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Savanna ecosystem project progress report 1975/1976

B J Huntley

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

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SINOPSIS

Die resultate van die tweede studieseisoen (Julie 1975 - Junie 1976) van 'n koöperatiewe, multi-dissiplinêre ondersoek van die struktuur en funksionering van 'n savanne-ekosisteem te Nylsvley in die noordelike Transvaal word kortliks bespreek.

Reënval gedurende die tydperk (684 mm) was effens bo die langtermyn gemiddelde van 630 mm. Primêre produksie en phytomassa is bepaal deur gebruik te maak van opbrengstegnieke vir die bogrondse kruidlaag, CO_2-gasuitruiling en destruktiewe monstering van houtagtige plante vir die bepaling van allometriese regressies. Grondmonsters is geneem vir die bepaling van ondergrondse veranderinge in wortelmassa. Voorlopige waarnemings is gemaak van die tempo en verspreiding van fotosintetiese produkte in geselekteerde grassoorte en die seisoenale variasie in die monofluoroasetaat konsentrasie van die giftige plant *Dichapetalum cymosum*.

In die verbruikerkomponent is ruimtelike en seisoenale veranderinge in die biomassa en bevolkingsgrootte en struktuur van soogdiere, reptiele, amfibieë, voëls en die hoofongewerwelde diere beraam. Voedingsstudies van geselekteerde voëls en insekte is uitgevoer. Die rol van endo- en ektoparasiete as beperkende faktore vir sekondêre produksie in rooibokke en beeste is ondersoek.

Beramings van die bevolkingstruktuur, biomassa en aktiwiteite van grond-arthropoda en mikro-organismes is binne die afbrekerkomponentprogram gemaak. Seisoenale skommelinge in die aktiwiteit van miskruiers, belangrike reduserende agente, is bepaal in verhouding tot misproduksie deur beeste en ander groot soogdiere.

Waarnemings van die stikstofinhoud van reënwater en die tempo van stikstofbinding is gemaak. Beramings toon dat die tempo van stikstofbinding in die *Burkea* savanne ongeveer 80 kg ha^{-1} jr^{-1} kan wees.

SYNOPSIS

The results of the second full season (July 1975 - June 1976) of a cooperative multi-disciplinary investigation into the structure and function of a savanna ecosystem at Nylsvley in the Northern Transvaal are briefly reviewed.

Rainfall during the period (684 mm) was slightly above the long-term average of 630 mm. Primary production and phytomass were measured using harvest techniques for above ground herbage, CO_2 gas exchange, and destructive sampling of woody plants for the determination of allometric regressions. Soil cores were taken for the estimation of below ground changes in root mass. Preliminary observations were made of rates and distribution of photosynthetic products in selected grasses and the seasonal variation in the monofluoroacetate concentration of the poisonous plant *Dichapetalum cymosum*.

In the consumer component, spatial and seasonal changes in biomass and population size and structure of mammals, reptiles, amphibia, birds and the

major invertebrate groups were estimated. Feeding studies were conducted on selected birds and insects. The rôle of internal and external parasites as limiting factors to secondary production was examined in impala and cattle.

Estimates of the population structure, biomass and activity of soil arthropods and micro-organisms were made within the decomposer component programme. Seasonal fluctuations in the activity of dung beetles, particularly important reducing agents, were determined in relation to cattle and other large mammal dung production.

Observations were made of the nitrogen content of rain water and the rates of nitrogen fixation. Estimates suggest that nitrogen fixation rates in the *Burkea* savanna would approximate 80 kg ha^{-1} yr^{-1}.

CURRENT TITLES IN THIS SERIES

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

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12. Savanna Ecosystem Project - Progress report 1975/1976. B J Huntley. March 1977. 42 pp.

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

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 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 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 1976-1979) - 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 objectives and detailed research programme of the Savanna Ecosystem Project were described in the first report of this series (Anon 1975) while the results of the 1974/75 season were reviewed by Hirst (1975). The present report reviews progress made during the 1975/76 season.

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Table 1 : Abbreviated list of completed and current research projects within the Savanna Ecosystem Project, 1974 to 1976.

No.	Project leader and report authorship	Short title
Abiotic Component		
1	De Jager (De Jager 1975, 1976)	Climate of Nylsvley
2	De Jager (De Jager 1975b)	CO_2 and moisture fluxes
3	Van Rooyen (Van Rooyen 1976)	Soil hydrology
4	De Villiers (De Villiers 1976)	Rainfall interception
5	Harmse (Harmse 1975)	Soils of Nylsvley
Primary Producers Component		
6	Coetzee (Coetzee et al 1976)	Vegetation of Nylsvley
7	Lubke (Lubke et al 1975, 1976, Lubke 1976)	Woody plant structure
8	Theron (Van Rooyen & Theron 1975)	Herbaceous plant structure
9	Grunow (Grunow 1975, 1976)	Aerial herbaceous standing crop
10	Grobbelaar (Grobbelaar 1975, Grobbelaar & Rösch 1976a)	*Dichapetalum cymosum*
11	Cresswell (Tew et al 1976)	Translocation
12	Cresswell (Tew & Cresswell 1976)	Photosynthesis
13	Cresswell (Cresswell et al 1976)	Transpiration
14	Rutherford (Rutherford 1975, Rutherford & Carr 1976)	Woody aerial standing crop
15	Van Wyk (Van Wyk 1976)	Underground phytomass
16	Venter (Venter 1976)	Seed production
Consumer Component		
17	Horak (Horak et al 1976, Horak 1976)	Parasites in cattle and impala
18	Nel (Bragg 1975, Temby 1976)	Small mammals
19	Skinner (Monro 1976)	Impala
20	Skinner (Carr 1976, Kingston 1976)	Large mammals
21	Skinner (Zimmerman 1976)	Cattle
22	Tarboton (Tarboton 1975, 1976 a,b)	Birds
23	Jacobsen (Jacobsen 1975)	Amphibia & reptiles
24	Holm (Holm et al 1976, Kirsten 1976, Scholtz 1976)	Phytophagous insects
25	Paterson (Levey 1976, Gandar 1976)	Phytophagous insects
Mineral Cycles Component		
26	Grobbelaar (Grobbelaar & Rösch 1976b)	Nitrogen fixation
27	Steyn (Steyn 1976)	Nitrogen in rainfall
Decomposer Component		
28	Endrödy Younga (Endrödy Younga 1976)	Arthropod reducers
29	Loots (Loots & Theron 1976, Olivier 1976)	Acari
30	Steyn (Steyn & Bezuidenhout, 1976)	Micro-organisms

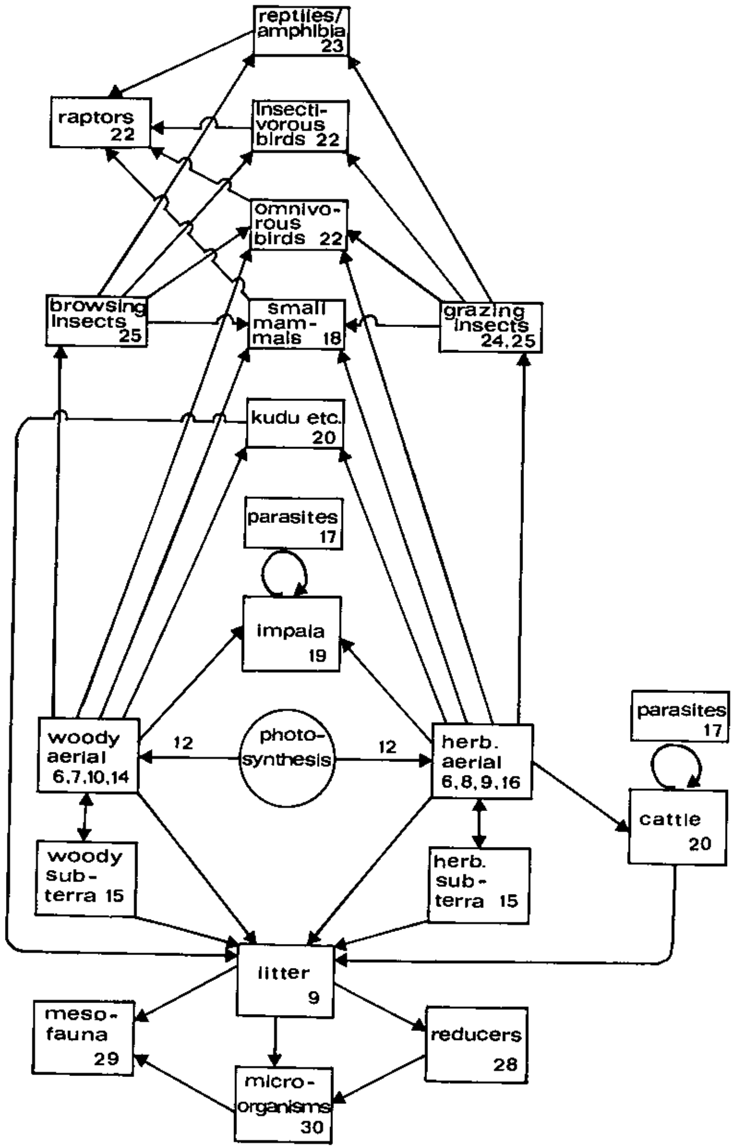

Figure 1 : Simplified conceptual model of Burkea africana *savanna indicating major trophic components and material pathways. Numerals refer to projects listed in Table 1. Controlling factors studied include climate (1,2) water balance (1,2,3,13) and nutrient status (5,26,27).*

INTRODUCTION

Phase I of the Savanna Ecosystem Project was initiated in mid-1974 with the principal objective of identifying and quantifying the major trophic components and material pathways within this deciduous broadleafed savanna ecosystem. By mid-1976 most of the pilot studies had been concluded, providing the basis for a general description of *Burkea africana* savanna and the development of a preliminary conceptual model of trophic inter-relations within the system, Figure 1.

Much of the information collected during Phase I will require considerable refinement before a meaningful budgeting model of the ecosystem can be built : the absence of studies on litter production, phenology and nutrient status was a serious deficiency in the preliminary research programme.

The present review provides a brief outline of the progress reported on by project participants during the 1975/76 season. No attempt is made to compare these results with studies in other ecosystems, nor are any early conclusions drawn : a comprehensive description of *Burkea africana* savanna at Nylsvley will be prepared at the conclusion of all Phase I projects.

CLIMATE

The climate of the Nylsvley area has been described by Hirst (1975) and Coetzee et al (1976). Routine meteorological observations and autographic recordings were made at three standard weather stations within the study area during the period under review (De Jager 1976). Hourly mean values of temperature and relative humidity and hourly totals of rainfall have been processed and monthly means and totals of these are presented in Figure 2. Precipitation during the 1975/76 season totalled 649 mm, only slightly higher than the 40 year mean of 630 mm.

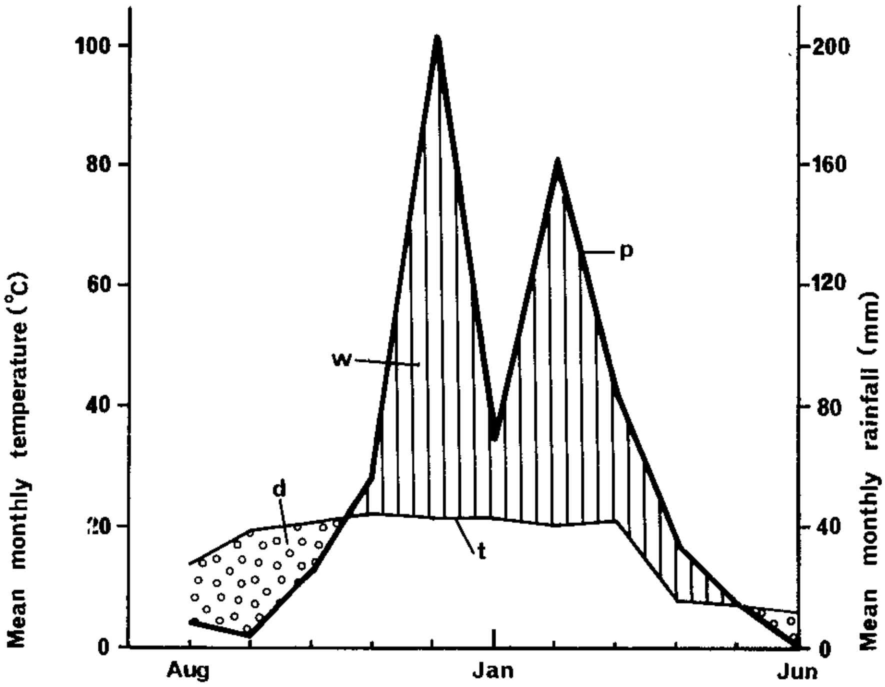

Figure 2. *Climate diagram for Nylsvley for the period August 1975 to June 1976. Key : t-mean hourly temperature; p-monthly rainfall; d-arid period; w-humid period.*

An automatic recording weather station capable of monitoring a wide range of system driving forces (De Jager 1975, Hirst 1975) is being installed in the intensive study site but has not yet begun operation. Once operational, the station will provide continuous records of a wide range of radiation, moisture, temperature, pressure and wind parameters.

