Revista Chilena de Historia Natural
67: 27 - 33, 1994

Host nutritional value in larval feeding preference of *Ormiscodes socialis* (Feisthammel) (Lepidoptera: Saturniidae) in Chile

Valor nutricional del hospedero en la preferencia trófica de las larvas de *Ormiscodes socialis* (Feisthammel) (Lepidoptera: Saturniidae) en Chile

JOSE E. FUENTES [1,2] and LESLIE. R. YATES [1]

[1] Departamento de Ecología, Facultad de Ciencias Biológicas,
Pontificia Universidad Católica de Chile
Casilla 114-D, Santiago, Chile
[2] Present address: Departamento de Ciencias Ecológicas, Facultad de
Ciencias, Universidad de Chile.
Casilla 653, Santiago, Chile

ABSTRACT

Field and laboratory work was performed to gather information to evaluate the hypothesis that host selection by larva of *Ormiscodes socialis* (Feisthammel) is fundamentally associated to nutritional value of the leaves. Evidence is reported which indicates that nitrogen content of leaves can account for the preferential utilization of the host by *O. socialis*, without excluding possible effects of other non nutritional factors not evaluated in this first approach to the problem.

Key words: Lepidopteran larvae, leaves nitrogen content, digestibility, assimilation efficiency, leaves ash content.

RESUMEN

Mediante observaciones de campo y ensayos de laboratorio se evalúa la hipótesis de que la selección de huésped de la larva de *Ormiscodes socialis* (Feisthammel) está asociada de manera fundamental al valor nutritivo de sus hojas. En este estudio se ha obtenido evidencia parcial que relaciona el uso preferencial de ciertas plantas, por parte de las larvas de esta especie, con la concentración de nitrógeno de las hojas de estas. Los resultados de este primer esfuerzo en poner a prueba esta hipótesis, no excluyen la posibilidad de que otros factores no-nutritivos puedan ser también de importancia en la selección de huésped.

Palabras claves: larvas de lepidóptero, nitrógeno, digestibilidad, eficiencia de asimilación, cenizas.

INTRODUCTION

Although a systemic approach to herbivory has been developed for the mediterranean chilean matorral (Etchegaray & Fuentes 1980, Fuentes et al. 1981, Montenegro et al. 1980, Walkowiak et al. 1984, Poiani & Fuentes 1985, Grez 1988), few investigations have analyzed a particular case study of herbivorous species. This second approach gives a more comprehensive understanding of herbivorous insect and plant relationships (Walkowiak et al. 1984).

Insects are the most important native grazers of shrubs in chilean matorral (Fuentes et al. 1981). A conspicuous member of this group is the larva of the lepidopteran *Ormiscodes socialis* (Feisthammel), which is a univoltine species in central Chile. Eggs are the wintering stage, eclotionating in August or September. Larvae growth and development continue until pupation occurs in November. Finally, adults began to appear in March and April laying their eggs for next spring generation. It seems that these larvae

(Recibido el 7 de mayo de 1993; aceptado el 12 de agosto de 1994)

are not strict specialists, because they are frequently seen in the field defoliating shrubs of *Muehlenbeckia hastulata* (J. E. Sm.) Johnst and *Acacia caven* (Mol.) Hook et Arn. and seldom can be found on *Lithrea caustica* (Hook et Arn.) and *Trevoa trinervis* Miers. More over, in laboratory assay the larvae are able to complete their development feeding on the leaves of *Schinus polygamus* (Cav.), *Schinus latifolius* (Gill. et Lindl.), *Pinus radiata* D. Don and the above mentioned *L. caustica* (F. Sáiz, pers. comm.). In localities where the first two host plant species are present, the larvae graze principally on *M. hastulata*, while where *M. hastulata* is absent the larvae are found defoliating *A. caven* specimens. This preliminary evidence suggest that *O. socialis* probably corresponds to a facultative specialist (Holdren & Ehrlich 1982), which uses fundamentally those plants with a higher trophic preference, that is, those plants wich are most suitable for their growth and development, i.e. their darwinian fitness (Wiklund 1981).

Of the multiple factors listed in the literature which could affect the diet breadth of herbivorous insects, including resource availability, plant antiherbivore defenses, predator or parasitoid attacks and nutritional quality of the hosts (Jaenike 1990), apparently the latter is the most relevant in our case.

