Trophic ecology of Lepidoptera larvae associated with woody vegetation in a Savanna Ecosystem

C H Scholtz

A report of the Savanna Ecosystem Project
National Programme for Environmental Sciences

SOUTH AFRICAN NATIONAL SCIENTIFIC PROGRAMMES REPORT NO

55

JUNE 1982

Issued by
Cooperative Scientific Programmes
Council for Scientific and Industrial Research
P O Box 395
PRETORIA
0001
from whom copies of reports in this series are available on request

Printed 1982 in the Republic of South Africa
by the Graphic Arts Division of the CSIR

ISBN 0-7988-2346-1

Author's address -

Dr C H Scholtz
Department of Entomology
University of Pretoria
PRETORIA
0001

PREFACE

The Savanna Ecosystem Project of the National Programme for Environmental Sciences is one of several national scientific programmes administered by the CSIR. The National Programme is a cooperative undertaking of scientists and scientific institutions in South Africa concerned with research related to environmental problems. It includes research designed to meet local needs as well as projects being undertaken in South Africa as contributions to the international programme of SCOPE (Scientific Committee on Problems of the Environment), the body set up in 1970 by ICSU (International Council of Scientific Unions) to act as a focus of non-governmental international scientific effort in the environmental field.

The Savanna Ecosystem Project being carried out at Nylsvley is a joint undertaking of more than fifty scientists from the Department of Agriculture and Fisheries, the Transvaal Provincial Administration, the CSIR, the Transvaal Museum, and eight universities. As far as possible, participating laboratories finance their own research within the project. The shared facilities at the study area and the research of participating universities and museums are financed from a central fund administered by the National Committee for Environmental Sciences and contributed largely by the Department of Environment Affairs.

The research programme of the Savanna Ecosystem Project has been divided into three phases - Phase I (mid 1974 to mid 1976) - a pilot study of the Nylsvley study area, in particular the description and quantification of structural features of the ecosystem, Phase II (mid 1976-1979) - studies in the key components and processes including the development of mathematical models, and Phase III (1979-1984) - extension to other sites and the study of management strategies for the optimal utilization of Burkea savanna ecosystems.

The present report forms part of both the description and quantification of the structural features of the ecosystem, and the study of key components and processes, focusing on the populations of Lepidoptera larvae associated with the main woody species and the impact that these larvae have on their host plants through the consumption of leaves and hence loss of photosynthetic area.

ACKNOWLEDGEMENTS

I wish to thank Dr E Holm of the Department of Entomology, University of Pretoria for supervising this project and for critically reading the manuscript.

ABSTRACT

This study represents a quantitative survey of a Lepidoptera community and deals with the trophic ecology of the 27 species of foliage-feeding Lepidoptera on the eight dominant woody plants in the Burkea africana-Eragrostis pallens savanna at Nylsvley. Food intake, growth and excretion by the eight dominant Lepidoptera species were measured in the field and monthly field surveys of standing crop of all species were carried out. The trophic ecology of the whole Lepidoptera system was extrapolated from these results. All feeding, growth and excretion data were expressed in dry mass per ground surface area.

Aspects of the biologies of the eight dominant species considered necessary to assess likely variations in the impact of foliage consumption by larvae eg number of generations per season, whether species are potentially eruptive or not, feeding techniques and specificity, are discussed.

The effect of Lepidoptera larvae on the woody vegetation is discussed. Removal of plant tissue by the larvae was insignificant in terms of mass, but comparable to that in other systems.

SAMEVATTING

Hierdie studie handel oor 'n kwantitatiewe opname van 'n Lepidoptera-gemeenskap en het te doen met die trofiese ekologie van 27 blaarvretende spesies op houtagtige plante in die Burkea africana-Eragrostis pallens savanne te Nylsvley. Voedselinname, groei en uitskeiding deur die agt dominante spesies is in die veld aangeteken en biomassa van alle Lepidoptera-spesies is maandeliks direk bepaal. Die trofiese ekologie van die hele Lepidoptera-sisteem is uit die resultate ekstrapoleer. Alle voedings-, groei- en uitskeidingsdata is uitgedruk in droë massa per eenheid grondoppervlakte.

Sekere aspekte van die biologie van die agt dominante spesies wat nodig beskou is om moontlike variasies in effek op blaarinname deur larwes te bepaal, byvoorbeeld aantal generasies per seisoen, of bevolkings-ontploffings moontlik mag voorkom, voedingstegnieke en spesifisiteit, word bespreek.

Die effek wat Lepidoptera-larwes op houtagtige plante uitoefen word bespreek. Verwydering van plantweefsel uit die sisteem deur larwes is ontbetekenisvol in terme van massa maar is vergelykbaar met ander sisteme.

TABLE OF CONTENTS

INTRODUCTION

The trophic ecology of larval Lepidoptera has not been reported on previously in South African ecosystems and little information is available on the biology of the non-economic Lepidoptera species in South Africa. Feeding studies elsewhere have usually been restricted to single species with the consumption data being derived from laboratory studies (Varley 1967; Winter 1971). Reichle and Crossley (1967) determined consumption in the field by means of sophisticated experiments using radio-isotopes. Many data on food intake are available from physiological studies but all these studies were done under controlled conditions (Evans 1939; Kasting and McGinnis 1962; Waldbauer 1962, 1964 and 1968; van den Berg and van den Berg 1973).

The objective of this study was to investigate the trophic ecology of the larval Lepidoptera populations on the dominant woody vegetation of the Savanna Ecosystem Project study area at Nylsvley, northern Transvaal (24°29'S, 28°42'E). The study was restricted to Burkea africana, Ochna pulchra, Terminalia sericea, Grewia flavescens, Strychnos pungens, Vitex rhemannii, Dombeya rotundifolia and Combretum molle, which are numerically the dominant woody plants at Nylsvley (Lubke, Clinning and Smith 1975). In total these plants account for more than 80% of the woody plant biomass in this area (Rutherford 1979). Vitex rhemannii had only low populations of one species (Scopula sp) which were not studied in detail and no lepidopterous larvae were recorded on either C molle or G flavescens.

Production, consumption and defaecation were measured in the field for those species which were considered to be of the greatest overall importance to the system. Importance was judged by noting which species reached high peaks of biomass, and also which had continuous generations throughout the season.

The most important species judged on these criteria were: Euproctis fasciata Walker (Lymantriidae), Maurilia arcuata Walker (Noctuidae) and Arcyophora carniola Hampson (Noctuidae) on T sericea (all have virtually continuous generations and fairly high biomass); Cirina forda (Westwood) (Saturniidae) and E fasciata on B africana (the former has one high biomass peak in mid-summer, the latter has continuous generations and fairly high biomass); Neobostra pyroxantha Hampson (Pyralidae) on O pulchra (has two high peaks of biomass in late summer); Anaphe reticulata Walker (Thaumetopoeidae) on D rotundifolia (has two high biomass peaks, one in mid- and the other in late-summer); and Phasicnecus sp (Eupterotidae) on S pungens (has four high peaks of biomass between October and April).

MATERIAL AND METHODS

Beating

Beating was carried out monthly to determine monthly standing crop biomass of foliage-feeding larvae on the dominant woody plants. Fifty branches each of B africana, T sericea and O pulchra were beaten. From a preliminary survey it was found that V rhemannii, C molle and G flavescens did not support significant populations of larvae and S pungens and D rotundifolia, although heavily defoliated at certain times of the year are sparsely distributed at Nylsvley, so it was decided to beat only 10 branches monthly of each of these species to monitor populations on these plants.

Branches were selected so that a whole small branch or the tip of a larger branch would fit over the beating tray. The beating tray consisted of a slightly concave sheet of white polystyrene measuring 50 x 100 cm, which was attached to a wire frame which could be hung around the beater's neck. This left both hands free to hold the beating stick, calipers and clipboard. The beating tray was held under the branch and the branch was beaten at the outside edge of the tray with a stout stick to dislodge the larvae. Legner and Oatman (1962), working in an apple orchard found that 95% of all larvae were dislodged by beating. In this study branches on which larvae were seen were beaten on a number of occasions and in all cases all the foliage-feeding larvae were dislodged. This holds true for free-living larvae but larvae which occur in webs (e.g. N pyroxantha on O pulchra) were not always dislodged. However, the webs of these larvae are conspicuous and in these cases the larvae were removed from the web by hand.

Beating was restricted to branches at roughly breast height and the diameters of the beaten branches were measured with calipers. From the diameter of the branch it is possible to estimate leaf surface area of the branch. J Tew (in litt) determined the ratios between the log of the diameters squared of branches and the log of leaf surface area for T sericea, B africana and O pulchra. He found that the relationship was very similar for these species. It was thus assumed for this study that it would also be similar for the other woody plants occurring in the study area. Tew determined the Leaf Area Index (LAI) for each of the three plants mentioned above and found that it was in the region of 0,2 in all three cases (0,272 for O pulchra, 0,240 for B africana and 0,219 for T sericea). As no LAI's have been determined for the other tree species concerned they were roughly estimated to be 0,1 as plant density of these species is considerably lower than that of the other three.[1] Larval biomass was expressed in g/ha of leaf surface area which was then

---

[1]Rutherford (1979) has recently provided more accurate estimates of Leaf Area Index for the major tree species, as follows (the estimates used in this paper are given in parentheses, for comparison): B africana 0,285(0,240); O pulchra 0,267(0,272); T sericea 0,098(0,219); D rotundifolia 0,015(0,100); S pungens 0,008(0,100). These differences will affect some of the calculations in this paper, but should not influence the overall pattern.

converted to g/ha of ground surface area using the LAI. All results are expressed as g/ha of ground surface area using this conversion.

