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THE GRASSLAND DYNAMICS OF MKAMBATI GAME RESERVE

Charles Michael Shackleton

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfillment of the requirements for the degree of Master of Science.

Umtata, March 1989

ABSTRACT

This work describes the coastal grasslands of Mkambati Game Reserve and their suitability for the present large herbivore complement. The initial description makes use of both field survey and quantitative sampling and multivariate analysis which facilitated the production of soil and vegetation maps at the scale of 1: 10 000. Suitability of these grasslands for herbivores is assessed in terms of both quantity and quality of food available and the present herbivore impact.

Local variation in soil type was considerable. Eight standard soil forms were distinguished as well as several others previously undescribed. Most of the soils were dystrophic although nutrient 'hot-spots' were common. This determined floristic composition of the various communities to some extent.

Three grassland communities and four subcommunities were recognized which contributed 81,5 % to the total area of the reserve. The remaining area comprised forest, wetlands, exposed rock and accommodation camps. Each grassland community was associated with particular ranges of the measured environmental variables.

The standing crop of the three communities was high relative to other areas of southern Africa. Absolute amounts varied seasonally, being highest in summer and lowest in winter. Partitioning between the phytomass, necromass and litter components also varied seasonally. Total standing crop increased with increasing interval since the last fire. Litter breakdown rates differed between communities and species.

Forage quality was poor being lowest in autumn and winter and

declining with age. This was probably a result of the dystrophic soils. Crude protein and phosphorus were limiting for several months of the year. Total forage quantity was in excess of the present herbivore needs although availability declined with age and during the non-growing season. However, the poor quality reduced the amount available such that present herbivore impact was low, at all times being less than 9 %. Removal by herbivores was highest several months after a fire when absolute amounts of various nutrients were at a maximum per unit area. Thereafter it declined to less than 1 % with aging of the sward.

The implications of the results for management are discussed and future research needs identified.

DECLARATION

I declare that this thesis is my own unaided work, except where acknowledged. This study was completed while I was employed by the University of Transkei. It is being submitted for the degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination to any other university.

day of 1989

PREFACE AND ACKNOWLEDGEMENTS

I undertook this project at the request of Mkambati Game Reserve (MGR) Board of Directors to contribute an understanding of the major, natural, biological processes operating in Mkambati Game Reserve. Such an understanding should assist in formulating management options for the area. This in turn would reveal the resources and options available for the promotion of economic gain, while taking cognizance of ecological constraints and conservation ethics.

The thesis is set out in chapters, each forming a cohesive unit of a particular aspect of the overall project. Chapters 2, 3 and 4 provide an overview of the physical setting of MGR in the form of a description of the study area, based on available literature, and detailed descriptions of the soils and grasslands based on field work. Chapters 5 and 6 present data pertaining to the growth, death and breakdown of vegetative material. The next two chapters, 7 and 8, are based on empirical data and are concerned with the palatability of the grasslands to herbivores and with present herbivore impact. These chapters are linked initially in the introduction and finally in Chapters 9 and 10, which deal with carrying capacity and recommendations, respectively. A chapter format was adopted as it is intended that most of these will form the basis for a scientific publication (one paper has already been published, two submitted and two are in preparation).

The various aspects covered by this thesis are part of a larger study. Aspects of the overall study referred to, but not included in the thesis, include seasonal estimates of root standing crop at the monitoring sites described in chapter 5, assessments of herbivore condition using kidney-fat and bone-marrow indices, key

species productivity and visitor perceptions. The reader should be aware also that this study was undertaken on a part-time basis which limited both the amount of time available and the timing of certain aspects. This was an important consideration in the adoption of particular approaches and methods over others.

Many people have contributed to this project and moulded my fundamental beliefs and philosophies which affected the approach adopted. These include my supervisors, official and unofficial, namely: Prof. J. E. Granger (the primary motivator of this project), Dr B. McKenzie, Prof. M.T. Mentis and Mr E. R. Robinson. Others include: Ms S. Bell-Cross, Ms U. Brown, Prof. G. Dardis, Prof. A. Dye, Mr A. Evans, Mr J. Feely, Mr P. Madasa and Prof. B. Walker.

Special thanks are due to Profs. A. Dye and P. Piacenza both of whom unselfishly gave their time and knowledge of various practical aspects of computers and chemical formulae, methods and materials. Special thanks are also due to Ms S. Bell-Cross and Mr J. Feely who undertook the arduous task of the final proof reading for typographical and grammatical errors.

Even more obviously my thinking has been influenced by people close to me, especially my parents and wife. Without my parents I would never have been in the career I enjoy so much. My wife, Sheona, played an integral role in this project in terms of her field assistance, support, enthusiasm and constructive debate and criticism at all times. Without Sheona this would have been a substantially lesser work.

Mr P. Zacharias (University of Natal) initiated the idea of determining the digestibility of the different grass species by an

in vitro method, rather than by determining crude fibre as initially planned. Furthermore, he was instrumental in putting the idea into practice by undertaking to have the samples analyzed in his laboratories, for which I am grateful.

The relatively smooth progression of this project would have been impossible without the willing logistic and technical support of Mr C. Barton and Mr D. Treadwell of the Science Workshop, University of Transkei (Unitra) and Mr I. Abboy, Ms K. Butler, Ms E. Dean, Ms K. Fields, Ms K. Kime, Mr A. Pretorius, Mr T. Strever and Mr N. Swart, all past or present members of the Department of Botany, Unitra.

Various staff members at MGR, both past and present, provided me and the project with support and information during the course of this study. I owe them all sincere thanks, especially C. Andrews, M. Andrews, N. Ayliffe, T. Ayliffe, M-L Koenig, P. Ruddle, H. Siebert, J. Siebert and T. Strever.

Herbarium specimens were identified by Ms A. Hutchings (formerly of Unitra), Dr R. Ellis (Botanical Research Institute, Pretoria), Dr B. Schire (Kew), Dr O. Hilliard (Natal) and staff of the Botanical Research Institute, Pretoria.

Funding of this project was from the Pondoland Survey Research Grant of the University of Transkei, for which I am sincerely grateful; as well as generous donations, provision of accommodation, labour and transport by Mkambati Game Reserve.

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LIST OF ABBREVIATIONS AND ACRONYMS

STANDARD ABBREVIATIONS

AU	Animal Unit
C	Celsius
Ca	Calcium
CP	Crude Protein
g	gram
ha	hectare
-k	exponential decay statistic
K	Potassium
kg	kilogram
km	kilometer
m	meter
mm	millimeter
m.a.s.l.	meters above sea level
Mg	Magnesium
n	number (sample size)
N	Nitogen
P	Phosphorus
RSA	Republic of South Africa
S	Sulphur
SD	Standard deviation
SE	Standard error
x	mean

DERIVED ACRONYMS

AGP	Above ground productivity
ASC	Above ground standing crop
BSC	Below ground standing crop
GBP	Grassland Biome Project
LB	Litter breakdown
LD	Litter decomposition
MGR	Mkambati Game Reserve

INTRODUCTION

1.1. OBJECTIVES OF THE STUDY

Recognition that vegetation and its management are the primary determinants of the potential stocking rate and secondary productivity of grasslands underlay the promotion of two aims for this study. These were: (i) to describe and map both the vegetation and soils of Mkambati Game Reserve (MGR) for management purposes; and (ii) to describe the seasonal changes in standing crop and acceptability to herbivores of the grasslands at MGR, and the influence of the present burning regime and stocking rate on these. Both of these aims were intended to provide data on the major community processes which could act as a baseline for future studies and management. Thus, a subsidiary objective was to propose objective management goals based on adequate knowledge of such community process. Fulfillment of these aims would be achieved by (i) the assessment of the status and condition of the sward, and (ii) monitoring standing crop, productivity, utilization, forage quality, and mass loss from litter under different treatments simulating possible management actions.

These aims were translated into specific questions to be answered during the course of this study:

(1) What is the range in structure, species composition and spatial distribution of the various grassland communities at MGR?

(2) Are the structure, species composition and spatial distribution of the different communities in any way correlated with particular biotic and/or abiotic factors?

(3) How is the plant biomass partitioned between the phytomass, necromass, and litter components during the year?

(4) What is the forage availability in the main communities, and how is it affected by seasonal changes in the partitioning of the standing crop between the above components?

(5) What is the palatability of the forage and how does it change seasonally?

(6) How do fire and herbivory affect the partitioning, forage availability and palatability?

(7) What is the upper stocking rate of MGR?

(8) What might be the consequences of altering fire and/or herbivory on community species composition, distribution, structure and partitioning?

1.2. OVERVIEW & RATIONALE

Until this decade community studies in the grassland biome have lagged behind those for other biomes in southern Africa. This has not been the case with studies of individual grass species where agricultural concerns have necessitated investigations into various aspects, such as production rates, palatability, responses to defoliation and fertilizer and water requirements. However, with the constitution of the Grassland Biome Project (GBP) and a brief synthesis of past and present research effort (Mentis and Huntley 1982, Tainton 1984) a greater degree of direction has been forthcoming.

The primary focus of grassland community studies has been descriptive floristic classification (eg Killick 1963, Werger 1973, Bredenkamp and Theron 1978) and quantification of primary production (eg le Roux 1979, Scotcher 1982, Everson 1985, Smith 1985). Further studies have been performed on various aspects of community processes including herbivory (eg Tainton 1972, Vorster

1975), determinants and driving variables (eg Rutherford 1978, Snyman and Opperman 1983) and the impact of fire on various processes, structure, and composition (eg Tainton and Mentis 1984, Everson 1985). Other community processes such as decomposition, nutrient cycling and root turnover have been neglected and require attention. Quite understandably, few researchers have attempted to determine all these factors for any one particular grassland community. The closest attempt has been that of Smith (1985) for Marion Island. To quantify and model all the processes in any one community requires co-ordination of several researchers, and therein lies the the value of the GBP.

Research into the grasslands of Transkei is very scanty indeed. A major contribution was the floristic description contained in Acocks' (1953) overview for southern Africa. He delimited and described eleven grassland veld types ("a unit of vegetation whose range of variation is small enough to permit the whole of it to have the same farming potentialities") occurring in Transkei. These comprise 10,2 % of the grassland biome in southern Africa (Mentis and Huntley 1982). According to Feely (1986) approximately 75 % of Transkei was mapped as grassland by Acocks (1953). Consequently it is important that research agencies in Transkei allocate adequate attention towards a greater knowledge of this biome. Most other studies in Transkei, usually of a localized nature with emphasis towards development plans, have deemed it adequate simply to paraphrase Acocks' work, with the exception of McKenzie (1984, 1987).

Of the eleven grassland veld types in Transkei none has had even elementary quantitative description or monitoring within Transkei, and only few of those extending into South Africa have been extensively studied there (eg Dohne Sourveld). Furthermore, very

few are represented in any conservation area (Edwards 1974). With increasing agricultural demands it is unlikely that a basic understanding of the these veld types will be achieved prior to widespread alteration through increased demand from subsistence farmers. Thus, baseline data will be lacking.

Over 80 % of MGR is grassland primarily of the Pondoland Coastal Plateau Sourveld veld type. Approximately 84 % of this veld type is situated within Transkei. This veld type is certainly worthy of investigation and elucidation of its community processes as it forms the upper reference point of productivity of 'natural' grass veld in South Africa (Acocks 1953). Furthermore, according to Acocks (1953) it is also the densest grassland in southern Africa. Insight into why the densest and potentially most productive grasslands occur here, and determination of the state variables that are responsible for this, should make an important contribution to the knowledge and management of grasslands elsewhere.

There has been no quantification of community processes for this region. As a result the management actions at MGR are based on knowledge extrapolated from the sourveld regions of the Natal Drakensberg (Granger and McKenzie 1981). It was stressed that these be modified, if necessary, following regular reassessment of their success in meeting the desired goals for MGR. Contrary to the recommendations of Johnson et al. (1980) and Granger and McKenzie (1981) monitoring programmes were not implemented to make these assessments and specific management actions suggested by Tinley (1978), Chapman (1980) and Granger and McKenzie (1981) have, on the whole, been ignored.

It was after the appointment of a director responsible for the

ecological management of MGR that the formulation of management options (as opposed to actions) derived from supportive data was proposed. The priority aspects for clarification were recognized as those listed by Johnson et al. (1980), "productivity, nutrient quality, season and frequency of burning, and grazing and browse monitoring" and the key questions were set up, in consultation, to cover these aspects.

The first two questions were posed on the assumption that it is not possible to undertake detailed studies into any aspects of fire regimes or stocking rates until an 'inventory' of the various vegetation types and their distribution have been obtained. The format of the other questions and the design of the study stemmed from: (i) the basic model of mass flow within a community presented by Singh et al. (1975) (see Figure 1.1.), and (ii) the expected seasonal changes in both partitioning of the above ground components and in forage quality as demonstrated for other grasslands throughout southern Africa (eg Scotcher 1982, Everson 1985, Conlong 1986).

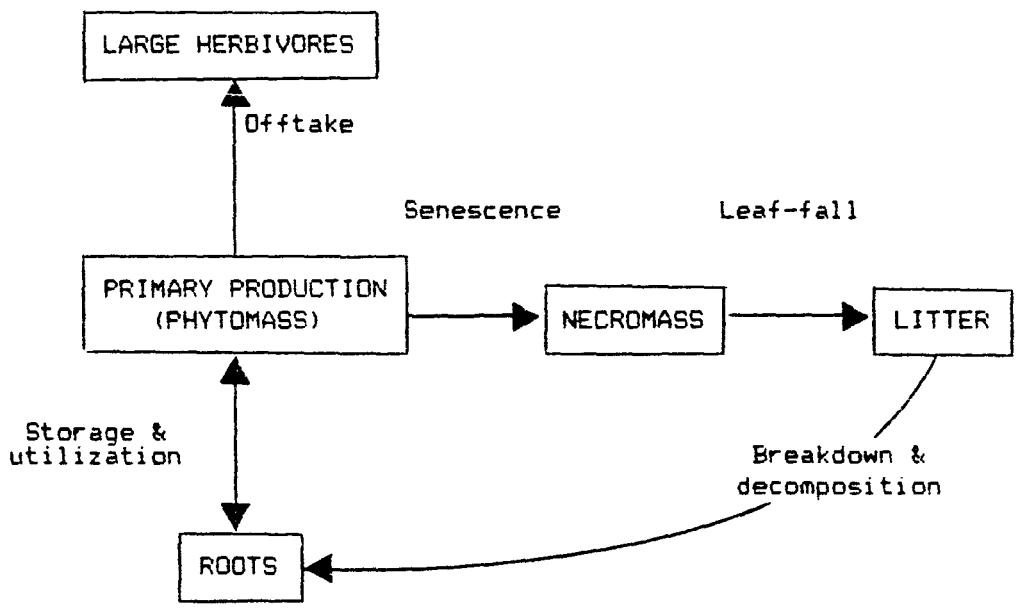


Figure 1.1. Schematic diagram of mass flow within a community

STUDY AREA

2.1. LOCATION

Mkambati Game Reserve is situated on the coast of northeastern Pondoland, Transkei (Fig. 2.1.). It covers an area of 7 720 ha and is delimited within the coordinates 31° 13' - 20'S and 29° 55' - 30° 04'E. It is bounded by the Mtentu river to the north and the Msikaba river in the south, with approximately 12 km of coastline forming the eastern limit. The only non-natural boundary is the inland fence in the west (approximately 300 m a.s.l.). The width of the reserve ranges from 5,5 km to 8,2 km. It is characterized by a combination of geomorphic, edaphic and phytogeographic factors that are not found elsewhere along the coast of southern Africa (Feely 1986).

2.2. GEOLOGY & GEOMORPHOLOGY

Mkambati Game Reserve is underlain by Paleozoic pre-Karroo sediments of the Natal Group sandstone (formerly Table Mountain sandstone) (Du Toit 1912, Sneesby 1933, Hobday **et al.** 1971, Johnson and Meyboom 1976), which form a narrow belt, approximately 16 km wide, parallel to the coast (Du Toit 1912, Hobday **et al.** 1971). These deposits, over 1 000 m thick, are characterized by a grain size of 0,5 mm to 1,0 mm and have a composition dominated by quartz with minor amounts of feldspar (Johnson and Meyboom 1976, Karpeta and Johnson 1979). Analyses from several sites by Hobday **et al.** (1971) revealed a high quartz content (70 - 98 %) with cementation primarily by silica. Having been laid down approximately 300 million years ago [probably in a shallow marine environment (Hobday **et al.** 1971, Johnson and Meyboom 1976)] they are the oldest sedimentary deposits in Transkei (McKenzie 1984). Although doleritic intrusions are common in Transkei few are present in this area (Du Toit 1912, McKenzie 1984), but several localized outcrops were noted at MGR during the course of this study. A small outcrop

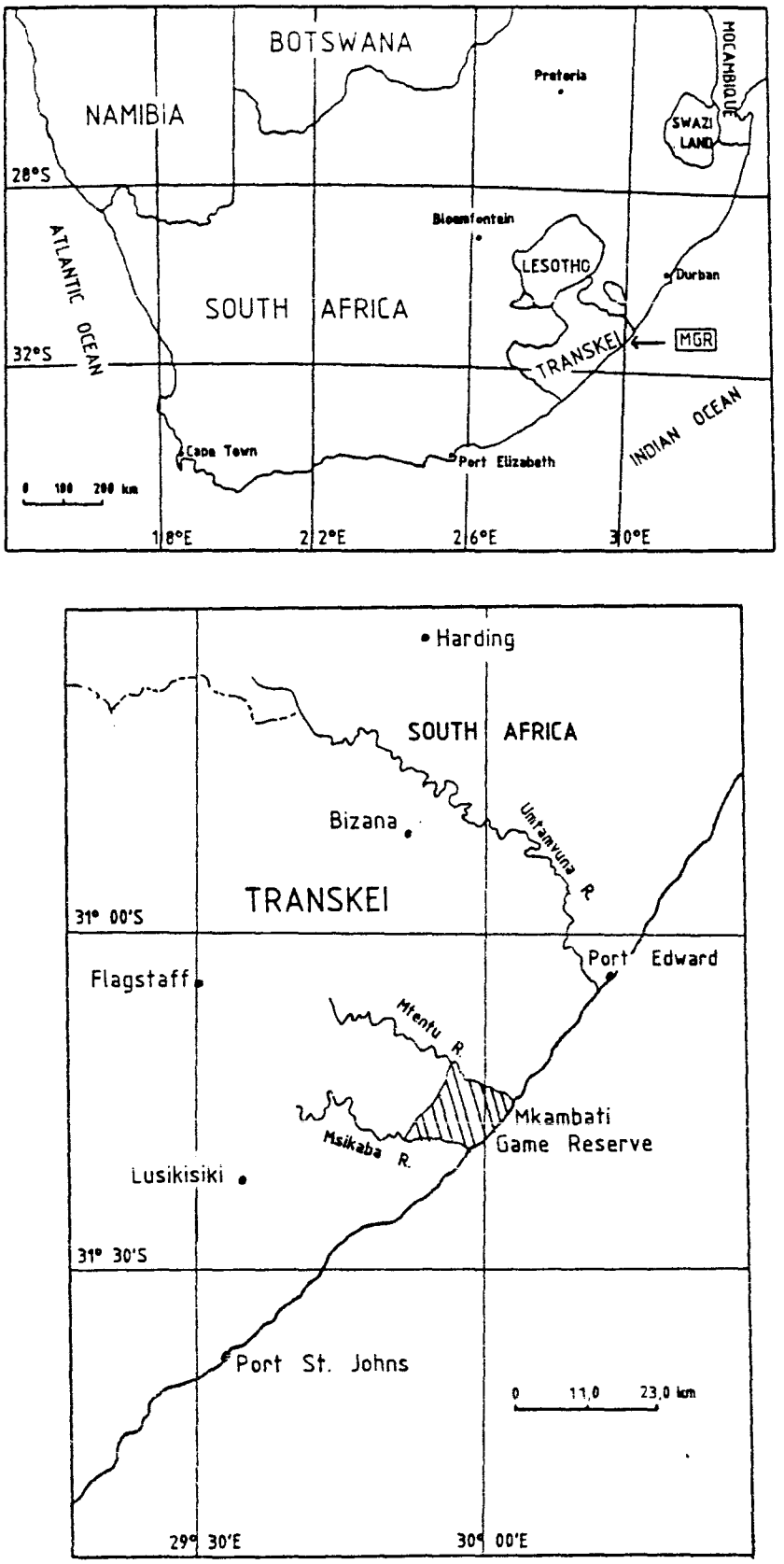


Figure 2.1. Location of Mkambati Game Reserve

of upper Cretaceous deposits were mapped at the coast in the present area that is MGR by Du Toit (1912), between the Mtentu River (northern boundary) and the Mgwetyana stream within the reserve to the south. Those to both the north and south are well known for their rich fossiliferous nature. The presence of these deposits was confirmed by the Geological Survey of 1976, although Tinley (1978) stated that their presence had not been confirmed. At several places along the coast Quaternary to Recent parabolic-type sand dunes were mapped by Tinley (1978). These are found only at or near the outlets of rivers and streams. Between the rivers and streams the land-sea interface is marked by abrupt rock faces of the Msikaba formation which is relatively resistant to weathering except along lines of weakness (Feely 1986). Consequently, both the shore and foreland are homeostatic, i.e. neither prograding nor degrading (Tinley 1985).

Situated at the southern end of the Natal monocline the terrain at MGR is a typical example of the Tableland topography described by Kruger (1983). King (1963) proposed that the structure of the shoreline was determined by the dynamics of the monocline. However, Maud (1961) and Partridge and Maud (1987) disputed this, stating that the primary factors influencing the coastal geomorphology in this region are the block structures and the structure of the rock ("structural control"). Nevertheless, it is the only unfaulted area along the south-eastern African coast where the regional dip is relatively low and away from the shore (J. Feely pers. comm.). Land facets are orientated parallel to the coast except where drainage systems have cut across them at right angles. Most of the slopes are less than 5 % except on scarp surfaces such that the rise from the sea (at the eastern boundary) to the inland boundary ($\pm$ 300 m a.s.l.) is gentle (Fig. 2.2.) with an average gradient of 3,8 %.

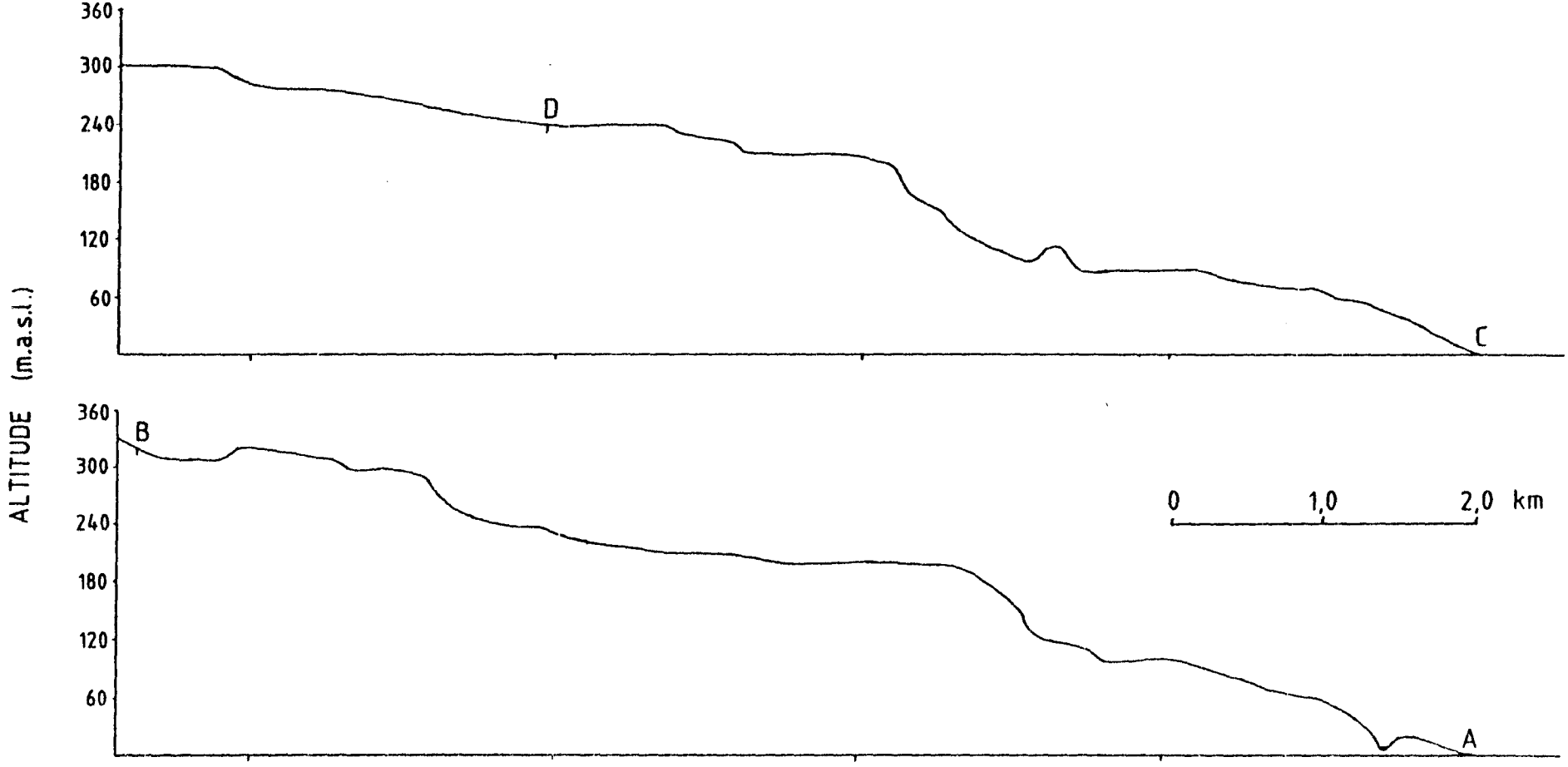


Figure 2.2. Cross sections of Mkambati Game Reserve (see map 1 for location of sections)

This gentle topography is the result of intense planation since the Tertiary and is interrupted by two steps parallel to the coast that were formed during intervals between periods of past geologic uplift (Du Toit 1912, King 1963, Tinley 1978). It is argued in a recent synthesis by Partridge and Maud (1987) that this uplift was considerably greater than previously thought. These steps are evident in Figure 2.2. at 85 m and 190 m and are characterized by steep surface gradients ranging between 10 % and 15 %. They mark the position of past shorelines. Superimposed on these periods of uplift were several episodes of alternating marine transgressions and regressions brought about by eustatic changes in sea-level evident in the various Cretaceous strata along the Pondoland coast north and south of MGR (Cooper 1974).

Traversing these gentle, stepped surfaces are three major perennial drainage systems, the Mtentu , Mkambati and Msikaba rivers, each with a deeply incised gorge. These also resulted from periods of uplift that initiated a greater erosion intensity due to the lowering of the base-level. Numerous smaller drainage systems with their total catchment within the reserve are orientated parallel to these major systems.

2.3. SOILS

On a broad scale, the coarse-grained strata of the Natal Group sandstones and the high rainfall have given rise to acidic, dystrophic, sandy soils (Tinley 1978), characterized by a weak structure, high permeability, but low available moisture capacity (Maud 1966). The soils of the MGR region were mapped by van der Merwe (1962) as Gley-like Podzolic Soils typical of the Natal coastal belt, where climate has been the dominant soil forming factor. The high temperature and rainfall have promoted the development of well weathered and leached soils with very little

clay mineral diversity. Kaolinite and illite are the most prevalent, with small amounts of montmorillonite (van der Merwe 1962, Maud 1966). Deposition of iron oxides in the B horizon may occur (van der Merwe 1962). In areas where igneous rock has intruded through the sandstone to near the surface parent material often overrides the effect of climate as the dominant soil-forming factor. This usually results in the development of soils with marked lateritic characteristics related to those of Red Ferrallitic Soils. Such soils are characterized by a red or reddish-brown colour (van der Merwe 1962).

Previous descriptions of the study area have stated that a further limiting factor, other than the very acidic and dystrophic nature of the soils, is their shallow depth or the development of ferricrete (Tinley 1978, Chapman 1980, Jooste **et al.** 1985). On the contrary, other than those forms characterized by shallow horizons (eg Mispah and Glenrosa), the soils at MGR are, on average, deep. Ferricrete is not prevalent and the primary limitation to rooting depth is saprolite and wet season waterlogging (see Ch. 3). Tinley (1982) is of the firm opinion that such severe alternation from excessive moisture during the wet season to excessive drying during the winter is the primary factor determining the distribution of grasslands. In some areas the saprolite itself forms a very deep horizon (>1,0 m). Signs of gleying and gley horizons are common at the base of the catenal sequence. Ferricrete is not common, possibly due to the low iron status of Natal Group sandstone and lateral eluviation rather than deposition in the B horizon (van der Merwe 1962).

In general, the soils have weakly structured, acidic [pH < 5,0 (in water)] A horizons, primarily orthic, but with a few sites characterized by a humic or organic topsoil (eg wetlands). The

majority of the soils are sandy loams or loamy sands. Where a B horizon is present the A horizon is deep (35 - 80 cm). Other than gleyed horizons the subsoil is an apedal red or yellow-brown horizon of the Hutton or Clovelly form, typical of Wood and van Schoor's (1976) generalized classification unit (Red and Yellow/Brown Apedal soils with an orthic epipedon) for this area. The sand content (%) decreases from the coast inland.

The soils were mapped and analyzed in greater detail during the course of this study and the results are reported in Chapter 3.

2.4. CLIMATE

According to the Köppen system MGR is classified as having a humid, temperate climate with sufficient rainfall in all seasons, a mean temperature above 1° C for at least eight months of the year, and the mean for the coldest month being above -3° C (Schulze 1947). On a broad subcontinental scale, this region experiences the climatic cycles typical of the south-eastern seaboard described by Tyson (1986). On a local scale, details of the major climatic variables are given below.

2.4.1. Rainfall

The average annual rainfall is 1 200 mm (56 years data) of which 61 % is received during spring and summer between September and February. A minimum of 50 mm is expected every month. The monthly distribution of the annual rainfall and number of rain days are illustrated in Figure 2.3. The nature of the rain is usually cyclonic although often convectional during summer. Thunderstorms are evident on average, for twenty days per annum, generally restricted to early spring (Tyson 1986).

The frequency distribution of annual rainfall (Fig. 2.4.)

illustrates that the median is close to the mean, reflecting a relatively even distribution. At extremes, one in ten years may experience unusually high rainfall of greater than 1 600 mm (400 mm > mean), whereas only one year in fifty is expected to receive less than 800 mm (400 mm < mean).

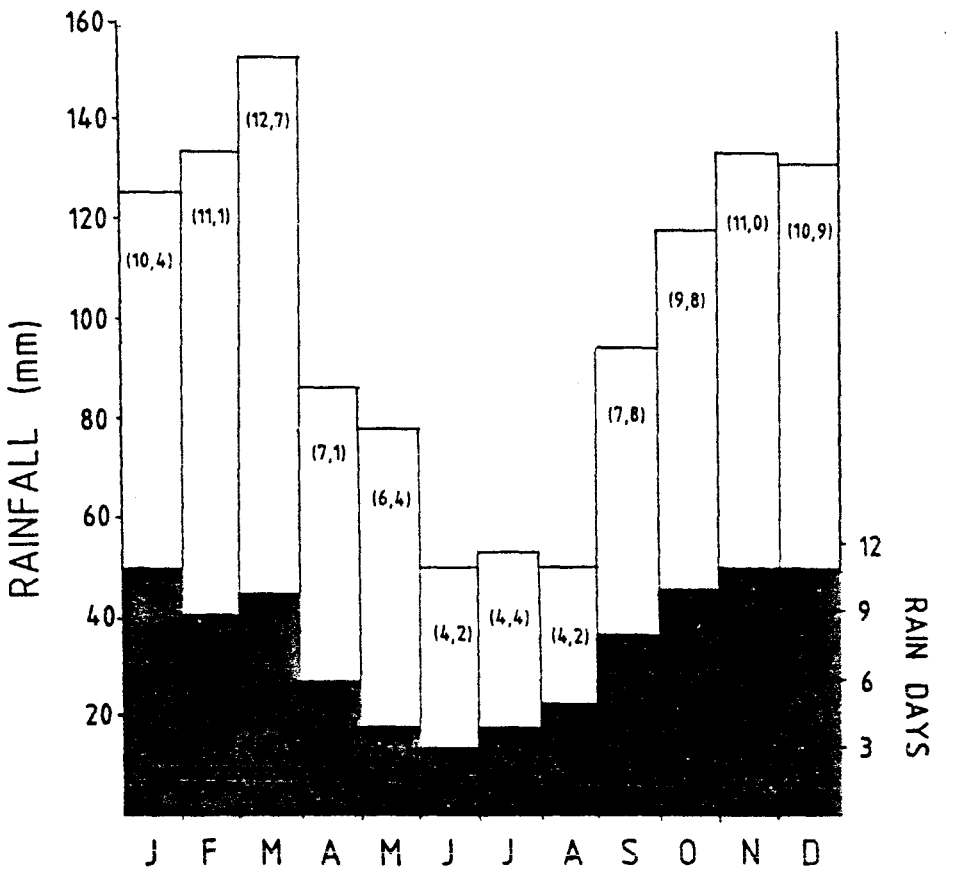


Figure 2.3. Monthly distribution of rainfall and number of raindays

Unfortunately, the recording of rainfall during the study period was erratic with several months being omitted. The last year with complete records was 1982. Alternative data from the nearest station, [Transkei Agricultural Corporation (TRACOR) - Mkambati Sugar Project, 15 km northwest] indicated that rainfall was close to the 'normal' during the beginning of this study, but the latter half of 1986 and early 1987 received considerably more rainfall than 'normal'.

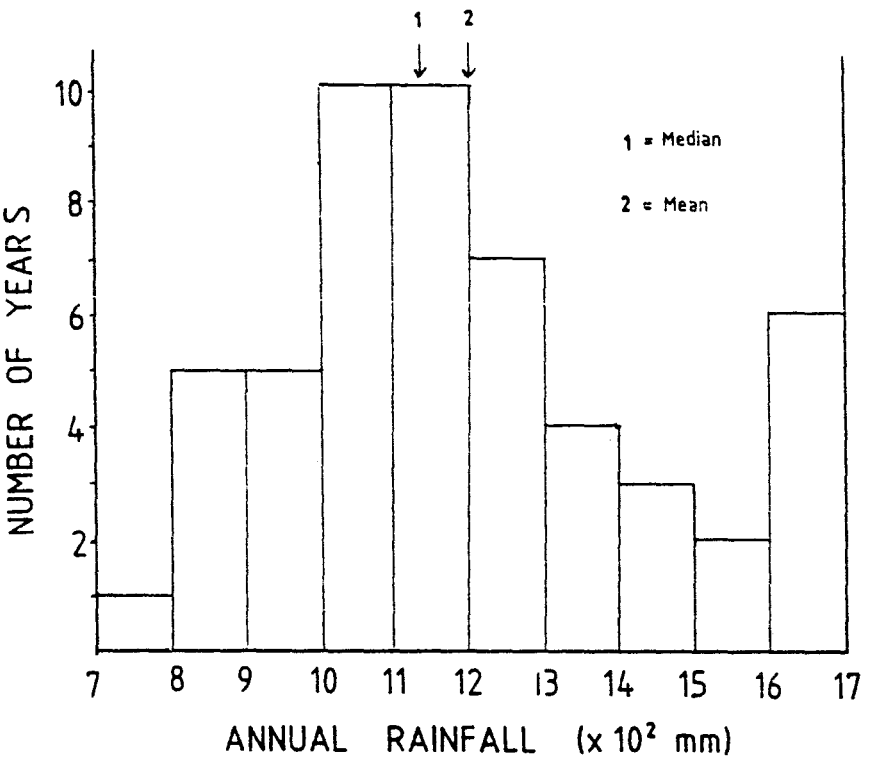


Figure 2.4. Frequency histogram of annual rainfall

Mkambati Game Reserve is situated on the periphery of the core area in southern Africa that experiences a quasi 18-year cycle of alternating wet and dry periods (Tyson 1986). These regions have, on average, nine years of which the majority will experience below average rainfall, followed by nine years of which most will have above average rainfall. This decade is experiencing years with mainly below average rainfall as reflected in the MGR records for 1980, 1981 and 1982 (lowest yearly total ever recorded at MGR). Extrapolating the data from TRACOR, the years 1985 to 1987 experienced a total rainfall close to the long term mean.

2.4.2. Temperature

Characteristic of its coastal location, MGR has a relatively equable temperature regime, both diurnally and seasonally. The mean annual temperature at Port St. Johns (50 km to the southwest, 31°

38'S; 29° 33'E) is 20,1° C and at Port Shepstone (75 km to the northeast, 30° 44'S; 30° 27' E) 20,6° C (Weather Bureau 1986). At both these stations the range about the mean is less than 7° C. As the records for both these stations are so similar, it may be presumed that MGR experiences a similar temperature regime. Thus only the data from Port St. Johns are reviewed to characterize MGR.

The warmest months are January and February. Minimum temperatures are recorded during July and August. Frost is absent [the lowest temperature ever recorded was 5,6° C (Sept. 1932)]. Temperature data from mid-1985 to mid-1987 from TRACOR are in reasonable agreement with those for Port St. Johns (lowest mean monthly minimum = 8,4° C; highest mean monthly maximum = 26° C). The data from Port St. Johns are summarized in Figure 2.5.

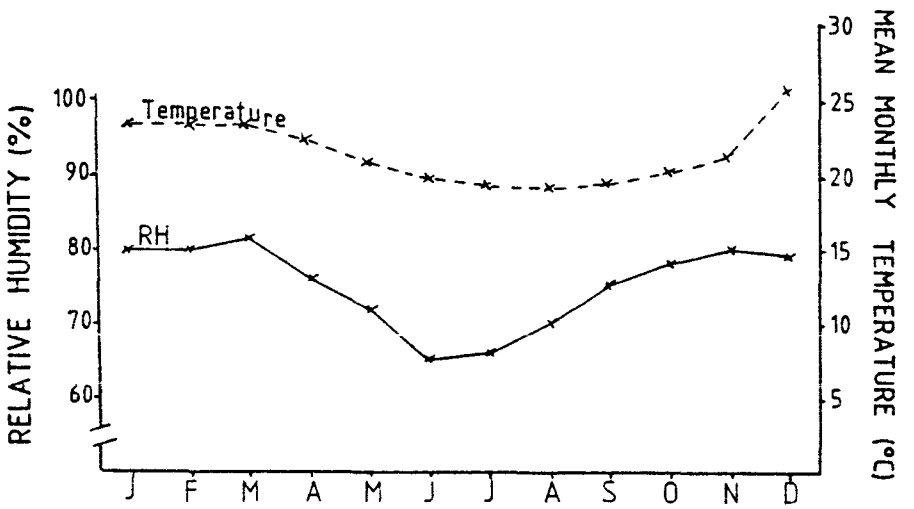


Figure 2.5. Mean monthly temperature and relative humidity at Port St. Johns

Diurnal temperature variations are also relatively small even in winter. Differences in the mean temperature at 08H00 and 12H00 are less than 6° C for all months of the year.

2.4.3. Relative Humidity

Relative humidity is high throughout the year with a yearly mean of 74 % and monthly means ranging from a low of 60 % (Fig. 2.5.) in June and July to 85 % from January to March (Weather Bureau 1986).

2.4.4. Wind

The winds blow predominately from the southwest [not northwest as reported by previous researchers; see wind rose diagram for Port St. Johns (Cawe **et al.** 1983)] and northeast parallel to the coast. Diurnal cycles of land and sea breezes are common. Maximum wind speeds are recorded during summer and spring (Jooste **et al.** 1985). The combination of strong winds and salt spray are likely to have a marked effect on the structure and composition of the vegetation adjacent to the shore.

2.5. SOIL MOISTURE

Soil moisture was measured at monthly intervals at three sites throughout the period of recording changes in standing crop (see Ch. 5). At each site fifteen samples were taken, one from each clipped quadrat in each of the three treatment plots (five quadrats per plot). The samples were taken to a maximum depth of 15 cm to coincide with the major rooting zone (Shackleton **et al.** 1988). After transporting the samples to the laboratory, the soil moisture status (%) was determined gravimetrically. The results are presented in Figure 2.6.

Soil moisture was highest during spring and summer from August through to February. Thereafter it declined through winter until the onset of the spring rains. These are only trends and there were marked exceptions with soil moisture 'droughts' during the rainy season or significant increments in mid-winter, reflecting variation in timing of precipitation.

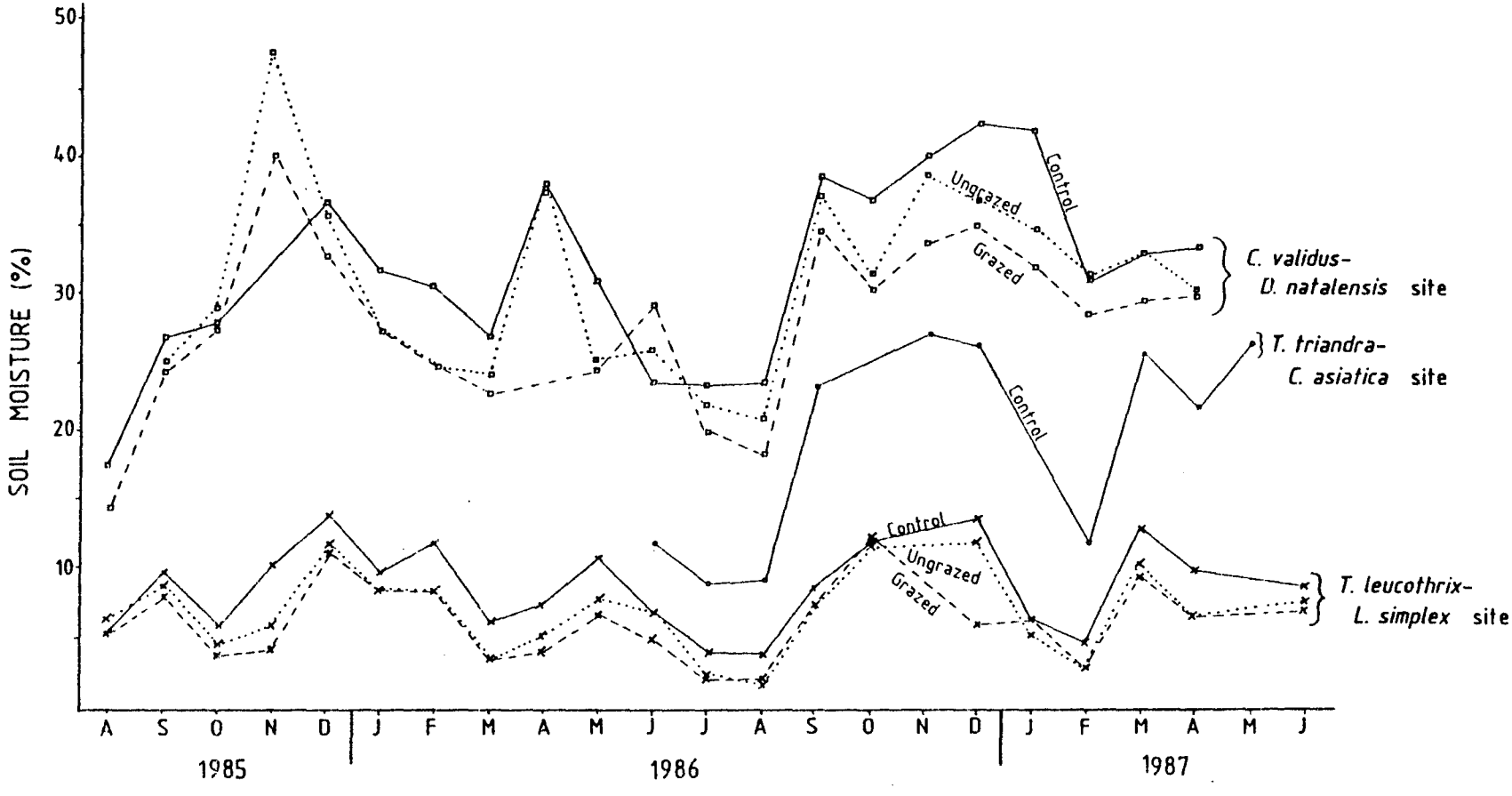


Figure 2.6. Soil moisture at three monitoring sites during the study

Soil moisture status was higher in unburnt grasslands, than recently burnt grasslands, at both the **Tristachya leucothrix - Loudetia simplex** and **Cymbopogon validus - Digitaria natalensis** sites. This is probably due to the higher litter loads in unburnt grasslands (Sect. 5.4.). The different moisture status at the three monitoring sites is due to differences in soil properties such as texture and organic matter (see Table 5.1.).

There was no significant statistical relationship between the soil moisture (%) and recorded rainfall during this study. However, there was a significant ($p < 0,05$) non-linear relationship between mean monthly soil moisture recorded during this study and the expected mean monthly rainfall expressed by the function $y = x/(ax + b)$ at the **C. validus - D. natalensis** and **Themeda triandra - Centella asiatica** sites. It was not significant for the **T. leucothrix - L. simplex** site.

2.6. VEGETATION

Biogeographically MGR is situated in the Indian Ocean Coastal Belt (Werger 1978), which extends all along the eastern seaboard of Africa from southeastern Somalia to Port Elizabeth (RSA). This overlaps with the Savanna Biome of Rutherford and Westfall (1986). I consider the latter is a misnomer for the coastal areas of Transkei because: (i) it bears no resemblance to the 'traditional' savanna generally characteristic of more arid regions, and (ii) it excludes coastal grasslands due to mapping scale constraints and temperature requirements. Therefore the description below was drawn mainly from the scheme of Werger (1978) and description of White and Moll (1978).

Due to sharp small scale changes in climate and soil the Indian Ocean Coastal Belt is divided into a mosaic of various vegetation

types ranging from edaphic grasslands to tall forest. The southern portion, referred to as the Tongoland-Pondoland Regional Mosaic extends from the Limpopo river (25° S) to Port Elizabeth. It is characterized by a relative absence of Guineo-Congolian linking species in favour of Afromontane, Karoo-Namib and Cape linking species. The latter are common in areas situated on nutrient deficient, sandy soils - common at MGR. According to White and Moll (1978) the woody component of the vegetation has been severely altered through the action of man during the last 600 years, but recent work has disputed this (Feely 1986). Thus, present knowledge indicates that significant portions of the coastal belt (including northeastern Pondoland) have been dominated by grasslands for the last 2 000 years, and probably throughout the Holocene. Consequently, by implication, the present disjunct, small patches of forest were not significantly more extensive than today for at least 10 000 years, contrary to general belief. Examination of a series of aerial photographs covering MGR dating back to 1932, indicated that the distribution of indigenous forest has hardly changed over the last 50 years.

The vegetation of MGR is probably a typical example of the edaphic grasslands that constitute part of the Tongoland-Pondoland Mosaic. Due to the equable climate productivity is high, permitting a high burning frequency of two or three times per annum, if so desired (White and Moll 1978, pers. obs.). This high burning frequency has promoted the dominance of fire tolerant and resistant species such as Tristachya leucothrix, Trachypogon spicatus and Themeda triandra; and if coupled with selective grazing promotes invasion and dominance by Aristida junciformis (White and Moll 1978).

On a finer scale the Tongoland-Pondoland Mosaic includes Acocks' (1953) veld types 1, 2, 3, 5, 6, 10, 23 and 24. By location MGR

should be classified as veld type 1, Coastal Forest and Thornveld, but the species composition makes it more akin to Pondoland Sourveld (no. 3). Except for the low abundance of **Themeda triandra** there is little difference between the flora of MGR and Acocks' (1953) description of Pondoland Sourveld, whereas it does exhibit several differences from veld type 1. Closer inspection of Acocks' (1953) map and comparison with the field situation leads me to conclude that the boundaries of all the veld types in this region should have been further to the east. Thus, Pondoland Sourveld extends to the coast (in this region) and 'Ngongoni veld extends further east than mapped.

Several local, qualitative surveys have been performed (Tinley 1978, Chapman 1980, Jooste **et al.** 1985), with most drawing heavily from Acocks' (1953) description and Tinley's (1978) report. The major discrepancy between reports of the various researchers concerned the existence of extensive swards dominated by **Aristida junciformis**. Whilst Tinley (1978) never mentioned such grasslands and Collinson (1981) clearly stated that MGR was relatively free of **A. junciformis**, Chapman (1980) stated that they were present and that MGR was in the process of becoming 'Ngongoni veld, and this was repeated by Jooste **et al.** (1985). After extensive qualitative and quantitative surveys of the reserve during this study it appears that this is not the case. Certainly, **A. junciformis** is present, especially along abandoned roads and moist sites on the fringes of wetlands as well as several very small areas where it is dominant, but otherwise it is not a major contributor to the biomass or cover over most of the reserve. The same controversy between researchers was evident at Dwesa Nature Reserve to the south, where both Moll (1974) and Tinley (1975) suggested dominance by **A. junciformis**; but quantitative analysis by McKenzie and Cowling (1979) refuted this. As a detailed quantitative description

of the grasslands was completed during the course of this study (see Ch. 4), only a broad overview of all the vegetation types is presented here.

Six major vegetation types are conspicuous at MGR, most with several communities. For ease of reference the most extensive communities have been summarized in Table 2.1.

Table 2.1. Major communities at Mkambati Game Reserve (areas are approximate)

VEGETATION TYPE	COMMUNITIES	DOMINANT GENERA/SPECIES
Forest	Dune	Mimusops, Brachylaena, Psychotria
	Swamp	Syzygium, Voacanga, Rauvolfia.
(662 ha)	Undifferentiated	Schleffera, Milletia, Trichilia.
	Mangrove	Bruguiera gymnorrhiza.
	Exotic	Eucalyptus spp.
Scrub	Stoebe-Athanasia	Stoebe vulgaris, Athanasia calva.
	Protea	Protea caffra.
(40 ha)	Exotic	Various (eg. Lantana sp. Hakea sericea, Acacia saligna).
Grassland	Short	Themeda triandra, Stenotaphrum secundatum, Ruellia cordata.
	Medium	Tristachya leucothrix, Loudetia simplex, Elionurus muticus.
(6 250 ha)	Tall	Cymbopogon validus, Digitaria natalensis.
	Aristida	Aristida junciformis.
Terrace	Strelitzia	Strelitzia, Gnidia, Rhoicissus.
Wetland	Perennial	various
	Seasonal	Eragrostis inamoena, Scleria spp.
(490 ha)	Reed	Phragmites australis.
	Prionium	Prionium serrata.
	Streambank	various
Beach pioneer		Ipomoea brasiliensis, Scaevola, Sporobolus virginicus.

This region is significant in terms of its conservation status through the presence of a relatively large number of endemics (van Wyk and Schire 1986) and outlying species that exhibit no contiguity with the rest of their distribution. To date one family (Rhynchocalycaceae), six genera (eg **Jubaeopsis, Pseudoscolopia**)

and more than 50 species have been listed as endemic to the region, 40 or more of which have been noted in the reserve (B-E. van Wyk pers. comm.). These span both woody species and forbs but no graminoids. Recently 16 undescribed species were collected in and around MGR (Jordaan 1987). The number of outlying species is difficult to assess from other researchers' collections, but at least three were collected during the course of this study (**Rhytachne rottboellioides, Eragrostis acrea** and **Sacrolepis indica**). A comprehensive checklist for the reserve is in preparation (specimens still awaiting identification). Presently the list comprises 906 species distributed throughout 488 genera and 136 families.

2.7. FAUNA

The latest census figures for the population numbers for each of the common, large herbivore species are given in Table 2.2. Numbers of the less common species such as reedbuck (**Redunca arundinum**), bushbuck (**Tragelaphus scriptus**) and duiker (**Sylvicapra grimmia**) are undetermined.

Table 2.2. Herbivore numbers at Mkambati Game Reserve

HERBIVORE SPECIES	COMMON NAME	NUMBER (10/'86)
Damaliscus dorcas phillipsi	blesbok	650 (- young)
Connochaetes taurinus	blue wildebeest	290
Equus burchelli	Burchell's zebra	98
Taurotragus oryx	eland	186
Oryx gazella	gemsbok	40
Aepyceros melampus	impala	80
Tragelaphus strepsiceros	kudu	40 (estimate)
Equus zebra	mountain zebra	40
Alcelaphus buselaphus	red hartebeest	140
Antidorcas marsupialis	springbok	60
TOTAL		1 624

Many of these species were introduced into the reserve during 1979 with the establishment of the reserve (see Sect. 2.8.3.) and did

not occur in the area historically (Skead, in press). From consideration of Table 2.3. which was derived from Skead's work it

Table 2.3. Animal species indigenous to the MGR region according to Skead (in press)

ANIMAL SPECIES	HISTORICAL STATUS IN THE AREA				
	PRESENT	POSSIBLE	DOUBTFUL	ABSENT	NO RECORD
Baboon	+				
Black-backed Jackal	+				
Blue Duiker	+				
Brown Hyena	+				
Buffalo	+				
Bushbuck	+				
Bushpig	+				
Common Reedbuck	+				
Dassie	+				
Eland	+				
Elephant	+				
Grey Duiker	+				
Hippopotomus	+				
Leopard	+				
Oribi	+				
Porcupine	+				
Red Hartebeest	+				
Serval	+				
Spotted Hyena	+				
Vervet Monkey	+				
Black Wildebeest		+			
Blesbok		+			
Lion		+			
Red Duiker		+			
Warthog		+			
Wild dog		+			
Black Rhinoceros			+		
Cape Grysbuck			+		
Kudu			+		
Ostrich			+		
White Rhinoceros			+		
Blue Wildbeest				+	
Burchell's Zebra				+	
Cheetah				+	
Gemsbok				+	
Giraffe				+	
Mountain Reedbuck				+	
Mountain Zebra				+	
Springbok				+	
Steenbuck				+	
Caracal					+
Clawless Otter					+
Klipspringer					+
Samango Monkey					+

is evident that approximately 40 % (in terms of numbers, 70 % in terms of species types of dominant species) of the total herbivore complement is not indigenous to the area. However, it must be borne in mind that the reserve was initiated as a hunting enterprise, and in such circumstances management was not concerned about the 'naturalness' of the species complement, but stocked solely with animals they believed clients would like to shoot (see Sect. 2.8.3.).

