

Savanna ecosystem project: Phase I summary and Phase II progress

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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 Agricultural Technical Services, the Transvaal Provincial Administration, the CSIR, the Transvaal Museum, and seven 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 Planning and the Environment.

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 to 1979) - studies in the key components and processes including the development of mathematical models, and Phase III (1979 to 1984) - extension to other sites and the study of management strategies for the optimal utilization of Burkea savanna ecosystems.

The objectives, organization and research programme of the project are described in detail in report no 27 of this series (Anon 1978). The results of Phase I are summarized and an outline of Phase II progress up to July 1977 is presented in the present report. A preliminary synthesis of Phase II findings will be prepared for publication before the end of 1978.

ABSTRACT

A summary of the results of the first phase (mid 1974 to mid 1976) of the South African Savanna Ecosystem Project being undertaken at Nylsvley in the northern Transvaal is presented. Phase I of this ten year study of the structure and functioning of a bushveld community was aimed at developing a quantitative description of the Study Area, in particular its soils, climate, vegetation and fauna. Details are provided of the main soil types, climatic variables, plant and animal communities, and in particular, the distribution of biomass in space and time. An outline is given of progress in Phase II – studies in key components and processes.

SAMEVATTING

'n Opsomming word gegee van die bevindinge van die eerste fase (middel 1974 tot middel 1976) van die Suid-Afrikaanse Savanne-ekosisteemprojek te Nylsvley in die noordelike Transvaal. Studies gedurende Fase I van hierdie tienjarige studie oor die struktuur en funksionering van 'n bosveldgemeenskap was gemoeid met die ontwikkeling van 'n kwantitatiewe beskrywing van die studiegebied, in besonder die grondsoorte, klimaat, plantegroei en fauna. Besonderhede word verskaf oor die belangrikste grondsoorte, klimatologiese veranderlikes, plant- en diergemeenskappe, met klem veral op die verspreiding van biomassa in ruimte en tyd. Die vordering gemaak gedurende Fase II, naamlik studies in sleutelkomponente en -prosesse, word kortliks bespreek.

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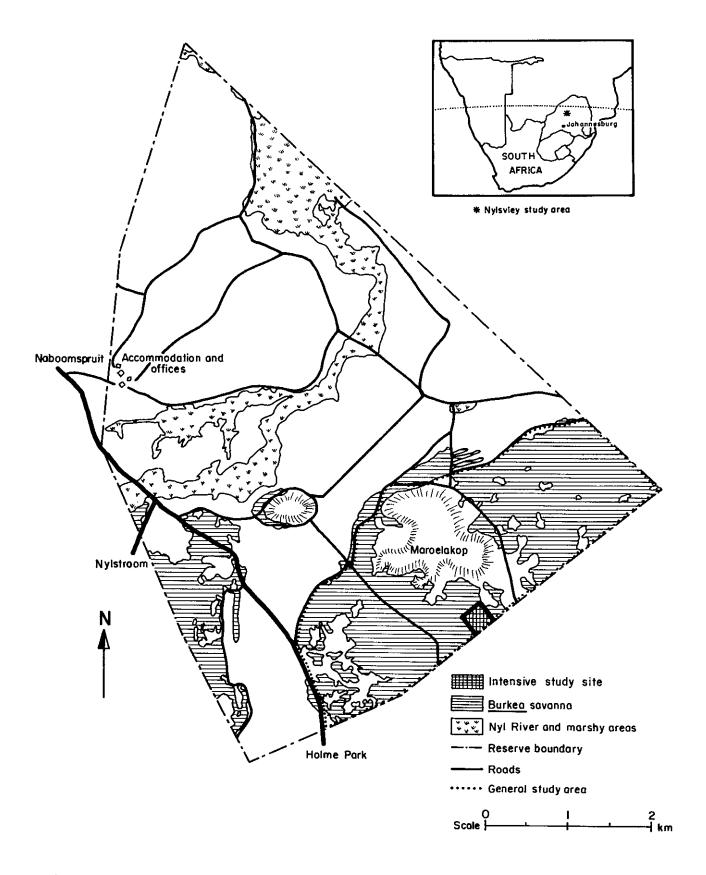


Figure 1. Nylsvley Nature Reserve, northern Transvaal. The Savanna Ecosystem Project Study Area occupies approximately 745 ha of the south-eastern sector of the Reserve.

INTRODUCTION

The Savanna Ecosystem Project was initiated in 1974 on the Nylsvley Provincial Nature Reserve, northern Transvaal, as a cooperative multidisciplinary effort to develop a holistic understanding of the structure and functioning of a typical southern African savanna (Anon 1978). The objectives of the project also included the development of simulation models, improved land-use strategies and the provision of an educational facility for training graduate students in interdisciplinary research. It is expected that the understanding gained from such studies would permit the prediction of the effects of various kinds of stresses on the ecosystem's stability.

The project was divided into three phases which have tended to overlap as the project has developed, viz:

Phase I (mid 1974 to mid 1976) - A pilot study of the Nylsvley Study Area

Phase II (mid 1976 to 1979) - Studies of key components and processes

Phase III (1979 to 1984) - Management and validation studies.

The pilot study included surveys of the soils, vegetation and vertebrate fauna of the Reserve as a whole, but most of the effort has been concentrated in a 745 ha Study Area dominated by Burkea africana savanna (Figure 1). For logistic reasons and in order to permit integration of research findings, studies of key components and processes have been conducted within an intensive study site of approximately 50 ha. The results of Nylsvley investigations will be compared with information gathered from a wide range of similar savannas during the Phase III validation studies.

Phase I activities were concluded in mid 1977 and it is now opportune to provide a summary of these results in addition to reporting briefly on progress made in Phase II studies.

PHASE I : PILOT STUDY OF THE NYLSVLEY STUDY AREA

The aims of the pilot study were outlined in the first description of the project (Anon 1975) as:

- To survey and map the soils and vegetation of the Reserve and describe its abiotic features and biotic components.
- To undertake a structural analysis of the vegetation of the Study Area, plan the intensive study site and install its weather recording and other facilities.
- To identify major components and pathways within the ecosystem.
- To determine standing crops of the components and their fluxes over a full year.
- To develop mathematical simulation models of the ecosystem based on the information gained above and from literature.
- To identify components and processes in the ecosystem, relative to the defined objectives, which have to be investigated further during Phase II.

Despite slight changes in emphasis, the execution of Phase I followed the set aims very closely and by mid 1977 most of the broader goals had been met. The division of research activities into six component groups was adhered to and it is useful to summarize the findings of the individual projects within these components.

ABIOTIC COMPONENT

Introduction

At the initiation of the project, very limited information was available on the major abiotic features of the Nylsvley Nature Reserve. A comprehensive soil survey of the whole Reserve, the preparation of large scale orthophoto topographic maps and the installation of meteorological stations were seen as first priorities.

Climate

The climate of Nylsvley has been briefly outlined by Hirst (1975) and Coetzee et al (1977). Long-term records for Mosdene and Nylstroom, respectively 10 km north-east and 25 km east-south-east of the Study Area, are summarized in Figure 2. The short-term records thus far available for the Study Area (Figure 3, Table 1) follow the general pattern illustrated by long-term data, but at the same time indicate the extent to which fluctuations in the pattern occur. While the long-term average monthly precipitation peaks from November to January, both 1975/76 and 1976/77 summers experienced a midsummer drought, that of the latter season resulting in considerably reduced herbage yields (Grunow 1977).

Meteorological instrumentation currently in use in the Study Area is listed in Table 2. The automatic weather station has not yet been commissioned.

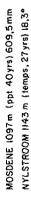
Rainfall in the Study Area for 1975/76 and 1976/77 seasons totalled 672 and 620 mm, falling on 74 and 64 days respectively, compared with a 40 year mean of 630 mm falling on an average of 62 days at Mosdene. During the 1975/76 and 1976/77 seasons 92% and 98% of the total rainfall was recorded during the period October through March.

The hottest months recorded at the Study Area during the two seasons for which data are available were January 1976 and January 1977 with mean monthly maxima of $22,2^{\circ}$ C and $24,2^{\circ}$ C (Table 1).

Ground frosts were recorded on 2! days in 1975, 22 days in 1976 and 18 days in 1977. The extreme grass minimum temperature was $-9.9^{\circ}C$, recorded on 1977.07.07.

The relative humidity of the air is consistently low in the early afternoon, often dropping to below 15% from July through September. Mean recordings at 08h00 for these months ranged from 57% to 70% while mean data for the same hours during the rain months of October through March ranged from 65% to 86%.

Daily evaporation from a USA class A pan during the period September 1976 to June 1977 reached maxima of 13,3 mm, 13,2 mm and 13,6 mm per day in September, November and January respectively. The monthly total evaporation varied from 125 mm in June to 258 mm in January with a September total of 241 mm. For the months September through April, the total evaporation was 1 630 mm. Using a theoretical pan factor of 0,6, this means that over this period the Burkea savanna could lose 980 mm of water or 155% of the annual expected rainfall (De Jager 1977).



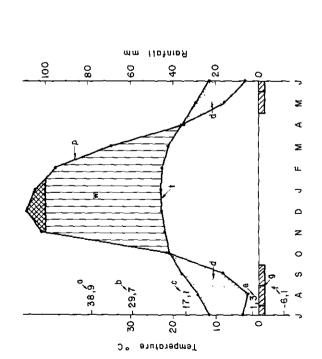


Figure 2. Composite climate diagram for Mosdene and Nylstroom showing long-term mean monthly temperature and

rainfall values.

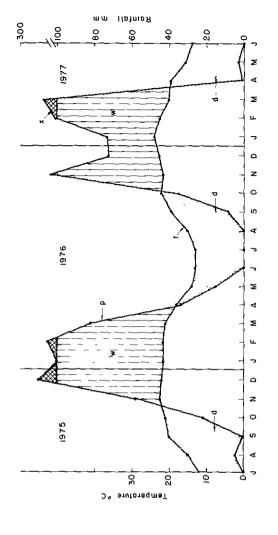


Figure 3. Climate diagram for the intensive study site, Nylsvley, July 1975 to June 1977.

p - monthly means of precipitation; daily range of temperature; d - arid period (dotted area); e - mean daily minimum of the coldest month; Key for Figures 2 and 3 : a - absolute maximum; b - mean daily maximum of the hottest months; c - mean f - absolute minimum; g - months with an absolute minimum below 0°C; t - monthly means of temperature; w - humid period (hatched area).