Larvae collected by beating were placed on a twig or leaf of the host plant and placed in glass vials with holes in the plastic stoppers. Directly after the beating was completed the larvae were closely examined, allocated to a size group and all colour patterns and other macroscopical morphological characteristics were recorded. It was found that colour was not always a reliable criterion, but that the positions of the markings were usually fairly constant, irrespective of the colour. Arbitrary size groups were used, namely very small: under 10 mm; small: 10-25 mm; medium-sized: 25-50 mm; large: greater than 50 mm.

The larvae were then described and allocated a field number, as identification to species level of most of the larvae was impossible, since no keys exist for the identification of South African lepidopterous larvae. Only after the emergence of the adults could most be identified. Even then, certain adults presented a problem as some of the reared species were found to be new or known, but undescribed, species.

Determination of biomass

The lengths and breadths of larvae collected by beating were measured and recorded (Figures 1, 2). The average measurements of all the larvae beaten from one host plant were used to calculate the biomass. Measuring larvae was complicated by the fact that certain larvae are very active. This was overcome by leaving them on a twig or a leaf of the host plant in a vial overnight. The following morning they were usually sufficiently inactive to make measurement possible. In very stubborn cases the larvae were cooled down with commercially available "ice-bricks".

To be able to determine the dry biomass of larvae in the field without removing them it was decided to draw up tables of biomass:size relationships for larvae. One hundred and sixty-six larvae of various easily obtainable species ranging in size from 5 x 1 mm to 85 x 16 mm were collected. These were measured with calipers and then dried in an oven at 110°C for periods ranging from four hours for small larvae to eight hours for large larvae. The times necessary to dry the larvae completely were determined by weighing the larvae and then placing them back in the oven. This was repeated until their mass remained constant. The mass of the dry larvae was determined on a Mettler micro-balance to 10^{-5} g.

Length, breadth and biomass data were then used in a multiple regression analysis. Six variables were used: log of biomass (Y); length (X_1); breadth (X_2); length squared (X_1^2); breadth squared (X_2^2) and length times breadth (X_1X_2).

From the regression it was found that it was necessary to use only breadth and breadth squared in the calculation of biomass as 94,5% of the variation in biomass can be attributed to these easily determined variables. Using breadth and breadth squared a multiple r of 0,9722 (= 94,518%) with a standard error of estimate of 0,2012 was obtained.

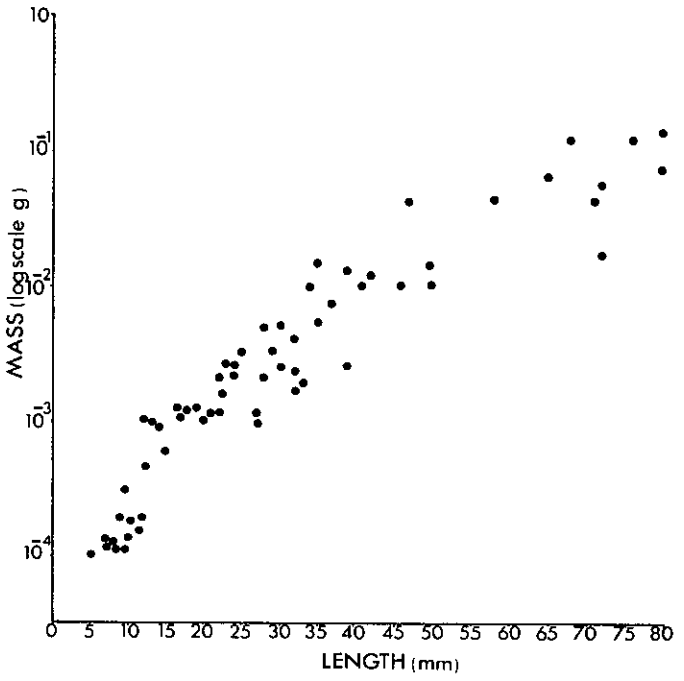

Figure 1. Relationship between larval mass and length.

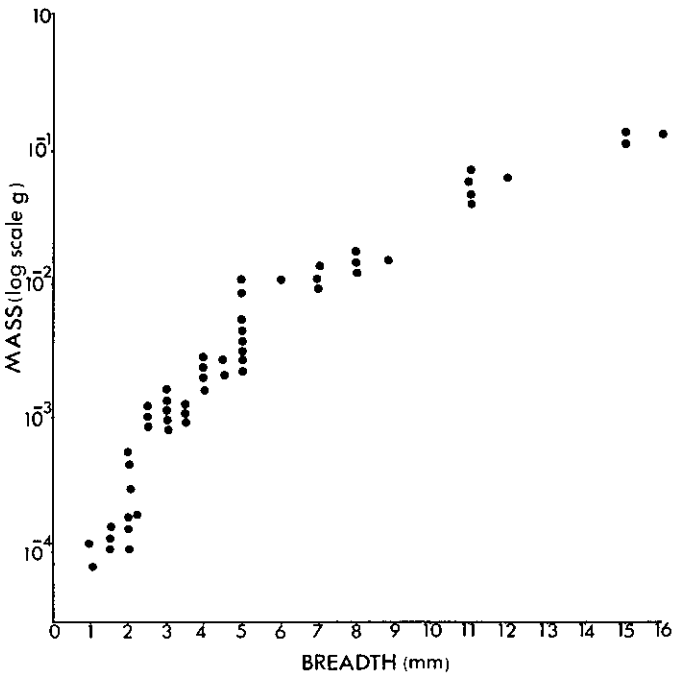

Figure 2. Relationship between larval mass and breadth.

By using breadth, breadth squared and length a multiple r of 0,9740 (= 94,86%) with a standard error of estimate of 0,1963 was obtained. It was felt sufficient to use breadth and breadth squared only (a far simpler equation) since using the longer equation with breadth, breadth squared and length improved the estimate by only 0,3%.

Hence the equation used to determine biomass from breadth and breadth squared was:

$$\frac{\log Y}{1000} = -0,19309 + 0,47415X_2 - 0,01681X_2^2 \qquad (1)$$

where Y = biomass in g dry mass
and X_2 = breadth in mm

Determination of consumption

Since the aim of the investigation was to assess consumption under natural conditions it was felt that consumption of leaf matter and amount of faeces excreted would be best determined in the field.

(a) Sleeving

When young larvae of approximately the same size were found in adequate numbers (at least five), they were measured and placed in nylon chiffon sleeves and these were tied over a twig of the host plant with a known number of leaves provided for food. Any leaves which had a portion missing were first removed from the twig.

Three sizes of sleeves were used, 80 x 45 cm, 55 x 30 cm and 30 x 15 cm. The choice of size depended on the number of larvae used for the experiment as well as on the size of the larvae and their likely food requirements.

It was assumed that the effect of sleeving on the microclimate within the sleeve would not affect the results significantly. Coarse chiffon was used in order not to affect the flow of air through the sleeves so that the temperature and humidity would remain approximately normal.

Larvae were supplied with crumpled paper or leaf litter in which to pupate in the sleeves, as certain ground-pupating larvae need to satisfy a positively thigmotactic sense before pupation takes place (Oldroyd 1970). These substrates were chosen so that it would be easy to separate the faecal pellets from them.

Ants, Crematogaster spp, were attracted to the bags and, on gaining entry, would kill and remove any pupae in the sleeves. To prevent the ants from having access to the sleeves, "Formex" (a tacky substance used commercially to keep ants out of fruit trees), was liberally applied to the base of the stem and branches on which sleeves were placed. This was not the ultimate solution as dust, leaves, grass and other debris stuck to the "Formex", thus forming bridges which the ants were quick to find. The band of "Formex"

(which remains sticky for a long time) was agitated weekly to prevent bridges forming, but nevertheless some losses were suffered.

(b) Leaf consumption and larval growth

To determine the average leaf size of the eight species of food plant, 500 intact leaves were randomly selected from each tree species and the surface area of the leaves determined in the field on a portable "Paton" electronic planimeter. From the results an average size leaf was calculated for each tree species.

The leaves used for determining the leaf surface area were taken to the laboratory where they were dried in an oven at 110°C for 24 hours. The dry mass of the sample was then determined on an electric Mettler top-pan balance and the dry mass of an average leaf was calculated for each host plant (Table 1).

Table 1. Average leaf sizes and dry masses of leaves for the eight dominant woody plants at Nylsvley.

TREE SPECIES	MASS OF AVERAGE LEAF (g)	AVERAGE LEAF SIZE (mm^2)
Terminalia sericea	0,0614	447,0
Burkea africana	0,0350	365,6
Ochna pulchra	0,2724	1 816,0
Strychnos pungens	0,0392	305,7
Dombeya rotundifolia	0,0840	731,6
Vitex rhemannii	0,0145	153,1
Grewia flavescens	0,0200	187,2
Combretum molle	0,1612	1 048,0

These results were subsequently used as standard measurements. When leaves were counted, and a sleeve containing larvae placed over them, they were regarded as "average" leaves and their dry mass was considered to be that of "average" leaves.

The larvae in the sleeve were measured at weekly intervals and the average size of all the larvae was calculated. The remaining leaves and parts of leaves (which were summed to estimate the number of complete leaves eaten) were counted. The faeces were removed, dried and the mass determined. The dry mass of the leaf matter consumed, as well as the loss of leaf area, was calculated from Table 1. When pupation occurred between weekly checks, the last measurement recorded was regarded as the size of the mature final instar larva.

It was decided to calculate consumption and defaecation for the whole larval stage. Where larvae were not obtained at the beginning of the first instar, their consumption up to that stage was estimated at five per cent of the total recorded. This estimate is derived from Waldbauer (1968) and Van den Berg and Van den Berg (1973) according to whom less than 10% of total consumption by lepidopterous larvae occurs in the first two instars. It was possible, however, to predict with reasonable accuracy when egg eclosion of the various species in the field would take place by noting time of adult emergence. Knowing the approximate duration of the egg stage it was in most cases relatively easy to find first instar larvae.

