky Jr. and J. G. Rodriguez eds. Nutritional Ecology of Insects, Mites, Spiders and Related Invertebrates. Wiley and Sons. New York.

Tanton, M.T. 1963. The effect of leaf "toughness" on the feeding of the mustard beetle Phaedon cochleariae Fab. Entomol. Exp. Appl. 5: 74-78.

Taylor, M.F.J. 1984. The dependence of development and fecundity of Samea multiplicalis on early larval nitrogen intake. J. Insect Physiol. 30 (10): 779-785.

Turner, C.E. 1985. Conflicting interests and biological control of weeds. Proc. VI Int. Symp. Biol. Contr. Weeds, 19-25 August 1984, Vancouver, Canada. Delfosse, E.S. (ed.). Agric. Can., pp. 203-226.

Turner, C.E., R.W. Pemberton, and S.S. Rosenthal. 1987. Host utilization of native Cirsium thistles (Asteraceae)

by the introduced weevil Rhinocyllus conicus (Coleoptera: Curculionidae) in California. Environ. Entomol. 16 (1): 111-115.

Waldbauer, G.P. 1964. The consumption, digestion and utilization of solanaceous plants by larvae of the tobacco hornworm, Protoparce sexta (Johan.) (Lepidoptera: Sphingidae). Entomol. Exp. Appl. 7: 253-269.

Waldbauer, G.P. 1968. The consumption and utilization of food by insects. Adv. Insect Physiol. 5: 229-288.

Wapshere, A.J. 1974. A strategy for evaluating the safety of organisms for biological weed control. J. Appl. Biol. 77: 201-211.

Watson, A.K. 1986. Host range of and plant reaction to Subanguina picridis. J. Nemat. 18(1): 112-120.

Weaver, C.R., and D.R. King. 1954. Meadow spittlebug. Ohio Agr. Exp. Sta. Res. Bull. 741.

Wilson, F. 1943. The entomological control of St. John's Wort (Hypericum perforatum) with particular reference to the insect enemies of the weed in Southern France. Austr. Council Sci. and Indus. Res. Bull. 169.

Zwolfer, H. 1970. Investigations on the host-specificity of Urophora affinis Frfld. (Dipt., Trypetidae). Weed Projects for Canada. Progress Report no. 25.

Zwolfer, H. 1972. Urophora siruna-seva (HO.) (Dipt.: Trypetidae), a potential insect for the biological control of Centaurea solstitialis in California. Commonwealth Institute of Biological Control Technical Bull. 12: 105-155.

Zwolfer, H. 1976. Investigations on Sphenoptera (Chilostethal) jugoslavica Obens. (Col., Buprestidae), a possible biocontrol agent of the weed Centaurea diffusa Lam. (Compositae) in Canada. Z. Angew. Entomol. 80: 170-190.

Zwolfer, H. and P. Harris, 1966. Ceutorhynchus litura (F.) (Col.:Curculionidae), a potential insect for the biological control of thistle, Cirsium arvense (L.) Scop., in Canada. Can. J. Zool. 44: 23-38.

Zwolfer, H. and P. Harris, 1984. Biology and host specificity of Rhinocyllus conicus (Froel.) (Col., Curculionidae), a successful agent for biocontrol of the thistle, Carduus nutans L. Z. Angew. Entomol. 97: 36-62.