Monthly evaporation class "A" pan Extr 11,0 13,2 12,8 (mm/day) 11,5 7,1 Total 234,1 210,4 258,3 185,6 118,0 138,5 134,9 125,3 (IIII) 18,0 38,0 29,0 25,0 Extr 29,0 21,0 18,0 15,0 28,0 38,0 14,0 11,0 14,0 21,0 17,9 12,9 (%)14h00 Mean daily 37,4 53,5 34,8 50,2 53,8 56,1 46,2 76,0 29,6 27,8 30,4 35,6 Relative humidity 49,6 48,8 7,44 50,4 61,4 45,2 29,9 26,2 (%) Extr min 27,0 50,0 54,0 61,0 65,0 18,0 51,0 36,0 39,0 24,0 41,0 31,0 40,0 39,0 59,0 62,0 6,44 41,9 8 08h00 Mean daily 75,3 62,4 85,0 85,6 85,4 81,2 57,0 69,7 64,1 65,1 68,2 70,0 67,3 9,97 85,6 79,8 62,9 65,2 8 Mean daily 6,64 62,8 70,5 62,9 65,8 58,0 46,0 50,3 58,9 59,4 56,0 63,5 73,5 62,5 46,7 43,7 47,4 45,7 (%) Mean 120cm 18,9 21,2 22,9 22,8 22,8 23,4 20,3 18,8 17,9 18,2 24,6 23,6 23,0 21,6 19,8 22,1 20,1 ව 22,1 Soil temperature Mean 60cm 16,9 24,9 18,6 22,4 24,2 24,2 24,5 23,9 22,0 16,6 24,2 23,4 26,2 23,3 25,1 18,9 16,2 17,4 26,1 23,7 20,2 9 24,5 29,0 Mean 20cm 14,4 17,3 22,4 24,2 21,5 16,7 14,4 14,3 16,7 21,6 25,6 27,0 28,4 26,9 23,3 22,8 18,3 15,2 ව Mean 10cm 18,0 24,6 28,0 15,3 26,7 27,5 25,8 22,2 17,0 14,8 17,6 22,6 26,0 23,9 23,2 24,4 14,1 25,1 28,9 28,9 17,8 14,6 9 Extr 7,5 12,0 8,2 13,0 12,2 9,5 2,5 2,0 ව Monthly air temperature Extr max 28,6 33,3 36,3 34,8 26,2 30,0 28,0 34.4 26,2 34,1 32,5 26,4 28,8 29,8 33,2 31,6 29,8 9 33,4 33,4 28,2 26,4 Mean daily 21,0 12,0 15,1 19,8 22,4 21,7 22,2 22,1 20,9 18,0 14,2 12,8 14,7 19,4 21,9 24,2 22,6 20,2 19,5 12,7 22,6 ව 15,7 13,7 Precipitation Actual Monthly rain total total days 0 13 ιŲ 0 0 0 2 œ 7 7 7 -0,2 57,7 102,6 149,7 81,9 34,1 15,1 73,0 105,2 178,7 (IIII 197,3 296,7 173,1 239,4 290,2 3 Monthly sunshine hours Max poss-396,0 389,6 334,4 345,1 354,7 418,6 375,2 341,4 329,4 314,8 389,6 396,0 358,7 375,2 341,4 334,4 371,1 345,1 354,7 314,8 Ξ September September November December February November December February October January October January August August March April April July March June July May June May 1975

Climatic records for station 2s, intensive study site, Hylsvley, from July 1975 to June 1977, Table 1.

Table 2. Meteorological instruments installed in the Study Area weather stations, Nylsvley.

*Maximum thermometer
*Minimum thermometer
*Wet-bulb thermometer
*Dry-bulb thermometer
*Thermohydrograph
Grass minimum thermometer
Campbell-Stokes sunshine recorder
Pressure plate anemometer
Lambrecht recording anemometer
*Standard raingauge
Casella recording raingauge
Recording evaporimeter
Class A evaporation pan

- l Solarimeter
- 1 Albidometer
- r l Net radiometer
- † l Quantum sensor
- 「 4 Tube solarimeters
- l6 Temperature sensors
- 5 Heat flux plates
- l Tipping bucket raingauge

- * Instruments at stations 1, 2 and 3. All others at station 2 only.
- Instruments connected to 48-channel data logger for continuous recording.

Geology, topography and soils

The Study Area occupies a sandy plateau at 1 100 m dropping gently towards the Nyl River floodplain (1 080 m) over most of its extent, although a fairly steep fall occurs along the northern margin of Maroelakop. The sands overlie sandstones, conglomerates and grits of the Waterberg system. The detailed topography of the Study Area has been mapped at a scale of 1: 2 500, (contour interval 2 m) and the results presented in a set of orthophoto map sheets.

The soils of the Reserve have been classified and mapped by Harmse (1977) who identified 17 soil forms and 34 soil series, Figure 4. The area occupied by and the characteristics of the more important forms and series of the Study Area are given in Table 3.

The dominant soil forms of the Study Area, ie Hutton, Clovelly and Mispah are pedologically distinguished according to the South African National Soil Classification System (Macvicar $et\ al$ 1977) on a basis of defined diagnostic horizons.

The Hutton form dominates the Study Area latosols. Its profile comprises an orthic A-horizon, generally of 5-30 cm depth, which is underlain by a

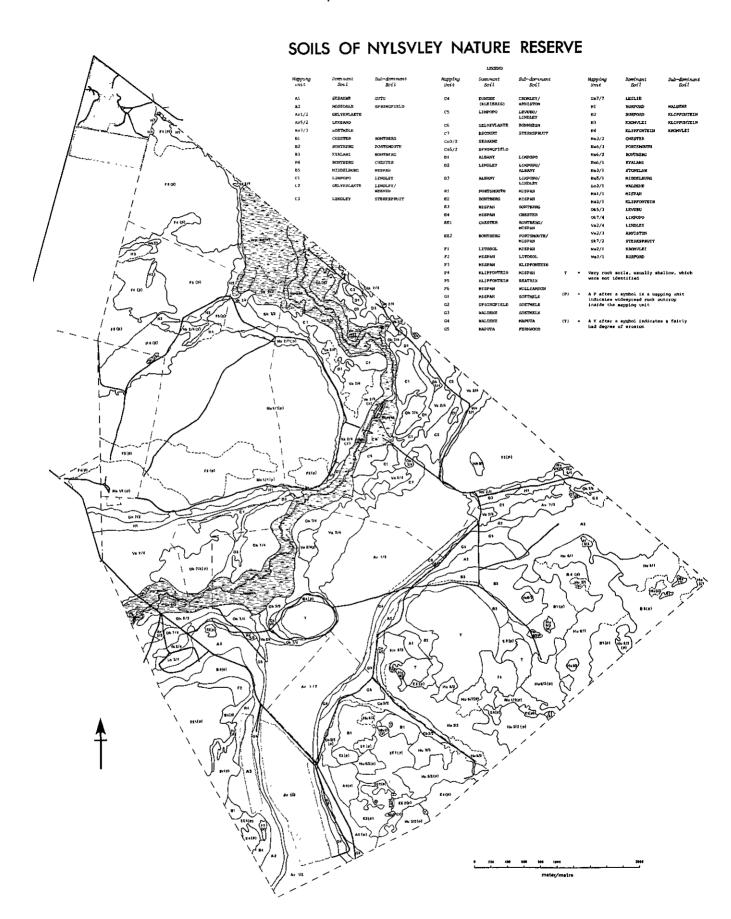


Figure 4. The soils of Nylsvley Nature Reserve. From Harmse (1977).

Summary of the characteristics of the main soil forms and series of the Study Area, Nylsvley, Data derived from Harmse (1977). Table 3.

(md	a N	17	61	19	10	2	26	71	20	20	16
atus (p	Ca	50	99	20	33	174	58	43	62	09	83
Mean nutrient status (ppm)	Mg	5	23	5	9	28	21	9	7	7	16
an nutr	×	יט	22	10	15	73	30	21	27	25	21
Ме	er.	2	Г	Ξ	'n	17	2	က	2	7	2
(H ₂ 0)	B hor	4,9	6,9	6,4	8,4	6,0	5,0	4,7	6,4	ı	5,1
рн	A hor	5,0	2,0	5,0	5,0	6,1	5,4	5,0	4,3	5,0	5,3
Phosphate Phosphate	content of B- horizon	Low	Low	Low	Low	High	Low	Low	Low	I	Low
Phosphate	content of A- horizon	Low	Low	Low	Low	High	Low	Medium	Low	Low	Гом
	Internal drainage	Good	Good	Good	Good	Good	Fair	Fair	Fair	Weak	Weak
Clay	content of B- horizon	9-0	6-15	6-15	6-15	6-15	6-15	9-0	6-15	6–15	6-15
	Diagnostic horizons	Orthic A, Red apedal B	Orthic A, Yellow-brown apedal B	Orthic A, Yellow-brown apedal B	Orthic A, Yellow-brown apedal B	Orthic A, Rock	Orthic A, Regic sand				
•	Area (ha)	187,8	91,9	90,06	61,4	44,1	74,8	37,4	9,1	29,7	8,4
C	Ser1es	Chester	Bontberg	Kyalami	Middelburg	Portsmouth	Mossdale	Sebakwe	Springfield	Mispah	Maputa
F	form and area	Hutton (475,8)					Clovelly (121,3)			Mispah (29,7)	Fernwood (8,4)

red apedal B-horizon of from 30-130 cm depth. Five soil series of this form were identified in the Study Area, four of which - Middelburg, Kyalami, Bontberg and Portsmouth, have a clay content of 6-15% in the B-horizon. The Middelburg and Kyalami soil series are distrophic, Bontberg is mesotrophic and Portsmouth is eutrophic in this horizon. The fifth series of this form, Chester, which is mesotrophic in the A-horizon has a B-horizon clay content of below 6%.

The Clovelly form exhibits an orthic A-horizon, generally of 5-30 cm depth, and a yellow-brown apedal B-horizon of from 35-130 cm depth overlying the Waterberg sandstone parent material. Two of the three series occurring in the Study Area - Mossdale and Springfield, have a clay content of 6-15% in the B-horizon but differ in the former being distrophic while the latter is mesotrophic in this horizon. The third series of this form, Sebakwe, has a B-horizon clay content of below 6%.

The Mispah form profile comprises an orthic A-horizon (5-30 cm depth) underlain by the parent rock. Only one series, Mispah, was identified in the Study Area.

Over 110 ha of the Study Area, in particular Maroelakop and surroundings, are occupied by rock outcrops where lithosols with no distinguishable soil horizons are found.