The data obtained in this way cannot be directly compared with results obtained from experiments where the insect's mass is determined periodically and where food of known mass is given, as is done in most feeding experiments. Such experiments are usually done under controlled laboratory conditions, whereas those of this project were done under natural conditions in the field. The effect of varying environmental conditions was considered to be vital for the data to have ecological significance and this would more than compensate for inaccuracies arising from field determinations. Crossley (1966) found that under controlled conditions a beetle species consumed 9-10 mg dry mass per day, while in the field the same species of similar size consumed 7-16 mg dry mass per day. The effect of the environment here is obvious. It is assumed that the same principle applies in the case of lepidopterous lavae.

(c) Defaecation

Faeces were collected from the sleeves at weekly intervals, dried and their mass determined. Larvae were left in the bags until pupation had taken place because if mature final instar larvae are removed before they have expelled their last gut contents this could affect faeces yield significantly. Waldbauer (1962) found that final instar gut contents could be as much as 9,3% of the fresh body mass.

Rearing in laboratory

Pupae were removed from the sleeves and taken to the laboratory where they were placed on sand in glass jars. The mouth of each jar was covered with a piece of chiffon which was held in place by a rubber band. A strip of stiff paper was placed in the bottle to provide the newly emerged adults with a place on which to climb during the expansion of their wings. If this is not provided the wings often do not develop completely which makes identification of the adults difficult.

Water was sprayed on the pupae at intervals of about one week to prevent desiccation. The pupae were kept at room temperature and normal light regime.

RESULTS

Trophic ecology of the dominant species

Consumption, excretion and secondary production were measured in the field and ingestion, faeces production, assimilation, secondary production and biomass (in g dry mass) are recorded in trophic flow diagrams (Figures 3a, 6a, 7a, 10a, 11a, 14a, 15a, 18a) for individuals of each species. In these diagrams I = amount of foliage ingested; NU = food eaten but not utilized; E = excretion; A = mass of food assimilated; P = production (ie increase in mass of larvae); R = that proportion of assimilated food lost during metabolic processes; B represents the final mass of larvae available to the next trophic level. I, NU, E and B were measured directly, P was calculated as the difference between the final mass of the larvae and the original mass (in the case of individuals the final mass of the larva less the mass of a first instar larva) and A was calculated as the difference between the mass of food consumed and the mass of faeces. B represents the final mass of the larva (in the case of individuals) and the total biomass figure for the season for all the populations (in the case of the total) for a particular host plant for the season.

Totals for all the populations on a host plant were calculated from the consumption data per unit of biomass. Each larva collected during sampling was measured and its consumption per unit of biomass was calculated from the specific results applicable to that species. The total consumption was then determined as the sum of the monthly results.

From the results of feeding experiments in the field, breadth (a function of growth) was plotted against average daily consumption (Figures 4, 5, 8, 9, 12, 13, 16, 17). These data were calculated from the increase in breadth (a function of mass) over seven days (14 days for E fasciata on B africana and N pyroxantha on O pulchra), and the total consumption over the same period divided by the number of days to give the average daily consumption. Individual efficiences were then determined for each species and are given in Table 2.

The tissue growth efficiency (TGE) is the efficiency with which digested food is converted to biomass and this will decrease as the proportion of digested food metabolized for energy increases (Waldbauer 1968). Thus TGE is affected by factors which influence the amount of energy devoted to the maintenance of physiological functions or the support of activity. It is not directly dependent upon digestibility, but it does vary with the level of nutrient intake.

The ecological growth efficiency (EGE) is the efficiency of conversion of ingested food to biomass. It is an overall measure of an insect's ability to utilize for growth the food which it ingests. Thus EGE varied both with the digestibility of the food and with the proportion of digested food that is converted to biomass or is metabolized for energy to maintain life (Waldbauer 1968).

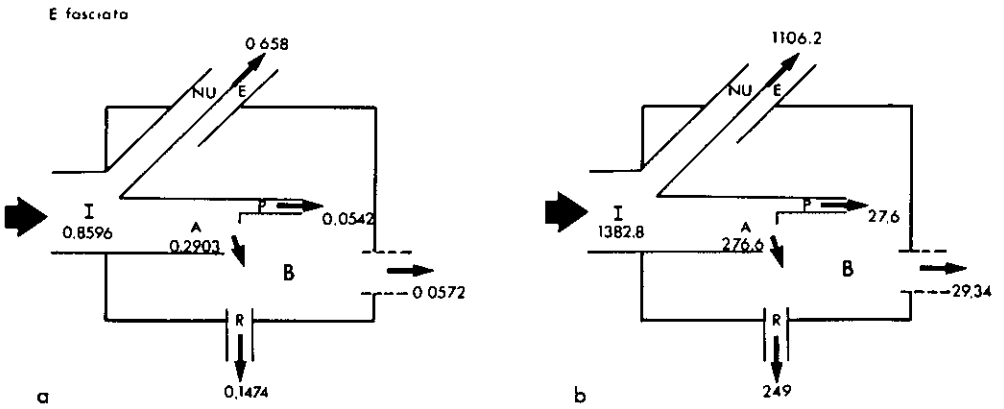

Figure 3. Trophic flow diagrams (expressed in g dry mass) for (a) one individual and (b) all the populations of E fasciata on T sericea for one season.
A = assimilation, B = biomass, E = excretion,
I = ingestion, Nu = not utilized, P = production
R = respiration.

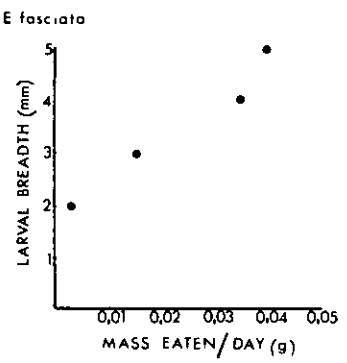

Figure 4. Dry mass of food consumed per size increase of E fasciata on T sericea.

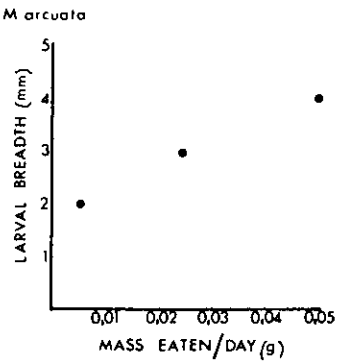

Figure 5. Dry mass of food consumed per size increase of M arcuata on T sericea.

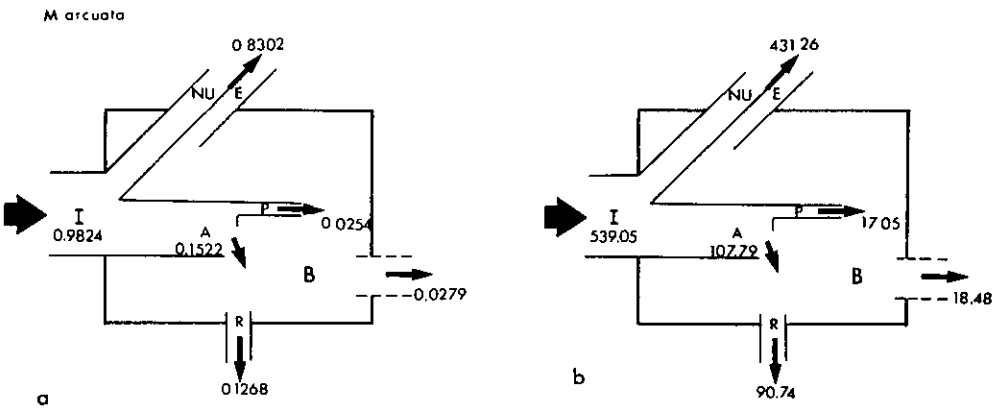

Figure 6. Trophic flow diagrams (expressed in g dry mass) for (a) one individual and (b) all the populations of M arcuata on T sericea for one season.

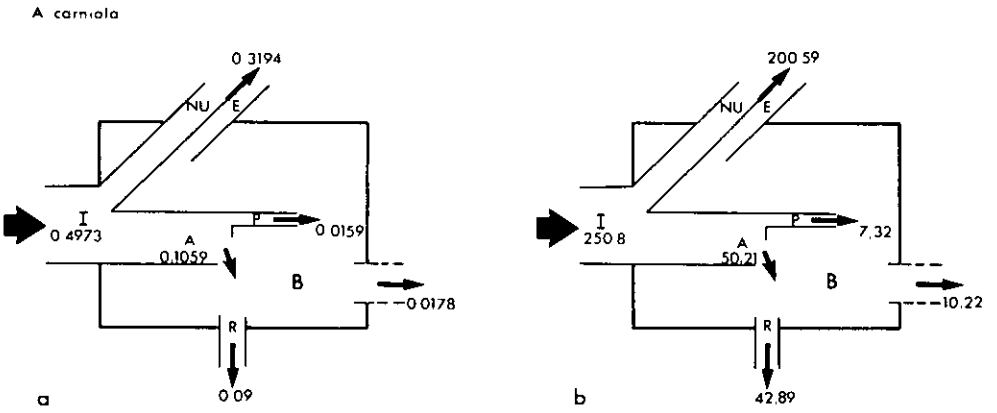

Figure 7. Trophic flow diagrams (expressed in g dry mass) for (a) one individual and (b) all the populations of A carniola on T sericea for one season.

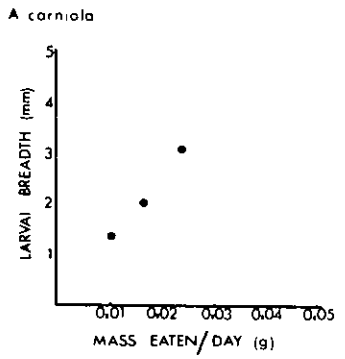

Figure 8. Dry mass of food consumed per size increase of A carniola on T sericea.