SOILS

The soils of the Nylsvley Nature Reserve have been classified and described by Harmse (1975) and are briefly outlined in Hirst (1975). No further studies have been conducted, but a detailed investigation of the role of mineral nutrients as control factors in *Burkea* savanna will be initiated during 1976.

Studies in the surface and sub-surface hydrology of soils in the ecosystem are also planned for 1976 (Van Rooyen 1976). This project will be integrated with others on precipitation and evaporation (De Jager 1976), rainfall interception (De Villiers 1976) and plant-water status (Cresswell, Tew and Ferrar 1976) towards the development of a mathematical model of the hydrological cycle in *Burkea* savanna at Nylsvley. Use will be made of a modified version of the model PROSPER (Goldstein and Mankin 1972) which simulates atmosphere-plant-soil-water relationships on a daily basis.

VEGETATION

The broadleafed savanna/microphyllous savanna mosaic

The vegetation of the study area has been classified and described on a basis of floristic, structural, pedological and anthropogenic characteristics (Coetzee et al 1976) but the biotic relations of the various communities on an African scale await interpretation. It is probable that detailed analysis of Phase I surveys will confirm the apparent relationships of *Burkea africana* - *Eragrostis pallens* savanna and *Diplorhynchus condylocarpon* - *Barleria bremekampii* savanna with the mesic and moist broadleafed savanna biome and the *Acacia* spp - *Eragrostis lehmanniana* savanna with the arid microphyllous savanna biome (Tinley 1975). The consequences of such relationships are of the greatest importance to any attempts at model building and extrapolation of Nylsvley data. Information gathered on the ecology of the *Acacia* spp - *Eragrostis lehmanniana* savanna cannot be linked with data on aspects of *Burkea africana* - *Eragrostis pallens* savanna. The studies on widely ranging species such as impala, kudu, cattle and many of the birds will have to account for the differences in time spent, activity patterns and niche structure and utilization within these various savanna types.

The role of the anthropogenically induced patches of *Acacia* savanna within the *Burkea* savanna is of very great importance due to their richer soil mineral status (Harmse 1975, Coetzee et al 1976) and consequently more nutritious herbage which is highly preferred by most of the larger mammals (Carr 1975, 1976; Monro 1976). Of particular interest is the apparent stability of these *Acacia* patches, which owe their origin to pastoral settlements abandoned over 50 years ago (Coetzee et al 1976). An understanding of the dynamic relations of the three savanna types within

Table 2. The percentage frequency and density of the most important woody species in all the sample areas of the Nylsvley study site, January 1976. Data from Lubke (1976).

Species	Percentage Frequency			Density (no/ha)		
	Total area 1974	Sample of area 1974	Sample of area 1976	Total area 1974	Sample of area 1974	Sample of area 1976
Ochna pulchra (<1m)	73,9	76,2	84,9	2585,8	2803,9	4709,6
O pulchra (1-3,5m)	60,8	62,3	63,7	1953,4	1997,1	2008,7
O pulchra (>3,5m)	2,1	2,4	2,4	15,8	9,6	9,6
Burkea africana (<4m)	43,8	50,0	58,7	368,0	408,7	536,5
B africana (4-7m)	9,3	7,2	7,2	38,6	29,8	29,8
B africana (>7m)	1,0	0,7	0,7	4,1	2,9	2,9
Grewia flavescens (individuals)	27,2	27,4	27,6	992,7	1092,3	1118,3
G flavescens (clumps)	27,1	27,4	27,6	195,3	220,2	240,4
Strychnos pungens (<1m)	19,3	19,5	20,0	169,9	163,5	242,3
S pungens (1-3m)	9,9	9,1	11,1	52,2	51,9	58,7
S pungens (>3m)	0,6	1,2	1,2	2,5	4,8	4,8
Terminalia sericea (<3m)	9,9	10,3	15,1	76,3	68,3	93,3
T sericea (3-5,5m)	5,3	5,3	5,3	31,7	25,0	26,9
T sericea (>5,5m)	0,6	0,7	0,7	2,9	2,9	2,9
Combretum molle	7,6	6,7	8,9	41,1	30,8	41,4
C zeyheri	2,8	1,9	3,1	18,9	10,6	19,2
Vitex rehmanii	9,3	8,2	9,1	105,3	68,3	89,4
Euclea natalensis	6,3	6,7	7,2	35,9	38,6	41,4
Lannea discolor	5,0	4,6	10,1	31,1	25,0	64,4
Dombeya rotundifolia	3,0	4,6	5,5	13,8	18,3	22,1
Securidaca longipendunculata	2,9	2,6	2,9	13,1	10,6	11,5
Asparagus suaveolens	2,3	2,4	3,1	16,9	22,1	28,9
Ozoroa paniculosa	1,7	1,7	2,2	8,8	8,7	10,6
Dichrostachys cinerea	1,4	2,4	2,9	10,8	23,1	25,0
Strychnos cocculoides	1,4	1,7	2,2	6,0	7,7	10,6
Ximenia caffra	1,1	0,2	0,2	4,8	1,0	1,0

the study area will be of fundamental importance to the development of management strategies but this aspect awaits study.

The structure and pattern of *Burkea africana* *savanna*

A detailed survey of the structure and pattern of the woody component of the study area's vegetation was undertaken during September 1974 (Lubke et al 1975, 1976) and changes monitored in January 1976 (Lubke 1976).

In the initial survey, five permanently marked belt transects, each sub-divided into 384 to 1 280 contiguous 5 x 5 m quadrats, were sampled for density, height, stem diameter, canopy cover, etc of all woody species. During January 1976 12,5 percent of the total area was re-sampled.

The frequency and density of all species with a frequency greater than 1,0% are presented in Table 2. The results of the 1976 survey conform closely with those of the 1974 survey except for a much greater frequency and density of woody plants in the lower height classes. Lubke (1976) suggests that these differences are probably due to seasonal effects, small leafless plants having been hidden in tall grass during the initial survey. Only *Strychnos pungens* showed a significant increase in numbers.

A survey of the structure of the herbaceous component of *Burkea* savanna was undertaken in 1975 (Van Rooyen and Theron 1975) but was not repeated during the 1975/76 season.

PRIMARY PRODUCTION

Definition of concepts and terms

During the initial stages of the project considerable variation existed in the use of terms relating to the concepts of primary production, standing crop, biomass, etc. At a Workshop held in April 1976, Tew (1976) proposed a series of definitions which have since been adopted for general use within the project.

The first set of terms apply to the plant(s) at any given time. Figure 3 gives the visual concept of the definitions and their abbreviations.

The second set of definitions apply to a dynamic situation where the biomass changes of the plant are considered between times t_1 to t_2, Figure 4.

From these terms a series of equations can be drawn up to describe the rates of production of the compartments (B, D, L, X). In terms of actual measurements in the field it is helpful to define ΔB as the apparent change in B from t_1 to t_2 :

$$\Delta B = B_2 - B_1$$

and similarly for ΔD, ΔL.

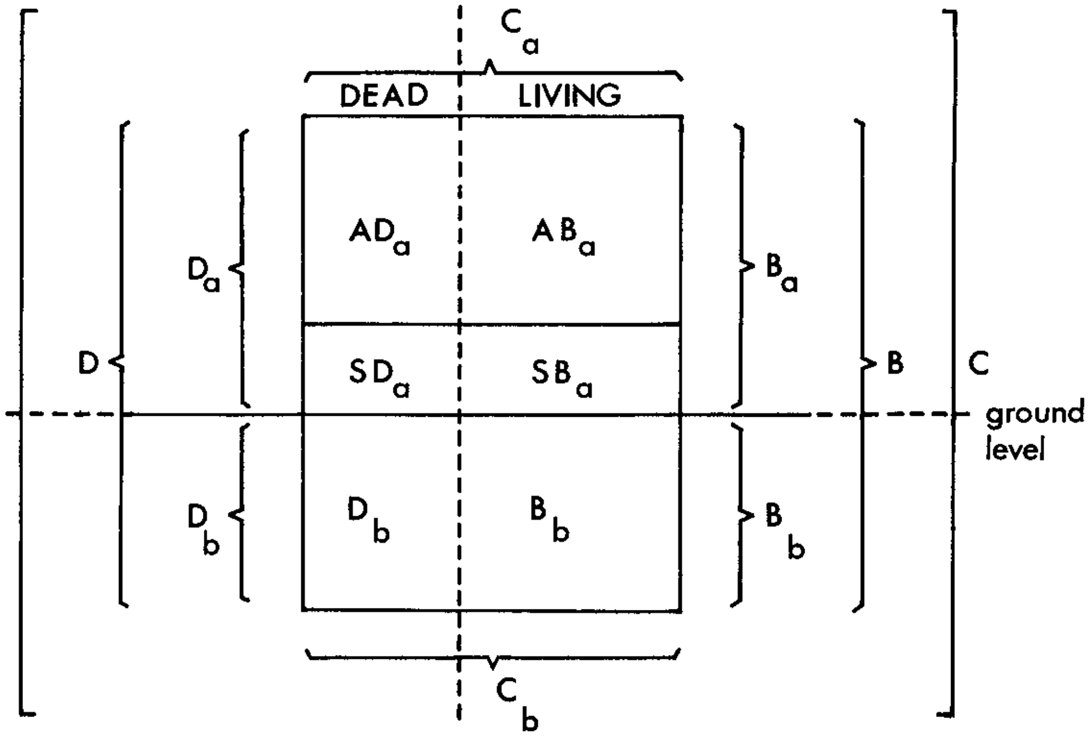

Figure 3. Definitions of terms used to describe a plant(s) at any given time on a mass basis. (From Tew 1976).