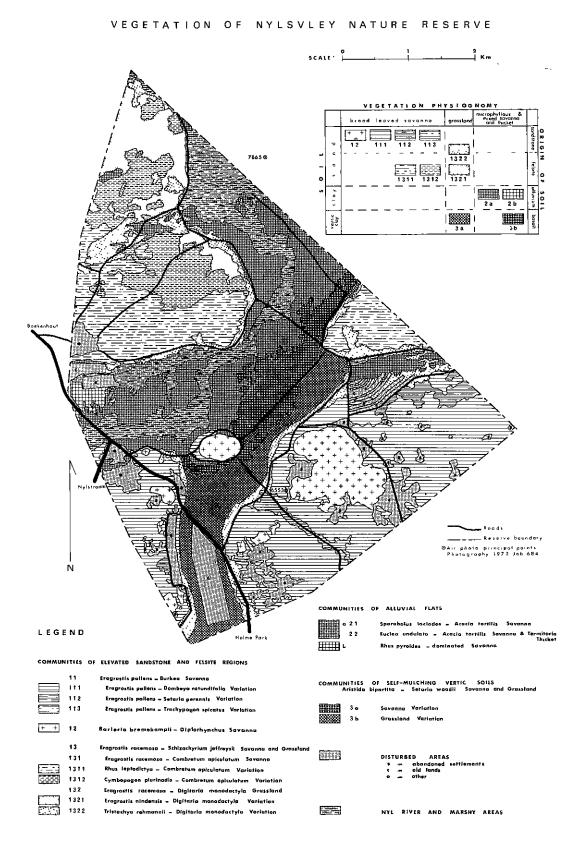


Figure 5. The vegetation of Nylsvley Nature Reserve. From Coetzee $et\ al$ (1977).

PRIMARY PRODUCER COMPONENT

Introduction

Phase I studies in the primary producer component were initiated with the classification, mapping and description of the plant communities of the entire Reserve. Concurrent botanical surveys were undertaken in the 745 ha Study Area and include the detailed structural analysis of both woody and herbaceous components of Burkea africana savanna within five permanent belt transects, the determination of changes in standing crop in various categories of the above ground herbaceous layer, the development and extrapolation of allometric relationships in woody species and the estimation of root biomass.

Vegetation survey

A detailed phytosociological classification of the whole Reserve was undertaken by Coetzee $et\ al\ (1977)$, Figure 5. A preliminary synopsis of the survey is provided by Hirst (1975) while a slightly expanded account of the plant communities of the Study Area follows, again based on Coetzee $et\ al\ (1977)$.

The vegetation of the Study Area comprises a mosaic of broadleaf communities on the deeper latosols and shallow lithosols and small patches of Acacia leptophyllous thorn savanna on sites of long-abandoned African villages. The relationships of these savannas with regard to the savannas of Africa as a whole is discussed by Huntley (1977) and supported by ornithological evidence by Tarboton (1978). The broadleaf communities include Eragrostis pallens - Burkea africana tree savanna on sands of the Clovelly, Hutton and Mispah forms (Figure 6) and Barleria bremekampii - Diplorhynchus condylocarpon savanna on the shallow lithosols of Maroelakop (Figure 7).

Eragrostis pallens - Burkea africana tree savanna

This community was shown by Coetzee et al (1977) to be differentiated by a large number of species including Grewia flavescens, Strychnos pungens, S cocculoides, Lannea discolor and Securidaca longipedunculata as constant differential species in the tree and shrub layer and the grasses Eragrostis pallens, Aristida argentea and A stipitata, the herbs Vernonia poskeana, Limeum viscosum, Cleome maculata, C rubella and the woody geophyte Dichapetalum cymosum in the field layer.

Coetzee $et\ al$ (1977) include three variations in this community, each correlated with edapho-climatic conditions.

(i) Eragrostis pallens - Dombeya rotundifolia variation

This variation is the most extensive and occupies approximately 430 ha on the upper and middle slopes of the Study Area on well-drained soils of the Hutton and Mispah forms and on soils transitional to the Clovelly form. Tree cover varies from 20-60%, ranging in height from seedlings and low



Figure 6. Burkea africana tree savanna. Shrub on left is Ochna pulchra and tree on right is Burkea africana.

juveniles up to approximately 15 m. Burkea africana, Terminalia sericea and Combretum molle dominate the tree stratum and the dominant shrubs are Ochna pulchra and Grewia flavescens. An average of 14 woody species was recorded per plot.

(ii) Eragrostis pallens - Setaria perennis variation

This variation occupies approximately 30 ha on distrophic Clovelly soils and differs from the Eragrostis pallens - Dombeya rotundifolia variation of upper slopes in the presence, height and cover of various woody species. Scattered individuals of Faurea saligna, up to 10 m tall, occur. The dominants in the tree and shrub layers are Burkea africana, Terminalia sericea and Ochna pulchra. Eragrostis pallens and Setaria perennis are dominant in the field layer. The average number of woody species recorded by Coetzee et al (1977) per plot was seven. Tree cover is considerably lower than in the first variation, usually less than 5%. Shrub cover is less than 10% and a field layer of up to 1,8 m high covers 30-75%.

(iii) Eragrostis pallens - Trachypogon spicatus variation

This variation, occupying approximately 25 ha, occurs along a moderately sloping drainage line west of Maroelakop on coarse-textured mesotrophic

Clovelly soils (Sebakwe series). The soils are better drained than the Mossdale series occupied by the former variation.

The woody component of this community resembles that of the previous variation, although *Terminalia sericea* generally has a higher cover than *Burkea africana* at heights above 3,5 m. Tree canopy cover can be up to 20%. An average of seven woody species was recorded per plot. *Trachypogon spicatus* and *Eragrostis pallens* are dominant in a 1,75 m tall field layer.



Figure 7. Barleria bremekampii and Diplorhynclus condylocarpon savanna on the shallow lithosols of Maroelakop.

Barleria bremekampii - Diplorhynchus tree savanna

The shallow lithosols of Maroelakop, its slopes and surrounding sandstone outcrops are occupied, over an area of approximately 130 ha, by this broadleaf savanna. Coetzee et al (1977) identify the following common differential species: the tree Diplorhynchus condylocarpon, the shrub Barleria bremekampii and the forbs Tephrosia longipes, Rhynchosia totta, Corchorus kirkii, Indigofera comosa, Asparagus saundersiae and Euphorbia neopolycnemoides. The community includes three variations.

(i) Pseudolachnostylis - Diplorhynchus variation

This savanna is typical of the Maroelakop area, where it occurs on various aspects and degrees of slope, with 30-60% rock cover. Diplorhynchus condylocarpon is the only dominant tree while Pseudolachnostylis maprouneifolia is a differential species. Dense stands of Canthium gilfillanii form the shrub layer, while the field layer of up to 1,50 m is dominated by Schizachyrium jeffreysii and locally, Setaria lindenbergiana.

(ii) Enneapogon scoparius - Diplorhynchus variation

In this variation, the trees are mainly 4-6 m tall with 5-20% cover while shrub cover varies from 1-15%. Combretum molle and Croton gratissimus are the dominant trees and Enneapogon scoparius is the dominant grass.

(iii) Burkea africana - Diplorhynchus variation

This variation occupies gentle, less rocky slopes with trees of between 4 and 6 m tall and up to 5% cover. Shrubs cover up to 5% while grasses and forbs have the highest cover in the community. Burkea africana and Diplorhynchus condylocarpon are the dominant trees and Loudetia flavida and Schizachrium jeffreysii the dominant grasses.

Acacia spp - Eragrostis lehmanniana tree savanna

Scattered throughout the *Eragrostis pallens - Burkea africana* tree savanna are small patches of leptophyllous thorn savanna occupying what are believed to be the sites of African villages abandoned at least 50 years ago (Figure 8). The soils of these sites, usually either Portsmouth or Bontberg series of the Hutton form, are more compacted and slightly richer in N, P and K than adjoining sands of the same series occupied by the *Burkea* savanna (Harmse 1977).

The vegetation is differentiated by *Eragrostis lehmanniana*, which is the only dominant grass and by *Solanum delagoense* and *Crotalaria pisocarpa*. Occasional *Sclerocarya caffra* trees of up to 20 m indicate the sites of abandoned villages.

The thorn tree savanna dominated by Acacia nilotica, A tortilis and Dichrostachys cinerea consists of a 2-6 m tree layer with up to 10% cover, a 0,5-2 m shrub layer with up to 5% cover, and a field layer of up to 0,8 m in which Schkuhria pinnata, Leucas neuflizeana and Eragrostis rigidior are typical species.

Structure of the tree and shrub strata

The structure of the woody component of *Burkea africana* savanna, in terms of frequency, density and various morphological parameters, was examined in September 1974, January 1976 and January 1977 (Lubke *et al* 1975, 1976; Lubke 1976, 1977).

The analyses were made in five permanently marked belt transects, each subdivided into 384 to $1\ 280$ contiguous $5\ x\ 5$ m quadrats. In the initial



Figure 8. Acacia spp thorn savanna. Acacia tortilis and A nilotica predominate in this community. Note abundance of Solanum delagoense in herb stratum.

survey, height, height to first branch, circumference of stem at main branch, circumference of stem at breast height, position of canopy, canopy cover, height of lowest leaves, leaf density, amount of dead wood, amount of insect damage, amount of browsing, amount of lichen cover, presence of fire scars and presence of parasites were recorded for all woody plants in all quadrats. In the subsequent surveys, only 12,5% of the quadrats were sampled. The percentage frequency and density of those species with an initial frequency of 1% or more is given in Table 4.

The mean number of woody plants, for all areas, all species and all height classes was 7 120 per hectare.

From Table 4 it will be noted that the results of the two latest surveys are more similar to each other than to the original survey, supporting an earlier conclusion (Lubke 1976) that differences between the 1974 and 1976 surveys could be accounted for by seasonal differences in data recording.

A canopy cover survey was carried out by Van Rooyen and Theron (1977). Total canopy cover was 27,5%. Highest canopy cover was obtained for Burkea africana (14,38%), followed by Ochna pulchra (5,78%), Terminalia sericea (2,68%), Vitex rehmannii (2,35%) and Grewia flavescens (1,54%). Other species recorded in the survey with lower cover percentages included Mundulea sericea, Maytenus heterophylla, Lannea discolor, Strychnos cocculoides, S pungens, Combretum zeyheri and Dombeya rotundifolia.

Table 4. The percentage frequency and density of the most important woody species in all the sample areas of the Study Area. Data from Lubke (1977).