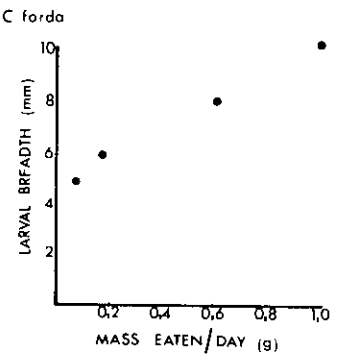

Figure 9. Dry mass of food consumed per size increase of C forda on B africana.

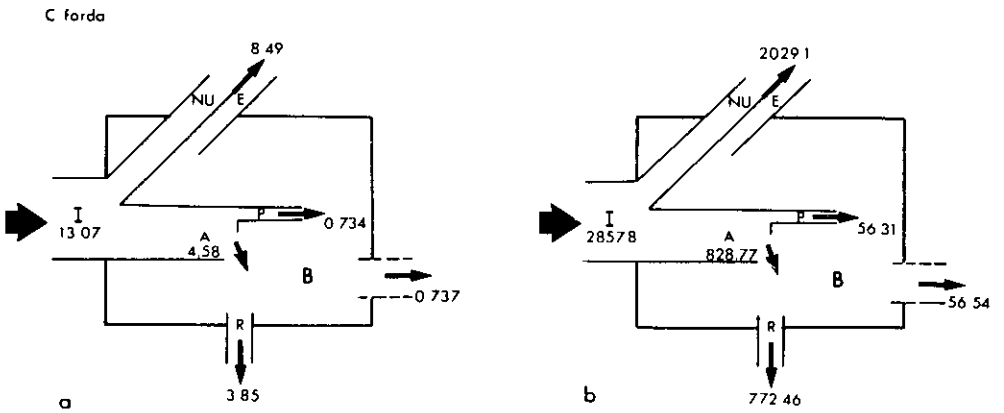

Figure 10. Trophic flow diagrams (expressed in g dry mass) for (a) one individual and (b) all the populations of C forda on B africana for one season.

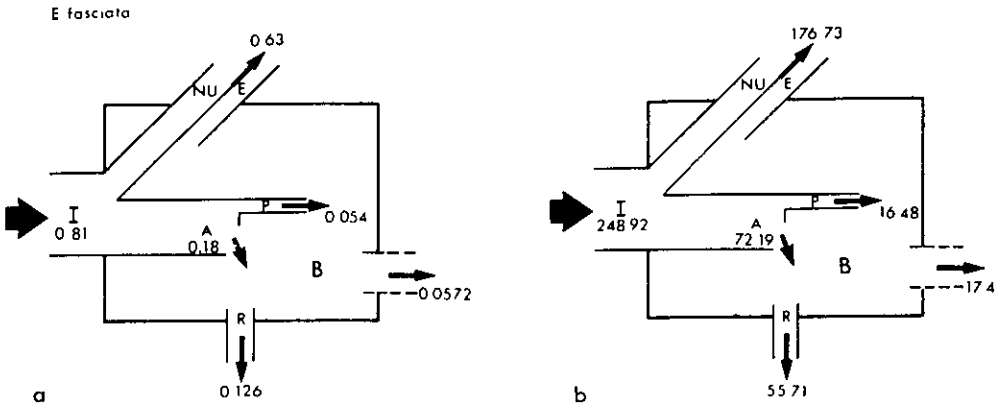

Figure 11. Trophic flow diagrams (expressed in g dry mass) for (a) one individual and (b) all the populations of E fasciata on B africana for one season.

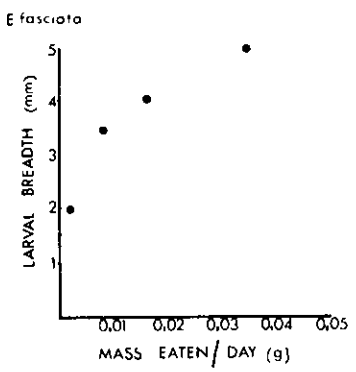

Figure 12. Dry mass of food consumed per size increase of E fasciata on B africana.

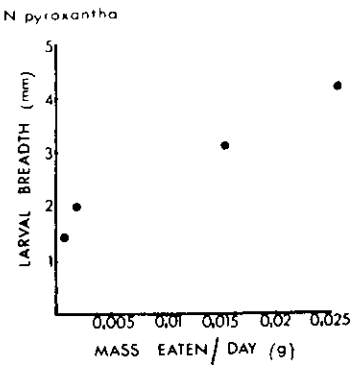

Figure 13. Dry mass of food consumed per size increase of N pyroxantha on O pulchra.

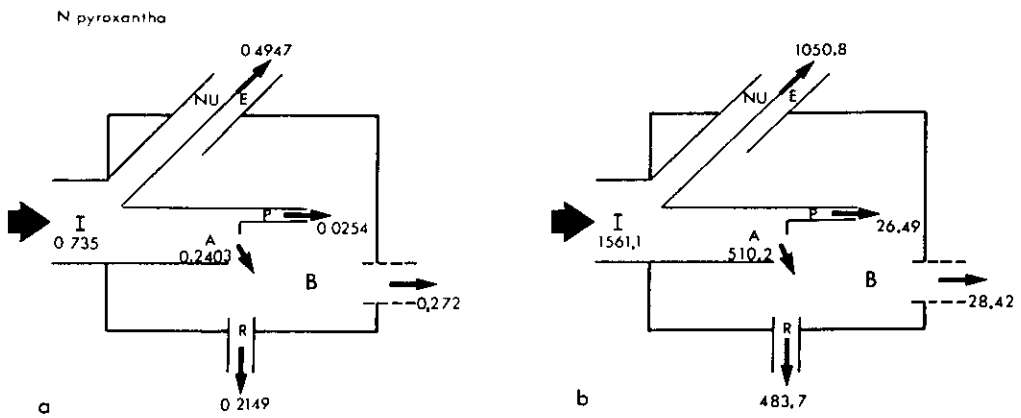

Figure 14. Trophic flow diagrams (expressed in g dry mass) for (a) one individual and (b) all the populations of N pyroxantha on O pulchra for one season.

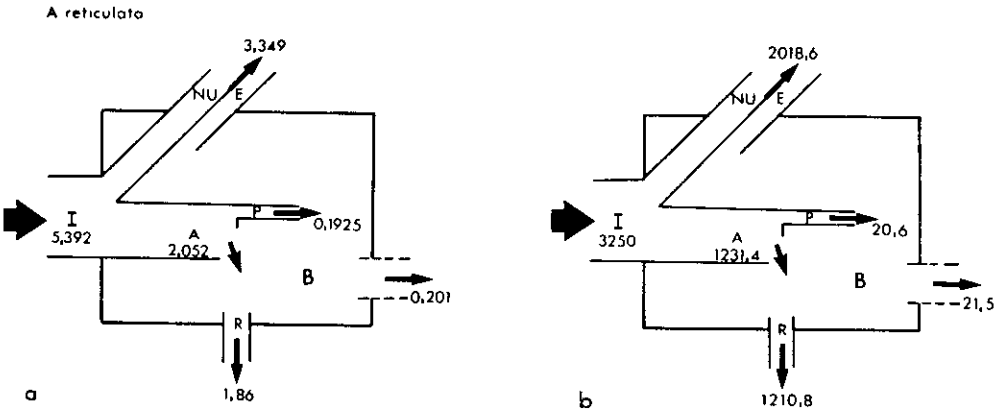

Figure 15. Trophic flow diagrams (expressed in g dry mass) for (a) one individual and (b) all the populations of A reticulata on D rotundifolia for one season.

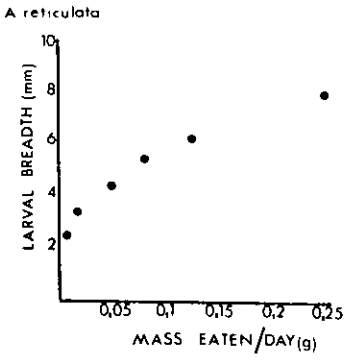

Figure 16. Dry mass of food consumed per size increase of A reticulata on D rotundifolia.

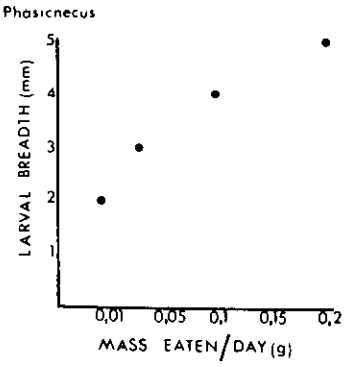

Figure 17. Dry mass of food consumed per size increase of Phasicnecus sp on S pungens.

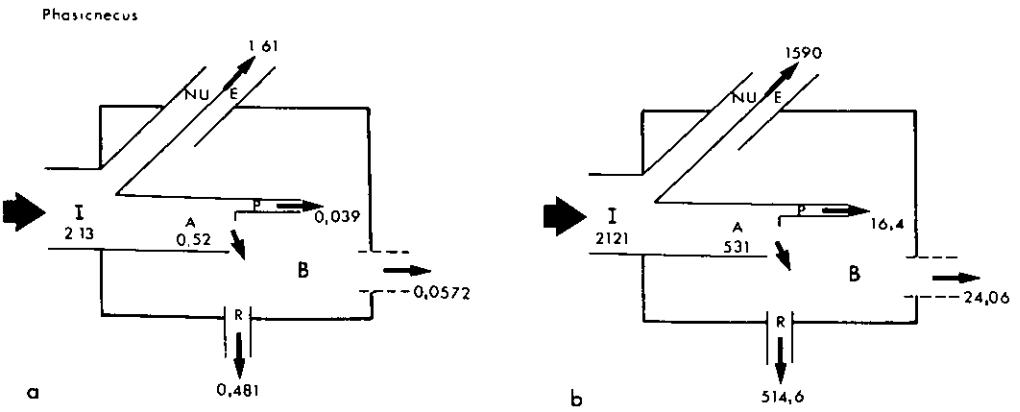

Figure 18. Trophic flow diagrams (expressed in g dry mass) for (a) one individual and (b) all the populations of Phasicnecus sp on S pungens for one season.

