AN ABSTRACT OF THE THESIS OF

Maret Silvia Pajutee for the degree of Master of Science

in Entomology presented in June 1980

Title: Food Utilization by Cinnabar Moth Larvae, Tyria jacobaeae L. (Lepidoptera: Arctiidae) in Relation to Feeding Site on the Host Plant, Senecio jacobea L., (Compositae)

Redacted for Privacy

Abstract approved:

The temporal and spatial distribution of larvae of the cinnabar moth (Tyria jacobaeae L.) correlates with changes in host plant quality. An observed change in diet preference occurs in the 2nd instar from low leaves to upper parts of generative plants. Timing of larval attack and foraging pattern was found to coincide with peak dry matter and nitrogen availability. There is a vertical gradient of increasing nitrogen in generative and vegetative plants.

A study of nutritional performance on diets of various plant parts revealed efficiencies of biomass conversion; rates of nitrogen consumption, accumulation and utilization efficiency can vary on diets of different plant parts as much as on diets of different plants.

Basal leaves of generative plants, which are avoided in the normative feeding pattern, did not support growth past the 4th instar. Gross growth efficiency was higher on high leaves containing more

nitrogen than on low leaves. Consumption rate varied resulting in a stable rate of nitrogen accumulation. Larvae-fed floral parts have lowered gross growth efficiency, due to an added metabolic or respiratory cost in eating flowers. However, they accumulated more nitrogen, due to increased consumption and efficiency of nitrogen utilization. This higher rate of nitrogen accumulation may be correlated with the higher fecundities observed in larvae fed on floral parts. Thus, the selection of floral parts as food could result in increased fitness of adults by increasing the component of fecundity.

Food Utilization by Cinnabar Moth Larvae, *Tyria jacobaeae* L. (Lepidoptera: Arctiidae) in Relation to Feeding Site on the Host Plant, *Senecio jacobea* L., (Compositae)

by

Maret Silvia Pajutee

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed June 1980

Commencement June 1981

APPROVED:

Redacted for Privacy

Professor of Entomology
in charge of major

Redacted for Privacy

Chairman of Department of Entomology

Redacted for Privacy

Dean of Graduate School

Date thesis is presented June 17, 1980

Typed by Donna Lee Norvell-Race for Maret Silvia Pajutee

p. "v" not used.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Food Utilization by Cinnabar Moth Larvae, Tyria jacobaeae L. (Lepidoptera: Arctiidae) in Relation to Feeding Site on the Host Plant, Senecio jacobea L., (Compositae)

I. INTRODUCTION

Through coevolution, biochemical systems of plants and phytophagous insects have become ecologically linked and to some degree mutually regulating. Much attention has been focused on the role of secondary plant compounds, which are thought to defend the plant from its enemies. It should be pointed out, however, that an adapted herbivore may not be inhibited by increases in the dose of these compounds (Blau et al. 1978). Mechanisms such as a high rate of detoxification and/or elimination, idiosyncratic resistance or lack of a susceptible target site can result in the physiological ineffectiveness of a phytochemical (Duffey 1980). Qualitative and quantitative changes in nutrients within the host plant may be of greater relevance to an obligate specialist. Southwood (1973) remarked on the implications of this in the study of insect foraging and performance:

> The different parts of the plant and of the same plant under different conditions and at different seasons all vary as to their biochemical composition. . . . It seems reasonable, therefore, to regard the many changes in insect feeding preference, developmental rate, fecundity and indeed, survival associated with changes in the growing condition of the host plant as evidence that, at many times, diet is far from optimal.

The larvae of the cinnabar moth, a specialized herbivore of the toxic weed, Tansy Ragwort, preferentially feed on floral parts of

generative (reproductive) plants (Bornemissza 1966, Van der Meijden 1976). Larvae fed on a diet including floral parts produce larger pupae, and adults which are more fecund than adults of larvae fed on leaf diets (Van der Meijden 1976, Rose 1978). My study examined the performance of larvae fed on different plant parts, in an attempt to find physiological mechanisms which may correlate to the observed effects of diet on fecundity. Because fecundity is a major component of insect fitness it is interesting to hypothesize that diet selection maximizes the absolute rate of population growth by increasing fecundity. I measured the variation in components of host plant food quality to determine the sensitivy of the insects' foraging pattern and performance to existing gradients among plant parts. In the following sections I will present an overview of the Cinnabar-Ragwort relationship and considerations in studying feeding strategies and nutritional physiology.

The Plant-Insect Relationship

Tansy ragwort (Senecio jacobaea L.) is an herb of European origin, first found in Western North America in 1913 (Harris et al. 1971). It is considered a problem weed because it invades marginal pastures, logged areas and roadsides, excluding desirable forage plants. Members of the genus Senecio contain pyrrolizidine alkaloids which cause cumulative, non-reversible liver damage in certain livestock. The plant is in the family Asteraceae (Compositae) and is basically a biennial in growth form, often becoming a perennial following

defoliation (Green 1974). Seeds germinate in Fall and Spring, the Fall germinating plants overwintering as small low-lying rosettes. The rosette grows in size during its first summer, producing more leaves. In the late Spring of the next season, the rosette usually produces a stem, with axillary stems near the top, which develops bright yellow flowers in June and July. Leaves on the second-year plant are ovate and dissected with long petioles, becoming more sessile and dissected near the top of the plant.

The cinnabar moth (Tyria jacobaeae L., Family Arctiidae) was introduced to Oregon from Europe in 1960 as a biological control agent for Tansy Ragwort. The adult is aposematically colored in a red and black pattern and is diurnal and non-feeding. The adult does drink water in the confines of a petri dish (Rose 1978). The larvae are specialists feeding on plants in the genus Senecio and related genera. The larvae selectively sequester dietary pyrrolizidine alkaloids (Aplin et al. 1968). Jacobine, jacozine, and jacoline are the dominant alkaloids found in the plant, making up 40-60% of the total alkaloid concentration, however they compose only 10-15% of the total alkaloid found in the insect (Aplin and Rothschild 1972). Seneciphylline, senecionine, and integerrimine, while not dominant in the plant compose 60-70% of the alkaloids found in the insect. Seneciphylline, which is present mostly as a water soluble N-oxide, is the major alkaloid stored by the insect. Tyria is rejected by many birds, mammals, reptiles, and amphibians, although chipmunks (Eutamias sp.) are known to consume adult body parts, leaving wings (Isaacson 1972). Avian

predators have been observed to feed selectively on cardenolide containing Monarch butterflies, eating thoracic muscles and abdominal contents, thus avoiding the exoskeleton where cardenolides are concentrated (Calvert et al. 1979). Schmidl (1972) discusses several other predators of the cinnabar moth affecting its successful colonization in Australia, particularly the mecopteran Harpobitticus nigriceps. Groups of larvae in recently logged areas are subject to heavy predation by carpenter ants; the more successful escape of solitary larvae may exert a selective pressure for larval dispersal (Myers and Campbell 1976). Repellent qualities reside in the skin of the larva and the hemolymph of the adult and pupa (Windecker 1939), although it is not clear how the pyrrolizidine alkaloids function in Tyrias distastefulness. Aplin and Rothschild (1972) believe they do play a role in the moth's defense mechanism, citing as evidence their analysis of four arctiid moths feeding on Senecio vulgaris: the two aposematic species stored alkaloids, while the two cryptic species did not. Arctiid moths in the genus Utetheisa--specialists on members of the Borage family, which contain pyrrolizidine alkaloids (PA's), secrete pyrrolizidine-derived pheromones (Culvenor and Edgar 1972). This has not been examined in Tyria. Volatile "esterifying acids" dissociated from the PA ring nucleus act as attractants and phagostimulants to adult moths in the Arctiidae and the closely related Ctenuchidae (Pliske 1975). Goss (1979) discounts the hypothesis that this feeding on dried and withered PA containing plants provides sex pheromone precursors as is the case in danaine and ithomiine butterflies, because

normal mating occurs in the absence of a PA source. However, females mated with males which had fed on the plants produced significantly greater numbers of eggs. Goss suggests the alkaloids may serve a nutritive function as a nitrogen source, the male contributing to egg production by transfer of a nitrogen-rich spermatophore. Radioactive tracer studies have shown male-contributed nutrients are used by females of three butterfly species for egg production and possibly for somatic maintenance (Boggs and Gilbert 1979). A possible nutritive role for PAs in Tyria has not been investigated, however the proportion of nitrogen contributed by alkaloids in leaves and flowers is relatively small, making up only 0.01 - 0.02% of the total nitrogen present.

The Foraging Pattern of Larvae

Adult Tyria emerge from early May to July, mating soon after emergence, and oviposition occurs within a day or two of mating. Eggs are laid in batches, approximately one batch per day for a period of 7 - 14 days (Rose 1978). Eggs hatch in about 10 - 13 days and the larval stage lasts about one month, the first four instars last 3 - 5 days each, and the fifth instar lasts 8 - 11 days (Green 1974). Inconspicuous pale green first instar larvae feed gregariously, skeletonizing the underside of basal or lower leaves on which they were laid. During the second instar the aposematic yellow and black banding pattern starts to appear and larvae move to the top of the plant, feeding in more loosely organized groups on flower buds and young leaves. Van der Meijden (1976) notes that the change in distribution pattern

accompanies the change in larval color pattern and this gregarious open exposure would heighten their conspicuousness to potential predators, a characteristic of aposematic animals. Gregariousness decreases with age, and after the second instar larvae move about the plant and between plants, tending to prefer the upper part of generative plants (Bornemissza 1966, Van der Meijden 1976). Van der Meijden distinguishes two phases of larval dispersal. In the first phase young larvae remain on the plant on which they hatched with a diet change from leaves only to leaves and flower buds or flowers during later instars. During the second phase of dispersal the older larvae may disperse to other generative plants, although food may be sufficient where they were. Green found over 50% of fifth instar larvae may leave non-overloaded, non-defoliated plants. Asking what might influence the distribution and disperal of cinnabar larvae, Van der Meijden offered these three factors:

1. Density of larvae. Survival of very young larvae increases with increasing egg cluster size up to an optimum size of 50 eggs (Green 1974). This may be because more individuals escape predation when a larger group is attacked, the attack on one individual evoking the escape reaction (dropping to the ground on a silken thread) in others (Dempster 1971). Under crowded rearing conditions, Van der Meijden (1976) found larvae had a higher growth rate, shorter developmental period, and produced smaller, lighter pupae (correlated with reduced fecundity) (Dempster 1971). There was also a decrease in pupal diameter when the period of gregarious living was

more prolonged. Fifth instar larvae are solitary feeders that actively maintain their spacing by head-flicking behavior. The frequency of this aggressive display is positively density-dependent and it may act as a proximate cue for disperal to other plants (Green 1974).

2. Food quantity. Green (1974) found that by leaving an overloaded plant, 33% of the larvae found a non-overloaded plant, and hence had increased their food supply. Density of host plants affects disperser success and inclination, with more larvae likely to disperse and succeed at higher plant densities (Green 1974, Myers 1976). Larvae which are subjected to even temporary food shortages show an increase in mortality and a decrease in the pupal size of surviving larvae (Van der Meijden 1976). Smaller pupae show a reduced percent emergence.

3. Food quality. Rose (1978) reared cinnabar larvae on diets of first-year plant leaves, second-year plant leaves (a mixture of leaves of all heights), shaded plant leaves, floral parts and a mix of the preceding four diets. Diet did not affect larval weights or developmental period. Instar survival, total larval survival, percent emergence, and female longevity also did not exhibit diet effects. However, female larvae which had been fed on floral parts produced larger pupae and laid more eggs which had a higher percent hatch. Male pupae were also larger on a floral diet. Van der Meijden also found no diet-related differences in pupation success and saw larger pupae produced by larvae-fed floral parts. Contrary

to Rose's results, he found a higher percent emergence and shorter developmental period for larvae receiving floral parts.

Food quality will be affected by the mechanical injury caused by feeding, which induces metabolic changes in plant tissue. Because of the persistance of larval feeding in localized plant populations over several months, cinnabar larvae usually feed on plants which have been previously injured by feeding. General changes in wounded plant tissue may include an increase in phenolics (Levin 1976), increases in protein content (Uritani 1976) and dessication, which concentrates sugars and other solutes. In Senecio jacobaea, mechanical removal of 50% of the leaves results in a 40 - 47 percent increase in total leaf alkaloids and N-oxides in undamaged leaves in two days (Rhoades 1979). Thus, as plant defoliation proceeds, larvae must ingest increasing amounts of PAs. No work has been done on dosage-dependent effects of PAs on insects.

Evolutionary Influences on Foraging Strategy

Natural selection tends to maximize fitness, the genetic contribution of the individual to future generations. Heritable traits which enhance an individual's fitness will be selected for and inherited by their offspring. Because individuals within a population may be in competition for limited food resources, an individual that obtains a maximum amount of energy or nutrients in a given time from a resource will be favored by natural selection. The pattern of allocation of resources to growth, maintenance, and reproduction is under genetic control and we expect selective pressures to favor patterns

of allocation which maximize an individual's fitness. The theory of optimal foraging suggests foraging patterns should also act to maximize on animals' fitness by maximizing the assimilation of energy or nutrients per unit time or unit expenditure. In considering what actual commodity in the utilization of a food resource is maximized or minimized by efficient foraging, we ask, what is the appropriate currency? It is often assumed that energy is a limiting factor and energetic efficiency is maximized in foraging (Emlen 1966). Time efficiency has also been considered relevant, that an animal would minimize time spent foraging to decrease its exposure to predators and abiotic stress (Schoener 1971). Slansky and Feeny (1977) argue that energy is often in superabundant supply and it may be more important for an organism to maximize the acquisition of certain limiting nutrients. They suggest for phytophagous insects a critical nutrient is organic nitrogen.

Studies of food utilization have been largely concerned with efficiency estimates of processes by which organisms acquire energy or nutrients. Odum and Pinkerton (1955) argue that in natural systems selection will tend to maximize the rate or power output of processes rather than efficiency. Therefore it may be more appropriate to look at rate of accumulation of a limiting nutritional component, rather than at the efficiency of its utilization.

The Importance of Nitrogen

Although Fraenkel (1953) at one time believed that all plants provided adequate nutrients for insects, it has more recently become

evident that plants are often nutritionally suboptimal and that the adaptation to a plant feeding habit presented a difficult evolutionary hurdle to insects (Southwood 1973). Southwood points out the low concentration of protein in plant tissues relative to insect tissues. Phytophagous insects have low efficiencies of conversion of food to biomass in comparison to predatory insects which consume tissue similar to their own in protein and sterol composition. If obtaining adequate nitrogen is a problem for herbivores, we would predict the following (from MacNeil and Southwood 1979):

1. The quality and quantity of nitrogen will influence insect growth and reproduction.
2. Insects should have evolved behavioral, physiological and ecological adaptations to decrease their vulnerability to low nitrogen levels in their host plants.
3. Restriction of availability of proteins and amino acids should be one of the evolutionary reactions of a plant to insect attack.

MacNeil and Southwood provide a review of the evidence that supports these three predictions. Recent studies of insect growth and feeding performance (Fox and McCauley 1977, Scriber 1977, Barbosa and Gremblatt 1979, and Scriber and Feeny 1979) have looked at the consumption, accumulation, and efficiency of utilization of nitrogen with indices developed by Slansky and Feeny (1977) in their work on Pieris rapae. Used in conjunction with nutritional indices which quantify growth, consumption and efficiency of food conversion to biomass (Waldbauer 1968), it is possible to evaluate feeding performance

on various diets and comment on the relative importance of food quality.

Slansky and Feeny (1977) found that over a range of food plants which differed in nitrogen content, the growth rates of Pieris larvae and the accumulation of nitrogen into larval biomass remained stable. This was due to compensatory changes in the rate of food consumption (RCR), the efficiency of utilization of dry matter (ECI and ECD), and the efficiency of nitrogen utilization (NUE). Larvae fed on low-nitrogen plants had high RCR, lower efficiencies of drymatter conversion (ECI and ECD) and higher NUE. There appeared to be a limit to how fast nitrogen could be accumulated because efficiency of nitrogen use declined with increased consumption rate. Thus larvae fed at a rate which maximized their rate of accumulation of nitrogen, eating more of low-nitrogen plants and less of high nitrogen plants and growth rates remained constant.

Research Objectives

The following questions concerning cinnabar moth larval foraging behavior are generated by the concepts and experiments discussed in the preceding section:

1. What are appropriate measures of food quality, and how does food quality vary between plant parts, between vegetative and generative plants, between plants of different sizes and seasonally?
2. Does timing of insect attack correlate with maximum availability of food and/or peaks in food quality?

3. Does the pattern of feeding correlate with differences in food quality within the plant?

4. Are there measurable parameters of physiological performance which strengthen the inference that diet selection maximizes fitness by increasing the component of fecundity?

5. How are rates of processes and efficiency related? Is power output favored over efficiency?

By answering some of these questions I hoped to test the hypothesis that measurable components of insect fitness are coupled to varying components of diet and that foraging behavior maximizes the acquisition of some limiting nutrient (particularly nitrogen) which may be coupled to fecundity. I predicted the following:

1. Larvae fed on the preferred diet of floral parts would demonstrate higher efficiencies of dry matter conversion and nitrogen utilization than leaf fed larvae. Larvae fed on plant parts which are avoided in the normative feeding pattern (basal and low leaves) would show lower efficiencies of dry matter and nitrogen utilization.

2. There are patterns in plant food quality which correlate to larval distribution in space and time. Parameters of larval growth and feeding performance are correlated with measures of food quality. If larval growth is limited by the availability of nitrogen in their food plants larvae will maximize the rate at which they can accumulate nitrogen. There will

be a stabilization of the rate of nitrogen accumulation due to physiological limitations in extraction and selection pressures to maximize power of processes.

I discuss my experiments in these three sections:

II Variation in host plant food quality.

III Correlation of larval feeding pattern and changes in the host plant.

IV Variation of feeding performance with diet--the utilization of dry matter and nitrogen.

II. VARIATION IN HOST PLANT FOOD QUALITY

Considerations in Choosing Measures of Food Quality

Different variables have been regarded as revelant indicators of food quality. In nutritional studies performance has been examined with respect to concentrations of dry matter (Schroeder 1976), calories (Slansky and Feeny 1977), soluble sugars (McNeil 1973), water (Scriber 1977), total nitrogen (Slansky and Feeny 1977), soluble nitrogen (McNeil 1973), amino acids (Emden and Bashford 1971), trace elements (Larsson and Tenow 1979), and secondary plant compounds (Reese and Beck 1976). Although caloric measurements have been done in several studies, no correlation between caloric value and growth has been found. Hickman and Pitelka (1975) suggest calorimetry is unnecessary for study of energy allocation patterns in plants because differences in dry weight are a good indicator of caloric differences in different plants and plant parts. Total nitrogen has proved to be a relevant measure of food quality (Slansky and Feeny 1977, Scriber 1977, Scriber and Feeny 1979) and although a more detailed assessment of available nitrogen in terms of soluble nitrogen or amino acid content would have been most useful, I chose to simplify my initial investigation by assessing only the total nitrogan levels in the plant. Total nitrogen has been found to be a good predictor of insect performance and behavior in other studies (McNeil and Southwood 1978). The convenient unit of plant material for analysis was usually one or two leaves which would have been insufficient in quantity for several analytical

procedures. Water content has been found to affect growth and efficiency of tree feeding lepidoptera (Scriber 1977). It may not be a limiting factor for forb-feeding insects because of the high water content (range 69 - 91%) of forbs (Scriber and Feeny 1979). Soluble sugars and trace elements have not been indicated as major determinants of feeding performance (MacNeil 1973), although sawfly larvae feeding on pine were found to concentrate phosphorus and to a lesser degree potassium, magnesium, sodium, and sulfur (Larsson and Tenow 1979). I chose to examine the sensitivity of insect performance to the following variables. This would indicate which areas of plant chemistry warranted further study: (1) dry matter content, (2) water content, (3) total nitrogen content, and (4) alkaloid content.

METHODS

General Procedure

Plants were obtained at sites in MacDonald Forest, Camp Adair and Mary's Peak, over two field seasons, 1978 and 1979. For any one comparison plants were from the same site. Plants were collected into plastic bags and fresh weights determined within an hour or two of collection. Material was oven-dried at 70°C to constant weight for dry weight determinations. Total nitrogen determination was done by micro-Kjeldahl Technique (Nelson and Sommers 1973). This measures all nitrogen present in the plant tissue including soluble and insoluble protein and alkaloid nitrogen. Plant material was ground by mortar and pestle to pass through a 40 mesh screen. The small amounts

of fibrous white material found in samples of ground floral parts was not analyzed. Attempts were made to analyze alkaloid content by a colormetric technique modified from Mattocks (1967, 1968) and Bingley (1968). Highly inconsistent results substantiated warnings I had received concerning the difficulties with this technique. I did not have access to alkaloid standards for chromatographic work and did not feel I could master more sophisticated techniques within given time constraints. Some values for alkaloid content of plant parts are available in the literature and these are used in my discussion.

Water and Nitrogen Content of Generative and Vegetative Plant Parts

Samples from plants of similar sizes were collected and analyzed as part of the feeding study done in this thesis. The definitions of the terms, "Floral parts," "High, Low, and Basal leaves" can be found in the Methods section of Part IV, Diet Effects on Feeding Performance. The term "Rosette leaves" used here refers to middle leaves of vegetative plants. Sample sizes of 20 were used for Floral, High, and Low plant parts. Sample sizes of 10 were used for Basal and Rosette leaves. One-way analysis of variance for unequal sample sizes was performed to test for significant differences between plant parts. A form of Student-Newman-Keuls test for unequal sample sizes was used to compare and separate significantly different means (Sokal and Rohlf, 1969).

Water and Nitrogen Content Within Vegetative Plants

The water and nitrogen content in sequential leaves of three vegetative rosettes was determined. Leaf position was identified by calling the lowest basal leaf "1" and proceeding numercially towards the apical meristematic leaves. Rosette size was measured by noting maximum height. Plants were collected on September 21.

Nitrogen Content Within Generative Plants

This analysis was done to determine how nitrogen content varies between individual leaves of flowering plants. Three plants were collected on June 20 and analyzed by individual leaves for nitrogen. Leaf position was identified by noting the distance of the leaf attachment in cm from the top of the plant.

Seasonal Variation of Dry Matter and Nitrogen Content in Generative Plants

Plants from Camp Adair were harvested and divided into floral parts and live leaves at approximately three-week intervals by Dr. Peter McEvoy and research associates. Dry weights of parts were determined by Dr. McEvoy's laboratory. I analyzed floral parts and leaves of three plants at four dates for nitrogen content. Using Dr. McEvoy's data on total dry weights of parts and my values for nitrogen content, I was able to calculate total standing crops of dry matter and nitrogen through the season.