A checklist of small mammals occurring at MGR based on recent trapping was compiled by van Niekerk (1987), and of birds by Vernon (1982) and Shackleton (in prep.). These have all been summarized by Shackleton (in prep.). Several further lists were compiled by Ruddle (undated) from a variety of texts for snakes, rodents, amphibians, fish and birds that should occur in the area. It must be noted that these are not based on visual sightings at MGR but from large scale maps with poor resolution. Consequently, there is the distinct possibility that some species recorded in these lists are not present at MGR, and never were.

2.8. HUMAN IMPACT

2.8.1. Pre-colonial

One of the factors contributing to Mkambati being proclaimed as a conservation area was its low settlement density (J.E. Granger pers. comm.) which minimized translocation of rural people to alternative sites. The low density settlement of this entire Tableland region had certainly been the case for the last 2 000 years (Feely 1986) and it was unlikely to have been any higher before that. There are several possible reasons for this pre-colonial, low density settlement including the high incidence of stock diseases (Bigalke 1979, L. Amaral pers. comm.), poor grazing

(therefore a low game density?), Tableland terrain (Feely 1986), deep soils with inadequate subsurface conditions for grain pits (Feely 1986), vegetation type (Feely 1986) and low incidence of subsurface dolerite (Hall 1981). Thus, it appears that this region was never settled in a similar fashion to the rest of coastal Transkei. However, evidence of exploitation of intertidal resources was recorded by Feely (1986) and Prins and Strever (1987) with the occurrence of marine shell-middens along the coast and in several rock shelters further inland. Prior to this, on the basis of discoveries to the north and south of MGR, it was likely that low scale exploitation by hunter-gatherers had occurred throughout the region for the last 150 000 to 500 000 years (Cawe **et al.** 1983). These hunters probably fired these grasslands on a frequent basis (Hall 1984, McKenzie 1984), promoting a fire adapted biota.

This exploitation was also practised within the reserve itself by late Stone Age hunters as evidenced by the recent discovery, in 1986, of several rock shelters with rock paintings, marine shell middens and pottery remains. Even more recently (Sept. 1987) further rock paintings have been found as well as a knapping site of the Stone Age period along with smelting slag indicative of Iron Age farmers (Prins and Strever 1987).

2.8.2. Colonial - 1978

The Tableland region was not immune to the political, sociological and economic developments of the eastern seaboard as a whole and Transkei in particular. Forces that had been in control for the past several thousand years were altered with regional upheavals as a result of Mfecane and the advent of European missionaries and settlers. Present day inhabitants are of the Mphondo people which have resided there since 1680, if not earlier (Feely 1986), but always at low density. The first European inhabitants of Pondoland

arrived in 1839 (Cawe **et al.** 1983) and by 1894 Pondoland had been annexed and was administered by the Cape Government (McKenzie 1984). Thus one would have expected that sooner or later the Tableland region would have been subjected to increased settlement due to increased population pressures brought about by greater political stability, influx of Africans evicted from the south of the Kei river by the Cape Government (McKenzie 1984), an increasing economic base, and improved basic health care.

However, the Mkambati area specifically did not experience such increments in settlement density during the 20th century, as it was proclaimed a leper colony in 1920 (Vincent 1984), administered by the Department of Health. Ruddle (pers. comm.) suggested that it was earlier than this. Land was allocated to the hospital and rehabilitation centres for agricultural purposes, which one presumes was to promote self-sufficiency and thereby reduce contact with the surrounding areas. The total extent of the "colony" is presently unknown but certain of the present accommodation complexes away from the main hospital are known to have been recuperation dormitories which indicate at least one third of the present area (if not the total area) was under the jurisdiction of the hospital. It is known that cattle were grazed on this land but stocking records are unavailable (P. Goss pers. comm.), although Vincent (1984) reported that at times there were up to 8 000 head. If that occurred over the present extent of the reserve it would have been the equivalent of 1,04 AU/ha; about five times the present recommended rate. It was evident from early aerial photographs (1932) that areas of the present reserve were cultivated especially in the vicinity of the hospital complex. This may be responsible for the location of particular grassland communities (S.E. Shackleton pers. comm.). It was also clear from past aerial photographs that what is presently MGR was divided into

large blocks, separated by fences, and that these were burnt on a controlled basis. The frequency and number burnt at a time is unknown. With the decreasing incidence of leprosy during the 20th century part of the hospital was redesigned to cater for people suffering from tuberculosis (TB) and the first patients were admitted in 1958 (Vincent 1984). With a reduction in the number of TB patients the land adjacent to the hospital was taken over by the Dept. of Finance (Transkei Government) in 1978 to be run as a hunting concern. The hospital was transferred to this operation in 1983.

2.8.3. Present management (1978 onwards)

After the transfer of the hospital lands to the Department of Finance a conservation area was proclaimed to be managed as a hunting concern. The concern was managed by private individuals but the government held 51 % of the shares. From the start, the area to be run in this manner certainly included all of the present reserve (see boundary delimitations in memorandum of agreement between the Secretary for Agriculture and Forestry and company directors 5/1/79). This partnership had the following objectives:

"(a) To encourage influential tourists to visit MGR thereby assisting in the economic and political recognition of Transkei;

(b) to operate a game lodge and to provide walking, driving, river and hunting safaris;

(c) to trade curios, skins and leathers;

(d) to arrange transport to and from the reserve by road and air;

(e) to obtain the services of qualified conservation officers;

(f) to trade in game;

(g) to market venison and export the same;

(h) to enter into finance agreements to the fulfillment of the above purposes."

To summarize the above, the primary objective of MGR was to generate revenue through the sale of game products in the form of hunting safaris, meat, trophies and skins whilst entertaining influential tourists/visitors (my emphasis), and thereafter the provision of other 'types' of safaris. No references were made to economic viability of such a venture, nor the ecological potential of the area to support such an enterprise. Several of the reconnaissance surveys performed to assess the area were requested after the initial stocking had commenced.

A move to fulfill the listed objectives was made with the delivery of at least 1 631 animals, including 959 blesbok, 75 eland, 66 zebra, 215 hartebeest, 135 gemsbok, 48 kudu, 9 giraffe, 6 springbok, 100 impala and 18 blue wildebeest, between March and October 1979 (MGR filed receipts). The exact number established is unknown due to animals killed in transport (were they replaced?), subsequent deaths within a few weeks, and incomplete records of further purchases and deliveries. Further plans to introduce tigers, Himalyan bears, cheetah and crocodiles (Bigalke 1979, MGR filed invoices) and various species of exotic game birds such as pheasant and grouse (J.E. Granger pers. comm.) never reached fruition. Several plans for construction of various hotels were likewise not carried through (Bigalke 1979, O' Connell et al. 1979, Agricultural Management Service 1982). The initial staff had no ecological expertise.

After complaints about the proposed introduction of exotic species, inadequate management and uncontrolled burning of the grasslands (J.E. Granger pers. comm.) several qualitative surveys were

undertaken to assess the suitability of the reserve for particular species, its carrying capacity and conservation status (Bigalke 1979, Chapman 1980, Johnson et al. 1980, Collinson 1981, Granger and McKenzie 1981). Despite these surveys it appeared that the managers were unwilling or unable to implement the various recommendations and guidelines, such that the Natal Parks Board refused to supply further animals. At the end of 1982 the second partnership was dissolved and the Transkei Government assumed total control and management of the reserve. Management policy and decisions were thereafter effected through a board of directors appointed by the government.

With the appointment of a director concerned with ecological management of the reserve a more streamlined and permanent, although unwritten, management policy was implemented and the daily running of the reserve was regularized. The reserve was divided into six management 'blocks' of approximately equal size (A - F; see Map 1) and a triennial burning cycle was proposed (Kime 1984). This would comprise an early winter burn the first year, a late winter burn the second, and no burn in the third year divided between the six blocks. Consequently, four of the six blocks would be burnt every year. At present this plan is not in operation and in essence the reserve is burnt on a biennial basis so that 50 % (three blocks) of the reserve is burnt each year. Firebreaks are burnt at the beginning of winter around the whole reserve and major forested areas, and between blocks. However, several forests have been burnt within the last three years and small patches of swamp forest and **Prionium serratum** are ignored and burnt indiscriminantly.

The provision of concentrated supplementary feeds during the winter ceased in the early 1980's. Approximately five animals are culled

each month to supply rations to employees. The trophies and skins are not sold. Roads and fences are maintained on a regular basis. Aerial censuses of the animal populations are conducted at irregular intervals.

Surrounding inhabitants are permitted to harvest thatch grass (**Cymbopogon validus**) within the reserve. Illegal stripping of bark for herbal medicines and poaching of large herbivores occurs, although not prevalent (N. Ayliffe, pers. comm.). Control of alien species is not regularized and is only via mechanical means. At some stage, the area north of the Mkambati river (± 50 % of the reserve) was proclaimed a 'Wilderness area' and closed to tourists. This area is now open for walking or guided landrover tours.

Reviewing whether or not the stated objectives have been achieved, it is clear that past and present management have fallen far short of the stated objectives, with only objectives (d), (e), to a limited extent, and (h) being attained, none of which serve to generate the intended revenue. Consequently, either the objectives should be reviewed and altered where necessary, or the actions and decisions required to implement them altered.

SOILS

3.1. OBJECTIVE

The purpose of this section was to determine the range in physical and chemical properties and the spatial distribution of the soil types at MGR.

3.2. OVERVIEW & RATIONALE

Soil mapping involves the recognition and delineation of various units of soil (forms, phases, associations, Great Soil Groups, etc.) that are homogenous and meaningful in terms of the objectives of the survey (van der Eyk **et al.** 1969). The primary objective of soil survey is to gather information for usually one of two very different reasons and end users, and, along with terrain maps it constitutes the primary basis for land-use classification (Young 1973, Davidson 1980). The first is agriculturally orientated, in which the properties and distribution of the various soils within a given area are described and mapped in great detail in order to assess their suitability for particular crop species (eg Maud 1966). The second has an ecological bias and aims to use soil data to interpret the distribution and dynamics of the biota. In this instance correlation of particular soil types and/or properties with vegetation (eg Tinley 1982, Walker 1982), or soil properties with animal distribution and impact (eg Downing 1979, Bell 1982) is important. It was with the latter objective (correlation of soils with specific grassland communities and animal impact on those communities) that a description and map of the soils at Mkambati was proposed. It was recognized that it would have secondary uses such as siting of roads and indications of agricultural potential, but discussion on these is limited as it was beyond the scope of the present study.

3.3. METHODS

There are two approaches in sampling an area for soil mapping purposes: (i) to place samples systematically along a predetermined grid system ("grid survey", Young 1976) over the whole survey area, or (ii) to correlate soils with landforms by mapping the various landforms from aerial photographs and topographical maps and then sampling selectively within each of the landforms ("free survey", Young 1976). The underlying approach in this study was that of grid-survey. Samples were taken throughout the reserve, but not in a rigid grid format. The density of samples in any specific area depended on changes in topography, vegetation and surface characteristics of the soil.

The production of a map of scale 1: 10 000 as desired for MGR implied a certain degree of detailed ground work. For such a scale, between four and nine sample points per hectare were proposed by White (1978), while Davidson (1980) quoted several lower figures in the region of 30 to 60 per km^2. As MGR will not be used for intensive arable farming (in the foreseable future) it was considered adequate to have fewer samples than recommended by White (1978) to meet the objectives of this study, and continue to map at 1: 10 000. This allowed the construction of overlays for the base, soil, vegetation and management maps. The total number of samples (1 825), at an average density of 0,24 samples/ha, was close to the estimate of Davidson (1980).

The position of these auger holes was recorded with the aid of aerial photographs (1: 30 000) and orthophotomaps (1: 10 000), as well as pacing the distance on the ground between holes. All the points were then transferred to a base map. Boundaries were then drawn between forms on the map, on the basis of the plotted points and aerial photographic interpretation.

In conjunction with the field samples [using a standard soil auger (120 cm long)] 41 soil pits were exposed for sampling and description throughout the soil profile. Pits were subjectively sited according to two criteria. The first was to characterize the mapped forms according to their physical and chemical characteristics - necessary for the determination of soil series. Thus, pits were sited in areas that were considered representative of each of the particular forms recorded from the auger samples. The second criterion was to locate pits in areas where sampling with an auger had been inadequate to determine the form. Soil forms from both pits and auger samples were classified according to the system of MacVicar **et al.** (1977). The samples removed from these pits were analyzed in the laboratory (after sieving and drying) for texture (Andressian Pipette method), carbon content (Walkley-Black titration method) and pH (in KCl suspension). All methods followed those outlined by the Fertilizer Society of South Africa (1980). The major cations from selected profiles were determined by the SASA laboratories at Mount Edgecombe Research Station, Natal.

3.4. RESULTS

Eight soil forms recognized in the Binomial Classification (MacVicar **et al.** 1977), as well as several previously undescribed forms, were recorded during this study. Recognized forms were: Champagne, Clovelly, Glenrosa, Hutton, Katspruit, Kroonstad, Mispah and Pinedene. The range in physical and chemical characteristics of each of these forms determined from the soil pits is provided in Appendix 1. The distribution of the various forms in the reserve is shown on Map 2 (a reduction of the original at a scale of 1: 10 000).

As to be expected, both the physical and chemical properties varied considerably between and within forms. In some instances, within

form variation was such that several series were present. Major differences between forms were associated with their catenal position, colour, number of horizons and texture. The variation in other factors measured or described was as great within forms as between them. Common to all forms were the low pH, dystrophic nature, apedal or weak structure of all horizons and the general absence of concretions. These properties are probably responsible for the low quality of available forage at MGR (see Sect. 8.4.), which in turn effects animal performance. A layer of reconstituted material (plinthite) between the A and B horizons was found in a few localized areas.

Many areas dominated by the Mispah form possessed a few pebbles at the base of the profile immediately above the R horizon. However, these pebbles rarely exhibited signs of weathering and could not be considered to represent a lithocutanic B horizon. Similarly, in some areas the Mispah form had slight, but noticeable, yellowing towards the base of the profile, but insufficient to be considered as a yellow apedal horizon and were consequently not classified as a Clovelly form. Mottling was generally absent except in gleyed horizons. Consistence of the A horizon was very friable or friable. The sub-soil horizons were usually friable to firm. pH was restricted to a very narrow range between 3,5 and 5,1, thus all profiles were very acid. Chemical analyses of selected profiles (Hutton, Clovelly, Pinedene) to facilitate determination of soil series indicated that phosphorus, potassium and calcium were very low. The low P levels coupled with moderate to strong P fixation, indicated that these profiles were deficient in plant available P for agricultural purposes.

3.5. DISCUSSION

The soils recorded during this survey fell into three broad

categories: (i) deep soils with a well developed sub-soil, (ii) shallow undeveloped soils on rock, and (iii) coastal soils and sands. Within each there were various subcategories which are summarized in Table 3.1.

Table 3.1. Soil groups at MGR (figures in parathenses are contribution to the surface area of the reserve)

1. Well developed soils with a deep subsoil:
   (a) ungleyed soils (ferrallitic soils) (16,2 %)
      - Clovelly, Hutton;
   (b) bottomland gleyed soils (hydromorphic soils) (8,5 %):
      (i) top horizon directly above the gleyed horizon
         - Katspruit, Champagne;
      (ii) top horizon and gleyed horizon separated by another horizon (2,7 %)
         - Pinedine, Kroonstad.
2. Shallow, undeveloped soils on rock (66,3 %):
   - Mispah, Glenrosa.
3. Coastal soils and sands (2,8 %):
   - Natal red sands (Berea Formation), Constantia, undeveloped dune sands.

3.5.1. Well developed soils with a deep subsoil

This category included soils of both typically mid-slope and bottomland soil forms. The gleyed soils, especially Champagne form, were strongly associated with wetland vegetation dominated by sedges (see Maps 2 and 3), and/or swamp forest dominated by **Syzygium cordatum** and **Voacanga thouarsii**. Both of these communities are adapted to very moist conditions which exclude most graminoids and trees (Bennett and Doss 1960, Orchard **et al.** 1985). The seasonal or permanent waterlogging, and the firm consistence of the

G horizon limits the agricultural potential of these soils. These characteristics give them a safe erosion rating except after compression of the soil and removal of the vegetation.

The ungleyed soils (Clovelly and Hutton forms) are typical of the eastern coastal belt (Harmse 1978). Depth and drainage are good, and the agricultural rating is high, based on physical characteristics under optimum management (Edwards and Scotney 1978, Anonymous 1982). However, the low pH and P, and the dystrophic nature of the soils (Appendix 1) in the reserve would severely limit production in the absence of fertilization and liming. All the areas with Hutton soils support the **Cymbopogon validus - Digitaria natalensis** community.

3.5.2. Shallow undeveloped soils on rock

The shallowness of these soils imposes a physical limitation to agriculture (Edwards and Scotney 1978). Such soils are best suited for natural pasture (Anonymous 1982). The shallowness also imparts a relatively high erosion potential if the vegetative cover is removed. This is ameliorated, to some extent, by the gentle topography within MGR. Soils of the Mispah form (Mispah series) were the most extensive in the reserve contributing 64,7 % of the total area. This was considerably less than mapped by Maud (1966). Being so extensive, there did not appear to be any association of specific vegetation types with this form. The lithocutanic B horizon of the Glenrosa form was not always easily discernable from auger samples and it is probable that some areas mapped as Mispah were, in fact, Glenrosa soils (presently mapped as contributing 1,6 % to the total area of the reserve).

3.5.3. Coastal soils and sands

This was a heterogeneous group with little in common except their

position close to the land-sea interface. Forms that had not been previously described by MacVicar **et al.** (1977) were common in this group. The most extensive was a humic phase of the Mispah form. It was characterized by shallow depth, no weathering of the subsurface rock, and a high organic matter content. The last excluded it from being an orthic horizon as defined by MacVicar **et al.** (1977), and the absence of a subsoil horizon differentiated it from other forms with a humic A horizon. A humic-phase Mispah was recorded by Campbell (1983) when characterizing soils of the fynbos biome, and he quotes several authors who also recorded such a form.

In several localized areas two subsoil horizons have developed beneath this humic topsoil. The first, being the middle horizon in a profile possessing three horizons, was initially considered an E horizon. However, it did not conform to the characteristics of an E horizon as defined by MacVicar **et al.** (1977) for three reasons : (i) the hue in both pits was two units less than permitted, (ii) it did not overlie a diagnostic horizon as the third horizon, i.e. a yellow-brown apedal horizon which was encountered only below 120 cm, and (iii) the overall absence of mottling and the fact that the amounts of organic matter and clay were not reduced relative to the underlying horizon. The second 'deviation' from the standard E horizon of MacVicar **et al.** (1977) highlights FitzPatrick's (1980) criticism of the present classification system; i.e. the determination of when a horizon is diagnostic is inconsistent and lacks a logical approach. If these deviations from the definition of an E horizon are viewed as unimportant (in making this decision the natural variability of soils must be borne in mind together with the artificial boundaries erected by most classification systems), then this profile could be classified as a Constantia form. In contrast, if the colour and depth criteria are rigidly applied then this profile does not conform to any of those in the

Likewise, the marine sands near the coast are not represented in the Binomial Classification. Two types were evident in MGR. The first was restricted to the vicinity of river mouths, and for the most part, was evident as exposed beaches. However, in some localities the sands had been stabilized, and supported dune forest vegetation. Typical species included **Mimusops caffra, Allophyllus sp.** and **Strelitzia nicolai.** The establishment of vegetation resulted in the incorporation of organic matter into the upper portion of the sand, to varying depths. However, the nature of the soil remained that of deposited sand and was consequently mapped as such.

The other soil with strong sand characteristics was typical of the Natal Red Sands (J.E. Granger pers. comm.). They were referred to as Berea-type sands by Tinley (1978) and as the Berea formation (Geological Survey 1976). King (1963) reported that these occur at irregular intervals all along the Natal coast to southern Mozambique. In the reserve, they stretch as a discontinuous belt across the reserve parallel to the shoreline. The belt is interrupted by major drainage features. In common with the sand under the dune forests this sand also exhibited incorporation of organic matter into the upper layers. This is, generally, more pronounced than under the dune forest and in places a definite orthic topsoil horizon is present. In such situations, the profile could be classified as a Hutton form on the basis of the orthic A horizon and red apedal B horizon. However, the properties are so distinctly different to the other Hutton profiles in the reserve that it was preferred to classify these soils as 'sands'. The transistion between the **Themeda triandra - Centella asiatica** community and the **Tristachya leucothrix - Loudetia simplex**

community was located along this belt.

3.5.4. Catenal sequence at MGR

With two exceptions, the marine sands and Hutton soils, the soils of MGR were derived from the same parent material (Natal Group sandstone) and under the same macroclimate (the area is not extensive enough to experience significant climatic differences within its boundaries). It can therefore be expected that the major factor determining the nature and differentiation of the soil at any given site is slope and its influence on drainage. Thus, the proximate cause is the movement or stagnation of water. As there appears to be a regular repetition of the soil sequence according to slope position, it is possible to employ the term 'catena', and use it as the basic mapping and discussion unit. This term has been commonly employed in description of soils in Africa (eg Morison et al. 1948, Boughey 1961). In the context of this study, these are "simple catenas" in that they obey the criterion that the whole slope must be situated on the same parent material (Bunting 1965). These are differentiated from "compound" catenas, where the parent material may differ along the slope (Young 1976).

The typical catenal sequence at MGR is a shallow, undeveloped soil of the Mispah or Glenrosa form at the top of a slope; followed by deeper well developed soils, usually a Clovelly form, occupying the mid-slope position; this, in turn, grades into a profile exhibiting gleying at the base, such as the Pinedene and Kroonstad forms; with Champagne or Katspriut forms, characterized by a well developed G or gleyed horizon, occupying the basal position of the catena. It is not intended to mean that soils on all the slopes conform to this sequence, as many are interrupted by ridges and rock outcrops which alter the drainage morphology in the vicinity. Morison et al. (1948) noted that micro- topography and climate often disturb the

'typical' catena of a region and in this event it was useful to differentiate phases.

The major deviations from the above sequence were: (i) the sandy areas directly adjacent to the coast, (ii) the absence of the Pinedine and Kroonstad forms from the sequence (thus, the Clovelly grades directly into a bottomland soil), and (iii) localized development of red apedal soils of the Hutton form, usually on upland sites. The Hutton probably develops over dolerite dykes that are not always visible at the surface, hence their red B horizon. Both de Villiers (1964) and van Eyk (1967) also recorded a correlation between dolerite dykes and red soils in Natal. In all locations where dolerite was visible at the surface within the reserve, Hutton soils were to be found. However, further investigation would be required to confirm this for MGR as red subsoils also develop where most of the iron present is in the ferric state (M.T. Mentis, pers. comm.).

The influence of topography on soil development was evident in (i) the relative increase in profile depth, (ii) development of a B horizon, and (iii) then a gleyed horizon, moving down the slope. The Mispah and Glenrosa forms were rarely deeper than 0,9 m before hard rock was encountered. More often, the effective depth of these two profiles was closer to 0, 5m. In comparison, profiles at the base of the catena were rarely less than 1,75 m. Often the base of the profile was not attained (maximum sampling depth was 2,3 m).

These three characteristics are brought about by the three causes of catenary differentiation (Young 1976). The first is the transport of material downslope under the influence of gravity. Except on steep slopes and/or highly erodible soils, mass movement of soil under gravity is rare and most movement of material is via

solution. The second cause is lateral eluviation and throughflow of fine particles and nutrients downslope. The third causal factor is the relative position and seasonal fluctuations of the water table. Soils on the crests of slopes do not experience periods of inundation due to rising of the watertable, in contrast to soils on the mid-slope and at the base. The rising watertable during the wet season results in the lower portions of soils on the mid-slope becoming partly or totally waterlogged on a seasonal basis. This promotes the development of subsoil horizons because the lower portion of the profile experiences different conditions relative to the upper portion. Near the base of the slope the period of inundation is longer and may even be permanent at the very base, resulting in the development of gley characteristics or a gley horizon. The increased moisture status of the profiles at the base of the slope also promotes the development of deeper profiles in this situation due to increased subsurface weathering (Bunting 1965).

Differentiation of different soil profiles in the same catenary position is poorly understood. For example, it is unknown why in some situations a Glenrosa form occupies the crest position, and at others a Mispah. De Villiers (1964) suggested that in such situations the pre-history of the site, before the present soil formation cycle, should be investigated. At the other end of the catena, differentiation into Katspruit and Champagne forms was evident, in some instances being adjacent. I suspect that this relates to the duration of waterlogging, with Champagne soils developing under permanently ponded conditions (van der Eyk et al. 1969, MacVicar et al. 1977). This causes anaerobic conditions and the rate of decomposition is suppressed, resulting in the characteristic black horizon, high in organic material (van der Eyk et al. 1969, Daubenmire 1974, MacVicar et al. 1977). Where the

topsoil experiences relief from such conditions for a significant part of the year, a Katspruit profile develops. Consequently, it would not be suprising to find a Katspruit soil fringing a Champagne on the upslope position or in bottomland areas but of greater slope where the water does not pond.

Differentiation between the gleyed soils with more than two horizons, namely Pinedene and Kroonstad possibly depends on the intensity of development of the underlying gleyed horizon. Thus, in a Kroonstad, I propose, the gleyed horizon is firm and well developed, creating a layer of low permeability to the rapid movement of water down the profile. This results in water moving laterally rather than vertically, giving rise to a E horizon (van der Eyk **et al.** 1969, MacVicar **et al.** 1977). On the other hand, I suggest on the basis of observations at MGR that the gleyed horizon of the Pinedene profile is not as well developed as the Kroonstad. Consequently, the vertical movement of water is not hindered to the same extent and therefore lateral movement is not as pronounced.

3.5.5. Comparison with other surveys

Previous soil surveys in this region may be grouped, on the basis of scale, into three groups. Firstly, small scale (1: 5 000 000 or smaller) which includes the whole of southern Africa (eg van der Merwe 1962, Harmse 1978). Secondly, medium scale, ranging from less than 1: 5 000 000 to 1: 250 000, which incorporates most maps attempting to cover the whole of Transkei (eg van Wyk 1967, Wood and van Schoor 1976). The third category, large scale, includes regional surveys at scales of larger than 1: 250 000 (eg Maud 1966). These three scales are analagous to the "exploratory survey, reconnaissance survey and detailed survey" categories of Young (1976). Descriptions by Cawe **et al.** (1984), McKenzie (1984) and Feely (1986) are succinct summaries of the major soil groups for

the whole or parts of Transkei based on the work of van der Merwe (1962) and Wood and van Schoor (1976).

With small scale mapping the soils of the MGR region were classified as Gley-like Podzolic soils of the Natal Coastal Belt by van der Merwe (1962). On the other hand, Harmse (1978) described them as a mosaic of several soil types. This included: (i) humic ferrallitic (red and yellow) soils, (ii) arenaceous sediments, (iii) acid, igneous rock derived lithosols, and (iv) weakly developed soils characteristic of arid regions. The poor resolution at such scales precludes any worthwhile comparison between the results of this study and the above two surveys. The medium and large scale surveys are more suitable.

The reconnaissance survey by Wood and van Schoor (1976) placed MGR in a region characterized by soils with a well developed apedal B horizon, with or without a plinthic intrusion. They were either Red or Yellow/Brown and included Hutton, Clovelly, Griffin, Avalon, Glencoe, Kranskop, Magwa, Inanda, Fernwood and Oakleaf Forms. This group of soils covers only 10 % of Transkei. Many of them share the same subsoil types as the forms encountered during this study, and the only difference is that they have a humic A horizon. Albeit a reconnaissance survey, no mention was made of gleyed soils in bottomland sites.

Of direct relevance to the Mkambati region were the large scale surveys by Maud (1966) and Nduliso (pers. comm.). The survey by Maud (1966), at 1: 50 000, included the area in which MGR lies. He mapped 90 % (approximately) of the reserve as "stony with patches of soil" with no further description. The remaining area was divided between coarse textured soils derived from Natal Group sandstone comprised of the Mkambati, Cutweni and Cartref forms

(8,2 %) and vlei soils of the Lingeni, Mkambati and Warrington forms (± 0,4 %). No test pits were sited within the reserve. Nduliso completed a survey of the agricultural lands adjacent to the reserve at a scale of 1: 10 000. The dominant catenal sequence was Mispah - Cartref - Katspruit, with Glenrosa and Clovelly forms in isolated patches. The Clovelly form appeared to replace the Cartref soils closer to the coast. Over 40 test pits were described. With the exception of the absence of the Cartref form, the results of this survey, including the catenal sequence, are in agreement with those of Nduliso. The chemical analyses from the few selected forms concur with the findings of van Wyk (1968) that soils derived from Natal Group sandstone are very acidic and nutrient poor.

3.6. SUMMARY

1. The several soil forms mapped at MGR are generally arranged in a catenal sequence (Mispah - Clovelly - Pinedene/Katspruit - Champagne).

2. Most of the soils are sandy, acidic, and dystrophic with few concretions.

3. The most extensive soil forms are Mispah (64,7 %), Clovelly (15,9 %) and Champagne (6,8 %).

GRASSLANDS

4.1. OBJECTIVES

The purpose of this section was to determine:-

(1) the range in structure, species composition and spatial distribution of the various grassland communities at MGR;

(2) whether or not the structure, species composition and spatial distribution of the different communities is in any way correlated with particular biotic and/or abiotic factors.

4.2. OVERVIEW & RATIONALE

Vegetation mapping and description usually forms the foundation of any synecological study. This is because: (i) it illustrates the spatial distribution of particular communities that may require more detailed studies, (ii) the juxtaposition of these communites (which may assist the interpretation of the spatial distribution of other communities in particular), and (iii) provides basic knowledge of the physiognomy and species composition of each community (in varying degrees of detail). Information on all of these are required before any management actions can be objectively implemented and assessed. For this reason, it was clear that the initial focus of this study had to be be orientated towards objective classification and ordination of the grasslands of MGR.

4.3. METHODS

The approaches commonly adopted in mapping and describing vegetation are reviewed by Kuchler (1967), Whittaker (1962, 1967, 1973), Shimwell (1971), Mueller-Dombois and Ellenberg (1974) and Greig-Smith (1983). There are advantages and disadvantages associated with each and the choice of any particular approach is

arbitrary but is influenced by the aims of the research and the multivariate analysis routines available (Scotcher 1982).

Data were collected in the field using the Braun-Blanquet approach (see Mueller-Dombois and Ellenberg 1974, Werger 1974). This was adopted in preference to a more quantitative sampling method (such as the wheel-point) as it provides a more comprehensive list of species (Novellie and Strydom 1987, Granger in prep), which was an important consideration since the flora of MGR had been poorly collected at the beginning of this study.

One hundred and thirteen sample quadrats (5 m x 5 m) were distributed throughout the reserve. The size of samples was arbitrarily selected as large enough to provide an adequate representation of species in each sample. The proportion of the total in each community identified during reconnaissance visits (on the basis of physiognomy, dominant species composition and abundance) was in approximate agreement with the contribution of that community to the total area, with a slight bias towards the smaller communities (a minimum of three quadrats per community as far as possible). Identified communities were (i) **Tristachya leucothrix - Loudetia simplex** community (assigned the prefix of 'L' - 78 quadrats), (ii) **Cymbopogon validus - Digitaria natalensis** community ('C' - 15 quadrats), (iii) **Themeda triandra - Centella asiatica** community ('T' - 8), (iv) unburnt moribund areas dominated by **Stoebe vulgaris** and **Athanasia calva** ('S' - 4), (v) several small areas dominated by **Aristida junciformis** ('A' - 3) or (vi) **Festuca costata** ('F' - 2), and a (vii) **Watsonia sp.** community ('W' - 3). Location of the individual quadrats was subjective in accordance with the Braun-Blanquet approach. Sampling was carried out between November and February in areas burnt in the previous winter (except the **Themeda triandra - Centella asiatica** community which failed to

burn). This period coincided with the flowering period for most species which aided identification. As only 50 % of the reserve is burnt each year, field sampling was spread over two growing seasons (1985/1986 and 1986/1987).

The following variables were recorded for each quadrat: (i) all species present and an estimate of their cover-abundance on the Braun-Blanquet scale as modified by Werger (1973), (ii) gradient (Abney level), (iii) altitude (from 1: 10 000 ortho-photographs), (iv) aspect (compass), (v) rockiness (estimated as a percentage of the ground cover), (vi) soil form according the the Binomial Classification of southern Africa (MacVicar **et al.** 1977) (auger sample), (vii) soil depth (auger sample), (viii) grazing (visual estimate of the percentage removed together with notes on species selected). A soil sample (5 - 20 cm below the surface) was taken from the centre of the quadrat for laboratory analysis of pH, texture, conductivity and organic carbon (see Sect. 3.3. for methods). As a consequence of inability to distinguish with certainty between vegetative material of **Rendlia altera**, **Diheteropogon filifolius**, **Elionurus muticus**, **Koeleria capensis** and **Bulbostylis sp.** in all quadrats, they were collectively recorded as 'wire grasses'.

Summarization and interpretation of the data was via TWINSPAN and DECORANA (Hill 1979a, b) after conversion of the cover-abundance values to a scale of 1 - 9. These two program were selected because of their availability at Unitra and their reputation as being the best multivariate methods currently available for vegetation analyses (Gauch 1982). Furthermore, the hierarchical nature of TWINSPAN and the efficiency of DECORANA in extracting meaningful axes that could be correlated with existing environmental gradients (Ter Braak 1986) were additional points in their favour. Whittaker

(1987), however, pointed out that the present techniques still fall far short of providing an adequate environmental interpretation of observed patterns. Due to their extensive use there are several descriptions and summaries of the basic algorithms, strong and weak points, etc. and the interested reader is referred to these rather than summarizing them here (Hill 1979a, b, Hill and Gauch 1980, Gauch 1982, Scotcher 1982, Conlong 1986, Granger in prep.). In each case default values of the program yielded the most satisfactory results after several iterations with altered pseudospecies cutoff levels and/or unequal weightings for species of differing abundance.

The ordination score of each quadrat on the first two axes was correlated (product-moment correlation coefficient) with each of the measured environmental variables. To permit correlation of aspect with the ordination scores, aspects of greater than 180° were converted to the mirror-image of aspects less than 180° as described by Wikum and Wali (1974). This was done after correction of the compass readings for the magnetic declination. For quadrats where soil depth was recorded as greater than 120 cm, a value of 180 cm was used in the calculation of correlation coefficients and mean depth per community.

It was possible that there were non-linear associations between vegetation types and site characteristics which would not be evident from the linear correlation of axis score and environmental variable. This was checked by the use of Correspondence Analysis (CA) described by Greenacre (1986). Organic matter was not included in the CA because of missing values.

The description of the vegetation was compiled from the interpretation of the results of TWINSPAN and DECORANA and field

notes.

The vegetation map (Map 3) was drawn from ground survey using 1: 30 000 aerial photographs and 1: 10 000 ortho-photographs and results obtained from the multivariate analyses.

4.4. RESULTS

4.4.1. Classification of the grasslands

The resultant hierarchical division of the sample plots from the TWINSPAN analysis is given in Figure 4.1. The top 100 species from the TWINSPAN analysis are tabulated in Appendix 2. A full species list for MGR is given by Shackleton (in prep.).

The short grassland immediately adjacent to the coast was recognized as being very different from the remainder of the reserve, with all eight quadrats (plus one from the pre-recognized **Watsonia sp.** community) being separated from the rest of the data set at the first level of division in the hierarchy. Indicator species were **Centella asiatica** and **Ruellia cordata.** At the second level of division the included **Watsonia sp.** quadrat was split off from the eight quadrats of this **Themeda triandra - Centella asiatica** community. Further divisions of this community were not recognizable in the field and were therefore ignored in the final dendrogram.

The main group of 104 quadrats on the positive side of the first division was divided into two groups of almost equal size at the second level. Each consisted of quadrats located in communities which differed widely in terms of floristics, physiognomy and habitat. Thus, this level did not yield meaningful results for classification.

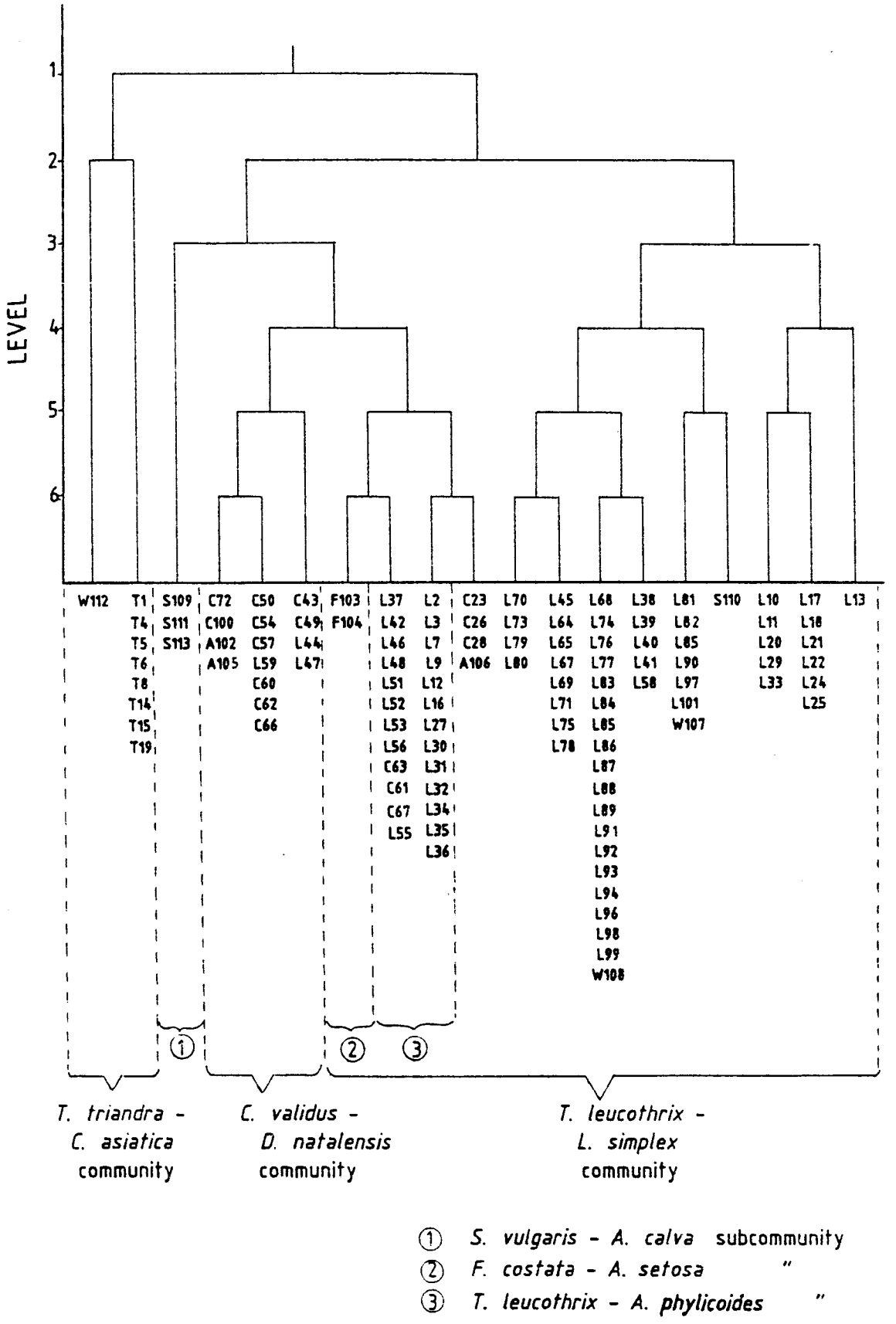


Figure 4.1. Dendrogram of TWINSPAN classification of MGR grasslands

On the other hand, the third level of division reduced each of these groups to recognizable units. In the first instance, three quadrats that represented unburnt grasslands invaded by woody species, primarily **Stoebe vulgaris** and **Athanasia calva**, were separated as a unit. These two species acted as indicators for the positive side of the division. The fourth quadrat placed in this community was not included in this group, probably because it had a greater number of species (50 as opposed to 34, 27 and 17 for the other three quadrats), giving it more species in common with the T. leucothirx - L. simplex community on the other side of the division at level two. From the field situation this is a mis-classification as these four quadrats were the only ones characterized by woody species (shrubs) and were therefore very distinct from the rest of the data set.

The 45 quadrats on the negative side of this division included samples from four of the communities identified during sampling. Successive divisions of this group, at the fourth, fifth and sixth levels isolated the two quadrats dominated largely by **Festuca costata**, although it was not selected as an indicator species. All the Cymbopogon validus - Digitaria natalensis quadrats were separated from those of the T. leucothrix - L. simplex community. Divisions within the C. validus - D. natalensis community appeared to have little practical interpretation beyond level four. The exception to this were quadrats C23, C26 and C28 which were all situated in management block A. This was noteworthy considering that the T. leucothrix - L. simplex quadrats of this block were also recognized as distinct from others of this community at level six. Similarly, soils of areas in this block dominated by C. validus and D. natalensis are different to other areas of the reserve also dominated by these two species (S.E. Shackleton pers. comm.). The TWINSPAN results, therefore suggest that the same holds

true for the areas not dominated by C. validus and D. natalensis. The lower level divisions also separated out quadrats of this community situated on Hutton (form) soils, but included these with quadrats intended to characterize areas dominated by Aristida junciformis. The partitioning of the A. junciformis quadrats between two groups at the fourth level, and the failure to isolate them by the sixth level, leads to the conclusion that these areas of the reserve (only 12,1 ha) are not worthy of recognition as a separate community for management purposes. This is beause they obviously share a large proportion of species in common with other communities, and were therefore not floristically distinct. Two T. leucothrix - L. simplex quadrats (L44 and L47) were included in the major grouping of C. validus - D. natalensis quadrats. This is considered a mis-classification as there is no obvious reason for their inclusion.

More difficult to interpret was the major division of the T. leucothrix - L. simplex quadrats at the second level. The majority of quadrats (55) form a major group of quadrats that are successively divided into smaller groups at the lower levels. The remaining 23 were included on the positive side at level two, along with quadrats from the C. validus - D. natalensis and F. costata communities. Several of the measured environmental variables associated with this group of quadrats were intermediate between those of the C. validus - D. natalensis and T. leucothrix - L. simplex communities (see Table 4.4.).

4.4.2. Ordination of the grasslands

From Figure 4.2. it is evident that the quadrats of both the T. triandra - C. asiatica and Stoebe vulgaris - Athanasia calva communities form very distinct units at the ends of the first and second ordination axes, respectively. To assist in the

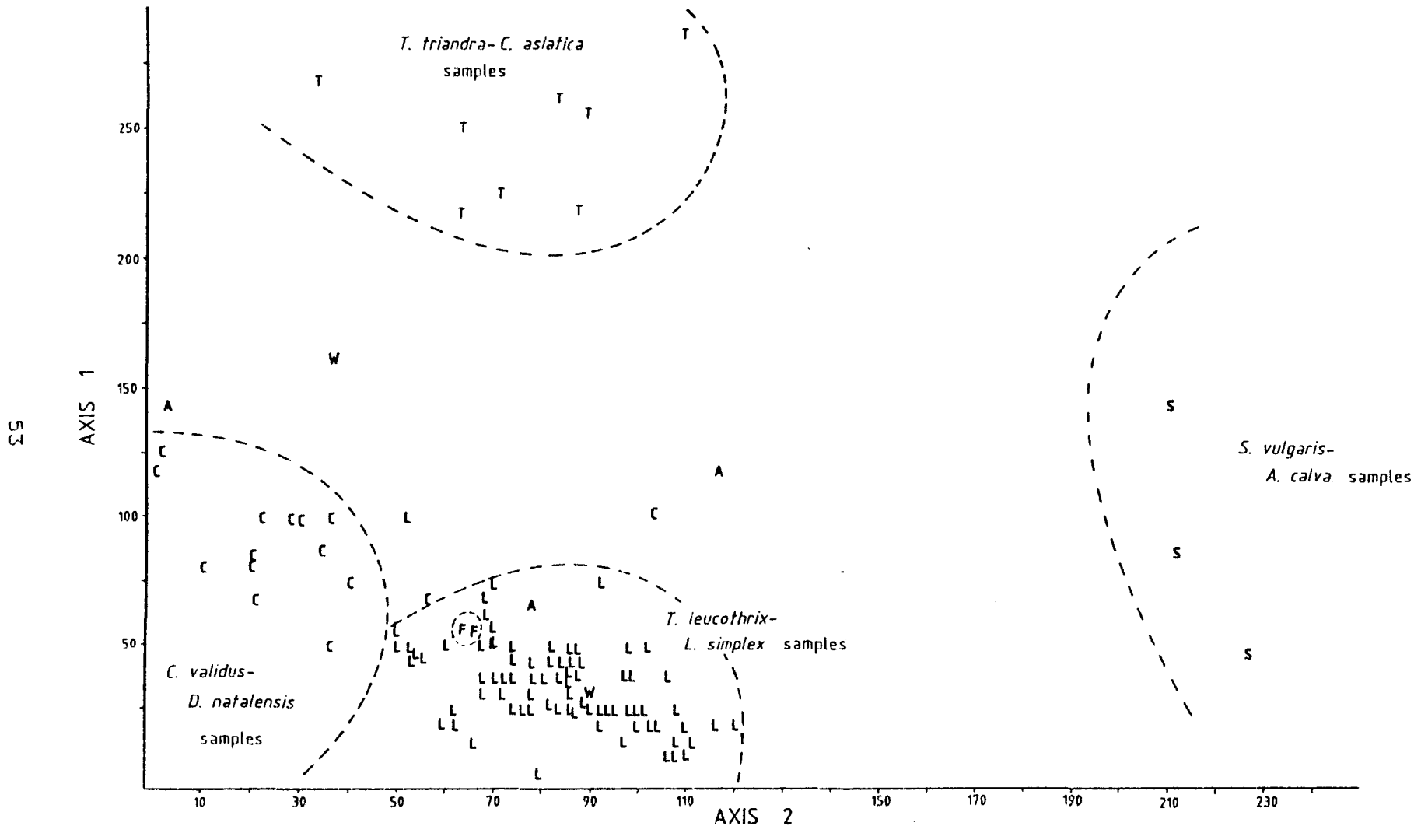


Figure 4.2. DECORANA ordination diagram of all samples

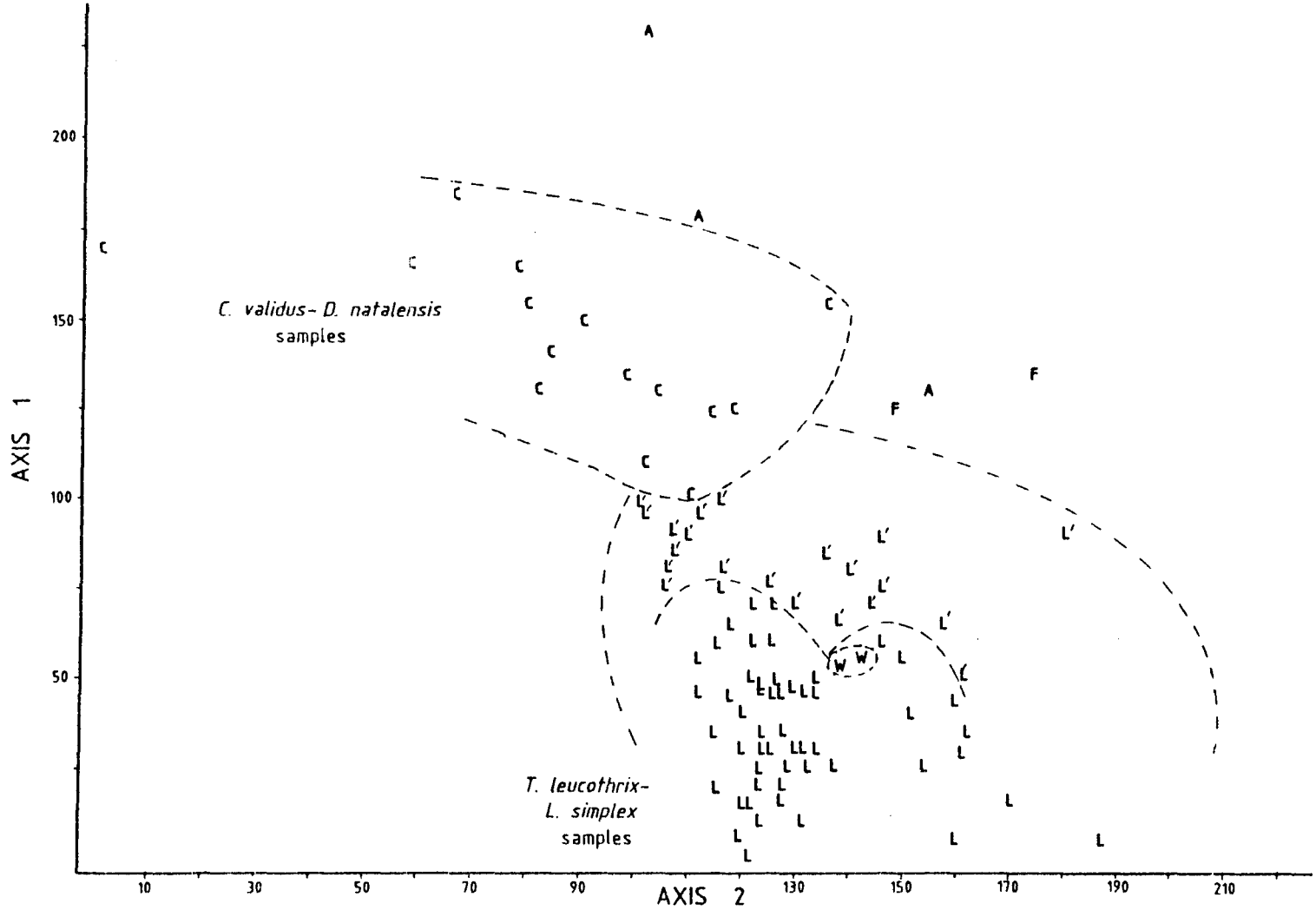


Figure 4.3. DECORANA ordination diagram omitting samples from the T. triandra - C. asiatica and S. vulgaris - A. calva communities

interpretation of these axes three additional iterations were performed successively:- (i) omitting the **T. triandra - C. asiatica** quadrats only; (ii) omitting the **S. vulgaris - A. calva** quadrats only; and lastly (iii) omitting quadrats from both these two communities. The last case is presented in Figure 4.3.

Substantiating the results of the TWINSPAN classification, the **C. validus - D. natalensis** quadrats were grouped together in both ordination diagrams. Furthermore, the quadrats from the **T. leucothrix - L. simplex** community that were included on the same side of the TWINSPAN dichotomy at level 3, along with the quadrats of the **C. validus - D. natalensis** community, are in an intermediate position between the two major communities. During field sampling these quadrats were not recognized as having close affinities with the **C. validus - D. natalensis** community because they lacked these two physiognomically distinct species. The reciprocity of the two techniques is not suprising since both are based on the reciprocal averaging algorithm.

Interpretation of the first two ordination axes was assisted through linear correlation of the ordination scores with each of the measured environmental variables. These have been summarized in Table 4.1.