Table 2. Individual efficiencies in terms of dry mass for eight dominant species of Lepidoptera at Nylsvley.
P = production, A = assimilation, I = ingestion.

	Tissue Growth Efficiency: $\frac{P}{A}$	Ecological growth Efficiency: $\frac{P}{I}$	Assimilation Efficiency: $\frac{A}{I}$
Terminalia sericea			
Euproctis fasciata	18,6%	6,3%	33,7%
Maurilia arcuata	16,7%	2,6%	15,5%
Arcyophora carniola	15,1%	3,2%	21,3%
Burkea africana			
Cirina forda	16,0%	5,6%	35,0%
Euproctis fasciata	30,0%	6,7%	22,2%
Ochna pulchra			
Neobostra pyroxantha	10,6%	3,5%	32,7%
Dombeya rotundifolia			
Anaphe reticulata	9,4%	3,6%	38,0%
Strychnos pungens			
Phasicnecus sp.	7,5%	1,9%	24,4%

Assimilation efficiency is the efficiency with which ingested food is utilized and represents that percentage of the total amount of food ingested that is eventually available for essential body functions.

The approximate average daily consumption of the populations was extrapolated for each month from the weekly consumption data obtained from the sleeved specimens of each species. From the size of the individuals, and the population estimates derived from beating, approximate average daily consumption figures for the populations were obtained from the results given in Figures 4, 5, 8, 9, 12, 13, 16, 17.

Consumption, excretion and secondary production of these populations, expressed in g dry mass, is recorded in trophic flow diagrams (Figures 3b, 6b, 7b, 10b, 11b, 14b, 15b and 18b).

Host-plants and associated lepidopterous larvae

Terminalia sericea

Twelve species of lepidopterous larvae were recorded on T sericea:

Euproctis fasciata Walker (Lymantriidae)

This polyphagous species was observed to feed on a number of plants at Nylsvley, namely T sericea, B africana, O pulchra, V rhemannii,

D rotundifolia, Lannea discolor, Ximenia caffra, Acacia tortilis and A caffra. Pinhey (1975) records it on Combretum platypetalum and unspecified species of Acacia, Cassia and Protea. Larvae are laminar feeders and leave only the rachis of the leaf.

At Nylsvley this species was recorded simultaneously on all the above-mentioned host plants, but the largest population was present on T sericea in the first generation and on B africana in the second generation. Complete larval development takes about 30 days on T sericea and about 55 days on B africana. It is not clear why B africana is the preferred host plant in the second generation. The fact that larval development takes nearly twice as long on B africana as on T sericea suggests that there must be strong selective pressures on them to utilize B africana. It is not known what these might be. Larvae of E fasciata do still occur on T sericea during the second generation, implying that the plant is still palatable and nutritious. Larval development is still quicker than on B africana.

The two generations per season of E fasciata on T sericea result in peak numbers of larvae being present in November-December and March.

Maurilia arcuata Walker (Noctuidae)

At Nylsvley this species was found to feed only on T sericea but Pinhey (1975) records it on unspecified species of Combretum, Myrica and Monotes. The larvae are laminar feeders and utilize the whole leaf excluding the rachis.

Maurilia arcuata has three generations per season and numerical peaks of the larvae are present in January (first generation), February-March (second generation) and April (third generation).

Arcyophora carniola Hampson (Noctuidae)

This species was only recorded on T sericea. The feeding pattern is that of a typical skeleton feeder, the rachis and several of the thicker veins not being eaten.

Arcyophora carniola has four generations per season and numerical peaks of the larvae are present in October (first generation), December (second generation), February (third generation) and April (fourth generation).

Altogether a total of 12 species of foliage-feeding lepidopterous larvae were recorded on T sericea.

From the results of the trophic ecology of E fasciata, M arcuata and A carniola it was calculated that an average of only 20,08% of ingested food is assimilated. Much of the ingested energy is lost during metabolic processes. In a laboratory study of Bombyx mori L, Hiratsuka (in Waldbauer 1968) found that 35-52% of assimilated energy was lost via respiration. A loss of 50% energy for a sedentary species is high and thus losses of about 80% are to be expected in natural populations. The

average percentage of ingested energy in terms of dry mass fixed by the main three species is 4,0%. This is the proportion of dry mass removed from the plant and fixed in the larvae which is available to the next trophic level.

The average daily consumption, based on consumption per unit biomass of E fasciata, M arcuata and A carniola, was used to determine the average daily consumption of all the populations on T sericea. Consumption (Figure 19) was determined for the monthly standing crop biomass (Figure 20). The average standing crops for two-month periods was calculated and the running averages of these were used to give a more probable figure for the consumption between the successive sample periods.

Faeces production was estimated as 80% of the amount consumed (Figure 19). This figure is derived from the results of A carniola, M arcuata and E fasciata in which faeces production amounted to 78,7%, 84,5% and 76,6% respectively of the amount of food consumed.

Monthly standing crop in g dry mass/ha is illustrated in Figure 20 and the estimated loss of photosynthetic area by T sericea as a result of consumption by all foliage-feeding Lepidoptera larvae on T sericea is shown in Figure 21.

Burkea africana

A total of nine species of foliage-feeding lepidopterous larvae were recorded on B africana:

Cirina forda (Westwood) (Saturniidae)

Cirina forda was only found feeding on B africana at Nylsvley. Pinhey (1975) records a number of other host plants without mentioning B africana, including unspecified species of Acacia, Albizzia, Carissa, Ekebergia, Euclea, Rhus, Warburgia, Aloe and Sideroxylon. Larvae are characteristic laminar feeders, leaving only the rachices and petioles of the compound leaves.

This species has two generations per year. First generation larvae are present on the trees from about the middle of October to about the end of November. Extensive defoliation of B africana trees is caused by the larvae of the first generation but this varies in intensity and severity from year to year. Larvae of the small second generation are present on the trees from about the middle of March until about the end of April but they do not appear to cause significant damage.

Euproctis fasciata

See the above discussion under T sericea on the host-plant preference and feeding pattern of this species.

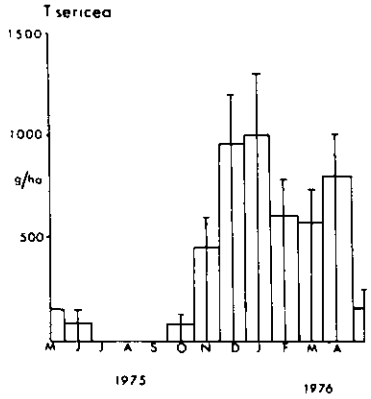

Figure 19. Total dry mass (g/ha) of T sericea foliage consumed (lines) and of faeces produced (blocks) by larvae.

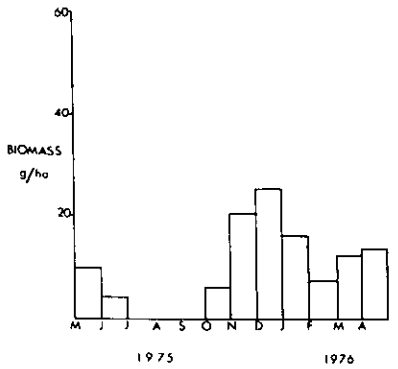

Figure 20. Monthly standing crop (g/ha) of foliage-feeding larvae on T sericea for one year.

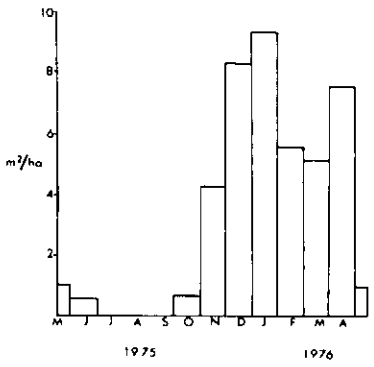

Figure 21. Loss of photosynthetic area (m^2/ha) on T sericea as a result of consumption by lepidopterous larvae.

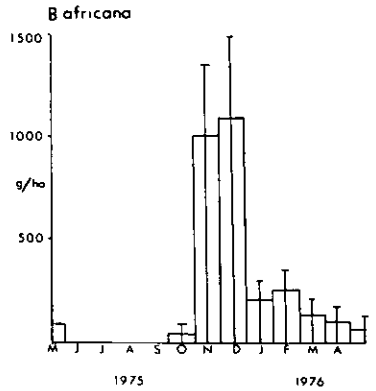

Figure 22. Total dry mass (g/ha) of B africana foliage consumed (lines) and of faeces produced (blocks) by larvae.

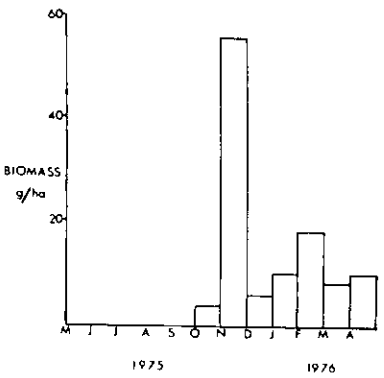

Figure 23. Monthly standing crop (g/ha) of foliage-feeding larvae on B africana for one year.

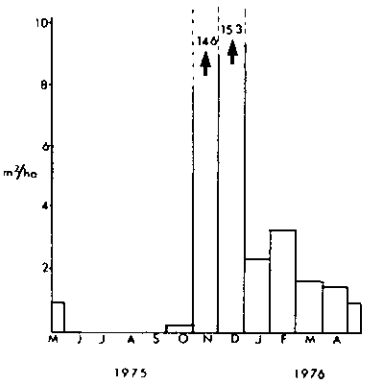

Figure 24. Loss of photosynthetic area (m^2/ha) on B africana as a result of consumption by lepidopterous larvae.

There are two generations of E fasciata per year on B africana and larvae are present from about the middle of November until around the middle of January and then again from near the end of February until about the end of April.