RESULTS

Variation in Water and Nitrogen Content Among Generative and Vegetative Plant Parts

Water content among the plant parts tested ranged from 85.54% to 89.74% (Table 1). Plant parts ranked in order of increasing water content are: Floral = High < Low = Rosette < Basal. Floral parts and High leaves, and Low and Rosette leaves were not significantly different at the 5% level in mean water content.

Nitrogen content ranged from 0.97% to 3.03% in parts tested (Table 1). Plant parts ranked in order of increasing nitrogen content are: Basal < Low < Rosette = High < Floral. Rosette and High leaves did not differ significantly at the 5% level in mean nitrogen content.

Variation in Water and Nitrogen Content Within Vegetative Plants

Among the four rosettes analyzed, water content was generally lower in basal and apical leaves than in leaves in mid-positions in the plant (Fig. 1). There was a trend in increasing water content among the first four leaves. Leaves in positions 4-9 had fairly constant water contents, while the top three to four apical leaves showed a decreasing trend.

Figure 2 illustrates intra-plant variation in nitrogen content. In the three rosettes analyzed there is a significant positive correlation between nitrogen content and leaf position at the 1% level.

TABLE 1

Water and nitrogen contents of various parts of generative and vegetative plants. Values are presented as a mean ± SE. Values followed by the same letter within a column are not significantly different at the .05 level as determined by Student-Newman-Keuls Test, done for unequal sample sizes.

Plant part	Water content (% fresh weight)	Nitrogen content (% dry weight)
Generative plants		
Floral	85.66 ± 0.48 a	3.03 ± 0.13 a
High leaves	85.54 ± 0.48 a	2.46 ± 0.13 b
Low leaves	88.06 ± 0.48 b	1.38 ± 0.13 c
Basal leaves	89.74 ± 0.59 c	0.97 ± 0.15 d
Vegetative plants		
Rosette leaves	88.37 ± .040 b	2.53 ± 0.11 b

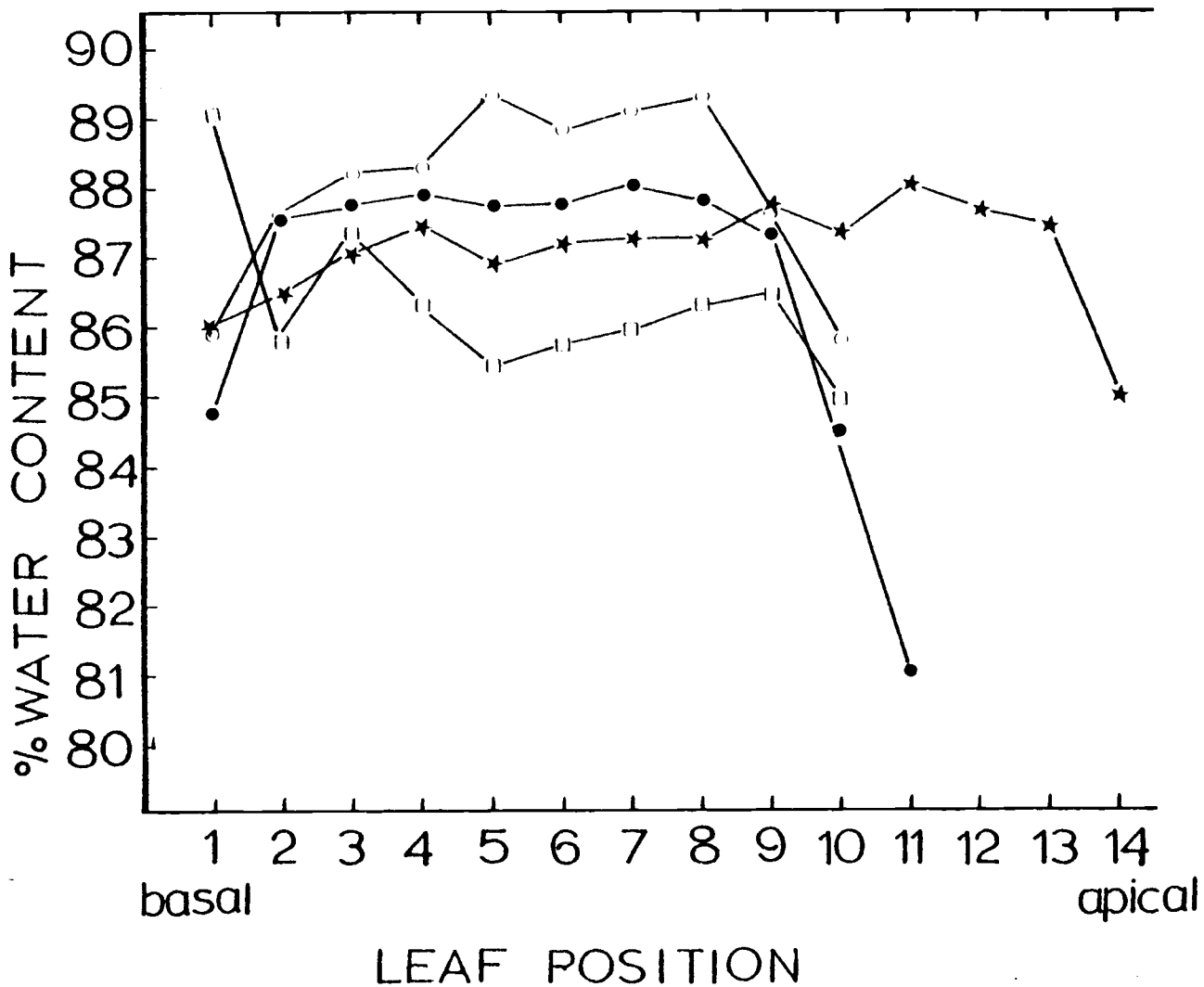

Figure 1. Variation in % water content with leaf position in vegetative rosettes. Symbols represent different plants.

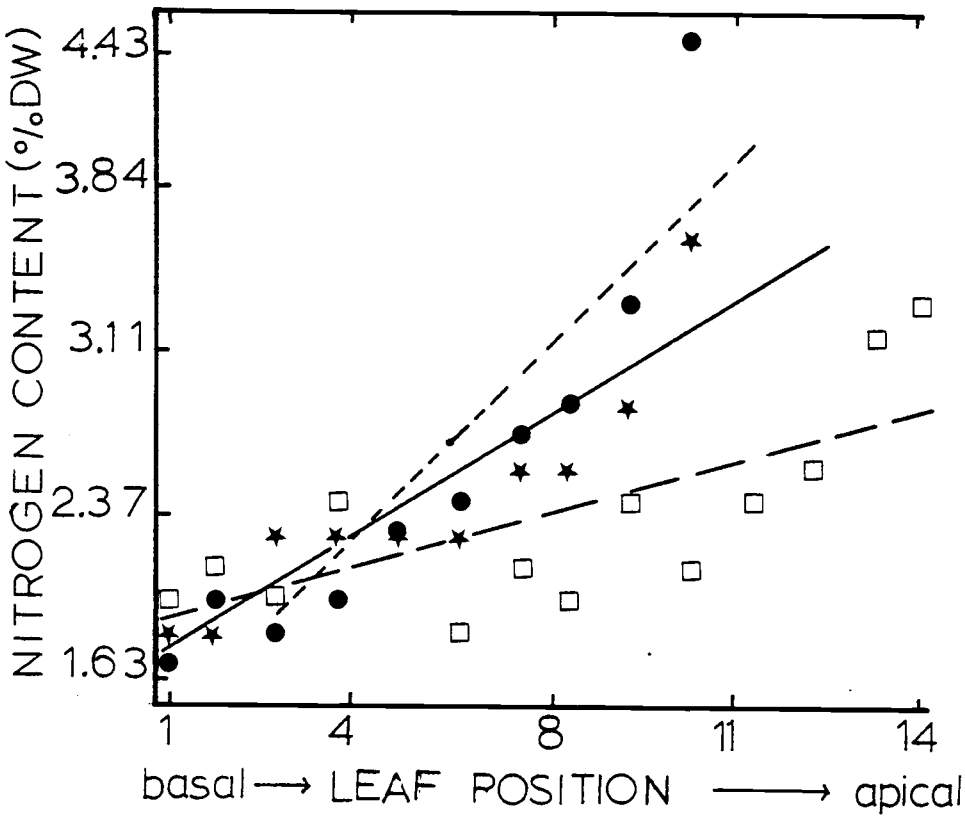

Figure 2. Intra-plant variation in nitrogen content in vegetative first-year rosettes. ★ = Rosette 1 : $r = 0.9015$, $n = 10$, $p < .001$; $y = 1.600 + 0.159x$. ● = Rosette 2 : $r = 0.9089$, $n = 10$, $p < .001$; $y = 1.097 + 0.266x$. □ = Rosette 3 : $r = 0.7399$, $n = 14$, $p < .001$; $7 = 1.773 + 0.078x$. Heights of plants are : Rosette 1, 35 cm; Rosette 2, 25 cm; Rosette 3, 57 cm.

The smallest plant, Rosette 2, showed the greatest amount of increase in nitrogen with ascending leaf position while the largest plant, Rosette 3, showed the least.

Variation in Nitrogen Content Within Generative Plants

Generative plants also showed an increase in nitrogen content with increasing height of plant tissue (Fig. 3). There is a very strong linear relationship; linear correlation coefficients of the three sets of plant analyses were highly significant, $p < .001$. Slopes of the three regression lines vary slightly with no obvious correlation to total plant height.

Seasonal Variation in Standing Crop of Dry Matter and Nitrogen in Generative Plants

The total standing crop of dry matter is at a maximum early in the season, on June 9, before extensive development of floral primordia (Fig. 4). Total dry matter declines after June 9, as the number of live leaves is reduced due to senescence. Floral dry matter peaks nearly seven weeks later on July 25. The pattern of the standing crop of nitrogen mirrors that of dry matter, with the peak of total nitrogen in plants on July 6. This peak is due to the high levels seen in leaves supplemented by increasing amounts of floral nitrogen. The peak of available floral nitrogen coincides with peak biomass of flowers on July 25. The standing crop of both dry matter and nitrogen in floral parts persists near the end of the measured season, when

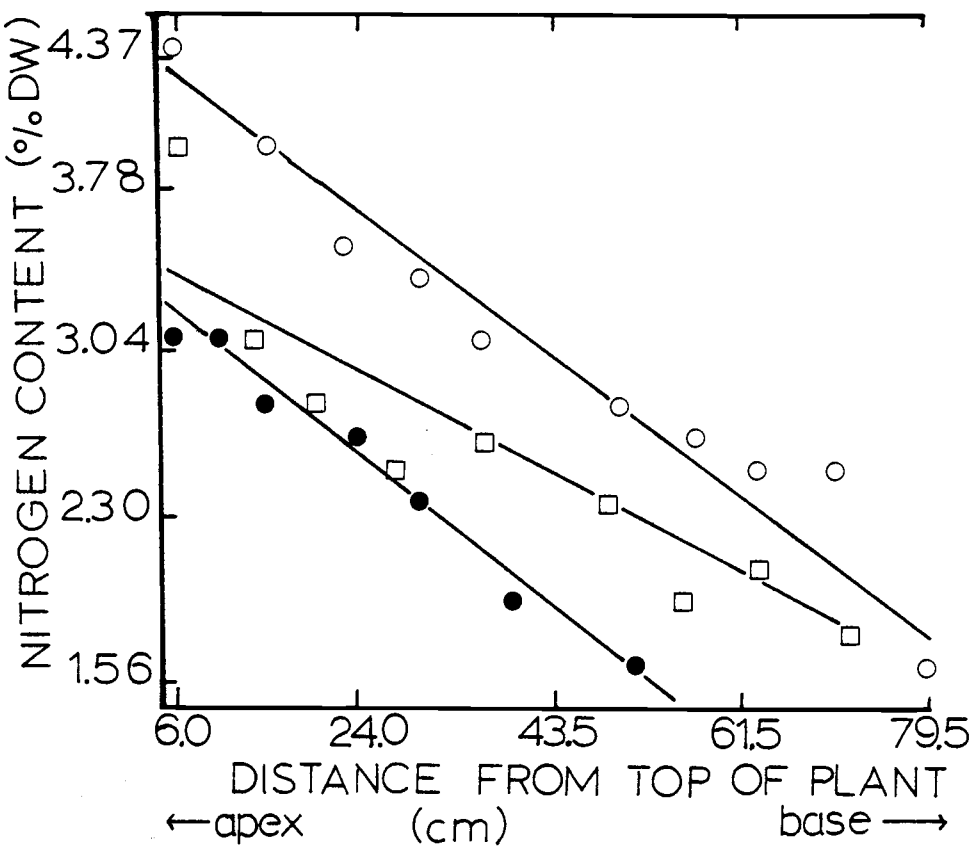

Figure 3. Intra-plant variation in nitrogen content in generative plants. ● = Flowering plant 1 : r = .9898, n = 7, p < .001; y = 3.423 - 0.035x. O = Flowering plant 2 : r = .9682, n = 10, p < .001; y = 4.488 - 0.033x. □ = Flowering plant 3 : r = .9108, n = 9, p < .001; y = 3.595 - 0.026x. Plant heights are : Plant 1, 51 cm; Plant 2, 81 cm; Plant 3, 72 cm.

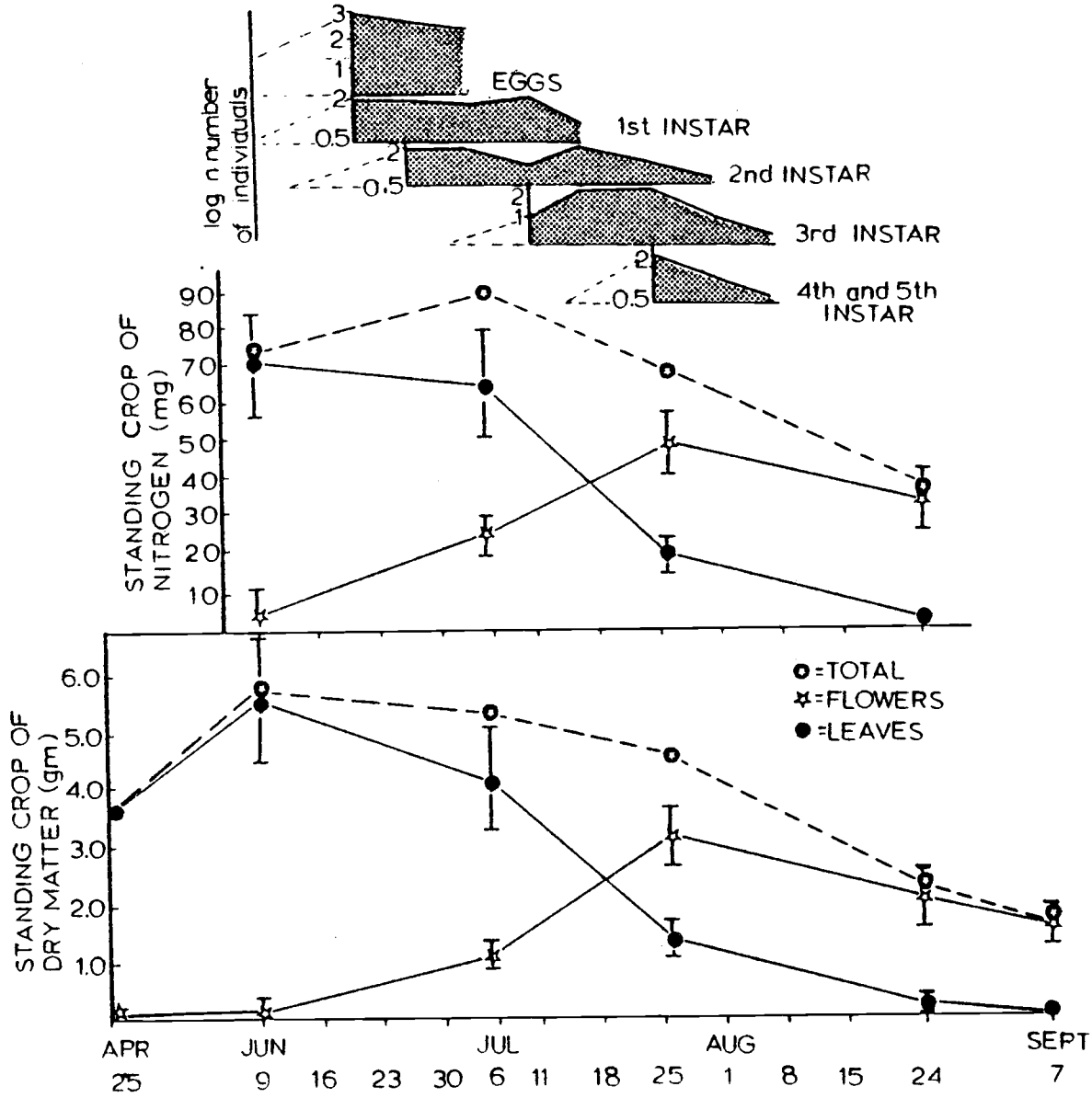

Figure 4. Seasonal changes in standing crop of dry matter and nitrogen in leaves and flowers and distribution of cinnabar moth life stages.

live leaves are virtually gone. However, flowers in August are mature and their physical presence does not imply they are a source of dry matter or nitrogen for the insect. In fact, larvae avoid feeding on mature flowers and seeds (personal observation).

III. LARVAL FEEDING PATTERN AND ITS CORRELATION TO HOST PLANT FOOD QUALITY

The purpose of this study was to confirm the change in larval feeding preference and document when this change occurred relative to plant development and changes in plant biomass, and water and nitrogen content.

METHODS

The site for the study was located on a roadside in MacDonald Forest, Benton County, approximately three miles on the Sulphur Springs turnoff from Lewisburg Road. Site selection was influenced by the following criteria: (1) a site where oviposition by females had been fairly synchronous, so that larvae on different plants would be in the same development stage, and (2) adequate density of eggs in a single site. Thus, early instar larval movements on lower leaves were not impeded by interference from older migrating larvae. As the season progressed migration occurred and was not controlled. Eight plants were observed with a total of 21 egg masses. Weekly observations were made on the following:

1. Plant height.
2. Location of eggs and larvae (expressed as their height on the plant).
3. Larval instar and number of individuals at each height.
4. Qualitative assessment of floral development and defoliation intensity.

Egg and larval locations were expressed in terms of relative height to allow comparisons between plants of various sizes. Relative height was calculated by dividing the height at which the insect was observed by total plant height. This presumes that developmental stages such as the flowering top, high sub-floral leaves, low rosette leaves, etc. are more relevant to a discussion of insect feeding than height of tissue above the ground. Observations continued until plants were defoliated and no larvae remained. The data obtained were used to plot distributions of larval instars over the host plant as they varied with time and compared to seasonal changes in host plant quality determined in Part II of this thesis. The studies of seasonal changes in food quality and changes in larval distribution were done at different sites which probably were asynchronous in terms of plant phenology. The food quality site (Camp Adair) is an open, sunny field which was approximately a week ahead of the MacDonald Forest site, a sunny, forested area, judging by observations at both sites.

RESULTS

Distribution of Life Stages on the Plant Over Time

The vertical distribution of individuals on the plant changed as the season progressed (Table 2). Figure 5 illustrates the percent of total number of individuals seen on plants in progressive stages of development and defoliation. Early in the season (June 21) plants have produced a stem with floral primordia and all individuals are

TABLE 2

Number of individuals in a particular life stage found at different relative heights on plant.