These results indicated that there was a complex of interrelated environmental variables (see Table 4.2.) correlated with the pattern illustrated in the ordination diagram. The primary axis, with an eigenvalue of 0,409, was highly correlated with soil conductivity, altitude (negative) and organic matter, and marginally correlated with the amounts of sand (negative) and clay (all quadrats considered). The first two were to be expected as there is an increase in altitude and distance from the sea across

Table 4.1. Correlation coefficients between the ordination scores and measured environmental variables

	ALL SAMPLES (Fig. 4.2.)		EXCLUDING EXTREME SAMPLES (Fig. 4.3.)	
VARIABLE	AXIS 1	AXIS 2	AXIS 1	AXIS 2
Conductivity	0,50 ***	0,23 *	0,41 ***	0,40 ***
Altitude	-0,34 ***	-0,34 ***	0,37 ***	-0,36 ***
% Sand	-0,24 *	0,44 ***	-0,59 ***	0,40 ***
% Clay	0,21 *	-0,38 ***	0,58 ***	-0,47 ***
Org. matter	0,49 ***	-0,54 ***	0,58 ***	-0,04 n.s.
pH	0,18 n.s.	0,34 ***	0,11 n.s.	-0,27 **
Slope	0,18 n.s.	0,14 n.s.	-0,01 n.s.	0,20 *
Aspect	0,16 n.s.	-0,05 n.s.	0,13 n.s.	0,10 n.s.
Soil depth	0,05 n.s.	-0,01 n.s.	0,04 n.s.	0,06 n.s.

n.s. $p > 0,05$ * $p < 0,05$ ** $p < 0,01$ *** $p < 0,001$

Table 4.2. Correlation coefficients between the measured environmental variables

	OM	pH	Sand	Clay	Depth	Alt.	Slope	Asp.
Conduct.	-0,42 ***	-0,30 **	0,04 n.s.	0,03 n.s.	0,04 n.s.	-0,24 *	0,28 **	0,16 n.s.
OM		0,05 n.s.	-0,74 ***	0,70 ***	-0,31 **	0,28 **	0,06 n.s.	0,04 n.s.
pH			0,14 n.s.	0,15 n.s.	0,20 *	0,15 n.s.	0,03 n.s.	-0,05 n.s.
% Sand				-0,96 ***	0,25 *	-0,49 ***	-0,10 n.s.	0,10 n.s.
% Clay					-0,30 **	0,50 ***	0,13 n.s.	-0,03 n.s.
Soil depth						-0,20 *	-0,08 n.s.	0,11 n.s.
Altitude							-0,11 n.s.	-0,21 *
Slope								0,18 n.s.

n.s. $p > 0,05$ * $p < 0,05$ ** $p < 0,01$ *** $p < 0,001$

the whole reserve. Such a correlation has been shown elsewhere for coastal regions (eg Westman 1981) and is associated with the

concomitant reduction in sodium chloride input. Omission of quadrats from the T. **triandra - C. asiatica** and **S. vulgaris - A. calva** communities did not alter the correlations except to strengthen the degree of correlation with soil texture. The second axis (eigen value = 0,233) showed correlation with the same variables and pH. However, the degree of correlation was less for conductivity, but greater for the amounts of sand and clay (negative). This indicates some degree of interaction between the two axes. There was a strong degree of interaction between altitude and both soil texture and conductivity. The third and fourth axes had eigenvalues of 0,150 and 0,107, respectively and were not considered further.

The results from CA merely tended to corroborate those obtained above. They are presented in Figure 4.4. and the breakdown of row and column contributions are provided in Appendix 3.

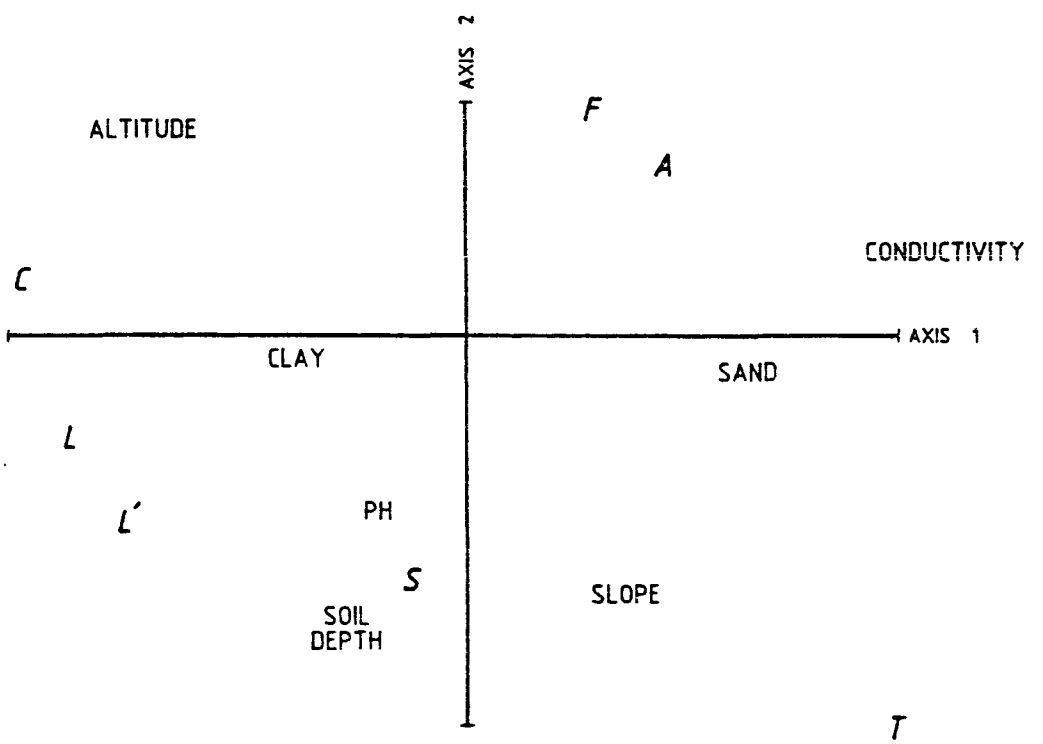


Figure 4.4. Correspondence analysis scatterplot (see Sect. 4.3. for symbol interpretation)

Axes one and two accounted for 69,2 % and 27,7 % of the inertia respectively. The greatest correlations with axis one were conductivity and altitude (negative). Thus, one extreme was characterized by the T. **triandra** - C. **asiatica** community associated with sandy soils, high conductivity and high slope and low altitude. At the opposing extreme was the C. **validus** - D. **natalensis** community at higher altitudes, with clay soils and low conductivity. The T. **leucothrix** - A. **phylicoides** subcommunity (see 4.4.3.2.1.) was intermediate between the T. **leucothrix** - L. **simplex** and C. validus - D. natalensis communities.

Environmental variables most closely associated with the second axis were altitude and soil depth. The S. **vulgaris** - A. **calva** subcommunity was strongly associated with pH and soil depth. This was the only feature highlighted by CA that was not evident from the previous analyses.

4.4.3. Grassland communities at MGR

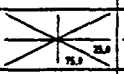
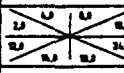
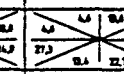
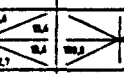
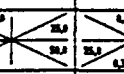
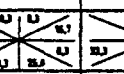
Synthesizing the results from the classification and ordination it was evident that several distinct grassland units were present in MGR. The term 'community' was used as a synonym for an association. Small areas within the major communities differring w.r.t. only the dominant species, or their 'invasion' by other species, were designated as subcommunities. The following descriptions of each community deal with the floristically dominant and more easily identified species as it is aimed at management personnel who often lack formal botanical training. The spatial distribution of these communities is depicted on Map 3. The name assigned to each community was drawn from two species, the first being the physiognomic dominant which is usually very abundant, and the second being an indicator species identified by the TWINSPAN analysis.

Physiognomic nomenclature followed that of Phillips (1971) rather than Edwards (1983) as the height divisions suggested by Phillips (1971) differentiated the various communities at MGR physiognomically. Under the system of Edwards (1983) most of the vegetation units fell into the same category and there was, therefore, no distinction between units except on floristics. As non-botanical personnel often identify more with physiognomy than floristics it was considered important to be able to differentiate the vegetation units at MGR on the basis of physiognomy. Phillips (1971) classified grasslands as dwarf (< 15 cm), short (15 - 45 cm), medium (46 - 100 cm), tall (100 - 200 cm) and high (> 200 cm). Each of the communities was associated with particular ranges of environmental variables (overlapping in some cases) which are summarized in Table 4.4.

4.4.3.1. **Themeda triandra - Centella asiatica** dwarf grassland community (quadrats T1, T4, T5, T6, T8, T14, T15, T19). Plates 4.1. and 4.2.

This was an easily identified dwarf grassland community (mean height was 13,1 $\pm$ 0,58 cm) adjacent to the sea shore. Indicator species were **Centella asiatica** and **Ruellia cordata**. This community had many preferential species, the most easily identifiable in the field being **Euryops leiocarpus, Stenotaphrum secundatum, Geranium ornithopodum, Moraea spathulata** and a short, slender form (ecotype?) of **Themeda triandra**. The last three were faithful to this community. Other faithful, but less abundant species included **Ehrharta calycina, Polygala fruticosa**, and **Crassula pellucida**. Total cover was usually 100 %, with forbs contributing a large proportion, especially **R. cordata, Isoglossa ovata** and **Tephrosia grandiflora**. In localized areas forbs were dominant and the sward appeared more as a herbland (**sensu** Edwards 1983). Moist areas were indicated by the presence of **Juncus kraussii** and smaller sedges, as well as an abundance of **Gazania rigens**. Where the sward had been

Table 4.4. Selected characteristics of the grassland communities and subcommunities at MGR

VARIABLE	COMMUNITY/SUBCOMMUNITY						
	T. TRIANDRA - C. ASIATICA	T. LEUCOTRICH - L. SIMPLEX	T. LEUCOTRICH - A. PHYLICOIDES	F. COSTATA - A. SETOSA	S. VULGARIS - A. CALVA	C. VALIDUS - B. NATALENSIS	A. JUNCIFORMIS - H. MIXTUM
No of samples	8	53	23	2	4	16	3
Altitude (m.a.s.l.)	13,0 ± 2,1 (0 - 22)	148,5 ± 10,6 (30 - 330)	201,8 ± 17,8 (45 - 305)	235,0 ± 20,0 (215 - 255)	123,3 ± 45,4 (60 - 258)	230,4 ± 45,4 (0 - 330)	217,3 ± 31,4 (155 - 255)
Slope (°)	3,8 ± 0,4 (2 - 5)	2,6 ± 0,3 (0 - 7)	2,3 ± 0,3 (0 - 6)	4,0 ± 2,0 (2 - 6)	3,8 ± 0,6 (2 - 5)	2,3 ± 0,5 (0 - 7)	2,0 ± 1,0 (0 - 3)
Aspect (% of Samples)							
Organic Matter (%)	5,0 ± 0,5 (3,5 - 8,3)	3,0 ± 0,1 (1,1 - 4,8)	3,4 ± 0,2 (2,2 - 4,8)	-	-	5,0 ± 0,4 (2,3 - 8,1)	-
Soil Depth (cm)	117,5 ± 14,6 (70 - 120+)	99,9 ± 8,2 (10 - 120+)	131,3 ± 12,8 (20 - 120+)	75,0 ± 25,0 (50 - 100)	110,0 ± 36,1 (60 - 120+)	108,1 ± 17,5 (20 - 120+)	96,7 ± 41,7 (50 - 120+)
Conductivity (s)	208,0 ± 23,7 (79 - 280)	66,6 ± 2,3 (43 - 120)	77,7 ± 3,5 (57 - 130)	310,0 ± 10,0 (300 - 320)	283,3 ± 16,7 (250 - 300)	78,2 ± 4,9 (54 - 135)	350,0 ± 28,9 (300 - 400)
pH	4,1 ± 0,1 (3,9 - 4,3)	4,0 ± 0,1 (3,8 - 4,4)	4,0 ± 0,1 (3,8 - 4,3)	3,8 ± 0,1 (3,7 - 3,8)	3,7 ± 0,1 (3,5 - 3,7)	4,1 ± 0,1 (3,9 - 4,5)	3,8 ± 0,1 (3,7 - 3,8)
Sand (%)	70,4 ± 1,7 (62 - 77)	75,9 ± 0,8 (63 - 89)	70,5 ± 1,6 (61 - 86)	59,0 ± 6,0 (53 - 65)	75,0 ± 4,0 (70 - 83)	52,1 ± 4,8 (21 - 79)	66,6 ± 6,0 (55 - 76)
Clay (%)	17,1 ± 1,6 (11 - 23)	13,0 ± 0,6 (4 - 22)	17,4 ± 1,5 (3 - 27)	24,0 ± 5,0 (19 - 29)	14,3 ± 2,3 (9 - 18)	30,1 ± 4,1 (8 - 60)	19,2 ± 4,6 (12 - 28)
Height of Sward (cm)	13,1 ± 0,6 (11 - 15)	31,0 ± 1,0 (22 - 50)	35,0 ± 2,0 (22 - 55)	48,5 ± 1,5 (47 - 50)	35,0 ± 3,0 (30 - 42)	64,3 ± 3,2 (47 - 100)	36,3 ± 4,4 (28 - 43)
No. of Species - Total	35,4 ± 1,9 (26 - 43)	56,3 ± 0,1 (44 - 72)	53,7 ± 1,9 (35 - 73)	56,0 ± 2,0 (54 - 58)	32,0 ± 7,0 (17 - 50)	53,2 ± 2,2 (38 - 67)	39,3 ± 2,8 (36 - 45)
- Graminoids	9,4 ± 0,6 (7 - 11)	13,9 ± 0,4 (8 - 20)	13,0 ± 0,5 (8 - 17)	12,0 ± 1,0 (11 - 13)	12,3 ± 1,4 (10 - 16)	13,3 ± 0,7 (7 - 17)	13,0 ± 1,0 (11 - 14)
- Forbs	26,0 ± 1,9 (18 - 33)	41,9 ± 0,8 (30 - 57)	40,7 ± 1,6 (27 - 59)	44,0 ± 1,0 (43 - 45)	19,8 ± 6,3 (7 - 37)	39,9 ± 1,9 (25 - 51)	26,3 ± 2,4 (23 - 31)
Cover (%)	94,5 ± 2,4 (80 - 100)	67,3 ± 1,7 (40 - 93)	71,4 ± 1,8 (60 - 90)	65,0 ± 15,0 (50 - 80)	51,3 ± 18,0 (15 - 95)	59,1 ± 2,6 (40 - 80)	61,7 ± 11,7 (40 - 80)

opened up (along roads, dung middens, etc.) **Stenotaphrum secundatum** often became dominant, forming a dense mat/lawn in which little else grew.

The total number of species per quadrat ($\bar{x}$ = 34,4 ± 1,93) was less than recorded in the other grassland communities. This was probably a reflection of the strong dominance of **Themeda triandra**, which always had a cover-abundance rating of '2b' (cover is between 13 % and 25 % irrespective of abundance) or more. The inland boundary of



Plate 4.1. Themeda triandra - Centella asiatica dwarf grassland



Plate 4.2. Stenotaphrum secundatum 'lawn'

this community was not very distinct (nor discernable on aerial photographs), with a gradual transition into the T. leucothrix - L. simplex community inland. The boundary was mapped where the slender ecotype of T. triandra ceased to be a conspicuous member of

the sward. The maximum width was 450 m, and the total area was 219 ha.

This community was associated with deep sandy soils of which Champagne, Mispah and coastal sands were the most prevalent. Soil conductivity was high - a result of the high input of sodium chloride from the sea-spray due to the proximity of the surf zone. Wind and salt-spray pruning of the few woody species associated with rock outcrops, especially **Carissa macrocarpa**, indicated that wind and salt-spray are important factors here, and it seems probable that they are responsible for the shortness of this grassland. Evidence in support of this view was provided by the fact that the tillers and/or shoots of most of the species were not reduced in length but had developed a prostrate growthform. Edwards (1967) ascribed the "dense mass of stunted, deformed individuals (grasses) with a neatly clipped canopy, gradually increasing in height away from the sea" of a similar grassland in the lower Tugela basin to salt-spray. Despite the relatively high fuel load (see Sect. 5.4.3.) this community does not burn except, possibly, in winters following very dry summers.

4.4.3.2. **Tristachya leucothrix - Loudetia simplex** short grassland community (53 quadrats). Plate 4.3.

In terms of area this was the dominant grassland in MGR, which, together with the **T. leucothrix - A. phylicoides** subcommunity, contributed 71,1 % (5 487,3 ha) to the total area. Together with the various subcommunities it was the most species-rich community of the reserve ($\bar{x}$ = 56,3 $\pm$ 0,11 species per quadrat), with a high cover-abundance of graminoids. Graminoids contributed over 80 % of the relative basal cover (Shackleton in prep.). Dominant grasses included **Tristachya leucothrix, Alloteropsis semialata**, wire grasses, **Trachypogon spicatus, Loudetia simplex** and **Diheteropogon**

amplectens. Common forbs were Gnidia kraussiana, Osteospermum imbricatum, Helichrysum adenocarpum, Senecio erubescens, S. bupleuroides, and Acalypha punctata amongst others. There were several indicator species, namely Syncolostemon parviflorus, Heteropogon contortus, Urelytrum agropyroides, Relhania sp. and Asclepias sp. Faithful species did not have much meaning for such a widespread community, where they may be locally absent. Recognition of faithful species for other communities and subcommunities was useful because of their limited distribution. Therefore preferential species were better indicators of this community. Easily identified preferential species included Callilepis laureola, Pentanisia prunelloides, Clutia hirsuta, Muraltia sp., Gnidia myrtifolia, Thunbergia atriplicifolia and Syncolostemon parviflorus. As this community covered such a wide area qualitative recognition of dominants was influenced by the patchy nature of some of the more conspicuous species and/or those in flower. Thus, immediately after a fire the profusion of inflorescences of T. leucothrix, Alloteropsis semialata, wire grasses and various geophytes, led to the impression that these species were the dominant species. However, surveillance during the autumn 18 months after a fire leads one to presume Loudetia simplex and Trachypogon spicatus are the dominant species because of the density of their inflorescences is high at a time when very few other species are flowering. Quantitative data collection overcomes this problem. Less abundant grasses included Eulalia villosa, Heteropogon contortus, Urelytrum agropyroides, Ctenium concinnum, Panicum ecklonii and Themeda triandra. Where present, the T. triandra in this community was of a more robust form than that of the T. triandra - C. asiatica community adjacent to the shoreline and they were easily differentiated.

The mean height was 31,0 cm three to five months after burning.

This community was found on all aspects and gradients throughout the reserve. However, it did occupy areas of different soil structure and chemistry to some of the other communities. The soils were sandy loams (mean % sand = 75,9 ± 0,82) with a maximum recorded clay content of 22 %. Conductivity and organic matter were lower than that of all other grassland communities units of the reserve, with means of 66,6 ± 2,28 umhos ($p < 0,005$) and 3,0 ± 0,1 % ($p < 0,01$), respectively. pH was also marginally lower. This community was recorded upon all soil forms encountered in the reserve with the exception of Champagne. Total cover-abundance was often lower on shallow soils.



Plate 4.3. **Tristachya leucothrix - Loudetia simplex** short grassland

4.4.3.2.1. Tristachya leucothrix - Athrixia phylicoides short grassland subcommunity (quadrats 2, 3, 7, 9, 12, 16, 27, 30 - 32, 34 - 37, 42, 44, 46 - 48, 51 - 53, 56)

Despite being separated from the rest of the quadrats dominated by T. leucothrix as early as the second level of the TWINSPAN classification, this unit was ranked only as a subcommunity because it was not readily discernable in the field on the basis of

floristics or physiognomy. As it was not recognized as a distinct vegetation unit during the reconnaissance phase of the study, it was not apportioned a fixed number of quadrats intended to characterize it. However, the results of both the classification and ordination suggested such a unit. Field validation of these results was inconsistent, as some areas were readily discernable as belonging to this vegetation unit, but not others, despite sampling there during initial data collection. Consequently, this subcommunity was not mapped on Map 3, but is possibly worthy of further investigation. Field recognition failed in most areas because the defining species were both scarce and inconspicuous. The dominants were the same as for the **T. leucothrix - L. simplex** community. Preferential species included **Panicum aequinerve, Oxalis sp., Ajuga ophrydis** and **Ledebouria revoluta**. The total number of species was similar to the T. leucothrix - L. simplex community although the height (35,0 $\pm$ 1,9 cm) was slightly greater.

Despite the difficulties of recognizing this subcommunity as representative of a distinct vegetation unit, the validity of this unit was supported by its clear association with different ranges of specific environmental variables. The mean altitude of 201,8 $\pm$ 17,8 m a.s.l. was intermediate between that of the **T. leucothrix - L. simplex** community and the **C. validus - D. natalensis** community, but the ranges overlapped and therefore this was a poor indicator. Conductivity was higher than the **T. leucothrix - L. simplex** community ($p < 0,005$) and similar to that of the **C. validus - D.** natalensis community. Overall soil texture was similar to the **T. leucothrix - L. simplex** community although there was more clay ($p < 0,005$).

4.4.3.2.2. **Festuca costata - Albuca setosa** medium grassland subcommunity (quadrats F103, F104). Plate 4.4.

In terms of species composition this subcommunity was not greatly different from the T. leucothrix - L. simplex community, differing primarily in the presence of Vigna sp. and the high abundance of Festuca costata. However, the tall growthform of the latter species, and its very dark green foliage made it visually very obvious as small patches within the main community, despite covering only a very small area (2,8 ha - hence only two quadrats). The mean height was 48,5 cm. The dark colour facilitated detection of these patches at long distances, which assists its collection by local weavers who use F. costata in weaving various household items. Other species present in abundance were T. leucothrix, Alloteropsis semialata, Panicum aequinerve, Acalypha punctata and wire grasses. The less abundant graminoids included T. triandra, Trachypogon spicatus and Eulalia villosa. The total number of species was 54 and 58 in the two quadrats, respectively. L. simplex was absent, a characteristic of the C. validus - D. natalensis community.



Plate 4.4. Festuca costata - Albuca setosa medium grassland

F. costata is also present in low abundance in the C. validus - D.

natalensis community, indicating its preference for the more clayey soils of the reserve. The two quadrats located in this subcommunity had a mean clay value of 24 ± 5 %, which was higher than all the other vegetation units except the **C. validus - D. natalensis** community. It therefore seems reasonable to speculate that these areas could be invaded by C. validus and D. natalensis. The soil environment differed from that of the C. validus - D. natalensis community in having a significantly higher conductivity. However, with only two samples this can be considered only as a generalization. Both quadrats were on a WSW aspect. Hilliard and Burtt (1987) noted that F. costata is often locally dominant in damp locations in the southern Natal Drakensberg.

4.4.3.2.3. **Stoebe vulgaris - Athanasia calva** short shrub grassland (heathland) subcommunity (quadrats S109, S110, S111, S113). Plate 4.6.

This vegetation unit was ranked as a subcommunity of the main grassland type, because it was believed to be simply an old, moribund expression of the main T. leucothrix grasslands, despite being very distinct within both the TWINSPAN and DECORANA analyses (and some areas having a low abundance of C. validus). The invasion of these species was facilitated by the absence of fire. All the areas sampled, in which these two woody species were dominant, were known not to have been burnt for at least five years. Exclosure plots erected in winter 1985 in a two year old sward of the T. leucothrix - L. simplex community had four established Athanasia calva plants by winter 1987 and two Rhus sp. by April 1988 (Plate 4.5.), i.e. after four years of protection from fire (see Ch. 5). The first plant was recorded in September 1986. Furthermore, extensive areas of A block, as well as a few areas of B block (see Map 1), were dominated by these two species during several reconnaissance visits in late 1984 and early 1985. With the onset

of a regular biennial burn cycle in winter 1985 this woody growth was removed. As yet there are no signs of any re-invasion, and with the current regularity of burning it is unlikely that there will be. Because the extent of this community is related to the period since the last burn, the total area will vary, but at the time of mapping it covered 33,1 ha.



Plate 4.5. 'Invasion' of **Athanasia calva** into the control plot at the **T. leucothrix - L. simplex** site

S. vulgaris and **A. calva** were the TWINSPAN indicator species as well as being the dominant and most conspicuous species in the field for this subcommunity. **Gnidia myrtifolia** was the only other species in the shrub layer, which had a mean height (n = 4) of 118,5 ± 27,49 cm. The herb stratum was moribund relative to the other grasslands of the reserve. Litter cover was always ranked as '03' (6 - 25 %) or greater which was not equalled in any other quadrats. Dominant species in the herb stratum were **Loudetia simplex**, **Trachypogon spicatus** and **Panicum deustum**. Preferential and

faithful species were **Eriochrysis pallida** and **Erica cubica**. Other preferentials included **Leonotis sp.**, **Aristea cognata**, **Helichrysum cymosum**, **Fimbristylis complanata**, **Xyris capensis** and **Dissotis canescens** amongst others. The mean height of the herb stratum was 35,0 ± 3,0 cm. Total species number varied considerably from one quadrat to another (17 to 50) with a mean of 32. General observation left the impression that most areas of this subcommunity had far fewer species than the surrounding grasslands.



Plate 4.6. **Stoebe vulgaris - Athanasia calva** short shrub grassland

In considering this subcommunity as only an older phase of the other grasslands of the reserve it was noteworthy that it was characterized by different ranges in soil pH and conductivity. It had a lower pH and higher conductivity ($p < 0,05$) than all the other communities but the **Festuca costata - Albuca setosa** subcommunity. This suggests two possibilities. All grasslands in the reserve may be invaded by these shrub species in the relatively prolonged absence of fire. Following such invasion **S. vulgaris** and **A. calva** alter the physical environment in a fashion analogous to the acidification of soils under pine plantations, hence the the

increased conductivity and decreased pH (thereby promoting facilitative succession?). Alternatively, these species only invade certain areas of the reserve, in the absence of fire, that have particular physical characteristics. These two possibilities require further investigation and subsequent recognition in the fire plan for MGR.

Values for the other measured environmental variables were similar to those of other communities. Soils were generally sandy in the A horizon, becoming moister with depth. Three of the four quadrats occurred on a Katspruit form. In terms of aspect, the quadrats were situated on northerly and easterly facing slopes, but more samples would be required to confirm this as a preference.

4.4.3.3. Cymbopogon validus - Digitaria natalensis medium grassland community (quadrats C23, C26, C28, C43, C49, C50, C54, C57, C60 - C63, C66, C72, C100). Plate 4.7.

Scattered throughout the reserve were patches of various sizes of medium grassland dominated by Cymbopogon validus and Digitaria natalensis. The total area of these patches was 536,0 ha (6,9 % of the reserve). This estimatation excludes the numerous, very small patches that could not be mapped at the scale of 1: 10 000. The indicator species for this community were C. validus, D. natalensis, Borreria natalensis, Eriosema salignum and Argyrolobium sp.. The more conspicuous preferentials included Scleria melanomphylla, Hypericum aethiopicum, Tritonia sp. and Hypoxis argentea. Small amounts of Aristida junciformis were not uncommon in this community. There was a marked absence of L. simplex and a low abundance of wire grasses. Rare, but faithful graminoids included Helictotrichon hirtulum and Harpechloa falx. Invasives such as Eragrostis curvula, E. plana and Sporobolus africanus were found mostly in this community (although in relatively low

abundance). The average height was 64,3 ± 3,15 cm three months after a fire, but heights of up to 85 cm were recorded in unburnt exclosure plots (see Sect. 6.3.2.). The maximum number of species recorded in a quadrat was 67, with a mean of 53,2 ± 2,2. As well as forming independant patches within the **T. leucothrix - L. simplex** community the dominant species of this community were also associated with forest margins and roadsides, indicating characteristics of early successional species. In the larger patches of this community there were obvious signs that the soil had been ploughed some time in the past. Fields were evident on the 1974 series aerial photographs where the largest patches of **C. validus** dominated areas are presently located.



Plate 4.7. **Cymbopogon validus - Digitaria natalensis** medium grassland

This community was prevalent towards the western regions of the reserve. Nearer the seashore it occurred in only very small patches, usually associated with termite mounds. It was found on heavier textured soils of the reserve, with significantly higher levels of clay and less sand than the widespread **T. leucothrix - L.**

simplex grassland ($p < 0,0005$). Conductivity and organic matter were significantly higher than the T. leucothrix - L. simplex community ($p < 0,005$), as was the nutrient status (S.E. Shackleton in prep.). Wherever Hutton soils occured in the reserve they invariably supported vegetation of this community. However, it was also found on most other forms recorded in the reserve, except Champagne. Its association with heavier textured soils, high organic matter, termite mounds, roadsides, forest margins, and Hutton soils, indicated a preference for sites with a high nutrient status and high moisture holding capacity but well drained. A tendancy for C. validus to follow drainage lines was noted by Hilliard and Burtt (1987) in the Natal Drakensberg. Previously Killick (1963) had pointed out that it prefers moist areas ("streambanks, gullies and forest margins") but added that it could also grow in comparatively dry conditions.

4.4.3.3.1. Aristida junciformis - Helichrysum mixtum short grassland subcommunity (quadrats A102, A105, A106). Plate 4.8.

This was ranked as a subcommunity as the quadrats were not isolated from those of the C. validus - D. natalensis community in the TWINSPAN analysis, indicating that there was a considerable number of species in common between areas dominated by C. validus, and those dominated by A. junciformis. However, their separation in the ordination diagram, and physiognomic difference in the field promoted the recognition of these areas as a separate vegetation unit, despite their small contribution to the total area of the reserve (12,1 ha).

As the name implies, A. junciformis was the dominant species contibuting more than 25 % (up to 75 %) to the cover-abundance. Other dominants differed between the three quadrats. For example,



Plate 4.8. **Aristida junciformis - Helichrysum mixtum** short grassland

A102 had a high abundance of **Borreria natalensis** with most other species ranked as 'r' (rare) or '+' (not abundant and less than 1 % cover), whereas **T. leucothrix, Cyperus obtusiflorus** and wire grasses were common in A105, but not in A106 where **Ctenium concinnum, T. triandra,** and **Diheteropogon amplectens** were the most abundant species after **A. junciformis.** The total number of species ranged from 36 to 45. The mean height was 36,3 $\pm$ 4,41 cm.

Each of the three plots was situated on a different soil form and thus the small sample size precluded anything but the broadest generalization about soil factors associated with this subcommunity.

4.5. DISCUSSION

4.5.1. Evaluation of the classification and ordination results

The TWINSPAN classification, in conjunction with the DECORANA

ordination and field observations provided an adequate description of the several grassland communities, which can form the basis for identifing management units. The 'validity' of the results of the multivariate analyses was assessed by division of the data set into subsets and re-running the program. The initial division was based on the year of data collection (therefore two subsets), and a second divided plots north of the Mkambati River from those to the south. In both instances the separation of communities was similar to that obtained using the whole data set.

It is important to stress that the final units were recognized on the basis of these three approaches together, and that one or another alone may well have yielded different vegetation units. For example, the **Watsonia sp.** areas were not differentiated as a unit by either the TWINSPAN or DECORANA routines (although a larger number of samples may have overcome this), but they were very obvious in the field on the basis of physiognomy and the dominance of **Watsonia** sp. The high abundance of this species in localized areas implies its specialized environmental requirements which were not measured in the course of field sampling. This specialist requirement could mean that these areas should be managed differently to maintain them (if it is desired). Hence these areas were included in Map 3, but not in the community descriptions. A further example is that of the **A. junciformis - H. mixtum** subcommunity which was not 'detected' by the TWINSPAN analysis, but the quadrats were separated from all others in the ordination diagram although not adjacent. Thus, one technique 'succeeded' where another 'failed', but coupled with field observations it was decided to accept this as a realistic vegetation unit. It may require different management to be maintained or eradicated as desired.

All in all, it might appear that the multivariate analyses merely substantiated the field observations, and identified the vegetation units recognized after the reconnaissance visits prior to sampling. However, that was not the case considering that the **T. leucothrix - A.** phylicoides subcommunity was not recognized during the reconnaissance and sampling stages, and hence was not allocated quadrats. However, the results from both the TWINSPAN and DECORANA analyses indicated the presence of a community intermediate between the T. leucothrix - L. simplex community and the C. validus - D. **natalensis** community which necessitated further visits for validation in the field. The final step of field validation is often omitted by researchers. However, it is important (Mueller-Dombois and Ellenberg 1974) in preventing the definition and description of vegetation units from tabulation and synthesis of field data, that are unrecognizable as separate entities in the field. This may be because the indicator and preferential species are (i) small and therefore difficult to detect, (ii) difficult to identify, or (iii) not abundant, thus precluding a different management regime for such an 'abstract' community.

The identification of environmental variables as the causal gradients in species composition suffers from the problem of non-linear responses of most species to environmental variables, a factor not accounted for by most ordination methods (Austin 1976). Likewise, there are few data to support the notion that turnover and replacement of species along a gradient follows a series of Gaussian curves (Austin and Austin 1980). This, and the number of variables correlated with the gradients extracted by DECORANA in this study, precluded anything but generalization about the most important factors governing species distributions [although DECORANA is influenced far less by non-linearities of ecological data than earlier ordination methods (Cowling 1982)]. Nevertheless,

the first ordination axis accounted for a considerable amount of variation that related to a reduction of maritime influence with increasing distance from the seashore. Nevertheless the possibility remains that the most important variables (those exerting the most influence) were not measured.

4.5.2. 'Appearance' and community nomenclature

Inclusion of a term descriptive of physiognomy in the names of each vegetation unit is important if these units are to be recognized by personnel unfamiliar with species identification (Kuchler 1967). Furthermore, it permits comparison of vegetation units and/or quadrats with little floristic similarity (Barbour et al. 1980), which may be useful after quantitative description of the other vegetation types of the reserve. However, physiognomy alone is inadequate for mapping of small areas in detail because several communities may share the same physiognomy, as is the case at MGR. In such instances floristic composition is necessary and desirable in that physiognomy alone rarely reflects local differences in environmental gradients as adequately as measures of species composition (Goldsmith and Harrison 1976). On the other hand it is successful for mapping large areas, showing convergence under similar macro-environmental conditions (Webb et al. 1970, Parsons and Moldenke 1975, Goldsmith and Harrison 1976).

Being an ecological study it was considered acceptable to distinguish ecotypes where necessary. This had little impact on the final description of the vegetation units except for the T. **triandra - C. asiatica** community, where the short, prostrate ecotype of T. triandra is both a dominant and faithful species. It is a noteworthy co-incidence that the orginal ecotype concept coined by Turesson was to explain the differences in height and growthform of individuals of one species growing at the coast from

those growing inland (McNaughton and Wolf 1979). The usefulness of the ecotype concept cannot be denied (Barbour **et al.** 1980), despite classical taxonomy weighting breeding behaviour equally, if not above, morphology or ecological requirements. With the present trend towards multivariate methods to analyse floristic data in conjunction with environmental data (Whittaker 1987) it is highly probable that ecotypes will gain more acceptance in community classification and ordination.

4.5.3. Comparison with other coastal areas of Transkei

Some of the vegetation units described for MGR are common along the coastal region of Transkei. Immediately south of the Msikaba River (the southern boundary of MGR) Cawe **et al.** (1983) described widespread grasslands dominated by T. **triandra** with T. **leucothrix**, A. **semialata**, D. **amplectens**, E. **villosa** and C. **concinnum** in abundance. They also noted a thin strip along the coastal forelands dominated by S. **secundatum** but this was not mapped as it was not visible on aerial photographs. McKenzie and Cowling (1979) and Hoffman (1983) recorded both a T. **triandra** dominated dwarf/short grassland adjacent to the coast (with differing abundances of **S. secundatum**), and a **Cymbopogon** spp. dominated tall grassland in both Dwesa and Hluleka Nature Reserves, respectively. A **Tristachya - Aristida** grassland also occurs in Dwesa NR. The major difference appears to be that the grasslands of MGR are rich in species relative to these two reserves. The mean number of species per quadrat (16 m^2), averaged across all non-wooded communities was 9,7 $\pm$ 0,92 and 15,9 $\pm$ 0,71 at Hluleka NR and Dwesa NR, respectively; whereas at MGR the mean for a 25 m^2 quadrat was 52,9 $\pm$ 0,93. Possibly such a comparison is misleading in that the grasslands of Hluleka NR and Dwesa NR are not sour, and it is well documented that sour grasslands have a greater species richness (eg Scotcher 1982, Granger in prep.).

The Cymbopogon community in Hluleka NR is dominated by C. plurinodis (Hoffman 1983), and that of Dwesa NR by C. excavatus with lesser amounts of C. validus (McKenzie and Cowling 1979), whereas this community in MGR is dominated by C. validus. The underlying geological strata of the Ecca Group and Beaufort Group in Dwesa NR and Hluleka NR respectively, have given rise to soils very different to those of MGR. Nonetheless, one still wonders whether differences in this community between the three reserves is not more of an identification error than anything else. This possibility is plausible considering that C. validus dominates the tall grasslands near Shinixi Point, only 15 km south of Dwesa NR (R. Lubke pers. comm.)

The Tristachya - Aristida community in Dwesa NR is the most species- rich grassland community in that reserve, located predominantly on sands (McKenzie and Cowling 1979). The T. leucothrix dominated areas of MGR bear little resemblence to this community in that they possess many more species, especially forbs, and lack the relatively high abundance of T. triandra and A. junciformis.

4.5.4. Comparison with other sour grasslands

Considering coastal grasslands north of MGR, there is little comparative quantitative work due to the high human population and agricultural pressures which have severely altered whatever coastal grasslands there once were. Edwards (1967) described S. secundatum grasslands immediately adjacent to the coast in the lower Tugela valley, as did Ward (1980) in the Isipingo Beach area in Natal. Edwards (1967) considered that these were located in areas of disturbance (grazing, trampling, or clearance of dune scrub), as noted at MGR.

Recently, quantitative data were analysed for the grasslands on the eastern shore of Lake St. Lucia which are, apparently, very similar to those at MGR in terms of rare species composition (R. Ellis pers. comm.) and structure (J.E. Granger, pers. comm.). The results from Conlong's (1986) work indicate that there is strong similarity between the **Alloteropsis semialata - Diheteropogon filifolius** community on the Eastern Shores and the T. leucothrix - **L. simplex** community of MGR. Dominant grasses in both areas include **T. leucothrix**, A. **semialata**, T. **spicatus** and D. **filifolius** (a constituent of the wire grass component at MGR). Abundant forbs in common include **Callilepis laureola**, **Pentanisia prunelloides**, **Acalypha** punctata, Thunbergia atriplicifolia, Tephrosia sp. and **Commelina** spp. However, the other communities described by Conlong (1986) do not have equals at MGR, those at Lake St. Lucia seeming to be dominated by species characteristic of more hydromorphic areas than MGR. Quantitative analysis of the wetlands at MGR may well reveal floristic similarities with the Lake St. Lucia system.

Possibly one of the most striking features of the MGR grasslands was the relative scarcity of T. **triandra**. Both Acocks' (1953) work and that of Cawe **et al.** (1983) just to the south described the grasslands as being dominated by this species. Furthermore, the major difference between the grasslands of MGR and those of the Natal Drakensberg appears to be the dominance of T. **triandra** in the Drakensberg as recorded by Killick (1967) and Scotcher (1982).

Ranking the species in Table 4.5. in relative order, after omitting T. **triandra**, highlights their similarities. The first two species are T. leucothrix and wire grasses. The next four species are usually a combination of any four of the following six species T. spicatus, H. contortus, A. semialata, L. simplex, E. villosa or D. amplectens. Actual abundances may differ markedly because of

the relative dominance or insignificance of T. triandra. Such a shift in dominance from T. triandra in favour of T. leucothrix, wire grasses, L. simplex and A. semialata might be interpreted by many as a replacement of decreaser species by increaser I and III species through under- and selective utilization of the grasslands of MGR (Tainton 1981). This assumes that these grasslands were once dominanted by T.triandra. Certainly Acocks recorded higher abundances of T. triandra in 1953 in Pondoland Sourveld.

Table 4.5. Comparative abundance of graminoid species at several locations

	Acocks a	This study b	This study c	Scotcher c
T. triandra	21,38	1,62	2,98	42,58
T. leucothrix	21,09	15,49	24,79	12,38
wire grasses	15,55	18,73	22,31	13,11
T. spicatus	12,87	11,81	6,82	7,29
D. amplectens	11,16	4,25	2,39	0,36
M. ceresiiforme	3,55	0,57	0,02	0,56
E. villosa	3,05	1,84	2,12	0,86
C. obtusiflorus	3,01	3,46	1.03	-
H. contortus	2,53	4,56	4,74	7,46
E. racemosa	1,78	0,22	-	0,08
A. semialata	1,39	6,01	18,01	0,45
A. junciformis	0,59	-	-	0,08
L. simplex	0,57	7,11	4,36	0,77

a - % relative abundance; b - wheel point; c - dry-weight-rank

4.5.5. Fire and 'invasion' of fynbos species

The incidence, at MGR, of a large number of species of fynbos affinities is worthy of comment. The most abundant fynbos species were Stoebe vulgaris, Athanasia calva, Erica cubica, E. natalensis, E. natalitia, Calopsis paniculata, Protea caffra, P. simplex, P. roupelliae, Leucodendron spissifolium, Leucospermum innovans, Agathosma ovata, and Muraltia lancifolia. Most of these species, although not all, were confined to unburnt grasslands or rock outcrops and terraces where they were, presumably, protected from

fire. In light of the present poor record of fire control it is important that management determine whether or not to attach some significance to these species, and if so, alter and implement the fire policy appropriately. Walker (1988) has interpreted an ordination axis for the Drakensberg grasslands as being age after a fire. In light of the results of this study and those of Walker (1988) I suggest that the National Working Group for Vegetation Ecology (NWVE) consider 'elevating' the time since the last fire to "compulsory status" for vegetation sampling and description along with the five variables already assigned such status (altitude, aspect, gradient, rock cover, lithostratigraphy). At present it is considered only as an optional measurement (NWVE minutes August 1985).

The invasion of woody species into unburnt areas of MGR indicates that these grasslands can support limited woody vegetation. However, the fact that forest and woodland require well drained sites (Tinley 1982) and the predominance of grassland vegetation on old planation surfaces and hydromorphic soils (Tinley 1982, McKenzie 1984, Feely 1986) indicates that it is unlikely that the whole of MGR would progress into forest in the absence of fire. There is strong inferential evidence that this region (Feely 1986) as well as most of the grassland-dominated eastern seaboard of Natal (Mentis and Huntley 1982) have been grassland for millenia. However, it is quite probable that the area of forest could be increased to a limited extent in isolation from fire, especially along the well developed terrace areas.

As an alternative to the extensive development of forest is the question whether or not the whole reserve could develop into Stoebe vulgaris - Athanasia calva shrubland? This is presently unknown pending determination of its requirements (see Sect. 4.4.3.2.3.),

but it is unlikely that it would cope with the wind and spray of the coastal forelands. In the possibility that large areas of the reserve could be dominated by S. vulgaris - A. calva shrubland, its development would hinge upon management aims.

4.6. SUMMARY

1. Several grassland communities and subcommunities were identified on the basis of floristic and physiognomic differences using TWINSPAN and DECORANA, complemented by field mapping and notes.

2. There is a complex gradient of interrelated environmental variables across the reserve from the seashore inland, with the various communities arranged along it.

3. Prolonged absence of fire probably promotes establishment of woody species.

STANDING CROP

5.1. OBJECTIVES

The objectives for this part of the study were to determine:

(1) the amount of forage in the main communities, and how it was affected by seasonal changes in partitioning of the plant biomass between the phytomass, necromass and litter components;

(2) how the plant biomass was partitioned between the phytomass, necromass and litter components during the year;

(3) how fire and herbivory affect the amount and accessibility of forage and its partitioning between the various components.

5.2. OVERVIEW & RATIONALE

Diet selection, in terms of both quantity and quality is primarily a function of the types and amounts of food on offer. These in turn determine the ecological carrying capacity (*sensu* Caughley 1976) of any particular region. Thus, it was necessary to determine the amount (this chapter) and quality (Ch. 8) of food on offer to herbivores at MGR. The former was to be achieved by estimation of the standing crop throughout the year. This approach followed that employed by Scotcher (1982) and Conlong (1986) in the sour grasslands of Natal.

Due to the confusion arising from the interchangeable use of the terms 'standing crop' and 'productivity' in the literature, it is important to distinguish between them at the start. In this study standing crop was defined as the total mass of standing organic material per unit area at a particular moment. It comprised standing live material (phytomass), standing dead material

(necromass) and unattached material (litter). It was distinguished here from 'biomass' by the inclusion of the litter component. There has been much inconsistency in the usage of these terms (Rutherford 1978, Grossman 1982). Furthermore, both have, at one stage or another, been used synonymously with productivity. Thus, peak standing crop is often equated with productivity (eg Conlong 1986), despite numerous studies showing that it is an underestimate since it neglects the death and decomposition of leaves during the time taken to attain peak standing crop (Singh **et al.** 1975, Williamson 1976, Smith 1985). Individual measurements of standing crop at one moment in time, ignoring previous and subsequent samples and the rate of transfer from one component to the next, will provide an estimate of forage availability. Definition and quantification of productivity at MGR are given in Chapter 9.

5.3. METHODS

One site was selected for monitoring in each of the three most extensive grassland communities (see Ch. 4); namely the **T. leucothrix - L. simplex** community, the **C. validus - D. natalensis** community, and the **T. triandra - C. asiatica** community. Site selection was based on topographic and vegetational homogeneity, lack of disturbance, accessibility, and representativeness of each community as a whole. Characteristics of each site are provided in Table 5.1.

At each site three plots, [30 x 30 m following the recommendations of the GBP (Mentis 1984)], were erected along the contour. Different treatments, corresponding to possible management options, were applied to each plot to permit pair-wise comparisons between the effects of burning and grazing (summarized in Table 5.2.). The **T. triandra - C. asiatica** site failed to burn satisfactorily in 1985 and therefore standing crop estimates were delayed until

Table 5.1. Selected characteristics of the three monitoring sites

	SITE		
	T. leucothrix - L. simplex	C. validus - D. natalensis	T. triandra - C. asiatica
ALTITUDE (m a.s.l.)	80	300	8
ASPECT (°)	163	27	132
GRADIENT (°)	3,5	1	3
DISTANCE FROM SEA (km)	1,0	6,8	0,06
CATENA POSITION	top	top	top
SOIL FORM	Clovelly	-	see Ch. 3
SOIL TYPE	Loamy sand	Silty clay	Sandy loam
A HORIZON:			
DEPTH (cm)	70 - 95	23	92
% GRAVEL	0,8	1,8	-
% SAND	85,4	23,7	76,2
% SILT	4,1	28,2	10,8
% CLAY	8,4	44,3	9,9
pH (KCl)	4,21	3,61	4,04
Field cap. (%)	34,7	48,9	40,0
B HORIZON: *			
DEPTH (cm)	25	25	100+
% GRAVEL	1,4	90,8	2,0
% SAND	77,8		64,9
%SILT	12,6	lateritic	6,7
% CLAY	1,8	horizon	26,2
pH	4,17		4,10
UNDERLYING MATERIAL	saprolite	saprolite	?

* At the T. triandra - C. asiatica site, the B horizon is the 3rd horizon.

Table 5.2. Experimental treatments of plots used in determination of standing crop

PLOT REFERENCE	TREATMENTS	
Grazed	Unfenced	Last burnt July 1985
Ungrazed	Fenced	" " " "
Control	Fenced	Last burnt July 1983?

another attempt at burning was made in 1986. The sward again failed to ignite in 1986. Consequently, there was no fire treatment for this community. Furthermore, the initial estimates of herbivore

offtake from this community (see Ch. 7) indicated that little or no grazing took place. Thus, when clipping commenced in July 1986 only one plot was clipped.

Time constraints precluded replication of the plot series within each community. In accordance with the community based approach of this study it was considered more important to include all the dominant communities, rather than study only one community but with more replicates. This precluded the use of inferential statistics to compare treatments within vegetation types. Between vegetation type comparisons would be based on pseudoreplication (Hurlbert 1984) and therefore inappropriate. However, multiple sampling within each plot provided an estimate of variation within the data. This would have permitted statistical analysis of treatments across all three sites, assuming the sites to be replicates. But, omission of the grazed and ungrazed treatments from the **T. triandra - C. asiatica** site left only two replicates for determination of treatment effects, which was considered insufficient. Hence no inferential statistics were applied.

5.3.1. Above ground standing crop (ASC)

Sample size and number were determined from the results of a short pilot study. Replicates of a series of different sized quadrats were clipped and the resultant material dried and weighed. From this the sample number and size was determined as five quadrats, each 1 x 0,5 m to obtain a SD of < 10 % of the mean. The time available determined that the interval between samples was one month. Each quadrat was randomly located within the plot using a co-ordinate system. Co-ordinates for the first three months' quadrats were drawn before the plots were burnt and all the plants or representative examples were identified and colour coded using varying numbers and colours of four-inch nails inserted into the

soil near the tuft. This permitted identification of tufts for separation into the species groups (see below) immediately after burning. Edge effects of fences were minimized by rejecting co-ordinates siting quadrats within 1 m of the fence. Each quadrat was clipped, using hand clippers, to stubble height. This varied for individual species depending upon whether the species was tufted or not, and ranged from 0 - 2,5 cm. Prior to clipping the height of the sward was measured at the centre of each quadrat which facilitated calculation of biomass concentration (grams per cubic centimeter) following McNaughton (1984).

During clipping the ASC was separated into several species or species 'groups'. These were Tristachya leucothrix, Loudetia simplex, Cymbopogon validus, Digitaria natalensis, Themeda triandra, Eulalia villosa, wire grasses (a combination of species characterized by their very filiform leaves, flowering immediately after a fire, and unpalatability to herbivores - including Elionurus muticus, Diheteropogon filifolius and Rendlia altera), sward (the remaining graminoid species, including sedges), forbs, and all unattached material was classified as litter. The selection of these species and groups was based on observations made whilst sampling quadrats for the community description (Ch. 4) according to three criteria: (i) their palatability, (i.e. had they been grazed?), (ii) abundance in each community, and (iii) the standard increaser and decreaser categories of Tainton (1981). It was intended that pairs of the above species would represent extremes for the selection criteria. Results for individual species are not presented here, but the sampling strategy is mentioned as the calculation of primary productivity (Ch. 9) was based on species peaks and not peaks in the total sward.

Litter was collected by hand both during and after clipping each

quadrat. This fraction was often contaminated with large amounts of soil (especially at the **T. triandra - C. asiatica** site). In these cases the soil and the litter were separated in the laboratory by flotation and sieving.

Following clipping a soil sample was taken from the centre of each quadrat, to a depth of 8 - 12 cm, for determination of soil moisture (gravimetrically). This was the depth attained by most of the root mass (Shackleton **et al.** 1988).

Material clipped from each quadrat was hand sorted in the laboratory into phytomass (attached green material), necromass (attached dead material) and flowering material. It was then dried at 45 - 50° C along with the litter until constant mass was achieved and then weighed to the nearest 0,1 g.

5.4. RESULTS

5.4.1. T. leucothrix - L. simplex site

5.4.1.1. Biomass concentration

Changes in biomass concentration and height of the sward throughout the study period are given in Figure 5.1. There is a clear distinction between treatments until January 1987. The control had the highest concentration, the grazed plot the least, and the ungrazed plot was intermediate between these two. Thereafter there was little difference between the plots, all being in the region of 1 mg/cc. Concentrations peaked in March and April (both years) and again in August/September. The lowest concentration was evident in winter (May - June).

The mass of the three components of standing crop (phytomass, necromass and litter) for each treatment throughout the study period is illustrated in Figure 5.2. The contribution of the

phytomass and necromass components to the biomass are summarized in Figure 5.3. All absolute figures are presented in Appendix 4.1.

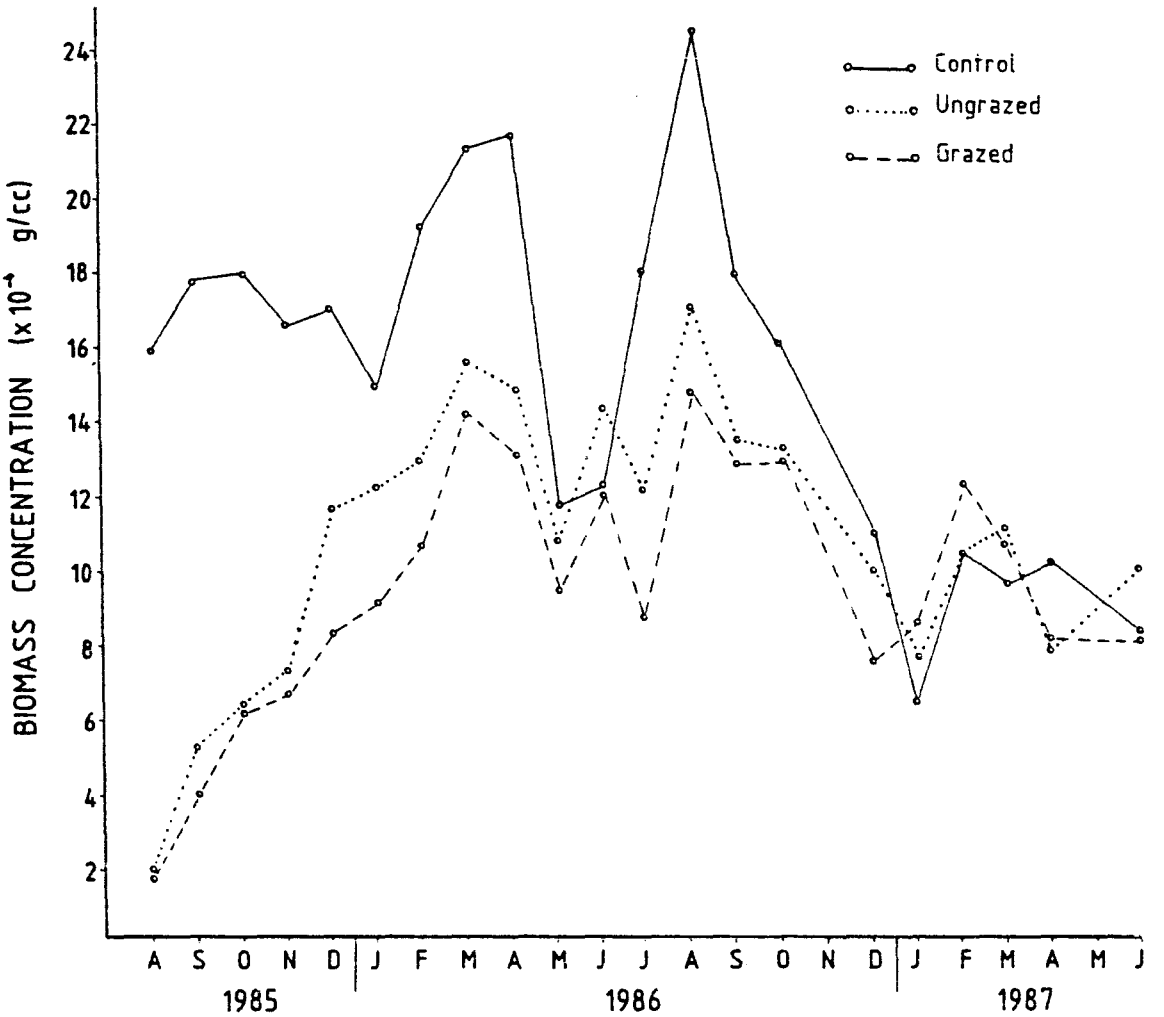


Figure 5.1. Biomass concentration at the **T. leucothrix - L. simplex** site

Total biomass showed a significant linear increase in both of the burnt plots over the period of study (grazed plot: $y = 10,3x + 104,2$; $r = 0,69$; $p < 0,001$; ungrazed plot: $y = 10,4x + 130,5$; $r = 0,62$; $p < 0,005$). The control plot exhibited an opposite trend, displaying a significant linear decrease during the course of the study ($y = 10,2x - 508,3$; $r = 0,65$; $p < 0,005$).