Foliar water and nitrogen content, which have been reported as important in determining food preference of defoliating insects (Scriber & Slansky 1981), are higher in *M. hastulata* leaves than in *A. caven*. Since *O. socialis* is not a specialist species, resource availability seems to have a relatively less importance (Tahvanainen & Root 1972). Furthermore, antiherbivore defenses, common in other plant species of the matorral, are absent or greatly reduced in *M. hastulata* (Fuentes et al. 1981) and in spite of the lack of information about these defenses in *A. caven*, considering the high level of defoliation found, we suspect they are ineffective in deterring these larvae. The effects of predators and parasitoids are unknown for this species, but all larval populations studied have shown important levels of attack by microhymenopterans and tachinids.

The aim of this study is to gather information which support the hypothesis that host selection of *O. socialis* larva is fundamentally related to nutritional value of the leaves, stablishing a hierarchization of their possible host species.

Two main questions are addressed in this study to attain this goal:

1. Which nutritional characteristics of host leaves could explain the shrub species utilization and trophic preferences of larvae?.
2. Is there any relationship between trophic preferences and assimilation efficiency?.

MATERIALS AND METHODS

Field work was performed at two localities, San Carlos de Apoquindo (33° 23' S; 70° 30' W) located 20 Km east of Santiago, and Lo Aguirre (33° 15' S; 70° 30' W) at a similar distance to the west of the city. Both hosts species, *M. hastulata* and *A. caven*, were present in San Carlos de Apoquindo, while *M. hastulata* was absent in Lo Aguirre. Other relatively abundant plants were incorporated in the analysis at each location, in order to have a contrast with non-host species. Thus, *Lithrea caustica* (Hook et Arn) was included in San Carlos de Apoquindo, and *L. caustica* and *Flourencia thurifera* (Mol.) DC. in Lo Aguirre. Five shrubs of each plant species were selected and sampled every two months for laboratory analysis of nutritional characteristics, obtaining three measures corresponding to mid winter (July), early (September) and late spring (November). A gross estimation of vegetative growth was established through presence-absence of young leaves. Leaf water content was determined gravimetrically by differences between fresh and dry weight, and nitrogen content with Kjeldahl method (Mc Kenzie & Wallace 1954) with three replicates for each sample. Leaf caloric content was determined with a Parr Adiabatic Calorimeter and ash content by incineration at 500 °C during 24 hours, both with three replications for each sample.

To perform a two way ANOVA of repeated measures (Snedecor & Cochran 1967) for plant species and month for each locality, the data were transformed to arcsine $\sqrt{x}$ in order to homogenize variances and to normalize the distribution (Sokal & Rohlf 1969).

Trophic preferences of last instar larva were estimated with the methodology described in Peterson & Renaud (1989), utilizing larvae collected in late spring sampling and deprived of food for 48 hours. During the tests, specimens were offered young fully expanded leaves. Results were analyzed with a Wilcoxon Mann Whitney test (Siegel & Castellan 1988).

Assimilation efficiencies (approximate digestibility *sensu* Scriber & Slansky 1981), expressed in terms of dry mass, water, caloric and nitrogen budgets, were estimated through short term feeding assays using last instar larvae of *O. socialis*. Food consumption and faecal output were estimated gravimetrically, using fresh leaves as a control to account for water losses during the experiments. Caterpillars were submitted to a starvation period of 48 hours, to empty the digestive tract, before the experiments began. The assays were done until larvae began to pupate and to void their guts naturally. Due to the small amount of faeces produced by a single larva, groups of five caterpillars were considered as the experimental unit. Results were expressed in per capita terms and analyzed with a two way ANOVA (Sokal & Rohlf 1969) for host species and locality.

RESULTS

Nutritional characteristics of plant species

The statistical analysis (ANOVA) reveals significant differences between plant species and months, and significant interactions, in the majority of the studied nutritional characteristics (Table 1).

Plant species foliar nitrogen content in both localities are shown in Fig 1. In mid winter and early spring *M. hastulata* presented the highest nitrogen levels in San