Date	Life Stage	Relative height of plants							
		0.125	0.25	0.375	0.5	0.625	0.75	0.875	1.0
Jun 21	eggs	331	122	34	25				
	1st instar	66		22					
Jun 27	eggs	132	96	31					
	1st instar	83							
	2nd instar	55		1	1				
Jul 4	eggs	53	17	21	44				
	1st instar	12	28	9					
	2nd instar			2	18	1	2	13	23
Jul 11	1st instar	26	5	1	44			14	
	2nd instar	1			1			6	7
	3rd instar							2	6
Jul 17	1st instar								10
	2nd instar	4		1		17	12	11	23
	3rd instar			1		3	2	1	64
Jul 25	2nd instar		5	7		2	5		
	3rd instar		3	12	5	4	8	7	42
	4th+5th instar	4	22	24	6	2	27	20	30
Aug 1	2nd instar		2		1				1
	3rd instar	1	1	1	1		2		3
	4th+5th instar	1	2		5	4	1	3	9
Aug 8	3rd instar			2					
	4th+5th instar		2			1		1	1

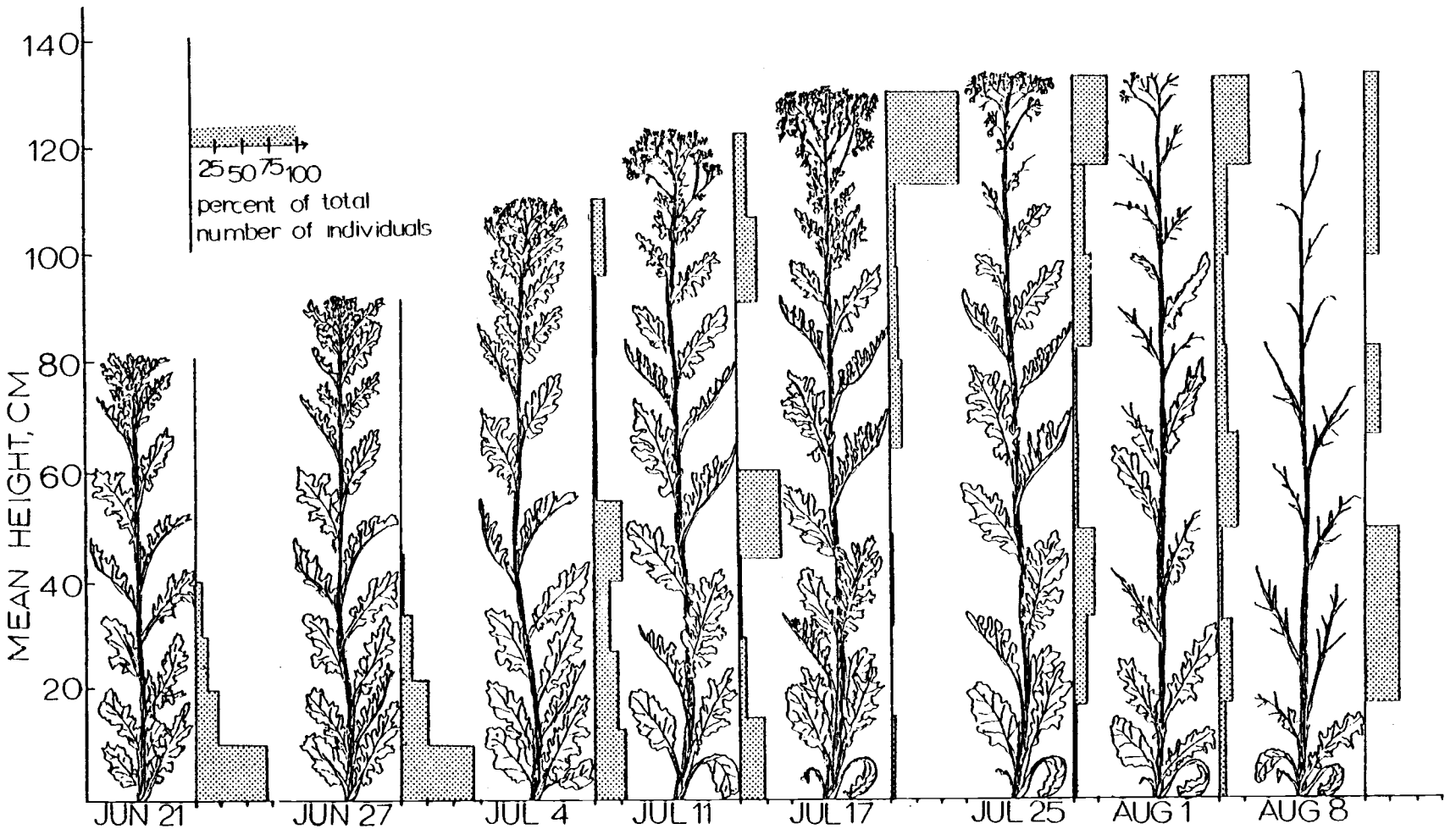

Figure 5. Change in percent of total number of individuals at different heights with plant development.

found on the lower half of the plant. As the plant elongates and floral development progresses, more larvae are found on the upper regions of the plant. By July 17, the peak of flowering for this site, nearly all larvae are found on the upper half of the plant. As the top of the plant is defoliated, larvae move to lower portions of the plant, spacing themselves more widely. Figure 6 illustrates the specific distribution of the different life stages. From June 21 to 27, eggs were the prevalent stage. All eggs were found below 0.5 relative height on the plant. First instar larvae were seen for a period of 4 weeks, from June 21 to July 17. They remained primarily on lower regions of the plant, below 0.5 relative height, feeding on the leaf on which they hatched and adjacent leaves. As flowering reached its peak from July 11 to 17, 16% of the 1st instar larvae were seen feeding on floral buds. Floral buds were eaten by first consuming the florets, leaving a scooped-out bract cup. Bracts and pedicels were then eaten. Distribution of 2nd instar larvae changed rapidly with all larvae below the 0.5 relative height on June 27 and 97% above 0.5 relative height the following week of July 4. There was a precipitous reduction in total numbers of 2nd instar larvae in July, from 59 larvae on July 4 to 15 larvae on July 11. The following week of July 17, 68 larvae were seen. This temporary disappearance of 2nd instar larvae has been observed by other investigators (Daryl Ehrensing, personal communication), and may occur because larvae leave the plant to molt. At the time of peak flowering (July 17), 2nd and 3rd instar larvae were the major stages found on the plants, in approximately equal numbers (68, 2nd instar; 71, 3rd instar). At this time 90% of

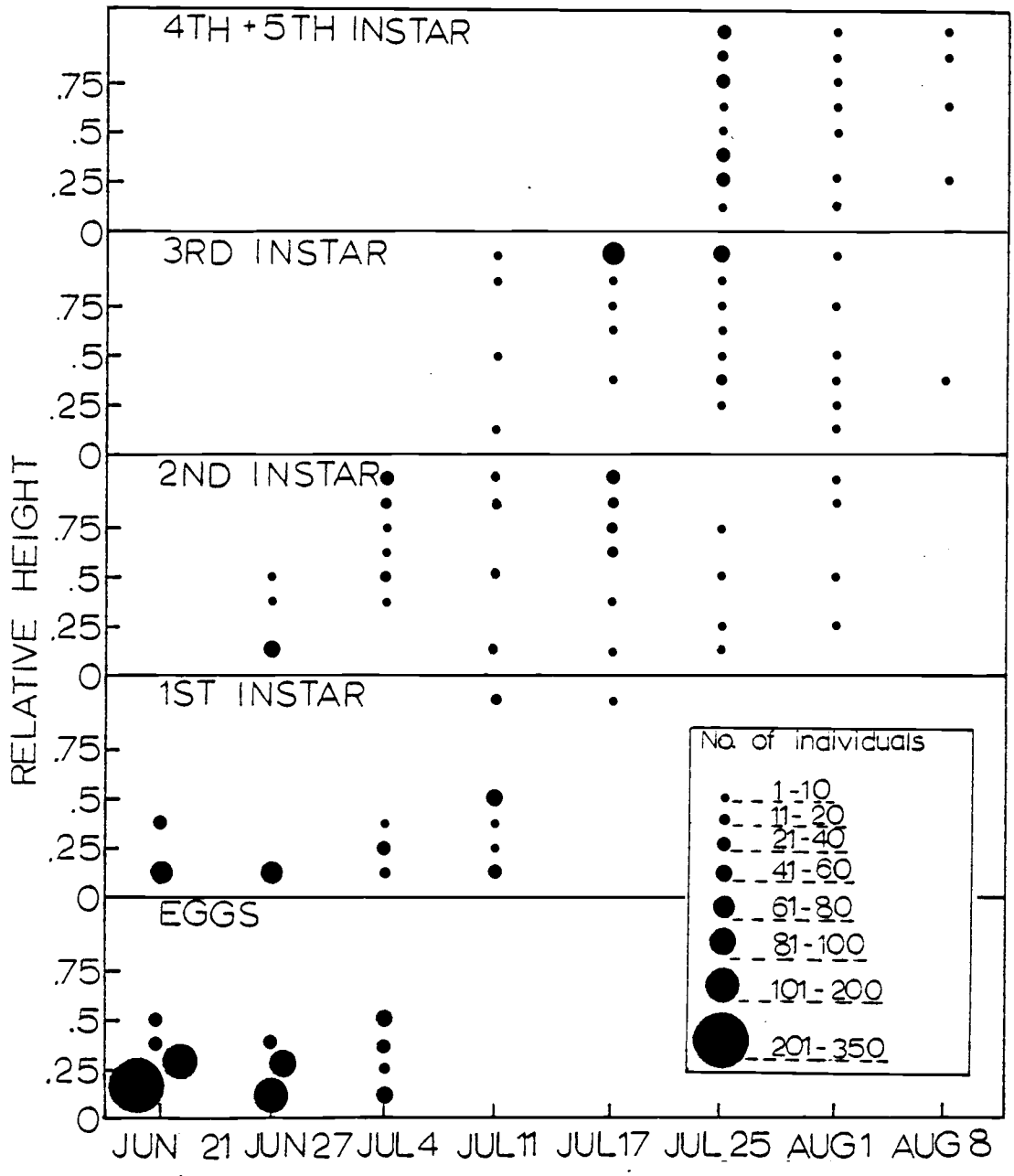

Figure 6. The distribution of life stages over plant height.

the 3rd instar larvae could be found on the floral parts of plants. As 4th and 5th instar larvae became prevalent and defoliation accelerated (July 25 to August 8), the trend seen in all stages present was a spacing-out over the plant. Data for August 1 shows a nearly even distribution of larvae over the plant with a concentration of individuals on the upper regions. By August 8 all plants were nearly completely defoliated, with only leaf petioles and basal leaves remaining. Only seven larvae were seen on all eight plants and these were found on remaining petioles of lower plant regions. Basal leaves were often found entire and uneaten on otherwise totally defoliated plants.

Estimates of Larval Cohort Consumption Rate

Isaacson (1972) determined the consumption rates of larval instars of the cinnabar moth in terms of grams dry weight eaten per day. I used the average values he presents for the 3rd, 4th, and 5th instar and his estimates of 1st and 2nd instar consumption rates to estimate consumption of the larval cohorts I observed (Table 3). These values were calculated by multiplying Isaacson's values for each instar by my data on numbers of each instar present at a particular date. The consumption of all instars present was totaled and averaged over the eight plants. Consumption by 1st and 2nd instars was assumed to be equal to or less than 0.003 g and consumption by 3rd instar equal to 0.015 g. Values used for consumption of mixed groups of 4th and 5th instars ranged from 0.16 g (approximately two-thirds 4th instar and one-third 5th instar larvae present) for July 25, to 0.25 g (one-third

TABLE 3

Estimated values of grams dry weight plant material consumed per day by a cohort of larvae.[1]

Date	Estimate of dry weight (gms) consumed per day by each cohort								Grams dry weight consumed/plant/day/cohort
	Plant # 1	2	3	4	5	6	7	8	$\bar{X}$ ± SE
Jun 21	0	0	0	0	0	0.14	0.05	0.07	0.03 ± 0.02
Jun 27	0.11	0.02	0	0	0.09	0.17	0.04	0	0.05 ± 0.02
Jul 4	0.03	0	0.08	0.04	0.04	0.14	0	0.02	0.04 ± 0.02
Jul 11	0.04	0.09	0.06	0.06	0.08	0	0	0.14	0.06 ± 0.02
Jul 17	0.40	0.10	0.42	0.21	0.09	0.03	0.003	0.08	0.17 ± 0.06
Jul 25	5.59	5.24	0.57	5.75	0.55	1.78	3.89	0.31	2.96 ± 0.85
Aug 1	0.29	0.25	0.25	0.52	0.25	3.82	1.09	0	0.81 ± 0.45
Aug 8	0	0.70	0	0.335	0	0	0.67	0	0.21 ± 0.11

[1] Consumption rates used for estimations from Isaacson (1972).

4th instar and two-thirds 5th instar larvae present) for August 1. On August 8 all larvae present were assumed to be 5th instars with a consumption rate of 0.335 g per day. A graph of cohort consumption rate in grams per day per plant (Fig. 7) shows a gradually increasing rate through July 17 with a dramatic 16-fold increase on July 25 to nearly three grams a day per plant. This is due to the higher numbers of 4th and 5th instar larvae present. The 5th instar consumes more than three-fourths of the foliage consumed by the larval stage (Isaacson 1972). Although daily consumption rates vary from plant to plant with the density of larvae present, there is remarkable synchrony of peak feeding intensity, occurring on all but one plant on July 25.

Seasonal Correlation of Larval Distribution and Food Quality

Figure 4 illustrates how the total numbers of larvae in each instar (expressed in log scale) correlates to seasonal patterns of dry matter and nitrogen abundance. The period of cinnabar moth presence correlates with dates of maximum standing crop of dry matter and nitrogen. However, larval density and the period of maximum consumption (July 25, discussed above), appear more closely atuned to peaks in floral biomass and nitrogen than to peaks of total biomass and nitrogen. Peak numbers of 2nd and 3rd instar larvae coincide with rising levels of floral dry matter and nitrogen. Recalling the possible asynchrony of the sites where plants and insects were collected or observed, in terms of plant phenology and larval development

it is clear a shift of the larval graphs to the right by one week would result in an even stronger correlation. The period of maximum consumption (July 25, or with shift allowing for site asynchrony to August 1), follows the peak of total biomass and nitrogen and appears more closely correlated to floral biomass and nitrogen. The decline in numbers of 4th and 5th instar larvae coincides with the decline of remaining live leaves and maturation of flowers. As noted earlier, flowers present late in the season have set seed and are not utilized by larvae as food.

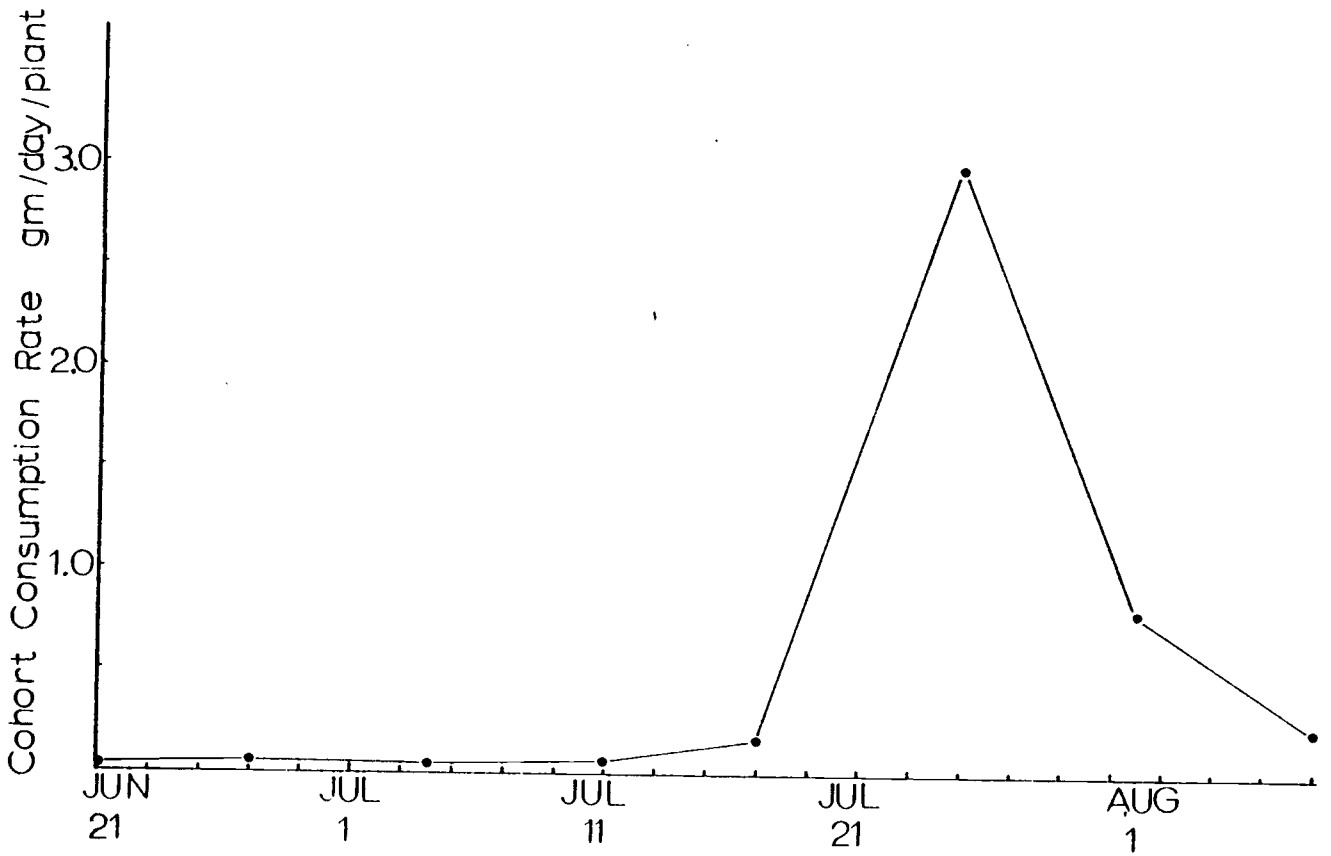

Figure 7. Changes in cohort consumption rate (gm/day/plant) with time.

IV. DIET EFFECTS ON FEEDING PERFORMANCE

METHODS

Considerations in Selection of Experimental Larvae

Larvae of the cinnabar moth, hatched from different egg masses, may show significant differences in weight in the 4th instar, possibly due to the quantity or quality of the food the parent obtained as a larva (Rose, 1978). Over the duration of the ovipositional period a female will lay progressively fewer eggs (Green, 1974) which are lighter in weight (Richards, 1978). Under suboptimum conditions hatching success is lower for later egg batches (Richards, 1978). First instar survival is highest at egg cluster sizes of around 50 (Green, 1974).

To minimize variation in larval performance due to genetic differences or lowered viability because of maternal nutrition or age, I used larvae hatched from one egg mass of optimum survival size (~50 eggs). Upon hatching larvae were randomly distributed to different diet treatments and synchronously molting larvae were used in the feeding study to eliminate effects of egg mass variability and developmental time.

The developmental stage used for the experiment was the 4th of a total of 5 instars. Waldbauer (1968) suggests the penultimate instar is the most convenient choice because of its fairly high consumption rate and a minimum weight loss during the premolt. The experimental period was defined physiologically, beginning with freshly molted

larvae and ending at the premolt stage.

Estimation of Percent Dry Matter and Nitrogen Content of Food

It was necessary to estimate the percent dry weight of fresh plant material prior to feeding in order to determine the dry weight of food consumed by the larva. This required selection and drying of an appropriate sample which would accurately estimate the actual percent dry matter of the fed plant material. Material was also required for analysis of nitrogen content and possibly alkaloid and caloric content.

The first year this feeding study was attempted my method of estimation was unsuccessful. Preliminary analysis had shown nitrogen content and dry matter increased in a linear fashion in leaves with height. Leaves are alternately arranged in Tansy Ragwort; thus a leaf would have to be taken from below or above the leaf fed and would be lower or higher in nitrogen content and dry matter. To resolve this problem in estimation of the fed leaf dry matter and nitrogen and have adequate material for feeding and analysis, I removed three adjacent leaves and cut the leaf blade from one side of the petiole, leaving the remainder of the leaf attached. The excised parts of the three leaves were weighed and dried for analysis while the remaining sections of leaves were weighed and fed with the petioles in a water-filled vial to help retain turgor. When uneaten leaves were removed from the feeding chamber the remaining petioles were excised and weighed and petiole weight subtracted from the initial weight. The remaining leaf material

was dried and weighed. This was to insure similarity of analyzed and fed plant material. When floral parts were fed a similar procedure was used removing buds and leaflets from one side, then after feeding removing the petiole. This was a time-consuming method and inaccurate because the petiole gained weight while in water thus causing the calculated initial fresh weight of leaf material to be too low.

The following procedure was used to determine nitrogen content and dry weights for the data reported here. For leaves, the leaf above and the leaf below the fed leaf were weighed and dried for analysis and the mean values of percent dry matter and nitrogen content were used to estimate values for the fed leaf. For floral parts the floral head was split, with one-half fed and the other analyzed. Admittedly there is an error introduced into calculations of dry matter and nitrogen consumed by analyzing whole leaves and whole floral heads when larval actually consume only selected parts of the offered food, first eating bud florets on floral parts and avoiding veins and petiole in leaves. It is not possible to obtain a sufficiently large sample for analysis from one leaf or floral head if only those parts are analyzed. Thus, estimates of nitrogen and dry matter consumed are probably low, florets and leaf laminae being higher in those commodities than petioles, stems and bracts. This has the effect of slightly lowering values of the parameters calculated. Because the error is constant and small, it should not affect comparisons among diets.

There is an inevitable discrepancy between the the estimated percent dry matter and the actual percent dry matter of the food. This error is reduced by limiting the amount of food offered so that the

proportion left uneaten is minimized (Waldbauer, 1968).

Determination of Parameters of Larval Growth and Efficiency

Larvae were obtained from hatching egg masses collected at the Sulphur Springs site in MacDonald Forest on June 18, 1979. Each leaf with an egg mass was placed in a covered container and the leaf petiole inserted in a water-filled vial with cotton plug. Egg masses and subsequent larvae were kept in a growth chamber with a 16-h light: 8-hour dark photoperiod and 25°C constant temperature. Humidity was maintained by keeping full pans of water in the bottom of the chamber. On June 22 all eggs had hatched and 1st instar larvae were transferred to four separate feeding treatments:

1. Floral = Floral parts (including floral buds, pedicels, small attached leaves, and main stem).
2. High = Leaves below the floral parts and above 0.5 relative height.
3. Low = Leaves from the bottom half (below 0.5 relative height) of the plant.
4. Basal = The leaves which were present in the 1st year rosette.

Plant material was changed daily. It was possible to determine the time of molting to the next instar by observing when larvae gathered on the lid of the container. This also allowed selection of a synchronously molting group for the feeding study. Four sets of ten

freshly molted 4th instar larvae were transferred from the feeding treatments to individual containers. The containers used were round 8-ounce waxed ice cream cartons with a hole in the side, allowing the stem or petiole of the food offered to be inserted in a plugged water-filled vial. The containers were lined with wax paper facilitating removal of feces, and were covered with a glass or plastic petri plate lid. Approximately every 24 hours larval fresh weights were measured, known amounts of fresh leaves were added and feces and uneaten food were removed. Feces and uneaten food were dried to constant weight at 70°C and weighed. Dry weight gained by the larvae was estimated by multiplying fresh weight gain by an average percent dry weight figure determined from several larvae from each diet treatment. Dry weight of food consumed was determined by standard gravimetric technique (Waldbauer 1968), subtracting the measured dry weight of uneaten food from the estimated dry weight of the food at the start of the feeding interval. The method for estimating initial dry weight is described above. Nitrogen content of larvae, feces and plant material allocated for analysis was determined by micro-Kjeldahl technique (Nelson and Sommers 1973). The amount of nitrogen gained by each larva was calculated by subtracting nitrogen content of the feces from nitrogen ingested by the larva. From this data the following quantities were determined for each larva over the duration of the 4th instar:

Biomass gained (mg dry weight)

Food ingested (mg dry weight)

Feces produced (mg dry weight)

Duration of instar (days)

Mean larval weight (mg dry weight) - by weighted average method (Waldbauer 1964)

Biomass nitrogen gained (mg)

Nitrogen ingested (mg)

Using the quantities, indices describing growth and utilization of dry matter and nitrogen could be calculated. The following indices as defined in current studies of feeding performance (Slansky and Feeny 1977, Scriber 1977, Scriber and Feeny 1979) were determined in my study:

RGR : Relative Growth Rate = biomass gained (mg dry weight)/mean larval weight (mg dry weight)/day

RCR : Relative Consumption Rate = food ingested (mg dry weight)/ mean larval weight (mg dry weight)/day

Utilization of Dry Matter

AD : Approximate Digestibility (also Assimilation Efficiency)

$$= \frac{\text{Food ingested (mg dry weight)} - \text{Feces (mg dry weight)}}{\text{Food ingested (mg dry weight)}} \times 100$$

ECD : Efficiency of Conversion of Digested Food

$$= \frac{\text{Biomass gained (mg dry weight)}}{\text{Food ingested (mg dry weight)} - \text{Feces (mg dry weight)}} \times 100$$

ECI : Efficiency of Conversion of Ingested Food

$$= \frac{\text{Biomass gained (mg dry weight)}}{\text{Food ingested (mg dry weight)}} \times 100$$

$$= \text{AD} \times \text{ECD}$$

Utilization of Nitrogen

RNAR : Relative Nitrogen Accumulation Rate

= Biomass nitrogen gained (mg)/mean larval weight (mg dry weight)/day

RNCR : Relative Nitrogen Consumption Rate

= Nitrogen ingested (mg)/mean larval weight (mg dry weight)/day

NUE : Nitrogen Utilization Efficiency

$$= \frac{\text{Biomass nitrogen gained (mg)}}{\text{Nitrogen ingested (mg)}} \times 100$$

Analysis of Data

For each experimental larva the following values were calculated: Mean % water content of ingested food (Plant Water), mean % nitrogen content of ingested food (Plant Nitrogen), relative growth and consumption rates (RGR, RCR), the three parameters of dry matter utilization (AD, ECI, ECD), and the three parameters of nitrogen utilization (RNCR, RNAR, NUE). Initial analysis involved generating computer scatter plots of rates and efficiencies versus the plant qualities of nitrogen and water content. Efficiency values were also scattered versus rate values. Scatter diagrams were examined for patterns indicating linear or curvilinear correlations and the associated product-moment correlation coefficients (r) were tested for significance. Matrices of correlation coefficients for all measured parameters were

calculated for data from all three diets, Low leaves, High leaves, Leaves (High and Low), and floral diet. This revealed whether an observed correlation between two parameters existed within one diet or between diets. Appendix 1 (a-e) lists correlation coefficients for various groups of diet data. If a significant correlation occurred, the linear regression model was determined, tested for significance and the coefficients of determination (r^2) examined. Single factor analysis of variance was used to examine diet effects on measured parameters. Significantly different means were separated by Duncan's Multiple-Range Tests.