From the results of the trophic ecology of C forda and E fasciata it was calculated that an average of only 28,6% of ingested food was assimilated. This is similar to that for lepidopterous larvae feeding on T sericea. An average of only 6,2% of the mass removed from the plant is fixed in the larvae and is consequently available to the next trophic level.

Consumption by all the populations sampled monthly on B africana was estimated from the specific consumption data of C forda and E fasciata. The consumption was determined for the monthly standing crop and the two-month running averages are given in Figure 22.

Faeces production was calculated to be 71% of the amount consumed (Figure 22) based on results from C forda and E fasciata in which faeces production was 65,0% and 77,8% respectively of the amount consumed.

Monthly standing crop is illustrated in Figure 23 and the monthly loss of photosynthetic area as a result of consumption by all foliage-feeding Lepidoptera larvae on B africana is recorded in Figure 24.

Ochna pulchra

Three species of lepidopterous larvae were recorded on O pulchra:

Neobostra pyroxantha Hampson (Pyralidae)

This species is only known to feed on O pulchra. The larvae are gregarious and live in webs spun between leaves.

Neobostra pyroxantha has two generations per year at Nylsvley and larvae reach high densities during both generations. First generation larvae are present from near the end of December to about the end of February and second generation larvae from the end of March until about the end of May. Between 12 and 21% of trees sampled had colonies of larvae and mean colony size was 3,6 and 5,8 larvae for the two generations respectively. These larvae cause extensive defoliation of O pulchra.

Neobostra pyroxantha was the only species numerous enough for detailed study on O pulchra and the trophic ecology of all Lepidoptera populations on O pulchra is based on that of N pyroxantha (Figures 13, 14a).

Total consumption of O pulchra foliage, and the amount of faeces produced, are recorded in Figure 25. Monthly standing crop is illustrated in Figure 26 and the loss of photosynthetic area as a result of consumption by Lepidoptera larvae on O pulchra is given in Figure 27.

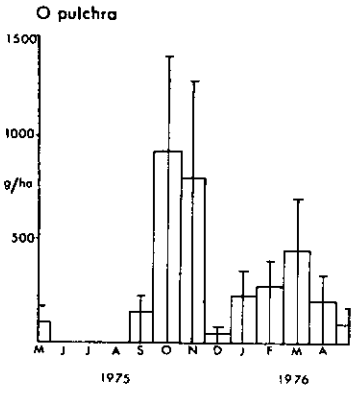

Figure 25. Total dry mass (g/ha) of O pulchra foliage consumed (lines) and of faeces produced (blocks) by larvae.

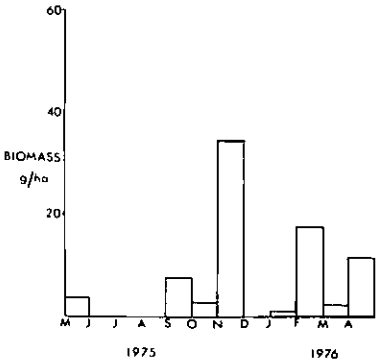

Figure 26. Monthly standing crop (g/ha) of foliage-feeding larvae on O pulchra for one year.

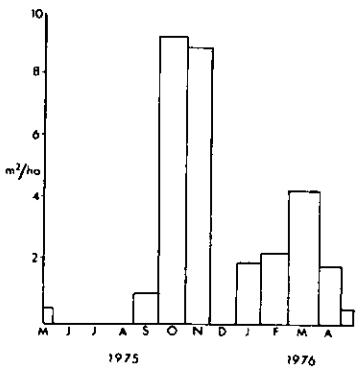

Figure 27. Loss of photosynthetic area (m^2/ha) on O pulchra as a result of consumption by lepidopterous larvae.

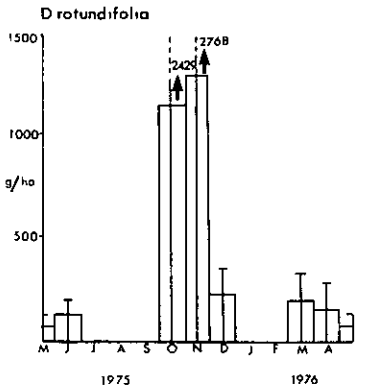

Figure 28. Total dry mass (g/ha) of D rotundifolia foliage consumed (lines) and of feaces produced (blocks) by larvae.

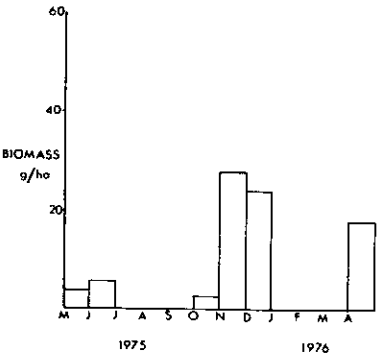

Figure 29. Monthly standing crop (g/ha) of foliage-feeding larvae on D rotundifolia.

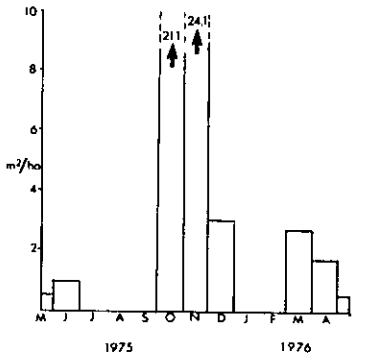

Figure 30. Loss of photosynthetic area (m^2/ha) on D rotundifolia as a result of consumption by lepidopterous larvae.

Dombeya rotundifolia

Only one species of foliage-feeding lepidopterous larvae was recorded on D rotundifolia:

Anaphe reticulata Walker (Thaumetopoeidae)

Larvae were found feeding on D rotundifolia and on one occasion on Grewia flavescens. Pinhey (1975) also records the larvae feeding on unspecified species of Diplorhynchus (presumably D condylocarpon, the only species in southern Africa). The larvae are gregarious and in feeding they skeletonize the leaves.

Anaphe reticulata has two generations per year and larvae are present between January and March and again between April and June. The larvae periodically cause extensive defoliation of D rotundifolia trees.

Trophic ecology of all the Lepidoptera populations on D rotundifolia is based on the results derived from A reticulata, the only species studied in detail. Total consumption of foliage, and total faeces produced, are given in Figure 28. Monthly standing crop is shown in Figure 29 and the loss of photosynthetic area by D rotundifolia, as a result of consumption by all Lepidoptera larvae, is illustrated in Figure 30.

Strychnos pungens

The larvae of only one Lepidoptera species were found feeding on this species:

Phasicnecus sp (Eupterotidae)

This species was only found feeding on S pungens. The larvae of the first few instars are typical window feeders, eating only the epidermis and mesophyll and leaving all vascular tissue uneaten. This feeding pattern is very characteristic and damage can be identified before the cryptic larvae are found. Later instar larvae are typical laminar feeders and leave only the rachices of the leaves uneaten.

Four peaks of Phasicnecus larvae were observed on S pungens, in October, December, February-March and April-May. Extensive defoliation of S pungens trees periodically occurs.

Total consumption of S pungens foliage, and total faeces produced, are recorded in Figure 31. Monthly standing crop is shown in Figure 32 and the loss of photosynthetic area as a result of consumption by Phasicnecus sp larvae on S pungens is illustrated in Figure 33.

Vitex rhemannii

Two species of Lepidoptera were found to feed on V rehmannii:

Scopula sp (Geometridae)

This small species was only recorded on V rhemannii. There are four or five continuous, overlapping generations per year.

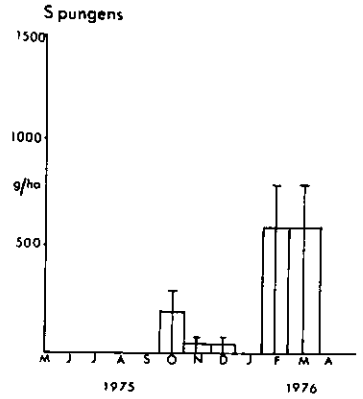

Figure 31. Total dry mass (g/ha) of S pungens foliage consumed (lines) and of faeces produced (blocks) by larvae.

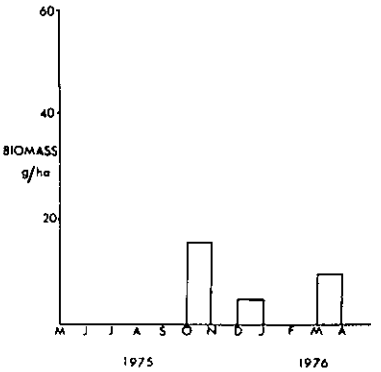

Figure 32. Monthly standing crop (g/ha) of foliage-feeding larvae on S pungens for one year.

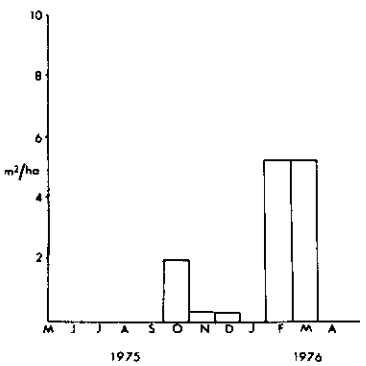

Figure 33. Loss of photosynthetic area (m^2/ha) on S pungens as a result of consumption by lepidopterous larvae.

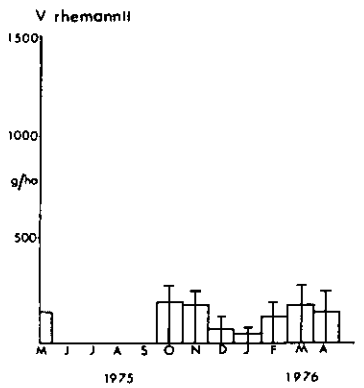

Figure 34. Total dry mass (g/ha) of V rhemannii foliage consumed (lines) and of faeces produced (blocks) by larvae.