Key :

AB_a = Available above ground biomass

SB_a = Stubble biomass (refers to grasses)
Woody biomass (refers to trees)

B_a = Above ground biomass

B_b = Root biomass

B = Total biomass (standing biomass)

AC_a = AD_a + AB_a Available above ground standing crop

SC_a = SD_a + SB_a Stubble (woody) standing crop

C_a = Above ground standing crop

C = Standing crop - summation of all mass

AD_a = Available above ground dead

SD_a = Stubble dead (refers to grasses)
Woody dead (refers to trees)

D_a = Above ground dead

D_b = Root dead

D = Total dead

C_b = D_b + B_b Below ground standing crop

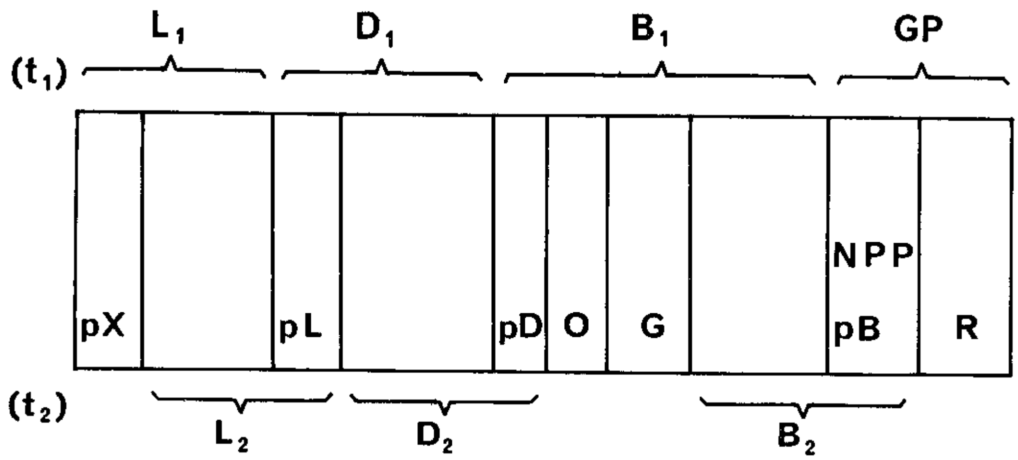

Figure 4. *Definitions of the terms that apply to the changes in mass of a plant(s) between time t_1 and t_2. (From Tew 1976).*

Key :

GP = Gross Production

B = Biomass

G = Loss to consumers

D = Standing dead

X = Decomposed (non-existent)

pB and similarly for the other terms = production of that term (ie amount that entered that compartment between t_1 and t_2).

NPP = Net Primary Production

R = Respiration by the living plant(s)

O = Other losses (exudation, parasitism)

L = Litter

$$NPP = pB = B_2 + G + O + pD - B_1 = \Delta B + G + O + pD$$

$$pD = D_2 + pL - D_1 = \Delta D + pL$$

$$pL = L_2 + pX - L_1 = \Delta L + pX$$

Combining these :

$$NPP = \Delta B + G + O + \Delta D + \Delta L + pX$$

Gross primary production is therefore :

$$GPP = NPP + R$$

NPP is by definition equal to the gross photosynthesis (P) minus the total respiratory component (R). The uptake of minerals (M) should also be considered as a positive mass term but as the ashed mass of most plant material is usually less than 5% of the dry mass it is not accounted for. An equation for NPP may therefore be written :

$$NPP = (P - R) + M = \Delta B + (G_1, G_2, \ldots) + O + \Delta D + \Delta L + pX$$

P = Gross photosynthesis

The following assumptions have been made :

- nothing falls off until it is dead;
- nothing decomposes except from the litter component.

If these assumptions do not apply then the production of the intervening compartments are over-estimated.

Herbaceous above-ground standing crop and production

Estimates of above-ground herbaceous standing crop and primary productivity were made using harvest and gas-exchange techniques.

Harvest methods were used by Grunow (1975, 1976) to measure above ground standing crop at intervals throughout the year, under trees and shrubs, and in the open. The standing crop was divided into available biomass, standing dead, stubble biomass, stubble dead and mass of litter. The harvested crop was separated taxonomically into *Eragrostis pallens, Digitaria eriantha* and other species.

During the 1974/75 season estimates were made in an ungulate-proof exclosure, but during the following season movable exclosures were used. After each harvest the exclosures were moved to the next sample site, so that the sites were protected only for the 4 or 8 weeks prior to clipping. Thirty 0,5 m^2 and forty 0,5 m^2 quadrats were clipped in protected and unprotected sites, respectively, every 4 weeks in open areas and every 8 weeks under trees and shrubs. In the latter, half of the quadrats (those under shrubs) were 0,25 m^2 in size (for practical reasons).

Above ground standing crop of *Eragrostis pallens* and *Digitaria eriantha* was determined by clipping 30 tufts in exclosures and 40 in unprotected sites, at 4-weekly intervals in the open and 8-weekly under trees and shrubs. Basal areas of the tufts were determined by transparency outlines, and gm^{-2} was then determined by weighting unit area production by basal cover estimates for the site. A summary of the above-ground standing crop data for grass biomass, standing dead, stubble biomass, stubble dead and litter is presented in Table 3.

The average net primary production in the open was 1,91 (previous year 1,33) times that produced under trees and shrubs : 57,8 vs 30,3 gm^{-2} (previous year 67,8 vs 50,9 gm^{-2} (Grunow 1975)). As in the previous year the maximal available above ground biomass in the open (108,2 gm^{-2}) was reached in February when it was 54,4% of total available above ground standing crop (198,8 gm^{-2}). The corresponding data for the under tree and shrub sub-habitat were : 48,3 gm^{-2}, January (ie 57,4% of 84,1 gm^{-2}). In both the pilot and current years there was more non-grass production under trees and shrubs than in the open. Available above ground standing dead showed no constant pattern, but was at a minimum during January and February, when it was nearly half of the maximum.

Table 3. Masses (in gm^{-2}) in different compartments of the grass layer in *Burkea africana* savanna, Nylsvley, October 1975 - September 1976. Data from Grunow (1976).

	Open			Under trees and shrubs		
	min	max	mean	min	max	mean
total available standing crop	108,2	208,0	171,2	68,1	84,1	76,3
grass biomass	21,8	108,2	57,8	12,0	48,3	30,3
grass standing dead	78,8	151,0	113,4	35,8	56,8	46,0
stubble standing crop	207,0	503,0	289,4	105,6	161,4	127,9
litter	210,8	394,0	271,1	795,8	1021,1	935,1

Average litter mass in the open sub-habitat was 2 700 kg ha^{-1} and under trees and shrubs 9 400 kg ha^{-1}. The ratio of grass to tree and shrub matter in the litter for the first few determinations varied from 1:2,7 to 1:4,6 for the two sub-habitats, respectively.

The average stubble mass present in the open sub-habitat was 3 000 kg ha^{-1} and under woods 1 300 kg ha^{-1}. In these the ratios of live to dead material worked out at 1:9,1 and 1:11,4. Available above ground standing crop was just less than 50 percent by mass of above ground standing crop.

Allowing for a biomass ratio of open : under trees and shrubs of 9:1 (Hirst 1975) a weighted mean maximum available above ground standing crop of 195,6 gm^{-2} is obtained. This is lower than the figure for the previous year : 240 gm^{-2} (Hirst 1975) but the experiment had been altered slightly. The weighted mean maximum available above ground biomass was 102,2 gm^{-2}. Forbs contributed approximately 12 percent to available above ground standing crop. The apparent rate of dry biomass production of 0,54 and 0,44 $gm^{-2}d^{-1}$ for the open and closed sub-habitats, respectively, was also lower than that calculated for the previous year and lower than that calculated by "trough-peak" analysis of the graphs which gave 0,72 and 0,53 $gm^{-2}d^{-1}$ respectively.

Standing crop and productivity figures for *Eragrostis pallens*, *Digitaria eriantha* and "other grasses" have not yet been calculated.

Attempts to determine net primary production using a differential CO_2 measuring cuvette in a gas analysis system were unsuccessful (Tew and Cresswell 1976). The measurements obtained using a static reference cell fluctuated to such an extent that the resulting data were too unreliable for interpretation. A considerably improved system is being developed (Ferrar 1976 pers comm).

The extrapolation of gas analysis data from leaf area to ground area requires the calculation of Leaf Area Index. Regressions were calculated for grass basal area to leaf area in *Eragrostis pallens*. Ratios of basal area to leaf area of tufts of *Eragrostis pallens* varied from 1:4 to 1:15 in open areas, during December and January. The ratio increased notably, especially in open areas, during December but was more constant in the January period. The sum of the tuft basal area (in cm^2) per square metre for *Eragrostis pallens* was 60,5 in shaded and 145,3 in open areas. The LAI calculated at the different times from the basal area to leaf ratio and the average basal area count per m^2 is presented in Table 4. The grass LAI changed with respect to time, which may be expected, so that calculations of productivity must take this change into account.

Table 4. Leaf area indices calculated for *Eragrostis pallens* during December 1975 and January 1976. Data from Tew and Cresswell (1976).

Date	Leaf Area Index	
	Shaded	Open
75:12:02	0,303	2,18
75:12:10	0,393	3,633
75:12:20	0,544	5,327
75:12:23	0,726	6,732
76:01:12	0,847	8,208
76:01:20	0,907	8,805

Woody plant standing crop and production

Allometric relationships between dimensions and mass of nine woody plant species were determined during the 1974/75 season (Rutherford 1975) while attention was concentrated during 1975/76 on measurement of shoot growth in *Burkea africana* and *Ochna pulchra* populations in two different parts of the study area, and on pilot work on rates of seasonal radial increase (Rutherford and Carr 1976).

Destructive measurement of seasonal growth was tested against non-destructive measurement of linear shoot growth. The former method was found to be unsuited for showing seasonal growth, but non-destructive measurements of current twig length, diameter and some other dimensions provided a clear progression of shoot growth. Using regressions established in the same tree populations, these measurements could be converted to mass units.

In both *Burkea africana* and *Ochna pulchra* linear twig extension was most rapid in the first few weeks of the season's growth. After the middle of October, however, there was a progressive reduction in growth rate which had actually ceased by the end of December in *Burkea africana*, while *Ochna pulchra* exhibited a second flush at the beginning of January.

The frequency distribution of twigs in linear extension classes for both *Burkea africana* and *Ochna pulchra* shows high variability of twig extension in each phase of growth.

To convert twig dimensions to twig mass and leaf mass (on a dry mass basis) various regressions were established. Some examples of these are cited in Table 5. Relations between twig dimensions and twig mass or leaf mass were all significant ($p \leq 0{,}001$).

Table 5. Regressions for the conversion of twig dimensions to twig mass and leaf mass (on a dry mass basis) for *Burkea africana* and *Ochna pulchra*. Data from Rutherford and Carr (1976).

	branched twigs	unbranched twigs
Burkea africana	$y = 0{,}338 + 0{,}0047\ p\ q$ $z = -15{,}845 + 3{,}718\ q$	$y = 0{,}157 + 0{,}0002\ p\ q^2$ $z = -13{,}556 + 3{,}224\ q$
Ochna pulchra	$y = 0{,}0055 + 0{,}0003\ p\ q^2$ $z = 1{,}736 + 1{,}208\ q$	$y = 0{,}007 + 0{,}007\ p\ q$ $z = -1{,}377 + 0{,}940\ q$
Twig mass = y; Twig length = p; Leaf mass on shoot = z; Basal twig diameter = q.		

During the course of the season's sampling it became clear that several different ways of stratifying or dividing shoots will be necessary in future shoot measurement programmes.

The ratio of leaf mass to current twig mass appears a functionally important parameter in the ecosystem since it reflects the composition of available browse; it indicates the proportion of photosynthetically active and non-active terminal growth and it provides a relative breakdown of current terminal growth into seasonal and perennial tissue in a deciduous system.

Initial above ground radial increment measurements on a mature *Burkea africana* (Rutherford and Carr 1976) suggest a basipetal movement of the time of maximum radial increment from 1 cm diameter twigs near the top of the tree in November/December to the base of the tree in January/February.

Radial measurements of the main trunk of a 2 m high *Ochna pulchra* showed the maximum rate of increase in early November, but with a slower but steady increase right through until April.

Some of the radial measurements showed different timing of maximal growth on opposite sides of the same trunk. The common excentricity of radial growth found in such stems may be related to this. A separate survey of radial growth excentricity from the destructive sampling of the previous season has shown that excentric radial growth is often pronounced and frequent in the larger individuals of all the species studied thus far.

Tew and Cresswell (1976) also conducted studies in the allometric relationships of leaf area to branch diameter in *Ochna pulchra*, *Burkea africana* and *Terminalia sericea*.

The regression of leaf area to the diameter of the trunk just below the node at the origin of the branch was tested. The regression for each species and the combined data showed high levels of significance. A high level of correlation was shown when leaf number was plotted in place of leaf area. The data were for the period of maximum leaf development only.

The three tree species were recorded in each of 200 25 m^2 quadrats. The diameter of the trunk at the first node was measured, squared, transformed to $\log_{10}$ of the value, and summed for each species, and an average sum per meter square was calculated. The LAI was then calculated from the regression analyses as described above.