Model I Regression Analysis may not be strictly appropriate for examining the relationship between nutritional parameters, since it assumes the existence of an independent variable which is measured without error. In my analysis the designation of one parameter as the independent variable was fairly arbitrary. Regression was used for its value in describing the form of a functional relationship between variables.

RESULTS

Diet Effects on Growth and Developmental Period

Relative growth rate was not shown to be significantly different among larvae fed on diets of high leaves or floral parts. Larvae fed low leaves showed a significantly higher growth rate (Table 4). However, larvae fed on low leaves were one day behind those fed high leaves or floral parts in molting to the 4th instar and had the lowest

TABLE 4

Variation in parameters of food quality and feeding performance with diet. All parameters showed diets effects as determined by single-factor analysis of variance. Values followed by the same letter did not differ significantly at the 0.05 level by Duncan's Multiple Range Test.

	Low leaves / $\bar{X}$ ± SE		High leaves / $\bar{X}$ ± SE		Floral leaves / $\bar{X}$ ± SE	
% H_2O	87.51 ± .24	a	86.00 ± .21	b	85.70 ± .26	b
% N	1.41 ± .05	a	2.40 ± .04	b	3.13 ± .06	c
RGR	0.35 ± .01	a	0.30 ± .005	b	0.31 ± .01	b
RCR	3.71 ± .28	a	1.55 ± .08	b	3.70 ± .35	a
AD	29.72 ± 4.19	a	31.36 ± 3.40	a	73.61 ± 2.22	b
ECD	48.16 ± 11.19	a	72.51 ± 10.62	a	12.78 ± 1.87	b
ECI	10.45 ± .82	a	20.02 ± .87	b	9.05 ± .91	a
RNCR	0.05 ± .004	a	0.04 ± .003	a	0.12 ± .01	b
RNAR	0.03 ± .004	a	0.02 ± .002	a	0.09 ± .01	b
NUE	50.90 ± 3.90	a	66.99 ± 2.08	b	81.69 ± 1.61	c

weights (both fresh and dry weight). Larvae fed on basal leaves were three days behind the rest in molting to the 4th instar. Of these larvae, 80 percent began losing weight on the second day of the 4th instar and were dead by the fourth day. No measure of feeding performance on basal leaves was possible.

Diet Effects on the Utilization of Dry Matter

Approximate digestibility (AD) or assimilation efficiency was 60 percent higher for those larvae fed on floral parts than for those fed on low or high leaves (Table 4). The AD values increased as consumption rates increased, showing significant correlations for all diets. Floral diet AD values showed the least relative increase with increased consumption, while High diet AD values showed the highest rate of increase (Fig. 8). Thus as food was consumed at a faster rate, a greater proportion of food was assimilated, the relative rate of increase being highest for diets of high leaves. ECD and ECI values increased as AD values decreased. This negative correlation was significant within diet treatments and among diets (Appendix I). This means as a greater proportion of food was assimilated, a smaller proportion of the assimilated food was converted into insect biomass and the overall ability to convert ingested food into tissue decreased.

The ability of larvae to convert digested food into biomass (ECD) was highest among leaf-fed larvae and lowest in larvae fed floral parts. The existence of three efficiencies over 100 percent in High leaf and Low leaf treatments (Appendix II), distorts the mean value determined, however I did not feel I could discard these points as

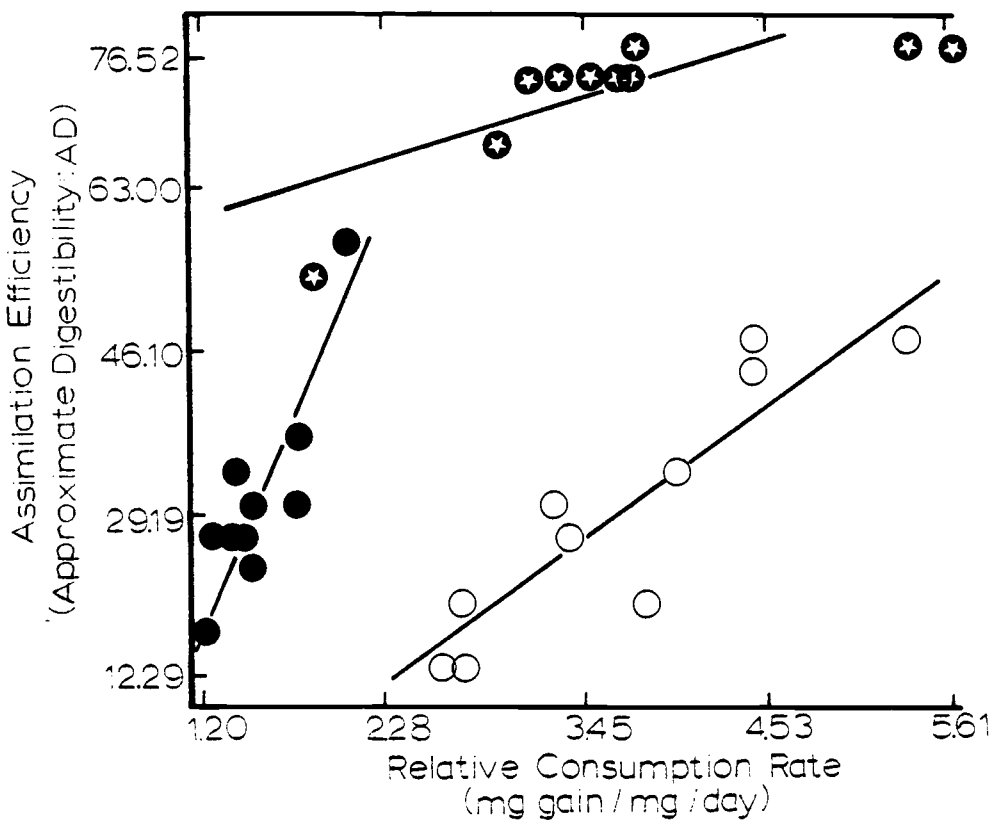

Figure 8. Relationship between approximate digestibility (AD) and relative consumption rate (RCR) of cinnabar moth larvae fed on diets of different plant parts. ✪ = Floral parts : $r = 0.7317$, $n = 10$, $p < .05$; $y = 56.590 + 4.599x$. ● = High leaves : $r = 0.8790$, $n = 10$, $p < .001$; $y = -24.770 + 36.3316x$. ○ = Low leaves : $r = 0.9184$, $n = 10$, $p < .001$; $y = -21.584 + 13.825s$.

outliers since the values used to calculate ECD are used in all other calculations. They reflect an error in estimating the amount of food ingested, the biomass gained by the larvae, or the amount of feces produced. Since fecal weight is measured directly the most likely source of the error is in the estimation of dry weight gained by larvae or in dry weight of food eaten. ECD decreased as RCR increased (Fig. 9), meaning the faster food was eaten the less efficiently it was converted to biomass.

The overall ability of the insect to convert ingested food into tissue (ECI) was 50 percent higher for larvae fed high leaves than those fed floral parts or low leaves. The ECI values of larvae on floral parts and low leaves were not significantly different. ECI is directly dependent on assimilation (AD) and the efficiency at which assimilated food is converted to biomass (ECD), since ECI = AD x ECD. the higher value of ECI for High leaf diets is mostly due to the greater ECD seen for larvae fed high leaves. ECI also was negatively correlated with RCR (Fig. 10).

The relative consumption rate of dry matter was lowest in larvae fed high leaves and less than half that found for larvae eating floral parts or low leaves. The RCR values of Floral and Low leaf diets were not significantly different.

Diet Effects on the Utilization of Nitrogen

Larvae fed on floral parts consumed and accumulated nitrogen at a significantly higher rate and utilized it more efficiently than larvae fed leaves (Table 4). The RNCR was 63 percent higher on floral

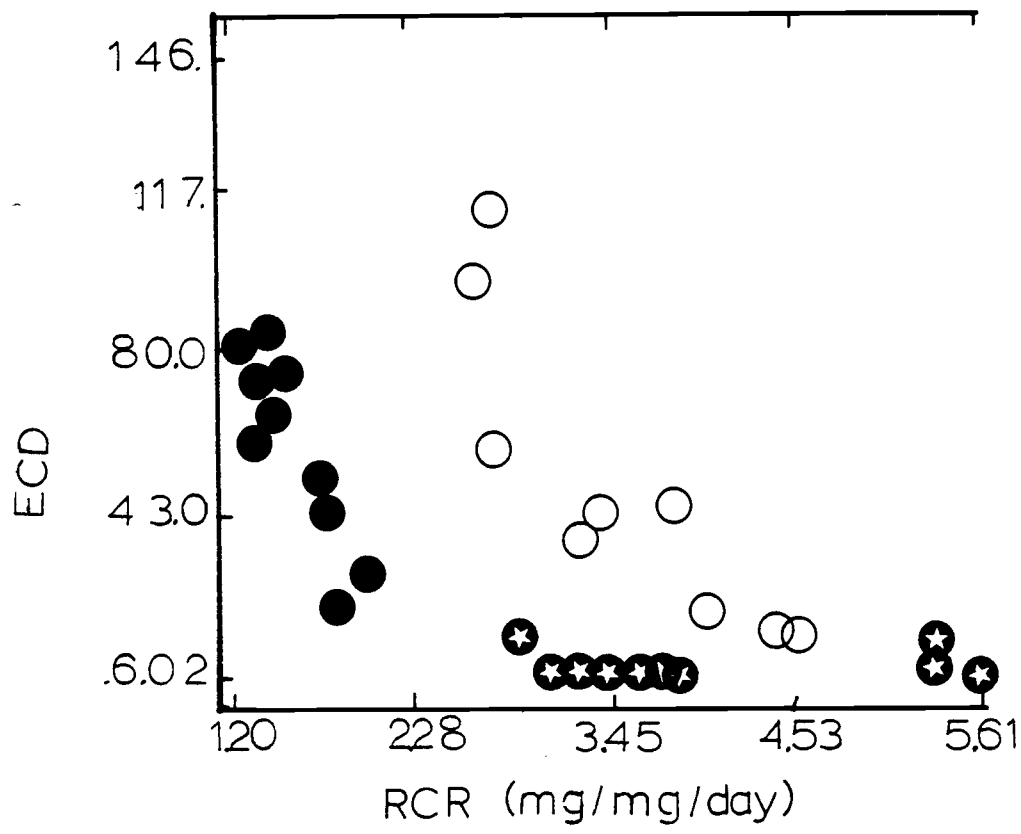

Figure 9. The relationship between relative consumption and efficiency of conversion of digested food to biomass. ★ = Floral parts. ● = High leaves. ○ = Low leaves. $r = -.6763$, $n = 30$, $p < .001$; $y = 101.453 - 19.082x$.

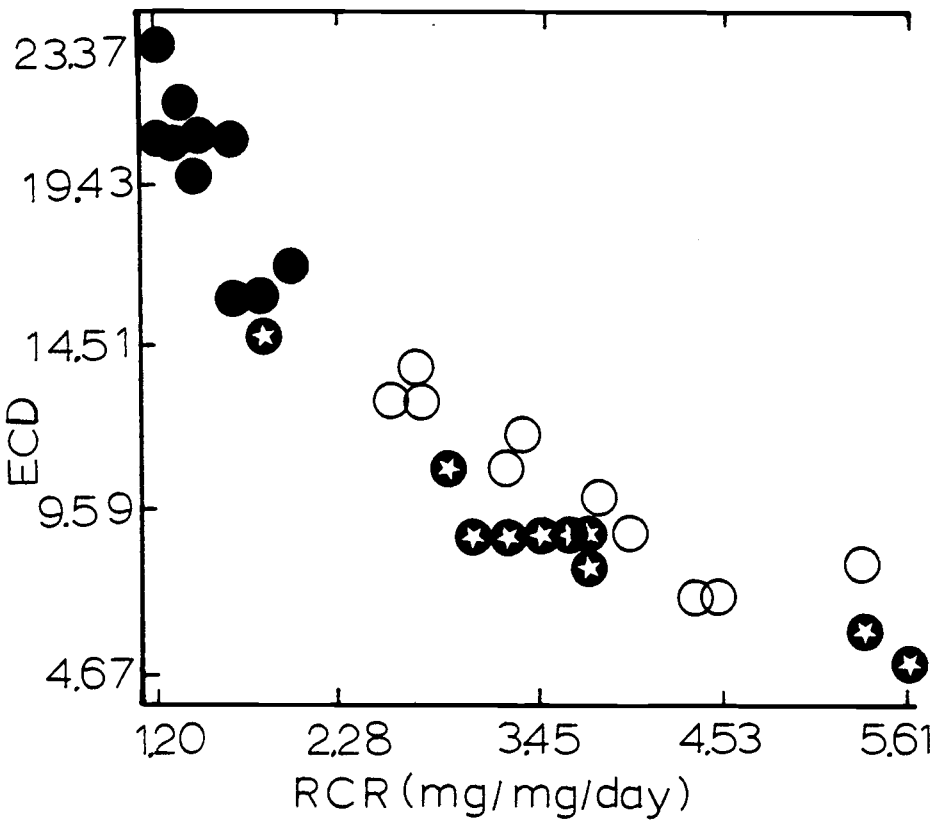

Figure 10. The relationship between the relative consumption rate and the efficiency of conversion of ingested food. ★ = Floral parts. ● = High leaves. ○ = Low leaves. $r = .9329$, $n = 30$, $p < .01$; $y = 25.101 - 3.994x$.

accumulation and consumption of nitrogen did not vary significantly between leaf diets. Plant parts ranked in order of increasing NUE are: Low < High < Floral. Larvae fed on floral parts utilized nitrogen 1.2 times more efficiently than larvae fed high leaves and 1.6 times more efficiently than larvae fed low leaves.

The proportion of food assimilated (AD) showed a strong positive correlation to the rate of nitrogen consumption (RNCR) and accumulation (RNAR) within all diets (Figs. 11 and 12). The rate of increase of AD levels off at higher nitrogen consumption and accumulation rates.

The efficiency of conversion of digested food to biomass (ECD) was strongly negatively correlated to RNCR and RNAR (Figs. 13 and 14). This correlation was significant within all diets.

The overall ability of the insect to convert ingested food to biomass (ECI) was also strongly negatively correlated to RNCR and RNAR within all diets (Figs. 15 and 16). Because ECI = AD x ECD, and since AD showed an increase with increased rates of nitrogen consumption, the decline in ECI must be due to the reduced efficiency of converting digested food at higher rates of nitrogen consumption. Nitrogen utilization efficiency (NUE) increased with respect to RCR for diets of high and low leaves ($p < .1$ level)(Fig. 17). NUE increased more rapidly in high leaf diets. For diets of floral parts NUE was stable over a range of RCR values. NUE showed a strong positive correlation with RNCR in low leaf diets only (Fig. 18). High leaf and Floral diets show relatively constant NUE values with changes

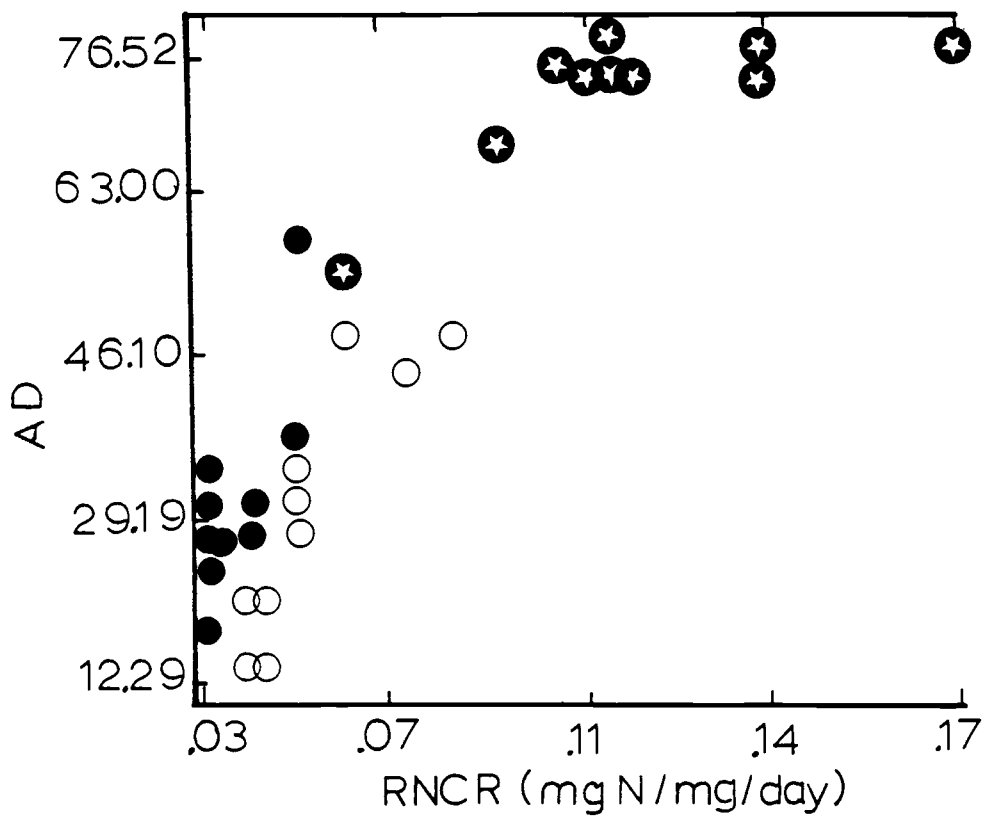

Figure 11. The relationship between the relative nitrogen consumption rate and approximate digestibility. ✪ = Floral parts. ● = High leaves. ○ = Low leaves. $y = 10.4145 + 509.588x$, $r^2 = .7856$.

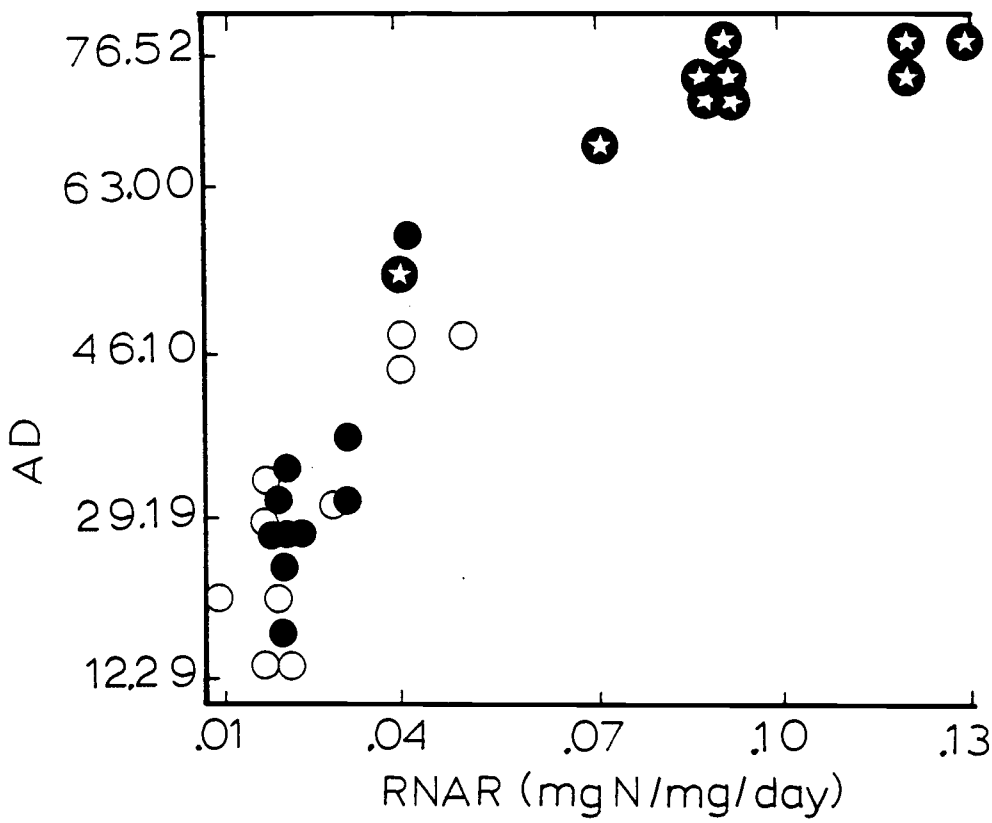

Figure 12. The relationship between the relative nitrogen accumulation rate and approximate digestibility. ★ = Floral parts. ● = High leaves. ○ = Low leaves. $r = .9239$, $n = 30$, $p < .001$.