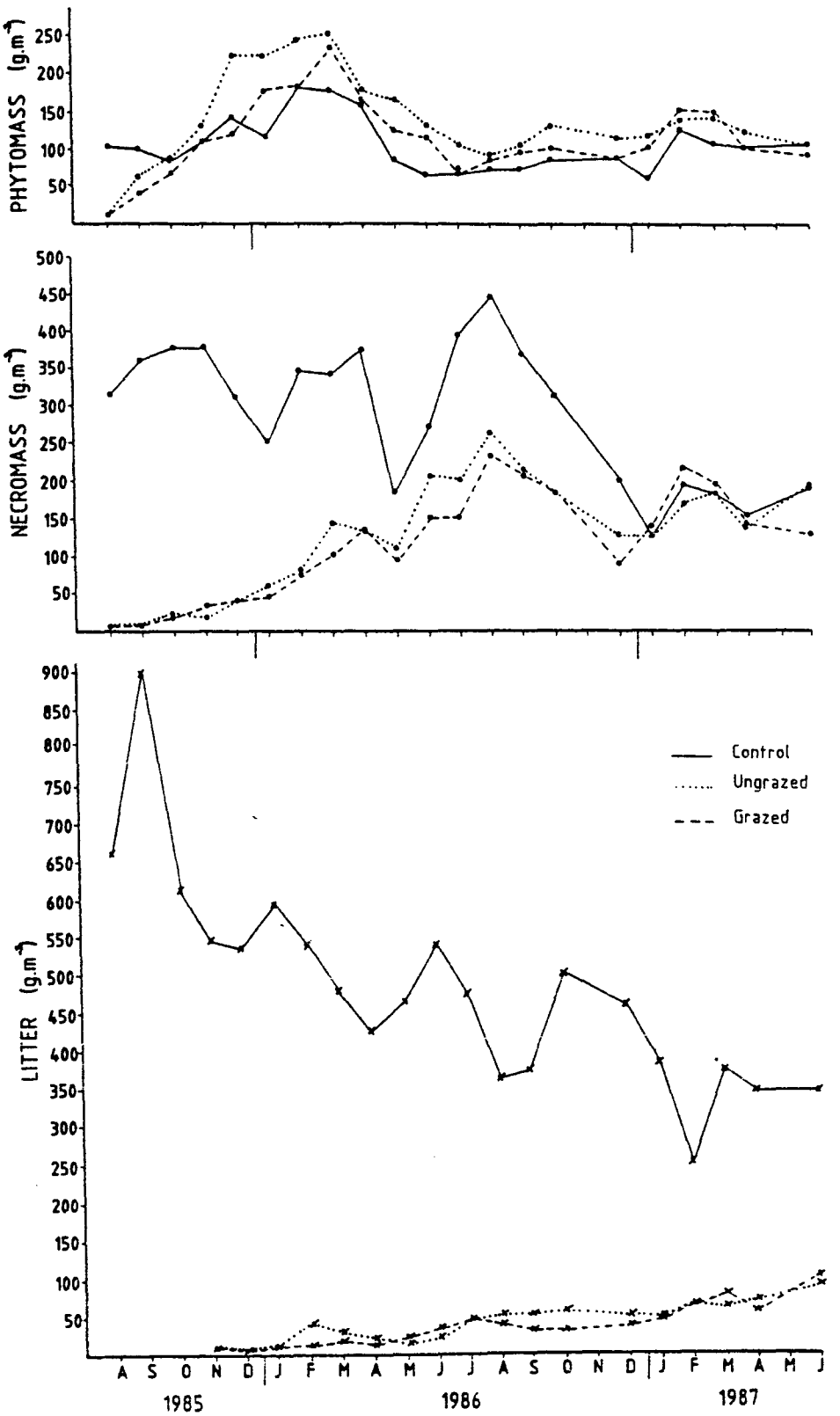


Figure 5.2. Above ground standing crop components at the T. leucothrix - L. simplex site

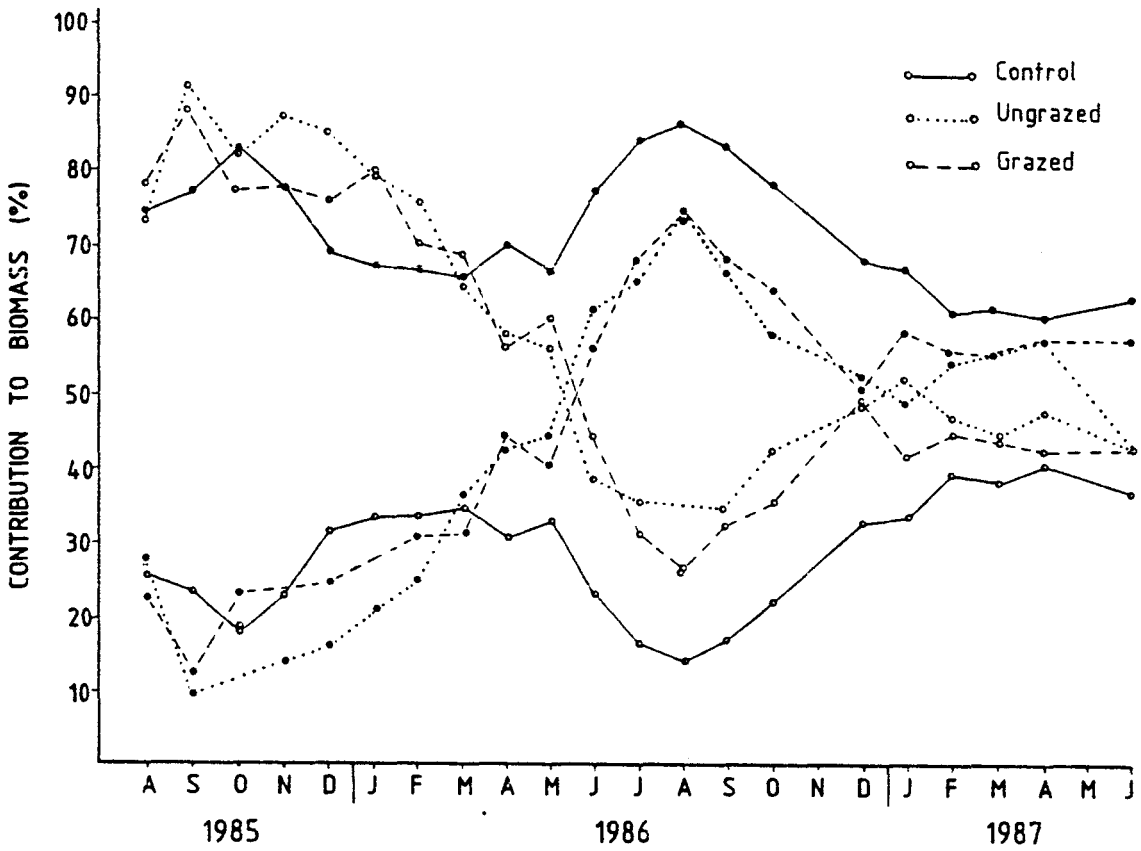


Figure 5.3. Contribution of phytomass and necromass to the biomass at the T. leucothrix - L. simplex site (o - phytomass, ● - necromass)

5.4.1.2. Phytomass

From these two figures it is evident that phytomass was greatest in the ungrazed treatment and there was little difference in phytomass between the grazed and control plots. Peak absolute phytomass was attained during February and March for all treatments. Peak relative percentage (of biomass) was achieved at the same time for the control plot (30 - 34 %) and for the grazed and ungrazed plots in 1987. The relative percentage phytomass showed no peak in the grazed and ungrazed plots in 1986 because they had just been burnt. Consequently, it was at a maximum immediately after the fire with a flush of new growth that declined steadily from January into winter. The decrease during March and April was rapid, averaging

1,75 g m^{-2} per day. The lowest absolute amounts were during winter (July and August), and were maintained well into the following spring due to the late onset of adequate rain in 1986/1987. The average winter amounts were approximately only 40 % of the peak summer values. The amounts present in the second summer were considerably less than in the first, both in absolute and relative terms. An unanticipated drop in phytomass occurred during January of each year, for which no explanation was evident.

5.4.1.3. Necromass

Control plot levels were higher than the other two treatments, although the difference declined as the two burnt plots accumulated mass with maturation. This conformed with expectations as the control plot had not been burnt for two years prior to monitoring, therefore substantial amounts of necromass had accumulated. All treatments had a bimodal pattern, with a major peak at the end of winter (August) and a minor peak in late summer through early autumn (February to March/April). These peaks were separated by declines during December/January and April/May. In the major peak, necromass contributed 74 % to the biomass in the two burnt plots and 85 % in the control plot.

5.4.1.4. Litter

The absolute amounts of litter showed a significant linear increase in the two plots burnt before monitoring began (grazed plot: $y = 3,8x - 11,34$; $r = 0,91$; $p < 0,001$: ungrazed plot: $y = 3,5x - 1,71$; $r = 0,89$; $p < 0,001$). This approximated an average rate of increment of 0,38 g m^{-2} d^{-1} and 0,35 g m^{-2} d^{-1} for the grazed and ungrazed plots, respectively. The contribution (%) to the ASC also increased linearly throughout the study; from 2 - 3 % three months after the fire to over 20 % by the end of the clipping period 20 months later. There was little difference between these two plots

in the amounts of litter at different dates. As with biomass, there was a net decrease in the control plot during the study period, indicating that decomposition was, on average, faster than litterfall. Absolute amounts at the end of the study were only slightly more than half of the amounts recorded when monitoring began. However, expressed as a percentage of the ASC, there was little change throughout the study (usually between 55 % and 67 %). The decrease was related to time by the following equation: $y = -17,1x + 675,0$ ($r = 0,82$; $p < 0,001$).

5.4.2. C. validus - D. natalensis site

5.4.2.1. Biomass concentration

The biomass concentration showed similar trends to the T. leucothrix - L. simplex community although the values were generally less (see Fig. 5.4.). Slight peaks were evident in March/April and again in August/September, separated by low values in May and January. The control plot had the greatest concentration a higher concentration than the grazed plot. For all treatments the concentration was less than the T. leucothrix - L. simplex plots until 1987 when there were no differences.

Biomass was higher in the control than the other two plots on all occasions. Moreover, all values were higher than those recorded at the T. leucothrix - L. simplex site for analogous treatments, indicating that this community was the more productive of the two. This also reveals that the lower biomass concentration at this site is a function of the taller physiognomy, and not a lower biomass.

The net increment in total biomass was significantly linear in all treatments although only marginally so for the control plot (grazed: $y = 29x + 60,6$; $r = 0,96$; $p < 0,001$: ungrazed: $y = 29,2x + 88,9$; $r = 0,93$; $p < 0,001$: control: $y = 12,4x + 679,6$; $r = 0,52$; p

< 0,02). This possibly indicated that the control plot was approaching a steady state.

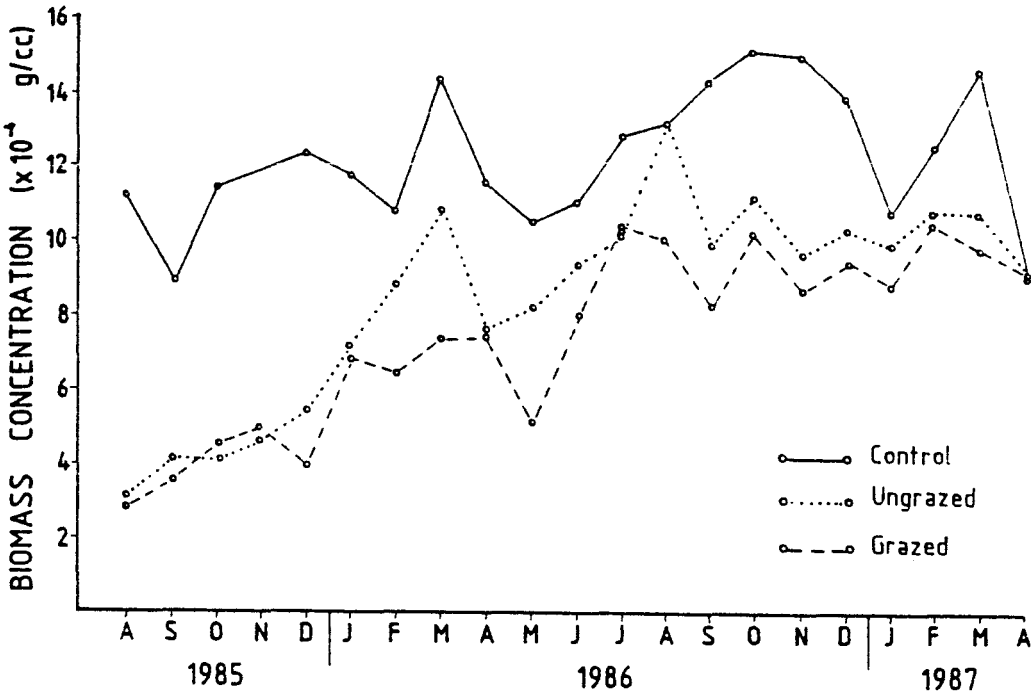


Figure 5.4. Biomass concentration at the **C. validus - D. natalensis** site

The absolute and relative percentage of each of the components of standing crop are presented in Figures 5.5 and 5.6, respectively. All recorded values, with standard errors, are shown in Appendix 4.2.

5.4.2.2. Phytomass

In general, peak amounts were achieved in February, with little difference in absolute amounts between the three plots (290,7; 250,8 and 295,3 g m^{-2} for the control, grazed and ungrazed plots, respectively). During the first year, phytomass was greater in the ungrazed plot than the grazed plot. Thereafter there was no difference between them. The control plot had the greatest amounts throughout the second year. The contribution of phytomass to the biomass was not as high as in the **T. leucothrix - L. simplex**

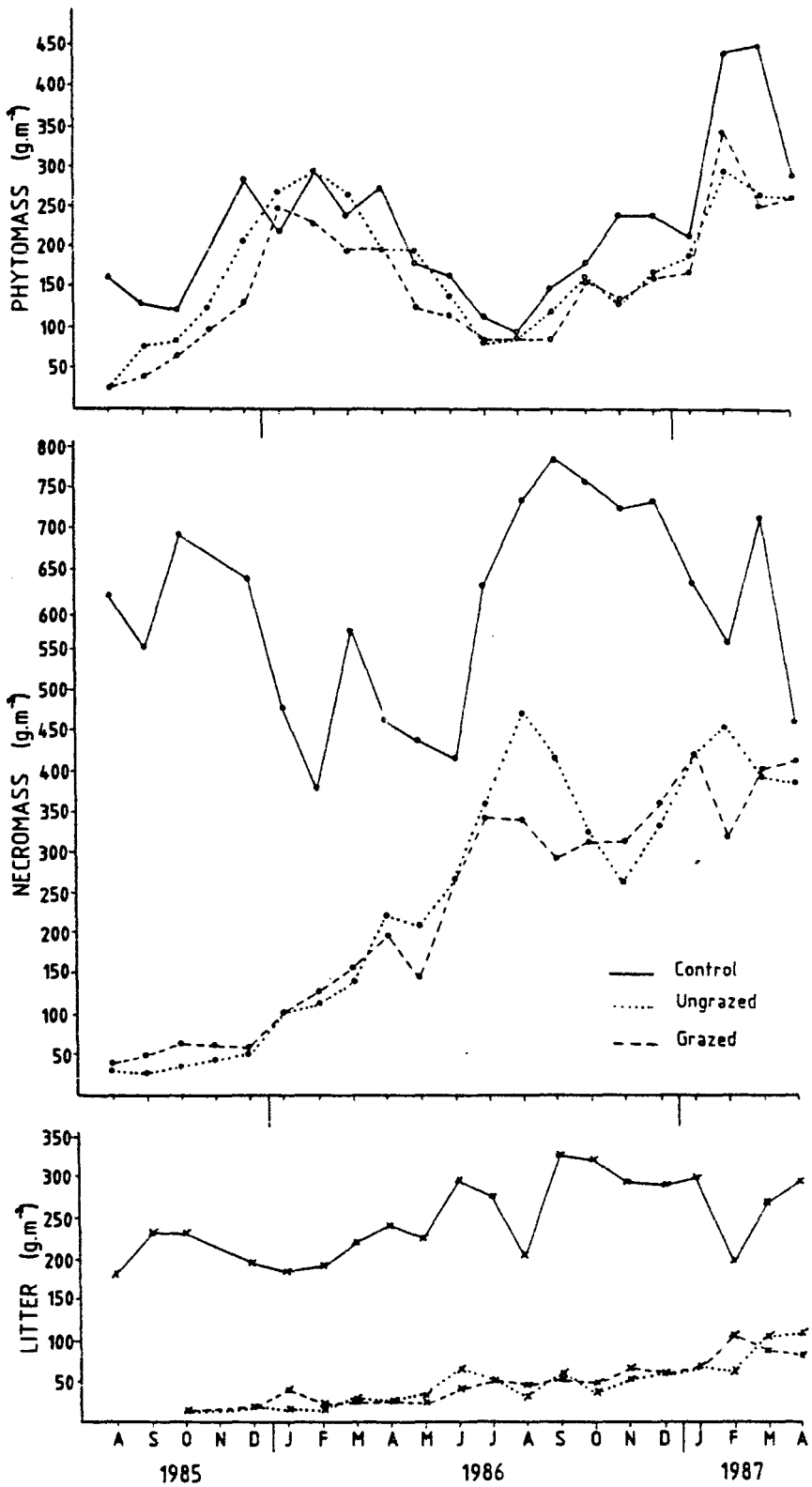


Figure 5.5. Above ground standing crop components at the **C. validus - D. natalensis** site

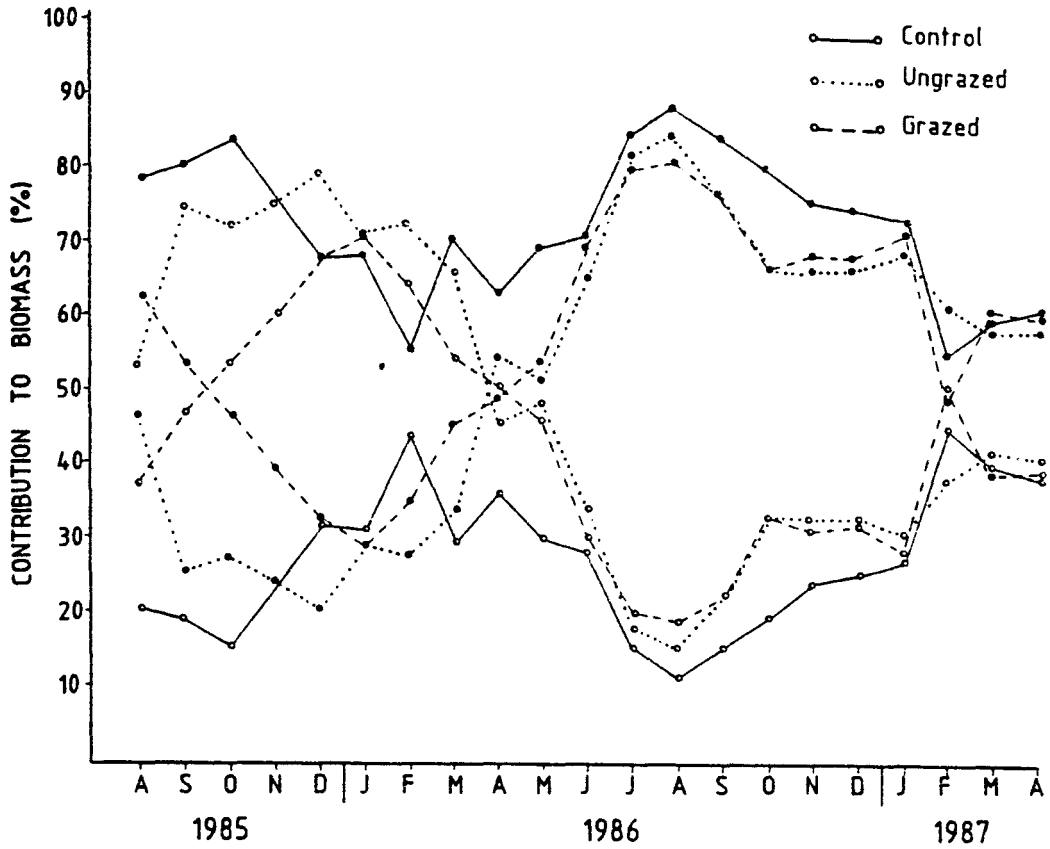


Figure 5.6. Contribution of phytomass and necromass to the biomass at the **C. validus - D. natalensis** site (o - phytomass, ● - necromass)

community immediately after the burn. This was because substantial amounts of charred, but not detached, material (especially from **C. validus** plants) contributed to the necromass component. Thus, there was steady a increment in the proportion of phytomass during the first few months. The percentage phytomass was highest in December (79,3 %) for the ungrazed plot, January (70,4 %) for the grazed plot, and February (44 %) for the control plot during the first growing season.

In the second summer, the percentage phytomass was considerably less in the grazed and ungrazed plots (at 51 % and 42 %, respectively) than the previous year. It was on a par with that of

the control plot (45 %) which was no different from the previous summer. The lowest amounts were recorded at the end of winter in July and August at approximately 45 g m^{-2}, or 15 - 20 %.

5.4.2.3. Necromass

As at the T. leucothrix - L. simplex site, the necromass component was asynchronous with the phytomass component, attaining maximum amounts in winter and least amounts in early summer. Again, a bimodal pattern was evident, with the major peak occurring between late winter and early spring, and the minor peak between late summer and autumn. Necromass was higher than at the T. leucothrix - L. simplex site for all treatments, as was total biomass. The two burnt plots had less necromass than the control plot but this difference declined steadily during the study period. At its peak, necromass comprised 80 - 85 % of the total biomass. The lowest values after the first year were approximately 66 % of the total biomass.

5.4.2.4. Litter

Litter levels were relatively low in the grazed and ungrazed plots, at less than 70 g m^{-2} until 18 months after the burn. There was no difference between these treatments, each showing a steady accumulation with time (grazed: $y = 4,2x - 2,59$; $r = 0,92$; $p < 0,001$: ungrazed: $y = 4,5x - 7,16$; $r = 0,90$; $p < 0,001$). Amounts in the grazed plot were consistently higher than those under the same treatment at the T. leucothrix - L. simplex site, but there was no difference between the ungrazed plots in the two communities. The control plot had higher levels than the two burnt plots, but less than the control plot of the T. leucothrix - L. simplex site. It also exhibited a significant marginal accumulation over time ($y = 4,9x + 194,43$; $r = 0,62$; $p < 0,005$). There was a large increase in winter over the autumn levels. The pattern was similar to that of

the necromass component. Relative contribution to the ASC in the two burnt plots was roughly equivalent to that of the T. leucothrix - L. simplex plots, ranging from approximately 4 % three months after the fire to 12 - 14 % by the end of the study. The control plot contributed a greater proportion to the ASC which was relatively constant, always less than 35 %. This proportion was far less than that measured in the control plot of the T. leucothrix - L. simplex site.

5.4.3. T. triandra - C. asiatica site

5.4.3.1. Biomass concentration

Despite the low height of the sward at this site the biomass was equal to, or higher than, that at the T. leucothrix - L. simplex site, but less than the C. validus - D. natalensis site (comparison between control plots only). This resulted in the biomass concentration being in the region of 50 % greater than at either of the other two sites (see Fig. 5.7.), always being above 1,7 mg/cc.

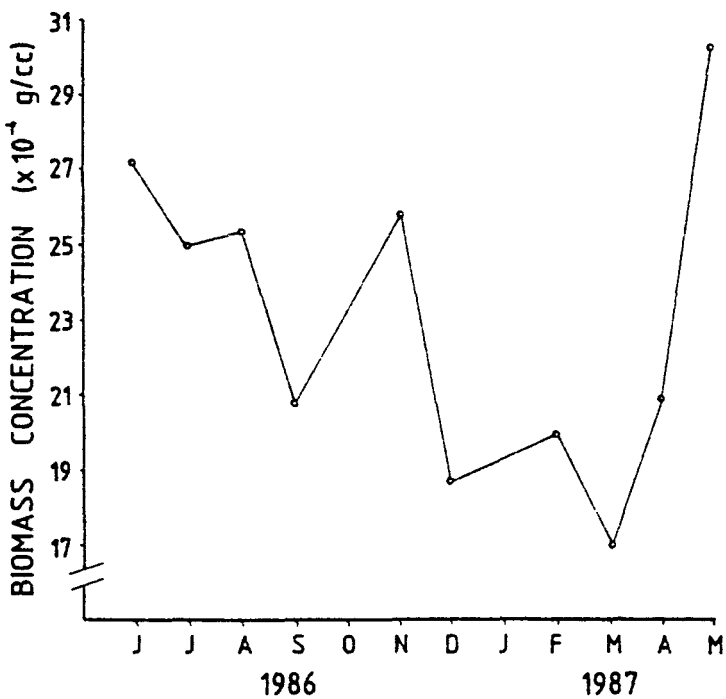


Figure 5.7. Biomass concentration at the T. triandra - C. asiatica site

Here, too, the net increment in biomass was linearly related to time ($y = 18,3x + 362,57$; $r = 0,79$; $p < 0,005$).

The contribution of litter to the total standing crop was less than the T. leucothrix - L. simplex control plot, but was still high at greater than 30 %, usually more than 40 % (see Appendix 4.3). This is less than that recorded at the C. validus - D. natalensis site. It was often greater than the contribution of the necromass component. Phytomass was the least with an average of 18,4 $\pm$ 1,35 % over the course of the monitoring period.

There being only a control plot, all the components of standing crop are presented on the same set of axes (Fig. 5.8.). Changes in relative contribution of phytomass and necromass are presented in Figure 5.9.

5.4.3.2. Phytomass

The contribution of phytomass to the biomass was relatively constant throughout the year except for a peak (up to 42 %) from February to April. With the exception of winter, the contribution to the biomass was on a par with that of the control plots of the T. leucothrix - L. simplex and C. validus - D. natalensis sites over the same period. Levels in winter were almost double those of the other two communities.

5.4.3.3. Necromass

As the inverse to phytomass, the necromass was also relatively constant and with lower winter values than either the T. leucothrix - L. simplex, or C. validus - D. natalensis sites. The lowest amount of 275,5 g m^{-2}, recorded in September, contributed 75,4 % to the biomass. The maximum and minimum contributions differed by only 21 %, indicating that the relative proportions were fairly

constant.

5.4.3.4. Litter

The litter component was usually severely contaminated with aggregated soil particles, often with pieces of litter cemented within, resulting in relatively inconsistent results. Amounts of litter fluctuated widely from one sampling date to the next obscuring any meaningful trends, although a slight positive increase was evident across the whole period ($y = 15,94x + 217,3$; $r = 0,70$; $p < 0,02$). In comparison to the other unburnt sites the mass of litter was slightly higher than that at the C. validus - D.

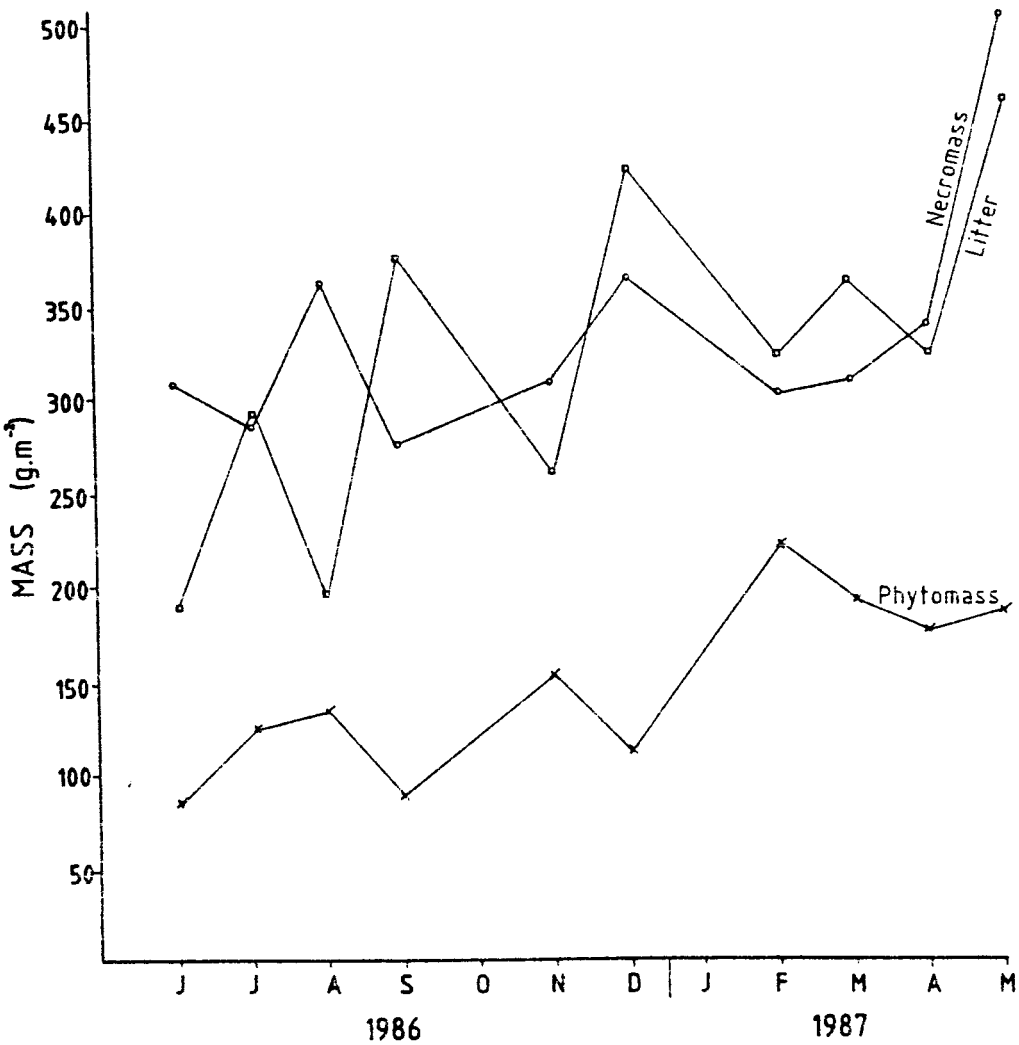


Figure 5.8. Above ground standing crop components at the T. triandra - C. asiatica site

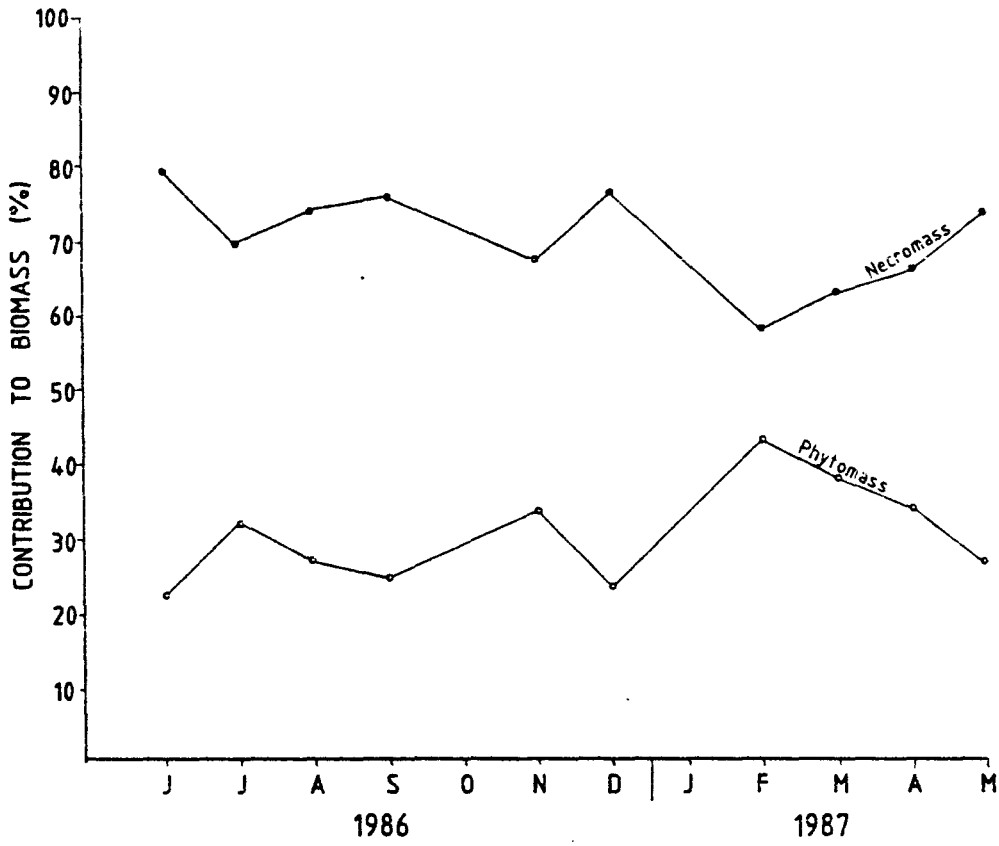


Figure 5.9. Contribution of phytomass and necromass to the biomass at the T. triandra - C. asiatica site

natalensis site, and slightly less than at the T. leucothrix - L. simplex site (although the difference was less by the end of the study due to the decline in litter mass at the T. leucothrix - L. simplex site). It generally contributed 30 - 45 % to the ASC, with a peak of 50,8 %. There were no seasonal trends in the contribution to the ASC.

5.5. DISCUSSION

5.5.1. Biomass concentration

Biomass concentration is not a widely measured parameter in natural systems, but has been measured in planted pastures by several researchers (eg Stobbs 1973a, 1973b, Chacon et al. 1978, Ludlow et al. 1982). Values recorded from the Serengeti grasslands

(McNaughton 1984) are of the same order of magnitude as those recorded during this study. Accepting McNaughton's (1984) extrapolation from the data of Ludlow **et al.** (1982), cow-sized herbivores at MGR would experience biomass concentrations less than that required for maintenance (0,8 g/cc) for up to 5 - 6 months after a fire. This is exacerbated if only the phytomass component is considered edible. Phytomass concentrations were never above this critical level at the C. validus - D. natalensis site, and only at irregular intervals at the T. leucothrix - L. simplex site.

The extent to which large, non-domestic, bulk grazers are influenced by physical characteristics of a sward, such as biomass concentration, has not been determined. However, McNaughton (1984) ascribed the preference and maintenance of grazing lawns by wild herbivores to the low biomass concentration in tall swards. Grazing lawns were very common at MGR (C. Shackleton in prep.), but further studies would be required to determine to what extent the short grass played a role in determining congregations of animals on these lawns. This is confounded by the higher soil nutrient status of these lawns relative to surrounding areas (S.E. Shackleton pers. comm.).

Extrapolation to a wild herbivore system encounters a number of difficulties. First, most wild herbivores are smaller than cattle and therefore require less absolute amounts of food. Hence the biomass concentrations required for maintenance will be lower. Second, in proportion to their smaller size, wild herbivores have smaller mouth parts, which will allow them to be more selective than cows for small-scale, high concentrations of biomass. Thirdly, most wild herbivores are more selective (for species and plant parts) than cattle which enables them to meet their energy requirements from proportionately less food, but of higher

quality. This again reduces the absolute amount of food required and hence the maintenance concentration. Nevertheless, the studies of Stobbs (1973a, b), Chacon et al. (1978) and Ludlow et al. (1982) have indicated the potential usefulness of biomass concentration as a measure of forage availability, and its application to natural systems warrants investigation.

5.5.2. Effects of fire

In agreement with other studies (eg Scotcher 1982, Everson 1985) the unburnt control treatment had a higher biomass and ASC ($p < 0,05$) than the two burnt treatments. However, the difference was either decreasing or had disappeared towards the end of the study. This indicated that it was unlikely that the sward of the control plots was older than two years at the start of the study. Additionally, there were significant differences in the absolute amounts and proportions of the various components between the burnt and unburnt treatments.

The contribution (%) of phytomass to the biomass, and the absolute amounts (after a lapse of 3 - 4 months after the fire) were always higher under the burnt ungrazed treatment relative to the unburnt control treatment (also ungrazed) at the T. **leucothrix - L. simplex** site. This indicates a greater accessibility and amount of edible material per unit area in burnt swards. At the C. validus - D. natalensis site, the proportion (and therefore the accessibility) was always greater in the burnt plot, but absolute amounts were generally less.

The unburnt plots had greater absolute amounts ($p < 0,005$) and proportions ($p < 0,005$) of necromass and litter. This serves to 'dilute' the accessibility of the more edible phytomass. Litter contributed up to 67,3 % and 34,7 % of the ASC at the T.

leucothrix - L. simplex and C. validus - D. natalensis sites, respectively.

5.5.3. Effects of grazing

From the results presented above it is evident that treatment effects were similar at the two sites where all three treatments were monitored. There was a reduction in biomass and ASC in the grazed plot relative to the ungrazed. This was expected as many studies have documented a similar decrease in ASC in open plots relative to exclosed plots (eg Pearson 1965, Spence and Angus 1971, Kumar and Joshi 1972, Sims and Singh 1978, Strugnell and Pigott 1978, le Roux 1979, McNaughton 1985). Averaged across both communities the difference was significant ($p < 0,005$), although small (12,8 % and 6,9 % at the T. **leucothrix - L. simplex** and C. validus - D. natalensis site, respectively), suggesting that food quantity was not limiting at MGR. This difference and its implications are discussed more fully in Chapter 8. This was the only difference between these two treatments as the proportions of the various ASC components were approximately equal. But there was a trend in the first few months for a higher proportion of phytomass in the ungrazed plot. This was probably due to the removal of phytomass in the grazed plot, reducing its relative contribution to the total.

5.5.4. Seasonality

The seasonality of growth patterns was relatively similar to that recorded by Scotcher (1982) in the Natal Drakensberg and Conlong (1986) in the Natal coastal grasslands. Peak ASC/biomass was achieved in March or April at MGR, April or May at St. Lucia, and April at Gaints Castle Game Reserve (GCGR). This coincided with the period of highest mean monthly rainfall at MGR and the end of the rainy season at both the Natal sites, yet biomass and rainfall were

not correlated. The month of peak ASC/biomass was more variable at Cathedral Peak ranging from December to June, although most plots experienced peak biomass between February and May (Everson 1985). The swards at MGR presumably attained peak ASC earlier in the year than the coastal grasslands at Lake St. Lucia in response to the shorter growing season before the onset of cooler temperatures.

Seasonal partitioning of the ASC between the various components was also similar. The lowest contribution of phytomass to the biomass ranged from 12 - 26,6 % at MGR, attained in August for all plots except the **T. triandra - C. asiatica** site which had the lowest percentage phytomass in June. Similar figures for GCGR were 5 - 25,2 % in August (grasses only), and 2 - 9,9 % in August at Cathedral Peak (biennially burnt plots only). The St. Lucia grasslands were distinctly different in that the amount of phytomass was greater than the necromass until 18 - 22 months after a fire. Thus, there was only a slight reduction in availability of green material for herbivores during the first winter after a fire. Lowest absolute values of phytomass at St. Lucia were reached in September or October except for the **Acroceras macrum** community. Obviously the necromass component followed patterns opposite to the phytomass component, with a maximum contribution in August and a minimum immediately after a fire and then again in March/April the following year.

5.5.5. Comparison to other sour grasslands

Considering the sour nature of MGR grasslands and their floristic similarity to the grasslands of the Natal Drakensberg, meaningful comparisons of biomass estimates for these two regions could be made. Such comparisons are hampered by the different ages of swards, a factor that is not always documented by researchers [eg the A. macrum community monitored by Conlong (1986)]. Regrowth of

swards at MGR immediately after a fire was considerably faster than recorded at various sites in GCGR by Scotcher (1982). The seasonal peaks were higher too. The lowest and highest wet-season peaks of 336,5 ± 95,9 g m^{-2} (**T. leucothrix - L. simplex** grazed plot) and 420,4 ± 46,5 g m^{-2} (**C. validus - D. natalensis** ungrazed plot) at MGR were 37 and 117 % greater, respectively, than the highest recorded at any of the one year old sites monitored by Scotcher (1982). Likewise, the peak of 492,9 g m^{-2} recorded by Scotcher (1982) for the 2 - 3 year old Bannerman Hut site was less (7,1 % and 46,5 % respectively) than the peak biomass recorded in the control plots (at both sites) of the same age. Peak values at GCGR were attained in April, at all sites, whilst at MGR the peak was as early as February, through to April.

Everson (1985) concluded that the grasslands in the Cathedral Peak area were among the most productive in southern Africa. All swards at MGR of less than one year had a higher peak in biomass than all six sites monitored by Everson (1985), except site 11B which at 396 g m^{-2} was on a par with amounts recorded at MGR. Older swards (12 - 24 months) at the **C. validus - D. natalensis** site were higher (2 - 102 %) than those at Cathedral Peak (of the same age). Peak biomasses of the **T. leucothrix - L. simplex** site were higher than predicted values for the annual winter burnt areas only, and were less than the areas burnt biennially in spring.

A similar comparison with the coastal grasslands on the eastern shores of Lake St. Lucia indicates that the ASC peaks at the **C. validus - D. natalensis** site were well above that recorded for all communities monitored by Conlong (1986). As Conlong (1986) did not provide appendices of values the comparison can only be approximate, using values read from small-scale graphs. ASC is compared, rather than biomass, as Conlong (1986) graphed ASC. The

grazed plot of the T. **leucothrix - L. simplex** site (0 - 12 months) had a peak ASC of 28 % or more greater than similar aged swards and treatments at St. Lucia except one site (**Cyperus natalensis** community) where the MGR value was 6 % less. The ungrazed treatment (0 - 12 months) had a 40 - 54 % greater ASC than all sites at St. Lucia of equivalent age. The lower difference between grazed plots of the two study areas possibly indicates that the level of herbivory is greater at MGR than around Lake St. Lucia [corresponding with the higher stocking rate at MGR (11,8 ha/AU and 13,8 ha/AU at MGR and the eastern shores, respectively)]. This is further supported by the non-detection of significant differences in ASC between open and exclosed plots at St. Lucia. Even the older swards (12 - 21 months = control plot) of MGR had higher peak ASC than the St. Lucia communities of equivalent age except for the **A. macrum** community. As the **A. macrum** community was a wetland community in dune slacks with a high water-table and relatively organic soils dominated by **A. macrum, Juncus krausii** and **Eragrostis inamoena**, it is possibly not an appropriate comparison.

It appears that the coastal grasslands around Lake St. Lucia had a higher peak biomass than the Natal Drakensberg grasslands, while the MGR grasslands had a higher peak than both. This indicates that coastal grasslands warrant further research. Until recently most attention has been given to the Natal Drakensberg grasslands - long thought to be the most productive in southern Africa. These results and those of Conlong (1986) indicate that the productivity of the Natal Drakensberg grasslands does not match that of the coastal areas.

5.5.6. ASC and abiotic variables

In the absence of corroborative evidence it is possible only to presume that the higher ASC of the coastal grasslands is due to the

more equable climate of these areas relative to the harsh inter-seasonal differences at higher altitudes. There is a well established relationship between precipitation and productivity (Whittaker 1975, Coe et al. 1976), explaining, to some extent, the high productivity of both these high rainfall regions. However, the linear relationship holds true only for regions with a mean annual precipitation of less than 700 mm. Above this amount the relationship between productivity and precipitation is less consistent. Cessation of growth in winter, despite the relatively even distribution of precipitation in coastal regions, indicates that rainfall is possibly not the most important environmental variable influencing growth patterns. The proportion of the mean annual rainfall expected in the three winter months (June - August) is 12,8 % and 14,0 % for the coastal areas of MGR and Lake St. Lucia, respectively. In the Natal Drakensberg the equivalent figures were less than half; 5,4 % at GCGR and 4,0 % at Cathedral Peak.

Temperature differences are greater than differences in rainfall between these two regions. Therefore, the standard relationship between productivity and temperature (Whittaker 1975, Rutherford 1978) may be more useful in explaining the differences in ASC (assuming that ASC and productivity are related). Mean annual temperature at MGR was 6,0^{o} C warmer than at Cathedral Peak, while the mean temperature of the coldest month (July) was 7,4^{o} C warmer and the mean daily minimum temperature of the coldest month was 8,4^{o} C warmer. Frost is mostly absent from the coastal areas, but both frost and snow are common in the Drakensberg. Using the equation of Leith [in Whittaker (1975)] the grasslands of MGR should exceed the productivity of Cathedral Peak by approximately 408 g $m^{-2}yr^{-1}$ (23,9 % higher). Not only is the climate more equable and conducive to higher growth rates in coastal areas relative to

montane areas, but the growing season is longer because of the higher temperatures and more even expectation of rainfall. Sims and Singh (1978) recorded a stronger correlation between the BSC and temperature than the ASC and temperature. The combination of temperature and precipitation in the measurement of evapotranspiration has yielded better correlations than either of those variables alone except in very arid environments (Rosenzweig 1968, Sims and Singh 1978). Unfortunately such data were not recorded at MGR. The soils are dystrophic in both regions and therefore cannot be used to explain the observed differences between such widely separated areas.

On a more localized scale standing crop and/or productivity have been shown to be influenced by a large number of variables such as soil type (McNaughton 1968, Rutherford 1978), fire (Hadley and Kieckhefer, 1963, Rutherford 1978), herbivory (McNaughton 1979, Rutherford 1978, Tomlinson 1986) and rockiness (Rutherford 1983). The C. validus - D. natalensis site, characterized by a higher ASC was located on a more clayey substrate than the other two sites. Studies quoted by Rutherford (1978) support this finding. However, this may simply be a reflection of the different height of the dominant species at this site.

5.6. SUMMARY

1. The grasslands of MGR have a high above-ground standing crop relative to others in southern Africa.

2. Accessibility of forage declines with aging of the sward after a fire.

3. Grazed swards have a reduced forage availability despite only a small proportion being removed by herbivores.

4. Patterns in relative proportions of the various components of above-ground standing crop are markedly seasonal, and therefore so is the accessibility of forage.

5. Fuel loads increase with age after a fire.

LITTER BREAKDOWN

6.1. OBJECTIVES

The objectives of this section were to determine:

(1) the rate of litter breakdown in the most extensive grassland communities of MGR;

(2) what might be the consequences for the communities (in partitioning of the above-ground standing crop) of altering the present fire regime.

6.2. OVERVIEW & RATIONALE

The processes of litter breakdown (LB) and decomposition (LD) have received little attention from researchers in southern Africa compared with Europe and North America (Huntley 1977). This is despite that quantification of LB rates has facilitated a much needed refinement in the calculation of primary productivity (Sims and Singh 1971, Smith 1985). Work that has been done deals with woody species and communities (eg Mitchell **et al.** 1986, Steinke and Charles 1986, Mitchell and Coley 1987, Steinke and Ward 1987) whereas decomposition in swards has been regretably neglected (Tainton 1984). Comparisons of LB and/or LD between herbaceous and woody material indicate the processes of LB and LD to be faster in the former (Singh and Gupta 1977, Morris **et al.** 1982).

It was considered necessary to gain some estimate of LB in the different swards at MGR for two reasons. First, such data were necessary for the calculation of AGP because they are required in the calculation of transfer rates from the necromass component to litter (see Ch. 10). Second, it was of interest to determine the proportion of the total litter that had fallen during the two year interval between burns that was still present at the end of the

biennial burn cycle. This would permit calculation of litter quantities removed by burning and breakdown, respectively.

6.3. METHODS

Rates of LB and/or LD may be determined by several methods which include: tracer techniques, individual leaf monitoring, paired quadrats, and litter bags (Wiegert and Evans 1964, Mason 1976, Swift **et al.** 1979). Despite their drawbacks, (Swift **et al.** 1979), litter bags are the most commonly used (Hunt 1977, Sims and Singh 1978, Stugnell and Pigott 1978), probably because they are the easiest and cheapest relative to the desired level of accuracy - the reason for employing them in this study. Mass loss from litter bags may be attributed to LB, LD and leaching.

Bags were constructed from nylon shade-cloth with a mesh size of 2 mm x 5 mm and closed with copper-coated staples. A large mesh size was selected to permit entry into the bag of all sizes of decomposer organisms, thus approximating the natural situation. Each bag was colour-coded to denote which species it contained using a small piece of coloured insulated wire attached to the corner.

Sufficient amounts of the necromass component of the six key species (**C. validus, T. leucothrix, L. simplex, D. natalensis, E. villosa, T. triandra**) and the wire grass complex were collected in August 1985 from a one year old sward. August was chosen to coincide with the end of the non-growing season as it was presumed that most of the material had entered the necromass component in the 2 - 3 months prior to collection and was therefore of relatively uniform age. This was dried at 60° C until constant weight. Samples of 10,0 g were then placed in the shade-cloth bags for all species except wire grasses and **T. triandra** for which 5,0 g

and 4,5 g were used, respectively. The pre-drying of the litter appeared to have no effect on the subsequent rate of LB in the field with the exception of **E. villosa** (Shackleton and Rogers, in prep.).

A total of eighteen bags for each species were placed at each of the three grassland monitoring sites (Sect. 5.3.) on 4 September 1985. This allowed for the collection of three bags for each species at approximately three month intervals, from each site. Bags were placed in the control plot to prevent disturbance by herbivores and/or wind in the burnt plots. In the absence of data indicating the contrary, it was assumed that the rate of LB was similar in the three plots. Each was placed on the soil surface between individual grass tufts.

Upon collection, foreign material was removed from the surface of the bags and each was then placed in a plastic bag, sealed and transported to the laboratory. There, the litter bags were placed in a convection oven at 60° C for five days (time required to attain constant mass - determined from the initial drying before bags were placed in the field).

When dry, the contents of the litter bags were hand sorted to remove any soil or other foreign matter and weighed to the nearest 0,1 g. When necessary, organic material was examined under 3x magnification to determine whether or not it was the same as the material originally placed in the bag. If the material was severely contaminated with soil the sample was placed in a solution of $MgSO_4$ with a specific gravity of 1,2 to separate the organic fraction from the soil in the manner described by Curry (1969). The $MgSO_4$ was then washed off with several rinses in distilled water

and the material redried and weighed.

Exponential decay statistics and constants were calculated using equation 6.1. (Mitchell et al. 1986, Steinke and Ward 1987).

$$\text{Natural log } (X_t/X_0) = -kt \quad \ldots\ldots\ldots\ldots\ldots \text{ (Eq. 6.1.)}$$

where: X_t dry mass remaining at time t

X_0 dry mass at beginning of the study

6.4. RESULTS

6.4.1. T. leucothrix - L. simplex site

Mass loss from the different species is illustrated in Figure 6.1. Mean values and standard errors are given in Appendix 5.