	Perc	entage freque	ncy	Density ha ⁻¹				
	July to October 1974	January 1976*	January 1977*	July to October 1974	January 1976*	January 1977*		
Ochna pulchra (<1m)	76,2	84,9	86,4	2 803,9	4 709,6	4 378,9		
0 pulchra (1-3,5m)	62,3	63,7	50,0	1 977,1	2 008,7	1 353,9		
0 pulchra (>3,5m)	2,4	2,4	2,7	9,6	9,6	11,5		
Burkea africana (<4m)	50,0	58,7	62,6	408,7	536,5	556,4		
B africana (4-7m)	7,2	7,2	6,5	29,8	29,8	27,9		
B africana (>7m)	0,7	0,7	0,7	2,9	2,9	2,9		
Grewia flavescens (individuals)	27,4	27,6	28,2	1 092,3	1 118,3	1 078,9		
G flavescens (clumps)	27,4	27,6	28,2	220,2	240,4	251,9		
Strychnos pungens (<1m)	19,5	20,0	23,5	163,5	242,3	295,2		
S pungens (1-3m)	9,1	11,1	8,0	51,9	58,7	41,4		
5 pungens (>3m)	1,2	1,2	1,9	4,8	4,8	7,7		
Terminalia sericea (<3m)	10,3	15,1	15,8	68,3	93,3	94,2		
r sericea (3-5,5m)	5,3	5,3	5,6	25,0	26,9	31,7		
ľ sericea (>5,5m)	0,7	0,7	1,0	2,9	2,9	3,9		
Combretum molle	6,7	8,9	6,8	30,8	41,4	32,7		
C zeyheri	1,9	3,1	1,9	10,6	19,2	12,5		
Vitex rehmaniı	8,2	9,1	9,2	68,3	89,4	84,6		
Euclea natalensis	6,7	7,2	6,6	35,6	41,4	47,1		
Lannea discolor	4,6	10,1	7,7	25,0	64,6	64,4		
Dombeya rotundifolia	4,6	5,5	5,6	18,3	22,1	30,8		
Securidaca longipenduncu- lata	2,6	2;,9	2,4	10,6	11,6	9,6		
Asparagus suaveolens	2,4	3,1	3,2	22,1	18,9	31,7		
zoroa paniculosa	1,7	2,2	2,2	8,7	10,6	9,6		
Dichrostachys cinerea	2,4	2,9	3,4	23,1	25,0	26,9		
Strychnos cocculoides	1,7	2,2	1,5	7,7	10,6	6,7		
Kimenia caffra	0,2	0,2	0,5	1,0	1,0	9,6		

Woody species biomass relations

Biomass relations of the 11 most important woody species have been studied in detail by Rutherford (1975, 1977) and Rutherford and Carr (1976). Initial studies focussed on establishing allometric regressions relating various dimensions to one another and to mass (Rutherford 1975), followed by measurements of shoot growth through the 1975/76 and 1976/77 seasons and during the latter season, the large scale field measurement of predictor variables for all woody plants in the five permanent belt transects established by Lubke $et\ al\ (1975)$. The combined area of the belt transects totalled 5,2 ha.

Allometric regressions were specifically derived for the dominant species Burkea africana, Ochna pulchra, Terminalia sericea and Strychnos pungens. For the less common species, Vitex rehmanii, Combretum zeyheri and Dombeya rotundifolia, regressions were quantitatively approximated using limited field data. For the rarer species, Securidaca longipedunculata, Strychnos cocculoides and Combretum molle, relations were approximated subjectively on a semi-quantitative basis. A combined species relationship was used for the remaining trees. The biomass of the multi-stemmed shrub, Grewia flavescens, was estimated using stem counts and mean ratios.

The biomass relations and leaf area of the 11 most important species, plus the sum for remaining species, are presented in Table 5. These data are derived from averaging the results from the five belt transects. The range in results from the various individual transects is illustrated in Table 6.

Structure of the herbaceous stratum

Wheel-point surveys (Tidmarsh and Havenga 1955) of the rooted basal cover of herbaceous species were undertaken in February 1975 and repeated in February 1977 in each of the five permanent belt transects (Van Rooyen and Theron 1975, 1977). A total of 10 000 points was recorded in each survey.

The results of both surveys are summarized in Table 7, from which it may be seen that the herbaceous layer of Burkea africana savanna comprises a predominance of graminoid species, with Digitaria eriantha and Eragrostis pallens each contributing 27% of the total basal cover of 5,96%. The seven species of forbs recorded in the 1977 survey accounted for only 0,23% basal cover, constituting 3,8% of the total herbaceous basal cover.

Changes in the total basal cover between the 1975 and 1977 surveys were not significant, nor were any of the 10 most important species of grasses found to have increased or decreased significantly in any of the belt transects.

Biomass relations of the herbaceous stratum

Harvest methods were used through the 1974/75, 1975/76 and 1976/77 seasons by Grunow (1975, 1976, 1977, 1978) to determine the herbaceous above-ground standing crop divided into various taxonomic and structural categories at periodic intervals. During the first season, the study was conducted in an ungulate - proof enclosure (Grunow 1975, Hirst 1975) while subsequent surveys were undertaken under grazing conditions sought to simulate the

Distribution of woody plant biomass, dead wood mass and leaf area amongst dominant species of Burkea africana savanna. Data from Rutherford (1977). Table 5.

Leaf area	m ² ha ⁻¹	2 854	2 266	216	325	587	263	148	107	9/	59	34	131	7 826
Dead wood	mass kg ha-1	519	42	204	977	13	28	=	12	6	23	7	14	1 859
	Leaf	400	289	160	47	82	98	21	15	14	12	ıΩ	20	1 100
	Current twig	99	36	10	86	14	0	7	4	0	_	_	C 4	236
Biomass kg ha ⁻¹	Branch wood	2 614	764	522	123	719	979	352	334	298	435	201	233	14 937
	Stem wood	5 697	1 047	1 042										14
- And the state of	Total	8 684	2 134	1 732	255	814	691	380	353	312	448	207	256	16 267
Species		Burkea africana	Ochna pulchra	Terminalia sericea	Grewia flavescens	Vitex rehmannii	Combretum zeyheri	Dombeya rotundifolia	Combretum molle	Strychnos pungens	Strychnos cocculoides	Securidaca longipedun- culata	Remaining species	All species

Table 6. Range in estimates of total biomass, dead wood mass and leaf area of woody plants in five belt transects. Data from Rutherford (1977).

Species	Minimum	value, kg	ha ⁻¹	Maximum value, kg ha ⁻¹							
	Total biomass	Dead wood	Leaf area	Total biomass	Dead wood	Leaf area					
Burkea	7 185 B*	404 C	2 278 C	9 957 A	629 D	3 366 D					
Ochna	586 D	11 D	675 D	3 753 A	71 A	4 170 A					
Terminalia	834 C	91 C	544 C	2 151 D	253 D	1 211 D					
Grewia	121 D	566 A	220 A	393 В	1 361 E	474 B					
Remaining species	15 C	1 C	23 C	545 E	30 E	247 E					
All species	12 637 C	1 450 C	5 715 C	20 020 A	2 334 E	10 094 A					

B* Belt transect from which data were collected.

range management patterns of the preceding 40 years (Grunow 1976, 1977; Huntley 1977). The latter study site was 42 ha in size and 25 mixed-breed steers grazed the area for periods of up to three weeks between January and April in 1976 and 1977.

Mean, maximum and minimum standing crop, divided into major compartments, for the three years are presented in Table 8.

Underground biomass relations

An attempt to measure the relative proportions of live and dead underground phytomass, separated into woody and non-woody components and by soil horizon, at frequent intervals through summer and winter, was initiated in November 1975. The soil core extraction and root washing methods used and preliminary results were described in detail by Van Wyk (1976, 1977) and summarized by Huntley (1977). During the 1976/77 season, improved methods were adopted and these probably account for the widely divergent results obtained for that season (mean underground phytomass of 1 545 g m $^{-2}$) compared with that of 860 g m $^{-2}$ for the previous season. Both sets of data were from the study site in which Grunow (1976, 1977) monitored changes in above-ground herbaceous standing crop.

The results for the 1976/77 season are summarized in Table 9. These data relate only to the open habitat, from which an average of 36 soil cores of 8 cm diameter were extracted to the depth of parent rock on each of seven

Table 7. Basal cover and frequency of the 15 herbaceous species of highest basal cover recorded in *Burkea africana* savanna at Nylsvley. Data from van Rooyen and Theron (1975, 1977).

	19	75	19	77	
Species	% basal % frequency		% basal	% fre- quency	
Eragrostis pallens	1,59	29,97	1,63	27,34	
Digitaria eriantha	1,46	26,69	1,64	27,51	
Diheteropogon amplec- tens	0,40	7,32	0,59	9,90	
Rhynchelytrum villosum	0,24	4,39	0,97	1,17	
Andropogon schirensis	0,23	4,21	0,24	4,03	
Perotis patens	0,20	3,66	0,16	2,68	
Aristida argentea	0,19	3,48	0,10	1,68	
Setaria perennis	0,18	3,29	0,16	2,68	
Elyonurus argenteus	0,16	2,93	0,12	2,01	
Panicum maximum	0,11	2,01	0,10	1,68	
Urelytrum squarrosum	0,10	1,83	0,12	2,01	
Fimbristylis hispidula	0,10	1,27	0,09	1,51	
Cymbopogon marginatus	0,07	1,27	0,05	0,84	
Themeda triandra	0,07	1,27	0,04	0,67	
Trachypogon spicatus	0,06	1,09	0,11	1,85	
Others	0,31	5,66	0,74	12,44	
Total	5,47	100	5,96	100	

sample dates. These results were compared with two test pits of one cubic metre volume that were extracted in August and September 1977 and found to comprise 1 718 and 1 403 g $\rm m^{-2}$ root mass respectively.

From the 1976/77 results, the mean root mass in open sites within Burkea savanna may therefore be expected to approximate 1 500 g m⁻², half of this

Table 8. Masses in g m⁻² of different compartments in the grass layer of Bunkea savanna, 1974-1977. Data from Grunow (1975, 1976, 1977).

	Date of max		1976.12.07 1976.10.13			1976.12.07 1977.02.03			1976.10.13 1976.10.13			1976.11.10 1976.10.13		1977.03.03 1977.02.03		1977.09.12 1976.12.07
7.61/9761	Mean		103,4	94,5		37,3	36,3		66,1 39,5	58,2		213,1 105,8 183,6		229,4 789,2 383,3		74,9 41,2 65,6
19	Мах		181,4	155,0		62,4 55,5	55,7		132,4	122,1		360,0 131,8 297,2		310,5 1 097,8 527,0		98,9 71,4 91,3
	Min		54,2 45,3	57,4		15,6 13,6	15,0		19,8	17,1		67,6 68,6 67,9		135,0 508,5 237,7		55,4 25,4 47,2
	Date of max		1976.04.13 1976.01.14			1976.02.10 1976.01.14			1975,10,22 1976.09.01			1976.12.19 1977.01.14		1975, 10, 22 1976, 01, 14		
975/1976	Mean		169,1 76,2	143,0		55,7 30,2	51,4		113,4	91,6		310,8 124,2 259,4		276,1 944,3 459,9		
	Мах		208,0 84,0	172,8		108,2 48,3	90,4		151,0	125,1		494,5 159,1 402,3		342,7 1 008,0 525,7		
	Min		68,3 68,1	94,4		21,8 12,0	19,1		78,8 35,8	67,0		201,9 94,3 172,3		203,5 836,8 377,7		
	Date of max		1978,02,04			1975.02.04			1975.06.03					1974.11.12 1974.11.12		
1974/1975	Mean		144,3	181,8		60,8 46,9	57,4		135,0	124,4				398,2 1 450,2 687,5		
19	Max		195,3	209,5		97,2 80,7	92,9		149,5	135,8				722,8 242,5 1 190,9		
	Min	0 07	140,8	129,8		30,6 18,8	28,8		99,1 59,4	88,2				253,5 835,5 413,5		
Compartment and	subhabitat	Available and apparrent above ground standing crop	Upen Under trees and shrubs	Combined subhabitats	Available and apparent above ground biomass	Open Under trees and	Combined subhabitats	Available and apparent above ground standing dead	Open Under trees and	Combined subhabitats	Stubble total	Open Closed Combined	Total litter	Open Closed Combined	Grass litter	Open Closed Combined

Table 9. Root mass values in g m⁻², from Burkea savanna, 1976/1977. Data from Van Wyk (1977).