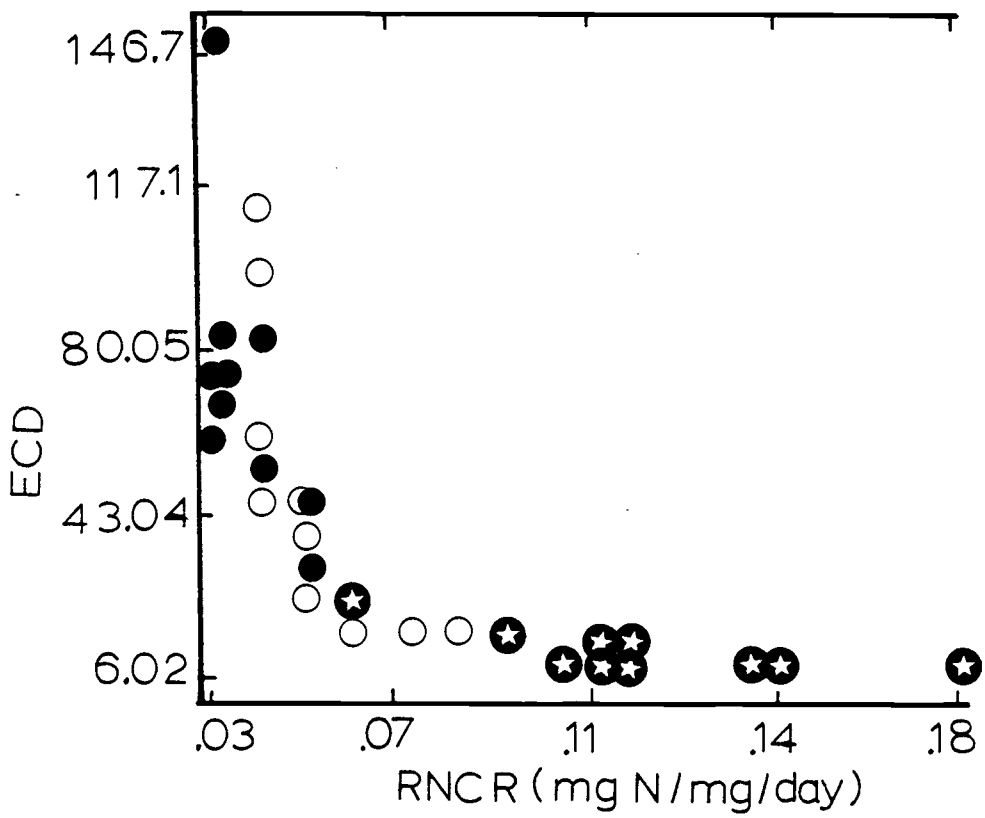

Figure 13. The relationship between relative nitrogen consumption rate and efficiency of conversion of digested food to biomass. ★ = Floral parts. ● = High leaves. ○ = Low leaves. Log y = -0.437 - 1.56 log x , r^2 = .8901.

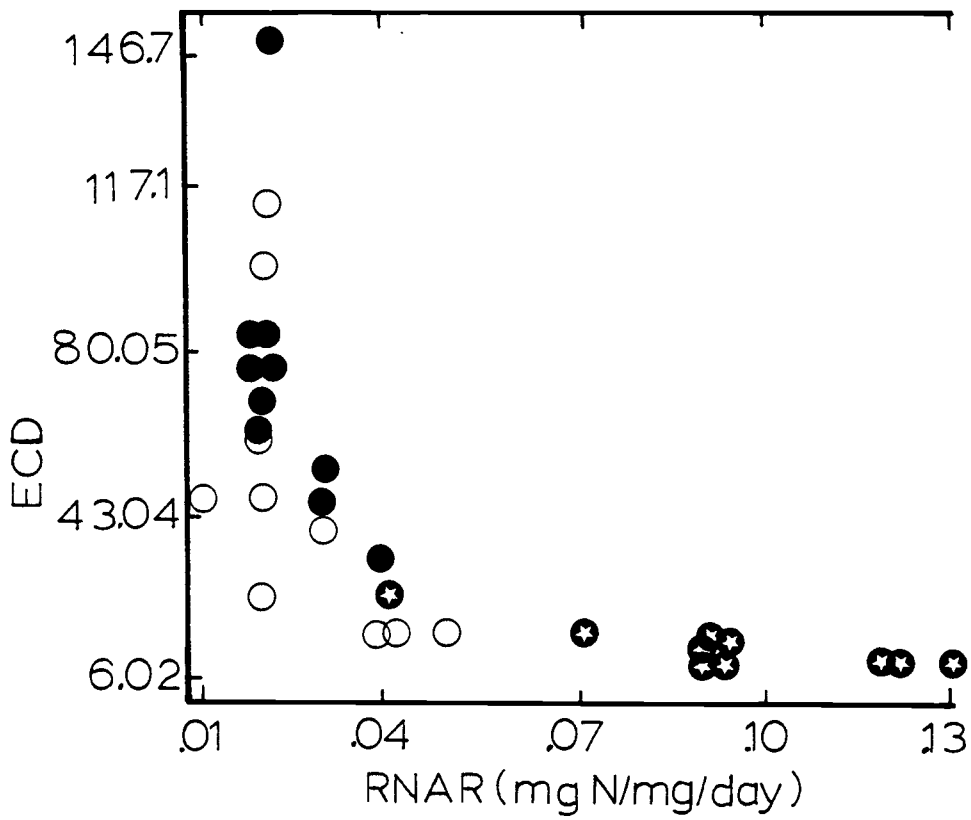

Figure 14. The relationship between relative nitrogen accumulation rate and efficiency of conversion of digested food to biomass. ✪ = Floral parts. ● = High leaves. ○ = Low leaves. Log y = -0.107 - 1.116 log x, r^2 = .7999.

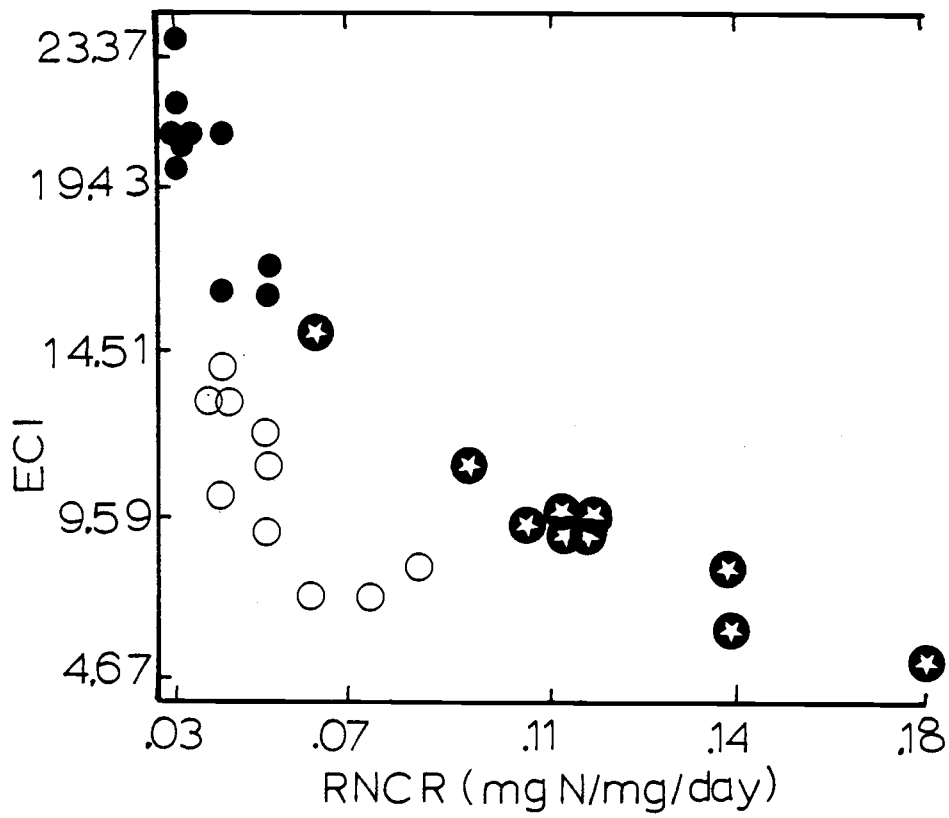

Figure 15. The relationship between the relative nitrogen consumption rate and efficiency of conversion of ingested food to biomass. ★ = Floral parts. ● = High leaves. ○ = Low leaves. Log y = 0.233 - 0.686 log x , r^2 = .7296.

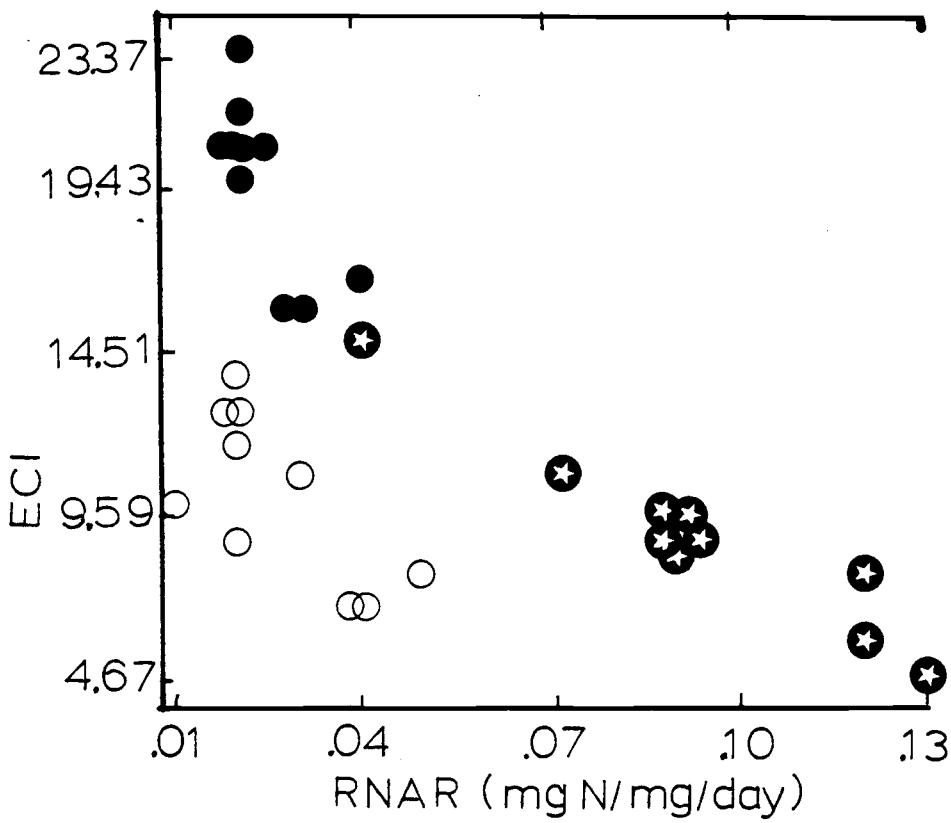

Figure 16. The relationship between the relative nitrogen accumulation rate and efficiency of conversion of ingested food to biomass. ★ = Floral parts. ● = High leaves. ○ = Low leaves. Log y = 0.480 - 0.419 log X , r^2 = .4789.

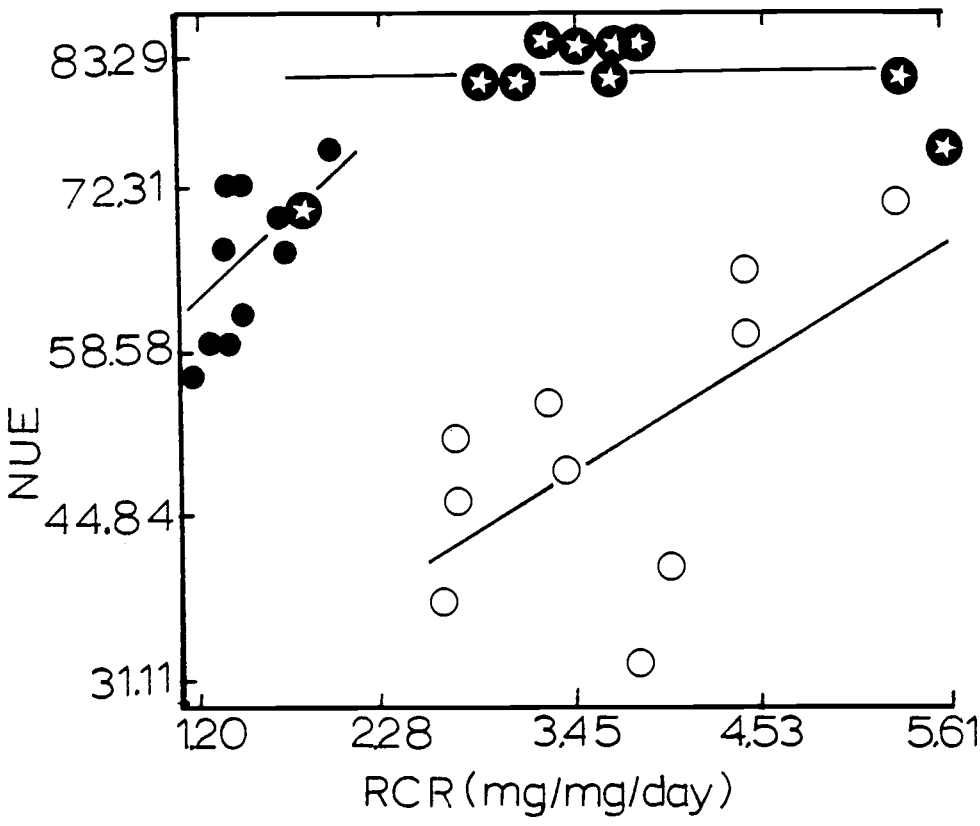

Figure 17. The relationship between the relative consumption rate and nitrogen utilization efficiency. ✪ = Floral parts: r = .1181, n = 10. ● = High leaves, r = .6029, n = 10. ○ = Low leaves, r = .6219, n = 10.

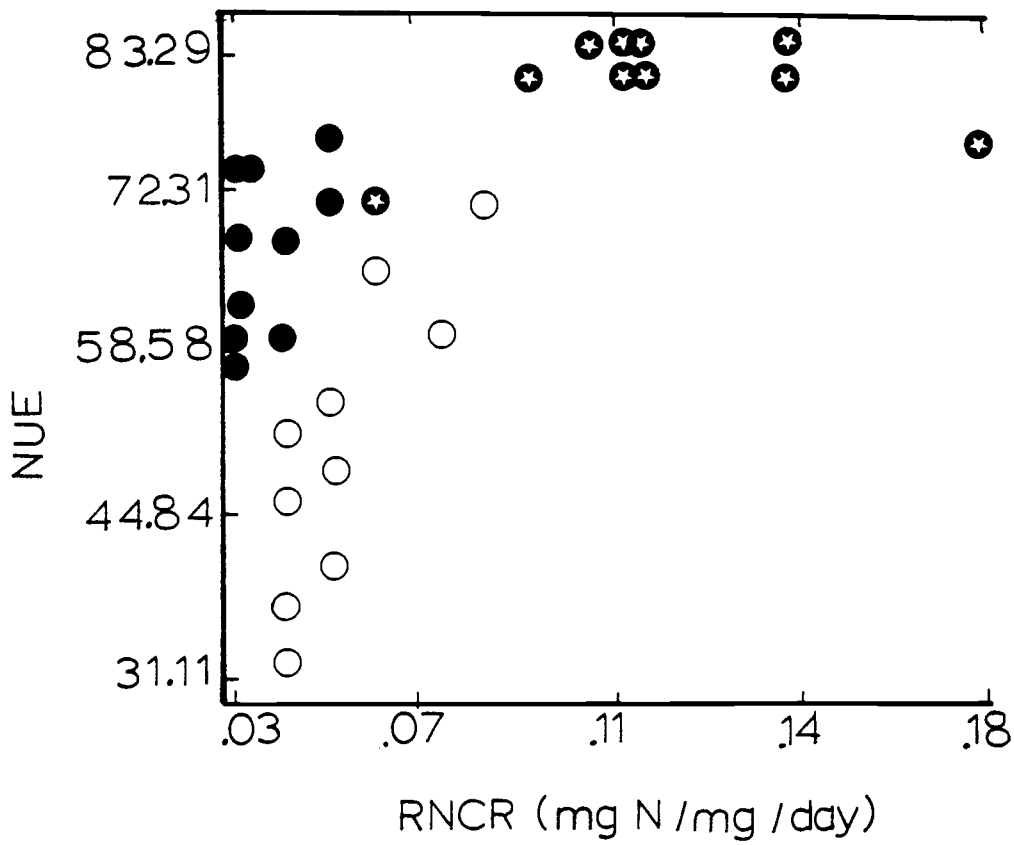

Figure 18. The relationship between relative nitrogen consumption rate and nitrogen utilization efficiency. ✪ = Floral parts. ● = High leaves. ○ = Low leaves. $r = .6303$, $n = 30$, $p < .001$.

in RNCR, with Floral diets showing the least effect. NUE showed a similar relationship to RNAR, with Low leaf diets exhibiting a strong positive correlation (Fig. 19). High leaf and Floral diets did not show significant correlations, but again the level of correlation was greater in High leaf diets than in Floral diets which demonstrated a fairly constant NUE.

Relationships Between Plant Water Content and Parameters of Feeding Efficiency

Relative growth rate (RGR) showed a significant correlation to plant water content (Fig. 20: $r = .4622$, $n = 28$, $p < .05$). Water content of larvae averaged around 86 percent, about the same as the water content of high leaves and floral parts and less than the water content of low leaves on which the highest RGR occurred.

There was a significant negative correlation between plant water and approximate digestibility (AD), ($r = -.4184$, $n = 30$, $p < .05$), the rate of nitrogen accumulation (RNAR), ($r = 0.4374$, $n = 30$, $p < .05$). and nitrogen utilization efficiency (NUE), ($r = -.6233$, $n = 30$, $p < .001$). These correlations could be an indirect result of variance in other factors which varied with water content. The strong negative correlation of plant water and plant nitrogen (Fig. 21), which is also strongly positively correlated to these parameters could have this effect. Water content was not significantly correlated to other parameters examined, neither within diets nor among diets (Appendix I).

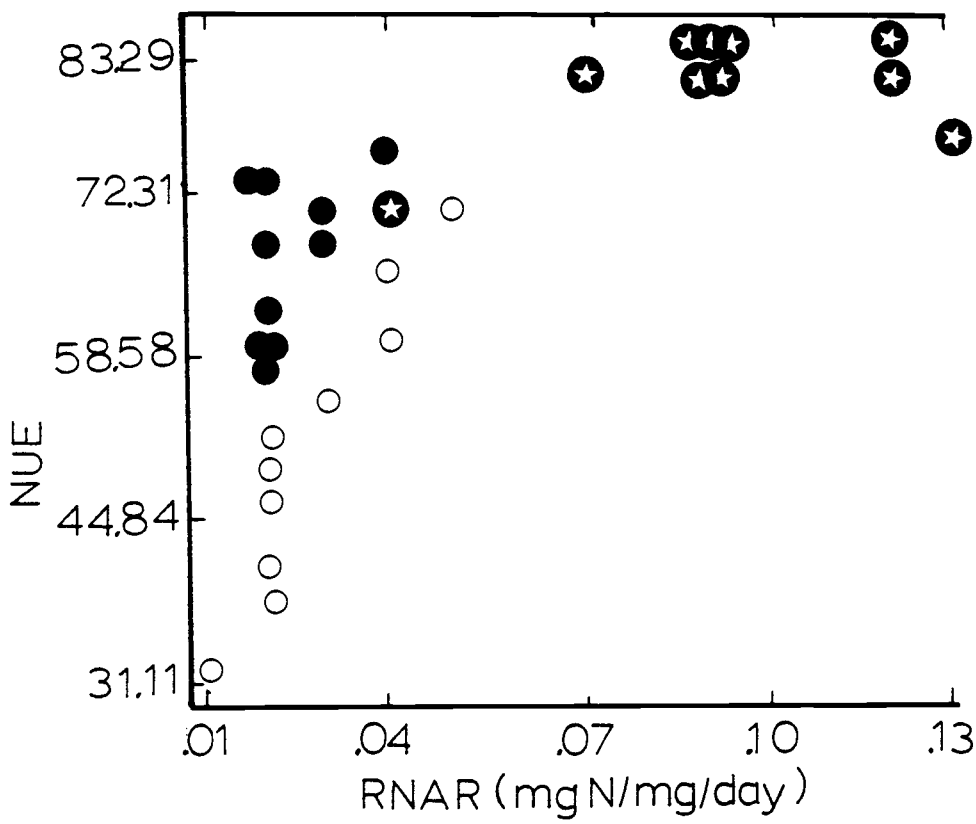

Figure 19. The relationship between the relative nitrogen accumulation rate and nitrogen utilization efficiency. ★ = Floral parts. ● = High leaves. ○ = Low leaves. Log y = 2.209 + .2788 log x , r^2 = .6041.

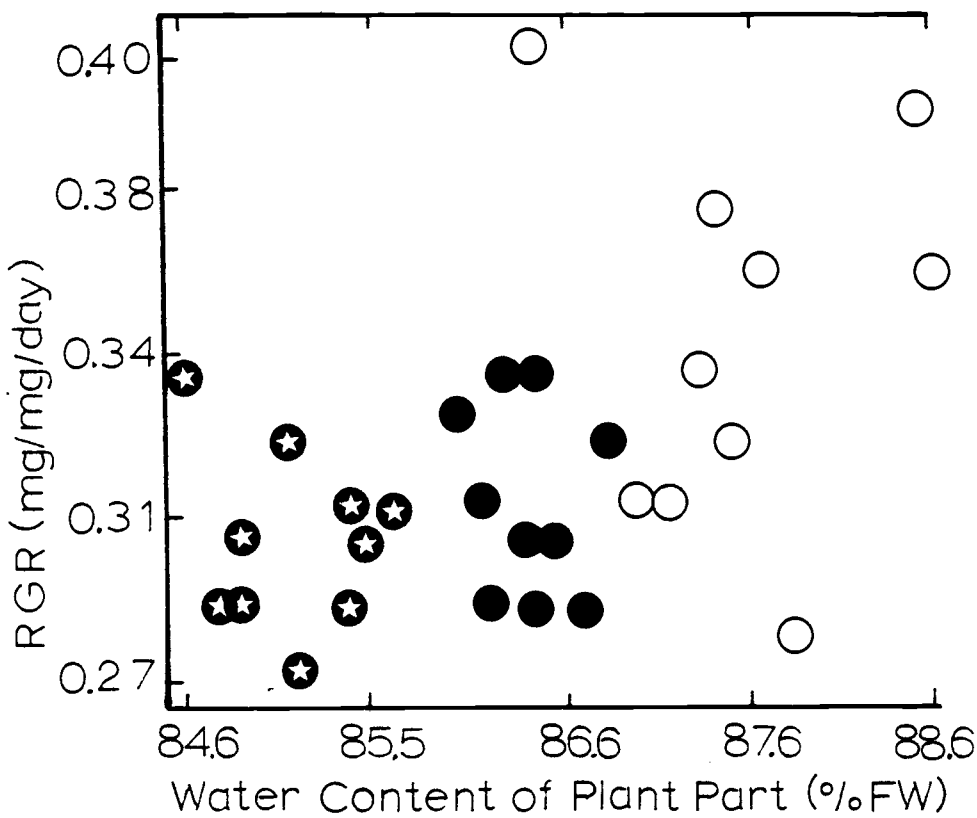

Figure 20. The relationship between plant part water content and relative growth rate. ★ = Floral parts. ● = High leaves. ○ = Low leaves. $r = .4622$, $n = 30$, $p < .05$.