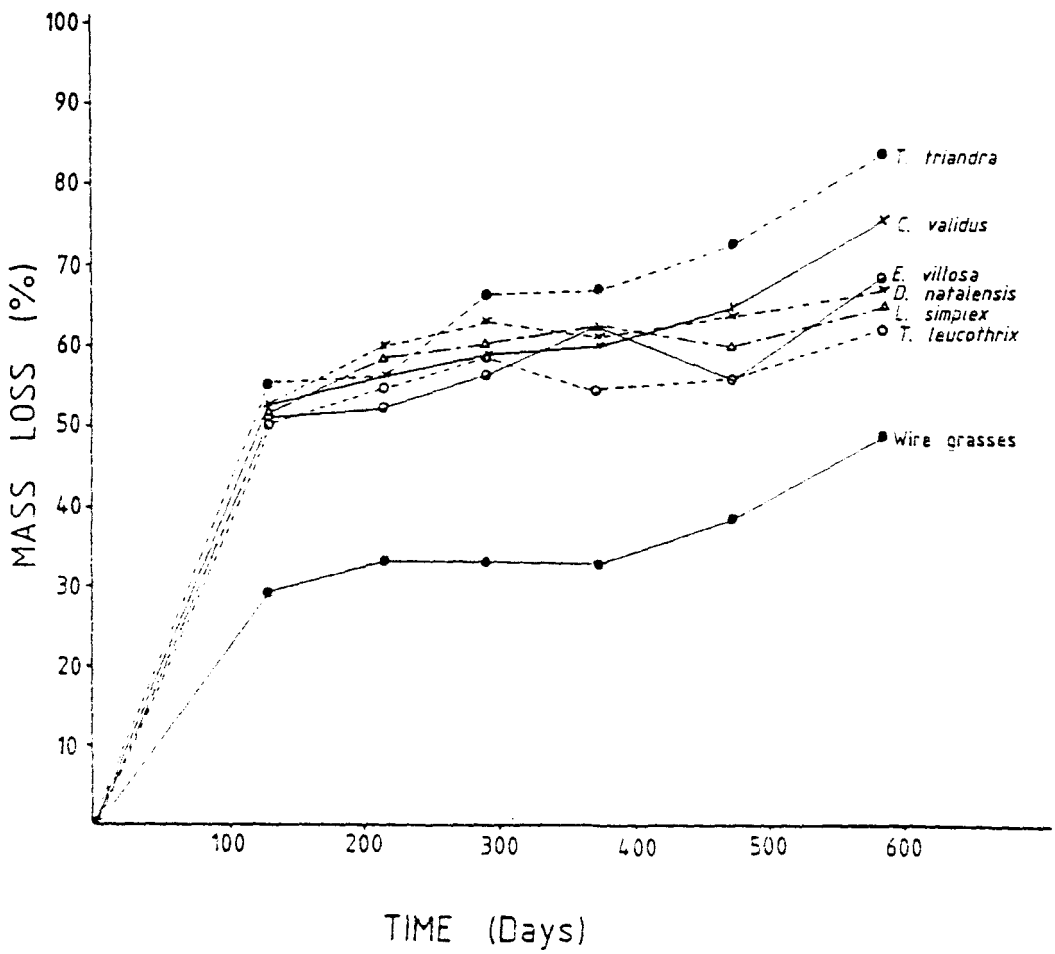


Figure 6.1. Litter breakdown at the T. leucothrix - L. simplex site

Litter from all species exhibited an exponential rate of decay, with a very rapid decrease in mass, usually greater than 50 % within the first three months. Thereafter, the rates of loss were relatively slow such that only a further 20 % was lost during the following seventeen months.

It was evident from the decay constants (-k) and their relative significance (Table 6.1.) that breakdown of the wire grass complex was significantly slower than all other species ($p < 0,005$). **T. triandra**, on the other hand, decayed significantly faster than all other species ($p < 0,01$) except C. validus. There were no significant differences between D. natalensis, L. simplex, T. leucothrix and E. villosa. Daily losses ranged from 0,08 % to 0,14 %.

Table 6.1. Exponential decay statistics for the litter bag study at the **T. leucothrix - L. simplex** site

SPECIES	k	k value signif #	TURNOVER (yr)	r	(P)	$\bar{x}$ daily loss (%) *
T. triandra	-0,11	a	8,82	0,78	0,05	0,14
C. validus	-0,09	ab	11,65	0,89	0,01	0,13
E. villosa	-0,07	bc	14,04	0,94	0,005	0,12
T. leucothrix	-0,06	c	16,69	0,98	0,001	0,11
L. simplex	-0,06	c	15,38	0,97	0,001	0,11
D. natalensis	-0,07	bc	14,43	0,96	0,001	0,11
Wire grasses	-0,04	d	23,99	0,97	0,001	0,08

r is the regression coefficient of mass with time fitted to the exponential curve

* Assumes a linear decay rate

\# Like letters denote no significant difference between two species

6.4.2. C. validus - D. natalensis site

The rate of breakdown is illustrated in Figure 6.2. The proportion of mass lost after twenty months ranged from 59 % for the wire grasses to 87 % for T. triandra. Exponential decay statistics were calculated as for the T. leucothrix - L. simplex site (Table 6.2.).

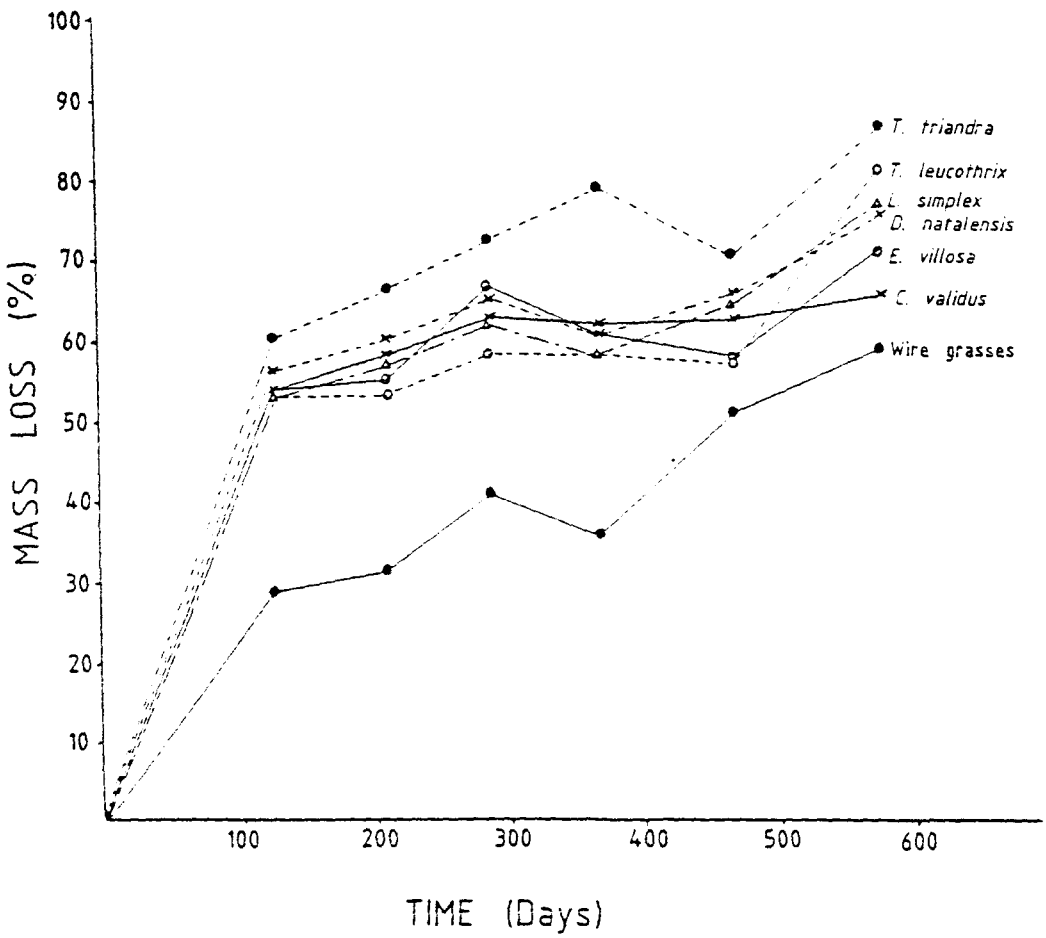


Figure 6.2. Litter breakdown at the C. validus - D. natalensis site

At this site the wire grass complex decomposed at a significantly slower rate than all the other species ($p < 0,05$) except C. validus. At the opposite end of the scale T. triandra showed the most rapid breakdown, significantly faster than all the other species except T. leucothrix. Breakdown rates of D. natalensis, L. simplex and E. villosa did not differ significantly and were

intermediate between the wire grass complex and T. triandra.

Table 6.2. Exponential decay statistics for the litter bag study at the C. validus - D. natalensis site

SPECIES	k	k value signif	TURNOVER (yr)	r	(P)	$\bar{x}$ daily loss (%)
T. triandra	-0,13	a	7,57	0,76	0,05	0,15
C. validus	-0,07	b d	14,83	0,97	0,001	0,11
E. villosa	-0,08	bc	12,82	0,92	0,005	0,12
T. leucothrix	-0,11	a c	9,50	0,84	0,02	0,14
L. simplex	-0,09	c	10,55	0,88	0,01	0,13
D. natalensis	-0,09	c	11,15	0,91	0,005	0,13
Wire grasses	-0,06	b d	17,24	0,82	0,02	0,10

6.4.3. T. triandra - C. asiatica site

Graphical representation of the results (Fig. 6.3.) indicates exponential mass loss with almost complete breakdown of T. triandra (90 %) and E. villosa (96 %) by the end of the study. There was no significant difference between the decay constants of these two species, and both had a significantly higher constant than most other species (Table 6.3.). As was the case at the other sites, the wire grass complex decayed at the slowest rate.

6.5. DISCUSSION

The pattern of LB - an initial rapid loss of mass that gradually slowed - conformed to the exponential decay curve. There appeared to be a slight increase in the rate of loss for all species during the second summer. This was confirmed by calculating the average daily loss for each interval between two collection dates. An

example, using values for **C. validus** from all three sites is provided in Table 6.4.

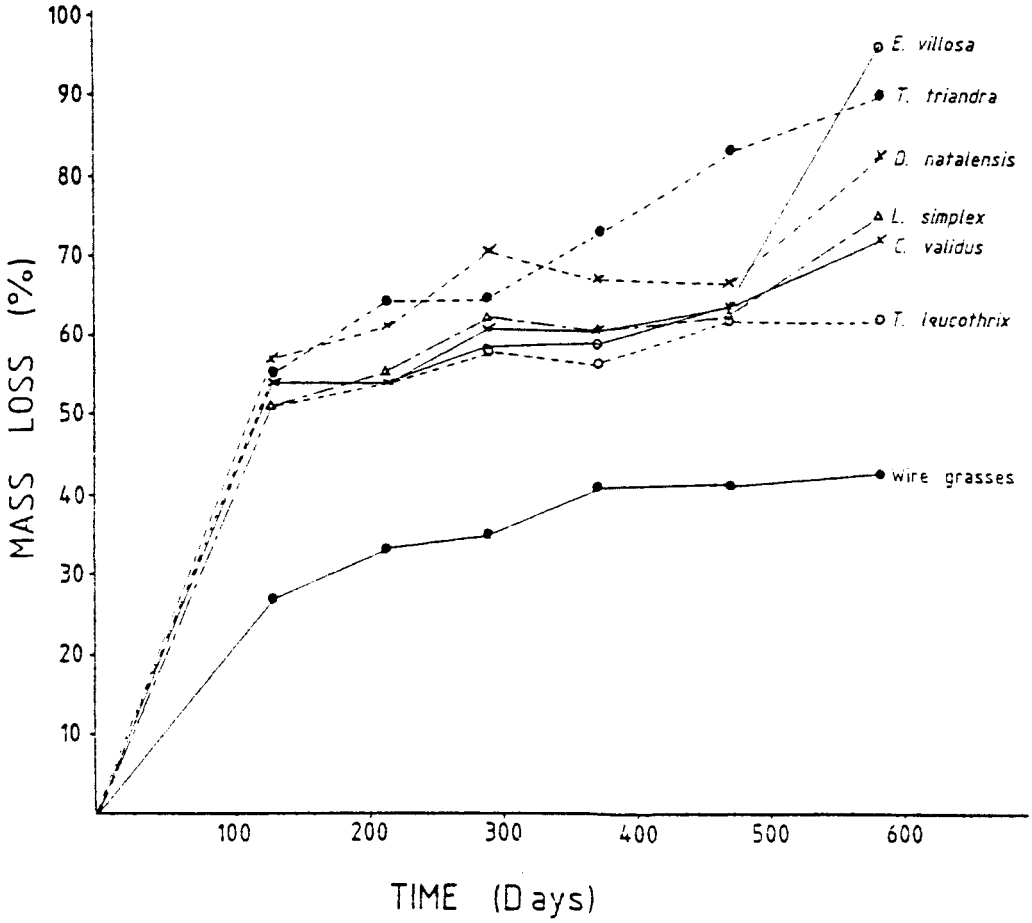


Figure 6.3. Litter breakdown at the **T. triandra - C. asiatica** site

Table 6.3. Exponential decay statistics for the litter bag study at the **T. triandra - C. asiatica** site

SPECIES	k	k value signif	TURNOVER (yr)	r	(P)	$\bar{x}$ daily loss (%)
T. triandra	-0,15	a c	7,06	0,66	n.s.	0,15
C. validus	-0,08	b	12,81	0,92	0,005	0,12
E. villosa	-0,23	a	4,97	0,67	n.s.	0,16
T. leucothrix	-0,06	b e	16,54	0,97	0,001	0,11
L. simplex	-0,09	bcd	11,43	0,89	0,01	0,13
D. natalensis	-0,11	bcd	8,93	0,83	0,02	0,14
Wire grasses	-0,04	e	28,76	0,97	0,001	0,07

Rates were generally similar between species at all sites, with the exception of **T. triandra** and wire grasses. **T. triandra** exhibited the most rapid breakdown at all sites. This is probably due to its lower crude fibre content than the other species (C. Shackleton in prep.). At the other extreme, wire grasses had a very slow rate of decay which correlated with their relatively high crude fibre content.

Table 6.4. Average daily loss of mass (%) of C. validus during intervals between collection of litter bags

SITE	COLLECTION DATE					
	1/86	4/86	6/86	9/86	12/86	4/87
T. leucothrix - L. simplex	0,41	0,07	0,03	0,01	0,00	0,04
C. validus - D. natalensis	0,42	0,05	0,07	0,00	0,06	0,12
T. triandra - C. asiatica	0,40	0,05	0,09	0,00	0,02	0,11

Calculation of a mean k value for each site, averaging k from each litter bag across all species (n=21), indicated that breakdown was significantly slower at the **T. leucothrix - L. simplex** site than at either the **C. validus - D. natalensis** or **T. triandra - C. asiatica** sites. There was no significant difference between the latter two. The higher soil moisture status at the **C. validus - D. natalensis** and **T. triandra - C. asiatica** sites (see Sect. 2.5.) and its influence on decomposer organisms could be expected to be responsible for the more rapid LB at these two sites. Wiegert and Evans (1964), Meentemeyer (1978) and Strojan **et al.** (1987) have all demonstrated the importance of the relative moisture status as a factor influencing the rate of LB. This was supported by the increase in LB at the end of the study during the moist summer

period. It was presumed that temperatures were comparable at the three sites.

6.5.1. Comparison with other grasslands

In the one published comparative study dealing with LB of graminoid material in RSA (Morris **et al.** 1982) the value of k ranged from -0,19 to -0,23 for different sites and species. This corresponded to a mean daily loss of 0,31 % - 0,33 % over the experimental period of 231 days. However, for the **Eragrostis pallens** litter bags (followed for 392 days), the value of k declined to -0,07 with a mean daily mass loss of 0,20 %. This is comparable with the results obtained at MGR. Singh and Gupta (1977) provided an extensive review of decomposition rates from several studies throughout the world. Mean daily losses of graminoid litter from litter bags ranged between 0,08 % and 0,24 %, and most were below 0,20 %. Values obtained during this study fell within this range.

6.5.2. Litterfall, breakdown and burning cycle

Extrapolating the figures derived during this study it was possible to estimate the proportion of the total litterfall in the two year period between burns that would be ashed by a fire. This was calculated on a community basis but weighted by the contribution of each of the monitored species to the total community. The LB rate of the other species in the sward was taken as the average of the seven species monitored. It was assumed that all species contributed to the litter fraction in proportion to their contribution to the biomass. Results were calculated for the grazed plots as they simulate the rest of the reserve.

At the **T. leucothrix - L. simplex** site the total litterfall within

the period between burns would be approximately 171,0 g m^{-2}. Immediately prior to burning approximately 107,6 g m^{-2} would be present on the ground and 63,4 g m^{-2} would have decomposed. Thus, 62,9 % of the total litterfall within the two year period would be ashed by fire on the present biennial burn programme. The corresponding proportions for the C. validus - D. natalensis site at different burning frequencies are summarized in Table 6.5.

Table 6.5. Proportion (%) of the total litterfall that would decompose under various burning cycles

BURN FREQUENCY	SITE			
	T. leucothrix - L. simplex		C. validus - D. natalensis	
	Decomposed	Burnt	Decomposed	Burnt
ANNUAL	24,2	75,8	34,0	66,0
BIENNIAL	37,1	62,9	46,2	53,8
TRIENNIAL	43,1	56,9	51,4	48,6

From this it is evident that there is an inverse relationship between the length of time between fires and the proportion of the total litterfall burnt. The corollary being that decomposition is faster under greater litter loads. This possibly explains the net decrease in absolute amounts of litter in the control plot at the T. leucothrix - L. simplex site (Sect. 5.4.1.4.). Should this be the case, it implies an alternating cycle of increases in litter followed by decreases in litter. Consequently, is a steady state ever attained?

With exception of the study of Dix (1960) there is little published empirical evidence to support the contention that LB is faster under greater litter loads. Dix (1960) concluded that as the litter

layer became deeper and more compact decomposition rates increased, until an equilibrium between production and decomposition was established. Apart from this evidence there are several additional circumstantial pointers to support this contention.

(i) It is well documented that an increase in moisture status can be correlated with faster rates of LB. As a well developed litter layer maintains a higher moisture status at the soil surface than areas without litter (Tomanek 1969), it therefore follows that rates of LB ought to be faster under large amounts of litter.

(ii) Large amounts of litter on the soil surface reduce the productivity of the biomass component (Penfound 1964). Consequently, input of litter is reduced and therefore the balance between litterfall and LB would be skewed in favour of LB relative to the situation with small amounts of litter.

(iii) Large amounts of litter may well provide a more suitable environment for decomposer organisms than little or no litter.

(iv) Olsen (1963) stated that the rate of LB and LD increased with community development. If a net increment in the amount of litter is a normal feature of "community development" then Olsen's statement is in agreement with the trends observed during this study.

From the above, it appears that there is no reason to reject the possibility of increasing rates of LB with accumulation of litter on the soil surface. However, the steady decrease in the amount of litter over a long period of time encountered in this study, has not been recorded elsewhere in references reviewed. Most of the

literature points to the establishment of an equilibrium between decomposition and production, given sufficient time (Dix 1960, Olsen 1963). The equations of Olsen (1963) indicate that such an equilibrium would be attained after 5/k years. From the results of this study therefore, equilibrium would not be attained until approximately 56 years had elapsed after a fire (mean k = −0,09; n=21).

Olsen (1963) also suggested that in the course of community development and succession there would inevitably be gradual or rapid changes in rates of production and LB influenced by new species of plants and animals, and in physical and chemical characteristics, i.e. rates would not be static. The alternating periods of increasing and decreasing decomposition rates suggested here accord with Olsen's statements. The long period of time required to achieve equilibrium certainly negates the possibility that it would be attained and fluctuations in driving variables and processes are more commonly encountered than equilibrium.

6.6. SUMMARY

1. Litter breakdown exhibited an exponential pattern.

2. Breakdown of litter was fastest at the moister **C. validus - D. natalensis** and T. triandra - C. asiatica sites than at the drier T. leucothrix - L. simplex site.

3. T. triandra was the most rapidly broken down (0,14 - 0,15 % per day), and wire grasses the slowest (0,07 - 0,10 % per day). There was little difference between the rates of LB of the other species, which were intermediate between these two species.

4. The proportion of the total litterfall that is burnt decreases

with increasing time between fires. Approximately 20 % less of the total litterfall is burnt under a triennial burning regime than under an annual burning regime.

HERBIVORY

7.1. OBJECTIVES

In this section the objectives were to determine:

(1) the seasonal forage availability of individual species in the different grassland communities;

(2) the levels of herbivory and preference ratios of individual species in each community, and how they change seasonally;

(3) how fire affects forage availability and acceptability of species and communities.

7.2. OVERVIEW & RATIONALE

The grasslands of Africa, including southern Africa, have evolved under complex selection pressures among which fire and grazing have been prominent (Mentis and Huntley 1982, Stuart-Hill and Mentis 1982, Hall 1984). Consequently, a knowledge of the structure and function of grasslands is incomplete without consideration of the herbivore component. Indeed, grasses that evolved in ecosystems without a significant herbivore component display properties very different to those that have (Mack and Thompson 1982). Similarly, community structure and function may be altered through the action of herbivores (Crawley 1983). Thus, any management policy aimed at sustaining large herbivores must be based upon a knowledge and understanding of herbivore habitat and dietary preferences along with other ecological requirements.

Various factors, both plant (Theron and Booysen 1966, Sinclair 1974, Tomlinson 1980, Owen-Smith 1982, Coley 1987, O'Reagain and Mentis 1988) and animal (Heady 1964, Jarman 1974, Owen-Smith 1982, Edwards 1983) combine to make herbivores favour particular areas, plant species or parts over others. At the plant species level this has led to their classification on the basis of their relative

contribution to the diet. Grunow (1980) distinguished between preferred species (those that contribute proportionately more to the diet of herbivores than their availability in the area), and principal food species (those that contribute the greatest proportion to the diet irrespective of availability). The latter are often considered key species in monitoring relative utilization of grasslands. Two more categories may also be recognized namely; non-forage or neglected species (those that are avoided or only eaten under very high stocking densities), and intermediate species. The last are species not usually taken and do not contribute greatly to the diet nor are preferred. But they are utilized more heavily as stocking densities increase. These categories are analogous to those recognized by Petrides (1975). Categorization of the constituent species of a region in this way facilitates refinement of carrying capacity estimates based on herbivore consumption rates.

7.3. METHODS

Estimates of herbage removal and species selection may be animal-based (Morgan et al. 1976) or plant-based (Barnes 1976). The former includes direct observation of grazing animals, fistulation, faecal analyses, etc., all of which are impractical for a multispecies, wild herbivore system. Plant based methods include visual rankings, exclosure plots, analyses of tiller and tuft size classes, etc. Such estimates have been used by Grunow and von Ginkel (1965), Du Plessis (1972), Kelly and Walker (1974), Scotcher (1982) and Conlong (1986) to yield the information sought in this study.

Exclosure plots, permanent or movable, were used by le Roux (1979), McNaughton (1984) and Conlong (1986). Both le Roux (1979) and McNaughton (1984) recorded large and significant differences in standing crop and productivity between exclosure plots and the

surrounding areas. On the other hand, Conlong (1986) failed to detect differences between exclosed and open areas and ascribed this to the low levels of herbivory. Thus, it appears that exclosure plots are best suited for areas sustaining large densities of herbivores and therefore able to measure a very definite impact. Other complications of the exclosure method are provided by Milner and Elfyn-Hughes (1968).

In this study, differences in standing crop between the fenced and unfenced plots were presumed to be a result of grazing by large herbivores (grazing by small mammals and invertebrates were assumed to be similar in both plots). Therefore a measure of total offtake from each site was possible. The methods have been described in section 5.3. However, considering that (i) no difference was recorded by Conlong (1986), (ii) the similarity of areas of the Eastern Shores of Lake St. Lucia to MGR, (iii) the sour nature of the grasslands at MGR, and (iv) the importance of such data to the management of the reserve, both the nature and the number of exclosure plots per community were viewed as insufficient. Since the time required to replicate plots could not be accommodated in the time available for field work, supplementary data were collected using visual rankings of individual species abundance and levels of herbivory.

Total removal and per species was estimated along several transects in each community throughout the reserve. Possible areas where transects could be sited within each management block were selected on the basis of accessibility, homogeneity of the vegetation, and adequate size. These were allocated a number and three were randomly drawn for each management block. Each transect comprised 100 quadrats (50 x 50 cm) five paces apart, giving a total transect length of 550 m. If habitat or vegetational homogeneity

altered along the transect preventing placement of all 100 quadrats within the same vegetation type, the remaining quadrats were situated at right angles to the main transect. All transects were assessed at approximately three month intervals. The specific location of the quadrats in each transect was not identical from one sample to the next three months later.

Initially transects were situated only in blocks burnt in 1985; six in the T. **leucothrix - L. simplex** community, three in the C. **validus - D. natalensis** community and two in the T. **triandra - C. asiatica** community (11 in total). After the 1986 burn a further nine were added; six in the T. leucothrix - L. simplex community and three in the C. validus - D. natalensis community.

In each quadrat the following were recorded: (i) total dry weight was ranked on a scale of 1 to 5 [DWR modification of Jones and Hargreaves (1979)]; (ii) the three most abundant species were ranked as 1, 2, and 3 respectively, in accordance with the method of t'Mannetje and Haydock (1963); and (iii) a visual estimate of grazing (%) of each species was made on the 8 point scale of Walker (1976). From this the contribution of each species to the dry weight of each community was calculated according to the method of Jones and Hargreaves (1979). All the transects within each community were pooled. The amount grazed (%) of each species was calculated according to equation 7.1.

$$\% \text{ grazing} = \sum_{n=1}^{k} (A_t \times A_n \times G_n) / (A_t \times A_n) \quad \text{——— eq. 7.1.}$$

where A_t = the rank of total grass abundance of all species in each quadrat (from 1 to 5)

A_n = rank assigned to species n according to the DWR method (top 3 species as 1, 2, and 3, respectively)

G_n = % grazing of species n (mid-point of each interval of an 8 point scale)

k = number of quadrats

Whenever a species was not sufficiently abundant to be ranked in the top three by the DWR method but had been grazed (i.e. $A = 0$, but G_n was positive) a minimum value of 1 % was assigned for A_n to avoid zero values of calculated grazing. Without this correction possible heavy utilization of less abundant species would be masked. Alternatively, this could have been overcome by assigning dry-weight ranks to more than the top three species. That would have required the derivation of new multipliers for the DWR method. Furthermore, it was unlikely that it would have been possible to rank more than the top three to five species accurately in such dense swards.

Seasonal changes in diet were assessed by testing for significant differences in diversity of food items recorded as preferred species as outlined by Zar (1974).

7.4. RESULTS

7.4.1. T. leucothrix - L. simplex community

The mean standing crop (all months considered) of the grazed plot was generally lower than the ungrazed plot. Only on two sampling dates (February and March 1987) was it higher in the grazed plot. The mean reduction (n=21 months) was 12,8 $\pm$ 13,68 %, although highly variable from month to month. Mean monthly reductions are given in Table 7.1., and seasonal means in Figure 7.1.

Table 7.1. Percentage increase/decrease in standing crop of the grazed plot relative to the ungrazed plot at the T. leucothrix - L. simplex site

MONTH	YEAR 1985	1986	1987
January		- 21,5	0,0
February		- 20,7	+ 19,8
March		- 14,9	+ 6,8
April		- 3,9	- 1,3
May		- 10,5	-
June		- 20,7	- 25,5
July	BURNT	- 28,2	STUDY
August	- 1,5	- 10,9	TERMINATED
September	- 22,4	- 7,0	
October	- 22,0	- 10,2	
November	- 8,2	-	
December	- 40,0	- 27,0	

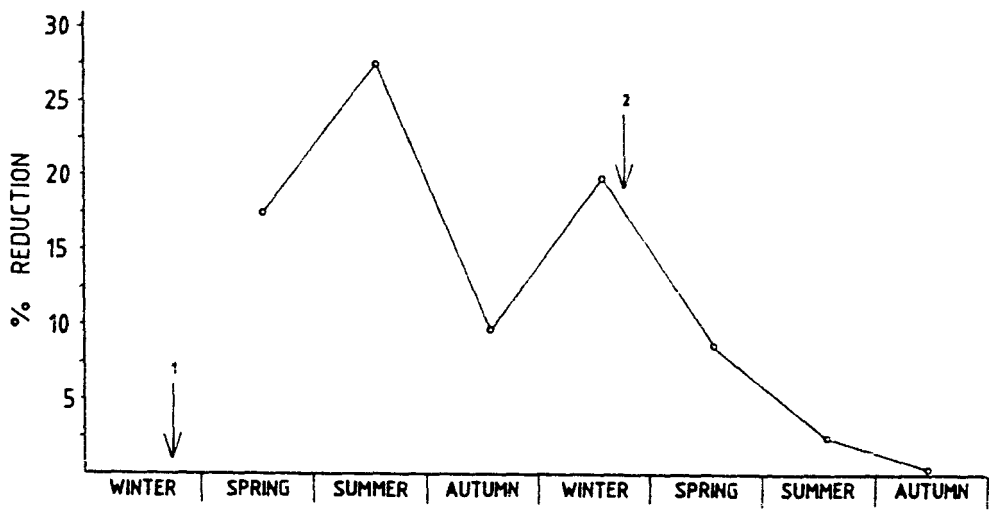


Figure 7.1. Seasonal levels of herbivory at the T. leucothrix - L. simplex site (expressed as the percentage reduction in standing crop of the grazed plot relative to the ungrazed plot). 1 = 1985 burn; 2 = 1986 burn

The total offtake determined from the grazing transects is provided in Table 7.2. It is evident that this method yielded much lower estimates of offtake than the exclosure method. This may be due to inherent differences in the two approaches, or that offtake was high at the T. leucothrix - L. simplex site specifically, relative

Table 7.2. Offtake from the T. leucothrix - L. simplex community

DATE BURNT	DATE SAMPLED						
	9/85	12/85	4/86	6/86	9/86	12/86	4/87
July 1985	3,27	1,15	1,17	1,49	0,94	0,17	1,32
July 1986	-	-	-	-	8,27	7,45	1,77

to the rest of the community. The latter is highly probable as it was noted that herbivores were attracted to the plot to graze the regrowth in areas of the plot that had been recently clipped for determination of standing crop. It is realistic to assume that although attracted by the clipped areas of the plot, unclipped areas were grazed too.

Offtake was highest immediately following the burn, decreasing significantly with aging of the sward ($y = 1/0,008x - 0,005$; $r = 0,897$; $p < 0,01$). There was a slight increase again at the beginning of the second dormant season; probably because by that time herbivores had redispersed throughout the whole reserve as the areas burnt in 1986 would, it is assumed, be of similar nutrient quality to areas burnt in 1985. The mean removal over the twenty month period was $1,36 \pm 0,36$ %. This figure assumes equal offtake throughout the whole community which was not the case (Sect. 7.5.). The few results for the areas burnt in 1986 showed that levels of offtake were much greater than in the preceding year.

Selection for particular species within the community was determined by calculating preference ratios (PR) for each species at each sampling date. Results for species that were preferred (i.e. PR > 1,0) on at least two sampling occasions are tabulated in Table 7.3. (results of the amount available, proportion grazed and contribution to the diet for all species are in Appendix 6).

Species are ordered in the table from those consistently preferred to those irregularly preferred. The total number of preferred species at any given date (including species preferred on one date only) is given at the bottom of the table.

Table 7.3. Species preference ratios for the **T. leucothrix - L. simplex** community (the upper figure refers to areas burnt in 1985 and the lower figure refers to areas burnt in 1986)

SPECIES	SAMPLING DATE 9/85	12/85	4/86	6/86	9/86	12/86	4/87
Eragrostis inamoena	-	3,8	14,4	3,9	43,3 -	1,6 -	32,7 -
Heteropogon contortus	4,7	1,9	1,2	3,8	1,3 0,4	0,5 0,9	5,6 0,3
Paspalum scorbiculatum	1,9	0,2	4,5	12,8	6,6 0,4	0,0 0,2	21,7 1,7
Setaria sphacelata	-	0,7	12,4	23,2	15,3 4,6	24,1 -	1,5 46,3
Tristachya leucothrix	1,0	1,8	1,9	1,3	0,9 0,6	2,3 2,0	1,3 1,8
Themeda triandra	1,6	1,3	0,6	1,3	0,8 0,9	1,0 2,0	0,4 1,4
Trachypogon spicatus	2,7	0,4	0,7	2,2	1,9 -	0,4 0,5	0,5 1,0
Scleria melanomphylla	-	2,2	0,0	0,4	3,1 -	5,9 0,1	0,0 0,0
Ctenium concinnum	1,5	1,9	0,1	0,0	0,4 0,3	0,0 0,4	0,0 0,4
Sporobolus centrifugus	2,3	8,2	-	-	- 0,9	0,0 1,8	- -
Alloteropsis semialata	0,2	1,0	0,6	0,6	0,6 1,1	1,2 1,3	1,6 1,7
Scleria bulbifera	1,0	0,2	2,0	0,0	0,0 -	0,2 0,1	0,0 0,0
Total number	10	9	8	7	7 6	6 6	11 12
% contribution to community	45,4	37,9	33,3	36,9	12,9 55,4	45,3 49,3	47,7 52,7
% contribution to diet	67,6	70,4	71,3	77,3	41,6 74,2	91,8 82,2	88,0 91,4

Several species were consistently selected, such as Eragrostis **inamoena**, **Heteropogon contortus**, **Setaria sphacelata**, **Tristachya** leucothrix and Paspalum scorbiculatum. Intermediate species included **Themeda triandra** and **Trachypogon spicatus**. The preference ratios of Ctenium concinnum and Sporobolus centrifugus declined with aging of the sward. Immediate post fire selection of Alloteropsis semialata in 1986 had not been evident in 1985. The preferred species constituted less than 50 % of the dry weight but usually contributed more than 70 % to the diet. The ratio of availability to contribution to diet ranged from 1:1,49 to 1:3,22.

Tristachya leucothrix contributed most to the diet on all occasions. The other principal food species on all occasions was **Alloteropsis semialata** (> 10 % of diet). **Trachypogon spicatus** and wire grasses comprised more than 10 % of the diet on one occasion each. Species consistently avoided were **Loudetia simplex**, Cyperus obtusiflorus and Urelytrum agropyroides.

Intake of the two principal foods declined in winter, with a concomitant increase in intake of **Heteropogon contortus**, Trachypogon **spicatus** and wire grasses. Grazing of the necromass component was noted during the winter months through to the second summer. In September and December 1986, the proportion of grazed quadrats with evidence of necromass grazing was 28,1 % and 21,1 %, respectively. Necromass grazing declined to 1 % in April 1987. The shift in diet between winter and both summer samples was greater than the two consecutive summers, although all were significant ($p < 0,01$).

7.4.2. C. validus - D. natalensis community

The increments and decrements in standing crop of the grazed plot relative to the ungrazed plot on a monthly basis are given in Table

7.4. The mean reduction (average of all months) was 6,91 ± 2,89 %. Seasonal figures are provided in Figure 7.2.

Table 7.4. Percentage reduction/increase in standing crop of the grazed plot relative to the ungrazed plot at the C. validus - D. natalensis site

MONTH	YEAR 1985	1986	1987
January		- 5,2	- 3,7
February		- 11,0	- 10,9
March		- 13,1	- 0,5
April		- 5,5	+ 3,9
May		- 34,0	STUDY
June		- 6,4	TERMINATED
July	BURNT	- 2,9	
August	+ 8,7	- 23,2	
September	- 13,3	- 29,4	
October	+ 12,0	- 3,8	
November	- 2,5	+ 16,6	
December	- 26,5	+ 5,6	

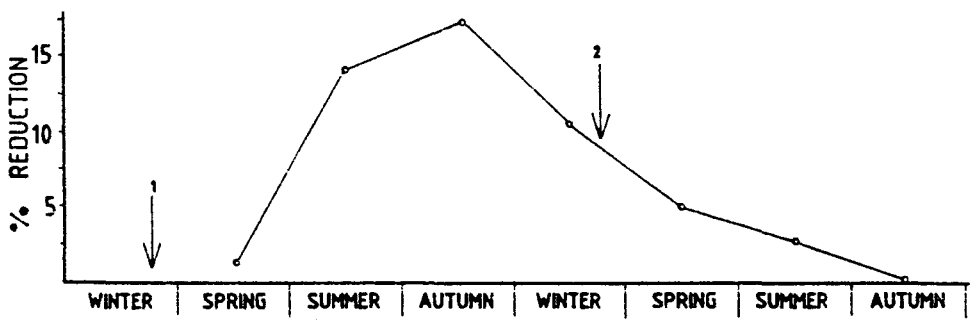


Figure 7.2. Seasonal levels of herbivory at the C. validus - D. natalensis site (expressed as the percentage reduction in standing crop of the grazed plot relative to the ungrazed plot). 1 = 1985 burn; 2 = 1986 burn

Like the T. leucothrix - L. simplex community the grazing transect data (Table 7.5.) yielded lower estimates of offtake than the clipping method. The mean offtake estimated by this approach was 2,78 ± 0,61 % (as an average over the whole community, ignoring areas of concentrated grazing), approximately double that of the T.

Table 7.5. Offtake from the C. validus - D. natalensis community

DATE BURNT	DATE SAMPLED						
	9/85	12/85	4/86	6/86	9/86	12/86	4/87
July 1985	2,69	3,85	5,16	3,45	2,76	0,98	0,57
July 1986	-	-	-	-	6,97	7,23	5,10

leucothrix - L. simplex community. Grazing was highest immediately following the burn and declined after the first summer ($y = 1/0,002x - 0,164$; $r = 0,80$; $p < 0,05$). Here, too, the proportion of available material removed from areas burnt in 1986 was considerably higher than those areas burnt in 1985.

Fewer species were preferred in the **C. validus - D. natalensis** community than in the T. leucothrix - L. simplex community (see Table 7.6.) although the ratios of availability to contribution were far higher. Species consistently preferred were Digitaria natalensis, (18 - 80 % of diet) Heteropogon contortus and, with maturation of the sward, Setaria sphacelata and Eragrostis plana. Festuca costata was selected immediately following a burn but was ignored thereafter, whilst Alloteropsis semialata was ignored in areas burnt in 1985, but preferred in areas burnt in 1986.

Digitaria natalensis was not only preferred but was also the principal food, contributing most to the diet on all occasions except immediately after the burn when Themeda triandra and Festuca costata contributed more. Despite having a low PR, C. validus was a principal food from April 1986 onwards. It contributed 39 % to the diet in June 1986, and in September 1986 it comprised 61 % of the diet, with a PR of 1,25. There appeared to be a major diet shift in favour of C. validus in winter, at the expense of D. natalensis which dropped from 80 % to 43 % and then increased to 77 % the

following summer. The diet in winter 1986 was significantly different to preceding and succeeding summers ($p < 0,01$), but the two summers were not ($p > 0,25$). Scotcher (1982) noted in the Natal Drakensberg that **C. validus** was selected by eland in winter, and both Matthews (1984) and Novellie (1985) recorded significant grazing of **C. plurinodis**. Avoided species in MGR were **Ctenium concinnum, Diheteropogon amplectens, Scleria melanomphyalla**, wire grasses and **Urelytrum agropyroides**. Grazing of necromass was not noted in this community.

Table 7.6. Species preference ratios for the **C. validus - D. natalensis** community

	SAMPLING DATE						
SPECIES	9/85	12/85	4/86	6/86	9/86	12/86	4/87
Digitaria natalensis	1,3	4,3	4,3	2,5	2,3 1,4	5,9 2,3	2,9 3,2
Heteropogon contortus	7,2	5,3	2,2	0,0	1,1 -	0,3 2,1	0,3 1,3
Setaria sphacelata	-	-	0,2	6,6	0,1 1,0	9,7 3,5	15,0 0,9
Panicum aequinerve	-	0,6	1,3	11,2	- -	0,0 -	- 0,5
Eragrostis capensis	1,5	-	-	3,0	- 1,1	0,0 1,7	- 8,3
Eragrostis plana	-	-	-	-	6,5 -	2,0 -	14,1 3,3
Alloteropsis semialata	0,2	0,0	0,3	0,7	0,2 1,6	0,7 1,2	2,7 1,2
Festuca costata	18,6	_	0,0	0,0	0,0 1,7	0,0 1,1	0,0 0,0
Cymbopogon validus	0,1	0,2	0,5	0,9	1,3 0,1	0,2 0,1	0,2 0,2
Total number	7	2	3	6	4 5	4 12	9 9
% contribution to community	33,1	19,1	16,4	19,1	61,9 69,1	13,3 37,7	27,9 34,0
% contribution to diet	89,6	82,1	68,4	46,9	91,2 95,2	79,2 87,7	84,6 84,9

7.4.3. T. triandra - C. asiatica community

Unfortunately no results were obtained from this community. Firstly, the application of the burn treatment was delayed, resulting in the absence of standing crop data. Secondly, two grazing transects were completed for this community for the first two sampling dates, but no grazing was recorded. Consequently the grazing transects were discontinued. This result is interesting in that prior to the commencement of the study, after a few reconnaissance visits, several people had stressed the fact that the herbivores used this community extensively, especially during the winter (Granger, pers. comm., Ruddle, pers. comm). Possible reasons for this result are presented in the discussion.

7.5. DISCUSSION

7.5.1. Effects of fire

The falloff in utilization with aging of a sward is a common feature of grassland grazing dynamics (Tainton 1981, Scotcher 1982). This is a result of three factors. (1) Estimates of utilization immediately after a fire could be higher because of reduced absolute amounts of food. Thus, herbivores may not be consuming greater amounts, but removal of the same amount constitutes a relatively higher proportion of the total available than a few months later. (2) During maturation of the sward following a burn several physical and chemical features change. Significant increments in the necromass component and concomitant decrements in phytomass reduce the availability of edible material as it becomes mixed with the more unpalatable necromass [green material fell from 87 % to 26 % of the total by the end of the first winter in the T. leucothrix - L. simplex grazed plot, and 70 % to 19 % in the C. validus - D. natalensis grazed plot (see Sect. 5.4.)]. The nutritional value of the phytomass component

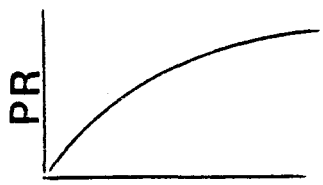
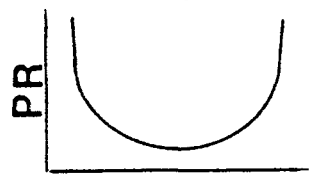
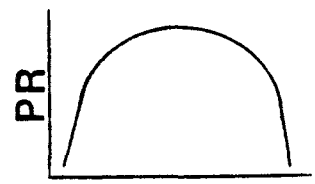
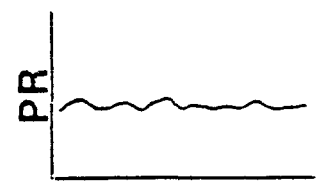
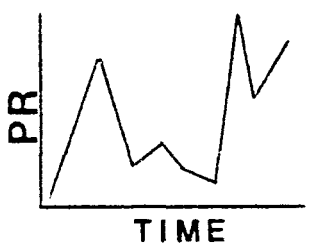
decreases, often to below levels needed by herbivores to maintain their body weight (see Ch. 8). (3) At the onset of winter many herbivore species concentrated their grazing at specific sites termed 'grazing lawns'. Measurable offtake from these grazing lawns would be high, but from most of the reserve it was low. After burning the alternative 50 % of the reserve in July, the herbivores were drawn to these areas so that swards older than 12 months remained relatively unutilized (< 1.0 %).

7.5.2. Seasonality

The selection of particular species altered during the year. Trends in the changes in PRs of the dominant species have been summarized in six idealized curves in Table 7.7. Owen-Smith and Cooper (1988) failed to detect meaningful patterns in PRs, and criticized the accuracy of results obtained from the usage of PRs as calculated during this study. They stated that estimates of abundance/availability in an area were: (i) open to distortion by uncommon or clumped species, and (ii) they were not representative of what an individual animal might encounter. They suggested the determination of acceptability indices as an alternative. However, that is only possible with the use of tame animals and was therefore not an option in the planning of this study. The effects of the first criticism were reduced by combining the results of the several transects in each community, rather than considering them individually. Despite these criticisms, definite trends were detected, and there was general consistency of trends for areas burnt in different years.

Several species had a high PR on the first sampling date and were constant at higher or lower levels thereafter (eg **L. simplex**). In such cases it was felt that the initial high value was probably a reflection of differential regrowth rates rather than true

Table 7.7. Changes in preference ratios of dominant species

	COMMUNITY	
	T. leucothrix - L. simplex	C. validus - D. natalensis
1. Decreasing with age 	- C. concinnum - E. villosa - S. centrifugus	- F. costata - H. contortus - S. centrifugus - T. triandra
2. Increasing with age 	- S. sphacelata	- S. sphacelata - A. semialata
3. Decreasing and then increasing 	- H. contortus - P. ecklonii	- T. leucothrix
4. Increasing and then decreasing 	- none	- C. validus
5. No change (relatively constant) 	- L. simplex - wire grasses - C. obtusiflorus - U. agropyroides	- S. melanomphala - wire grasses - P. scorbiculatum - U. agropyroides - D. amplectens
6. Erratic 	- A. semialata - D. amplectens - P. scorbiculum - T. triandra - T. spicatus - T. leucothrix - E. inamoena - S. bulbifera - S. melanomphala	- D. natalensis

preference, and the pattern after the first date received greater consideration (although the first date was not ignored). Owen-Smith and Cooper (1988) termed forage species 'palatable' only if they were consistently selected throughout the year. Furthermore, they considered that utilization during the new leaf stage of growth in woody species should have no influence on the palatability ranking of a species. This would probably be analogous to down-weighting of results for the immediate post-fire period employed here. The three sample dates for areas burnt in 1986 generally (there were some exceptions) conformed to the initial trends for each species within each community recorded in 1985.

There were similarities between the behaviour of some species within the two communities; for example **Setaria sphacelata**, Sporobolus centrifugus, Urelytrum agropyroides and wire grasses. However, other species exhibited different trends in the two communities. The major differences were those species showing no trend at all (no. 6) in one community, but exhibiting trends in the other. This was to be expected as the species composition of the two communities differed, which would influence species selection (Matthews 1984). There was no correlation between species trend and assignment of the species to the standard decreaser/increaser categories of Foran **et al.** (1978).

Grazing of dried material, usually in winter, is quite a common phenomenon in African grasslands (McNaughton 1985, O'Reagain and Mentis 1988). At MGR it was more pronounced at the end of winter and spring in the **T. leucothrix - L. simplex** community. If the shortage of available palatable species is such that herbivores have to ingest necromass it is not hard to view **C. validus** as a principal food species. These results and those of Matthews (1984) and Novellie (1985) suggest that **Cymbopogon spp.** may not be as

unacceptable as often presumed.

7.5.3. Comparison with other grasslands

In agreement with most other published figures for terrestrial systems, the proportion of standing crop and productivity consumed by herbivores at MGR is very low. Crawley (1983) estimated that the majority of studies recorded a figure of less than 10 % utilization of available forage. The mean consumption from the T. **leucothrix** - L. **simplex** community measured using an exclosure plot was higher than 10 % (i.e. 12,8 %) but this was probably an overestimate (see Sect. 8.3.1.). Scotcher (1982) recorded a range of utilization between 0,0 % and 5,54 % for sourveld grasslands of the Drakensberg. Higher levels were recorded at MGR only during the post-fire summer. The mean level of utilization determined from the exclosure plots indicated higher levels of utilization at the T. **leucothrix** - L. **simplex** site.

Results from the grazing transects (spread throughout each community) indicated greater utilization of the C. **validus** - D. **natalensis** community. The significant degree of area selection for the C. **validus** - D. **natalensis** community ($p < 0,001$) relative to the T. **leucothrix** - L. **simplex** community (C. Shackleton in prep.), the artificial nature of permanent exclosure plots, and the replication of grazing transects throughout the reserve leads me to accept the grazing transect data as a more realistic reflection of the 'true' situation.

Many of the trends in utilization and preference of species observed during this study agree with those recorded elsewhere. For example, the initial selection of **Festuca costata** immediately after a burn has been recorded by Scotcher (1982) and Shackleton and Walker (1985). Both of these studies also recorded utilization of

wire grasses such as **Elionurus muticus**, **Diheteropogon filifolius** and **Rendlia altera** immediately after a fire, whereafter utilization fell off rapidly. **Loudetia simplex** was actively avoided at MGR as was recorded by Tomlinson (1980) in Zimbabwe. On the other hand, other species showed trends opposite to previous studies. For example, **Heteropogon contortus** was consistently selected in both communities at MGR, yet Shackleton and Walker (1985) found that it was never utilized in North-eastern Mountain Sourveld, whilst Scotcher (1982) recorded utilization in spring declining during the rest of the year. In a summary paper looking at principal food species (not necessarily preferred), Grunow (1980) indicated that **Themeda triandra** was one of the most highly utilized species across a variety of veld types and herbivores, yet it rated very poorly at MGR (possibly because of its low abundance). **Setaria spp.** rated well too. **Heteropogon contortus** received an intermediate ranking whilst **Diheteropogon amplectens** was rated poorly.

7.5.4. General

It is important to note that the the calculation of mean intensity of herbivory masks the fact that grazing intensity is neither temporally nor spatially uniform. Grazing intensity in recently burnt areas is approximately 300 % greater than in older swards. The relative decline over time is quite dramatic. Furthermore, the figures obtained for MGR excluded grazing lawns (except for one initiated along part of transect C2 in the **C. validus - D. natalensis** community). Inclusion of these lawns would increase the calculated value of mean offtake although the total offtake would still be very low. Assuming a reduction in standing crop of 80 % in the grazing lawns, covering a total area of 115 ha, the increment in offtake averaged over the whole reserve would be in the region of 0,5 %.

The inclusion of non-preferred species in the diet is often difficult to explain, especially if it has a low PR and yet is a principal food. There are a number of possible reasons, summarized by Crawley (1983), all of which may apply at MGR. The high proportion of principal but non-preferred species in the diet of herbivores at MGR is indicative of the low abundance of palatable species and the generally poor quality grazing afforded by Pondoland Sourveld (see Ch. 8).

Grazing of forbs was negligible possibly because of the absence of browsers. The most frequently grazed forb species were all legumes (eg **Lotononis pulchra, Tephrosia grandiflora, Eriosema** spp., **Indigofera fastigiata,** etc.) together with **Acalypha punctata, Watsonia densiflora, Gnidia myrtifolia** and **Hypoxis sp.**

Failure to detect grazing in the **T. triandra - C. asiatica** community maybe for one or two reasons. Firstly, herbivores may not utilize this community enough to permit observable measurements of removal. Secondly, problems inherent in the sampling procedure may have promoted non-detection of low levels of herbivory. This is unlikely in light of the low levels detected in the other two communities. It is feasible that the fine leaved nature of the dominant species, **Themeda triandra** may have made detection of eaten leaves very difficult. Furthermore, the fragile and prostrate growthform characteristic of this community may result in the complete removal of a tiller upon grazing, thereby precluding visual estimates of removal. Marked plants would probably be the best means of measuring grazing in this community.

Based on the results in this chapter and the indicator species from the vegetation classification it is possible to identify certain 'key' species. These would be the most useful to monitor with the

implementation of a monitoring programme. Of top priority would be Digitaria natalensis, Cymbopogon validus, Heteropogon contortus and Loudetia simplex.

7.6. SUMMARY

1. Herbivory levels are low at MGR, being generally less than 5 %.

2. Levels are highest in the summer following a burn and decrease thereafter with maturation of the sward.

3. The C. validus - D. natalensis community experiences higher intensities of herbivory than the T. leucothrix - L. simplex or T. triandra - C. asiatica communities.

4. There is marked species selection [and area selection (C. Shackleton in prep.)], which differs between winter and summer.

5. During winter herbivores include less palatable species and material in their diet.

NUTRIENTS

8.1. OBJECTIVES

The objectives of this section of the study were to determine:

(1) the acceptability of the grasslands and how it changes seasonally;

(2) how fire and herbivory affect forage acceptability.

8.2. OVERVIEW & RATIONALE

It is a complex task to determine the quality of the diet available to herbivores, and whether or not it is adequate to meet their needs. The complexity arises from several factors. (1) Nutrient differences between various food items (species, parts, age, etc.). This means that selection for particular foods must be assessed before measurement of availability is meaningful. (2) Requirements differ from one individual herbivore to the next according to differences in species, age, sex, physiological condition, past nutritional status, etc. (Heady 1964, Crawley 1983, Robelin and Geay 1984). This in turn, may effect their selectivity. (3) It is often desirable to ensure that any given diet supplies all the nutritional requirements. Since seventeen different nutrients are necessary for maintenance (minerals and amounts required to maintain body mass) and growth in herbivores (Dyer 1969), this is often not feasible in terms of time and expense. Not only are the concentrations of specific minerals important, but also the ratios of various pairs of minerals (Du Toit **et al.** 1940, Dyer 1969, Bransby 1981, Mackie and Therion 1984).

Most recommendations on nutrient requirements were obtained from trials involving domestic animals. In such situations the availability and selection of food items can be controlled, and the

differences in requirements between species, ages, sizes, etc. can be determined. In the absence of contradictory data, these results have been extrapolated to wild herbivores. Determination of dietary quality is considerably more difficult in free-ranging, wild herbivores than domestic animals, enforcing the adoption of plant-based methods rather than animal-based methods. However, there are distinct differences between the quality of actually ingested food and that determined by plant-based methods, which usually underestimate the possible availability and ingestion of protein and minerals, and overestimate the possible ingestion of fibre (Weir and Torrel 1959, van Dyne and Heady 1965, 't Mannetje 1984). Hence, fistulated animals should be used if possible. This could be achieved using hand-reared, tame animals, but that is impracticable in a multispecies situation such as MGR.