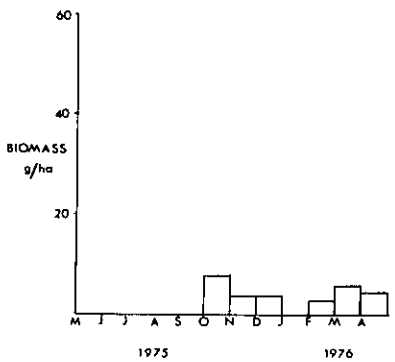

Figure 35. Monthly standing crop (g/ha) of foliage-feeding larvae on V rhemannii for one year.

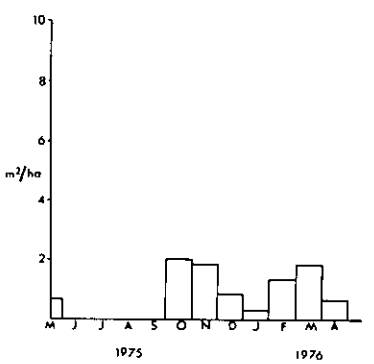

Figure 36. Loss of photosynthetic area (m^2/ha) on V rhemannii as a result of consumption by lepidopterous larvae.

Trophic ecology of all populations on V rhemannii was based on the results of Arcyophora carniola (Figures 7a, 8) as Scopula sp, the dominant species on V rhemannii, is similar in size to A carniola and it was therefore assumed that their trophic ecology would be similar. Total consumption of V rhemannii foliage, and the total faeces production, are recorded in Figure 35. The loss of photosynthetic area as a result of larval consumption is recorded in Figure 36.

Grewia flavescens and Combretum molle

No significant numbers of larvae were recorded on either of these host plants.

Overall trophic ecology of Lepidoptera on the dominant plants of the Burkea savanna.

Lepidoptera larvae removed 2,2% of the foliage produced per ha in one year. This is based on a figure of 1 000 kg/ha/year of foliage production from the eight woody species dealt with (Rutherford 1979). Larvae on T sericea removed 25,3% of the total; on B africana 16,7%; on O pulchra 19,9%; on D rotundifolia 26,4%; on S pungens 8,4%; and on V rhemannii 3,3%. The total monthly consumption data and faeces production are summarized in Figure 37.

The monthly biomass of all Lepidoptera larvae present on the dominant plants is recorded in Figure 38 and a trophic flow diagram illustrating the overall amounts (in g dry mass ha^{-1}) of consumption, excretion and secondary production is given in Figure 39.

DISCUSSION

Lepidoptera larvae removed 2-3% of the foliage produced by woody plants in one year at Nylsvley. This effect is small but is comparable to results obtained in other systems. Bray (1964) recorded figures of 7-12% for all foliage-feeding insects in a North American deciduous forest system. Varley (1970) reported a figure of 6,9% of foliage removal by Lepidoptera larvae in an oak forest, but this was determined during a high population peak and this figure would probably be considerably lower during an average year.

The impact of leaf consumption is usually taken to be the removal of photosynthetic area, resulting in reduced primary production. Total impact is, however, not truly reflected in such figures. Funke (1971) has pointed out that the extent of damage cannot be judged solely by the amount eaten. The place of attack, the stage of development of the plant or its organs and the season of attack must also be taken into account. The spread of consumption over time may be significant as certain trees may be heavily defoliated early in the season, though this need not necessarily be reflected in the final average figure. Franklin (1970) notes that damage to and consumption of leaves late in the season has far less effect on the tree than that occurring early in the season, but this difference in effect is difficult to assess.

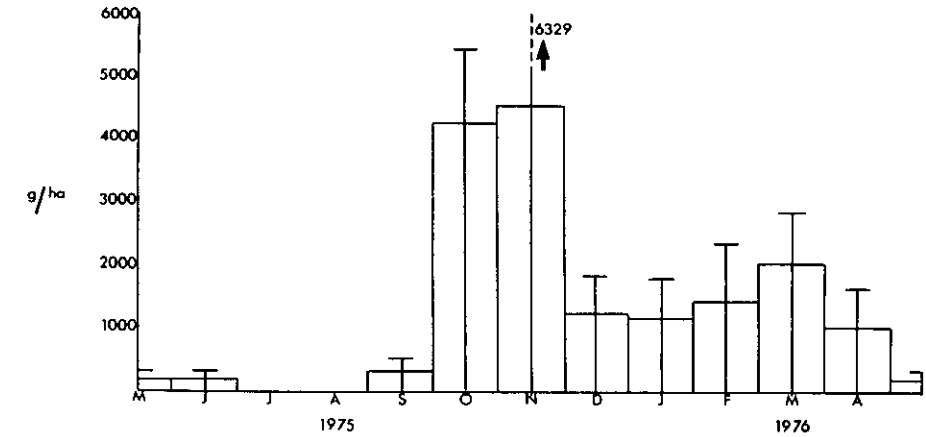

Figure 37. Total dry mass (g/ha) of foliage of the eight dominant woody plants consumed (lines) and of faeces produced (blocks) by larvae.

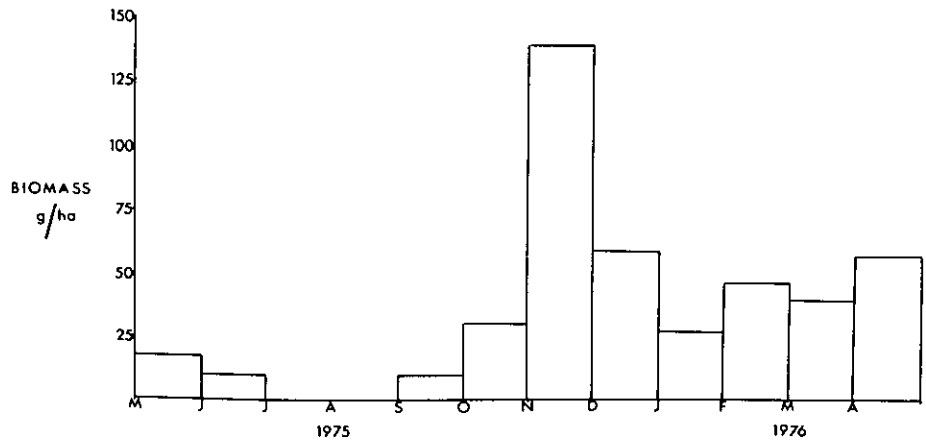

Figure 38. Monthly biomass of all Lepidoptera larvae present on the eight dominant woody plants at Nylsvley.

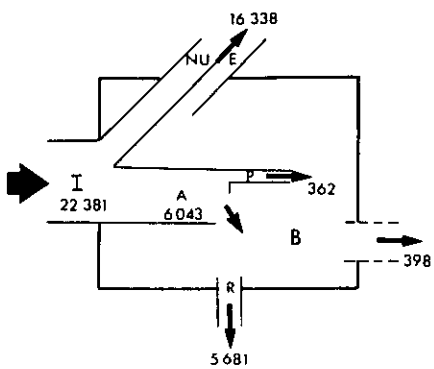

Figure 39. Trophic flow diagram (expressed in g dry mass ha^{-1}) for the whole complex of foliage-feeding Lepidoptera larvae associated with the eight dominant woody plants at Nylsvley.

The average tissue growth efficiency (P/A) of all species of Lepidoptera associated with woody vegetation at Nylsvley was 16,5% (range 7,5 - 30,0) the average ecological growth efficiency (P/I) was 4,2% (range 1,8 - 6,7) and the average assimilation efficiency (A/I) was 26,6% (range 15,5 - 38,1). These figures, except for the ecological growth efficiency, are within the limits for natural populations as reported by Odum (1971) and Welch (1968). The ecological growth efficiency, however, appears rather low compared to results of the above-mentioned authors.

Variation in efficiencies, it appears, must be attributed to physiological and behavioural properties of the species and to the host plant, because these efficiencies varied for different species on one host plant as much as between host plants.

The average percentage of dry mass assimilated that was lost in maintenance was 83% for all species studied, which is slightly higher than the average of 70% reported by Engelmann (1966) for natural populations.

It is not clear why C molle and G flavescens have no significant lepidopterous larvae associated with them. C molle has hairy leaves and G flavescens coarse leaves. This does not appear to deter other insects as certain beetle species are very partial to C molle. G flavescens, however, has generally low insect diversity (Holm et al 1976).

REFERENCES

Bray J R 1964. Primary consumption in three forest canopies. Ecology 45, 165-167.

Crossley D A 1966. Radioisotope measurement of food consumption by a leaf beetle species Chrysomela knabi Brown. Ecology 47, 1-8.

Engelmann M D 1966. Energetics, terrestrial field studies and animal productivity. In: Advances in ecological research 3, 73-115. Cragg J B (ed). Academic Press, London and New York.

Evans A C 1939. The utilization of food by certain lepidopterous larvae. Transactions of the Royal Entomological Society of London 89(2), 13-22.

Franklin R T 1970. Insect influences on the forest canopy. In: Ecological Studies 1. Analysis of temperate forest ecosystems, 86-99. Reichle D E (ed). Springer Verlag, Heidelberg, Berlin, New York.

Funke W 1971. Food and energy turnover of leaf-eating insects and their influence on primary production. In: Ellenberg H (ed) Ecological Studies 2. Methods and results of ecosystem research in the German Solling Project, 81-93. Springer Verlag, Heiderlberg, Berlin, New York.

Holm E, Kirsten J F and Scholtz C H 1976. Final report on primary feeding on woody vegetation. Report to National Committee for Environmental Sciences, CSIR, Pretoria. 12 pp Mimeograph.

Kasting R and McGinnis A J 1962. Quantitative relationship between consumption and excretion of dry matter by larvae of the pale western cutworm, Agrotis orthogonia Morr. (Lepidoptera : Noctuidae). Canadian Entomologist 94, 441-443.