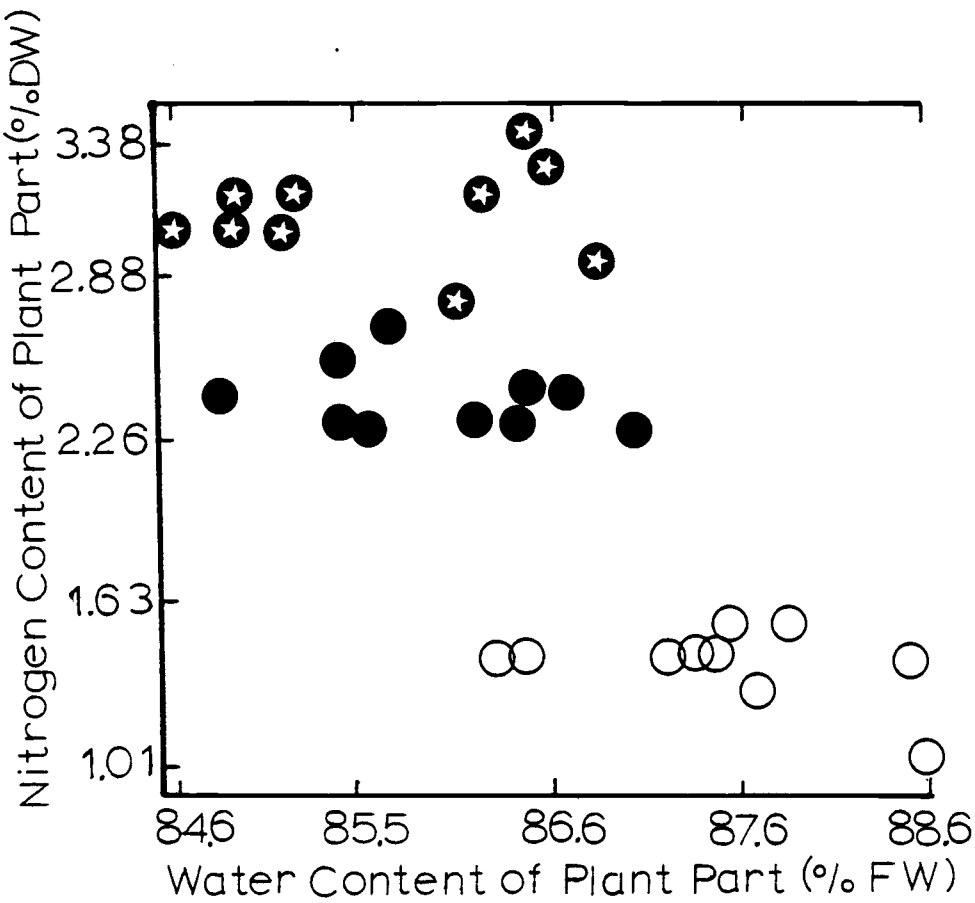

Figure 21. The relationship between plant part nitrogen content and water content. ✪ = Floral parts. ● = High leaves. ○ = Low leaves. $r = -.7250$, $n = 30$, $p < .001$.

Relationships Between Plant Nitrogen Content and Parameters of Feeding Efficiency

Relative growth rate (RGR) is negatively correlated with plant nitrogen content over all diets (Fig. 22). RGR appeared independent of nitrogen content in larvae fed on low leaves. Within High leaf and Floral diets, the correlation was insignificant at the 0.05 level, however the negative correlation was stronger in Floral diets.

Relative consumption rate (RCR) was negatively correlated with Floral nitrogen, at the $p < .1$ level (Fig. 23). No significant relationship was seen within separate leaf diets, however considered together they showed a strong negative correlation at the $p < .001$ level.

The proportion of food assimilated (AD) showed a strong positive correlation to increasing nitrogen levels when examined over all diets (Fig. 24). The correlation within separate diets was insignificant, except for the Floral diet which showed a positive correlation at the $p < .05$ level.

The efficiency at converting digested food to biomass showed separate trends in Floral and leaf diets (Fig. 25). When ECD values are examined, excluding the three values over 100 percent, it is clear that ECD increases with increasing plant nitrogen for leaf diets considered together and for the Floral diet. The ECD of larvae fed on floral parts is much lower than expected, considering the trend of increase with increasing nitrogen seen in leaves. The relationship of ECI with plant nitrogen shows a similar pattern. There is an increase

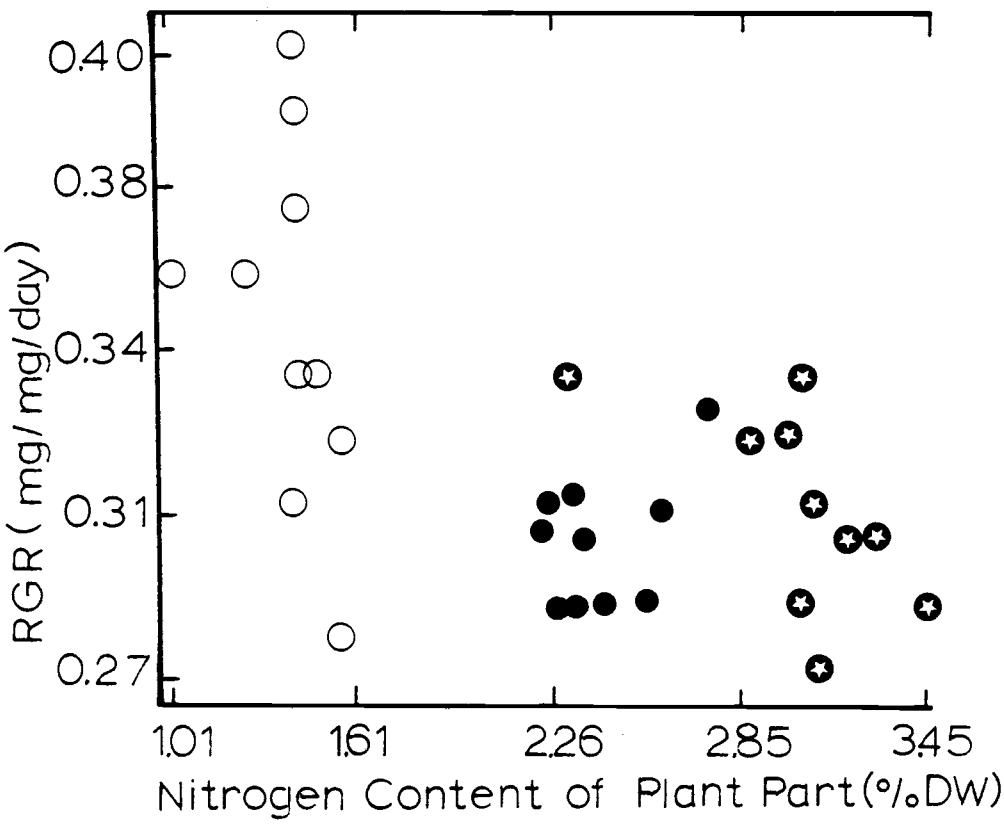

Figure 22. The relationship between plant part nitrogen content and relative growth rate. ✪ = Floral parts. ● = High leaves. ○ = Low leaves. $r = -.5928$, $n = 39$, $p < .01$.

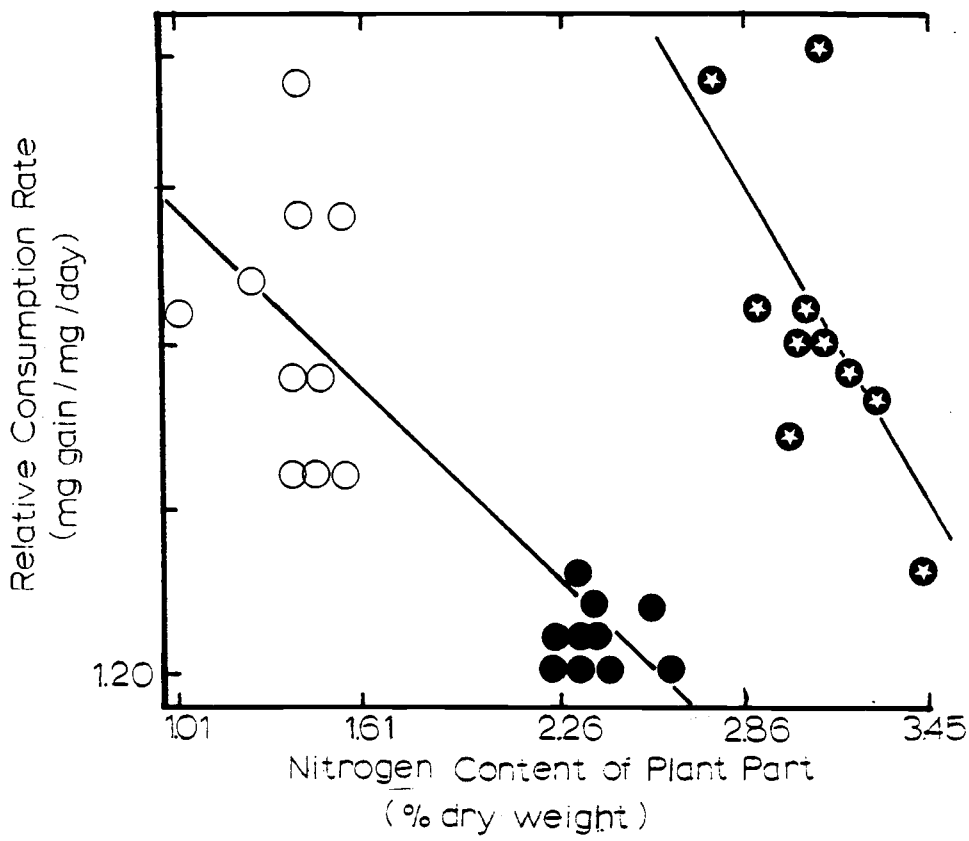

Figure 23. The relationship between the nitrogen content of plant parts and relative consumption rate (RCR) of cinnabar moth larvae. ✪ = Floral parts: 4 = -0.6306, n = 10, $p < .1$; $y = 14.549 - 3.470x$. ● = High leaves: $r = 0.9766$. ○ = Low leaves: $r = -0.1909$. Leaves together: $r = -0.8555$, $n = 20$, $p < .001$; $y = 6.590 - 2.0797x$.

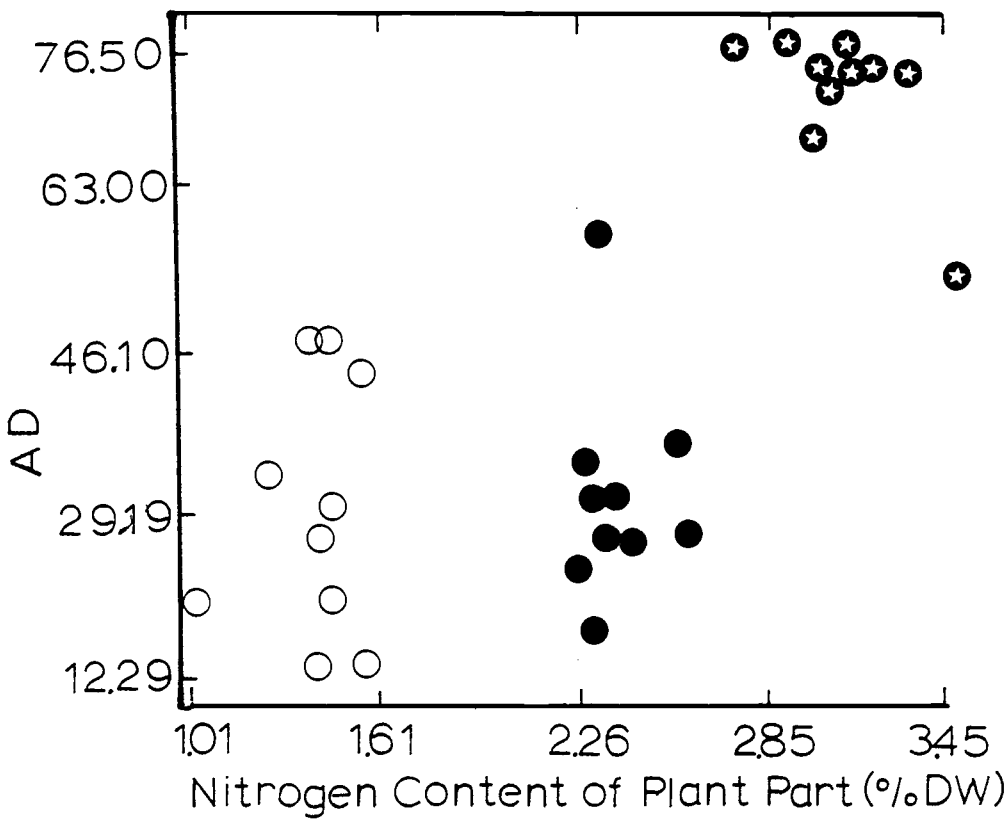

Figure 24. The relationship between the nitrogen content of plant parts and approximate digestibility. =Floral parts. = High leaves. =Low leaves. $y = -7.254 + 22.556\,x$, $r^2 = .5126$.

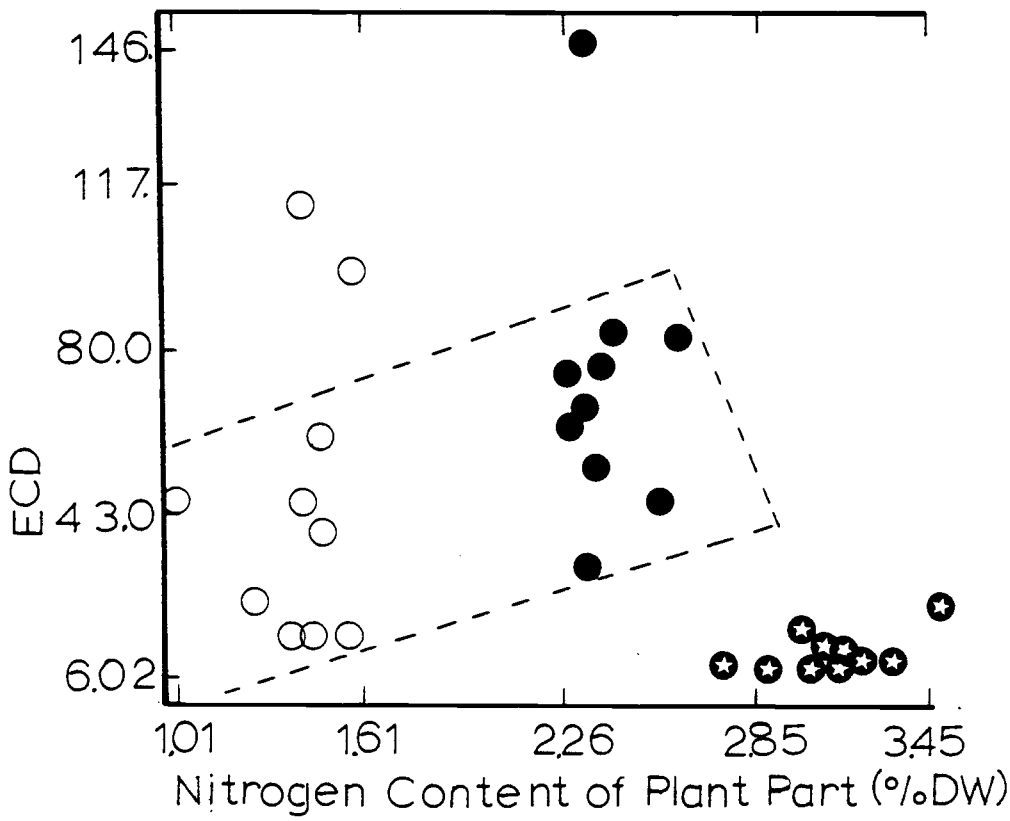

Figure 25. The relationship between the nitrogen content of plant parts and efficiency of converting digested food to biomass. ✪ = Floral parts; r= .6626, n= 10, P< .05. ● = High leaves. ○ = Low leaves. Leaves together:r= .3456, n= 20, P> .1. (Includes outliers).

in ECI with increasing nitrogen in leaf diets considered together and in the Foral diet considered separately (Fig. 26). Again, the ECI values of Floral diet fed larvae were much lower than expected considering the trend seen in leaves.

As the nitrogen content of leaves fed increased, the relative rate of nitrogen consumption (RNCR) appeared to decline slightly (Fig. 27). However, the means of RNCR on High and Low leaf diets are not significantly different. Regression analysis of leaf data revealed a r^2 value of 0.2640, meaning only 26 percent of the observed variation in RNCR can be accounted for by the regression. The RNCR values on Floral diets with higher nitrogen content were high and slightly negatively correlated with nitrogen. Similar trends are seen with the relationship of relative nitrogen accumulation rate (Fig. 28). Floral diet RNAR values are high and slightly negatively correlated ($r = -.5722$, $p < .1$) leaf diets the correlation is near zero ($r = -.5722$, $p < .1$) leaf diets the correlation is near zero ($r = .0606$). This suggests a stable rate of nitrogen accumulation over different levels of plant nitrogen in larvae fed on leaves. Larvae fed on Floral diets accumulate nitrogen at a relatively faster rate than leaf fed larvae and although variability appears high for RNAR values, there is also some stabilization of RNAR, since as nitrogen content of floral parts increases accumulation of nitrogen does not increase. Figure 29 illustrates that for higher nitrogen content diets the plateau level of nitrogen accumulation can be reached at lower consumption rates than on diets lower in nitrogen. Larvae fed on floral diet accumulate the most nitrogen when consumption rates are high and floral nitrogen

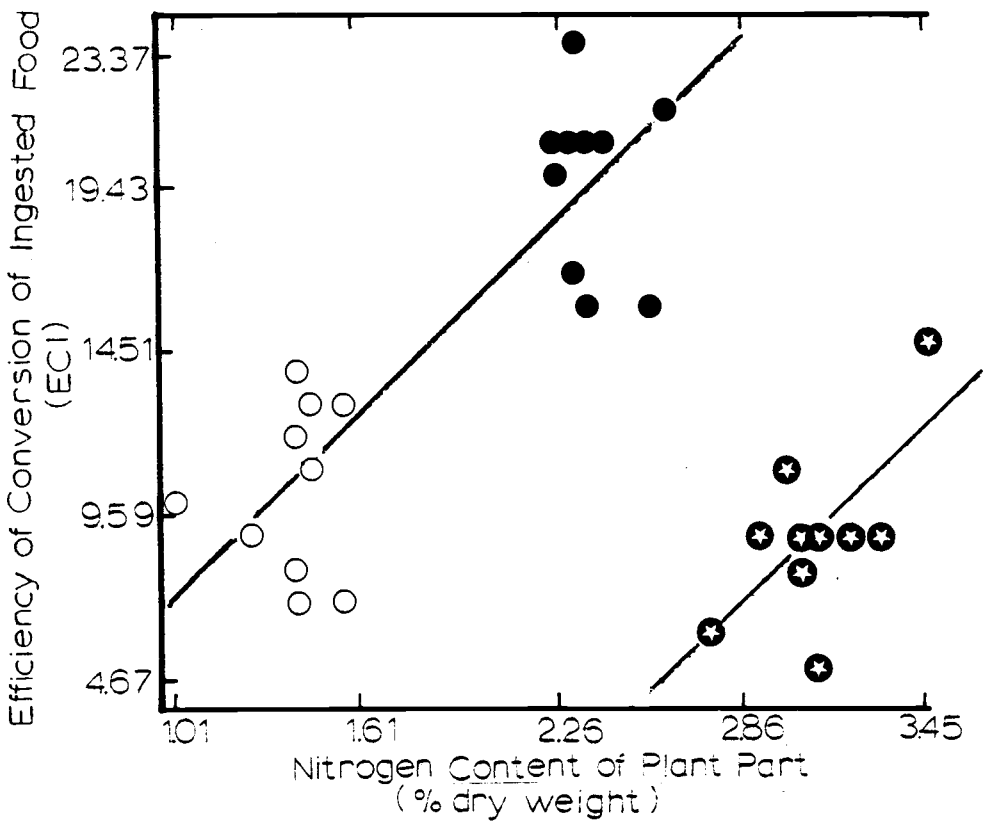

Figure 26. The relationship between nitrogen content of plant parts and relative consumption rate (RCR) of cinnabar moth larvae. ✪ = Floral parts: $r = 0.6287$, $n = 10$, $p < .1$; $y = -18.678 + 8.871x$. ● = High leaves. ○ = Low leaves. Leaves together: $r = .8513$, $n = 20$, $p < .001$; $y = 01.912 + 9.001x$.