It was necessary to obtain some indication of the palatability [specific characteristics of the feed that influence herbivore preference or avoidance (Bransby 1981); in this study restricted to chemical characteristics] of the different swards and species at MGR as forage quality rather than quantity may be the limiting factor to herbivore populations. This has been shown elsewhere in Africa (Talbot and Talbot 1963, Sinclair 1975), and more specifically in the sour grasslands of the Natal Drakensberg (Mentis 1978, Scotcher 1982), hence the possibility that the same applied in the sour grasslands of MGR could not be ignored.

8.3. METHODS

The palatability of grass has been both positively and negatively related to several physical and chemical properties of herbage. These include protein content, anthocyanin levels, crude fibre, moisture, breaking tension of the leaves and phosphorus content, among others (Heady 1964, Theron and Booysen 1966, Stanley-Price

1977, Downing 1979, Tainton 1981).

Since there is a large body of evidence indicating that protein is one of the most frequently limiting nutrients, given sufficient energy (Sinclair 1975, Bransby 1981, Scotcher 1982). It was evident that it should be the primary focus of nutritional analyses for this study. Crude protein (CP) was determined as 6.25 x % N (Afolayan and Fafunsho 1978, Bransby 1981). Likewise, the importance of fibre as having a negative effect on ingestion was recognized (van Soest 1965, Bransby 1981) and was, therefore, to be included in the analyses. However, the inability of laboratories in southern Africa to differentiate the various fractions of crude fibre (which includes some digestible fractions, such as hemicellulose, but excludes other indigestible fractions such as lignin) via the van Soest method (1967) promoted a more indirect determination by assessment of digestibility rather than crude fibre as such. Digestibility is one of the most important factors determining herbage quality (Bransby 1981), and is generally negatively correlated with fibre (Stanley-Price 1977, Heard 1980). The nutrient poor soils and sour vegetation prompted the inclusion of standard vegetation analyses for various minerals: these included potassium, phosphorus, sulphur, calcium and magnesium. All analyses were undertaken by the South African Sugar Association laboratories at Mount Edgecombe (Natal) with the exception of digestibility determinations which were done by Mr P. Zacharias of the Department of Grasslands Science, Agriculture Faculty, University of Natal (Pietermaritzburg) using an *in vitro* cellulase technique (Zacharias 1986).

Phytomass clipped from the three treatment plots for estimates of ASC (see Ch. 5) was used for the analyses. Analyses were conducted for each of the key species at each site and each treatment, pooled

from the five clipped quadrats. The amounts of Themeda triandra and **Eulalia villosa** (from the **T. leucothrix - L. simplex** site only) were generally insufficient for individual analyses and were therefore included in the sward fraction. Expense precluded the analysis of replicate samples and hence there was no statistical treatment of the data. On occasions there were insufficient amounts of particular species and therefore not all the minerals could be quantified. Results are presented for the total grass phytomass (which does not include forbs) as a whole and not for individual species. The mean percentages were weighted by the contribution of each species to the total phytomass of grasses. All results are expressed as a percentage of the dry mass of phytomass.

8.4. RESULTS

8.4.1. T. leucothrix - L. simplex site

8.4.1.1. Crude protein (CP)

The CP (%) recorded for the three treatment plots over the duration of the study is illustrated in Figure 8.1. Absolute values are provided in Appendix 7.1. Both burnt plots exhibited high levels (> 10 %) immediately after the burn. Levels decreased rapidly, so that by February they were similar to the unburnt plot. It is evident that the CP in the ungrazed plot was lower than that in the grazed plot for most of the months recorded. After the decline in CP following the burn, the values for the control plot were also higher (generally) than those in the ungrazed plot, but on a par with those for the grazed plot. Ignoring the high post-fire levels, values in summer were usually 30 - 50 % higher than the winter levels. The lowest CP levels were recorded in July or August.

8.4.1.2. Digestibility

The mean digestibility was consistently lower in the control plot

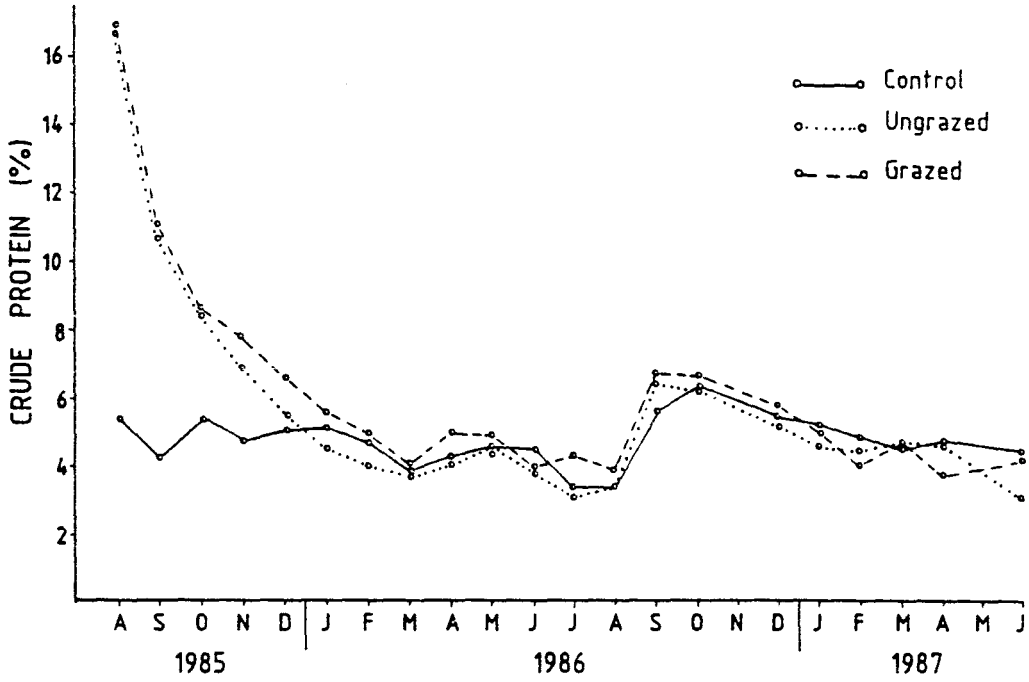


Figure 8.1. Crude protein of grass leaves at the T. **leucothrix** - L. **simplex** site

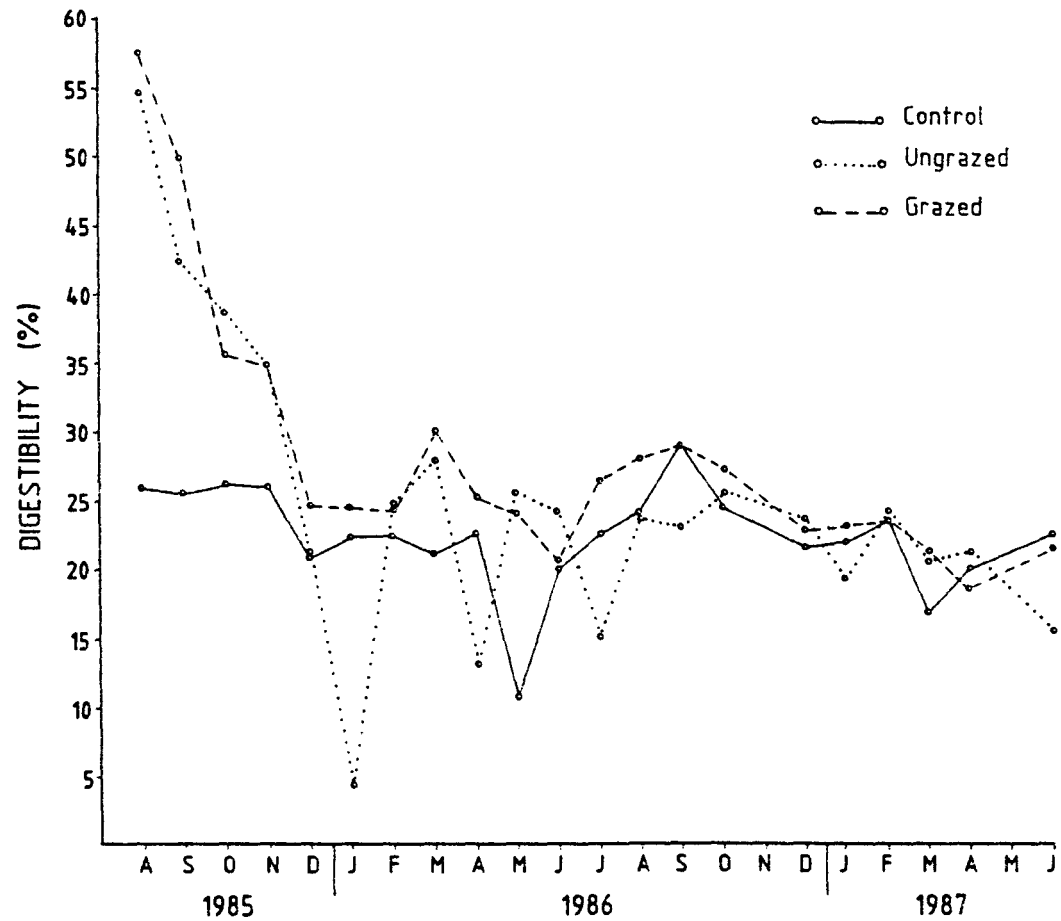


Figure 8.2. Digestibility of grass leaves at the T. **leucothrix** - L. **simplex** site

than the other two plots (Fig. 8.2.). There appeared to be little difference between the grazed and ungrazed plots. Values were high immediately after the burn, but decreased rapidly, being on a par with the control plot by December. There was no marked seasonal differentiation, thus sward age had a greater influence on digestibility than did season. Most values fluctuated between 23 % and 32 %.

6.4.1.3. Minerals

It is evident from Figure 8.3. that there were both seasonal and treatment differences in the concentrations of some minerals, but not others. Both P and K showed a rapid decline following the fire, and strong seasonal differences thereafter. The lowest winter values (0.03 % P and 0.65 % K, respectively) occurred in July and August and peak values were in early spring (September and October). On the other hand, Ca and Mg exhibited little response to the fire, and no seasonal trends, with values remaining relatively constant under all three treatments (0.20 - 0.30 % Ca and 0.12 - 0.25 % Mg). A large number of missing values (insufficient material) detracted from a meaningful interpretation of the trends in the concentration of S, but it did appear that values were high following a fire (relative to the unburnt plot), declining rapidly, and with little change after December. With respect to the actual values recorded there were some treatment effects over and above the effect of the fire. For instance, Ca was generally higher in the ungrazed plot relative to the grazed plot, whilst the opposite held true for S. There were no differences in concentrations of Mg, K and P between these two plots. The control plot was characterized by the lowest concentrations of Mg and Ca, but had the highest concentrations of K (after the decrease following the burn).

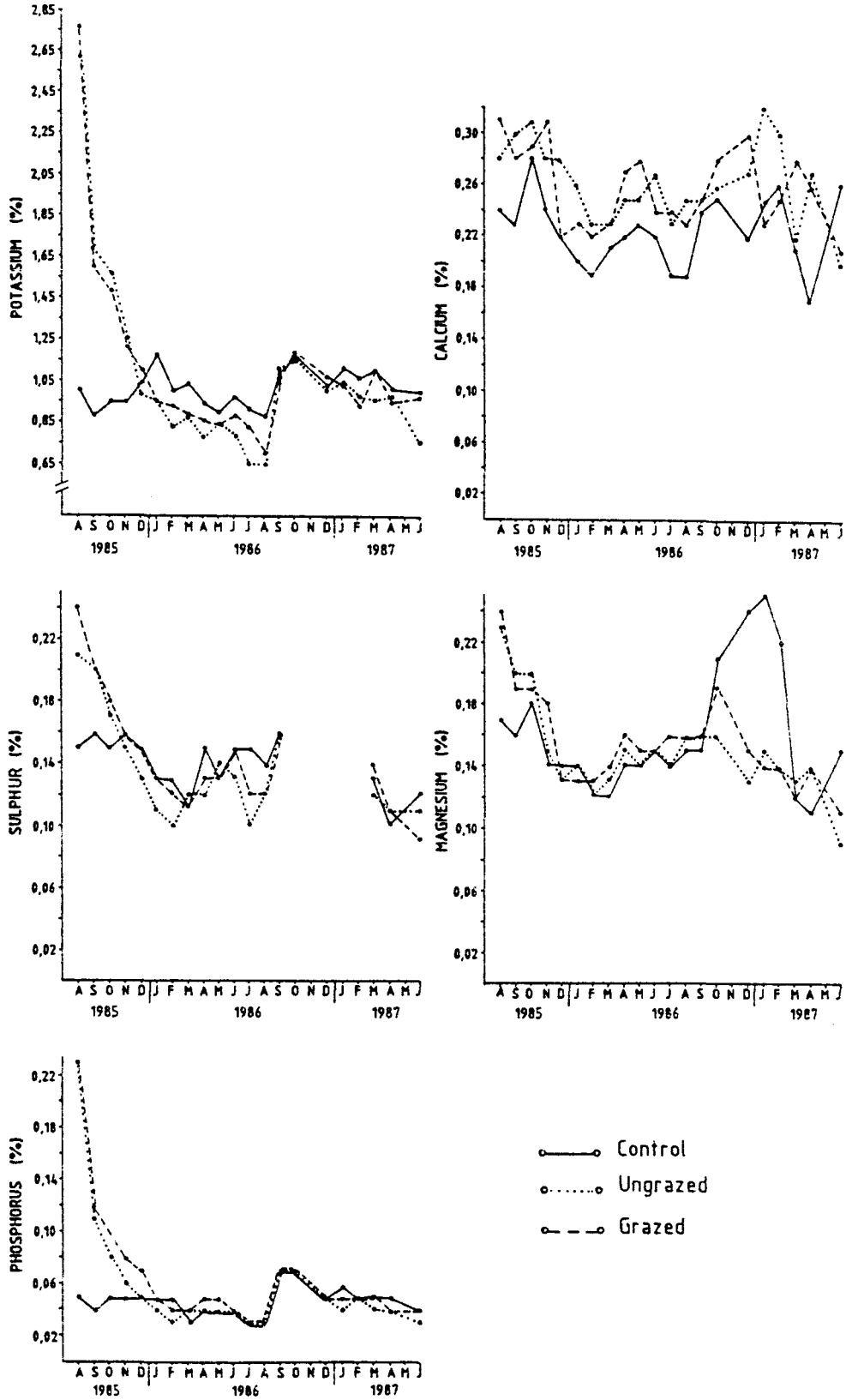


Figure 8.3. Nutrient content of grass leaves at the T. leucothrix - L. simplex site

8.4.2. *C. validus - D. natalensis site*

8.4.2.1. Crude protein (CP)

With the exception of a few months, CP was higher in the grazed plot than in the ungrazed plot (Fig. 8.4. and Appendix 7.2.). This was also the case at the T. leucothrix - L. simplex site. The control plot had the lowest values of all the treatments. Overlooking the effect of the burn, seasonal differences were evident. Crude protein was lowest (< 3 %) in late winter (July or August). Levels in spring were almost double those of winter, but declined steadily through summer to the low winter levels. A small peak was evident in May, as was recorded at the T. leucothrix - L. simplex site. This corresponds with the increased phytomass and reduced necromass recorded at that time (see Sect. 5.4.2.). Values for all treatments were less than those recorded for analogous plots at the T. leucothrix - L. simplex site.

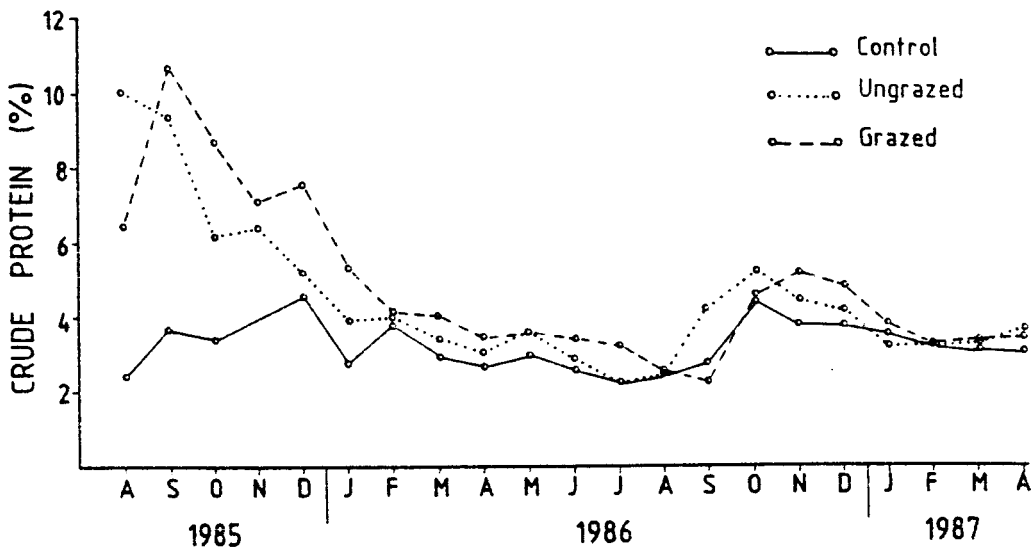


Figure 8.4. Crude protein of grass leaves at the C. validus - D. natalensis site

8.4.2.1. Digestibility

Figure 8.5. illustrates the monthly digestibility (%) of the sward

under the three treatments at the C. validus - D. natalensis site. The digestibility for the ungrazed treatment was often less than the grazed plot, and rarely greatly higher. The control plot generally was 2 - 3 % lower than the other two plots. There was a steady decline in digestibility throughout the study, even in the control plot, which was not interrupted by seasonal trends. As with CP, digestibility was lower than at the T. leucothrix - L. simplex site.

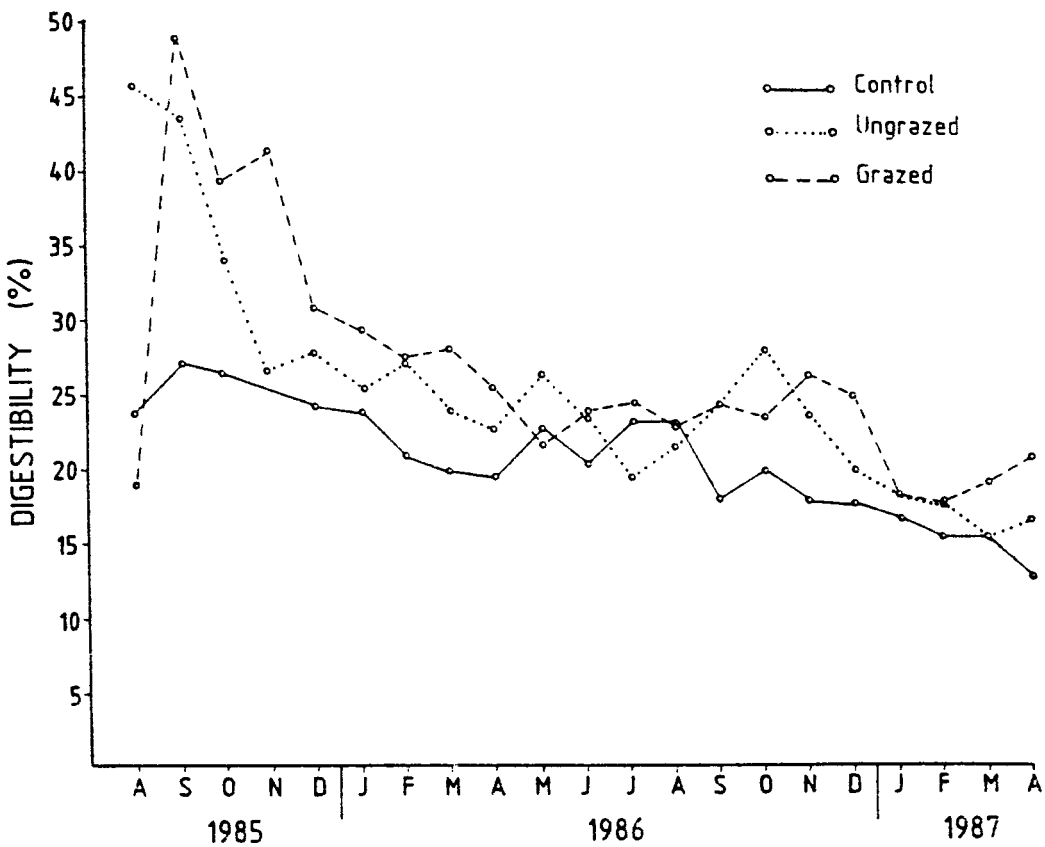


Figure 8.5. Digestibility of grass leaves at the C. validus - D. natalensis site

8.4.2.3. Minerals

The new growth after the burn had higher concentrations of P, K, and S (as far as could be determined in light of a number of missing values), relative to the unburnt sward (Fig. 8.6.).

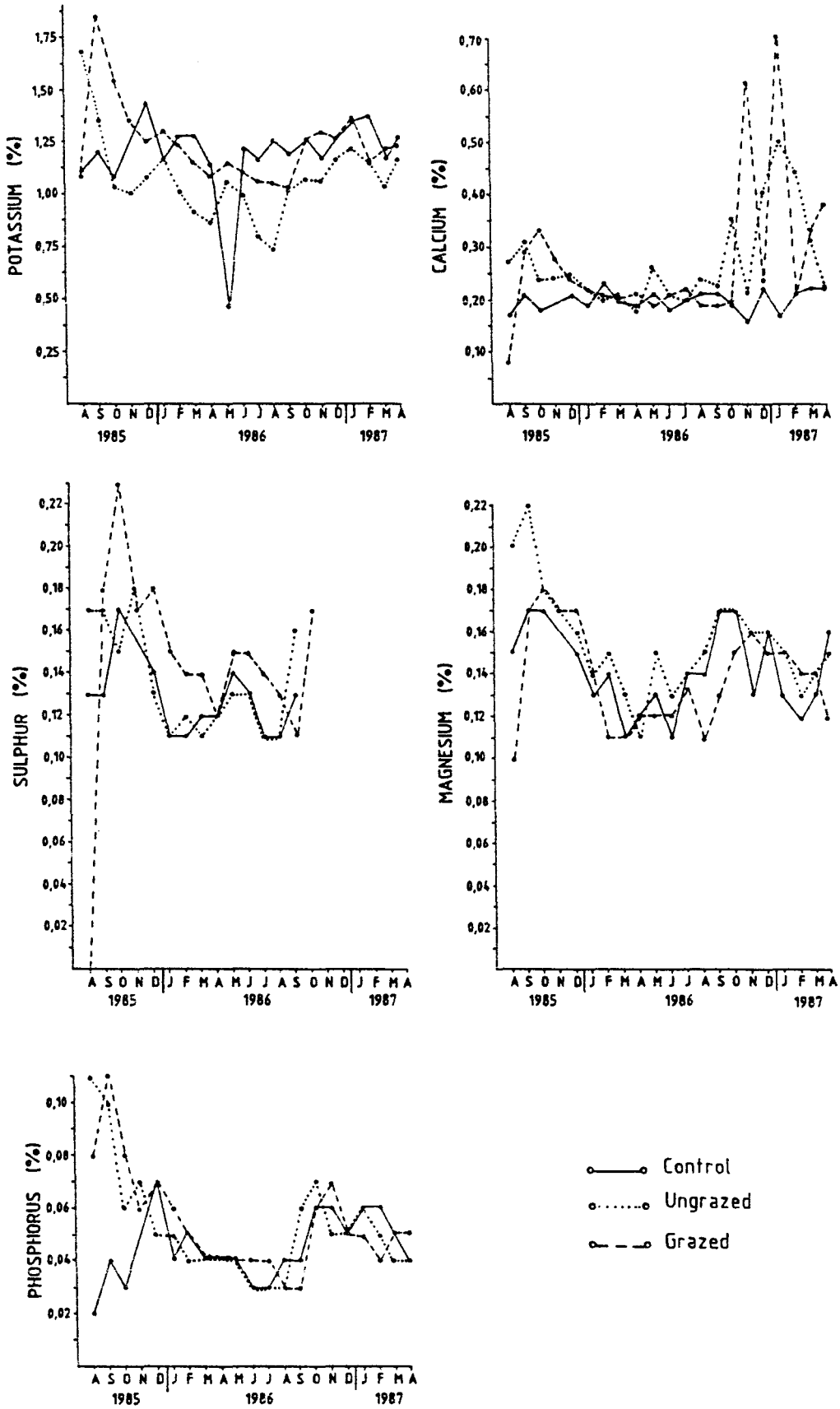


Figure 8.6. Nutrient content of grass leaves at the C. validus - D. natalensis site

Concentrations of these three minerals decreased rapidly after burning. Seasonal differences were evident thereafter in P and K. Concentrations of Ca did not follow any discernible pattern during the study period. Magnesium declined throughout the study in the two burnt plots. There were treatment differences in the concentrations of some of the minerals. Levels of K were lower in the ungrazed plot relative to the grazed plot, whilst the levels of Mg were higher. In agreement with the results from the T. **leucothrix - L. simplex** site, the control plot had low levels of Mg and Ca although the difference was less or had disappeared by the end of the monitoring period. Similarly, levels of K were highest in the control plot once the high post-fire concentrations had declined in the other two plots. Values of Mg and Ca were generally lower (with exceptions for some months) than those recorded at the T. **leucothrix - L. simplex** site, but K was higher.

8.4.3. T. **triandra - C. asiatica** site

8.4.3.1. Crude protein (CP)

Crude protein varied between 3,9 % and 7,5 % (Fig. 8.7. and Appendix 7.3). Monthly values were comparable to the values recorded in the unburnt plot at the T. **leucothrix - L. simplex**

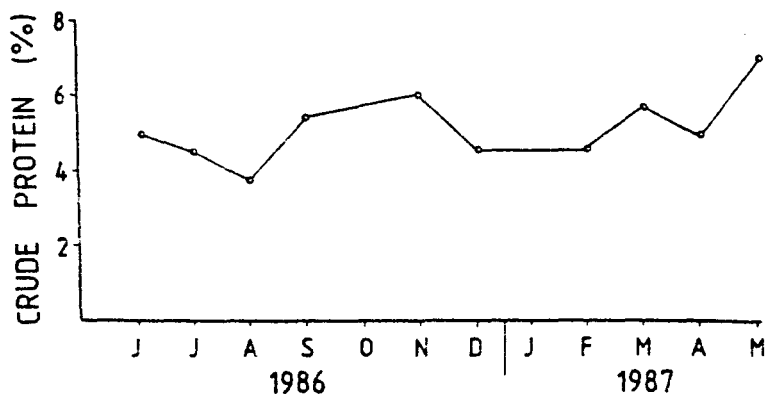


Figure 8.7. Crude protein of grass leaves at the T. **triandra - C. asiatica** site

site. but were substantially higher than those recorded at the C. **validus - D. natalensis** unburnt site, over the corresponding period. The lowest level of CP was attained at the end of winter, in August.

8.4.3.2. Digestibility

The monthly levels of digestibility (%) are presented in Figure 8.8. They exhibited similar trends to CP, declining during the late winter at the start of monitoring, and then increasing at the onset of spring (in September). The highest level was recorded in May (as was the highest % CP). Nevertheless, there was little difference throughout the monitoring period as a whole, and values were relatively constant. Values were generally less than those recorded at the unburnt plot of the T. **leucothrix - L. simplex** site. However, they were higher than those recorded at the unburnt plot at the C. **validus - D. natalensis** site, with the exception of the lowest values attained in late winter.

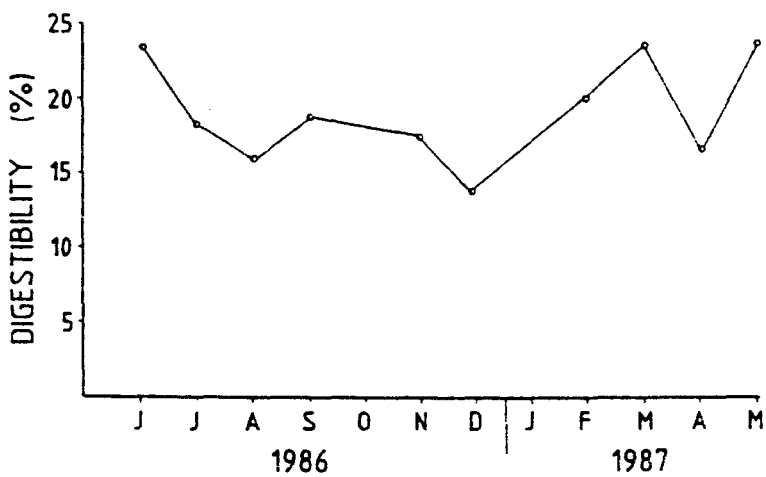


Figure 8.8. Digestibility of grass leaves at the T. **triandra - C. asiatica** site

8.4.3.3. Minerals

As at the other two sites, there were marked seasonal differences in the concentration of most of the minerals recorded (Fig. 8.9.).

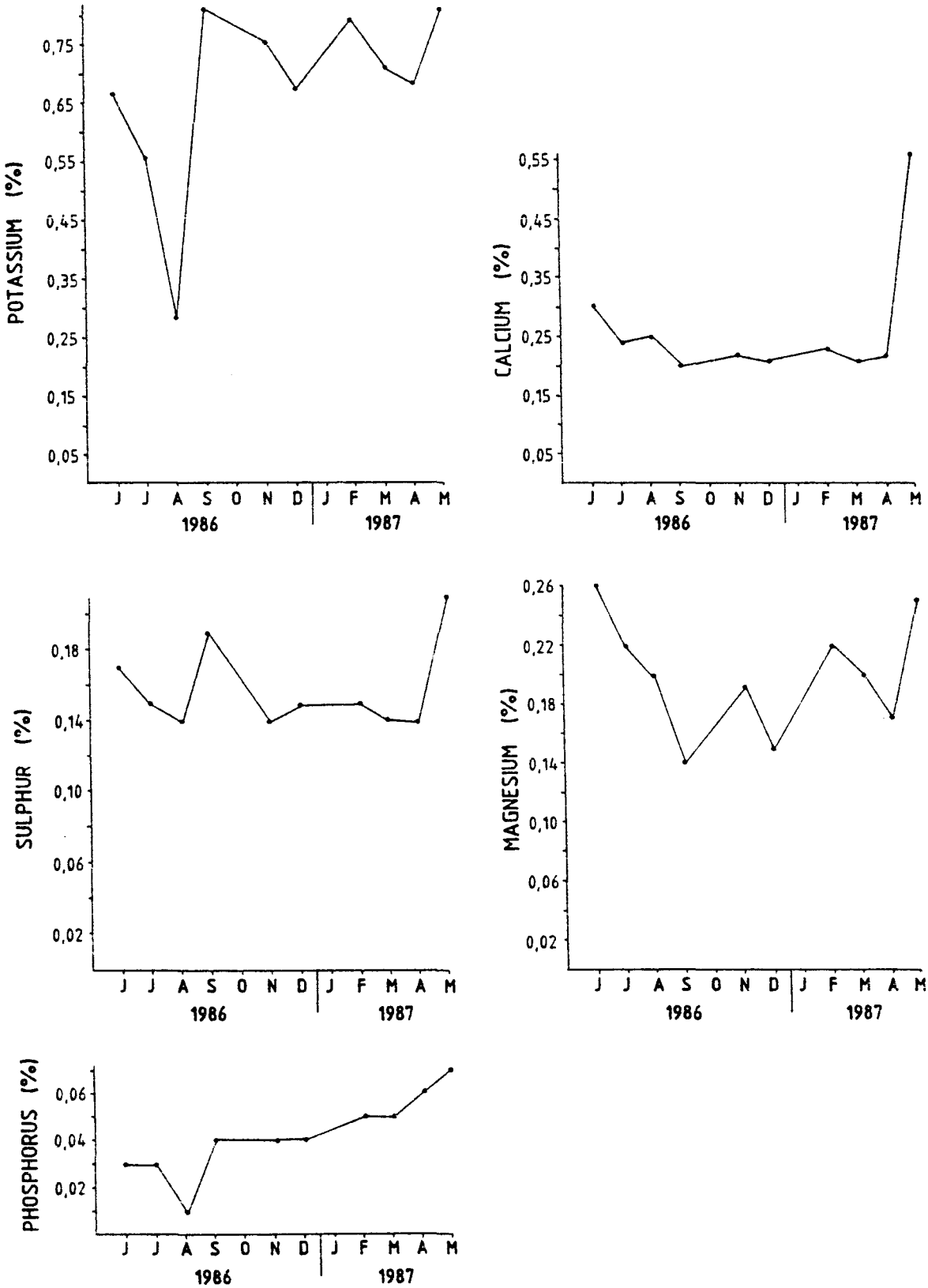


Figure 8.9. Nutrient content of grass leaves at the T. triandra - C. asiatica site

most noticeably of P and K. The lowest concentrations of P, K and S were recorded in late winter (August), and the highest in late autumn (May). Calcium and Mg were at their lowest values in September, one month later than the above mentioned three, but the highest values were recorded also in May. Concentrations of Mg, Ca and S were usually higher than at the T. **leucothrix - L. simplex** and C. **validus - D. natalensis** sites, but K was lower than at either of these two sites.

8.5. DISCUSSION

Acocks (1975) ascribed the low incidence of grazing in this region to the "very sour" nature of the grasslands. The results presented here indicate that these grasslands are indeed very sour, being deficient in both CP and P. However, statements regarding the nutritional quality of the grasslands must take cognizance of the effects of both season and fire. Once-off measurements and subsequent interpretations and generalizations (eg O' Donovan undated, Chapman 1980) could well promote misleading conclusions or recommendations. For instance, O'Donovan (undated) recorded 6 % CP in "freshly burnt" grasslands at MGR, and yet results presented here indicate that values are above this for at least 4 - 5 months after a fire. It is thus appropriate that these factors (season and fire) are considered individually before general statements can be made. Furthermore, in discussing these results it is important to bear in mind that nutrient quality determined from clipped samples is not an accurate reflection of what is available to herbivores. Herbivores are selective for particular areas, plant species, and plant parts.

Except for areas of concentrated grazing (where all species were grazed) and highly preferred species (such as **Setaria sphacelata**,

Digitaria natalensis and Heteropogon contortus) it was observed that removal of herbage was largely confined to the tips of leaves. Wilkinson et al. (1970) and Stobbs (1973a, b) have shown that the upper layers of grass swards usually have a higher CP content and digestibility than the basal layers. Samples collected during this study were clipped to ground level in most instances (see 5.4.) and therefore these results are 'average' values. Weir and Torrel (1959), Van Dyne and Heady (1965) and Fourie et al. (1986) demonstrated convincingly, through the use of oesophageally fistulated animals, that samples clipped to ground level (including all species in the sample area) had a lower CP content and higher fibre than the material collected via the fistula. Furthermore, without replication of treatments, only trends can be considered, but consistency across the sites lends some degree of credence to these trends.

8.5.1. Seasonality

Seasonal differences in the nutritional status of African grasslands have been reported by many researchers (Du Toit et al. 1940, Plowes 1957, Sinclair 1975, Afolayan and Fafunsho 1978, Scotcher 1982, Toisma et al. 1987). Indeed, the decline in sward quality during the non-growing season forms the basis for the traditional separation of grazing lands in southern Africa into "sweetveld" and "sourveld" (Tainton 1981). Both experience a decline in quality in the dormant season, but in sweetveld it is not significant and therefore grazing is possible throughout the year. In sourveld the decline in quality is marked, such that domestic animals experience weight loss during the dormant season if supplementary feeds are not provided. Other differentiating characteristics of sweetveld and sourveld are summarized by Tainton (1981).

8.5.1.1. Crude protein

In sourveld, CP is highest during the growing season (which differs between climatic regions). Peaks are usually attained early in the season with the onset of rain, with a steady decline thereafter until the lowest values are reached in late winter (Scotcher 1982, Everson 1985). This was the case at MGR with peak values for grass phytomass in unburnt swards recorded in October/November (maximum 6.22 % and 4.43 % at the T. **leucothrix** - L. **simplex** and C. **validus** - D. **natalensis** sites, respectively); and lowest values in July/August (minimum of 3.38 % and 2.34 % at the T. **leucothrix** - L. **simplex** and C. **validus** - D. **natalensis** sites, respectively).

8.5.1.2. Digestibility

Digestibility has not been one of the standard herbage-quality analyses in southern Africa (Bransby 1981), and therefore, comparative data for the subregion are lacking. It is known that the digestibility of tropical species is less than that of temperate species [average of 13 % less (Corbett 1978)] in response to the gross differences in macro-climatic variables. Temperature is the most important of these, there being a drop of 0,6 - 1.0 % in digestibility per 1° C increase in growth temperature (t' Mannetje 1984). Hence, there should be no reason to doubt that digestibility experiences seasonal fluctuations. Furthermore, as digestibility is improved with higher N and other minerals in low quality herbage (Ellis **et al.** 1984), it is presumed that digestibility would follow the seasonal trends in CP and minerals (see 8.5.1.3.).

However, examination of the results from both the unburnt plots and the second year from the burnt plots (unaffected by fire), indicates that there was very little change in digestibility throughout the year. Differences between the maximum and minimum

values were rarely in excess of 10 %. Peak values (25 - 28 %) were attained in spring (September/October), but the timing of the lowest values (10 - 19 %) was variable, falling between February and May. Bransby (1981) cautioned against placing too great an interpretative value on small changes in digestibility of less than 5 %. In light of the small differences between the peak and lowest values it would probably be unwise to generalize about seasonal trends here.

In contrast to the results of Stanley-Price (1977) and others, there was no positive correlation between digestibility and CP in the unburnt plots. However, the consistency of a positive correlation between these two has been questioned by the results of Dugmore **et al.** (1986) whom measured a significant negative relationship between CP and digestibility of **Pennisetum clandestinum**.

8.5.1.3. Minerals

There was no uniform response in the concentrations of the various minerals to time of year. Most exhibited an increase in spring over the levels of late winter. This increase was only slight in magnitude and not maintained in Mg and Ca. In contrast, P and K displayed distinct seasonal differences, being highest in spring and summer and lowest in winter. This is in agreement with the results of Du Toit **et al.** (1940) and Scotcher (1982), although the degree of the seasonal contrast differed between regions. McDowell **et al.** (1984) noted a decrease in the concentration of minerals during the dry season, but they did not cite specific elements. Contrary to expectation, manifestation of mineral deficiency symptoms in domestic herbivores is more prevalent during the wet season (McDowell **et al.** 1984). This is ascribed to the increased demand due to the rapid rate of growth of herbivores during this

period (whilst energy and protein availability are at their highest), rather than reduced concentrations of minerals in the foliage.

8.5.2. Effects of fire

There are numerous publications regarding the effects of fire on the nutrient status of both vegetation and soils (summarized by Schirge and Penderis 1978, and Booysen and Tainton 1984). Many of the studies present contradictory evidence which is probably partly responsible for the great deal of research attention this topic has received. The majority of the literature does, however, indicate that fire enhances the concentration of nutrients in grasses (eg Tainton and Mentis 1984). However, this enhancement is maintained for differing lengths of time according to vegetation type and nutrient investigated. Various authors proposed that these increases, however short-lived, were a consequence of the solubilization of the ash resulting from the fire, with the exception of N and S that were volatilized (Daubenmire 1968). Complementary studies investigating the effects of fire on soil nutrient levels seem to indicate that the increased nutrient concentrations in the vegetation are also a result of the mineralization of soil nutrients, especially N and P (Kellman et al. 1985, Brown and Mitchell 1986, Stock and Lewis 1986). This increases their availability to plants.

8.5.2.1. Crude protein

In this study, the CP of the burnt plots was approximately three times greater than that of the control plot in the first sample after the fire. It then declined steadily, attaining values comparable to those of the control plots 5 - 6 months after the fire. These results are comparable to those of other sourveld regions. Peak values recorded by Scotcher (1982) and Everson (1985)

in the sourveld regions of the Drakensberg following a fire were slightly lower than those recorded at MGR, but reduction to pre-fire levels was reached in the same time span.

8.5.2.2. Digestibility

Published work on the influence of fire on digestibility levels seems to be scarce. However, it is well known that digestibility decreases with plant maturation (Heard 1980, Bransby 1981, Leng 1984), and hence it can be expected that digestibility of food taken from a recently burnt sward would be high. This was evident in the results above. Digestibility was approximately double that measured in the unburnt plot for 2 - 3 months after the fire. Thereafter it declined, and was comparable to the unburnt sward by December/January.

8.5.2.3. Minerals

There are few data on the effects of grazing on mineral concentrations from comparable vegetation types, except for those of Scotcher (1982). He recorded a definite increase in P and K, and lesser increments in Mg and Ca following a fire relative to unburnt plots. The peak in Mg was the least sustained (2 - 3 months), followed by P (4 - 5 months) while the longest was K (7 - 8 months). Calcium responded variably in the different plots. In terms of magnitude and duration of the enhanced mineral concentrations following a fire the results recorded at MGR are very similar to those of Scotcher (1982). The stimulation of Mg and Ca levels were the least in magnitude and duration (2 - 3 months for Mg: Ca was variable). Stimulation of K and P concentrations was greater and was evident over a longer period: 3 - 5 months for K, and 4 - 6 months for P.

8.5.3. Effects of grazing

Responses induced in the nutrient quality of vegetation to grazing are usually similar to those induced by burning. Consequently, it appears that plants respond to defoliation **per se** and the manner of defoliation is less important, although it may effect the magnitude of the response. For example, stimulation of CP content occurs under both burning and mowing treatments, but is greater under burning (Tainton **et al.** 1977). This must be a consequence of the increased availability of minerals for regrowth under the burn treatment through solubilization and mineralization as mentioned above. Nevertheless, the similarity of trends serves to suggest that the major effects of defoliation are a result of promoting regrowth of young tissues undergoing active cell division. Unfortunately, but understandably, many of the investigations into the effects of grazing on nutrient content have simulated grazing via clipping or mowing. Such an approach will, therefore, not detect effects of saliva (Reardon **et al.** 1972, 1974). Furthermore, clipping and mowing experiments are usually confined to individual species. Detection of differences attributable to grazing in natural grassland, where there are several species, may simply be a consequence of changes in species composition in grazed areas relative to ungrazed areas; and that the different species may be inherently higher or lower in certain nutrients.

8.5.3.1. Crude protein

At both sites CP levels were higher in the grazed plot relative to the ungrazed plot. The same effect of grazing was recorded by Husband and Taylor (1932), Roberts and Opperman (1966) and Fourie **et al.** (1987). In the last study results were not consistent, but there were indications that as the stocking rate increased so did the concentration of CP in ingested herbage. They suggested that it was a consequence of increased consumption of shrubs (**Grewia flava**)

under higher stocking rates.

8.5.3.2. Digestibility

Leng (1984) suggested that a means of maintaining a high intake by cattle would be to maximize digestibility by increasing stocking rates to sufficient levels that the sward was kept in a young, vegetative state. This implies that sward digestibility is improved under grazing. This is consistent with the earlier statement about defoliation simply promoting regrowth which is characterized by higher nutrient concentrations and digestibility. However, no differences in digestibility were evident between the grazed and ungrazed treatments during this study.

8.5.3.3. Minerals

Less investigation of the effects of grazing on the concentration of various minerals has been made. Undersander and Naylor (1987) reported that concentrations of P and K were lowered with increased clipping frequency of **Agropyron elongatum**. The results for Ca and Mg were opposite, indicating that increasing clipping frequency resulted in higher concentrations. In contrast, Roberts and Opperman (1966) found that P levels were increased with clipping, as did Henrici (1935) for a shrub (**Phymaspermum parvifolium**). Results at MGR were not consistent between sites, and without replication are of doubtful validity. At the **T. leucothrix - L. simplex** site Ca was lower in the grazed plot than the ungrazed plot, but S was greater. At the **C. validus - D. natalensis** site Mg was lower in the grazed plot and K was higher.

8.5.4. Herbivore requirements

From the above it is evident that analytical results pertaining to the quality of herbage available to herbivores must be accompanied by details of: season of sample collection, age of sample and, if

possible, defoliation regimes implied by stocking rates. Consistent with the results from other sourveld regions it is possible to state that the quality of food available to herbivores at MGR is highest in spring and early summer, thereafter declining to its lowest in winter.

In assessing herbivore requirements there appears to be some inconsistency in the literature concerning the minimum levels required. Although CP has been shown to be deficient in many regions, the maintenance requirement proposed by various authors is very different, ranging from 4 - 9 %. This probably results from non-specification of the animal species concerned. Sinclair (1974) stated that 5 % is the most commonly used limit, and hence it will be employed here. Table 8.1. summarizes herbivore requirements for a variety of nutrients.

Table 8.1. Nutrient requirements of herbivores (a - antelope; c - cattle)

NUTRIENT	REQUIREMENT (%) FOR MAINTENANCE	& GROWTH	REFERENCE
CP	5.0 a		Bransby (1981)
	8.0 c		" "
	6.6 c		O' Reagain & Mentis (1988)
	5.5 - 9.0		Stelfox and Hudson (1986)
	4.0 - 8.0		Sinclair (1974)
	7.0		Everson (1985)
	5.0 a		Owen-Smith & Novellie (1982)
Ca		0.14	Du Toit **et al.** (1940)
		0.25 c	Dyer (1969)
		0.20	Bransby (1981)
K		0.34	Du Toit **et al.** (1940)
		0.10 c	Dyer (1969)
		0.07	Bransby (1981)
Mg		0.10 c	Dyer (1969)
		0.07	Bransby (1981)
P		0.20 c	Siegmund **et al.** (1961)
		0.20 c	Dyer (1969)
		0.20	Bransby (1981)
S		0.15 c	Dyer (1969)

From Table 8.1. and the results from this study it is evident that the only nutrients that may be limiting to herbivores at MGR are CP and P. This is a common feature of southern African grasslands, and deficiencies of the other measured minerals are rare (Du Toit et al. 1940, Bransby 1981, Kreulen and Jager 1984). The CP content of clipped samples is approximately 67,6 ± 3,52 % (n = 13) of that measured in fistula samples [determined as the mean difference of the original values recorded in the studies by Weir and Torrel (1959), van Dyne and Heady (1965), Pratchett et al. (1977) and Fourie et al. (1986)]. After compensation of the winter values recorded at MGR by this figure, the CP levels remain strongly limiting in the C. validus - D. natalensis areas and marginally so in the T. leucothrix - L. simplex areas. If a minimum requirement for maintenance of greater than 5 % was accepted then the severity of the CP shortage would be even greater. This winter shortage was well correlated with the observed decrease in fat reserves measured by both kidney-fat and bone-marrow indices (C. Shackleton in prep.).

The shortage of P was not related to season. It was below maintenance requirements throughout the year except after a fire. That some animals experience this deficiency was confirmed by the observation of oestophagia by domestic herbivores just outside the perimeter of the reserve (Plate 8.1.).

Other deficiencies were suggested after observation of gemsbuck licking soil on two occasions. Such behaviour is often a sign of a mineral deficiency (Kreulen and Jager 1984). Most commonly, soil licking is attributed to a deficiency of Na. However, the proximity of the sea detracts from its likelihood in this case.



Plate 8.1. Osteophagia by domestic herbivores outside MGR

Sinclair (1974) demonstrated that the dry season level of CP was a factor limiting buffalo populations in east Africa. Similarly, Mentis (1978) proposed that low dietary quality in winter, in conjunction with adverse climatic conditions, was responsible for limiting herbivore populations in the Natal Drakensberg. This has been supported by the work of Scotcher (1982). As the herbivore populations at MGR have been only recently established it is difficult to predict future trends in numbers. The similarity of the dominant grasslands of MGR to those of the Natal Drakensberg (Ch. 4), suggest the potential for the same mechanisms to be in operation at MGR. This implies that herbivore populations are, or will be, limited by the quality of food available. Consequently, if MGR management still abides by the initial objective for the reserve, i.e. to maximize animal production, the use of supplementary foods is recommended during the winter. Alternatively, an earlier burn could be considered.

With respect to burning, it is important to consider the improved quality in conjunction with the reduced quantity immediately after a fire (Sect. 5.4.). Combining both these factors indicates that nutrient stocks (absolute amounts per unit area) as opposed to concentrations (as percentages) are reduced (Table 8.2.). As the nutrient stocks are less, herbivores would have to forage over greater areas and for longer periods because of reduced biomass (Young and Corbett 1972). This will, however, be overcome to some extent by increased rumination time through ingestion of high quality forage (Tainton and Mentis 1984). Thus, the optimum combination of grazing quality and quantity exists in burnt grassland only 5 - 6 months after the fire. Peak levels of herbivory recorded during this study occurred, generally, several

Table 8.2. Nutrient stocks (g m^{-2}) and concentrations of grass phytomass in recently burnt grassland at the **C. validus** - D. natalensis site (data for the grazed plot)

Days after	NUTRIENT											
	N		P		K		S		Ca		Mg	
fire	stock	%	stock	%	stock	%	stock	%	stock	%	stock	%
19	0,03	0,89		0,07	0,03	0,93				0,07		0,08
40	0.42	1,84	0,03	0,12	0,44	1,95	0,04	0,18	0,08	0,33	0,05	0,22
68	0,62	1,53	0,04	0,09	0,65	1,59	0,09	0,21	0,17	0,43	0,09	0,23
89	0,82	1,21	0,05	0,07	0,96	1,43	0,12	0,17	0,28	0,41	0,16	0,23
117	1,31	1,32	0,08	0,08	1,31	1,32	0,19	0,19	0,37	0,37	0,25	0,25
144	1,25	0,95	0,09	0,07	1,80	1,36	0,20	0,15	0,41	0,31	0,26	0,20
178	2,15	0,86	0,13	0,05	3,23	1,29	0,35	0,14	0,78	0,31	0,41	0,16
208	1,81	0,77	0,09	0,04	2,83	1,20	0,35	0,15	0,77	0,33	0,39	0,17
236	1,20	0,61	0,08	0,04	2,17	1,11	0,25	0,13	0,54	0,27	0,31	0,16

* Underlined values are the peak values after the fire.

months after the fire (Sect. 8.4.), which supports the above contention. Consequently it is recommended that the burn programme is staggered so as to provide swards of different ages, which attain their optimum combination of quality and quantity several weeks apart.

8.6. SUMMARY

1. The grasslands of MGR are deficient in CP and P, the degree of which depends on season and age of the sward after burning.

2. Forage quality is highest in spring and summer in unburnt swards, and is improved by burning.

3. The enhancement of nutrient levels by burning lasts only for a few months.

4. During winter nutrient quality is lowest, and the most severe shortages are manifest in July and August.

CARRYING CAPACITY

9.1. OBJECTIVE

The objective of this section was to partially synthesize results from the preceding chapters for the determination of the herbivore stocking rate for MGR.

9.2. OVERVIEW AND RATIONALE

The determination of the carrying capacity (CC) of natural areas for wild herbivores remains an elusive goal for the wildlife manager and researcher. Part of the problem stems from the use of the same term to describe two very different situations dependent upon management objectives. On the one hand "carrying capacity" has been used to describe the density of animals for maximum sustainable yield; and on the other hand, it has been applied to the density of animals that a given area may sustain without effecting long-term (detrimental) changes in the vegetation and environment, i.e. the density at which there is an equilibrium between the animal species and the resources upon which it/they depend. The first is of importance to the manager interested in economic returns, whilst the latter is of relevance to the manager of classical conservation areas where the goal is to maintain the environment and ecosystem in its 'natural state' (if such a state exists). Caughley (1976) proposed that the former be referred to as "economic carrying capacity" and the latter as "ecological carrying capacity" as a means of distinguishing the aims of different management policies. These terms have been successfully adopted in the subsequent literature.

As implicated by Caughley's (1976) differentiation between economic CC and ecological CC, the management objectives for an area are of prime importance in determination of the desired stocking rate.

This applies to all forms of possible management ranging from standard commercial pastoralism, through subsistence pastoralism to game ranching and conservation (Mentis 1978, 1984). Carrying capacity is further dependent upon several properties of each specific management unit. These include; (i) the types and ratios of the herbivore species stocked, (ii) the net primary production, (iii) the proportion of the net primary production that is edible to the species stocked, (iv) topography and (v) veld condition (Edwards and Coetzee 1971, Mentis 1976). The last, in turn, depends on many factors; including soil type, past and present land use, and floristic composition, all of which are interrelated. The interrelationships between these variables, and the fact that some of them are constantly changing leads to the result that the CC of a particular area is never constant (Sinclair 1981, Emslie 1985, Hardy and Mentis 1986). This tends to make the quantification of a static CC a rather meaningless pursuit. It would be better to allow systems to attain their 'own' equilibrium. Alternatively only broad boundaries of animals numbers should be proposed, rather than one figure. The first option is not always viable due to the artificial nature of many conservation areas (Hanks et al. 1981, Owen-Smith 1983), although the dire consequences often predicted under such circumstances are rarely manifested (Caughley 1981).