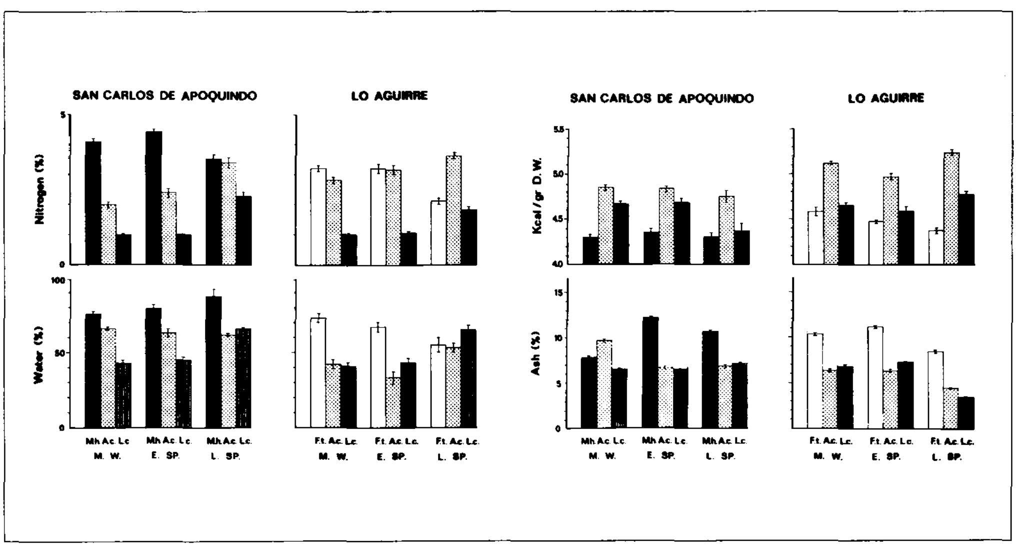

Fig. 1: Ash, energy, water and nitrogen contents of *Muehlenbeckia hastulata* (M. h.), *Acacia caven* (A. c.), *Lithrea caustica* (L. c.) and *Fluorencia thurifera* (F. t.) leaves, in both field locations during mid winter (M. W.), early spring (E. SP.) and late spring (L. SP.). Energy is expressed as Kcal/g of dry weight (D W). Statistical analysis (ANOVA) is shown in Table 1. Deviation bars are 2 SE from the mean.

Contenido de nitrógeno, agua, energía y ceniza de las hojas de *Muehlenbeckia hastulata* (M. h.), *Acacia caven* (A. c.), *Lithrea caustica* (L. c.) y *Fluorencia thurifera* (F. t.), para ambas localidades durante invierno medio (M. W.), primavera temprana (E. SP.) y primavera tardía (L. SP.). La energía está expresada como Kcal/g de peso seco (D W). El análisis estadístico (ANOVA) se muestra en la Tabla 1. Las barras de desviación expresan 2 EE en relación a la media.

Carlos, but similar values were also registered in late spring in *A. čaven* leaves. In Lo Aguirre *F. thurifera* had a higher nitrogen content during mid winter, *F. thurifera* and *A. caven* presented similar levels of this element in early spring, and finally *A. caven* reached the highest foliar nitrogen level in late spring. Summarizing, *M. hastulata* and *F. thurifera*, wich began their vegetative growth early in the year, showed a decrease tendency in nitrogen content throught time, whereas *A. caven* and *L. caustica*, which started growing later, showed a nitrogen increase in late spring.

M. hastulata had the highest leaf water content throught all the study period in San Carlos (Fig. 1), while in Lo Aguirre *F. thurifera* presented more leaf water in mid winter and early spring. *L. caustica* was the species with higher water leaves content in late spring.

In both study sites the highest caloric value of the leaves throught the sampling period, was observed in *A. caven* (Fig. 1). Of the studied species in San Carlos, *M. hastulata* had the highest ash content except in mid winter, and *F. thurifera* was the plant with more ash content in Lo Aguirre (Fig 1).

Feeding preference essays

The larvae of the *O. socialis* population of San Carlos, showed significant preferences for *M. hastulata* leaves over *L. caustica* and for *A. caven* over *L. caustica*. No significant preference was observed between *M. hastulata* and *A. caven* (Table 2).

Likewise, larvae from the Lo Aguirre population preferred *A. caven* leaves over *L. caustica* and *F. thurifera*, and *L. caustica* leaves over *F. thurifera* (Table 2). Furthermore, an extra test with *M. hastulata* and *A. caven* was performed in this population coming from a locality without *M. hastulata*; the results showed no significant preferences (Table 2).

Assimilation efficiency essays

Digestibility results expressed in terms of dry mass, nitrogen, water and caloric budgets are shown in Table 3. ANOVA for nitrogen and calories assimilation efficiency didn't show any significant differences in plant species or localities. However, the differences in water assimilation efficiency between both plant species and locality are significant. Tukey

TABLE 1

Results of ANOVA for leaf nitrogen, water, calories and ash content between plant species and months, and interaction for each locality (n = 5).