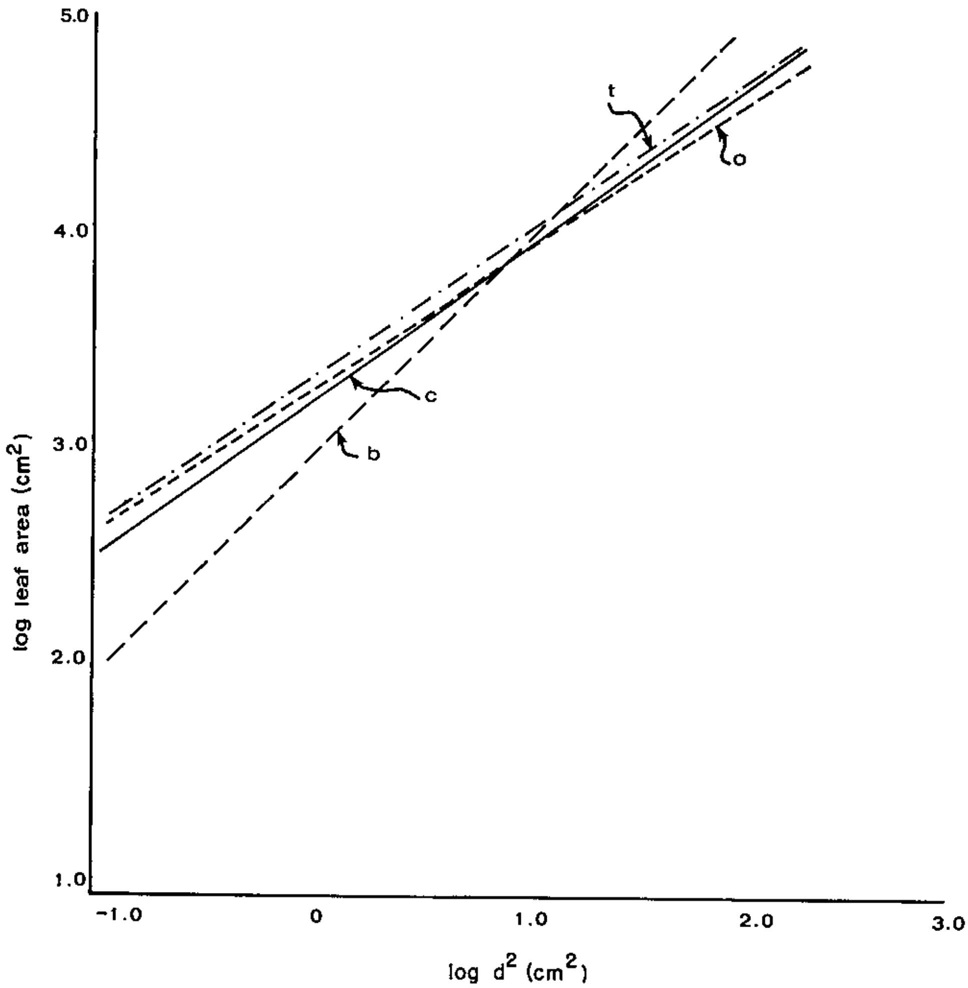

Figure 5. *Regressions of log of the leaf area and the log of the stem diameter² (just below node). (From Tew and Cresswell 1976).*

The allometric regressions of the log of the leaf area to the log of the diameter squared of the branch below the node for *Terminalia sericea* and *Ochna pulchra* are very similar (Figure 5). The line for *Burkea africana* is steeper than those for the other two species. A combination of data results in a common line for all the species which is very close to the line for the two species *Ochna pulchra* and *Terminalia sericea*. The regression of the log of the leaf number and the log of the diameter squared shows *Burkea africana* and *Terminalia sericea* to be similar, with the line for *Ochna pulchra* being steeper.

Sums of the log of the diameter squared of the trunk just below the first node per unit ground area are given in Table 6. The LAI was then calculated from the allometric regression lines for each species individually and from the common regression line (Table 7).

Table 6. Sum of log $d^2 \cdot m^{-2}$ for *Terminalia sericea, Burkea africana* and *Ochna pulchra*. Data from Tew and Cresswell (1976).

Species	$\Sigma \log d^2 \cdot m^{-2}$
T sericea	0,067
B africana	0,114
O pulchra	1,212

Attempts to measure net primary production of woody plants by gas exchange techniques were unsuccessful due to instrumentational problems (Tew and Cresswell 1976).

Table 7. Leaf area indices determined from allometric regressions for *Terminalia sericea, Burkea africana* and *Ochna pulchra*. LAI calculated from individual species regressions, LAI' calculated from combined regression line. Data from Tew and Cresswell (1976).

Species	L A I	L A I
T sericea	0,282	0,219
B africana	0,181	0,214
O pulchra	0,301	0,272
Total	0,764	0,731

Below ground standing crop and production

Estimation of the underground standing crop of herbaceous and woody plant roots were made from soil cores extracted by means of a specially developed soilbore (Van Wyk 1976). The cores were 8 cm in diameter and from 80 to 100 cm depth dependent on depth of the parent rock. Cores were collected monthly during summer and six-weekly during winter. One hundred cores were collected at each sampling date, 50 from under trees on alternate dates, otherwise all samples were collected in open areas within the study plot utilized in the herbaceous above ground standing crop studies of Grunow (1976).

Cores were divided into 20 cm sections and washed in a rootwasher to separate roots from soil. The coarser roots of each section were hand separated into woody and grass roots. This was only done for roots with a diameter of more than 1 cm. Finer roots were all lumped. Sub-samples were extracted and microscopically investigated to determine the ratio of woody and non-woody roots.

Live/dead ratio of grass roots was determined by means of the TTC-method (Knievel 1973). The method was not wholly satisfactory because some of the finer roots disintegrated during preparation and because formasan absorption rates varied between samples. Results for the period November 1975 to July 1976 give a total underground root standing crop of 860 gm^{-2} surface area. Grass roots account for roughly one third of this mass (Table 8). During winter approximately 15 percent of the grass roots were dead. No estimate of root production, either for grasses or woody plants, could be determined from currently available data.

Translocation

Preliminary studies in the translocation and distribution of photosynthetic products in *Eragrostis pallens* were undertaken during the review period (Tew et al 1976). Leaves of *E pallens* were enclosed in a circular glass chamber through which $^{14}CO_2$ was passed at a rate of 40 lh^{-1} for a maximum period of 30 minutes. The $^{14}CO_2$ was prepared from 25 m Ci of barium carbonate (60 m Ci m $mole^{-1}$). The end concentration of CO_2 was between 300 and 315 vpm.

Tew et al (1976) report that $^{14}CO_2$ incorporated into the leaves of *E pallens* was rapidly translocated into the root base, stubble and the unlabelled leaves of the same tuft over a period of 6 hours. After a week of translocation the root tips constituted the major sink, with little activity remaining in the above ground tuft. The old inflorescence stalk and the standing "dead" material were minor sinks at certain periods during the growing season, and may function as temporary storage sites. The storage of photosynthates in these aerial organs suggest a loss term in the net primary production equation if these were removed by grazing or fire. The rhizosphere also became labelled before the peak in the rate of translocation to the root tips suggesting a probable requirement for organic carbon in the rhizosphere prior to root growth. The seasonal effect is that the sinks for the photosynthetically derived carbon varied in capacity as well as there being different sites at different times, as shown by the high level in the green inflorescence stalks during their initiation.

Table 8. Dry mass in gm^{-2} of roots extracted from soil cores during the period November 1975 to July 1976. Data from Van Wyk (1976).

	grass roots	woody roots	total
1975:11:16 open	162,875	457,288	620,160
1976:01:04 open and under trees	353,532	521,360	874,892
1976:01:26 open	228,608	452,800	681,408
1976:02:17 open and under trees	254,940	736,018	990,958
1976:05:20 open	237,790	634,296	872,086
1976:05:20 open and under trees	426,180	560,840	987,020
1976:07:05 open	229,534	761,700	991,234
Average	270,494	589,186	859,680

CONSUMERS

Population dynamics and biomass assessment

A primary objective of the pilot phase of the project was the determination of mean and seasonal biomasses and rates of population and biomass change in all consumer species. As a first approximation the consumer compartment was sub-divided into eleven groups - cattle, impala, other large mammalian herbivores (including kudu, duiker, warthog, steenbok), small mammals (mainly omnivores), reptiles, amphibia, insectivorous birds, omniverous birds (including seed-eaters) raptors, woody plant feeding invertebrates and herbaceous plant feeding invertebrates. Large carnivores are insignificant within the study area.

Attempts to determine the overall mean biomass of these groups met with varying success. Data for cattle and impala were probably within 10 per cent of the population mean, but confidence limits for the other groups were wide. Much of the information collected awaits analysis and at this stage only a brief outline of the main findings is possible.

Cattle

In order to maintain the grazing management system practised on Nylsvley during previous decades, cattle were introduced into the study area during the midsummer for the four months January through April. On 1976:01:01, a mixed herd of 156 crossbred cattle were brought into the study area, with

Table 9. List of indigenous mammals recorded in the study area, Nylsvley. (From Temby 1976, Jacobsen 1976).

Order Insectivora	
Elephantulus brachyrynchus	Shortsnouted elephant shrew
Erinaceus frontalis	Hedgehog
Crocidura bicolor	Tiny musk shrew
Crocidura cyanea	Reddish-grey musk shrew
Order Chiroptera	
Eptesicus capensis	Cape serotine bat
Nycterus thebaica	Egyptian slit-faced bat
Order Primates	
Galago senegalensis	Lesser galago
Cercopitheous aethiops	Vervet monkey
Order Carnivora	
Proteles cristatus	Aardwolf
Hyaena brunnea	Brown hyaena
Canis mesomelas	Black-backed jackal
Ictonyx striatus	Polecat
Mellivora capensis	Honey badger
Genetta genetta	Small spotted genet
Paracynictis selousi	Selous' mongoose
Herpestes sanguineus	Slender mongoose
Ichneumia albicauda	White-tailed mongoose
Atilax paludinosus	Water mongoose
Mungos mungo	Banded mongoose
Order Tubulidentata	
Orycteropus afer	Aardvark
Order Lagomorpha	
Pronolagus crassicaudatus	Red rock hare
Lepus saxatilus	Scrub hare
Order Rodentia	
Cryptomys hottentotus	Common mole-rat
Hystrix africae-australis	Porcupine

Table 9. Continued.

Pedetes capensis	Spring hare
Graphiurus murinus	Dormouse
Paraxerus cepapi	Bush squirrel
Otomys angoniensis	Angoni vlei rat
Lemniscomys griselda	Single-striped mouse
Rhabdomys pumilio	Four-striped mouse
Leggada minutoides	Pygmy mouse
Praomys natalensis	Multimammate mouse
Aethomys chrysophilus	Red veld rat
A namaquensis	Namaqua rock rat
Tatera leucogaster	Bushveld gerbil
T brantsi	Brant's gerbil
Saccostomus campestris	Pouched mouse
Dendromus melanotis	Grey pygmy climbing mouse
D mystacalis	Lesser climbing mouse
Steatomys pratensis	Fat mouse
Order Artiodactyla	
Phacochoerus aethiopicus	Warthog
Tragelaphus strepsiceros	Kudu
Sylvicapra grimmia	Grey duiker
Redunca arundinum	Reedbuck
Aepyceros melampus	Impala
Raphicerus campestris	Steenbok

58 more being added to the herd on 1976:02:05. The herd was removed on 1976:05:03. A total of 13 cattle died while in the study area, due mainly to heartwater but also due to poisoning by *Dichapetalum cymosum* (Zimmerman 1976). The mean cattle biomass (wet-mass) during this period ranged from 56,20 kg ha^{-1} on 1976:02:11 to 63,94 kg ha^{-1} on 1076:04:21, slightly more than one half of the biomass carried during the previous season when overgrazing occurred in several areas (Grunow 1976, pers comm).