Currently, the view is held that the low soil fertility of many African rangelands in combination with several other factors (selective grazing strategies, migration to 'follow' a sequence of seasonally changing food abundance, influence of fire on both the vegetation and grazing dynamics of herbivores) serve to lower the ecological CC of areas dominated by wild herbivores relative to areas under domestic herbivores (Bell 1982, Scotcher 1982, Rowe-Rowe and Scotcher 1986). This was evident from the survey by Mentis and Duke (1976) which indicated that areas under wild herbivores

exhibited evidence of "overgrazing" and deterioration of grasslands when stocked at the recommended agricultural rate. Generally, evidence of degradation was noted at stocking rates well below the agricultural stocking rate. This led Mentis and Duke (1976) and Mentis (1977) to propose that stocking rates for wild herbivores should be at least half of, if not lower than, those for domestic herbivores. This is hardly surprising, bearing in mind that the agricultural stocking rates are recommended for cattle (bulk grazers) based on a well managed system of prime veld, rotational grazing, and supplementary feed during winter and autumn. Emslie (1985) added that as the recommended agricultural stocking rates are conservative, and that farmers stock to maximize yield and not the number of animals per unit area, the ecological CC for cattle was higher than the recommended stocking rate. Hence the ecological CC for wild herbivores would certainly be less then the 50 % reduction proposed by Mentis and Duke (1976). Recently Rowe-Rowe and Scotcher (1986) suggested that the ecological CC of the Natal Drakensberg for wild herbivores was approximately ten times lower than the recommended agricultural stocking rate of 1 AU per 5,0 ha. Similarly, Shackleton (1984) recorded that the stocking rate at Mount Sheba Nature Reserve (North-eastern Mountain Sourveld) was also approximately 10 % of the recommended agricultural stocking rate (it was an open system with relatively free access in and out of the reserve). This estimate is in agreement with that of Sharkey (1970) who concluded from a review of the ecological CC of various regions around the world that the ecological CC for domestic herbivores was in the region of ten times greater than that of wild herbivores. He suggested that this was so because of the greater natural and induced soil fertility, and high yielding plant species that characterize domestic systems.

The stated aims of MGR were to deal in game products (Sect. 2.8.3.)

and hence it was important to determine the economic CC. However, current, but unwritten, management policy appears to be concerned more with the ecological CC. As the economic CC is always less than the ecological CC (Caughley 1976, Mentis 1984, Thompson 1986) determination of the ecological CC for MGR sets an upper limit to the total density of herbivores that are desirable in the reserve. From hereon CC refers to the ecological CC unless otherwise stated.

9.3. METHODS

The calculation of CC has never been accurately determined from empirical data in Africa. Consequently, several methods have been attempted to approximate it. Five methods were used here, each a supposed refinement of the preceding one, and the results compared. Present herbivore numbers refer to the figures from the last census (October 1986) unless stated otherwise. All census figures are from aerial counts as a mean of three counts and/or observers (P. Ruddle pers. comm.). Herbivore numbers were converted to AU using Equation 9.1. Here, an AU was defined as the herbivore biomass consuming energy at the same rate as an average steer of 450 kg (Meissner 1982) [Mentis and Duke (1976) used a value of 456 kg, and Rowe-Rowe and Scotcher (1986) used a value of 455 kg]. This successfully accounted for the higher proportional energy requirements of smaller herbivores (Mentis 1977).

$$\text{species X} = \frac{450^{0.75}}{\text{Mean body mass of species X}^{0.75}} \text{ AU} \quad \ldots \text{(Eq. 9.1.)}$$

In using AU it was recognized that it was an oversimplification in that it neglects the fact that smaller herbivores require food of higher quality, which is generally scarce, especially in sourveld regions (Mentis 1977). It is therefore incorrect to equate the

impact of 4,84 blesbok to that of one steer in accordance with Equation 9.1., although it is the best approximation presently available.

Mean body masses were taken from Mentis and Duke (1976) which were derived from a representative sample including both males and females, as well as sub-adults.

Method 1. This employed the recommended stocking rate for the MGR region (Mentis and Duke 1976). The area available was corrected for the non-utilizable areas of the reserve (forests, rocky areas, wetlands, and tourist camps) in the manner of Grobler and Jones (1980). The contribution of these areas to the total of the reserve was determined from Maps 1 - 3 using a digital planimeter.

Method 2. Using the data from chapters 5 and 6 the primary production was calculated. In accordance with the community approach to this study, ANP was calculated with data for the sward as a whole, after summing the data for the individual key species. The method adopted was the summation of increments in phytomass with no statistical constraints. Increments in the necromass and litter components were also summed if they occurred concomitantly with increments in the phytomass component. Thus, plant senescence and litterfall were accounted for. Losses through decomposition at each time interval were also included using Equation 9.2. (Smith 1985).

$$D = \frac{Lp + Lt}{2} \cdot rt \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad \text{Eq. 9.2.}$$

where: Lp is the mass of litter at the start of the time interval
Lt is the mass of litter at the end of the time interval
r is the instantaneous rate of decomposition
t is the length of the time interval (days)

The mean decomposition rate (r) at all sites was calculated as the average LB rate measured for all the key species and species groups (see Ch. 7). Peak-trough analysis was also attempted and yielded marginally lower estimates of ANP in the first year after the burn and markedly lower estimates in the second year after the burn at both sites. Translocations to and from the BSC were not included in any of the calculations.

The daily intake requirements of the various herbivore species were determined from the literature. The annual grassland production was then divided by the yearly requirements to determine the number of AU that could be maintained. This was adjusted by the standard "carry over" of a certain proportion of the productivity for the subsequent years growth (Edwards and Coetzee 1971, Heady 1975).

Method 3. This considered the contribution of only the palatable species to the total available. However, it was illustrated in chapters 7 and 8 that palatability of individual species varied throughout the year. Hence the total DWR contribution (%) of all the preferred species was taken from Table 7.3. and Table 7.6. for the **T. leucothrix - L. simplex** and the **C. validus - D. natalensis** communities, respectively. The proportion of palatable species in the remaining grassland communities was assumed to be the average of these two communities. The degree to which the proportion in the other communities deviated from this assumed value was not of great importance because of their relatively small areas. This approach was used by Conlong (1986), but his determination of which species were palatable and which not was subjective and not based on empirical observations.

Method 4. This was based calculation of the absolute amounts of nutrients determined as limited using the data of total ASC (Ch. 5)

and nutrient levels (Ch. 8). From these, annual production of CP and P was determined, in the same manner as method 2 for ASC, and weighed against daily requirements of herbivores.

Method 5. Most of the above approaches considered mean values for the year and neglected the periods of high and low availability of resources (dry matter, CP, etc.) during the year. This approach quantified the 'store' of resources at the end of the growing season and attempted to determine whether or not it was sufficient to supply the needs of herbivores during the non-growing season, during which time it was assumed there was no replacement.

9.4. RESULTS & DISCUSSION

9.4.1. Herbivore numbers

The present number of herbivores and AU of each species is provided in Table 9.1. Changes in the total number of AU, and individual species over the past six years are given in Table 9.2. and Figure 9.1., respectively.

Table 9.1. Present herbivore numbers at MGR

HERBIVORE SPECIES	NUMBER	MASS (kg)	NUMBER/AU	AU EQUIVALENTS
Blesbok	700*	55	4,84	144,6
Blue Wildebeest	290	182	1,97	147,2
Eland	186	385	1,12	166,1
Red Hartebeest	140	182	1,97	71,1
Burchell's Zebra	98#	216	1,73	56,6
Impala	80#	41	6,03	13,3
Springbok	60#	28	8,03	7,5
Gemsbok	40	160	2,17	18,4
Mountain Zebra	40	221	1,70	23,5
Total	1 634	229 738		648,3

* Estimate as midpoint between the last two censuses, as the October 1986 count of blesbok did not include young, and the previous count was an estimate.

These figures are most certainly overestimates at the time of writing.

Table 9.2. Total animal numbers since 1982

DATE	5/82	3/84	10/84	3/85	11/85	10/86
TOTAL NUMBER	1 573	1 590	1 440	1 670	1 829*	1 634
ANIMAL UNITS	615	646	590	665	721	648

* Total number of blesbok was only an estimate

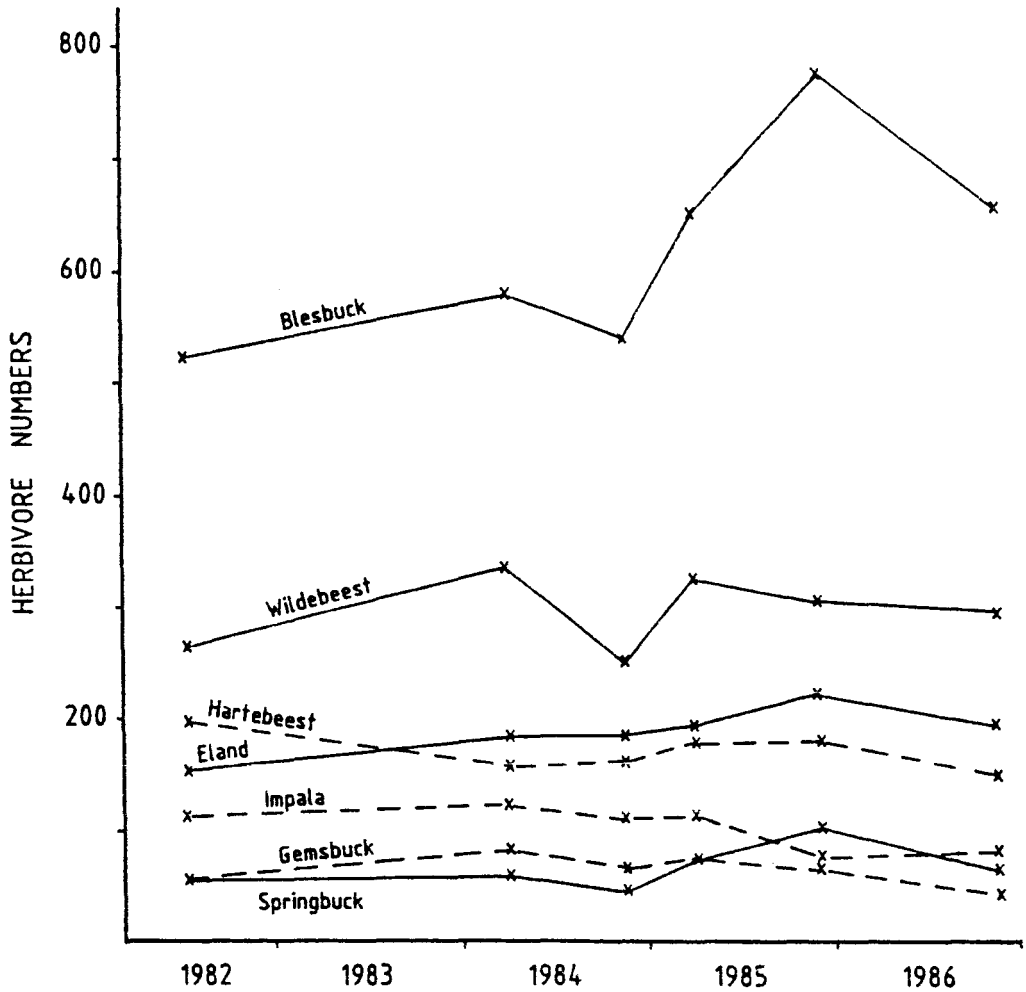


Figure 9.1. Changes in herbivore populations since 1982

From the above it is evident that herbivore numbers remained relatively constant between 1982 and 1986 (if the November 1985 count is ignored because of the inaccurate count of blesbok which

were the most numerous in the reserve). The minimum and maximum figures differed by only 16 %. Figure 9.1. indicates that the numbers of impala, mountain zebra and gemsbok remained steady or declined, suggesting that they were ill adapted for this region. Decline in these species has been balanced by increments in the number of blesbok, eland and Burchell's zebra. It was noteworthy that the mean density of eland (3,13 km^{-2} - calculated on the basis of grazable area plus area of indigenous forest) was the third highest in Africa [compared to the data reviewed by Scotcher (1982) Table 4.4.6] and the calving percentage is still high (pers. obs.).

9.4.2. Carrying capacity

Method 1. Agricultural stocking rate

The recommended stocking rate for wild ungulates in this region (extrapolated from Natal) is 5 - 6 ha/AU (Mentis and Duke 1976). A mean figure of 5,5 ha/AU was used in the subsequent calculations. Presumption that the total area (7 720 ha) was available to herbivores resulted in a recommended CC of 1 403,6 AU. The CC calculated by Chapman (1980), Ruddle (1984) and Jooste et al. (1985) was slightly higher because their estimates were based on the area of the reserve being 8 000 ha and a recommended stocking rate of 4 - 5 ha/AU. O'Donovan (undated) used a recommended stocking rate of 1,7 ha/AU which effectively increased the proposed CC to 4 705 AU. However, he did not show the derivation of such a high stocking rate, nor provided a reference. Hence, this estimate must be considered anomalous.

Comparison of this calculated figure with the present number of AU leads to the conclusion that MGR is understocked. This conclusion was shared by authors of the previous surveys, although the degree of understocking varied in accordance with the estimates of total

area and stocking rate employed. However, calculation of CC in this manner has several drawbacks (which are rarely mentioned), some of which serve to reduce the estimate and others that serve to increase it.

(1) This calculation assumes that the total area of the reserve is available to herbivores. This is clearly not realistic, as wetlands, campsites, forests, rock outcrops, etc. are not utilized by the herbivore complement at MGR. Therefore the calculated CC should be reduced by the proportion of the unavailable/ungrazable sites to the total area. Grobler and Jones (1980) estimated that only 49 % of the Whovi Wild Area in Matopos National Park was utilized by herbivores, and after reduction of the calculated CC to account for this, there was a closer agreement between the calculated CC and the actual number of AU. The extent of these unavailable sites in MGR is presented in Table 9.3.

Table 9.3. Extent of areas unavailable to herbivores.

SITE	AREA (ha)
Indigenous forest	558,1
Wetland	486,8
Exposed rock	271,2
Exotic forests	103,2
Accommodation areas	30,7
Total	1457,0

Thus, approximately 19 % of the reserve is unavailable to herbivores. Reduction of the calculated CC by this figure resulted in a recommended stocking rate of 1 140 AU. Despite this adjustment it still appears that MGR is understocked, being at only 57 % of the calculated CC.

(2) Wildlife areas are, of necessity, continuously grazed systems, i.e. the grazing period extends throughout the year with no rest

period. The CC recommended by Mentis and Duke (1976) takes this into account. Nevertheless, they comment that the conversion has limitations. The statement later in their paper to the effect that their figures were probably overestimates for sourveld regions because of the enforced continuous grazing system, is usually overlooked. This figure must therefore be viewed as an upper limit rather than a mid-point around which herbivore numbers may fluctuate.

(3) The CC of wild herbivores was calculated by Mentis and Duke (1976) as the CC for domestic stock over the grazing period of a particular vegetation type, extended to a continuous grazing system. Once again, most researchers making use of the figures of Mentis and Duke (1976) failed to acknowledge that the CC for domestic stock referred to a system under optimum conditions and management, although it was clearly stated in their paper. However, wild herbivore systems are rarely managed along similar lines of optimum management. Recognition of this fact serves to emphasize that the calculated CC using this approach must be regarded as an upper limit. Indeed, Mentis and Duke (1976) concluded that areas stocked according to the recommended rate invariably displayed signs of deterioration and that their figures should be reduced.

(4) Being an extrapolation from the recommended stocking rate for domestic herbivores this estimate fails to account for the relatively selective grazing strategies of wild herbivores, especially the smaller species. This selectivity has arisen as a consequence of the need to obtain food of adequate quality in relatively poor quality grasslands. Thus, a large proportion of primary production that is edible to cattle is inedible to wild herbivores. Hence, CC determined in the above manner is an overestimate.

(5) Due to the preference of herbivores for burnt areas (Rowe-Rowe 1982) the influence of the controlled burning programme serves to introduce a rotational grazing system for certain times of the year. Directly after a burn only 50 % of the reserve is utilized, thus, the recommended CC should be halved during this period. If this is accepted, then the present numbers are slightly over the CC.

(6) It has been suggested that estimates based on the recommended agricultural stocking rates must be viewed as conservative (Emslie 1985). This arises from two comment that (i) agriculturalists are usually conservative in order to reduce resource degradation and large economic losses during unpredictable large-scale climatic fluctuations and, (ii) their estimates are not based on system processes. But as agricultural estimates are orientated more towards maximum sustainable yield rather than ECC, these points have little effect on calculation of CC.

(7) The CC calculated in this manner is an extrapolation from that recommended for domestic herbivores under an agricultural management system. Under such situations the objective is to maximize animal production which is generally achieved at some level below the CC. By this reasoning, this method should result in an underestimate of the CC for wild herbivores.

Method 2. Productivity of the MGR grasslands

Any determination of CC based on the measurement of above-ground net primary productivity (ANP) is reliant upon the method used to calculate ANP itself. The classic paper of Singh et al. (1975) discusses the various methods available for the calculation of ANP from harvest data, and the drawbacks associated with each. The nature of the data collected during the course of this study permitted calculation of ANP using any of the approaches reviewed

by Singh et al. (1975). That adopted is outlined in section 9.3. Results are presented in Table 9.4.

Table 9.4. Above-ground net primary production (ANP)

COMMUNITY	TREATMENT	SITE ANP ($g\ m^{-2}\ yr^{-1}$)		COMMUNITY ANP ($10^6\ kg\ yr^{-1}$)	
		1st yr	2nd yr	1st yr	2nd yr
T. leucothrix - L. simplex (5 460,2 ha)	Grazed	360,9	333,5	19,7	18,2
	Ungrazed	436,4	138,8	23,8	7,6
	Control	344,4	197,5	18,8	10,7
C. validus - D. natalensis (533,7 ha)	Grazed	446,5	429,1	2,4	2,3
	Ungrazed	430,1	566,0	2,3	3,0
	Control	256,6	796,7	1,4	4,3
T. triandra - C. asiatica (217,7 ha)	Control	-	658,1		1,4

It is possible to gain a rough estimate of the number of AU that can be supported in any given area after calculation of ANP (Edwards and Coetzee 1971, Conlong 1986). This is achieved by division of the total ANP in the reserve by the daily requirements of herbivores. Total ANP for the reserve was taken as the sum of that measured in the ungrazed plots as that simulates ANP without herbivores. This yielded a total ANP value of $27,5 \times 10^6$ kg yr^{-1}.

Quoted figures of daily requirements for domestic herbivores are variable. Edwards and Coetzee (1971) suggested a rough estimate of 10 kg day^{-1} per AU whilst le Roux (1979) used a figure of 12,5 kg day^{-1} per AU. Butterworth and Brandl (1980) calculated a basal metabolism figure of 6,1 kg day^{-1} per AU. According to Walker (pers. comm.) the daily requirement is approximately 9 % of an animal's metabolic mass (which is the equivalent to 8,8 kg day^{-1}

per AU). Conlong (1986) used the figure of Butterworth and Brandl (1980). However, as that refers to basal metabolism it is an underestimate of the requirements under normal activities. Furthermore, it does not reflect the different requirements due to changing demands during pregnancy, lactation, or rutting. Intake requirements for basal metabolism during pregnancy and lactation are available but the sex ratios of the herbivore species at MGR are unknown. Hence the figure of Edwards and Coetzee (1971) was opted for in subsequent calculations [it is also approximately the mean between the estimates of le Roux (1979) and Walker].

Using the figure of Edwards and Coetzee (1971) it was calculated that the yearly ANP at MGR could sustain 7 534 AU. This was 6,6 times greater than that calculated by the recommended agricultural stocking rate in method 1 above. However, as with method 1, this approach had several drawbacks.

(1) Meissner (1982) quoted several references reporting that wild herbivores in subtropical regions ingest less food material than domestic species of comparable size. Accepting this would imply that the result from this calculation, using requirements of domestic species, is an underestimate.

(2) The final CC is highly dependent upon which figure of daily requirements are accepted. Thus, if the figure of Butterworth and Brandl (1980) is used (as did Conlong 1986) the result would be an underestimate as the daily requirement of 6,1 kg refers to basal metabolism only. However, the figure accepted here appears to be representative of those reviewed, and therefore, the calculated CC can be accepted as representative.

(3) It ignores the compartmentalization of the ANP into phytomass, necromass and litter, and therefore assumes that all the ANP is

edible. Consequently, the calculated CC is an overestimate. This problem is sometimes ignored by researchers (eg Conlong 1986) which may have severe management implications. If only phytomass is considered the ANP of the **T. leucothrix - L. simplex, C. validus - D. natalensis** and **T. triandra - C. asiatica** communities is 13,8 x 10^6, 1,6 x 10^6 and 0,6 x 10^6 kg yr^{-1}, respectively. On this basis, the number of AU that could be supported would be 4 384.

(4) It ignores palatability of the constituent species, assuming that all the material is edible. However, both physical and chemical characteristics act to deter ingestion of particular species and thus they will be avoided by herbivores. Consequently, without correction for this, the figure calculated above is an overestimate. Method 3 (below) takes cognizance of the proportion of palatable species.

(5) It assumes a steady supply throughout the year and therefore fails to account for possible periods of short supply i.e. winter (see method 5). Thus, this figure may again be considered an overestimate.

(6) A proportion of the ANP should remain unutilized and carried over for the following season's growth. If this is not done so, this figure should be considered as too great. Edwards and Coetzee (1971) stated that at least 25 % (if not more) of ANP must be left for this purpose, whilst Heady (1975) suggested a 50 % carry over was standard rangeland practice. As the grasslands of MGR appear to be very productive, the minimum value of 25 % is suggested. This serves to reduce the CC to 3 288 AU.

Method 3. Contribution of palatable species

It is well known that most herbivores are selective at various scales (for areas, species and plant parts). This especially so for

the concentrate grazers that dominate the herbivore complement at MGR. Hence, calculations based on total ANP are invalid because not all of that ANP is acceptable, and as implied in the approach of Conlong (1986) only palatable species should be considered if dealing with concentrate grazers. Consequently, the mean contribution of palatable species to the total in MGR was determined and is provided in Table 9.5. The same rationale cannot be applied to bulk and roughage eaters which make some use of unpalatable species.

Table 9.5. Mean contribution of palatable species throughout the study period

COMMUNITY	AREA (ha)	CONTRIBUTION OF PALATABLE SPECIES (% ± SE)
T. leucothrix - L. simplex	5 460,2	37,1 ± 4,5
C. validus - D. natalensis	533,7	27,3 ± 6,3
Other grasslands	265,7	32,2

These proportions may be applied to either the estimates of ANP or the areas for each community. In this way, the annual production of palatable species in the three communities would be 8,8 kg yr^{-1} in the **T. leucothrix - L. simplex** community, 0,6 kg r^{-1} in the **C. validus - D. natalensis** community and 0,5 kg yr^{-1} in the **T. triandra - C. asiatica** community. This translated into an estimated CC of 2 750 AU. Accepting the principle of a 25 % carryover results in a reduction of this figure to 2 063 AU.

It is possible to use these proportions to determine the area of a "mythical reserve" of which all the species of the constituent grasslands were edible (Conlong 1986). This is provided by the sum of the products of the second and third columns (as a proportion)

in Table 9.5. This resulted in a figure of 2 257,0 ha. If stocked at the recommended rate of 5,5 ha/AU (Mentis and Duke 1976) the recommended CC would be 410 AU.

As with the previous methods inaccuracies can be identified in this approach due to several factors.

(1) This approach was based on empirical observations of which species were preferred and which were not. However, other species were grazed even if they were not preferred. Reasons for this were provided in chapter 8. Thus, this estimate should be considered as an underestimate.

(2) The observations of what was and was not eaten would be influenced by the present stocking rate and herbivore complement of the reserve. If the reserve is understocked, herbivores may not be utilizing species of marginal, but acceptable, palatability because of a relative abundance of highly palatable species. However, if the reserve is overstocked, herbivores may well be utilizing unpalatable species in an attempt to ingest sufficient food.

(3) The palatability rating of any particular species may change. This was indeed the case (see ch. 7). This is overlooked by some authors (eg Conlong (1986). However, this may be negated to some extent through empirical observation of what is and what is not selected - as attempted here. But the inclusion of intermittently palatable species results in the estimate of CC being too great.

(4) The palatability status of individual species may be influenced by the herbivores themselves. A marginally unpalatable species would be ignored until the herbivore density increased sufficiently for them to utilize such species. Once grazed, the regrowth may be significantly more palatable than the old growth. In this way its palatability rating is increased. Thus, the calculation of CC in

this manner for a reserve that is not severely overstocked would result in an underestimate. However, this would probably not be significant.

(5) Although the method recognizes that species differ in their palatability it ignores compartmentalization in the various ASC components (as with method 2). If only phytomass of the palatable species is considered the estimate of CC will be reduced. The ANP of phytomass in the various communities was 5,1 x 10^6 kg yr^{-1} in the T. **leucothrix - L. simplex** community, 0,4 x 10^6 kg yr^{-1} in the C. **validus - D. natalensis** community, and 0,2 x 10^6 kg yr^{-1} in the T. **triandra - C. asiatica** community. Thus the effective CC would be approximately 1 562 AU. With a 25 % carry over, the estimated CC would be 1 172 AU.

(6) Calculating the area of a 'mythical' reserve with totally edible material and then applying the recommended stocking rate is inaccurate because the recommended stocking rate is based on the species composition and therefore accounts for the inedible species. If all the species were edible the recommended stocking rate would be greatly increased. This was not recognized by Conlong (1986) when he adopted this approach.

Method 4. Nutrient stocks

It was demonstrated in chapter 9 that the concentrations of crude protein (CP) and phosphorus (P) were limiting during particular times of the year. In a manner similar to method 2 the productivity of these nutrients can be calculated and then weighed up against herbivore requirements. Calculation of nutrient productivity is based on absolute amounts per unit area which may be derived from the the product of the concentration (ch. 8) and phytomass (ch. 5). This was done for CP and P and the results are presented in Table 9.6.

Table 9.6. Annual production of crude protein and phosphorus

NUTRIENT	COMMUNITY	PRODUCTION (g/m^2 /yr)	AREA (ha)	TOTAL COMMUNITY PRODUCTION (kg/yr)	MEAN DAILY PRODUCTION (kg/day)
Crude Protein	T. leucothrix L. simplex	15,25	5 460,2	832 680,5	2 281,3
	C. validus D. natalensis	15,00	533,7	80 055,0	219,3
	T. triandra C. asiatica	16,81	217,7	36 595,4	100,3
	TOTAL		6 211,6	949 330,9	2 600,9
Phosph-orus	T. leucothrix L. simplex	0,13	5 460,2	7 098,3	19,4
	C. validus D. natalensis	0,15	533,7	800,6	2,2
	T. triandra C. asiatica	0,14	217,7	304,8	0,8
	TOTAL		6 211,6	8 203,7	22,4

The daily requirements of domestic herbivores for CP and P is approximately 0,07 % and 0,003 % respectively, of their body mass (ARC 1965). This is the equivalent of 0,315 kg CP day^{-1} per AU and 0,0135 kg P day^{-1} per AU.

On the basis of the figures for CP, MGR could, therefore, support 8 257 AU. This is the highest estimate calculated so far.

However, refinement of this figure in the manner adopted for the previous calculations serves to reduce it considerably. Thus, if only palatable species are considered the production of CP is approximately 938,5 kg day^{-1}, permitting a CC of 2 979 AU. Looking at the phytomass component only in conjunction with the biennial burn and an 25 % carryover results in a CC of 650 AU.

If the figures for P are used, it is estimated that the CC would be 1 659 AU, more than double the present numbers. The lower estimate based on P appears to indicate that P, rather than CP, is the more limiting factor. Adjusting this estimate to exclude unpalatable species reduces the CC to 963 AU, and incorporation of the relevant reductions for the biennial burn and 25 % carryover results in a figure of 212 AU.

As with the above methods, this one also has several generalizations/drawbacks that limit its accuracy.

(1) It is based on absolute mass rather than metabolic mass which is not as accurate (Mentis 1977).

(2) It ignores seasonal differences of abundance or scarcity. Hence, at particular times of the year, the CC could be higher than calculated, whilst at others it would be lower. But if the most critical shortage is of only short duration than the herbivores may survive through until a subsequent period of increased production. In contrast, if it is too long a duration then the above is an overestimate.

(3) More importantly, it ignores the foraging time required to meet the daily requirement. Thus, in absolute terms the standing stock per unit area may be adequate, but if the concentration is very low (as was shown in Ch. 9), herbivores would have to ingest and digest large amounts of food to obtain the required quantities. Under such circumstances there may be insufficient foraging and rumination time to ingest the required amounts, and therefore, the calculated CC would be an overestimate. Whether or not this applies to the CC based on CP adjusted for palatable species only is unknown because it is highly probable that the CP concentration in the palatable species is considerably higher than the other species. This

calculation based on palatable species only would serve to reduce the dilution effect.

Method 5. Seasonal availability of phytomass and CP

A problem common to all the above estimates is that they failed to account for seasonal differences in supply of required resources. And yet it is clear that if resources are inadequate they should be most limited during the non-growing season, during which time they are not renewed. This may apply to both quantity and quality of food. The peak amounts of phytomass and CP are presented in Table 9.7.

Table 9.7. Peak phytomass and CP stores

COMMUNITY	AMOUNT (kg/ha) Phytomass	CP	AREA (ha)	COMMUNITY TOTAL (kg) Phytomass	CP
T. leucothrix - L. simplex	2 329	140.0	5 460,2	12 716 806	764 428
C. validus - D. natalensis	2 500	134.4	533,7	1 334 250	71 729
T. triandra - C. asiatica	2 210	141.3	217,7	481 117	30 761
	TOTAL			14 532 173	866 918

Assuming a non-growing period of 180 days and the daily requirements given in methods 2 and 4 the store of phytomass at the end of the growing season could support 8 073 AU throughout the winter period. Even if only palatable material is considered it is clear that there was no shortage of material for the present number of herbivores on a mass basis. The same appears to apply for the store of CP which, at 866 918 kg, should be able to support 15 536 AU throughout the winter period. Correction of both these values as in the above methods results in a calculated CC approximately double the present number (Table 9.8.)

Despite being a refinement upon several of the above methods there are still inaccuracies inherent in this method.

(1) Herbivores can survive a period of shortage by mobilization of body reserves and tissues (Hardy and Mentis 1986) as was the case at MGR (C. Shackleton in prep.). Thus, although the store of CP is inadequate to meet daily requirements it does not necessarily follow that there will be increased mortality. The shorter the period of non-replenishment, the greater is the probability that the herbivores will survive. However, whilst 'weathering' a period of short supply by utilization of body reserves there may be increased mortality due to disease and weakness induced by their poor nutritional status. Consequently, this method underestimates the CC, but does indicate that animals will experience mass loss during the non-growing season.

9.5. GENERAL DISCUSSION

9.5.1. Carrying capacity of MGR

If nothing else, the wide range in the results, summarized in Table 9.8., serves to emphasize the difficulties and ignorance surrounding the calculation of the CC for a given area. The calculated CC ranges from less than 100 AU to over 15 000 AU and even then reasons for inaccuracies have been identified with each approach. This certainly leads to questioning the applicability of the results, indeed, the very concept of carrying capacity itself.

In this respect, methods 4 and 5 which incorporated aspects of the quality of the vegetation would appear to be the most realistic approaches. The general agreement between the final values in methods 1 and 3 with that of 4.1. lends further credence to method 4. The values obtained from these three approaches suggest that MGR

is presently close to CC or marginally overstocked, especially as most of the inaccuracies in the approaches suggested that they overestimate CC.

Table 9.8. Summary of values of carrying capacity for herbivores at MGR calculated according to different methods

METHOD	ADJUSTED FOR -	CC (AU)	
1. Agricultural		1 404	
	- non grazable areas		1 140
	- biennial burning		570
2. Productivity		7 534	
	- proportion of phytomass		4 384
	- biennial burn		2 192
	- 25 % carryover		1 644
3. Palatable species		2 750	
	- proportion of phytomass		1 562
	- biennial burn		781
	- 25 % carryover		586
4.1. CP productivity		8 257	
	- palatable species		2 979
	- proportion of phytomass		1 734
	- biennial burn		867
	- 25 % carryover		650
4.2. P productivity		1 659	
	- palatable species		963
	- proportion of phytomass		565
	- biennial burn		283
	- 25 % carryover		212
5.1. Peak stocks of phytomass		8 073	
	- palatable species		2 910
	- biennial burn		1 455
	- 25 % carryover		1 091
5.2. Peak stocks of CP		15 536	
	- palatable species		5 611
	- proportion of phytomass		3 267
	- biennial burn		1 634
	- 25 % carryover		1 226

Accepting that the upper CC of MGR is approximately 600 AU, then it is considerably greater than that recorded in other sourveld regions. The similarity of the MGR grasslands to those of the Natal

Drakensberg have been indicated in earlier chapters, and hence the discrepency in estimates of CC casts doubt upon this figure. The higher productivity of the coastal grasslands, longer growing season and less severe winters may ameliorate this difference to some extent. The effect of these factors require investigation, where possible.

Rowe-Rowe and Scotcher (1986) estimated the CC to be only 10 % of that of the recommended agricultural stocking rate for the sourveld grasslands of the Natal Drakensberg. Their estimate was substantiated by the numerical stability of herbivore populations in the Natal Drakensberg, having been more or less constant over the last six decades without any active management. Rowe-Rowe and Scotcher (1986) quote data from Southgate (1979) from another area of the Drakensberg which is in agreement with their estimate. As previously stated, Shackleton (1984) similarly recorded a very low stocking rate for wild herbivores on sourveld grassland in the eastern Transvaal, although it was not known whether the populations had been stable for a long period or not. In agreement with the findings of Rowe-Rowe and Scotcher (1986) Sharkey (1970) concluded that the maximum recorded CC of wild herbivores was only 10 % of the maximum for domestic herbivores after reviewing several sources from around the world.

However, acceptance of that the CC of MGR is only 10 % of that of the recommended agricultural stocking rate (± 58 AU) is problematic in that it is inconceivable that any reserve could be stocked to 1 100 % of the CC (there are presently 648 AU in MGR) without signs of massive deterioration in both habitat and vegetation. Definite signs of localized heavy grazing are evident and it is my impression that these have increased in size and number during the course of this study. These areas are favoured by the concentrate

grazers, which is a common feature of most sour grasslands under wild herbivores. However, the impression that these areas are increasing does suggest that the present herbivores numbers are close to or slightly greater than CC.

In light of (i) the general agreement between methods 1, 3 and 4.1., (ii) the findings of Mentis and Duke (1976) that the agricultural stocking was an overestimate for wild herbivores, (iii) recognition that most of qualifications attached to the various methods adopted to calculate CC suggested that the results were overestimates, (iv) the increase in heavily utilized areas, (v) the winter stress experienced by the herbivores, and (vi) the form of rotational grazing imposed by the biennial burn, I suggest that MGR is marginally overstocked. This is further supported by the decline in numbers of the species ill adapted to this area (gemsbok, impala, springbok) following an initial increase in their numbers. Moreover, it appears that the reproductive rate of the blesbok, which are well suited to this region, has declined (Andrews pers. comm.).

Thus, I envisage that animal numbers will decline over the next few years, or the extent of the heavily grazed areas will increase significantly, which could, after some optimum is attained, lead to a lowering of the ecological CC in the long term. However, it is likely that animal numbers will level off and there is no need for control of animal numbers. In this frame I suggest that 500 - 600 AU be considered the CC of MGR over the next few years, after which herbivore reproductive rates and condition of the grasslands should be reviewed. Whether or not management should attempt to actively contain the herbivore numbers within these limits is discussed in chapter 10.

9.5.2. Carrying capacity and the environment

Several attempts have been made over the last two decades to relate CC to abiotic variables. In this way the differing CC of various regions could be explained as well as lending a predictive capacity for unstudied areas. The first models related CC to rainfall or effective moisture status (Rosenzweig 1968, Coe et al. 1976) as these was perceived as the factor controlling productivity. This approach yielded satisfactory results for regions with an annual rainfall of less than 700 mm per annum, but the relationship between rainfall and productivity diminished under greater precipitation values. It was inferred from this that some other factor limited production where rainfall was adequate.

Recent syntheses by Botkin **et al.** (1981) and Bell (1982) suggested that soil nutrient status was the other factor, and as such, should be incorporated into the modelling of productivity. This parallels work demonstrating the importance of food quality in determination of available herbage. Botkin **et al.** (1981) and Bell (1982) contend that CC can be related to soil nutrient status because the latter determines food quality. Thus, low soil nutrient status yields low quality food and hence the CC is low. In the same way, high soil nutrient status leads to a high CC. This must be considered in conjunction with the rainfall regime as that determines the amount of food. However, under high rainfall leaching of soils is intense, resulting in a low nutrient status. This limits the productivity and reduces the quality of available herbage. Thus, the highest CC should be evident in regions of intermediate rainfall where there is adequate moisture for high productivity, but only limited leaching, thereby promoting production of good quality forage. This relationship was summarized by Botkin **et al.** (1981) in Figure 9.2.

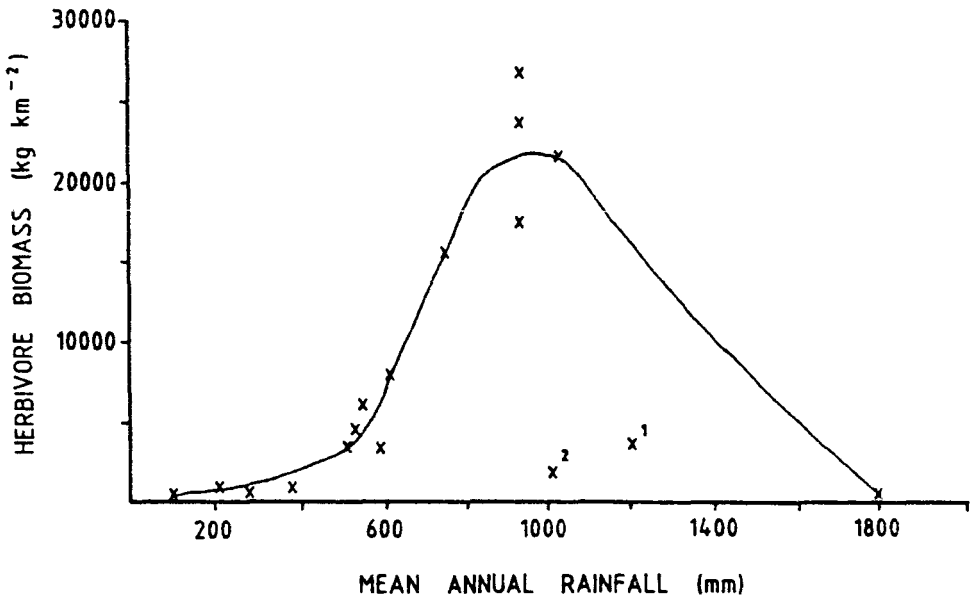


Figure 9.2. Herbivore biomass as a function of mean annual rainfall [adapted from Botkin **et al.** (1981): 1 = MGR, 2 = GCGR]

However, Scotcher (1982) indicated that this relationship did not hold for the Natal Drakensberg. It clearly does not apply for MGR either. This is a result of the data used by Botkin **et al.** (1981) being from areas with a high nutrient status relative to the dystrophic regions of the Natal Drakensberg and MGR (Scotcher 1982). It appears, therefore, that the curve in Figure 9.2 should be displaced to the left. The data reviewed by Bell (1982), with a few exceptions, certainly substantiates this (Fig. 9.3).

It is worthy of comment that most of the areas on Bell's (1982) figure with a mean annual rainfall of greater than 850 mm have a basement geology (i.e. situated on Precambrian strata) and a low herbivore biomass. Moreover, these areas are characteristically dominated by large herbivores such as elephant (**Loxodonta africana**) and buffalo (**Syncerus caffer**). Data from MGR includes it in that

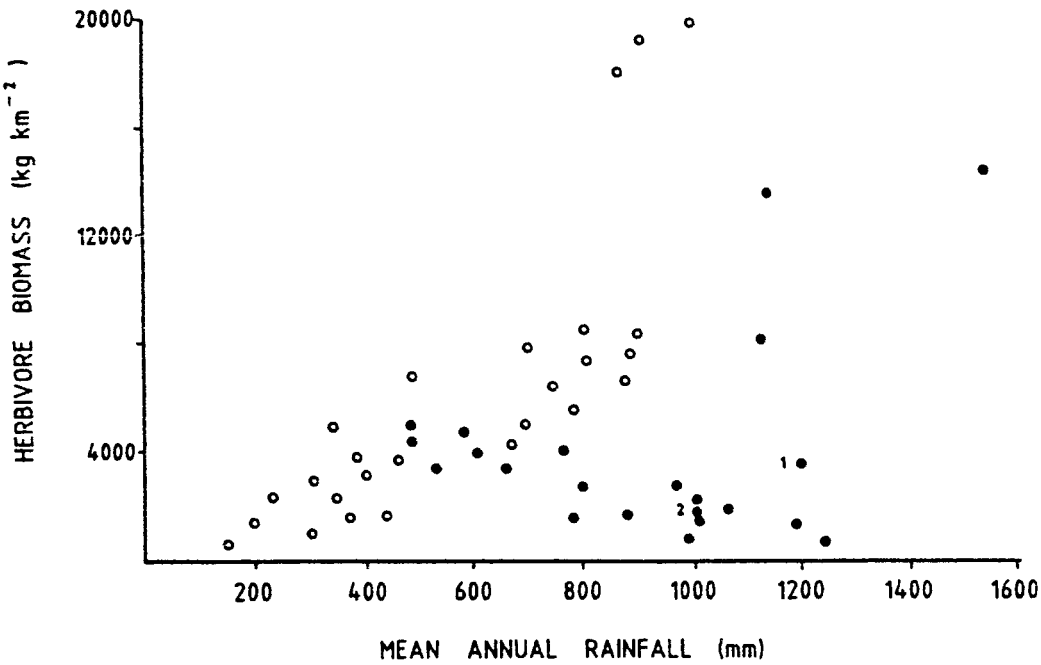


Figure 9.3. Herbivore biomass as a function of mean annual rainfall [adapted from Bell (1982); 1 = MGR, 2 = GCGR; o = non-basement geology, ● = basement geology]

Note: the three extreme points at the top of Figure 9.3. are anomalous and reasons for this are suggested by Bell (1982)

area of the figure. However, such a position is anomalous in that it does not have a basement geology [although the mapping scale used by Bell (1982) would possibly classify it as being on a basement geological type], nor is it dominated by large herbivores. Bell (1982) did, however, note several dystrophic grassland areas as exceptions. These were dominated by small herbivores as is the case at MGR. Bell (1982) concluded that community structure in these areas was displaced. Alternatively, the non-conformity of MGR to this relationship may serve to indicate the artificiality of the herbivore complement at MGR. The decline in numbers of impala, gemsbok and springbok support the obviously poor consideration of historical and ecological factors in the initial stocking of the reserve.

9.6. SUMMARY

1. In light of the similarity of these grasslands to those of the Natal Drakensberg (in terms of species composition, productivity, seasonality, fire response and forage quality), and the low quality of forage at MGR, it is probable that the CC is below the recommended agricultural rate, as is the Natal Drakensberg.

2. The carrying capacity of MGR should not be viewed as static and herbivore populations should not be maintained at a particular level. Rather, numbers should be able to fluctuate within broad limits.

3. It is recommended that the lower and upper limits for MGR be 500 AU and 600 AU, respectively, over the next few years.

4. Adherence to these limits should be reviewed after five years and appropriate recommendations made.

SYNTHESIS AND RECOMMENDATIONS

Following description of the soils and grasslands of MGR, data were presented to quantify each of the variables and processes outlined in the original model (see Fig 1.1). For critical evaluation, the study can be divided into three sections: (i) description of the soils and grasslands of the reserve, (ii) determination of standing crop of the grasslands, and (iii) assessment of the suitability of the grasslands for herbivores. From these various conclusions can be drawn, on which, in turn, several management and research recommendations can be made.

10.1. MGR - soils and grasslands

Chapters 3 and 4 provide the basis for improved management based on a knowledge of the various edaphic and vegetative units in the reserve. As such this is an accepted conventional starting point for any research aimed at promoting more objective and knowledge-based management of the biota of any area.

Three soil associations were identified, each composed of several forms. The arrangement of these associations in relation to topography was generally repetitive and thus conformed to the catena concept. At the top of slopes, shallow, undeveloped soils of the Mispah and Glenrosa forms were predominant. These graded into deeper, well-developed soils of the Clovelly and Hutton forms at the mid-slope position, to deep hydromorphic soils at the base of the slope (Pinedene, Katspruit and Champagne forms). In terms of area of the reserve, the most extensive forms in each of these groups were Mispah (64,7 %), Clovelly (15,9 %) and Champagne (6,8 %).

In some instances the delimitation of the various soil associations

correlated well with particular vegetation types. For instance, hydromorphic soils usually supported seasonal and/or perennial wetland vegetation and soils of the Hutton form generally underlay the **C. validus - D. natalensis** grassland community. More specifically, the distributions of the grassland communities were associated with particular ranges of soil variables, rather than soil forms (see later). This inventory of the soils, and soil-vegetation units, coupled with knowledge of the erosion potential of each form is an invaluable aid in deciding the correct location of roads. This is especially necessary where they are presently the cause of accelerated erosion or are impassable during the wet season due to waterlogging.

Critical evaluation indicates that the results of the multivariate procedures applied to the vegetation data substantiated the identification of the original vegetation units discerned in the field. The most extensive grassland communities were the **T. leucothrix - L. simplex** short grassland (71,1 % of the reserve), **C. validus - D. natalensis** medium grassland (6,9 %) and the **T. triandra - C. asiatica** dwarf grassland (2,8 %). Forests and wetlands comprised 7,2 % and 6,3 % of the total area, respectively. The extent of the shrub grassland subcommunity dominated by **S. vulgaris** and **A. calva** appeared to be related to fire frequency although this requires further investigation.

Correlation between the various grassland communities and specific edaphic and physiographic variables emphasized the distinctiveness of the communities recognized. Thus, the **T. leucothrix - L. simplex** short grassland was associated with sandy soils of a lower nutrient status than the clayier soils characteristic of the **C. validus - D. natalensis** medium grassland community. The **T. triandra - C. asiatica** dwarf grassland adjacent to the seashore was associated

with soils with a high conductivity and organic matter content relative to other communities. These habitat - vegetation associations also enhanced insight into the relationships between communities and their successional trends. Thus, where two or more communities or subcommunities are not associated with mutually exclusive ranges of the measured environmental vaiables, it is possible that one may expand at the expense of another as environmental pre-requisites are similar.

Using the areas of each community, and Map 3 it is now possible to define more rational boundaries for the management compartments/blocks. This refinement will take into account the ungrazable areas of each compartment, as presently some blocks are of widely differing areas, thereby causing an imbalance in food supply between the two years of the burning cycle. Compartment boundaries may further be refined to ensure that there are equal proportions of each community within each compartment, so that localized heavy grazing is not promoted by burning of the majority of the favoured **C. validus - D. natalensis** community in one compartment. This second refinement would also balance the productivity of the various compartments.

10.2. Determination of standing crop

Determination of standing crop indicated that forage availability was heavily influenced by season reflected in marked differences in partitioning of ASC between the phytomass, necromass and litter components between winter and summer. Thus, peak levels of phytomass of between 45 - 55 % in summer decreased to 15 - 26 % of the biomass in winter. Availability was also a function of the age of the sward which also affected this partitioning. Peak absolute values of total ASC are the highest recorded in southern African grasslands to date. However, these differred between treatments and

different aged swards. Herbivory reduced total ASC marginally (< 8 %) but had little influence on the partitioning into the above components.

Although calculation of AGP is highly dependent upon the method used, the results support Acocks' (1953) suggestion that these grasslands are probably the most productive in southern Africa. In common with the dystrophic soils elsewhere in southern Africa, this is a reflection of the high precipitation characteristic of such areas (Scotcher 1982). This high rainfall together with the equable coastal temperature regime, are the most probable factors which ensure that the coastal grasslands of this region are more productive than the more intensively studied montane grasslands of similar species composition (Sect. 5.5.5).

In evaluating this aspect of the study three shortfalls are evident. (i) Separation of standing crop into key species and species groups was extemely time consuming. Furthermore, the high variability of the resultant data detracted from the usefulness of this approach in lending any insight into the role of these species in community dynamics. (ii) Non-replication of the sample sites precluded the use of inferential statistics. The rationale at the commencement of this study was that it was more important to monitor the three most extensive communities, rather than several sites in the most extensive community only. An additional factor which precluded the sampling of additional sites was the labour necessary to separate clipped material into key species. However, a result of this non-replication is the lack of any indication of the extent to which site-specific differences contributed to the measured overall differences in ASC between communities. (iii) Low sample number of clipped quadrats. Although sample number was determined from a pilot study, and the resultant variation was

usually relatively low (< 20 %) in comparison to other productivity studies, more samples would have been a more efficient use of the time available than the separation of clipped material into key species and species groups.

Further improvement may have been gained by increasing the overall emphasis of the LB study. This would involve placement of bags in the field monthly, or seasonally rather than just once as done during this study. However, such a refinement was not efficient in terms of the primary objectives of the study (see Ch. 1). Such work could, however, yield very profitable results if undertaken at MGR in the future.

10.3. Suitability of the grasslands for herbivores

This aspect of the study revealed that the present herbivore complement had little impact on the productivity of the grasslands of the reserve since the animals consume less than 8,0 % of the available forage (Ch. 7). In contrast to the grasslands, however, both Tinley (pers. comm.) and Dutton (pers. comm.) have predicted and observed extensive damage to the forests, and endemic woody species in MGR.

The low herbivore impact on the grasslands is attributed to the poor nutrient quality of the grasslands and the dominance of concentrate grazers in the herbivore complement. Crude protein was low (< 5,0 %) from March through to August in the two most extensive grassland communities. This deficiency was temporally ameliorated by burning which increased CP levels 200 - 300 % for two to three months immediately following the fire. Phosphorus appeared to be deficient for herbivore requirements throughout the year except in burnt grasslands. However, the improvement in P concentration after burning was shortlived, and levels declined to

below maintenance requirements within two months. Digestibilty also declined rapidly after a fire being generally less than 35 % within 4 - 5 months after the fire. It rarely exceded 30 % in the older unburnt swards.

This has resulted in pronounced area and species selection. Preferred species (PR > 1) generally comprised more than 70 % of the diet but usually represented less than 45 % of the forage available in the **T. leucothrix - L. simplex** community and less than 30 % in the **C. validus - D. natalensis** community (Sect. 7.4.).

Two interrelated criticisms may be levelled at this aspect of the study. Firstly, plant-based estimates of utilization were used, which are less accurate than animal-based methods. However, no animal-based method is as quick and accurate as the methods employed here unless tame animals are used. The adoption of tame animals was not feasible because of the diversity of ungulates at MGR. Furthermore, this aspect was recognized, and estimates of herbivore requirements were corrected, as far as possible, for this (Sect. 8.5.4.). The second problem relates to the extrapolation of nutrient requirements from domestic stock to wild herbivores. Unfortunately, empirical studies of the nutritional requirements of the various species of wild herbivore still need to be attempted. Until then, extrapolation from domestic herbivores will remain the standard procedure.

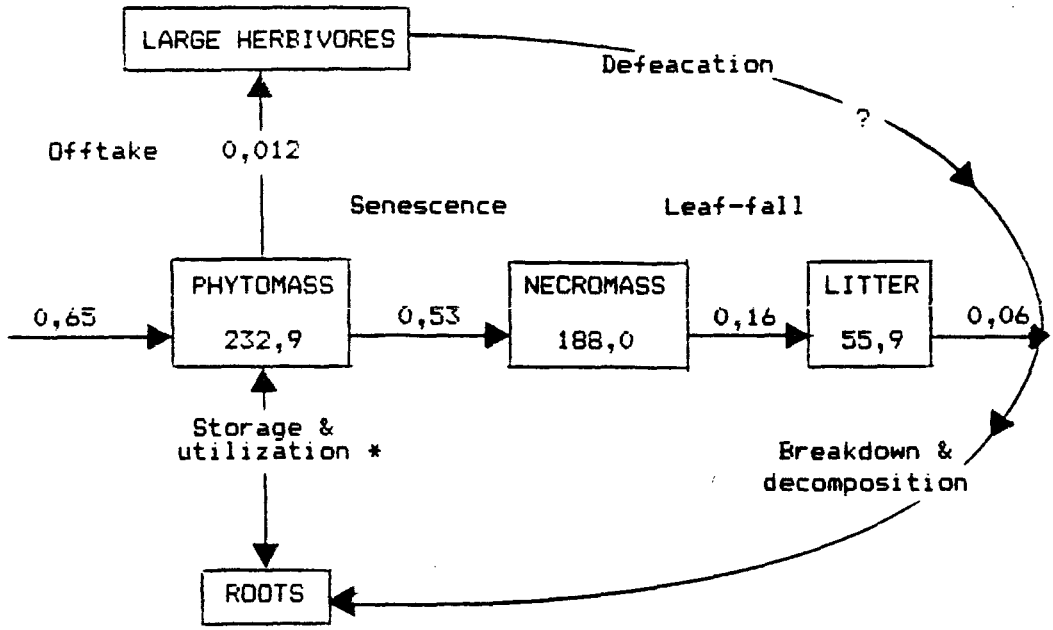
10.4. General synthesis

The initial approach of this study was based on the approach of the IBP grasslands programme. This led to the adoption of Fig 1.1. as the basic model of mass flow within a community which would determine the amount of food available for herbivore consumption. Mean annual values for the various variables in Fig 1.1. and

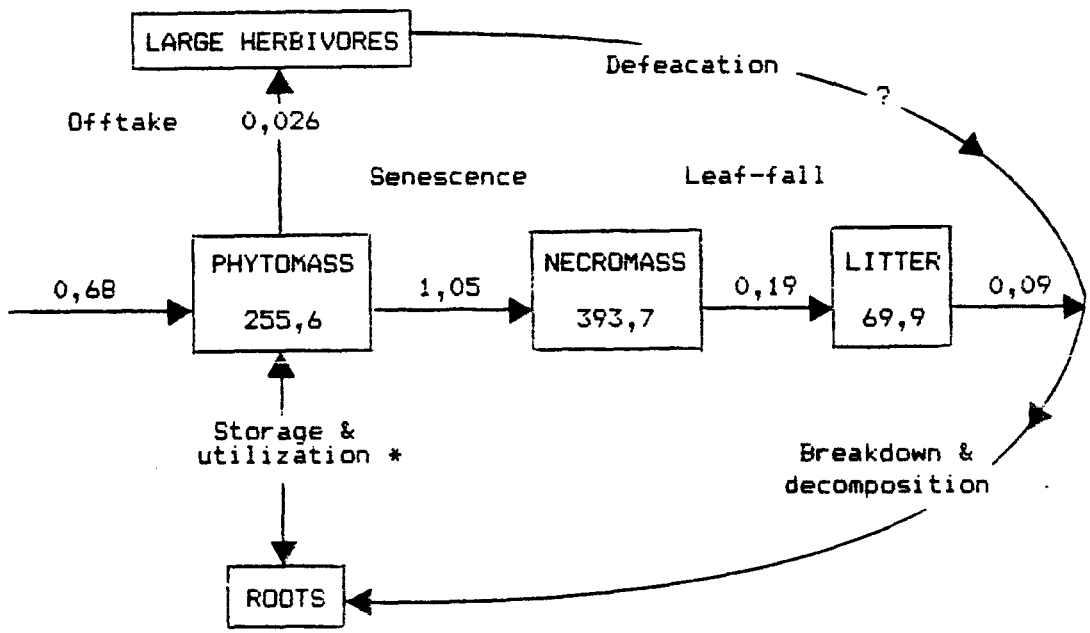
transfer processes are provided in Fig. 10.1. for two of the three communities monitored.