Sampling date	No of cores	Mixed roots	Thick roots	Total
October 1976	33	776	631	1 407
November 1976	18	1 019	570	1 589
December 1976	40	918	494	1 412
January 1977	40	976	726	1 702
February 1976	40	476	753	1 229
April 1977	40	690	867	1 557
July 1977	40	393	1 528	1 921
Average	36	750	796	1 545

being woody plant material the other half being herbaceous. Approximately 75% of the root biomass lies in the uppermost 20 cm of the soil profile. Preliminary results of live/dead ratios determined by the TTC method (Knievel 1973) indicate that about 30\% of the root mass is dead in winter and about 13% dead in summer.

CONSUMER COMPONENT

Introduction

Phase I objectives for the consumer component included the survey of faunal composition and structure, the estimation of biomass changes in terms of space and time for the dominant species and functional groups and preliminary investigations into the food requirements and preferences of selected taxa. Studies in the energetics and indirect influences on primary production of key species form an integral part of Phase II activities and will be outlined in the latter part of this report while a comprehensive review of Phase II progress will be published before the end of 1978.

Faunal composition

A major effort was made during the pilot study to inventorise all vertebrates and invertebrate taxa within the Study Area. Annotated checklists for the Reserve as a whole have been published on the birds (Tarboton 1977) and for amphibia, reptiles and mammals (Jacobsen 1977), while preliminary checklists are in preparation for invertebrates of the Study Area.

One of the more important findings of the faunistic survey was the often distinctive animal communities associated with the two main vegetation types of the Study Area. The avian faunas of Burkea savanna and Acacia savanna have been shown to be related to the Brachystegia "moist savanna" and to the South West Arid savanna respectively (Tarboton 1978). Marked differences between the Burkea and Acacia savanna faunas were reported by Ferrar (1977) for termites; Gandar (1977) for orthoptera; Holm (1977) for lepidoptera and coleoptera; Jacobsen (1977) for reptiles and Temby (1977) for small mammals. The affinities of these faunas with the major zoogeographic patterns in southern Africa awaits study. The need to distinguish between ecological information gathered from either of these two savanna types when attempting to synthesize data from the Study Area mosaic during model building has already been stressed (Huntley 1977).

Phase II studies will, where funds permit, be undertaken in both *Burkea* and *Acacia* savannas to allow quantification of functional differences; the major focus will, however, be on *Burkea* savanna.

Anurans

The greatest diversity of anuran species was found along the Nyl River floodplain, but the fauna of the Burkea savanna is nevertheless surprisingly rich despite its distance from permanent water. Eighteen species of anurans have thus far been recorded in the Reserve (Jacobsen 1977) of which ll occur in the Study Area. The most common species are northern mottled toad Bufo garmani, common rain frog Breviceps mossambicus and short-toed running frog Kassina senegalensis.

Reptiles

The Nylsvley reptile survey proved extremely rewarding and 57 species have thus far been listed, many of these constituting new locality records of rare species, while one series of specimens appears to belong to an undescribed species. The Study Area fauna comprises 48 species including 3 tortoises, 18 lizards, 1 amphisbaenid and 26 snakes. The most common species are leopard tortoise Testudo pardalis, Cape dwarf gecko Lygodactylus capensis, variable skink Mabuya varia, Cape rough-scaled sand lizard Ichnotropis capensis, white throated monitor Varanus exanthematicus, spotted bush snake Philothamnus semivariegatus, Herald snake Crotaphopeltis hotamboeia, vine snake Thelotornis capensis, short-snouted sand snake Psammophis sibilans and Cape centipede-eater Aparallactus capensis.

Birds

Tarboton (1977) provides a checklist of the birds of Nylsvley, which lists 325 species of which 197 are resident, 64 migrant, 14 sporadic, 13 vagrant and 37 of uncertain status. In a detailed study of the bird populations of an Acacia and Burkea sample area, Tarboton (1978) found 130 species in the former and 120 species in the latter savanna type (Table 10).

Table 10. The number of bird species recorded in two 150 ha sample plots in Acacia and Burkea savannas, subdivided into different consumer classes and status classes (pR = permanent resident, sR = seasonal resident, sp = sporadic). Data from Tarboton (1978).

			Status class of species								
Consumer class	Total s	species	pI	₹	sI	₹	вþ				
	Acacia	Burkea	Acacia	Burkea	Acacia	Burkea	Acacia	Burkea			
III Raptor	13	14	0	2	0	0	13	12			
III Insecti- vore	67	71	22	30	10	20	35	21			
I Fructivore	4	4	2	0	1	1	1	3			
I Granivore	19	10	6	3	6	2	7	5			
Mixed diet	27	26	11	14	5	6	11	6			
Total	130	125	41	49	22	29	67	47			

Mammals

Jacobsen (1977) lists 62 indigenous mammals for the Reserve, 46 of these having been recorded from the Study Area. The mammalian fauna of the Study Area includes 4 insectivores, 2 bats, 2 primates, 2 lagomorphs, 18 rodents, 11 carnivores, 1 tubulidentate and 6 ungulates. The most common species in the Study Area are tiny musk shrew Crocidura bicolor, shortsnouted elephant shrew Elephantulus brachyrhynchus, Cape serotine bat Eptesicus capensis, scrub hare Lepus saxatilus, Natal red rock hare Pronolagus crassicaudatus, bush squirrel Paraxerus cepapi, porcupine Hystrix africae-australis, spring hare Pedetes capensis, grey pygmy climbing mouse Dendromus melanotis, Bushveld gerbil Tatera leucogaster, red veld rat Aethomys chrysophilus, multimammate mouse Praomys natalensis, black-backed jackal Canis mesomelas, slender mongoose Herpestes sanguineus, white-tailed mongoose Ichneumia albicauda, banded mongoose Mungos mungo, warthog Phacochoerus aethipicus kudu Tragelaphus strepsiceros, grey duiker Sylvicapra grimmia, impala Aepyceros melampus and steenbok Raphicerus campestris.

Invertebrates

In view of the great diversity of invertebrates in savanna ecosystems and severe constraints on manpower and financing, it was decided that the pilot study should include a general survey of the arthropod fauna using a variety of sampling procedures, as a first approximation to a comprehensive faunal survey. The aim was to determine the characteristics of the invertebrate fauna of the Study Area, in particular to identify those groups which through abundance, biomass, consumptive or indirect effects have the greatest influence on the ecosystem's functioning.

A general survey of above ground arthropods was initiated in 1974 by Holm and co-workers and is summarized in Huntley (1977). Subsequent surveys of invertebrate primary and secondary consumers have concentrated on the insect fauna of the herbaceous stratum (Gandar 1976, 1977), the woody plant feeding coleoptera (Levey 1976, 1977) and lepidoptera (Scholtz 1976), social insects (Kirsten 1976, Holm and Kirsten 1977, Nunn 1976), root feeders (Mostert 1977) and spiders (Ferreira 1977). Surveys of reducer and decomposer groups will be described in the section on that component.

The preliminary surveys produced over 7 000 specimens of over 1 000 species, but this is probably less than half the above-ground arthropod fauna. Despite the limitations of the preliminary checklist, it is likely that at least the most important species are included. Lepidoptera and coleoptera each accounted for one third of the species collected while diptera and hymenoptera were poorly represented, possibly due to sampling bias (Holm, Kirsten and Scholtz 1976).

Faunal density and biomass

Introduction

As one of the principal aims of the pilot phase, an attempt was made to determine the biomass of individual consumer species and groups and their variation in space and time. In most cases, estimates of biomass were

derived from various capture techniques repeated at monthly intervals over a 12 to 24 month period. The reliability of data varies from acceptable levels of accuracy (~ 10% of population mean) for cattle and other large ungulates, and certain bird and insect species, to "order of magnitude" estimates for less common vertebrates and many invertebrates. Population dynamics studies have thus far only been undertaken for a limited number of lepidoptera and orthoptera; more intensive studies of this nature will be undertaken in Phase II. The data for density and biomass changes have to be refined considerably before the dynamics of the ecosystem as a whole can be interpreted.

Reptiles and anurans

The vast quantity of data collected by Jacobsen (1975, 1977) on the reptile and amphibian populations of two trapping grids, one of 49 ha and the other of I ha, during the period June 1975 through June 1977, await analysis. Preliminary findings on the density and biomass fluctuations of the snake population of the 49 ha Burkea savanna sampling area are presented in Figure 9. The low records for July and August are explained by the hibernation of most species during this cold period.

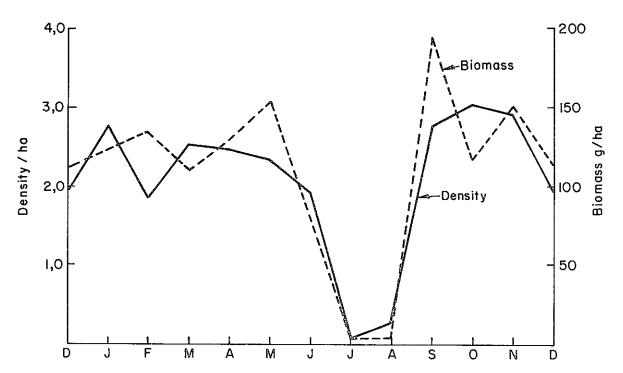


Figure 9. Fluctuations in the density and biomass of snakes in a 49 ha trapping grid, December 1975 to December 1976. Data from Jacobsen (1977).

The mean density and live biomass of snakes in the Burkea savanna at Nylsvley probably approximates 3 snakes and 150 g ha⁻¹. The most abundant reptile, common dwarf gecko Lygodactylus capensis was estimated to number between 195 to 262 animals ha⁻¹, while the commonest lizard was the Cape rough-scaled sand lizard Ichnotropis capensis with between 6,9 and 11,4 animals ha⁻¹ (Jacobsen 1975).

Birds

The avian population of a 150 ha sampling plot in the Study Area, and another plot of the same area in the *Acacia* savanna 5 km distant was studied in detail during a 15 month period in 1974 to 1975 (Tarboton 1978).