Impala and other indigenous large mammals

A total of 46 indigenous mammal species have thus far been recorded in the study area (Table 9, Jacobsen 1976, Temby 1976). Only two of these (impala and kudu) make a substantial contribution to the total mammalian biomass within the study area, while even these species formed only 14 percent of the probable vertebrate biomass in the four months during which cattle utilized the study area (Monro 1976 pers comm).

A series of ground counts of larger mammals was begun in December 1975 and has been continued at approximately six-weekly intervals. Kingston (1976) describes the methods adopted and the results of the first four counts which are presented in Table 10. Subsequent surveys indicate that the overall larger mammal biomass (excluding cattle) would approximate 8,0 kg ha^{-1} during the 1976 winter (Monro 1976 pers comm).

Table 10. Total numbers of mammals counted during ground censuses, Nylsvley study area. From Kingston (1976).

	17/12/75	16/2/76*	29/3/76	18/5/76	Mean	Mean per ha
Cattle	0	194	200	20	103,5	0,134
Impala	126	71	127	103	106,8	0,138
Kudu	10	7	13	24	13,5	0,017
Warthog	8	34	16	5	15,8	0,020
Duiker	13	36	16	9	18,5	0,024
Steenbok	3	18	7	14	16,0	0,021
Reedbok	2	2	1	0	1,3	0,002
Jackal	0	4	0	0	-	-
Vervet	0	4	1	0	-	-
Banded mongoose	0	1	20	0	-	-

* Observers spaced at 50 m intervals instead of 100 m

The distribution, movement and general behaviour of impala, kudu and warthog was studied intermittently from May 1975 through May 1976 (Carr 1976). In all these species a distinct pattern of movement to and from the study area at the beginning and end of the rains was noted, as was a preference by all species for *Acacia* savanna as opposed to *Burkea* savanna.

Carr (1976) noted that *Acacia* savanna comprises only 82 ha of Camps 1, 2 and 3, which have a combined total area of 571 ha. Impala were more or less evenly distributed over these Camps during the wet season, but began to centre their activities around the various *Acacia* patches as the dry season approached. During the latter part of winter the majority of the study area impala population moved to the *Acacia* savanna in other parts of the Reserve, returning to the fire-breaks surrounding the study area during the pre-spring flush and to the study area itself during the rains.

Small mammals

Attempts to estimate the seasonal and spatial variation in small mammal biomass have been unsuccessful due to the extremely low populations of all species (Bragg 1975, Temby 1976). *Burkea* savanna proved particularly depauperate, only 5 animals were captured in 2 100 trap nights using a 10 x 10 grid of 100 Sherman traps during March 1976 (Temby 1976).

Both *Acacia* and *Diplorhynchus* savanna types have much richer small mammal faunas; a total of 8 animals of 5 species were caught in 100 traps on one night in the former and 6 animals in 50 traps in the latter habitat on particularly successful occasions (Temby 1976 pers comm). In all areas however, recapture results have been inadequate for biomass or home range determinations. Large-scale fluctuations in population would nevertheless be detected should they occur. Hares and spring-hares have been counted using night strip census techniques and preliminary results suggest that the latter species may be an important constituent of the consumer component within *Acacia* savanna.

Reptiles and amphibians

The survey of the reptile and amphibian population initiated by Jacobsen (1975a, 1975b) continues to provide details on population size, structure and seasonal fluctuations. By the end of May 1976 a total of 1 348 lizards of 16 species, 277 snakes of 21 species and 1 218 frogs of 11 species had been captured, measured, marked and released (Jacobsen 1976 pers comm). Recaptures totalled 388 lizards, 41 snakes and 38 frogs.

Preliminary analyses of the initial results for May through November 1975 are presented by Jacobsen (1975b). The most abundant reptile was the common dwarf gecko, *Lygodactylus capensis*, 270 specimens having been collected during the initial study. Schnabel population estimates of this species range from 195 to 262 animals ha^{-1} with males constituting 74% of captures. The animals generally restrict their movements to within a radius of 5 metres of their arboreal habitat. These geckos live for at least two years, reaching sexual maturity at 8 months and breeding throughout the year.

The most frequently captured lizard was the Cape rough-scaled sand lizard *Ichnotropis capensis*, 336 animals having been caught during the first five months of study. A sex ratio of 100 males to 61 females was possibly due to trapping bias. Recaptures for this species were always from the trap in which they were originally caught, indicating a limited home range in the vicinity of the trap. Schnabel index estimates indicate a population of 6,9 to 7,8 animals ha^{-1} from May to October and 11,4 ha^{-1} in November. Eggs were laid in November and December, hatching in January and February. The species attains sexual maturity at 10 months and dies within six months.

The most commonly captured snakes were the olive grass snake *Psammophis sibilans*, vine snake *Thelotornis capensis* and redlipped snake *Crotaphopeltis hotamboeia*, of which 61, 18 and 17 individuals were captured (Jacobsen 1975b). The olive grass snake's population approximated 3,7 ha^{-1} during September and October 1975. Vine snakes were seldom captured in traps, but were frequently caught by hand when found on *Grewia flavescens* shrubs, apparently their favourite habitat. Most snake species increased in numbers during September and October, dropping rapidly in November. Jacobsen (1975b) suggests that the increase may correlate with increased activity during the mating season and therefore greater chance of being seen and captured.

Large numbers of frogs were found to aestivate in the *Burkea* savanna, emerging only during and after periods of rain (Jacobsen 1975b). Of the 338 specimens of seven species captured, marked and released during September and October 1975, 191 were running frogs *Kassina senegalensis*, 71 were leopard toads *Bufo regularis* and 54 were common blaasops *Breviceps m adspersus*. Although no movement patterns had been determined from the initial study, Jacobsen (1975b) suspects that the frogs move out of the *Burkea* savanna to the wetlands during rains and return to aestivate at the onset of the cold season.

Birds

Tarboton (1971, 1975, 1976b) has described the avifaunal population of the Nylsvley area in general and the *Burkea* savanna in particular. Details of the composition and biomass of the 152 species recorded in *Burkea* savanna during the 1974-1975 period are given in Tarboton (1975) and summarized in Hirst (1975).

In the initial general survey of the avifauna of *Burkea* savanna, the black tit *Parus niger* was found to be a dominant resident insectivore. It was thus selected for a more intensive study aimed at relating its population characteristics to biotic and abiotic variables in the ecosystem. Tarboton (1976a) reports progress on the first six months study, December 1975 to May 1976. The aims of this study were to monitor black tit numbers through the year and relate where possible changes to productivity/mortality and immigration/emigration, to monitor changes in age structure, social structure and spacing in the population, and to quantify the foraging strategy and food composition through the year and relate this to food availability.

The black tit population was found to comprise about 45 birds in the 400 ha study area. This population was dispersed in groups or pairs which defended permanent territories against conspecifics. Groups were probably the result of the imbalanced sex ratio in the population (1,7 males : 1,0 females) where surplus males remained attached to the parental group (Tarboton 1976a).

Invertebrates

A general survey of the arthropod fauna of the *Burkea* savanna commenced in 1974 and over 1 000 species identified from the 7 000 specimens so far collected (Holm 1976). Although still incomplete, the results give a good indication of the proportional diversity of families and a general measure of species abundance. Lepidoptera and Coleoptera accounted for one third of all species while Diptera and Hymenoptera were poorly represented due possibly to sampling bias. Orthoptera were well represented, while most small orders were low in diversity, except Dyctioptera and Odonata. Heteroptera and Homoptera were found to be extremely diverse.

Amongst non-insect arthropods, the spiders were extremely well represented and Holm (1976) suggests that they would account for far above 50% of the insect predator biomass.

The following families were found to be best represented within the most important trophic groups :

Sap-suckers	:	Cicadellidae, Pentatomidae.
Leaf-eaters	:	Noctuidae, Chrysomelidae, Curculionidae and Scarabaeidae (sub-fam Melolonthinae

and Rutelinae). Probably also Acrididae and Grillidae on grass.

Predators : Most important : Arrachnoidea. Also Carabidae, Mantidae, Formicidae and probably other Hymenoptera, followed by predatious Diptera (mainly Asilidae) and Odonata.

Decomposers : (timber) Cerambycidae (probably also Isoptera)
(dung) Scarabaeidae
(other) Tenebrionidae, Formicidae.

Woody plant feeding invertebrates

Following the general survey of the arthropod fauna in *Burkea* savanna a study was initiated on the seasonal fluctuation of biomass, host selection and consumption rates of leaf eating insects within the woody plant component. Preliminary results, for the period September 1975 through April 1976, are presented by Holm, Kirsten and Scholtz (1976), Scholtz (1976a, 1976b) and Levey (1976).

Beating of branches was carried out at monthly intervals to determine the monthly biomass of foliage feeding larvae on the dominant woody plants. Fifty branches each of *Terminalia sericea, Burkea africana* and *Ochna pulchra* were beaten, while ten branches each of *Vitex rehmannii, Combretum molle, Grewia flavescens, Stychnos pungens* and *Dombeya rotundifolia* were sampled. Feeding experiments were conducted in the field. Larvae of a known size were released in chiffon bags placed over branchlets with a known number of leaves. Larvae were measured weekly to determine growth and the number of leaves eaten were counted and recorded. Faeces were removed from the bags, dried and their mass determined.

The results obtained included monthly standing crop, consumption and defaecation rates, secondary production, loss of photosynthetic area and energy fixed in larvae and available to the next trophic level.

Terminalia sericea was found to carry about twice as many species of leaf eaters than any other host plant, while diversity in *Grewia flavescens* and *Strychnos pungens* was low. *Terminalia sericea* has about equal numbers of Lepidoptera and Coleoptera species while in *Burkea africana* the difference in these orders was also relatively small. In most other host plants the Coleoptera species far outnumbered the Lepidoptera. *Vitex rehmannii* and *Strychnos pungens* carried about twice as many sap-sucking as beetle species. Sap-suckers outnumbered Lepidoptera considerably in *Burkea africana, Ochna pulchra* and *Dombeya rotundifolia* and even more markedly in *Strychnos pungens* and *Vitex rehmannii*, while the difference was small in *Terminalia sericea*.

Numerical abundance did not coincide with diversity. Most host plants had individual loads of about 150 insects, *Dombeya rotundifolia* being the exception with as many as 630, while *Grewia flavescens* carried an average of only 35. Numbers were more equally spread among host plants than were species, for while Coleoptera and especially the sap-suckers far outnumber the Lepidoptera in species diversity, these differences were absent in terms of numbers of individuals, and in the sap-suckers the situation was reversed since they were generally lowest in numbers of individuals.

Biomass estimates were based on monthly branch beating samples of 8 selected host plants. The mass was estimated per insect species from length/mass tables while biomass per hectare was derived from leaf area indexes and structural data drawn from Tew and Cresswell (1976) and Lubke et al (1975). The quantitative methods and statistical tests applied to these data are described by Scholtz (1976b). The results showed that Coleoptera and Lepidoptera were approximately equal in biomass while sap-suckers totalled three times the biomass of either of these two orders.

The average standing crop of all phytophagus insects throughout the year was about 135 gm ha^{-1} with the highest average of about 300 gm ha^{-1} in March and the lowest about 60 gm ha^{-1} in August (Holm, Kirsten and Scholtz 1976).

Nearly one third of the Coleoptera biomass was concentrated on *Dombeya rotundifolia* while *Grewia flavescens* had the least. Lepidoptera biomass was about equal on the three dominant host plants, followed by *Dombeya rotundifolia*. *Grewia flavescens* and *Combretum molle* were completely free of Lepidoptera. The sap-suckers comprised one third of the biomass dependent on *Strychnos pungens* while *Ochna pulchra, Terminalia sericea, Combretum molle* and *Vitex rehmannii* all carried high loads with *Dombeya rotundifolia, Grewia flavescens* and *Burkea africana* carrying low loads. *Strychnos pungens* supported the highest overall biomass of leaf-eating insects, followed by *Terminalia sericea.*

Fluctuations in biomass for all host plants and groups of feeders showed marked peaks and troughs. Fluctuations in biomass on *Ochna pulchra* and *Burkea africana* paralleled one another.