Legner E F and Oatman E R 1962. Foliage-feeding Lepidoptera on young non-bearing apple trees in Wisconsin. Journal of Economic Entomology 55, 552-554.

Lubke R A, Clinning C F and Smith F R 1975. A quantitative ecological survey of the woody vegetation of the Nylsvley study area. Report to the National Committee for Environmental Sciences, CSIR, Pretoria. 123 pp. Mimeograph.

Odum E P 1971. Fundamentals of ecology. 3rd edn. Saunders, Philadelphia, London, Toronto.

Oldroyd H 1970. Collecting, preserving and studying insects. Hutchinson Scientific and Technical, London.

Pinhey E C G 1975. Moths of southern Africa. Tafelberg Publishers Ltd, Cape Town.

Reichle D E and Crossley D A 1967. Investigation on heterotrophic productivity in forest insect communities. In: Petrusewicz K (ed) Secondary productivity of terrestrial ecosystems. Polish Academy of Sciences, I B P, Warsaw, Poland.

Rutherford M C 1979. Aboveground biomass subdivisions in woody species of the Savanna Ecosystem Project study area, Nylsvley. South African National Scientific Programmes Report 36, 1-33.

Van den Berg M A and van den Berg M M 1973. The food assimilation and duration of larval instars of three saturniid forest pests. Journal of the Entomological Society of southern Africa 36, 165-173.

Varley G C 1967. Estimation of secondary production in species with an annual life-cycle. In: Petrusewicz K (ed) Secondary productivity of terrestrial ecosystems: 447-457. Polish Academy of Science. Warsaw, Poland.

Varley G C 1970. The concept of energy flow applied to a woodland community. In: Watson A (ed) Animal populations in relation to their food resources, 389-404. Blackwells, Oxford and Edinburgh.

Waldbauer G P 1962. The growth and reproduction of maxillectomized tobacco hornworms feeding on normally rejected non-solanaceous plants. Entomologia experimentalis et applicator 5, 147-158.

Waldbauer G P 1964. Quantitative relationships between numbers of fecal pellets, fecal weight and the weight of food eaten by tobacco hornworms Protoparce sexta (Johan). (Lepidoptera : Sphingidae) Entomologia experimentalis applicator 7, 310-314.

Waldbauer G P 1968. The consumption and utilization of food by insects. In: Beament J W L, Treherne J E and Wiggelsworth V B (eds) Advances in insect physiology. 5. 229-228. Academic Press, New York.

Welch H 1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. Ecology 49, 755-759.

Winter K 1971. Studies in the productivity of Lepidoptera populations. In: Ellenberg H (ed) Ecological studies 2. Methods and results of ecosystem research in the German Solling Project, 94-99. Springer Verlag, Heidelberg, Berlin, New York.

TITLES IN THIS SERIES

1. *A description of the Savanna Ecosystem Project, Nylsvley, South Africa. December 1975. 24 pp.

2. *Sensitivity analysis of a simple linear model of a savanna ecosystem at Nylsvley. W M Getz and A M Starfield. December 1975. 18 pp.

3. *Savanna Ecosystem Project - Progress report 1974/1975. S M Hirst. December 1975. 27 pp.

4. Solid wastes research in South Africa. R G Noble. June 1976. 13 pp.

5. *Bibliography on marine pollution in South Africa. D A Darracott and C E Cloete. June 1976. 131 pp.

6. *Recycling and disposal of plastics waste in South Africa. R H Nurse, N C Symington, G R de V Brooks and L J Heyl. June 1976. 35 pp.

7. *South African Red Data Book - Aves. W R Siegfried, P G H Frost, J Cooper and A C Kemp. June 1976. 108 pp.

8. South African marine pollution survey report 1974-1975. C E Cloete and W D Oliff (editors). September 1976. 60 pp.

9. Modelling of the flow of stable air over a complex region. M T Scholtz and C J Brouckaert. September 1976. 42 pp.

10. Methods and machinery for pulverising solid wastes. M J Simpkins. October 1976. 29 pp.

11. *South African Red Data Book - Small mammals. J A J Meester. November 1976. 59 pp.

12. Savanna Ecosystem Project - Progress report 1975/1976. B J Huntley. March 1977. 41 pp.

13. Disposal and recovery of waste paper in South Africa. G R de V Brooks. April 1977. 35 pp.

14. South African Red Data Book - Fishes. P H Skelton. July 1977. 39 pp.

15. A checklist of the birds of the Nylsvley Nature Reserve. W R Tarboton. September 1977. 14 pp.

16. *Grondsoorte van die Nylsvley-natuurreservaat. H J von M Harmse. September 1977. 64 pp.

17. Description and manual for the use of DRIVER - an interactive modelling aid. P R Furniss. September 1977. 23 pp.

18. South African Red Data Book - Large mammals. J D Skinner, N Fairall and J du P Bothma. November 1977. 29 pp.

19. *Introducing you to satellite operated Data Collection Platforms (DCP's). C C Stavropoulos. September 1977. 9 pp.

20. A phytosociological classification of the Nylsvley Nature Reserve. B J Coetzee, F van der Meulen, S Zwanziger, P Gonsalves and P J Weisser. December 1977. 31 pp.

21. An annotated checklist of the amphibians, reptiles and mammals of the Nylsvley Nature Reserve. N H G Jacobsen. December 1977. 65 pp.

22. *Cooperative National Oceanographic Programme. SANCOR. January 1978. 19 pp.

23. South African Red Data Book - Reptiles and amphibians. G R McLachlan. February 1978. 53 pp.

24. *Guidelines for the disposal of dangerous and toxic wastes so as to minimize or prevent environmental and water pollution. R T Rudd. January 1978. 12 pp.

25. Richards Bay mesometeorological data. Vertical profiles of air temperature and wind velocity and surface wind statistics. M T Scholtz, E T Woodburn, C J Brouckaert and M Mulholland. March 1978. 104 pp.

26. *Studies of mineralization in South African rivers. G C Hall and A H M Gorgens (editors). March 1978. 24 pp.

27. Nylsvley - A South African Savanna Ecosystem Project: objectives, organization and research programme. March 1978. 37 pp.

28. *A description of the Fynbos Biome Project. June 1978. 25 pp.

29. *Savanna Ecosystem Project - Phase I summary and Phase II progress. B J Huntley and J W Morris. July 1978. 52 pp.

30. *Review of Coastal Currents in Southern African Waters. T F W Harris. August 1978. 106 pp.

31. *Report of the Task Group on Fermentation Technology. R J Andrews, J A de Villiers, P M Lategan, F G Neytzell-de Wilde, J P van der Walt and Professor D R Woods. September 1978. 16 pp.

32. South African programme for the SCOPE mid-term project on the ecological effects of fire. September 1978. 36 pp.

33. Fire in South African ecosystems: an annotated bibliography. G U Schirge and A H Penderis. October 1978. 114 pp.

34. *Inland water ecosystems in South Africa : a review of research needs. R G Noble and J Hemens. November 1978. 150 pp.

35. *South African Antarctic Research Programme, 1978-1982. SASCAR. December 1978. 39 pp. Out of print but partially replaced by No 50.

36. *Aboveground biomass subdivisions in woody species of the Savanna Ecosystem Project Study Area, Nylsvley. M C Rutherford. January 1979. 33 pp.

37. *Marine Line Fish Research Programme. SANCOR. April 1979. 17 pp.

38. *The Southern Ocean - South African Cooperative Research Programme. SANCOR. May 1979. 26 pp.

39. The Transfer of Pollutants in Two Southern Hemispheric Oceanic Systems. Proceedings of a workshop held at Plettenberg Bay, South Africa, 23-26 April 1979. October 1979. 188 pp.

40. Fynbos ecology : a preliminary synthesis. J Day, W R Siegfried, G N Louw and M L Jarman. December 1979. 166 pp.

41. *Bibliography of Marine Biology in South Africa. D A Darracott and A C Brown. February 1980. 250 pp.

42. Advances in understanding phosphorus cycling in inland waters - their significance for South African limnology. A J Twinch and C M Breen. March 1980. 22 pp.

43. Terrestrial ecology in South Africa - project abstracts for 1978. February 1980. 92 pp.

44. A manual of methods for use in the South African Marine Pollution Monitoring Programme. R J Watling. July 1981. 82 pp.

45. Threatened plants of Southern Africa. A V Hall, M de Winter, B de Winter and S A M van Oosterhout. May 1980. 244 pp.

46. South African legislation with respect to the control of pollution of the sea. André Rabie. January 1981. 73 pp.

47. Terrestrial ecology in South Africa and South West Africa - project abstracts for 1979. May 1981. 107 pp.

48. A bibliography of seabirds in the waters of southern Africa, the Prince Edward and Tristan Groups. J Cooper and R K Brooke. December 1981. 297 pp.

49. National Geoscience Programme. The Evolution of Earth Resource Systems. SACUGS. June 1981. 42 pp.

50. South African Antarctic Biological Research Programme. SASCAR. July 1981. 54 pp.

51. South African Marine Pollution Monitoring Programme 1979-1982. R J Watling and C E Cloete (editors). July 1981. 52 pp.

52. Structural characterization of vegetation in the Fynbos Biome. B M Campbell, R M Cowling, W J Bond and F J Kruger in collaboration with D P Bands, C Boucher, E J Moll, H C Taylor and B W van Wilgen. August 1981. 19 pp.

53. A bibliography of fynbos ecology. M L Jarman, R M Cowling, R Haynes, F J Kruger, S M Price and G Moll. August 1981. 73 pp.

54. A description of the Benguela Ecology Programme 1982-1986. SANCOR: (W R Siegfried and J G Field editors). March 1982. 39 pp.

55. Trophic Ecology of Lepidoptera Larvae associated with woody vegetation in a Savanna Ecosystem. C H Scholtz. June 1982. 29 pp.

*Out of print.

8363106