Resultados de la ANOVA para el contenido de nitrógeno, agua, calorías y ceniza foliares entre especies de plantas y meses, e interacciones para cada localidad (n = 5).

NUTRITIONAL CHARACTERISTICS	PLANT SPECIES				MONTH				INTERACTIONS			
SAN CARLOS	SS	MS	F	P	SS	MS	F	P	SS	MS	F	P
Nitrogen	0.0541944	0.027097	320.3	<0.001	0.0047299	0.002365	28.0	<0.001	0.0080613	0.02015	23.8	<0.001
Water	0.6626276	0.331381	812.1	<0.001	0.1036560	0.051828	127.0	<0.001	0.128086	0.032022	78.5	<0.001
Calories	1820882	910441	77.1	<0.001	177992	88996	7.53	<0.05	144782	36196	3.06	<0.05
Ash	0.0399853	0.019992	41.8	<0.001	0.0000062	0.000003	0.01	=0.9 N.S.	0.0216567	0.005414	11.3	<0.001
LO AGUIRRE												
Nitrogen	0.0378085	0.018904	306.9	<0.001	0.0005377	0.000269	4.36	<0.05	0.0093765	0.002344	38.1	<0.001
Water	0.4208828	0.210441	218.3	<0.001	0.1047297	0.052365	54.3	<0.001	0.297412	0.074353	77.1	<0.001
Calories	3075797	1537899	566.8	<0.001	78858	39429	14.5	<0.001	263649	65912	24.3	<0.001
Ash	0.0735371	0.036768	77.0	<0.001	0.0291	0.01455	30.5	<0.001	0.0024679	0.000617	1.29	=0.3 N.S

test reveals that the larvae of Lo Aguirre have higher water assimilation efficiencies than the larvae of San Carlos when they are fed both plants leaves ($p<0.05$ Tukey test). Furthermore, only the population from Lo Aguirre showed significant differences between plant species, being more efficient in water terms on *A. caven* leaves than on M. *hastulata* ($p<0.05$ Tukey test).

DISCUSSION

Since at both localities these lepidopteran larvae are found feeding on shrubs whose leaves have a higher nitrogen level, this nutritional element seems to account for the preferential utilization of the host species. Even though at San Carlos de Apoquindo, *M. hastulata* leaves also had the highest water and ash contents, at Lo Aguirre the larvae were seen defoliating exclusively on *A. caven* leaves which had the lowest water content of the plant studied. Otherwise, the caloric content of *A. caven* is the highest on both localities and therefore could not explain the preferential utilization of *M. hastulata* in San Carlos de Apoquindo.

Feeding preference tests conducted under laboratory conditions established no preferences between *M. hastulata* and *A. caven* leaves. This result could be explained in terms of nitrogen content, because during the assays larvae were offered leaves of *M. hastulata* and *A. caven* with no significative differences in nitrogen (late spring in Figure 1; $p=0.1$ Wilcoxon Mann Whitney test N. S.); the same outcome was attained analyzing nitrogen content in terms of wet biomass ($p=0.2$ Wilcoxon Mann Whitney test N. S.)(Paine & Vadas 1969). In all the other tests performed, the larvae preferred the more nitrogenous plant offered, with the only exception of *F. thurifera* which was sistematically rejected. This feeding avoidance would be explained on the basis of allelopathic soluble exudates produced by this plant, which apparently also affect the feeding preferences of goats acting as allelochemical deterrent against herbivory (Fuentes *et al.* 1987).

The importance of nitrogen content in food preferences of herbivores, has been reported in a great number of studies with a wide taxonomic range of vertebrates (Milton 1979, Owen-Smith & Novellie 1982, among others) and invertebrates (White 1978, Scriber & Slansky 1981, Strong *et al.* 1984). Particularly, for the mediterranean matorral of central Chile, similar trends has been found for native and introduced ungulates, lagomorphs and rodents (Simonetti & Fuentes 1983, Simonetti et al. 1984, Veloso & Bozinovic

TABLE 2

Results of feeding preference test of last instar larvae of *Ormiscodes socialis* in both localities. Test were performed with late spring foliage (November).
= not significant difference, > significant difference at 0.05 level and >> significant difference at 0.001 level with Wilcoxon Mann Whithney test (n = 30).