Herbacious plant feeding invertebrates

Preliminary studies in this component were restricted to grass-eating insects. Gandar (1976) reports on pilot surveys conducted in three *Burkea* savanna communities during March and April 1976. The three communities were dominated by the grasses *Digitaria eriantha - Eragrostis pallens, Hyperthelia dissoluta - Eragrostis lehmanniana* and *Eragrostis pallens - Diheteropogon amplectens.*

Grasshoppers were found to contribute at least half of the biomass of grass-eating insects. Local and ephemeral outbreaks of, for instance, the beetle *Astylus atromaculatus* (Coleoptera), aphids, caterpillars and mites occasionally overshadowed the grasshoppers.

Grasshopper densities in mid-March and mid-April ranged from 1,79 to 7,76 m^{-2} and 1,71 to 4,44 m^{-2} respectively. *Pnorisa squalus* was the commonest grasshopper in all sample areas, with *Pseudoarchyptera carvalhoi, Oedaleus carvalhoi* and *Orthochtha dasychnemis* the most abundant co-dominants in the three areas. Species diversity ranged from eight species in the *Eragrostis-Diheteropogon* community to 18 species in the *Hyperthelia-Eragrostis* community.

Social insects

Kirsten (1976) described studies in the quantitative ecology of social Hymenoptera. These studies included the estimation of colony densities, biomass per colony, food intake per colony and the foraging activity of the dominant social Hymenoptera.

Colony density estimates for the Formicidae ranged from 0,224 to 0,602 colonies m^{-2} with a mean density of 0,408 colonies m^{-2}. Wasp colonies ranged from 0,7 colonies ha^{-1} during October and December 1975 but dropped to 0,3 colonies ha^{-1} during January and February when four colonies were destroyed by *Hoplostomo fuligeneus*. Bees in the study area were of very low density with only 0,03 colonies ha^{-1} recorded.

Estimates of ant density were made using capture/recapture methods in which large sub-samples of ants from four colonies were marked with P^{32} isotopes and recaptured after a period of 5 to 6 days. The results of these estimates are presented in Table 11. Density and biomass data for bees and wasps are not yet available.

Table 11. Numbers (m^{-2} and biomass (in g ha^{-1}) of foraging ants, January to April 1976. Data from Kirsten (1976).

	January	February	March	April
Crematogaster				
numbers	10 000	33 000	33 000	46 000
biomass	7,1	23,4	23,4	32,7
Camponotus				
numbers	30 000	30 000	33 000	23 000
biomass	254,4	254,4	279,4	195,1
Size group 1				
numbers	70 000	133 000	190 000	193 000
biomass	16,1	30,6	43,7	44,4
Size group 2				
numbers	103 000	130 000	253 000	260 000
biomass	8,2	10,4	20,2	20,8
Total				
numbers	213 000	326 000	509 000	522 000
biomass	285,8	318,8	366,7	239,0

A total of 48 species of ants were collected and identified of which the dominant species are seven *Crematogaster* spp, four *Camponotus* spp and seven *Pheidole* spp.

Three wasp species were recorded; *Balenogaster junceus, Polistes marginalis* and *Rhopalina capensis*. The dominant species was *P marginalis*.

Feeding behaviour

Parallel to attempts to determine the seasonal and spatial variation of biomass and population size of the consumer component, studies were initiated in the feeding behaviour of several groups. The principal aim was the determination of the overall impact of consumers on primary producers as a first step towards obtaining an understanding of energy conversion processes and efficiency within *Burkea* savanna.

Cattle

A detailed study in the feeding behaviour of Afrikander steers was begun in May 1976 (Zimmerman 1976). Preliminary results indicate that cattle on Nylsvley have a marked preference for the forage available in *Acacia* savanna compared with that of *Burkea* savanna. Furthermore, the study group of Afrikaner steers spent 53,7% of their grazing time feeding under trees in vegetation with a mean canopy cover of 32,5%. Zimmerman (1976) suggests that as the cattle did not appear to be seeking shade, they were probably seeking out *Panicum maximum* growing under the trees.

During continuous 24 hour behavioural observations in May the steers were noted to spend 10 hours 25 minutes feeding, compared with 8 hours 42 minutes in March. Furthermore, the grazing time : rumenating time ratio in May was 1:1,57 compared with 1:1,93 and 1:1,92 in March, suggesting that the digestibility of the plants was dropping.

Using fistulated steers, Zimmerman (1976) found that the dry matter bite size of animals eating *Panicum maximum* was 0,53 grams/bite. Total intake per animal per day had not been determined, but initial studies gave a faecal output ranging from 2,4 to 2,7 kg dry matter for steers averaging 250 kg live mass. Steers of similar live mass were gaining approximately 0,5 kg per day.

During the period 1976:03:04 to 1976:05:01, the average water consumption for the whole cattle herd was approximately 10,4 litres per animal per day. Daily water consumption showed no correlation with humidity but did correlate positively with temperature (Zimmerman 1976).

Impala

Field observations of impala feeding behaviour were extremely difficult due to the highly nervous state of animals in the study area. A preliminary study of grazing preferences was nevertheless undertaken in the 2,2 ha enclosure in which 13 two-year-old impala were held prior to release in the study area. The relative frequency of occurrence of the 10 most abundant herbaceous species in the enclosure and the average amounts of these removed, was estimated at weekly intervals during a six week period. The results of the survey (Table 12) indicate that *Panicum maximum* and *Digitaria eriantha* were the most preferred grasses and that *Solanum panduraeforme* and *Justicia anagaloides* were frequently eaten forbs.

The microscopic analysis of impala rumen contents collected from animals shot in the study area during 1975 has commenced. A key to the epidermal patterns of all grasses thus far collected in the study area is being compiled and will be used in this and other studies on the feeding preferences of consumer species.

Other mammals

Observations on the feeding behaviour and consumption of other mammal species were limited to occasional sightings and do not merit comment at this stage.

Table 12. Relative frequency of occurrence of herbaceous plants in a 2,2 ha enclosure and amount of above ground biomass removed by 13 impala during a six week study period. Data from Monro (1976).

	Observer	1	2	1	1	2	2
Species	Relative freq %	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6
Digitaria eriantha	32,8	12,4	14,3	30,4	18,8	17,6	32,3
Panicum maximum	32,7	15,1	13,8	33,0	40,1	30,6	50,5
Eragrostis spp	11,5	3,2	5,5	13,3	8,4	4,3	13,1
Sporobolus fimbriatus	6,4	13,5	3,2	26,4	18,6	8,2	21,1
Mosdena leptostachys	4,5	0	0,3	0	0	0,3	6,0
Justicia anagaloides	4,2	8,1	13,4	32,8	33,2	17,6	54,8
Aristida congesta	3,3	4,3	0,7	1,7	0	1,7	7,2
Cynodon dactylon	2,0	4,0	9,6	18,6	7,1	20,6	39,3
Solanum panduraeforme	1,5	27,8	24,9	31,3	22,8	76,9	95,0
Stipagrostis uniplumus	1,2	0	0,7	0	0	0,9	1,5

Reptiles and amphibians

A large number of stomach contents of the more abundant reptiles and amphibians have been collected (Jacobsen 1975b) but await analysis.

Birds

A detailed study in the ecology of the black tit *Parus niger* was initiated in 1976 (Tarboton 1976). Preliminary results indicate that black tits were wholly insectivorous during December to May and that caterpillars formed 92% of their diet. Each bird ate an estimated 68 food objects per day or 50% of its body weight. Groups travelled about 10 km per day about their territories, spending 95% of their time searching for food, and engaged in territory disputes once every two hours. Most food was sought, and found, in foliage (respectively 56% and 68%). *Terminalia sericea* and *Burkea africana* were the main tree species in their feeding ecology, accounting for 82% of their search effort and 53% of their success. Monthly fluctuations in the tit's utilization of different tree species probably reflect changes in prey density on those trees.

Invertebrates

Consumption estimates for the main insect groups were extrapolated from biomass using various conversion factors (Holm, Kirsten and Scholtz 1976, Scholtz 1976a). For Coleoptera the consumption ratio of 0,72 $g.g^{-1}d^{-1}$ (Crossley 1966) was used while for the Lepidoptera a factor of 1 $g.g^{-1}d^{-1}$ was used. Consumption data for sap suckers have not yet been determined.

It appears that the Lepidoptera are responsible for about two thirds of the leaf consumption on trees with as much as three quarters in the case of *Ochna pulchra*. The leaf consumption estimates provided by Holm, Kirsten and Scholtz (1976) approximate 1,7 $gm^{-2}yr^{-1}$ for the leaf eaters on woody plants. This figure approximates 2% of the total leaf production of roughly 800 kg $ha^{-1}yr^{-1}$ (Rutherford 1976 pers comm). The woody plant leaf consumption estimate may rise to three or four percent if groups not covered by the techniques utilized are included. It may consequently be assumed that most of the leaf production goes to litter.

The effect of feeding on the woody vegetation by lepidopteran larvae and the monthly standing crop changes in lepidopteran larvae was studied during the period September 1975 to April 1976 (Scholtz 1976a, 1976b). Fourteen species of Lepidoptera were reared on *Terminalia sericea*, eleven of which were foliage feeders. The remaining three species were galligenous and were probably fairly important as controlling factors of primary production. Three foliage feeding species were regarded as dominant. They were *Maurilia arcuata* (Noctuidae), *Euproctis fasciata* (Lymantriidae), and an undescribed noctuid.

Six species were reared on *Burkea africana* of which five were foliage feeders. The sixth species was an undescribed bud borer. The larvae of this species were responsible for the destruction, in spring, of 67% of the buds on trees under two metres height and 16% on trees taller than two metres (Scholtz 1976).

Ochna pulchra was the host of four species of Lepidoptera of which one reached high peaks and defoliated many small trees. *Dombeya rotundifolia, Vitex rehmannii* and *Strychnos innocua* were host to one important species each whereas *Grewia flavescens* and *Combretum molle* had no significant larvae associated with them.

The importance of foliage feeders may be underrated by looking only at figures of gross consumption. Feeding occurs in marked peaks and even at the low averages indicated above, some host plants such as *Burkea africana* may occasionally be completely denuded with a consequent second flush, which in turn may have a whole chain of ecological consequences (Scholtz 1976a). Moreover, some of the primary feeders on woody vegetation do not only remove biomass and photosynthetic area, but inhibit the growth of the host plant to a significant degree. These insects include bud borers, stem borers and gall formers.

Information on the feeding behaviour of grass- and forb-eating invertebrates was not available for this review but studies are currently in progress.

Limiting factors

Parasites

Internal and external parasitism plays a limiting role in domestic livestock production in many parts of South Africa. A survey was initiated in 1975 (Horak 1975, 1976a, 1976b; Horak, Londt and Stewart 1976) of parasites in or on impala and cattle utilizing the study area, their numbers and seasonal incidence and their possible role as limiting factors.

Two to four impala were culled each month from February 1975 until February 1976 and total parasite counts done on each of these animals.

At least 16 helminth species (Table 13) were recovered from impala but, with the exception of the animals culled during November and December 1975, adult worm burdens never reached levels that could be considered pathogenic. Burdens of over-wintering immature worms exceeded 10 000 in individual animals culled from May to September 1975 (Horak 1976a).

Five of the helminth species recovered (*Haemonchus placei, Trichostrongylus axei, T colubriformis, T falculatus* and *Cooperia pectinata*), are parasites that are normally encountered in cattle but the present results suggest that they are also well adapted to impala.

At least six species of ticks and four species of lice were recovered from the impala. The ticks are the same as those encountered on cattle, while the lice are host-specific. *Amblyomma hebraeum*, the tick which transmits heartwater, and *Hyalomma truncatum*, the vector of sweating sickness, appear not to find impala suitable hosts. Large burdens of immature ticks were recovered from the impala culled from April to July and from September to November 1975. It would seem that impala are efficient hosts in maintaining immature tick populations in the project area (Horak 1976, Horak et al 1976).