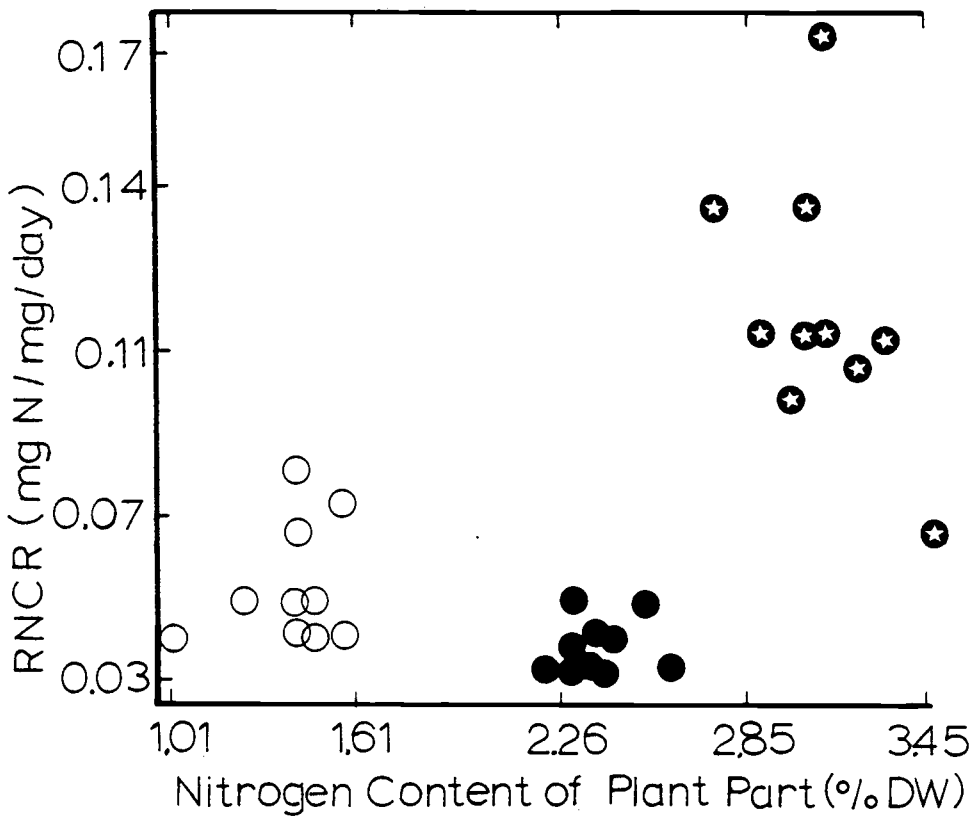

Figure 27. The relationship of nitrogen content of plant parts and the rate of nitrogen consumption ✪ = Floral: r= -.4726, n= 10, P > .1. ● = High leaves. ○ = Low leaves. Leaves together: r= -.5171, n= 20, P < .05.

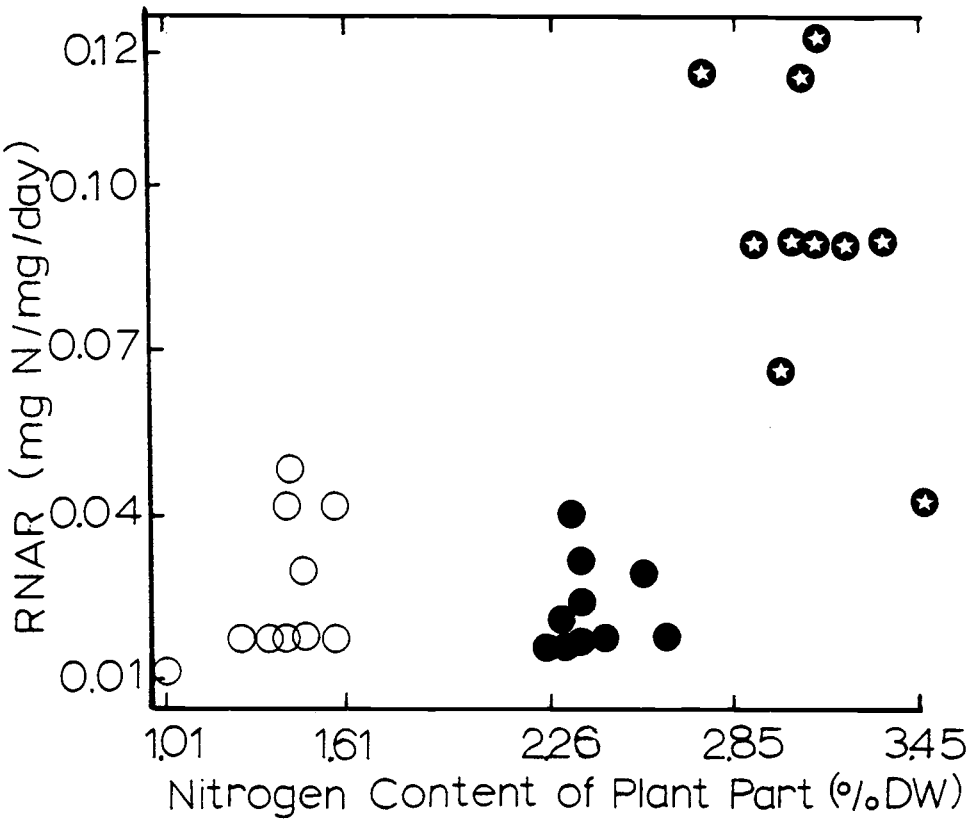

Figure 28. The relationship of nitrogen content of plant parts and the relative rate of nitrogen accumulation. ✪ = Floral parts: r= -.5722, n= 10, P < .1. ● = High leaves; ○= Low leaves. Leaves together: r= -.0606, n= 20, P > .1.

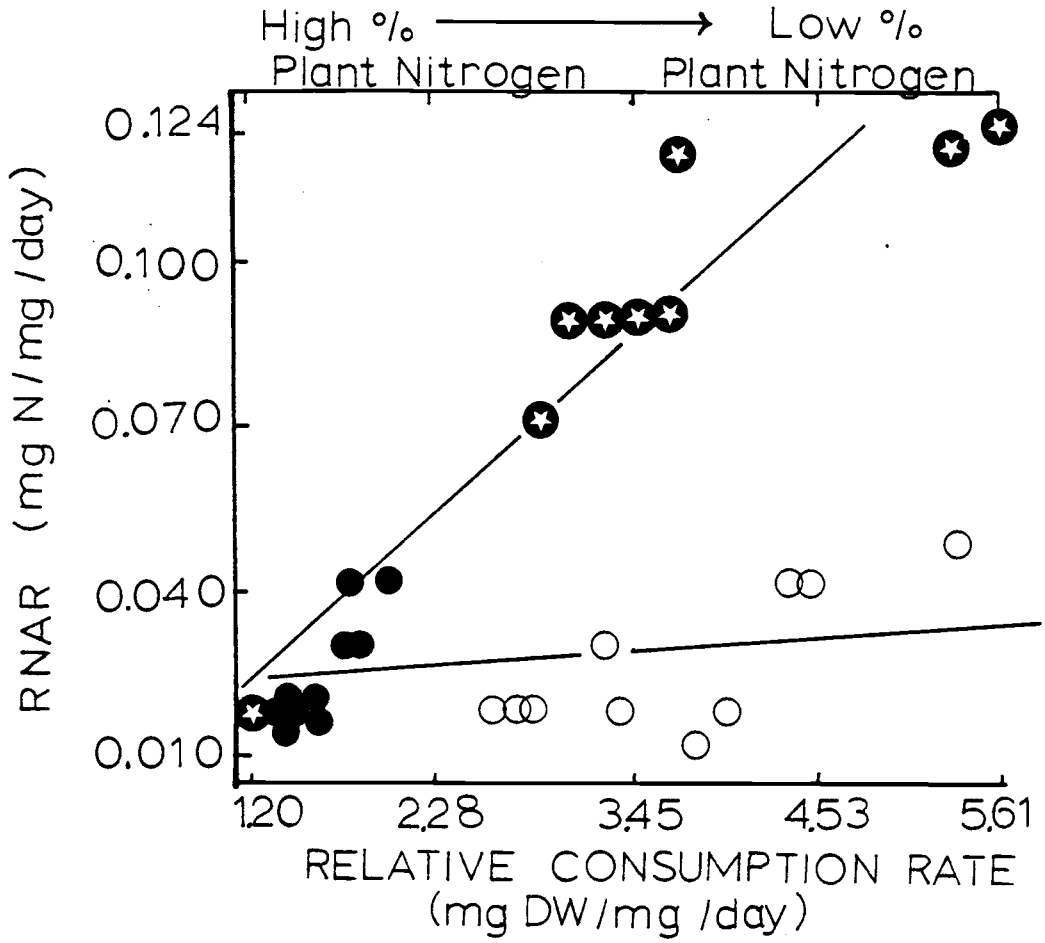

Figure 29. The relationship between the relative consumption rate (RCR) and relative nitrogen accumulation rate (RNAR). ✪ = Floral parts: $r = 0.9022$, $n = 10$, $p < .001$; $y = 0.015 + 0.021x$. ● = High leaves. ○ = Low leaves. Leaves together: $r = 0.5030$, $n = 20$, $p < .05$; $y = 0.015 + 0.004x$.

content is lowest.

The efficiency of nitrogen utilization (NUE) was positively correlated to nitrogen content of plant parts when examined over all diets (Fig. 30). Within diet group correlations were not found. As previously discussed, NUE showed increases with increasing values of RNCR and RNAR at the low levels of nitrogen found in low leaves.

DISCUSSION

Spatial and Temporal Changes in Plant Food Quality

The pattern of variation in dry matter and nitrogen content I observed within the plant and seasonally agrees with the general understanding of energy allocation and nitrogen metabolism in plants. Plants have a vertical age structure, with parts at different heights changing in function and value to the plant as they mature and senesce (Harper 1977). Apical regions and young leaves are dependent structures, active in the reduction of nitrate, which is transported to them along with carbon skeletons, from lower regions of the plant (Steward and Durzan 1965). They accumulate amino constituents from this assimilation of nitrate. Older leaves are exporters of the organic materials produced in them by photosynthesis. Photosynthetic enzymes are prominent proteins, the total amounts of leaf protein reaching a maximum when the leaf has fully expanded (Beevers 1976). With leaf senescence, there is a rapid decrease in soluble nitrogen and protein content. I found younger leaves (high on the stem) to have a higher nitrogen content than older (low) senescing leaves.

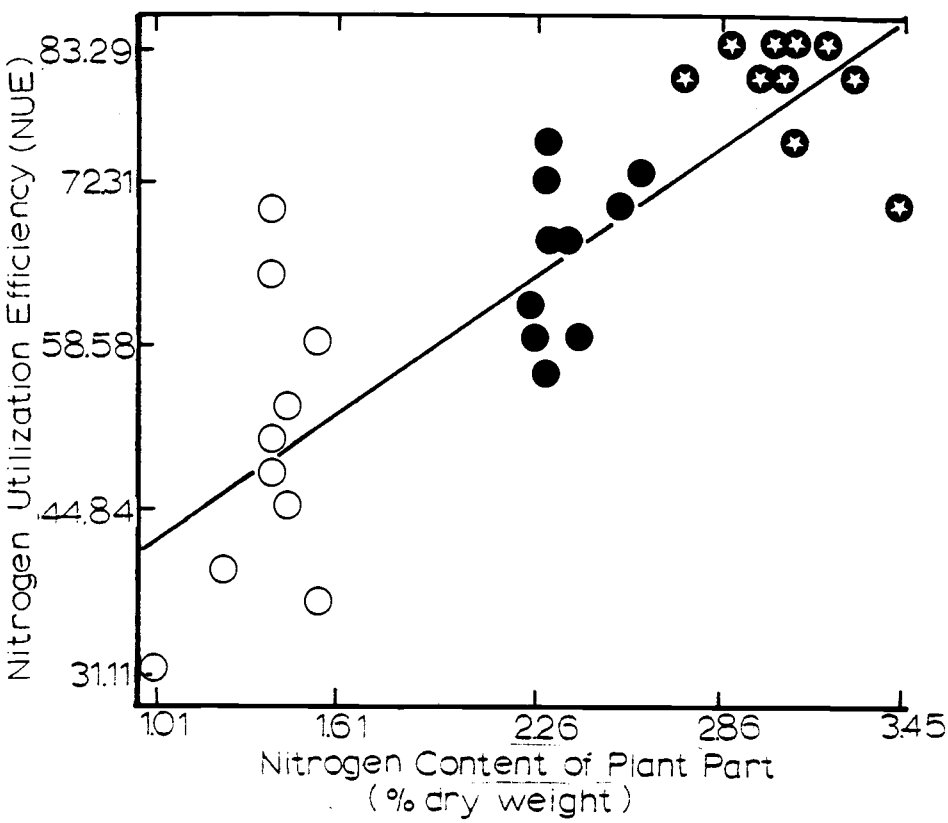

Figure 30. The relationship between nitrogen content of plant parts and nitrogen utilization efficiency (NUE) of cinnabar moth larvae. ✪ = Floral parts. ● = High leaves. ○ = Low leaves. $r = 0.8397$, $n = 30$, $p < .001$; $y = 26.144 + 17.467x$.

Reproductive tissues have generally higher caloric values and higher percentages of dry matter than vegetative parts (Hickman and Pitelka 1975). Floral parts have also been shown to be higher in nitrogen content than leaves (Woodwell et al. 1975). This agrees with my findings of the higher dry matter and nitrogen content of floral parts.

The steepness of the gradient in nitrogen content within a plant is striking. By feeding on floral parts of a plant, rather than basal leaves, a larva can feed on tissue that is 2 to 3 times higher in nitrogen content.

Although my attempt to examine alkaloid content of plant tissues was unsuccessful, the probable variation in alkaloid content can be surmised from the literature. Alkaloids are known to be prominent in actively growing tissues. Alkaloid content of leaves increases during cell enlargement and vacuolization then decreases as leaves age (Robinson 1979). Flowers of Senecio jacobaea have been shown to contain at least twice as much alkaloid as leaves (Dickenson and King 1978). Floral alkaloid content may be as much as four times higher than leaf (P. Cheeke, personal communication). Aplin and Rothschild (1972) showed seasonal variation in the relative amounts of alkaloids present in Senecio. Total percent of alkaloids, dry weight, varied from 0.33 in bolting rosettes in May to a peak of 0.79 in July, declining to 0.23 in December. The increase in relative amounts of seneciphylline along with jacozine accounts for the higher percent of alkaloids found in July. This is interesting because seneciphylline

is known to be the major alkaloid stored by cinnabar moth larvae, actively concentrated above levels found in the plant. There are also differences in relative concentration of individual alkaloids among plant parts. Swick (1979) found senecionine and seneciphylline in much higher concentrations in flowers than other plant parts of Senecio. The alkaloids which are prevalent in the plant (jacoline, jacozine, and jacobine) are found in highest concentrations in leaves and are not actively concentrated by the insect. Aplin and Rothschild suggest oviposition behavior of adults may be explained by their preference for plants which are rich in seneciphylline early in the season. Possibly larval feeding preference is influenced by selection of alkaloid-rich (and/or seneciphylline-rich) floral parts. The specific distribution of alkaloids in Senecio warrants further study.

Correlation of Timing of Attack and Feeding Site with Variation in Plant Food Quality

My results show the timing of cinnabar moth attack to be correlated with the period of peak standing crops of dry matter and nitrogen in leaves and flowers. The main concentration of larval feeding pressure seems more closely atuned to the peak in floral biomass rather than total plant biomass. Green (1974) found the numerical peak of fifth instar cinnabar moth larvae which consume 75 percent of the total food eaten by a larva in its lifetime, coincided with early flowering in Tansy Ragwort. Phenological adaptations of other herbivores to their host plant's nutritional status have been observed. Feeny (1970) found the larval feeding of winter moth on oak correlated

to seasonal changes in tannin content and leaf protein; early spring feeding occurs at a time of maximum leaf protein content and minimum tannin content. Peaks in population density of the aphid, Holcus mollis, coincide with periods of high nitrogen availability in its host plant (MacNeil 1970). Maximum numbers of 2nd and 3rd instar larvae of the cinnabar moth were found at a time when floral biomass and available nitrogen were at a maximum. These instars consume far less food than later instars. If their feeding preference for floral parts is of adaptive significance, this allows a greater percentage of the population to feed on high quality food early in their life cycle. In holometabolic insects soluble storage proteins are synthesized by the fat body at the highest rate during early to mid-larval instars (Chen 1978). When feeding stops in the pre-pupae, proteins are selectively sequestered by the fat body for later release and degradation for de novo synthesis of adult proteins. Thus, the quality of food consumed in early instars affects reserves for the synthesis of adult proteins which include vitellogenins, the yolk proteins needed for egg production. Fourth and 5th instar larvae in heavily infested areas are often faced with eating only low leaves and remaining petioles of higher leaves. As floral buds mature, and the pappus for seed dispersal develops, the proportion of indigestible cellulose and lignin increases. Thus flowers may be more digestible early in their development, especially to a leaf-feeding insect unadapted to eating seeds and their associated structures.

Rose (1978) observed a later emergence date (about 11 days later) for pupae of cinnabar moth fed on floral diets. Thus, offspring of

larvae fed floral parts would be less likely to find floral buds. However, if eating leaves selects for early emergence, the offspring of larvae which did not find floral buds would be more likely to find them in the following year. Most larvae have pupated by the time the standing crop of dry matter and nitrogen have reached very low levels.

Variation in feeding site correlated to host plant food quality is an adaptation seen in many insects (MacNeil and Southwood 1978). The mirid, Leptopterna dolabrata, shows a change in feeding site from leaves to flowers, at a time when maximum growth is occurring and gonadal development is beginning (MacNeil 1973). At this part of its life cycle when the demand for nitrogen is high, it feeds on the young seed in flowers which are high in nitrogen and avoids leaves whose levels of nitrogen are falling. There may be demands for nitrogen in early instars of the cinnabar moth which are met by this change in feeding habit. I observed a preference of flower-eating larvae for the florets of the floral bud. These were eaten first leaving the involucral bracts and receptacle. Analysis of a few samples of florets and bracts revealed florets to be nearly twice as high in nitrogen as bracts, and higher in water content.

Nutritional Parameters as a Measure of Host Plant Utilization

The values of the various nutritional parameters I determined fall in the range reported in other nutritional studies (Scriber 1977, Slansky and Feeny 1977, Scriber and Feeny 1979). It is striking that I found nutritional indices varying as much with diets of plant parts

of a single plant species as others have found with diets of different plant species. This suggests great caution should be employed in nutritional studies, so that similar plant parts from different plant species used for feeding performance comparisons which are of comparable stages of development.

Nutritional indices are useful in evaluating general feeding performance, however they do not identify the specific factors which influence performance. The use of artificial diets with known amounts of nutrients or non-nutrients added improves the resolution of nutritional assessments (Reese 1978). More sophisticated studies can also measure the timed-specific growth of organs and tissues as correlated to food utilization (Woodring et al. 1979). In a study of this type, it is not possible to state conclusively what aspect of plant food causes the variation in performance observed. Nitrogen, however, appears to play a dominant role in the growth of herbivorous insects and the results of this study are in general agreement with the theory of nitrogen utilization presented by Slansky and Feeny (1977).

Feeding Performance of Larvae on Leaves

Slansky and Feeny (1977) predict the following concerning utilization of food and, specifically, nitrogen:

1. The consumption rate is adjusted to maximize nitrogen accumulation rate (and hence growth rate).
2. The rate of nitrogen accumulation is limited by declining nitrogen utilization efficiency at higher consumption rates.

3. The consumption rate on a plant is adjusted to the lowest value at which maximal nitrogen accumulation can be achieved since net growth efficiency declines with increasing consumption rate.

I found the gross growth efficiency of ECI of cinnabar larvae fed on leaves increased with increasing levels of nitrogen. Larvae consumed smaller amounts of more nutritious leaves. The proportion of assimilated food and the ability to convert assimilated food to biomass increased as nitrogen levels in leaves increased. Therefore, it appears larvae fed on leaves were more efficient at utilizing their food source when fed on leaves of a higher nitrogen content. Barbosa and Gremblatt (1979) found higher gross and net growth efficiencies for gypsy moth larvae fed on diets highest in nitrogen content. The relatively constant growth rate I observed for larvae fed on diets with differing amounts of nitrogen was due to a decline in both gross growth efficiency (ECI) and the efficiency of converting digested food to biomass (ECD) with increasing consumption rates. Decreased gut retention time (MacNeil and Southwood 1978) and increased costs in terms of loss of digestive enzymes and respiratory losses during feeding (Slansky and Feeny, 1977) may account for this. Although an increased consumption rate led to a decline in gross growth efficiency, it allowed larvae fed on less nutritious diets to consume and accumulate nitrogen at a rate equal to that of larvae fed more nutritious diets. Food high in nitrogen was easier to assimilate and the proportion assimilated increased with the rate of consumption of nitrogen,

but gross growth efficiency declined as nitrogen was eaten at a faster rate. Nitrogen was utilized more efficiently when present in higher concentrations, but the efficiency of utilization was not affected by how fast it was consumed. Therefore, eating more nitrogen did not mean the larvae accumulated more nitrogen. Larvae feeding on leaves must sacrifice their gross growth efficiency to maintain a fairly constant rate of nitrogen accumulation, however their gross growth efficiency is higher when fed foods higher in nitrogen content.

Feeding Performance of Larvae on Floral Parts

The relationships of nutritional indices and food quality differed in several significant ways from predicted trends for larvae fed on floral parts. Floral parts have a high nitrogen content, yet consumption rate is high. As the larvae consume more plant tissue of higher nitrogen content, they accumulate more nitrogen (Fig. 29). There is some stabilization of nitrogen accumulation rate. Larvae fed on floral parts accumulate relatively more nitrogen than leaf-fed larvae because of higher nitrogen consumption rate and higher nitrogen utilization efficiency. Slansky and Feeny (1977) saw unusually high NUE values for a given NCR for larvae fed on Dentaria and highly fertilized collards; they suggested this was due to a greater proportion of easily digestible nitrogen in these plants. It is possible the high levels of alkaloid in flowers impose costs for their active sequesteration and concentration. Although the cinnabar moth is considered an adapted herbivore, there may be dosage-dependent effects

of alkaloid, higher amounts requiring detoxification systems to be employed. A metabolite which is a fragment of a pyrrolizidine alkaloid was found in analysis of cinnabar pupae and adults, indicating the moth alters some alkaloids metabolically (Aplin and Rothschild 1972). There may be an increased respiratory burden imposed in eating flowers. Larvae must remove florets from the involucral bract encasement and handling of flower parts could incur a higher respiratory rate. This could be tested easily by measuring respiration rates of larvae on different diets.

Why do larvae eat floral parts preferentially if they must sacrifice growth efficiency? Part of the answer may lie in the increased fecundity observed for larvae fed on floral parts (Van der Meijden 1976, Rose 1978). In view of my results, this may be attributable to their higher nitrogen accumulation, due to both a high rate of nitrogen consumption and a high efficiency of utilization. Nutrition in larval stages often influences the fecundity of adults, especially when adults are non-feeding (Engelmann 1970). Nitrogen accumulation will effect available reserves of proteins necessary for synthesis of adult tissues and yolk proteins.