The avian population of these two savannas varied from an early summer density of 11,85 birds ha^{-1} in Acacia and 5,86 birds ha^{-1} in Burkea to a peak of 16,00 and 9,00 birds ha^{-1} in midsummer, dropping to a minimum of 9,25 and 3,99 birds ha^{-1} in winter following emigration of non-residents and dispersal or mortality. The live biomass of the Acacia savanna bird population was more than twice that of the Burkea savanna (Table 11).

Table 11. Avian biomass (kg 100 ha⁻¹) in early summer in *Acacia* and *Burkea* savannas. From Tarboton (1978).

Consumer class	Acacia	Burkea
raptors	2,1	3,6
insectivores	18,6	12,1
fructivores and granivores	8,2	1,5
mixed diet	55,6	23,5
Totals	84,6	40,7

Small mammals

An intensive study of the small mammal population of Burkea savanna was initiated in April 1974 (Bragg 1975) and continued until April 1977 (Temby Despite exhaustive sampling with a variety of trapping techniques, returns were very poor and indicate that the small mammal population of the Study Area is exceptionally low when compared with other South African ecosystems. Mean kill trap success in the Burkea sampling area was only 0,35% for 4 000 trap nights in 1976 while live capture with Sherman and pitfall traps resulted in only 0,24% success. The extremely low trapping returns, and the bias resulting from differing responses to bait type, trapping techniques, weather and other factors, preclude the use of standard formulae for the determination of population densities and biomasses for the smaller mammals. Jacobsen (pers comm 1977) was unable to determine accurate biomass estimates but found a clear seasonal variation in the capture returns for Dendromys melanotis (Figure 10) with a peak in autumn (April/May) and a trough in spring (September/November). This general trend was also found amongst the other small mammals.

Biomass estimates were made for spring hare, scrub hare and yellow-footed squirrel, which approximate 0,1; 0,23 and 2,0 individuals per hectare or live biomasses of 0,03; 0,047 and 0,0043 g $\rm m^{-2}$ respectively for Burkea savanna.

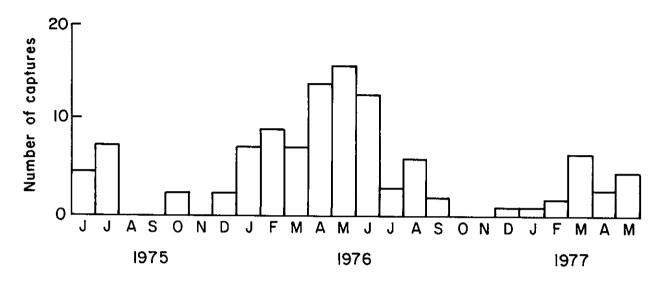


Figure 10. Variation in numbers of *Dendromys melanotis* captured per month in a 1 ha trapping grid from June 1975 to May 1977. Data from Jacobsen (pers comm 1977).

Indigenous ungulates

Of the six species of wild ungulate present in the Study Area, only two (kudu and impala) make an appreciable contribution to the total ungulate live biomass during the summer period when cattle are present. Population estimates were made at frequent intervals from December 1975 to December 1977 (Table 12) and indicate that the indigenous ungulate live biomass probably ranges from 8 kg ha⁻¹ in midwinter to about 10 kg ha⁻¹ in summer.

The spatial distribution of ungulate biomass has not been studied in any detail. Carr (1976) reported that the movement patterns of impala tend to follow herbage availability and quality, with the Study Area population widely dispersed during the wet season, becoming concentrated in the Acacia patches towards winter and in late winter moving to the Acacia savanna of the Nyl floodplain before returning to the pre-spring green flush of the Study Area firebreaks. The other ungulates are dispersed through the Study Area at a low density in both Burkea and Acacia savannas.

Cattle

According to the previous owner of Nylsvley, cattle were grazed in the Study Area during the period January through April almost every year during the past four decades (Grunow 1974). The short summer grazing period was necessary to avoid cattle losses due to their feeding on the poisonous woody geophyte *Dichapetalum cymosum*. The cattle biomass in most years was ca 150 kg ha⁻¹ during the four month grazing period.

Table 12. Population estimates for six indigenous ungulates, Nylsvley Study Area, December 1975 to August 1977

Date	Impala	Kudu	Warthog	Duiker	Steenbok	Reedbuck
75.12.17	126	10	8	13	13	2
76.02.16	71	7	34	36	18	2
76.03.29	127	13	16	16	7	1
76.05.18	103	24	5	9	14	o
76.06.21	106	3	1	32	22	0
76.08.17	64	3	7	16	13	0
76.10.06	110	39	6	18	5	0
77.11.16	61	26	14	9	13	0
77.01.13	108	17	7	9	14	0
77.03.11	119	25	18	18	9	0
77.06.03	99	9	4	22	5	0
77.08.19	154	27	8	18	10	0
Mean animals 100 ha ⁻¹	12,89	2,10	1,32	2,23	1,48	0,05

In order to maintain the traditional management practice through Phase I, cattle were introduced to the Study Area annually in January and kept on until late April. During 1975, the cattle live biomass averaged 116 kg ha⁻¹ but due to severe overgrazing in some areas it was reduced to 61 kg ha⁻¹ in 1976 and to 65 kg ha⁻¹ in 1977, for the four months January through April. The cattle were divided into two or three herds and moved between the various subdivisions of the Study Area at approximately fortnightly intervals.

At the end of the 1975 grazing period, several parts of the Study Area had been overgrazed but during 1976 and 1977 no signs of range deterioration were noted.

Invertebrates

The pilot study of invertebrate density and biomass comprised three components, the first including invertebrates on woody plant species, the second covering the invertebrates of the herbaceous strata and the third

the insects of the soil surface and litter environments. Most of the latter group form part of the reducer and decomposer component and will be discussed later.

The methods and results of the studies on leaf-eating insects in the tree and shrub component are described in detail by Holm, Kirsten and Scholtz (1976) and Levey (1976, 1977) and are summarized in Huntley (1977). The average dry biomass of primary consumers on woody plants was estimated at 135 g ha⁻¹ with a minimum of 60 g ha⁻¹ in August and a peak of 300 g ha⁻¹ in March (Holm, Kirsten and Scholtz 1976).

The invertebrate primary consumers of the herbaceous strata in both *Burkea* and *Acacia* savannas were investigated over a two year period, January 1976 to December 1977 (Gandar 1976, 1977). The results indicate that *Acacia* savanna supports more than twice the phytophagous insect biomass than does *Burkea* savanna (Table 13).

Table 13 Average dry biomass of groups of phytophagous insects within the herbaceous stratum of *Burkea* and *Acacia* savannas at Nylsvley. Data from Gandar (1977)

	Вг	ırkea	Acacia		
	Biomass kg ha ^{-l}	Percent of total	Biomass kg ha ^{-l}	Percent of total	
Acridoidea	0,76	76	2,32	93	
Other orthoptera	0,06	6	0,02	1	
Lepidoptera	0,05	5	0,03	1	
Hemiptera	0,08	8	0,08	3	
Others	0,05	5	0,05	2	
Total	1,00		2,50		

Grasshoppers (Acridoidea: Orthoptera) account for 76% of the biomass in Burkea and 93% in Acacia. Other groups of importance included Phasmidae, Gryllidae and Blattidae within the Orthoptera and in particular certain species of Lepidoptera, Hemiptera, Acarina, Coleoptera, Thysanoptera and Psocoptera, but none of these was present in sufficient numbers or biomass to exert an observable consumptive influence on the vegetation. Occasional eruptions of local importance included army worm Spodoptera exempla (Lepidoptera) which for a brief period had a live biomass of 1,3 g m⁻² on a patch of Cenchrus ciliaris in Acacia savanna, and an outbreak of Astylus atromaculatus (Coleoptera), also on Cenchrus ciliaris.

DECOMPOSER AND REDUCER COMPONENT

Introduction

Little is known of decomposition and reduction processes in African savannas and virtually nothing was previously known of these key processes in Burkea savanna. As the savanna trees are deciduous, an important Phase I project established the level and timing of tree leaf litter production. Other inputs to the component, including wood and herbaceous litter, were identified and quantified where possible. The main macro- and micro-organisms responsible for decomposition and reduction were also identified and their quantities estimated.

Litter, carcass and dung production

A measure of woody plant litter input was obtained during 1977 (Huntley and Osborn 1977) by means of 50, and later 100, litter baskets of 0,25 m² area each distributed in a stratified random design through a 0,8 ha Burkea africana savanna study site. Large mammals were excluded from the study site by a two metre tall game-proof fence. Litter fall for the period 77.04.07 to 77.11.14 totalled 160 g m^{-2} comprising 84,8% leaves, 9,4% twigs, 5,5% fruit and seeds and 0,3% bark and bud scales. The major portion of litter came from Burkea africana (35,4%), Ochna pulchra (34,6%) followed by Combretum spp (10,3%) and Vitex rehmannii (7,7%). From the available data it would appear that the total litter input for the season would approximate 170 g m $^{-2}$, an estimate which compares well with measures Standing crop of of tree and shrub biomass increment from the savanna. litter was estimated on 76.10.18 and on 77.07.12 by collecting all litter and decomposing organic material above the soil surface. A total of 50 0,5 $\rm m^2$ quadrats (76.10.18) and 100 1 $\rm m^2$ quadrats (77.07.12) adjacent to the litter baskets were sampled. The total litter standing crop amounted to 1 853 g m⁻² on 76.10.18 and 1 342 on 77.07.12. The litter collected on 77.07.12 was subdivided into branches (87 g m⁻²), twigs (16 g m⁻²), leaves (534 g m⁻²), fruit and seeds (12 g m⁻²), grass (44 g m⁻²) and unrecognisable fragments of 1 to 10 mm diameter (184 g m⁻²), 0,5 to 1,0 mm diameter (177 g m^{-2}) and organic matter of less than 0,5 mm diameter (288 g m^{-2}). accurate measure of the input of wood to the litter layer has yet to be made.

Peak season herbaceous litter standing crop has been obtained by Grunow (1977) in open and closed subhabitats. In the open subhabitat grass litter peaked at 81,4 g m $^{-2}$ in January 1977 while in the closed subhabitat grass litter peaked at 45,9 g m $^{-2}$ in December 1976.

Detailed information on the seasonal and spatial distribution of animal carcass and dung production in Burkea savanna is still not available. Hirst (1975) estimated a total dry mass for cattle dung of 20 to 24 g m⁻².

Soil arthropods

Loots (1975), Loots and Theron (1976), Prinsloo (1975) and Olivier (1976) have reported on the composition and biomass fluctuations in the soil mesofauna. Their findings indicate that termites and dung beetles are probably the most important primary decomposers and reducers, with

oligochaetes, millipedes, centipedes and isopods of little, if any, significance. Both Acari and Collembola are important bacterio- and fungiphages and preliminary studies of their seasonal fluctuations in number and biomass have been undertaken.