At 28 day intervals during the four month period that cattle utilized the study area, two calves were treated with a multiple therapeutic dose of an anthelminthic, returned to the herd and slaughtered 29 days later. Prior to slaughter the calves were not dipped for varying periods of time.

Ten species of helminths were recovered from these calves. *Impalaia tuberculata* and *Cooperioides hamiltoni*, both parasites of impala, were recovered in very small numbers from some of the calves. The only external parasites recovered were six species of ticks (Table 13).

Haemonchus placei, Cooperia pectinata and *Trichostrongylus* spp found most cattle and impala suitable hosts, but little danger appeared to exist of cross transmission of other helminths between the two species of large mammals. The ticks *Rhipicephalus appendiculatus* and *R evertsi* appeared equally well adapted to cattle and impala.

Five species of ticks were recovered from calves sampled at two weekly intervals. Adult ticks were generally present in peak numbers during

Table 13. Internal and external parasites recovered from cattle and impala in the Nylsvley study area, February 1975 through February 1976. Data derived from Horak (1976a, 1976b).

Internal parasites	Impala	Cattle
Trematoda		
Fasciola gigantica	x	
Paramphistomum sp	x	x
Cestoda		
Moniezia sp	x	
Nematoda		
Bigalkenema sabie	x	
Cooperia pectinata	x	x
C punctata		x
Cooperioides hamiltoni	x	x
C hepaticae	x	
Gongylonema pulchrum	x	
Haemonchus placei	x	x
Impalaia tuberculata	x	x
Oesophagostomum radiatum		x
O columbianum	x	
Strongyloides sp	x	
Trichostrongylus axei	x	x
T colubriformis	x	x
T falculatus	x	x
Trichuris sp	x	
External parasites		
Acarina		
Amblyomma hebraeum	x	x
Boophilus sp	x	
Hyalomma rufipes	x	x
H truncatum		x
Ixodes sp	x	
Rhipicephalus appendiculatus	x	x
R evertsi	x	x
R simus		x
Phthiraptera		
Damalinia aepycerus	x	
D elongata	x	
Linognathus nevelli	x	
L sp	x	
Diptera		
Lipoptena sp	x	

February declining rapidly thereafter. An exception is the red-legged tick *Rhipicephalus evertsi* which remains present albeit in reduced numbers. Immature brown ear ticks *R appendiculatus*, showed a rapid increase in numbers from 1976:04:21 onward. Very few other immature ticks were encountered.

A study group of 150 cattle were examined for clinical signs of tick borne disease and for maggot infestation when they were mass measured at two weekly intervals during the period January through April 1976. Blood smears were examined for antibodies to *Anaplasma* spp (gall sickness) and for *Babesia* spp (red water) in February and early May. Of the 150 animals examined, four probably died due to heartwater, two further exhibited symptoms of heartwater and lost a mass gain equivalent to 8 to 10 weeks growth, four animals exhibited symptoms of sweating sickness and lost an equivalent of six weeks growth while 8 animals were infected with maggots of the fly *Chrysomyia bezziana* and lost an equivalent of four weeks growth (Horak, Londt and Stewart 1976).

The acquisition of fairly large numbers of helminth parasites by the drenched calves exposed for a period of 28 days in the project area required that the effects of these parasites on productivity be investigated. The study group of 150 cattle were divided into three equal groups. One group was treated once with an anthelminthic, another at two-weekly intervals and a third was not treated at all. The animals were mass measured at two weekly intervals and faecal worm egg counts were done during a period of three months. At the conclusion, the group treated once had gained a mean of 35,6 kg (16,9% of original body weight), that treated two-weekly 37,0 kg (17,3%) and that left untreated 37,9 kg (17,1%). The egg counts of the first group fell to zero after treatment but rose gradually thereafter, those of the second remained virtually negative after treatment while those of the untreated group rose slightly and then dropped to the original level.

It would appear that the level of helminth infestation had no effect on gain in mass over a three month period.

Dichapetalum cymosum (*gifblaar*)

The importance of this toxic woody geophyte as a limiting factor to cattle production in *Burkea* savanna was discussed by Hirst (1975) in the 1974/75 progress report. Grobbelaar and Rösch (1976b) have continued studies in the seasonal variation in the monofluoroacetate content of leaves, phenology and methods of eliminating the species with various herbicides. The fluctuation in the concentration of monoflouroacetate in *Dichapetalum* leaves during the 1975-1976 season paralleled that of the previous year, both in levels and timing (Grobbelaar 1976 pers comm). The effects of the herbicide treatments have not yet been determined.

DECOMPOSERS AND REDUCERS

Litter, carcass and dung production

Detailed information on the seasonal and spatial distribution of plant litter, animal carcass and dung production in *Burkea* savanna is not yet available. Rough estimates indicate an end-of-season standing crop of plant litter of between 3 to 30 tonnes ha^{-1} in open and closed sub-habitats respectively, while Hirst (1975) estimated a total dry mass cattle dung input of 20 to 24 gm^{-2}.

Studies on woody plant litter input and decomposition rates will be initiated during the 1976/77 season. Litter fall will be measured with 50 x 50 cm wire mesh litter baskets distributed at random through a 0,8 ha study plot. Measurements will be made weekly or bi-weekly of total litter input, sub-divided into leaves, leaf scales, twigs, branches etc at species level.

Data are available for two years on seasonal fluctuation in herbaceous litter standing crop (Grunow 1975, 1976 - Table 3). An attempt will be made to measure nett herbaceous litter production during the 1976-77 season.

The rate of mass loss of leaf samples of seven species will be determined at 3 and 5 weekly intervals. The samples will be placed in nylon bags of 5,0 mm and 0,5 mm mesh size and 120 replicates of each will be carefully placed on the litter surface in six sub-habitats of *Burkea* savanna. Samples will be removed at 3 to 5 week intervals and their mass loss, N, P, S and lignin-cellulose ratios determined on one half while the other half will be used for biomass determination using plate counts and ATP measurements.

Studies on the organisms responsible for plant litter and animal carcass and dung reduction and decomposition commenced in 1974 with preliminary quantitative and qualitative investigations into the soil micro-organisms and mesofauna of *Burkea* savanna.

Soil arthropods

Loots (1975), Loots and Theron (1976a, 1976b, 1976c), Prinsloo (1975) and Olivier (1976) have reported on the composition and biomass fluctuations in the soil mesofauna. Their findings indicate that termites and dungbeetles 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 bacteria- and fungiphages, and their seasonal fluctuations in number and biomass are being studied.

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.

Soil micro-organisms

Studies in soil micro-organisms began in 1976 by Steyn and Bezuidenhout (1976a, 1976b). Monthly soil samples were collected at three depths (0-5, 5-15, and 15-30 cm) from six sub-habitats within *Burkea* savanna.

Total bacteria, fungi and actinomycete propagule and colony counts were made on five replicates of each sample. The overall trends shown in the results are summarized in Tables 14 and 15. Total counts decreased significantly with depth and from mid-summer to mid-winter. Highest counts were recorded between grass under *Burkea*, lowest counts in open grassland between *Burkea* clumps.

Table 14. Total propagule and colony counts per g dry soil, for bacteria and fungi collected from three soil depths on 1976:01:07 in *Burkea* savanna, Nylsvley. Data from Steyn and Bezuidenhout (1976).

Soil depth, cm	bacteria	fungi
0 - 5	$3,4 \times 10^6$	25×10^3
5 - 15	$1,5 \times 10^6$	13×10^3
15 - 30	3×10^5	7×10^3

Table 15. Average propagule and colony counts per g dry soil of actinomycetes, bacteria and fungi, samples in mid-summer and mid-winter. Data from Steyn and Bezuidenhout (1976).

	actinomycetes	bacteria	fungi
1976:01:07	3×10^6	5×10^6	25×10^3
1976:07:08	3×10^5	4×10^5	20×10^3

Table 16. A T P content, in f g g^{-1} dry soil, of soil samples collected in *Burkea* savanna. Data from Steyn and Bezuidenhout (1976).

Soil depth, cm	1976:04:06	1976:09:01
0 - 5	$1,50 \times 10^6$	$2,0 \times 10^6$
5 - 15	$2,5 \times 10^5$	$1,0 \times 10^6$
15 - 30	1×10^5	$0,5 \times 10^5$

Total biomass of soil samples was estimated from the measurement of the ATP content of sub-samples. Results parallel those for propagule counts in terms of seasonal variation and decrease with depth (Table 16). Significant differences were not recorded between samples collected under *Burkea* trees and in open grassland.

Estimates of soil respiration were made at monthly intervals in six *Burkea* savanna sub-habitats using both field and laboratory techniques (Steyn and Bezuidenhout 1976a). Direct measurements of CO_2 production in the field were highest under *Burkea* and lowest in open grassland, dropping from 510 and 420 mg CO_2h^{-1} m^{-2} on 1976-04-06 to 10 and 0 mg $CO_2h^{-1}m^{-2}$ nett CO_2 efflux on 1976:09:09.

Laboratory measurements of CO_2 production from soil samples gave similar seasonal and spatial trends and in addition showed a rapid drop in CO_2 production from soil samples collected at increasing depths.

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.

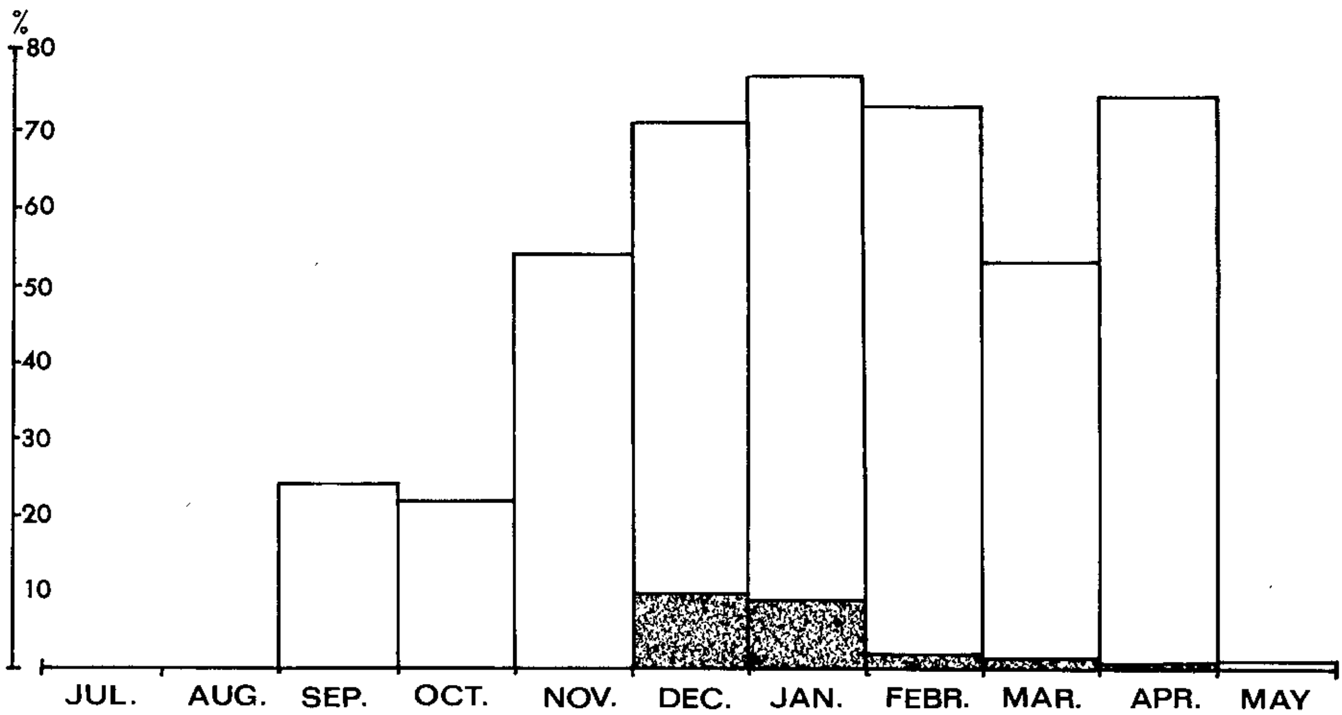

Figure 6. Total dung removal between July 1975 and May 1976. Portion removed by dung rollers (Scarabaeinae) is shaded. (From Endrödy-Younga 1976).