Resultados de los test de preferencia trófica en larvas de último instar de *Ormiscodes socialis* para ambas localidades. Los test fueron realizados con follaje de primavera tardío (Noviembre).
= diferencia no significativa, > diferencia significativa al nivel 0.05 y >> diferencia significativa al nivel 0.001 con el test de Wilcoxon Mann Whitney (n = 30).

SAN CARLOS	LO AGUIRRE
M. hastulata = *A. caven* (p=0.27)	*A. caven* > *L. caustica*
M. hastulata > *L. caustica*	*A. caven* >> *F. thurifera*
A. caven >> *L. caustica*	*L. caustica* > *F. thurifera*
	M. hastulata = *A. caven* (p=0.22)

1993). Althougth, nitrogen content of a plant is only one of the many variables that would be relevant for herbivores (like allelochemical, moisture or fiber levels), their importance is critical for growth, reproduction and survival of many organisms (Mattson 1980).

In relation to assimilation efficiency, Slansky & Feeny (1977) found that larvae fed on plants with low levels of nitrogen showed a higher ingestion rate, lower digestibility and higher nitrogen assimilation efficiency than those fed on plants with high levels of nitrogen. According to their results we would have expected larvae fed on *A. caven* leaves to have higher ingestion rates, lower digestibility and higher nitrogen assimilation efficiency than larvae fed on *M. hastulata* leaves. However, against our predictions, significative differences were not detected between larvae feeding on leaves from both species. Slansky & Feeny (1977) utilized leaves over a wide range of nitrogen content (1.5 to 6.0%) to feed their larvae, while the larvae used in our assays had been grown in the field eating leaves with a lower variation in their nitrogen content (4 to 3.1%). Besides, in this work larvae were fed leaves from both plant species which did not differ significantly in their nitrogen contents. In spite of the short duration of our tests, we believe that the differential host plant utilization by these larvae populations from different localities, have not guided them to a state of local specialization, because the larvae have not lost their capacity to use the alternative host (Singer 1982).

Establishing an analogy with nitrogen budget predictions of Slanky & Feeny (1977), our results of water assimilation efficiency conform well with their reasoning, since the population of Lo Aguirre had higher efficiencies on *A. caven* than on *M. hastulata*, whose leaves had a lower content of water

In summary, we report correlational evidence which support the hypothesis that nitrogen content of the plant leaves can account for the preferential utilization of hosts by *O. socialis* larvae, without excluding possible effects of other non nutritional factors that we did not evaluate. The ecological relevance of this first approach to this problem, needs to be complemented with future research related to adult females oviposition preferences, and larval survival and future adult reproduction success on different host species.

TABLE 3

Assimilation efficiencies of the larvae of *Ormiscodes socialis* on different host plant species, in terms of digestibility (dry biomass), nitrogen, water and caloric budgets for both localities. Data are presented as percentages (%) and in x = Arcsine √ (%/100) transformation. Standard errors are shown in parenthesis. Due to the small amount of faeces produced by a single larva, groups of five caterpillars were considered as the experimental unit. Results were expressed in per capita terms and analyzed with a two way ANOVA for host species and locality. Significance level are given in the text. n = 3.

Eficiencias de asimilación de las larvas de *Ormiscodes socialis* en diferentes plantas hospederas, en términos de presupuestos de digestibilidad (biomasa seca), nitrógeno, agua y calorías para ambas localidades. los datos son presentados como porcentaje (%) y como transformación x = Arcoseno √ (%/100). Los errores estándar son mostrados entre paréntesis. Debido a la pequeña cantidad de fecas que produce una larva, se consideró como unidad experimental grupos de cinco orugas. Los resultados fueron expresados en términos per capita y analizados con ANOVA de dos vías para las especies de hospedero y localidad. Los niveles de significación están dados en el texto. n = 3.

PLANT SPECIES	DRY MASS		NITROGEN		WATER		CALORIES	
	%	X (SE)	%	X (SE)	%	X (SE)	%	X (SE)
SAN CARLOS								
M. hastulata	19.21	0.45 (0.04)	29.92	0.57 (0.08)	25.93	0.53 (0.05)	29.39	0.57 (0.02)
A. caven	30.53	0.58 (0.04)	29.84	0.57 (0.07)	33.89	0.81 (0.02)	32.87	0.60 (0.08)
LO AGUIRRE								
M. hastulata	30.91	0.59 (0.02)	25.04	0.52 (0.05)	52.57	0.62 (0.06)	34.65	0.62 (0.04)
A. caven	21.21	0.48 (0.03)	14.43	0.38 (0.03)	71.77	1.01 (0.06)	25.63	0.53 (0.03)

REFERENCES

ETCHEGARAY J & ER FUENTES (1980) Insectos defoliadores asociados a siete especies arbustivas del matorral. Anales del Museo de Historia Natural de Valparaíso 13:159-166.