In terms of biomass, the most important mesofaunal groups were identified by Loots and Theron (1976) as Araneae and Pseudoscorpions followed by insects, Oribatei, Mesostigmata, Astigmata and Trombidiformes. Although the least important in terms of biomass, the latter order was numerically dominant. Within the Trombidiformes, the bacteriophage and fungiphage family Nanorchestidae was dominant. The fungiphage family Ameronothridae was dominant within the Oribatei, while the Ascidae were the most important Mesostigmata. The Astigmata were of little importance.

Fifteen species of termite (Table 14) have been recognised from the Study Area (Ferrar P 1977, pers comm 1978). The most common species in Burkea savanna are Aganotermes oryctes (also in Acacia savanna), Microtermes albopartitus, (also in Acacia savanna), Cubitermes pretorianus and Microcerotermes parvus. Of the 15 species, at least four are humus feeders and most of the rest feed on rotting wood and leaf litter. The biology of the termites is still being investigated.

Results of core sampling by means of a 7,5 cm diameter cylindrical corer to a depth of 18 cm indicated densities of subterranean termites in Burkea savanna comparable to those in other African savannas while densities in Acacia spp savanna were much lower and more variable. In Burkea savanna a mean of 2 540 termites m^{-2} was obtained from 14 sampling dates through 1977. The maximum was 8 204 termites m^{-2} (November) and the minimum was 596 termites m^{-2} (July). In Acacia savanna a mean of 690 termites m^{-2} was obtained from 13 sampling dates. The maximum was 3 223 termites m^{-2} (March) and no termites were found in four samples taken between June and September, inclusive. Ferrar P (1977) reports that conversion of mean number of termites per core to unit area is crude and likely to be an overestimate.

Soil micro-organisms

Soil microbial activity has been monitored at monthly intervals for two years by means of viable propagule counts (plate counts), carbon dioxide evolution determinations, both in the laboratory and in situ, and ATP assays from 18 samples (Steyn and Bezuidenhout 1977a, 1977b). Maximum, mean and minimum values for bacterial, actinomycetal and fungal propagule counts from soils in the Burkea shaded subhabitat are given in Table 15. Average values obtained for all subhabitats were 10^6 , 5 x 10^5 and 10^4 g⁻¹ soil for bacterial, actinomycetal and fungal propagule counts, respectively. Values obtained are in the ranges expected although actinomycete counts were remarkably high.

Maximum, mean and minimum values for ATP content of and ${\rm CO}_2$ evolution from soils of the open subhabitat are given in Table 16. Average values were 2,33 x 10^6 fg ATP g⁻¹ soil and 1 866 mg ${\rm CO}_2$ evolved m⁻²d⁻¹ (*in situ*) and ca 2,55 x 10^{-3} mg g⁻¹d⁻¹ soil as determined by respirometry in the laboratory.

Table 14. Checklist of termite species found at Nylsvley. Data from P Perrar (1977) and pers comm P Ferrar (1978).

Family	Sub-family	Мате	Habitat	Notes
Kalotermitidae	Kalotermitinae	? Bifiditermes sp	Acacia and Burkea	Nests in and feeds on dead branches of living or recently-dead trees
Termitidae	Apicotermitinae	Aganotermes oryctes Sands	All areas	Humus feeder; one of commonest termites
Termitidae	Macrotermitinae	Macrotermes ukuzii Fuller	Burkea, possibly also Acacia	Feeds on dead wood and grass and other litter; builds broadly conical mounds - all those examined seemed to be long dead
Termitidae	Macrotermitinae	Microtermes sp 1 (albo- partitus Sjöstedt)	Abundant in <i>Acacia</i> and Burkea	Feeds on wood and other litter
Termitidae	Macrotermitinae	Microtermes sp 2	Near turf vlei	Found in dead wood and in foraging galleries in soil
Termitidae	Nasutitermitinae	Fulleritermes coatini Sands	Burkea only	Uncommon; believed to feed on wood and probably other litter
Termitidae	Nasutitermitinae	Trinervitermes dispar (Sjöstedt)	Burkea only; principally open areas	Harvests grass but does not store it in its nest
Termitidae	Nasutitermitinae	Trinervitermes sp 2 Trinervitermes sp 3	Burkea only	Presumably harvesting; habits not yet investiga- ted
Termitidae	Termitinae	Cubitermes pretorianus Silvestri	Common in <i>Burkea</i>	Humus feeding; football-sized nests almost invariably occupied by other termite species and by ants
Termitidae	Termitinae	Microcerotermes parvus (Haviland)	Very common in Burkea; less common in Acacia	Feeds on fallen wood litter and old dung and probably on other litter
Termitidae	Termitinae	Microcerotermes sp 2	Found in Burkea	Habits similar to preceeding species
Termitidae	Termitinae	Procubitermes sp	In <i>Burkea</i>	Humus feeder; reasonably common
Termitidae	Termitinae	Promirotermes sp	In <i>Burkea</i>	Humus feeder; moderately common
Termitidae	Termitinae	Amitermes sp	Near turf vlei	Apparently humus feeder

Table 15. Maximum and minimum values of five replicates for viable actinomycetal, bacterial and fungal propagule counts (g⁻¹ soil) from soils of various subhabitats. Data from Steyn and Bezuidenhout (1977).

	Actinomycetes		Bacteria		Fungi		
	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum	
Value	33,8x10 ⁵	0,4x10 ⁵	41×10 ⁵	0,6x10 ⁵	8,6x10 ⁴	0,3x10 ⁴	
Subhabitat	Burkea, between grass tufts, 0-5cm	Ochna, O-5cm	Burkea, between grass tufts, 0-5cm	Open, 5-15cm	Burkea, between grass tufts, 0-5cm	Burkea, away from grass tufts, 15-30cm	
Date	77.01.12	76.08.02	76.01.07	76.11.12	77.04.08	77.03.03	

Dung-feeding arthropods

During the 1975/1976 summer season a pilot study was undertaken to establish the general biology of dung-feeding arthropods at Nylsvley. Aspects investigated included the composition and fluctuation of populations, seasonal changes in rate of dung removal, changes in the agents responsible for dung removal and the influence of dung age on removal rates. Preliminary findings are presented by Endrödy-Younga (1976a, 1976b). Particular attention was devoted to the reduction of cattle dung. The amount of dung removed ranged from 0% during July and August to over 70% through December, January and February. The rate of dung removal on a daily basis varied according to the season, in winter no dung had been removed after 10 days, in early spring 24% had been removed after 10 days and during summer as much as 77% was removed during the first day.

Dung removed by rollers (Scarabaeinae) was measured separately from that removed by diggers (Coprinae, Aphodiinae). While the diggers bury dung under the pellet, the rollers are important in dispersing dung away from the site of deposition. Dung dispersal was substantial at the beginning of the season but virtually the entire quantity was dug into the soil beneath the pellet towards the end of the season.

The composition of the coprophagous fauna was characterized by the large variety and populations of some digging groups such as Oniticellini, Aphodiinae and Onthophaginae, as well as moderate numbers of Coprinae. *Pachilomera* spp were the commonest dung rollers.

Table 16. Mean, minimum and maximum values for in situ $\rm CO_2$ efflux (130 replicates), respirometric $\rm CO_2$ measurement (156 replicates) and ATP content assay (156 replicates) in the open subhabitat over the year from 76.04.06 to 77.04.20.

	Mean value at monthly intervals	Minimum value (date)	Maximum value (date)	
In situ CO ₂ effux mg CO ₂ m ⁻² d ⁻¹				
litter	533	86 (76.08.02)	903 (77.03.08)	
soil	809	104 (76.08.02)	2 220 (77.12.09)	
roots	524	37 (76.06.11)	1 553 (77.01.13)	
total	1 866	226 (76.08.02)	4 367 (77.01.13)	
Respirometric CO ₂ measurement mg CO ₂ g ⁻¹ soil d ⁻¹ x 10 ⁻³				
soil depth 0-5 cm	4,87	2,12 (76.08.02)	1 263 (77.01.13)	
5-15 cm	2,17	0,12 (76.08.02)	705 (77.01.13)	
15-30 cm	0,61	0,06 (76.07.08)	206 (76.11.12)	
ATP content fg ATP g ⁻¹ soil x 10 ⁶				
soil depth 0-5 cm	4,09	0,50 (76.10.04)	14,90 (77.12.09)	
5-15 cm	2,10	0,18 (76.07.08)	10,90 (77.11.12)	
15-30 cm	0,81	0,05 (76.07.08)	7,80 (77.12.09)	

MINERAL CYCLING COMPONENT

Introduction

Burkea savanna occurs on sands known to be deficient in a number of nutrients. Phase I projects were aimed at identifying and measuring quantities of limiting nutrients present and establishing the rate of nitrogen fixation in the soil.

Nutrient status of Nylsvley soils

Determinations of nutrient status have been carried out by various project participants (Table 17). Walker and Horne (1977) reported that the level

Table 17. Nutritional status of A-horizon soils (Hutton form, Bontberg Series) in ppm from the two main subhabitats.

	Number	Under <i>Burkea</i> canopy			Open subhabitat		
	of rep- licates	Mean	Max	Min	Mean	Max	Min
Macronutrients							
Nitrate nitrogen	9	19,0	27,0	12,1	19,6	25,7	16,7
Ammonium nitrogen	9	35,5	42,4	27,4	36,7	42,0	29,1
Total nitrogen	9	421,5	604,2	270,0	426,7	602,2	270,1
Phosphorous	76	2,4	5	1	3,3	21	1
Potassium	76	40,2	110	12	32,6	222	11
Calcium	76	83,4	258	16	78,5	296	21
Magnesium	76	24,0	68	5	22,6	81	5
Micronutrients					-		
Iron	3	41,1	55,6	30,6	74,9	122,2	11,2
Manganese	3	4,9	6,0	3,2	5,9	8,4	3,0
Zinc	3	8,1	21,6	0,6	28,9	80,3	1,2
Copper	3	0,38	0,42	0,34	0,45	0,56	0,38
Sulphur	3	0,94	1,01	0,81	1,48	1,88	1,23
Aluminium	3	0,42	0,48	0,34	0,62	0,67	0,53

of total nitrogen in the soil was very low and showed little variation over an experimental area in *Eragrostis pallens - Burkea africana* tree savanna. The pH, at about 4,0 in KCl, is low and soils are more acidic under tree canopies than in the open. The exchangeable cations, calcium, magnesium and potassium are in sufficient concentrations to be non-limiting to plant growth. Harmse (1977) reported A-horizon nitrogen percentages in the range 0,040 to 0,047 for Kyalami, Portsmouth, Chester and Bontberg series and 0,025 for Middelburg series soils of the Hutton form, the dominant soil of the Study Area.

Three sites for each of the open and under canopy subhabitats have been sampled for pilot micronutrient analyses. All micronutrients tested for were in adequate concentrations to be non-limiting to plant growth in the sandy soil of the Study Area. Zinc was found in particularly high concentrations, and was extremely highly concentrated in one sample. Further samples need to be taken, however, to verify whether this is a representative concentration of zinc in the area as a whole.