Table 17. Monthly changes of dung removal rates. The figures represent percentages of dung removed from measured 1 litre pellets, and are averages of five replications (Endrödy-Younga 1976a).

Year	Month	Number of days after setting									
		1	2	3	4	5	6	7	8	9	10
1975	July	0	0	0	0	0	0	0	0	0	0
	August	0	0	0	0	0	0	0	0	0	0
	September	10	20	20	22	24	24	24	24	24	24
	October	15	19	22	22	22	22	22	22	22	22
	November	54	54	54	54	54	54	54	54	54	54
	December	64	71	71	73	*	*	*	*	*	*
1976	January	74	76	77	*	*	*	*	*	*	*
	February	45	63	73	*	*	*	*	*	*	*
	March	46	48	53	*	*	*	*	*	*	*
	April	64	73	74	*	*	*	*	*	*	*
	May	1	1	1	*	*	*	*	*	*	*

* Dung removal not measured.

Preliminary findings are presented by Endrödy-Younga (1976a, 1976b). Particular attention was devoted to the reduction of cattle dung. Amount of dung removed (Figure 6) ranged from 0% during winter (July, August), to over 70% through summer (December, January, 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 only 24% had been removed after 10 days, while in summer as much as 77% was removed during the first day (Table 17). A study on the influence of dung age on removal rates showed that the number of *Gymnopleurus* beetles attracted to dung decreased considerably after the first day and slowly thereafter (Figure 7).

An important aspect studied was the mode of removal. Dung removed by rollers (Scarabaeinae) was measured separately to that removed by diggers (Coprinae, Aphodiinae etc). While the diggers bury dung under the pellet, the rollers are important in dispersing dung away from the site of dung deposition. The proportion of dispersed dung was substantial at the beginning of the season whereas towards the end virtually the entire quantity was dug into the soil under the pad.

The composition of the coprophagous fauna was characterised by the large variety and populations of some digging groups such as Oniticellini, Aphodiinae, Onthophaginae, etc, as well as moderate numbers of Coprinae. The limited populations and importance of the largest dung beetles, *Heliocopris* spp was noteworthy, as was that of the Scarabaeini, except Pachilomera spp (Endrödy-Younga 1976a).

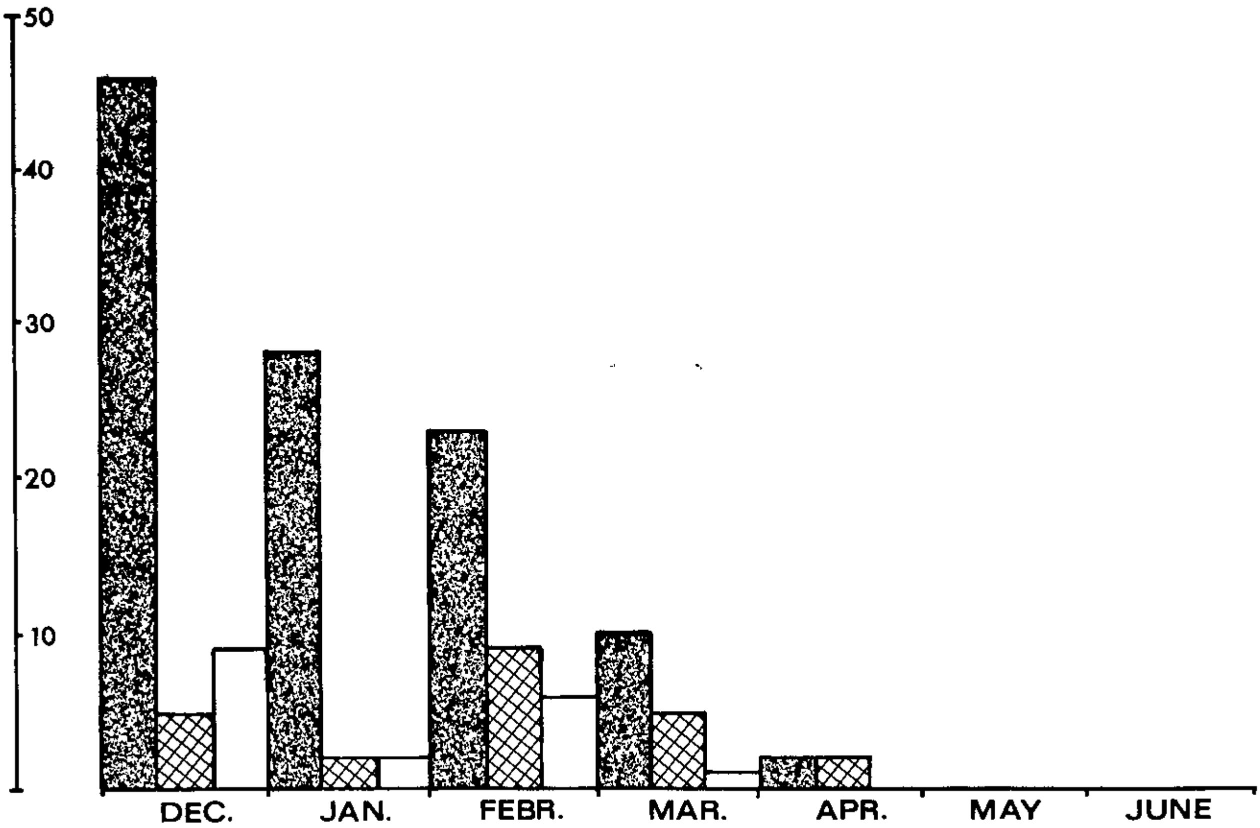

Figure 7. The numbers of a Gymnopleurus species attracted to dung of varying ages. Shading of histogrammes represents different ages of dung tested : black 1 day, shaded 2 days, white 3 days old. (From Endrödy-Younga 1976).

Wood reducers

A pilot study was conducted from January to June 1976 to determine the number of wood borer species active on the dominant plant species. From the initial sampling it would appear that the wood borers are generally host specific although there may be a correlation between the density of the wood of the host plants and the species that infest them. Preliminary results (Table 18) show that *Burkea africana* and *Terminalia sericea* possess the greatest diversity of species when compared with such hosts as *Combretum molle, Dombeya rotundifolia, Grewia flavescens, Lannea edulis, Ochna pulchra, Ozoroa paniculosa, Securidaca longipedunculata, Strychnos innocua* and *Vitex rehmannii* (Hasenjager 1976).

MINERAL CYCLES

The lack of a comprehensive project into the role of nutrients as limiting factors within the *Burkea* savanna remains a serious deficiency within the research programme. Current studies are limited to a survey of the rate of nitrogen fixation and a preliminary study on the dynamics of mineral release from parent materials.

Nitrogen fixation

Studies in the rate of nitrogen fixation using whole soil cores (25 cm^2 surface by 40 cm depth) incubated with acetylene under aerobic conditions were continued through the 1975-76 summer (Grobbelaar and Rösch 1976a). Appreciable rates of nitrogen fixation were only recorded during the five months December through April. Only a small percentage of the 40 samples collected each month showed any signs of nitrogen fixation (Table 21), with the major contribution to total fixation usually being contributed by very few samples.

Grobbelaar and Rösch (1976a) estimate that the total rate of nitrogen fixation on *Burkea* savanna would approximate 80 kg $ha^{-1}yr^{-1}$, surprizingly high considering that only one of the several hundred samples collected was in the immediate vicinity of a nodule forming legume species. Grobbelaar and Rösch (1976b) conclude that nitrogen fixation in *Burkea* savanna is probably mainly due to an intimate association between the roots of non-legume angiosperms and micro-organisms.

MODELLING

Modelling activities have developed along two distinct, but complementary lines : a general "accounting" model and several models of subsystems within the ecosystem (Starfield and Furniss 1976).

The accounting model covers all of the biotic elements of the ecosystem, which are considered in approximately 60 compartments. The model deals with the inter-compartmental flows in terms of dry mass, on a weekly basis. It lacks any internal mechanisms for changing these flow rates, but merely summarises the appropriate data, to give a representation of the ecosystem, and a check on the validity of the data.

Table 18. Number of woodboring arthropod species recorded from woody plants at Nylsvley, June 1976. Data from Hasenjager (1976).

Host Plant	FAMILIES						Total No of Spp/Host Plant
	Brenthidae	Bostry-chidae	Buprestidae	Ceramby-cidae	Curculio-nidae	Scolytidae	
Burkea africana	0	1	1	4	0	1	7
Combretum molle	0	0	0	0	0	0	0
Dombeya rotundifolia	0	0	0	1	1	0	2
Grewia flavescens	0	0	2	0	0	0	2
Lannea discolor	0	1	0	2	0	0	3
Ochna pulchra	0	1	0	2	0	0	3
Ozoroa paniculosa	0	0	0	1	0	0	1
Securidaca longipen-dunculata	0	0	0	0	0	0	0
Strychnos pungens	0	0	0	0	0	0	0
Terminalia sericea	0	0	2	3	0	0	5
Vitex rehmannii	0	0	0	0	0	0	0

The subsystem models differ from the accounting model in that they involve considerable internal structure, and are intended to simulate the behaviour of part of the ecosystem, both under normal conditions and in response to change. This cannot be achieved in a model of the ecosystem as a whole, but a model of a subsystem allows reasonable realism without unreasonable complexity. The development of these models involves gaining understanding of their behaviour, which is most rapidly achieved when the models can be manipulated as computer programmes in an interactive system, in which the time between successive runs of a model, with perhaps a change in a parameter value between runs, is a matter of seconds.

To facilitate this kind of interaction with the models, a DRIVER programme has been written (Furniss 1976). This is based on a set of "reference information" which contains values for the parameters and variables of the model and information defining the form of the output from the model. Any of the reference information can be changed, and the model run, using a simple set of commands entered from a terminal keyboard. DRIVER is usually used in conjunction with a VDU (visual display unit), which displays both the user's entries and output from the computer. It also generates hard copy output from a printer.

The models developed, using DRIVER, during the review period, include HERBY and PLANT. HERBY is a model of the food selection behaviour of large herbivores. It includes a simple, logistic model of plant growth, and simulates the amounts of different food plants eaten by a herbivore (or a number of herbivores), taking account of the differing preferences and availabilities of the plants. On the basis of a workshop attended by a number of project participants, the model is being improved (HERBY 2), although the basic method of simulating the changing amounts taken is not being altered.

PLANT is a model of the growth of a plant during a year, and is more complex than the plant submodel in HERBY. The plant is considered in several separate organs, and much of the model is involved in simulating the transfer of material between these organs, as the phenology and organ sizes change.

Work has been started on a model of the decomposition of litter (meaning all dead material on or in the soil). This model will initially be a specialised accounting model, dealing with transfer and loss rates of various constituents of organic matter between different classes of litter (classified by origin and size). Later, the effects of changing conditions (especially temperature and humidity) will be included.

DATA PROCESSING

Quantifiable information collected in the various research projects is recorded on standardized data forms and submitted to the project Data Processing Unit established in the Botanical Research Institute, Pretoria. All data processing required by project researchers is undertaken by the Unit, making use of the Department of Agricultural Technical Services' Burroughs system.

Four main computer programmes for data accessioning and validation are now in operation (Morris 1976). P/ECOSYSTEM/TAPEREAD reads magnetic tape and stores contents on temporary disk, P/ECOSYSTEM/INPUT is the main data accessioning programme from temporary to permanent disk store, P/ECOSYSTEM/EDITOR constructs formats for each data form and P/ECOSYSTEM/TIDY removes used and error records from temporary disk.

More than 4 000 data forms have been processed and routine summaries of climatic data are now available to project participants on request. A detailed data processing manual is being prepared to facilitate direct use of the data banking service by researchers.

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