FUENTES ER, J ETCHEGARAY, ME ALJARO & G MONTENEGRO (1981) Shrub defoliation by matorral insects. In: Di Castri, Goodall & Spech [eds]. Ecosystems of the world, Vol 11: Mediterraneam Type Ecosystems. Elsevier, 345-359.

FUENTES ER, GA ESPINOZA & G GAJARDO (1987) Allelopathic effects of the Chilean matorral shrub *Flourencia thurifera*. Revista Chilena de Historia Natural 60:57-62.

GREZ AA (1988) *Procalus malaisei* y *Procalus lenzi* (Coleoptera: Chysomelidae): dos especialistas del matorral. Revista Chilena de Entomología 16:65-67.

HOLDREN C & P EHRLICH (1982) Ecological determinants of food plant choice in the checkerspot butterfly *Euphydrias editha* in Colorado. Oecologia 52:417-423.

JAENIKE J (1990) Host specialization in phytophagous insects. Annual Review of Ecology and Systematics 21:243-273.

MATTSON WJ (1980) Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11:119-161.

MC KENZIE H & H WALLACE (1954) The Kjeldahl determination of nitrogen: A critical study of digestion conditions - temperature, catalyst, and oxidizing agent. Australian Journal of Chemistry. 7:55-70.

MILTON K (1979) Factors influencing leaf choice by howler monkeys: A test of some hypothesis of food selection by generalist herbivores. American Naturalist 114:362-378.

MONTENEGRO G, M JORDAN & ME ALJARO (1980) Interaction between Chilean matorral shrubs and phytophagous insects. Oecologia 45:346-349.

OWEN-SMITH N & P NOVELLIE (1982) What should a clever ungulate eat?. American Naturalist 119:158-178.

PAINE R & R VADAS (1969) Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. Marine Biology 4:79-86.

PETERSON C & P RENAUD (1989) Analysis of feeding preference experiments. Oecologia 80:82-86.

POIANI A & ER FUENTES (1985) Efecto de los insectos defoliadores sobre manchones de matorral: casos mono y multiespecíficos. Revista Chilena de Historia Natural 58:47-56.

SCRIBER J & F SLANSKY (1981) The nutritional ecology of inmature insects. Annual Review of Entomology 26:183-211.

SIEGEL S & N CASTELLAN (1988) Nonparametric statistics for the behavioral sciences. Mc Graw Hill Book Co., 2 nd ed., New York.

SIMONETTI JA & ER FUENTES (1983) Shrub preferences of native and introduced Chilean matorral herbivores. Oecologia Applicatta 4:269-272.

SIMONETTI JA, G MONTENEGRO, M JORDAN & R ARRANZ (1984) Morpho-chemical correlates of the palatability of two Chilean shrubs. Oecologia Plantarum 5:369-373.

SINGER M (1982) Quantification of host preference by manipulation of oviposition behaviour in the butterfly *Euphydrias editha*. Oecologia 52:224-229.

SLANSKY F & P FEENY (1977) Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. Ecological Monographs 47:209-228.

SNEDECOR G & L COCHRAN (1967). Statistical methods. The Iowa State University Press. Iowa.

SOKAL R & F ROHLF (1969) Biometry. W. H. Freeman and Co. San Francisco.

STRONG DR, JH LAWTON & TRE SOUTHWOOD (1984) Insects on plants: Community patterns and mechanisms. Harvard University Press. Cambridge.

TAHVANAINEN J & R ROOT (1972) The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). Oecologia 10:321-346.

VELOSO C & F BOZINOVIC (1993) Dietary and digestive constraints on basal energy metabolism in a small herbivorous rodent. Ecology 74:2003-2010.

WALKOWIAK A, J SIMONETTI, I SEREY, M JORDAN, R ARRANZ & G MONTENEGRO (1984). Defensive pattern in shrubs of central Chile. A common strategy?. Oecologia Plantarum 5:191-199.

WHITE TCR (1978) The importance of a relative shortage of food in animal ecology. Oecologia 33:71-86.

WIKLUND C (1981) Generalis v/s Specialist oviposition behaviour in *Papilio machaon* (Lepidoptera) and functional aspects on the hierarchy of oviposition preferences. Oikos 36:163-170.