Nitrogen fixation

Grobbelaar and Rösch (1976a) reported that nitrogen fixation in the soils of Nylsvley is in the order of 80 kg $ha^{-1}y^{-1}$. They consider that this value is unrealistically high and may be an overestimate as the acetylene reduction technique used is not consistently reliable.

MODELLING COMPONENT

Introduction

Modelling has been an integral part of the project since its inception. The first model to be developed was of the whole ecosystem (Getz and Starfield 1975) and since then various models and submodels have been built. Models are seen as heuristic tools to be used by researchers themselves with the assistance of trained modellers where necessary. The development of DRIVER, an interactive modelling aid (Furniss 1977), has been of assistance in this regard and has facilitated the building of many of these models.

The main objectives of the Data Processing Unit are to store project data permanently, make such data available to researchers on request, to manipulate data by computer to satisfy modelling requirements and to carry out routine statistical analyses of data sets for researchers.

Modelling

The first project model was a simple linear model of the savanna ecosystem (Getz and Starfield 1975), developed as an aid for the planning of the research programme. Estimates for standing crop and annual intercompartmental flow rates were obtained from participants (Table 18). The sensitivity of the 15-compartment model to changes in its parameters was analysed and recommendations were made concerning future research. Compartments and flows singled out for further study on the basis of this sensitivity analysis included rates of flow to and from and standing crop of the insect compartments, dynamics of the moribund grass compartment and the small herbivore compartment.

Although playing a small role overall, herbivore-carnivore interaction required study and refinement in the decomposer and reducer compartments was urgently required. Stress was placed on the need to gather information on the seasonal fluctuations of components.

As the model was based on the extremely limited information available at the time, it is not surprising that some of the recommendations are no longer considered to be of high priority. On the other hand, some, such as the need for a detailed study of decomposition and reduction processes, were adopted and have proved valuable.

DRIVER is a FORTRAN-language computer programme which was developed within the project. The programme has two aims. Firstly, it enables researchers with little or no computer background to exercise existing mathematical models after very little instruction. Secondly, it enables modellers and participants to implement their models on a computer without having to concern themselves with input-output routines. An instruction manual for DRIVER has been published (Furniss 1977).

Table 18. Average yearly standing crop values used in first linear model (Getz and Starfield 1975) and current estimates.

		mass (g m ⁻²)			
	System component	1975 estimates	1977 estimates		
Primary	grass	240	95		
producers	forbs	16	15		
	shrubs and trees	760	1 627		
Dead vege- tation	moribund grass	60	58		
tation	standing dead trees and shrubs	23	186		
	litter	30	383		
Herbivores	*impala	0,9	0,6		
	* kudu	0,5	0,4		
	*small herbivores	0,5	0,1		
Herbivorous	grass-eating insects	0,75	0,1		
insects	browsing insects	0,4	0,01		
Secondary	* carnivores	0,4	0,005		
consumers	* insectivores	0,01	0,02		
* wet mass, others are dry mass value					

Data processing

As a service to participants, a central data banking and processing office was established at the Botanical Research Institute, Pretoria. Data collected are encoded on partly standardised data sheets and stored on computer disk files. Summarization, manipulation and statistical analysis of these data are carried out by computer.

The computer data bank now contains over 10 000 records, of which 2 000 are of weather observations. The bank has recently been re-structured into three tiers -

- (a) Archive data including copies of all raw data from projects which do not have data included in tier (b). These data will not be stored on the computer.
- (b) Raw data for projects with large amounts of data and where extensive data manipulation and summarization by computer are required. Summaries of these data will be made by computer for inclusion in tier (c).
- (c) Summarized data for projects where summarization can be done by hand, data are submitted in summarized form.

PHASE II: STUDIES OF KEY COMPONENTS AND PROCESSES

Phase II Aims

- To undertake a selected number of studies of components and processes within the Nylsvley Study Area, identified during Phase I to contribute to the long-term objectives of the ecosystem project.
- To develop mathematical models to simulate the dynamics of structure and function within the ecosystem and to reflect advances and understanding achieved during Phase II.
- To design validation experiments to be carried out during Phase III, so that the models developed during Phase II can be tested at other comparable sites elsewhere.
- To design experiments to be carried out during Phase III, in which the effects on the ecosystem of such management factors as fire, different grazing strategies and fertilizer application can be investigated.

Although Phase II was originally planned to commence in 1976, many of the Phase I descriptive studies were modified at an early stage to examine certain Phase II questions. As the overall programme developed, the division of Phase II into a number of themes became necessary and these themes will be followed in presenting a sketch of progress in the Phase. A detailed synthesis of Phase II findings will be compiled for publication before the end of 1978.

Theme I: Pattern and dynamics of the Burkea/Acacia savanna mosaic

The mosaic of Burkea africana and Acacia spp savannas in the Study Area have been described in the Phase I summary. An understanding of the dynamics within and between these two communities is regarded as fundamental to the development of management models for the Nylsvley savanna. Preliminary investigations based on an analysis of changes in the distribution of the mosaic components in the Nylsvley area and in the ratio of trees: shrubs: open patches in Burkea savanna as shown in aerial photographs during the last 30 years has been initiated by Walker and coworkers. Changes in the structure of both herbaceous and woody components of the five belt transects in Burkea savanna (Van Rooyen and Theron 1977, Lubke 1977) have already been referred to.

Theme II : Climatic characteristics of the Burkea savanna

The development of predictive models relating microclimatic variables to macroclimate in <code>Burkea</code> savanna is seen as the major objective within this theme. The choice of microclimates to be modelled have been selected by the climatologist in consultation with biologists. While a considerable volume of data is being collected by the three standard weather stations in the Study Area, the collection of microclimatic information has been delayed because of the continued malfunction of the electronic automatic weather station.

Theme III: Water relations within Burkea savanna

Water availability is believed to be the major determinant of the structure and efficiency of Burkea savanna at Nylsvley and detailed information on water cycling through the ecosystem as a whole and on water relations of individual species is regarded as a high priority. The seasonal and spatial distribution of rainfall is being monitored by the standard weather stations (De Jager 1977), its interception loss is being estimated by De Villiers (1977) and its fate within the soil monitored by Van Rooyen The interception loss study was initiated late in the 1976/1977 summer and no results are currently available although a study in a similar, but perhaps slightly denser savanna near Pretoria indicated a 23% loss due to interception (De Villiers 1976). The monitoring of hydrological conditions, in particular the drying cycle, in four subhabitats of Burkea savanna by means of a neutron depth and surface probe was initiated early in 1977 (Van Rooyen 1977). Research in the water physiology of selected plant species is seen as an urgent priority but had not been initiated by the end of the period under review.

Theme IV: Factors influencing primary production

Considerable progress has been made in the estimation of biomass accumulation rates in the herbaceous (Grunow 1977) and woody (Rutherford 1977) components of the Nylsvley savanna, providing baseline data on the gross patterns of primary production over a series of years during which varying climatic conditions prevailed. More detailed studies of primary production have been initiated by Cresswell and Ferrar (Ferrar P J 1977), initially by means of measurements of short-term $^{14}{\rm CO}_2$ incorporation rates as an estimate of photosynthetic capacity. More accurate and more detailed studies will be possible once the controlled environment system currently in development for use in both phytotron and the field has been completed.

Theme V: The fate of photosynthate

Attempts to quantify the translocation and distribution of photosynthetic products with respect to leaf age and time of season in the dominant grasses of Burkea savanna were abandoned after considerable effort (Tew, Cresswell, Ambler and Baldwin 1976). More general studies of changes in the distribution of photosynthate included those of Rutherford (1977) and of Van Wyk (1977). The former study includes investigations of the sequence of radial increment from canopy to root in woody plants and the latter has attempted to measure seasonal changes in the underground biomass of woody and herbaceous species simultaneously to similar above-ground measurements being made by Grunow (1977) and Rutherford (1977).

Theme VI: Factors affecting faunal dynamics and secondary production

Numerous Phase I studies examined various aspects of faunal population composition and dynamics and these studies have been referred to in the Phase I summary. Two projects focussed on factors affecting faunal productivity — in particular in terms of cattle production. Grobbelaar studied the pattern of monofluoroacetate activity in gifblaar Dichapetalum cymosum (Grobbelaar and Rösch 1976b) which is extremely toxic to domestic

stock but of unknown influence on indigenous herbivores, while Horak (1975, 1976a, 1976b, 1977, 1978a, 1978b), Horak $et\ \alpha l$ (1976) studied the incidence and role of various internal and external parasites in cattle and impala.

Theme VII: Influence of consumers on primary production

The influence of consumers on primary production varies considerably and with little relation to the size or abundance of the consumer in question. Preliminary studies of these influences were devoted to the direct consumptive effects, measured mainly in terms of herbage removal, rather than on the influence of such removal on net primary productivity. Studies thus far completed include Gandar (1977) on insects of the herbaceous stratum, Scholtz (1976) on lepidopterous larvae, Monro (1977) on impala, Temby (1977) on various small mammals and Zimmerman (1977) on cattle. The removal of herbage by these groups and species probably approximated between 10 to 15% of net herbage production.

Theme VIII: Decomposition and reduction processes in Burkea savanna

Encouraging progress has been made in decomposition and reduction studies. Phase I studies on litter production (Huntley and Osborn 1977, Grunow 1977) have provided data on the rates and kinds of input into the component from primary producers, while a meaningful idea of the kinds and patterns of activities of reducer and decomposer insects and micro-organisms has been obtained from the studies of Endrödy-Younga (1977), Steyn and Bezuidenhout (1977), Ferrar P (1977) and Holm and Hasenjager (1977). Current studies are centred on determining the rates of decomposition and mineral release from woody plant leaves, grass leaves and woody material of ten selected species. Substrate condition is being measured in terms of cellulose, hemi-cellulose, lignin, sugars and the levels of N, P and K.

Theme IX: The role of nutrients as limiting factors in Burkea savanna

A preliminary fertilization trial, using applications of N, P and K at four levels and several different combinations has been started by Walker and Horne (1977). The detailed study of the nitrogen cycle in *Burkea* savanna has also been planned for early initiation.

Theme X: The ecological effects of fire in Burkea savanna and
Theme XI: The influence of various management practices on the ecology
of Burkea savanna

Neither of these themes have been investigated as yet.

PHASE III : VALIDATION STUDIES AND THE DEVELOPMENT OF MANAGEMENT STRATEGIES FOR BURKEA SAVANNA

The value of the hypotheses and models developed during Phase II will depend on the degree to which they can be successfully applied in other savanna ecosystems. Phase III will therefore be devoted to the design and execution of validation experiments and the interpretation of results in terms meaningful to the land manager. Every effort has been made to anticipate the nature of management questions to which answers will be required during the planning and execution of the research programme.

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