CONCLUSION

Patterns of food quality of Senecio jacobaea correlate with the timing of cinnabar moth larval attack and foraging behavior. The timing of larval feeding coincides with peaks of available dry matter and nitrogen. Gradients of dry matter and nitrogen within the plant correlate with changes in larval distribution. From the second instar

on, larvae consume floral parts preferentially which are highest in dry matter and nitrogen content. The rate of biomass gain or growth rate was not significantly greater for larvae fed high nitrogen content food, in fact larvae fed the poorest quality food gained biomass at the fastest rate. However, biomass gain may have little effect on overall fitness and feeding performance, as evidenced by higher pupal weights and shorter developmental times for larvae fed floral parts (Van der Meijden 1976, Rose 1978).

A pertinent finding of this study to other studies of nutritional physiology is the range of variability of nutritional indices possible on a single plant species diet. This encourages careful choice of plant parts for testing feeding performance on a range of plant species to minimize effects due to intra-plant differences in food quality.

The gross growth efficiency of larvae eating high leaves which contain more nitrogen is higher than that of larvae eating less nutritious low leaves. Consumption rate is inversely proportional to leaf nitrogen content so that a stable rate of nitrogen accumulation is achieved over a range of nitrogen concentrations in leaves.

Larvae feeding on floral parts show a lowered gross growth efficiency, although they consume more food of a higher nitrogen content. Assimilation of flowers is high so the lowered gross growth efficiency is due to added energetic costs of metabolic processes or respiratory increases. Larvae fed on flowers accumulate more nitrogen, due to both higher nitrogen consumption rate and higher utilization efficiency. This might be due to increased digestibility of floral nitrogen.

It seems likely there is a correlation between this higher nitrogen accumulation and higher fecundity seen in adults which fed on floral parts. Thus selection of floral parts as food could result in increased fitness of cinnabar moth adults by increasing the fecundity component. Biomass gain, and efficiency of food utilization, are not relevant measures of fitness in this case.

BIBLIOGRAPHY

Aplin, R. T., M. H. Benn, and M. Rithschild. 1968. Poisonous alkaloids in the body tissues of the cinnabar moth (Callimorpha jacobaeae L.). Nature (Lond.) 219:747-748.

Aplin, R. T., and M. Rothschild. 1972. Poisonous Alkaloids in the Body Tissues of the Garden Tiger Moth (Arctia caja L.) and the Cinnabar Moth (Tyria jacobaeae L.) Proceedings on the 2nd International Symposium on Animal and Plant Toxins 2:579-595.

Barbosa, P., and J. Gremblatt. 1979. Suitability, Digestibility and Assimilation of Various Host Plants of the Gypsy Moth (Lymantria dispar L.). Oecologia (4361), pp. 111-120.

Beevers, Leonard. 1976. Nitrogen Metabolism in Plants. London: Edward Arnold (Publishers), Ltd.

Bingley, J. B. 1968. Solvent and Temperature Effects in the Determination of Pyrrolizidine Alkaloids with 4-Dimethylamino benzaldehyde. Anal. Chem. 40:1166-1167.

Blau, P. A., P. P. Feeny, L. Contardo, D. S. Robson. 1978. Allylglucosinolate and Herbivorous Caterpillars: A Contrast in Toxicity and Tolerance. Science 200:1296-1298.

Boggs, C. L., and L. E. Gilbert. 1979. Male Contribution to Egg Production in Butterflies: Evidence for Transfer of Nutrients at Mating. Science 206:83-84.

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

Calvert, W. H., L. E. Hedrick, and L. P. Brower. 1979. Mortality of the Monarch Butterfly (Danaus plexippus L.): Avian predation at Five Overwintering Sites in Mexico. Science 204:847-851.

Chen, P. S. 1978. "Protein Synthesis in Relation to Cellular Activation and Deactivation." In M. Rockstein (ed.) Biochemistry of Insects. New York: Academic Press, pp. 145-203.

Culvenor, C. C. J., and J. A. Edgar. 1972. Dihydropyrrolizidine secretions associated with coremata of Utetheisia moths. Experientia 28:627-28.

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

Dickinson, J. O., and R. R. King. 1978. "The Transfer of Pyrrolizidine Alkaloids from Senecio jacobaea into the Milk of Lactating Cows and Goats." In: Keeler, R. G., K. R. Van Kampen, and L. F. James (eds.), Effects of Poisonous Plants on Livestock. New York: Academic Press, pp. 201-208.

Duffey, S. S. 1980. Sequestration of Plant Natural Products by Insects. Ann. Rev. Ent. 25: 447-477.

Emlen, J. M. 1966. The tole of time and energy in food preference. Am Nat. 100:611-617.

Engelmann, F. The Physiology of Insect Reproduction. Oxford: Pergamon Press, 1970, 307 p.

Feeny, P. 1970. Seasonal changes in Oak Leaf Tannins and Nutrients as a Cause of Spring Feeding by Winter Moth Caterpillars. Ecology 51:565-581.

Fox, L. R. and B. J. Macauley. 1977. Insect Grazing on Eucalyptus in Response to Variation in Leaf Tannins and Nitrogen. Oecologia 29:145-162.

Fraenkel, G. 1953. The nutritional value of green plants for insects. Trans. 9th International Congress of Entomology, Amsterdam (1951) 2:90-100.

Goss, G. J. 1979. The Interaction Between Moths and Plants Containing Pyrrolizidine Alkaloids. Environ. Ent. 8(3):487-93.

Green, W. Q. 1974. An Antagonistic Insect/Host-Plant System: The Problem of Persistence. Ph.D. thesis, University of British Columbia. 247 p.

Harris, P. et al. 1971. Senecio jacobaea L., tansy ragwort (compositae). In: Biological control programmes against insects and weeds in Canada. Technical Communication No. 4, Commonwealth Institute of Biological Control. Farnham Royal, England, pp. 97-104.

Hickman, J. C., and L. F. Pitelka. 1975. Dry weight indicates energy allocation in ecological strategy analysis of plants. Oecologia 21:117-121.

Isaacson, D. L. 1972. Population Dynamics of the cinnabar moth, Tyria jacobaeae (Lepidoptera: Arctiidae). MS. Thesis, Oregon State University, 65 p.

Larsson, S., and O. Tenow. (1979). Utilization of Dry Matter and Bioelements in Larvae of Neodiprion sertifer. Geoffr. (Hym., Diprionidae) Feeding on Scots Pine (Pinus sylvestris L.). Oecologia 43(2):157-172.

Levin, D. A. 1976. The Chemical Defenses of Plants to Pathogens and Herbivores. Ann. Rev. Ecol. Syst. 7:121-159.

Mattocks, A. R. 1967. Spectrophotometric Determination of Unsaturated Pyrrolizidine Alkaloids. Anal. Chem. 39:443-448.

Mattocks, A. R. 1968. Spectrophotometric Determination of Pyrrolizidine Alkaloids--Some Improvements. Anal. Chem. 40:1749-1750.

McNeil, S. 1973. The Dynamics of a Population of Leptopterna dolabrata (Heteroptera: Miridae) in Relation to its Food Resources. J. Animal Ecol. 42:495.

McNeil, S. and Southwood, T. R. E. 1978. The role of nitrogen in the development of insect/plant relationships. Biochemical Aspects of Plant and Animal Coevolution. (Ed. by J. B. Harborne), pp. 77-98. New York, London: Academic Press.

Myers, J. H., and B. J. Campbell. 1976a. Predation by Carpenter Ants: A Deterrent to the spread of Cinnabar Moth. J. Entomol. Soc. Brit. Columbia 73:7-9.

Myers, J. H., and B. J. Campbell. 1976b. Distribution and dispersal in populations capable of resource depletion: a field study on cinnabar moth. Oecologia 24:7-20.

Nelson, D. W., and L. E. Sommers. 1973. Determination of total nitrogen in plant material. Agron. J. 65:109-112.

Odum, H. T., and R. C. Pinkerton. 1955. Time's speed regulator: the optimum efficiency for maximum power output in physical and biological systems. Am. Sci. 43:331-343.

Pliske, T. E. 1975. Attraction of Lepidoptera to Plants containing Pyrrolizidine Alkaloids. Environ. Ent. 4:455-473.

Reese, J. C. 1978. Chronic Effects of Plant Alkachemicals on Insect Nutritional Physiology. Ent. Exp. and Appl. 24:425-431.

Reese, J. C., and S. D. Beck. 1978. Interrelationships of Nutritional Indices and Dietary Moisture in the Black Cutworm (Agrotis ipilon) Digestive Efficiency. J. Insect Physiol. 24:473-479.

Richards, L. R. 1978. Maternal Influences on Size in the Cinnabar Moth. MS. Thesis, University of British Columbia. 53 p.

Rhoades, D. F. "Evolution of Plant Chemical Defense against Herbivores," pp. 3-54. In: G. A. Rosenthal and G. H. Janzen (ed.), Herbivores--Their Interactions with Secondary Plant Metabolites. New York: Academic Press, 1979.

Robinson, T. "The Evolutionary Ecology at Alkaloids," pp. 413-448. In: G. A. Rosenthal and D. H. Janzen (ed.), Herbivores--Their Interactions with Secondary Plant Metabolites. New York: Academic Press, 1979.

Rose, S. D. 1978. Effect of Diet on Larval Development, Adult Emergence and Fecundity of the Cinnabar Moth (Tyria jacobaeae L.). MS. Thesis, Oregon State University, Corvallis, Oregon. 92 p.

Schmidt, L. 1972. Studies on the control of Ragwort, Senecia jacobaeae L., With the Cinnabar Moth, (Callimorpha jacobaeae L.) (Arctiidae: Lepidoptera), in Victoria. Weed Res. 12:46-57.

Schroeder, L. A. 1976. Energy, matter and nitrogen utilization by the larvae of the Monarch butterfly (Danaus plexippus). Oikos 27:259-264.

Schoener, T. W. 1971. Theory of Feeding Strategies. Ann. Rev. Ecol. and System 2:369-403.

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

Scriber, J. Mark and P. Feeny. 1979. Growth of Herbivorous Caterpillars in Relation to Feeding Specialization and to the Growth Form of their Food Plants. Ecology 60(4):829-850.

Slansky, Frank and P. Feeny. 1977. Stabilization of the Rate of Nitrogen Accumulation by Larvae of the Cabbage Butterfly on Wild and Cultivated Food Plants. Ecol. Mongr. 49:209-228.

Sokal, R. R., and F. J. Raholf. Biometry. San Francisco: W. H. Freeman and Company, 1969. 776 p.

Southwood, T. R. E. 1973. The insect/plant relationships--an evolutionary perspective. In: "Insect/Plant Relationships" (van Emden, H. F., ed.), pp. 3-30. Symp. R. Ent. Soc. Lond. No. 6. Oxford: Blackwell Scientific.

Steward, F. C., and Durzan, D. J. 1965. "Metabolism of Nitrogenous compounds." In: Plant Physiology, A Treatise, Vol. IV-A, Metabolism: Organic Nutrition and Nitrogen Metabolism. Steward, F. C. (ed.). New York: Academic Press, pp. 399-686.

Swick, R. 1979. Dietary Factors Influencing the Toxicity of Senecio jacobaea in Animals. MS.Thesis, Oregon State University, Corvallis, Oregon.

Taylor, F. 1978. Foraging Behavior of Ants: Theoretical Considerations. J. Theor. Biol. 71:541-565.

Uritani, I. 1976. Protein Metabolism, pp. 509-521. In: R. Heitefuss, and P. H. Williams (eds.). Physiol. Pl. Path., Vol. 4.

van der Meijden, E. 1976. Changes in the Distribution Pattern of Tyria jacobaeae during the Larval Period. Netherlands Journal of Zoology 26(1):136-161.

van Emden, H. F., and Bashford, M. A. 1971. The performance of Brericoryne brassicae and Myzus persicae in relation to plant age and leaf amino acids. Entomol. Exp. Appl. 14:349-360.

Woldbauer, G. P. 1968. The consumption and utilization of food by insects. Rec. Adv. Insect Physiol. 5:229-88.

Windecker, W. 1939. Z. Morphol. Okol. Tiere 35(1):84.

Woodring, J. P., C. W. Clifford, and B. R. Beckman. 1979. Food Utilization and Metabolic Efficiency in Larval and Adult House Crickets. J. Insect Physiol. 25:903-912.

Woodwell, G. M., R. H. Whittaker, and R. A. Houghton. 1975. Ecology 56:318.

APPENDICES

Appendix 1a. Coefficients of correlation between pairs of parameters of food quality and feeding performance over all diets (28 degrees of freedom).

	Water	Nitrogen	RGR	RCR	AD	RNAR	NUE	ECD	ECI	RNCR
Water	--	--	--	--	--	--	--	--	--	--
Nitrogen	-.7250 †††	--	--	--	--	--	--	--	--	--
RGR	.4622 †	-.5928 ††	--	--	--	--	--	--	--	--
RCE	.2530	-.1248	.2813	--	--	--	--	--	--	--
AD	-.4184 †	.7160 †††	-.2363	.5244 ††	--	--	--	--	--	--
RNAR	-.4374 †	.6666 †††	-.2548	.6081 †††	.9239 †††	--	--	--	--	--
NUE	-.6233 †††	.8397 †††	-.4114 †	.1114	.8197 †††	.7444 †††	--	--	--	--
ECD	.1434	-.3256	-.0008	-.6763 †††	-.8228 †††	-.6842 †††	-.5152 ††	--	--	--
ECI	-.1484	.0022	-.2008	-.9329 †††	-.6208 †††	-.6619 †††	-.1821	.7800 †††	--	--
RNCR	-.3281	.5605 ††	-.1848	.7196 †††	.8864 †††	.9776 †††	.6303 †††	-.7137 †††	-.7513 †††	--

†indicates statistical significance at P<0.05 level.
††significance at P<0.01 level.
†††significance at P<0.001 level.

Appendix 1b. Coefficients of correlation between pairs of parameters of food quality and feeding from floral diets (8 degrees of freedom).

	Water	Nitrogen	RGR	RCR	AD	RNAR	NUE	ECD	ECI	RNCR
Water	--	--	--	--	--	--	--	--	--	--
Nitrogen	.1112	--	--	--	--	--	--	--	--	--
RGR	-.0328	-.5472	--	--	--	--	--	--	--	--
RCR	-.1691	-.6306	-.0521	--	--	--	--	--	--	--
AD	-.0884	-.6692 †	.2486	.7317 †	--	--	--	--	--	--
RNAR	-.3000	-.5722	-.1423	.9022 †††	.8167 ††	--	--	--	--	--
NUE	-.1669	-.4937	.4074	.1181	.6818 †	.3884	--	--	--	--
ECD	.2471	.6626 †	-.0618	-.8570 ††	-.9491 †††	-.9328 †††	-.5658	--	--	--
ECI	.2471	.6287	.0685	-.9336 †††	-.8773 †††	-.9706 †††	-.4072	.9773 †††	--	--
RNCR	-.2650	-.4726	-.2842	.9279 †††	.7200 †	.9595 †††	.1609	-.8718 ††	-.9450 †††	--

†indicates statistical significance at P<0.05 level.
††significance at P<0.01 level.
†††significance at P<0.001 level.

Appendix 1c. Coefficients of correlation between pairs of parameters of food quality and feeding performance from leaf diets (high and low) (18 degrees of freedom).

	Water	Nitrogen	RGR	RCR	AD	RNAR	NUE	ECD	ECI	RNCR
Water	--	--	--	--	--	--	--	--	--	--
Nitrogen	-.7945 †††	--	--	--	--	--	--	--	--	--
RGR	.4912 †	-.6710 ††	--	--	--	--	--	--	--	--
RCR	.7664 †††	-.8555 †††	.5588 †	--	--	--	--	--	--	--
AD	.0182	.0773	-.0332	.3526	--	--	--	--	--	--
RNAR	.1642	-.0606	.0136	.5030 †	.8002 †††	--	--	--	--	--
NUE	-.5271 †	.7208 †††	-.4094	-.3380	.5679 ††	.5328 †	--	--	--	--
ECD	-.2519	.3456	-.2326	-.6463 ††	-.7966 †††	-.5981 ††	-.1240	--	--	--
ECI	-.6815 †††	.8513 †††	-.4856 †	-.9512 †††	-.3223	-.4648 †	.4020	.6869 †††	--	--
RNCR	.5413 †	-.5171 †	.3455	.8560 †††	.6276 ††	.8179 †††	.0532	-.7140 †††	-.8161 †††	--

†indicates statistical significance at P<0.05 level.
††significance at P<0.01 level.
†††significance at P<0.001 level.

Appendix 1d. Coefficients of correlation between pairs of parameters of food quality and feeding performance from high leaf diets (8 degrees of freedom).

	Water	Nitrogen	RGR	RCR	AD	RNAR	NUE	ECD	ECI	RNCR
Water	--	--	--	--	--	--	--	--	--	--
Nitrogen	-.3022	--	--	--	--	--	--	--	--	--
RGR	.2879	-.1687	--	--	--	--	--	--	--	--
RCR	-.1860	.0766	.5162	--	--	--	--	--	--	--
AD	-.0967	-.0290	.7164 †	.8790 †††	--	--	--	--	--	--
RNAR	-.1842	-.0711	.4868	.9401 †††	.8486 ††	--	--	--	--	--
NUE	-.3053	.4436	.6015	.6029	.5987	.5067	--	--	--	--
ECD	.2813	-.0948	-.4325	-.8230 ††	-.8357 ††	-.6449 †	-.5904	--	--	--
ECI	.3506	-.1192	-.2014	-.9286 †††	-.7203 †	-.8213 ††	-.4721	.8456 ††	--	--
RNCR	-.1096	.2688	.1850	.8301 ††	.7108 †	.8668 ††	.3455	-.6131	-.8026 ††	--

†indicates statistical significance at P<0.05 level.
††significance at P<0.01 level.
†††significance at P<0.001 level.

Appendix 1e. Coefficients of correlation between pairs of parameters of food quality and feeding performance from low leaf diets (8 degrees of freedom).

	Water	Nitrogen	RGR	RCR	AD	RNAR	NUE	ECD	ECI	RNCR
Water	--	--	--	--	--	--	--	--	--	--
Nitrogen	-.5160	--	--	--	--	--	--	--	--	--
RGR	-.0411	-.3756	--	--	--	--	--	--	--	--
RCR	.5572	-.1909	-.0235	--	--	--	--	--	--	--
AD	.2588	.0677	-.2154	.9184 †††	--	--	--	--	--	--
RNAR	.2098	.4451	-.2442	.7470 †	.8295 ††	--	--	--	--	--
NUE	.0211	.4753	-.1318	.6219	.7459 †	.9446 †††	--	--	--	--
ECD	-.2192	.1325	.1390	-.8340 ††	-.9168 †††	-.5865	-.4722	--	--	--
ECI	-.4854	.0905	.3856	-.9135 †††	-.9298 †††	-.6995 †	-.5378	.8832 †††	--	--
RNCR	.3585	.2265	-.0949	.8991 †††	.9026	.9268 †††	.8322 ††	-.7305 †	-.8151 ††	--

†indicates statistical significance at P<0.05 level.
††significance at P<0.01 level.
†††significance at P<0.001 level.

Appendix 2. Parameters of food quality and feeding performance of cinnabar moth larvae determined over diets of different plant parts. Underlined values are impossible.

		Plant H_2O (% FW)	Plant N (% DW)	RGR	RCR	AD	RNAR	NUE	ECD	ECI	RNCR
	F1	85.14	3.01	0.32	2.93	68.48	0.07	80.95	15.91	10.89	0.09
	F2	85.28	3.15	0.27	5.70	77.56	0.13	75.48	6.02	4.67	0.18
	F3	86.52	3.34	0.30	3.16	76.29	0.09	82.81	12.40	9.46	0.11
	F4	86.49	3.50	0.29	1.90	55.76	0.04	70.42	27.70	15.45	0.06
Floral	F5	86.05	2.79	0.33	5.40	78.96	0.12	81.90	7.85	6.20	0.14
Parts	F6	86.89	2.93	0.32	3.76	79.90	0.09	85.28	10.76	8.61	0.11
	F7	84.56	3.10	0.34	3.63	75.92	0.09	82.59	23.40	9.42	0.11
	F8	84.96	3.25	0.30	3.29	73.58	0.09	85.88	12.41	9.13	0.10
	F9	86.19	3.13	0.31	3.47	74.60	0.09	85.55	12.05	8.99	0.11
	F10	84.92	3.06	0.29	3.77	75.04	0.12	86.04	10.27	7.71	0.14
	H1	84.83	2.39	0.29	1.76	31.41	0.03	67.70	51.86	16.29	0.04
	H2	86.22	2.35	0.29	1.20	15.80	0.02	58.34	154.08	24.35	0.03
	H3	85.48	2.58	0.29	1.82	37.12	0.03	70.22	43.41	16.12	0.05
	H4	85.50	2.35	0.31	1.48	31.19	0.02	74.66	67.11	20.93	0.03
High	H5	87.01	2.29	0.31	1.53	25.63	0.02	62.80	79.12	20.28	0.03
Leaves	H6	85.71	2.64	0.31	1.39	27.74	0.02	73.57	80.47	22.32	0.03
	H7	86.44	2.38	0.30	1.43	27.08	0.02	67.92	76.65	20.76	0.03
	H8	86.74	2.41	0.29	1.37	26.19	0.02	60.04	81.62	21.38	0.04
	H9	85.61	2.26	0.30	1.40	34.27	0.02	59.15	61.56	21.10	0.03
	H10	86.45	2.34	0.34	2.07	57.19	0.04	75.49	29.22	16.71	0.05
	L1	86.47	1.44	0.41	3.40	26.74	0.02	48.51	45.56	12.18	0.05
	L2	87.86	1.56	0.28	4.48	44.88	0.04	60.79	14.86	6.67	0.07
	L3	87.19	1.43	0.31	4.44	46.64	0.04	66.26	16.10	7.51	0.06
	L4	88.49	1.41	0.39	5.35	47.21	0.05	70.11	16.41	7.81	0.08
Low	L5	87.39	1.50	0.34	3.32	29.68	0.03	54.34	37.08	11.01	0.05
Leaves	L6	86.32	1.50	0.34	2.77	20.69	0.02	45.19	62.65	12.96	0.04
	L7	87.56	1.57	0.32	2.71	12.58	0.02	38.84	100.42	12.63	0.04
	L8	87.70	1.28	0.36	4.06	34.08	0.02	41.93	27.42	9.35	0.05
	L9	87.49	1.41	0.37	2.76	12.29	0.02	51.93	116.12	14.29	0.04
	L10	88.63	1.01	0.36	3.82	22.40	0.01	31.11	44.96	10.07	0.04