This holist approach by the IBP illuminated several ill-defined correlations between AGP and various abiotic factors such as rainfall, temperature, growing season length, radiation loads, latitude, etc. (Sims and Singh 1971, 1978). Furthermore, it assisted in identifying gaps in existing knowledge of the basic processes and calculation of AGP (van Dyne **et al.** 1978). The construction of such strategic models co-ordinated by the IBP are, however, now deemed to be 'out-moded' (van Dyne **et al.** 1978). This is primarily because of their great cost and the inapplicability of the generalized results (derived from the synthesis of results from several geographically distinct sites) to specific systems (Huntley 1987). The enormous complexity of the resultant models, poor resolution of predictive results and mathematical contraints were further reasons for scaling down of the IBP after several years (Rigler 1975, Watt 1975). However, there is little doubt that a tactical modelling approach can be useful for small, localized systems such as MGR (Innis 1975, Matthews 1984). However, their 'success' may depend upon the the degree of homogeneity within the system, although they have been employed with varying degress of 'success' (and realism) in large heterogeneous conservation areas (e.g. Starfield **et al** 1981, Pellew 1983). Here too, the greatest benefit of this approach would probably be the identification of gaps in knowledge about the major driving forces and processes which aid objective appraisal of opposing management options.

Serious criticism of the scheme in Fig 10.1. could be that it has little predictive capacity and no relevance to the determination of stocking rate since the system at MGR is limited by nutrients, and not by mass. However, the construction of a similar model for CP



a. **T. leucothrix -L. simplex** community [30.07.85 - 22.07.86 (374 days)].



b. **C. validus - D. natalensis** community [15.07.85 - 24.07.86 (374 days)].

Figure 10.1. Schematic diagram of mass flow within the two burnt grassland communities at MGR. [Blocks = g m ; Transfer arrows = g m day]. * Storage and utilization assumed to balance out over the yearly period

may now be attempted. The present model has little predictive capacity because the driving variables were not identified, except herbivory, which was shown to be of little importance. However, within the time constraints it would have been unrealistic to attempt detailed recording of the possible driving variables during the course of this project. However, it has assisted greatly in constructing a framework of relationships that should serve as a useful guide to further research.

A further important omission from the model is the return of mass and nutrients to the soil via herbivore dung. Determination of this was not considered a priority in assisting management of the reserve. For the present values may be substituted from the literature. But this aspect has now been identified as requiring quantification to complete the model. Preliminary root studies were included in Fig 1.1. and were reported by Shackleton **et al.** (1988), and were therefore not reported here.

Lastly, no consideration was given to the impact of insectivorous herbivores (termites, grasshoppers, etc). However, this is usually low in grasslands (Crawley 1983) and is not amenable to management - hence its omission. However, it has been suggested that impact of insect herbivores increases disproportionately with increases in AGP (Andrzejewska and Gyllenberg 1980). Therefore, as MGR has been shown in this study to have a high AGP, insect impact may be worthy of investigation.

The final question posed in chapter 1 related to determination of the 'most appropriate' burning cycle and stocking rate for MGR. In that sense it is predictive as consideration must be given to the possible consequences of altering the present situation. This has been attempted below, drawing on both data and conclusions from

various chapters of this thesis, as well as relevant literature.

10.4.1. Burning regime

The present burning frequency at MGR is based on research in the montane grasslands of Natal. The similarity of the grasslands at MGR to those of the Natal Drakensberg with respect to species composition, seasonality and productivity was illustrated by this study. Hence, such an approach was acceptable in the absence of data to the contrary. However, the data derived from this study now permit a rationale revision of this policy at MGR.

Fire frequency is often considered a controversial question in southern Africa. But much of the controversy arises from ill defined management goals for the area in question. Determination of an optimal frequency at MGR was based on consideration of the effects of fire on; (i) on individual species, (ii) the structure and function of the various communities, and (iii) herbivory. Considering the stated aims of MGR (Sect. 2.8.3.) only the third approach should be reviewed here. However, as alternative management goals could be adopted in the future all three approaches should be contemplated as far as possible. Each is considered below in terms of the effects of an annual burn, the present biennial burn, and a triennial or longer burning frequency. At no stage is the absence of fire considered as a management treatment because all available, published evidence, together with data from this study, indicates that fire is essential for the maintenance of sour grasslands. Thus, Scotcher's statement (1982) concluded that "fire is probably the most important factor in maintaining ecosystem stability in the Drakensberg and can in fact be regarded as a major and regular perturbation" probably applies equally well to the grasslands at MGR.

10.4.1.1. The influence of burning frequency on individual species

The influence of different burning frequencies on the long term vigour and abundance of individual species has not received much research attention, and hence only generalizations may be made here.

It may be expected that an annual burn would cause the eventual decline of any species that failed to reproduce within the time period between consecutive burns. However, this would apply only if existing individuals were adversely affected by fire, and there were no refuges (areas where fire could not destroy newly established individuals). A combination of both these factors is relatively rare, hence most species at MGR would survive regular annual burning, although some may experience a decline in abundance and/or productivity. Species that would be most notably affected would be fire intolerant species such as **Prionium serrata** which grow in environments characterized by a low fire frequency. This contention is supported M. Jordaan (pers. comm.) who attributes the elimination of this species from large areas of Natal to uncontrolled burning. Woody species attempting to establish within the grasslands (eg **Athanasia calva, Stoebe vulgaris, Protea sp.,** forest margin species) are, as observed during the course of this study, adversely affected by frequent burning.

A group of species favoured by annual burning are the geophytes which usually flower only after a fire has most of the ASC. This in turn would favour animal species dependent upon geophytic plants as a primary food source (several game birds).

A biennial burn caters well for both geophytic species and grassland species that require two years to achieve a major sexual reproductive output, such as **C. validus**, and **L. simplex**. It also

shares the negative aspects of annual burning but to a lesser extent.

A triennial burn, or longer would permit the establishment of some woody species where local edaphic conditions are suitable, with a concomitant reduction in flowering frequency of geophytes.

10.4.1.2. The influence of burning frequency on communities

The present fire policy excludes all forests from being burnt by stipulating that burning should commence by burning outwards from forest margins (Kime 1984). Although this is standard management practice over most of southern Africa, forests can, and do, recover from periodic fires (Granger 1984), as they must have done before the advent of controlled burning and fire breaks. The recovery of forests subjected to differing frequencies and severities of burning has not been investigated. The poor implementation and control of the burning programme over the last three years at MGR has resulted in severe damage to several extensive forests (pers. obs.). On the other hand, burning of small patches within the grasslands is difficult to avoid without disproportionate costs and labour. Hence it is necessary that forest patches be rated in terms of importance (size, species composition, fire accessibility, potential for expansion, ease of implementation of protection measures, etc.). Forests with a high importance rating (eg swamp and dune forest) should then be permenantly protected by fire-breaks, and all fires in the vicinity burnt away from the forest. Forests with a medium importance rating would not be protected by fire-breaks, but fires should be set just beyond the forest margins. Thus, unscheduled fires may burn into the forest dependent upon fire intensity. Forests with a low rating would not recieve any protection measures. In this instance patch burning leading to a mosaic of different aged areas within the reserve is a feasible

option (see 10.1.4.3.). This rating should be undertaken by suitably trained personnel.

It has been suggested (see Ch. 4) that the biennial programme prevents any of the grassland communities developing towards a shrubland. In the interests of promoting biotic diversity (animal and plant), but to the detriment of grazing potential, it is suggested that a proportion (say, 10 - 15 %) of the reserve be burnt less frequently to encourage development of a shrubland community.

There is little information considering the effects of burning frequency on wetland vegetation. Downing's (1966) work and my personal observations at MGR suggest that fire is generally detrimental to wetland communities, irrespective of frequency. This is especially so in the shallower ones, Nevertheless, wetlands at MGR must have been subject to fire before the advent of a controlled fire policy. Again the question is one of frequency. Hence the same approach as that outlined for forests is recommended.

The effects of fire frequency on grassland communities are usually assessed in terms of productivity and species composition. The short term results from this study indicate that productivity declined when fire was excluded from the T. **leucothrix** - L. **simplex** community for more than two years. Hence burning should occur no less than once every three years. Conversly, at the C. **validus** - D. **natalensis** grassland production in the absence of fire continued to improve relative to the burnt plots. Thus, intervals between burns could be longer than at present in this grassland, although this may be detrimental to the production of new tillers (S.E. Shackleton, pers. comm.).

Long term trials in sour grasslands in Natal led to the conclusion that there was little difference in production between annual, biennial and triennial burning treatments (Tainton et al. 1978). Similarly, McKenzie (1984) demonstrated the potential for swards of Dohne Sourveld that had been excessively grazed over six decades to almost match the productivity of a "benchmark" site after only two years of protection.

Species composition may alter in the absence of fire (Staples 1930, Everson and Tainton 1984), usually towards less palatable species and then some form of wooded community (Granger 1984, Tainton and Mentis 1984). The last phase would only occur in regions where the edaphic, climatic and biotic factors were conducive towards woody growth, and this probably is not the case for the whole of MGR. However, the work of Everson and Tainton (1984) indicates that it is only absence of fire that has a major effect on species composition, and that there was little or no effect induced by different fire frequencies over periods as long as forty years. Everson and Tainton (1984) concluded that a high proportion of decreaser species was maintained with frequent defoliation, brought about by either an annual burn, or a biennial burn with grazing. The latter case is currently the situation at MGR.

An annual burn may favour decreaser species except in the case of species that do not reproduce sexually in less than one year, such a **C. validus**, **L. simplex** and **Protea simplex**. S. Shackleton (in prep.) has indicated that tillering rates in C. validus may be promoted by annual burning, but does not take into account maintanence of the population by seed input, and possible reduced vigour of vegetatively produced tillers. On the other hand, it would favour geophytes.

A biennial burn with grazing appeared to be equivalent to an annual burn in terms of its effect on species composition (Everson and Tainton 1984). This regime is also suitable for biennial species and geophytes, being detrimental only to the development of woody communities.

Triennial burning would probably be similar to biennial in terms of its effect on communities. Less frequent burning would possibly result in a change in species composition as recorded in the unburnt areas of the reserve, as well as the undesirable accummulation of moribund material. Such an accummulation would increase the severity of non-scheduled fires by increasing the fuel load.

10.4.1.3. The influence of burning frequency on herbivory

Determination of fire frequency orientated towards the large vertebrate component of a community is often at odds with that recommended for the plant component - usually the long term losses outweigh short term gains. At MGR it was shown that nutrient content of the sward, more specifically CP and digestibility, declined after a burn, equilibrating after the second year. Furthermore, forage accessibility was greatest in the first year whilst the palatable phytomass was exposed and 'undiluted' by increasing amounts of unpalatable necromass. Results (Sect. 8.5.4.) demonstrated that the nutrient stocks, a function of both forage mass and nutrient concentration, were highest about six months after a burn, decreasing thereafter. Consequently, an annual burn would potentially be the best to maximise large vertebrate performance.

However, an annual burn programme may be detrimental to smaller mammals and game birds. Available literature, reviewed by Tainton

and Mentis (1984), clearly indicates that populations of such species are promoted by intervals of greater than one year between fires, up until some maximum period whereafter populations decline due to the accumulation of moribund material. Hence a biennial or triennial programme would be appropriate at MGR if due consideration is given to maintaining large populations of these species and thereby promoting biotic diversity. Again, this clearly demonstrates the importance for defining unambiquaous management goals in resolving possible ecological and management conflicts.

Such conflicting management demands may be accommodated by burning different areas of the reserve according to different burning programmes, resulting in a mosaic of unevenly-aged swards. The same effect could be achieved by burning a varying proportions of the reserve per year, but the exact areas being determined randomly. Under such a programme there would be no need for defined burning compartments, and a patch system could be adopted. This latter option would also negate any theoretical possibility that the fauna and flora become 'adapted' to a particular burning frequency and thereby experience deleterious effects after any fire outside the normal programme.

If either scheme were implemented it must be borne in mind that large vertebrates always favour freshly burnt areas (Rowe-Rowe 1982, Bothma 1989) and differential burning of particular areas will led to increased utilization of those areas, and decreaseed utiliztion of the remaining areas under a constant stocking rate. Hence it could mean that the present stocking rate would have to be reduced if less than 50 % of the reserve was burnt per year. Such an option is therefore undesirable under the present management goals.

However, such a burn moasic would be advantagous in that it would (i) promote maximisation of biotic diversity of both animal and plant species and communities; (ii) result in improved dispersal (because of small size of blocks) of the game throughout the reserve thereby enhancing veld condition and game viewing; (iii) facilitate easier control of fire and protection of sensitive areas because the management blocks would be smaller, (iv) decisions to burn may be event driven rather than routine and as such probably is in accord with the inherent dynamics of the system (Walker **et** al. 1986). Hence it is recommended that this option be seriously considered by the management of MGR. Details of the rotation for various areas of the reserve are given by Shackleton (in prep.). Should this be considered unsatisfactory, then the present biennial regime appears to be the most appropriate, but with more blocks of smaller areas.

10.4.2. Herbivore numbers and composition

Options open to the management of MGR are to increase, decrease or maintain the present number of herbivores within the reserve. Because biological systems are dynamic and interactive there is no absolute number of animals that the reserve should support (Sinclair 1981), but the consequences of major increments or decrements can be inferred, drawing from the data collected during this study.

The present number of herbivores has little impact on the amount of food available to them, being limited by quality. Thus, MGR may be considered a non-interactive system. Because of this, an increase in the number of animals would probably increase the number and extent of the heavily utilized, localized patches, usually associated with high nutrient spots. Although perhaps aesthetically unpleasant relative to the 'lush swards' surrounding such patches

it appears that these do recover rapidly once grazing pressure is reduced. This occurs towards the end of winter when animals are attracted to newly burnt areas elsewhere in the reserve (pers. obs.). Consequently, provided that such localized grazing does not lead to accelerated soil erosion, invasion of persistant, unpalatable species (eg **Aristida junciformis, Pteridium aquilinum**) or alien species (eg **Rubus sp.**) then the stocking rate could be increased. The latter two species have been noted on a few of the grazing lawns at MGR. The localized nature of these grazing lawns make monitoring relatively easy. Since the unavailability of nutritious food items during the winter was the major present/potential attribute of the vegetation influencing herbivore performance at MGR, the provision of supplementary foods during this period would increase the number of animals that could be supported. Whether that would be cost efficient would have to be determined by the present management.

Theoretically, it is projected that should the herbivore numbers be allowed to increase, then, at at some point negative feedback factors will occur causing the herbivore populations to become more or less constant around some mean density. Scotcher (1982) has proposed that this situation has been attained by eland populations in the Natal Drakensberg. The dire consequences often predicted about uncontrolled increases in populations of African herbivores have rarely been fulfilled (Caughley 1981). Where they have, it has usually been in the face of a major episodic event, usually drought. However, droughts are relatively infrequent in moist coastal grasslands of southern Africa characterized by their equable climate. Unfortunately, the inability of the present management to supply up to date census figures (those for 1988) prevented calculation of long term reproductive rates here. It was therefore not possible to determine whether or not populations have

been stable since 1986. Furthermore, discontinuation of regular counts precludes the calculation of instantaneous rates of population increase and hence also theoretical projections of CC according to logistic growth equations. Once such 'stability' is attained reproductive rates are low and hence the fulfilment of the major management aim of promoting income from animal products would be reduced, although game viewing potential would be maximized.

One aspect that would have to be considered if the number of herbivores was increased would be the species complement, especially the browsers. The smaller, isolated forests scattered throughout the grasslands of the reserve have definitely experienced significant herbivore impact since establishment of the reserve, with the result that many areas appear to be becoming more open (pers. obs., P. Dutton pers.comm., T. Strever pers. comm.). K. Tinley (pers. comm.) attributes this to the introduction of historically non-indigenous browsers. Furthermore, the need for increasing the proportion of bulk grazers has to be addressed. Results from this study indicate that **C. validus** is utilized by the present herbivore complement, and that this community is highly favoured. In conjunction with the impact of thatch harvesters [see data from S. Shackleton (in prep.) for quantitative assessment], there appears little need for alteration of the present ratio solely for the control of **C. validus**.

The removal of historically non-indigenous species should be seriously considered. This is especially so for those species that appear to be ill-adapted to the area and show declining populations (gemsbuck, springbuck, impala and possibly red hartebeest). Removal of these species by trophy hunters in the near future would provide some return on the funds spent in order to translocate these species to the reserve initially. Should this not be done, and the

populations continue to decline then no return on that expenditure will be realized.

An alternative option would be to reduce the present herbivore numbers. The findings in chapter 9 indicate that should be done. This would be unlikely to have major detrimental consequences on either the vegetation or present animal reproductive rates. It may lead to an increase in reproductive rates and thereby promote income from the sale of animal products. However, it would reduce game viewing satisfaction.

The final option would be to maintain herbivore numbers at approximately their present levels. Data collected during this study indicate that the influence of the herbivores on the grassland vegetation is slight. The present number and extent of areas subject to heavily concentrated grazing is not unacceptable. Thus, maintanence of the present herbivore numbers is a viable option, provided that monitoring of the extent of these areas is undertaken on a continuous basis.

As previously indicated the selection of any particular management option depends upon clearly defined management goals. This is well illustrated in the case of the question of desired stocking rates for MGR. If revenue is to be maximized from animal products then direct income from meat, skins, trophies, etc. will generate higher yields than tourism (Anderson 1983). In this respect herbivore numbers should be lowered by 10 % and reproductive rates monitored over the following four years. If reproductive rates increase over the present, then a further 10 % reduction should be implemented and the effects on the reproductive rate again monitored. In this way active management will yield the required data for estimation of CC and maximal sustainable yield from the logistic growth

equation during the 'normal' management of the reserve.

If tourism is to be the primary management objective at MGR then large numbers and a wide variety of herbivore species are desirable. In this respect numbers should be allowed to equilibrate naturally. Periodic culls could be maintained to boost income. However, the low forage quality available to herbivores will probably limit the maximum numbers without supplementary feeding at densities below those of sweetveld areas. Therefore promoting game viewing as the primary income generater would not equal that from dealing in animal products directly unless significantly more accommodation units were constructed. This was confirmed by the results of a visitor survey (C. Shackleton in prep.). Results indicated that 60,2 % of the respondents (122) visited MGR to fish and enjoy the beaches. Only 14,5 % listed game viewing as the reason for their visit. In ranking the time spent in various listed activities during their stay 24,6 % of the respondents did not spend any time viewing game. Only 11,5 % spent most of their time game viewing, with the largest group of respondents (32 %) ranking it only third, usually after fishing, and batheing. With only 14,5 % of respondents listing game as a reason to visit MGR it is unlikely that any increase in herbivore numbers will promote increased tourism, although introduction of other species may.

10.5. Proposed management goals for MGR

It is evident throughout this chapter that the courses of action open to the policy makers and managers of MGR are determined by the overall aims for the reserve. The only existing documented aims place considerable emphasis on animal production in order to generate income. Regrettably, as stated in Section 2.8.3., most of these aims have not been achieved. Furthermore, major decisions which affect both the conservation and game managment of the

reserve are invariably made on an **ad hoc** basis by personnel lacking the appropriate knowledge and/or experience (eg the culling of 25 % of the herbivores in 1988, cancellation of aerial censuses, removal of monitoring plots, hiring of personnel, non-development of the education centre). Moreover, with the relatively high turnover of senior personnel in the reserve steps taken to achieve these goals have differed from one manager to the next, none of which have been recorded in a policy/management document. Swings of comparable extremes have also occurred with attempts to formally define management goals (J.E. Granger pers. comm.).

It is further evident that the present documented goals place considerable emphasis on the animal component and its potential to earn revenue, possibly at the expense of the balanced conservation ethics in the policy documents of reputable conservation bodies. Consequently, I suggest that the existing documented goals be reviewed by a multi-disciplinary team and judged whether or not they are appropriate. If they are considered appropriate reasons why they have not be attained should be identified and resolved. If they are considered inappropriate a new, and binding, policy document should be drawn up. It is imperative that this assessment of the present aims, and their possible ammendment be undertaken by recognized 'experts' in the conservation and game management fields, as well as the financiers and staff of the reserve. Possible participants and interested parties are suggested by Shackleton (in prep.)

In this context it may prove useful to attempt to construct some decision aiding tool using artificial intelligence to guide future management of the reserve. Tools available include decision analysis and expert systems (Starfiled and Bleloch 1986, Starfield and Louw 1986), both of which are presently being introduced, on a

limited experimental basis, into the management systems of agriculture and conservation agencies (eg Michalski et al. 1983, Danilewitz et al. 1988, M.T. Mentis, pers. comm.). Their potential is enormous (see Starfield and Bleloch 1986) and serious consideration should be given to their application at MGR in light of the high turnover and inexperience of the staff. Construction of an expert system may be attempted by the above-mentioned multidisciplinary team.

Until such a panel has been constituted and formulated firstly a realistic set of management goals for MGR, and secondly, a sound strategy to attain these, I propose that the aims outlined below substitute the present management goals. These have been adapted from the IUCN strategy, and as such, should be applicable to most conservation areas, including MGR. At present management either fails to take congnizance of these generally accepted principles, or, in some instances has promoted the opposite. It is not intended that these be binding, but that they can serve as a starting point. They are presented in order of priority, and hence management conflicts are resolved in favour of the higher ranked aim.

1. Maintenance of essential ecological processes and life-support systems.

2. Maintenance, or improvement, of biotic diversity.

3. Promotion of sustainable utilization of species and ecosystems.

4. Generation of revenue from the reserve but not at the expense of failing to accomplish the preceding aims.

5. Promotion of the local economy and labour training.

6. Assist with both formal and informal education of Transkeians in the biological and conservation fields.

7. Promotion of objective understanding of the controlling processes of the reserve which will assist in the refinement of management options and actions.

At present only the first aim is achieved, mainly by non-interference. Success with the remainder is varied, from not at all to moderate.

Following acceptence and/or revision of such aims it is then possible to assess options that will work towards their attainment such as the maintenance of the wilderness area or not, reintroduction of controlled hunting or not, traditional and commercial exploitation of plant products or not, maintenance of non-indigenous populations or not, etc. Finalization of options will then permit consideration of the actions necessary to achieve the stated aims.

As such, it is recommended that the following actions be implemented in order to work towards the achievement of the above objectives.

1. Combat of accelerated soil erosion where it presently occurs along present and past roadsides (especially in the wilderness area).

2. Implementation of a trial burn mosaic pattern to promote biotic diversity with concommitant evaluation of the programme by appropriate personnel.

3. Initiate regular veld assessment of the different management blocks, compiling records from year to year. The monitoring sites

established during this study can form the basis for this. hence, it is important that they be maintained.

4. Implement regular censuses of herbivore populations. Ground counts would be adequate in the open grasslands of MGR.

5. Negotiate the sale of skins and trophies of the monthly culled animals. Look at the feasibility of re-introducing trophy hunting to replace the monthly culling.

6. Implement and maintain a regular alien plant control programme.

7. Open up the presently redundant education centre for educational groups and research facilities.

8. Negotiate with the Transkei Herbalists Association for the managed and sustained utilization of indigenous products for medicines.

9. Continue the determination of physiological condition on all culled animals, compiling accurate records.

10. Determine the desirability of maintaining non-indigenous herbivore populations, and possible substitution with indigenous species (eg oribi).

The two actions listed below are of importance in the near term and as such should be implemented as soon as possible.

1. Organize and host a 'goals' workshop at MGR to draw up a binding policy document.

2. Computerise records of all management actions, and data collected above.

10.6. Research recommendations

1. Assessment of present, and monitoring of future browser impact. This stems from the observations P. Dutton, K. Tinley and T. Strever, all of whom have been familar with the MGR region for considerable time. They have all stated that browser impact is severe and action should be taken to reduce it. However, whether or not this is indeed the case requires clarification. Present levels of browser damage may simply be an adjustment of the system after re-introduction of browsers in 1979, and therefore may be acceptable.

2. Establish and monitor sites to receive different frequencies of burning (0, 1, 2, 3, 5 year cycles and randomly).

This study has provided some insight into the influence of burning on the suitability of the grasslands for herbivores. However, this was only in the short-term, and longer term monitoring is desirable. Most importantly, the eclusion of fire from trial areas will allow investigations of plant succession which is suggested below.

3. Establishment and monitoring of sites to determine secondary successional trends and changes, if any.

4. Experimental manipulation to determine optimum levels for sustainable utilization of all indigenous products that may be harvested (**C. validus**, **Juncus krausii**, **Flagellaria guineensis**, all fern species, various wildflower species (mostly Composites), trees and bulbs for traditional medicines).

Consideration must be given to these aspects for two reasons. Firstly, it provides income for the reserve, thereby reducing state subsidies. This supports the maintenance of the area as a reserve

rather than turning it over to agriculture. Secondly, it promotes good socio-economic relations with the surrounding people.

5. Determination of the role of termitaria in the establishment of grazing lawns.

Initial observations during this study suggest that termitaria play an important role in the grazing dynamics of the herbivores at MGR. This arises from the observation that areas of concnetrated grazing are often associated with extinct or extant termitaria. This may be a result of the change in concentration of selected nutrients within the soil, which is reflected in the vegetation.

6. Determination of the primary production and seasonal palatability of grazing lawns (can they be artificially induced?).

As these are the primary sites of herbivore grazing, investigation of their dynamics and longevity are required.

7. Investigate the contribution of seasonally dry wetlands to the herbivore diet during winter.

This study was confined to the grasslands of the reserve. However, some grazing of wetlands does occur, both continuosly (by reedbuck), and seasonally in those that exhibit considerable desiccation during the winter months. It is importnat to determine whether or not these areas provide forage of a higher nutrient quality than the surrounding grasslands duing the winter months. And if so, whether these areas play a significant role in maintaining herbivore condition during this time.

8. Investigate the determinants of swamp forest (can they be artificially induced?).

Mkambati Game Reserve boasts the southernmost distribution of swamp forest in southern Africa. Consequently it can be expected that it is in a marginal enviornment. Thus, the indescriminant burning of patches of swamp forest, coupled with possibly significant browser impact, require that its determinants be investigated. This would provide an indication of whether or not there are potential areas into which it may expand within the reserve.

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APPENDIX 1. Soil forms of MGR [in alaphabetical order, with profiles not desrcibed by MacVicar et al. (1977) given at the end]

Note 1. The following abbreviations have been used.

General: (W) = wet, (D) = dry, nr = near, incr = increasing, undtm = undetermined

Colours: Yell = Yellow, Org = Orange, Brwn = Brown, Blk = Black

Consistence: Fr = Friable, V. fr = Very friable, Mod = Moderate

Note 2. Depth has been expressed in centimetres, textural classes as percentages and slope in degrees.

FORM	CHAMPAGNE	
SERIES	STRATFORD	
LOCATION		
PIT NO.	25F, 28E, 36D	
CATENA	Bottom	
SLOPE	1 - 4	
VEGETATION	Perennial wetlands	
PHYSICAL		
HORIZON	O	G
DEPTH	55 - 85	25 - 80
COLOUR (W)	2,5Y 2/0 - 10YR 3/1	2,5Y 4/0 - 2,5Y 5/2
MOTTLES (Colour)		Org, Yell, Brwn
(Abundance)	Absent	Common
STRUCTURE	Apedal - Weak	Apedal
CONSISTENCE (W)	V. Fr - Firm	Fr - Firm
CONCRETIONS	Absent	Absent
TRANSITION	Clear	
ROOTING DEPTH	Throughout	
TOTAL DEPTH	110 - 150	
C - HORIZON	Rock	
CLAY	18,9 - 29,9	17,3 - 39,2
SILT	13,8 - 18,1	6,8 - 10,0
SAND (TOTAL)	48,5 - 65,8	46,5 - 71,7
(FINE)	10,4 - 17,5	11,9 - 17,2
(MEDIUM)	19,2 - 30,0	14,5 - 26,5
(COARSE)	17,8 - 24,4	15,1 - 28,0
CHEMICAL		
pH (KCl)	3,7 - 3,9	3,5 - 3,8

FORM	CLOVELLY
SERIES	MOSSDALE/OATSDALE/CLOVELLY
LOCATION	
PIT NO.	4A, 5F, 18B, 19B, 20B, 30E, 33F, 41C,
CATENA	Mid
SLOPE	2 - 4
VEGETATION	T. leucothrix - L. simplex or C. validus - D. natalensis grassland

PHYSICAL

HORIZON	A	B
DEPTH	40 - 92	20 - 150
COLOUR (W)	2,5YR 3/0 - 10YR 2/2	7,5YR 4/6 - 10YR 5/8
(D)	10YR 4/1 - 10YR 5/2	7,5YR 5/8
MOTTLES (Colour)		Red
(Abundance)	Absent	V. few, incr with depth
STRUCTURE	Apedal - Weak	Apedal
CONSISTENCE (W)	V. Fr - Loose	V. Fr - Firm
CONCRETIONS	Absent	Absent
TRANSITION	Gradual - abrupt	
ROOTING DEPTH	1/2 through B	
TOTAL DEPTH	89 - 230	
C - HORIZON	Saprolite/Rock (pebbles common nr base)	
CLAY	8,4 - 35,8	1,8 - 48,9
SILT	3,2 - 12,2	4,6 - 12,5
SAND (TOTAL)	40,8 - 85,4	32,3 - 82,1
(FINE)	15,0 - 23,9	13,1 - 24,4
(MEDIUM)	14,8 - 60,5	10,7 - 51,5
(COARSE)	1,1 - 25,3	1,9 - 27,9

CHEMICAL

pH (KCL)	3,6 - 4,2	3,6 - 4,2
P (ppm)		1 - 2
PDI		0,19 - 0,73
K (ppm)		16 - 48
Ca "		26 - 48
Mg "		25 - 103
Na "		10 - 33
Al		10 - 75
S value		2,23 - 4,46

FORM GLENROSA

SERIES KANNONKOP/MARTINDALE/SAINTFAITHS

LOCATION

PIT NO.	2A, 8B, 9B, 24F, 34D
CATENA	Crest
SLOPE	0 - 8,5
VEGETATION	All communities

PHYSICAL

HORIZON	A	B
DEPTH	23 - 82	48 - 86+
COLOUR (W)	5YR 2,5/1 - 10YR 3/2	strong mottling
MOTTLES (Colour)		Org, Yell, Brwn, Blk, Grey
(Abundance)	Absent	V. Common
STRUCTURE	Apedal - Weak	Apedal - Weak
CONSISTENCE (W)	Friable	V. Fr - Firm
CONCRETIONS	Absent	Highly decomposed pebbles & quartz usually grading into saprolite
TRANSITION	Abrupt	
ROOTING DEPTH	Top of B-horizon	
TOTAL DEPTH	210 +	
C - HORIZON	Saprolite/Pebbles/Rock	
CLAY	9,6 - 44,3	38,7 - 57,3
SILT	3,7 - 28,2	2,5 - 14,9

SAND (TOTAL)	23,7 - 83,7	20,5 - 51,7
(FINE)	11,8 - 56,0	7,2 - 35,0
(MEDIUM)	0,7 - 32,8	6,2 - 17,1
(COARSE)	0,3 - 15,0	0,1 - 7,1
CHEMICAL		
pH (KCl)	3,6 - 4,2	4,0 - 4,6

FORM	HUTTON
SERIES	FARNINGHAM/BALMORAL/HUTTON/LICHTENBERG
LOCATION	
PIT NO.	3A, 6C, 27E
CATENA	Mid - top
SLOPE	0 - 3
VEGETATION	C. validus - D. natalensis grassland

PHYSICAL

	A	B
HORIZON		
DEPTH	75 - 92	98 - 150
COLOUR (W)	5YR 3/2 - 7,5YR 3/2	2,5YR 3/6
MOTTLES (Colour)	-	Yell (v. faint)
(Abundance)	Absent	Few (incr with depth)
STRUCTURE	Apedal - Blocky	Apedal
CONSISTENCE (W)	V. Fr - Firm	V. Fr - Firm
CONCRETIONS	Absent	V. few
PERMEABILITY	Rapid	Rapid
TRANSITION	Gradual	
ROOTING DEPTH	140 +	
TOTAL DEPTH	190 - 240	
C - HORIZON	?	
CLAY	15,1 - 49,8	33,2 - 46,9
SILT	3,2 - 12,3	1,0 - 8,9
SAND (TOTAL)	24,0 - 80,0	22,0 - 58,0
(FINE)	11,3 - 54,8	9,3 - 41,9
(MEDIUM)	7,4 - 57,1	6,4 - 32,3
(COARSE)	1,5 - 7,2	2,1 - 6,3
CHEMICAL		
pH (KCl)	3,7 - 4,1	4,1 - 5,1
P (ppm)		1 - 2
PDI		0,13 - 0,52
K (ppm)		23 - 40
Ca "		49 - 141
Mg "		78 - 217
Na "		21 - 53
Al		1 - 51
S value		2,39 - 8,19

FORM	KATSPRUIT
SERIES	KATSPRUIT
LOCATION	
PIT NO.	15B, 22F, 29E
CATENA	Bottom
SLOPE	2 - 7
VEGETATION	Seasonal wetland, moist grassland

PHYSICAL

HORIZON	A	G
DEPTH	47 - 68	80 - 140+
COLOUR (W)	5YR 2,5/1 - 10YR 3/1	2,5Y 5/2 - 10YR 4/3
(D)	2,5YR 4/0	
MOTTLES (Colour)	-	Various
(Abundance)	Absent	Many
STRUCTURE	Weak	Apedal
CONSISTENCE (W)	V. Fr - Mod	Fr - Shear
CONCRETIONS	Absent	Absent
PERMEABILITY	Rapid	Slow
TRANSITION	Gradual	
ROOTING DEPTH	120+	
TOTAL DEPTH	135 - 220+	
C - HORIZON	Rock	

CLAY	12,5 - 18,3	16,6 - 35,5
SILT	3,7 - 10,3	3,0 - 8,3
SAND (TOTAL)	67,1 - 80,8	58,8 - 77,3
(FINE)	17,8 - 54,1	17,4 - 39,5
(MEDIUM)	26,4 - 33,1	18,8 - 29,7
(COARSE)	0,3 - 24,3	0,3 - 25,7

CHEMICAL

pH (KCl)	3,7 - 3,8	3,4 - 4,0

FORM KROONSTAD
SERIES AVOCA/MKAMBATI

LOCATION

PIT NO. 14B, 13B, 17B, 32E, 37D
CATENA Bottom
SLOPE 0 - 3
VEGETATION **T. leucothrix - L. simplex grassland & Watsonia sp community**

PHYSICAL

HORIZON	O	E	G
DEPTH	50 - 86	22 - 45	40 - 150+
COLOUR (W)	5YR 2,5/1 - 2,5Y 2/0	10YR 5/3 - 2,5Y 6/2	7,5YR 5/2 - 2,5Y 5/2
(D)	10YR 6/4	10YR 8/2	
MOTTLES (Colour)	-	Org, Yell, Blk	Various
(Abundance)	Absent	Abs - few	Many
STRUCTURE	Apedal - Weak	Apedal	Apedal
CONSISTENCE (W)	V. fr - Firm	Fr - V.firm	V. fr - Firm
CONCRETIONS	Absent	Absent	Absent
PERMEABILITY	Rapid	Rapid	
TRANSITION	Gradual - Abrupt	Clear - Abrupt	
ROOTING DEPTH	A & E horizons only		
TOTAL DEPTH	115 - 230+		
C - HORIZON	?		

CLAY	8,4 - 17,6	1,4 - 22,6	3,9 - 21,6
SILT	1,6 - 10,0	1,1 - 11,4	1,2 - 8,6
SAND (TOTAL)	66,0 - 84,8	60,7 - 93,4	63,6 - 94,3
(FINE)	19,4 - 51,1	16,9 - 47,2	19,3 - 49,4
(MEDIUM)	27,2 - 46,0	24,6 - 44,6	25,9 - 47,9
(COARSE)	0,5 - 21,8	0,3 - 24,9	0,3 - 18,4

CHEMICAL			
pH (KCl)	3,7 - 4,7	3,6 - 4,9	3,4 - 4,6
P (ppm)		1 - 2	
PDI		0,65 - 0,71	
K (ppm)		25	1 pit only
Ca "		24	"
Mg "		23	"
Na "		25	"
Al		85	"
S value		2,30	"

FORM MISPAH
SERIES MISPAH

LOCATION
PIT NO. 26F, 35D, 39D, 40D
CATENA Mid - top
SLOPE 0 - 3
VEGETATION All communities

PHYSICAL	
HORIZON	A
DEPTH	10 - 90
COLOUR (W)	5YR 3/1 - 10YR 3/1
(D)	5YR 4/1
MOTTLES (Colour)	-
(Abundance)	Absent
STRUCTURE	Weak - Apedal
CONSISTENCE (W)	V. fr - Fr
CONCRETIONS	Absent
TRANSITION	Abrupt onto rock
ROOTING DEPTH	Throughout
TOTAL DEPTH	10 - 90
C - HORIZON	Rock
CLAY	12,2 - 36,4
SILT	5,2 - 12,4
SAND (TOTAL)	45,2 - 79,1
(FINE)	14,5 - 22,1
(MEDIUM)	19,0 - 31,3
(COARSE)	16,4 - 31,5
CHEMICAL	
pH (KCl)	3,6 - 3,7

FORM PINEDENE
SERIES OUWERF

LOCATION
PIT NO. 11A, 31E, 38D
CATENA Mid - Bottom
SLOPE 1 - 5
VEGETATION Seasonal wetlands, moist grasslands

PHYSICAL			
HORIZON	O	B	G
DEPTH	38 - 93	28 - 120	30 - 50
COLOUR (W)	5YR 2,5/1 - 7,5YR 2/0	10YR 4/4 - 10YR 5/6	10YR 6/4 - 2,5Y 8/4

(D)	10YR 4/1	10YR 6/4	
MOTTLES (Colour)	-	-	Org, Brwn
(Abundance)	Absent	Absent	Many
STRUCTURE	Apedal - Weak	Apedal	Apedal
CONSISTENCE (W)	Fr - V. Firm	V. Fr - Firm	V. Fr - Firm
CONCRETIONS	Absent	Absent	Absent
PERMEABILITY	Rapid	Rapid	
TRANSITION	Gradual - Clear		Gradual
ROOTING DEPTH		110	
TOTAL DEPTH		130 - 180+	
C - HORIZON		Saprolite	
CLAY	14,5 - 23,4	19,7 - 28,7	20,0 - 22,3
SILT	8,9 - 10,1	5,3 - 12,3	7,2 - 9,3
SAND (TOTAL)	60,3 - 70,7	55,2 - 75,0	65,6 - 68,6
(FINE)	14,8 - 17,7	13,3 - 20,6	21,5 - 25,8
(MEDIUM)	26,0 - 26,5	23,2 - 27,0	16,8 - 34,7
(COARSE)	19,3 - 26,9	18,8 - 28,8	12,4 - 23,0
CHEMICAL			
pH (KCl)	3,6 - 3,7	3,6 - 3,8	3,4 - 3,5
P (ppm)		1	
PDI		0,36 - 0,53	
K (ppm)		23 - 25	
Ca "		24 - 36	
Mg "		23 - 57	
Na "		24 - 36	
Al		69 - 106	
S value		2,30 - 2,80	

BEREA TYPE SANDS

LOCATION			
PIT NO.	6B, 7B, 23F		
CATENA	Mid - crest		
SLOPE	2 - 12		
VEGETATION	T. leucothrix - L. simplex or T. triandra - C. asiatica grassland		
PHYSICAL			
HORIZON	A		B
DEPTH	15 - 80		120+
COLOUR (W)	5YR 3/2 - 10YR 3/2		2,5YR 3/6 - 2,5YR 4/6
MOTTLES (Colour)			Yell, Brwn
(Abundance)	Absent		Rare/Faint
STRUCTURE	Apedal		Apedal
CONSISTENCE (W)	V. Fr		Fr - Firm
CONCRETIONS	Absent		Absent
TRANSITION		Gradual	
ROOTING DEPTH		Throughout	
TOTAL DEPTH		220+	
C - HORIZON		?	
CLAY	8,7 - 15,1		11,4 - 46,9
SILT	1,7 - 3,3		1,0 - 4,5
SAND (TOTAL)	79,9 - 87,1		47,4 - 85,2
(FINE)	15,6 - 57,3		12,4 - 53,0
(MEDIUM)	28,5 - 57,1		25,8 - 32,3
(COARSE)	0,1 - 7,2		0,1 - 2,7

CHEMICAL		
pH (KCl)	4,1 - 4,4	4,1 - 4,4

UNDEFINED (CONSTANTIA?)

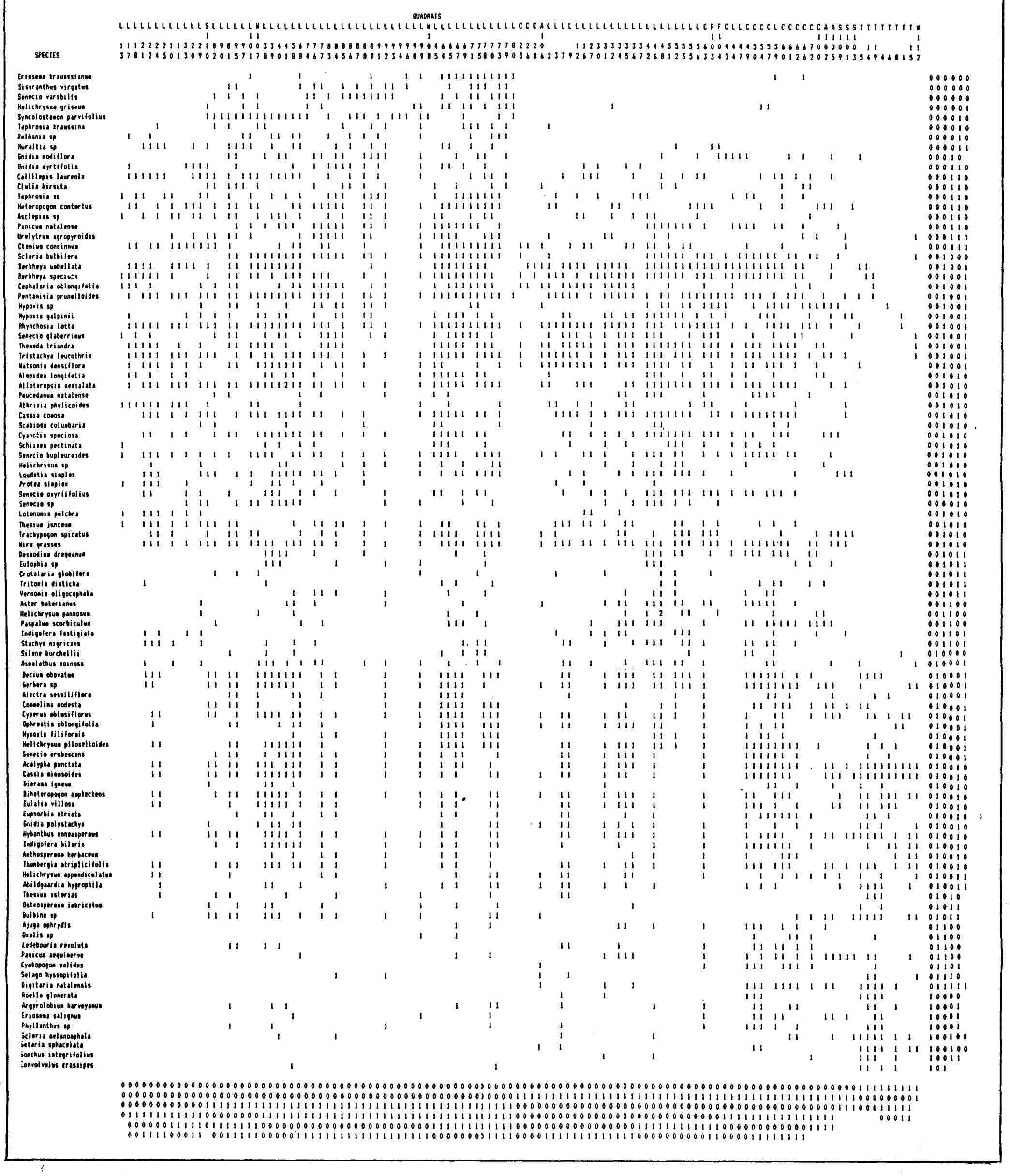
LOCATION

PIT NO.	12B, 21F
CATENA	Bottom
SLOPE	0 - 2
VEGETATION	T. triandra - C. asiatica grassland

PHYSICAL

HORIZON	Upper	Mid	Basal
DEPTH	60 - 92	48 - 70	70+
COLOUR (W)	5YR 2,5/1	10YR 2/2 - 3/2	10YR 4/6 - 6/6
MOTTLES (Colour)	-	Yell, Brwn	Org, Brwn
(Abundance)	Absent	Medium	Few
STRUCTURE	Apedal	Apedal	Apedal
CONSISTENCE (W)	V. Fr	V. Fr - Fr	V. Fr - Firm
CONCRETIONS	Absent	Absent	Absent
TRANSITION	Gradual - Clear		Clear
ROOTING DEPTH		55 - 110	
TOTAL DEPTH		220+	
C - HORIZON		?	
CLAY	9,9 - 17,6	17,6 - 24,8	3,2 - 26,2
SILT	7,0 - 10,8	3,8 - 5,4	3,3 - 6,7
SAND (TOTAL)	76,2 - 77,6	65,8 - 74,1	64,9 - 90,5
(FINE)	39,5 - 57,2	37,2 - 48,8	39,7 - 46,7
(MEDIUM)	14,1 - 31,8	12,6 - 33,5	11,4 - 41,7
(COARSE)	4,9 - 6,3	3,4 - 4,7	2,1 - 13,7
CHEMICAL			
pH (KCl)	3,9 - 4,0	4,0	4,1 - 4,3

Appendix 2. Classification results from the TWINSPAN program



Appendix 3. Row and coloumn contributions from the Correspondence analysis program

ROW CONTRIBUTIONS

I	NAME	QLT	MAS	INR	k=1	COR	CTR	k=2	COR	CTR
1	Altitude (al)	999	297	342	-351	748	369	203	251	310
2	Slope (sl)	605	5	5	128	112	1	-269	493	10
3	Soil depth (sd)	976	188	139	-130	158	32	-295	818	411
4	Conductivity (co)	1000	349	420	406	958	582	85	42	63
5	pH	924	7	2	-93	175	1	-191	748	7
6	Sand (sa)	873	120	67	-61	47	4	-257	826	199
7	Clay (ca)	317	34	25	-179	306	11	-33	11	1

COLUMN CONTRIBUTIONS

J										
1	T. triandra - C. asiatica (TC)	986	110	264	423	519	198	-401	468	447
2	T. leucothrix - L. simplex (TL)	922	104	121	-345	714	125	-186	207	91
3	T. leucothrix - A. phyllicoides (TA)	980	128	158	-401	912	208	-110	68	39
4	F. costata - A. setosa (FA)	982	181	91	116	186	24	239	796	261
5	S. vulgaris - A. calva (SA)	982	156	78	262	958	108	-41	23	7
6	C. validus - D. natalensis (CD)	946	128	196	-452	931	264	59	16	11
7	A. junciformis - H. cymosum (AH)	982	192	92	193	543	72	173	438	145

Appendix 4.1. Standing crop (g m^{-2}) at the T. leucothrix - L. simplex site

TREATMENT			DATE 1985 Aug	Sep	Oct	Nov	Dec	1986 Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	1987 Dec	Jan	Feb	Mar	Apr	May	Jun
	- Phytomass	$\bar{x}$	8.9	18.6	66.6	107.8	119.4	175.2	181.6	232.9	162.5	123.8	116.1	68.8	84.3	94.2	102.0	-	87.5	103.1	153.2	149.5	105.4	-	93.0
G		SE	0.8	3.8	2.0	3.9	14.1	9.3	33.6	36.6	11.7	12.8	8.9	8.3	9.4	8.0	20.9		14.0	20.5	24.2	16.9	11.4		14.7
R	- Necromass	$\bar{x}$	2.9	7.2	20.2	21.8	39.2	16.8	75.6	103.6	132.4	94.2	148.5	149.8	231.0	200.4	178.1	-	87.7	137.3	210.9	193.1	146.2	-	128.4
A		SE	1.1	1.0	1.1	5.6	6.7	9.2	11.4	11.4	16.6	21.7	13.3	10.0	8.4	12.9	29.4		7.8	14.0	18.2	21.0	22.9		20.1
Z	- Litter	$\bar{x}$	-	-	-	12.4	5.5	10.4	14.3	15.8	13.8	22.6	36.3	47.0	40.2	32.7	33.5	-	41.2	56.4	66.2	79.4	56.0	-	93.0
E		SE				2.0	0.8	2.0	2.5	3.4	1.8	2.5	3.9	6.2	4.2	3.8	2.4		5.9	6.7	5.7	7.7	6.0		9.9
D	- Total	$\bar{x}$	11.8	55.8	86.8	151.9	164.0	232.4	271.5	352.3	308.6	240.6	300.9	265.6	355.4	327.3	313.6	-	216.5	296.8	430.3	421.7	307.6	-	325.0
		SE	1.4	4.6	2.3	10.4	16.8	17.1	46.2	44.9	24.8	32.9	18.8	22.2	16.0	16.8	51.0		25.1	34.7	65.1	41.9	35.2		41.0
U	- Phytomass	$\bar{x}$	8.8	65.5	88.9	132.0	223.9	222.4	243.7	253.2	178.2	132.6	128.9	106.2	92.8	106.7	128.8	-	114.3	117.4	138.7	140.9	120.2	-	107.0
N		SE	1.3	5.2	8.0	8.4	23.5	17.7	32.7	18.1	15.5	20.3	9.1	6.2	11.6	15.1	12.9		17.6	15.5	12.2	17.0	7.9		15.3
G	- Necromass	$\bar{x}$	3.2	6.4	22.3	19.9	40.0	60.3	80.6	142.1	128.6	110.8	204.9	198.5	261.1	210.0	183.0	-	125.7	122.6	165.3	179.9	137.8	-	198.3
R		SE	0.3	0.4	9.6	2.3	2.7	8.7	13.5	13.3	9.1	30.0	16.7	23.4	20.0	38.4	26.4		18.1	32.2	22.7	29.5	14.9		38.2
A	- Litter	$\bar{x}$	-	-	-	11.0	6.8	10.5	43.7	29.2	21.6	19.5	26.4	46.9	50.8	52.4	55.9	-	53.8	50.2	65.6	62.2	74.4	-	103.6
Z		SE				3.7	1.4	2.7	19.2	5.9	5.0	1.4	3.1	6.5	11.8	6.0	11.7		5.7	7.7	8.7	5.1	7.0		14.6
E	- Total	$\bar{x}$	12.0	71.9	111.2	163.0	270.8	293.2	368.0	424.6	328.3	262.9	360.2	351.6	404.7	369.2	267.7	-	293.8	286.1	369.7	383.1	329.4	-	389.4
D		SE	1.4	5.2	13.1	10.4	22.9	26.7	42.8	33.5	22.9	45.9	25.3	25.1	32.0	56.6	33.6		35.5	31.5	35.5	42.7	20.6		47.9
C	- Phytomass	$\bar{x}$	105.0	102.1	83.1	105.8	142.6	117.0	177.9	175.9	159.3	80.4	69.0	73.9	72.0	71.7	85.0	-	92.0	61.0	123.9	109.9	98.0	-	104.6
O		SE	2.0	10.0	26.9	19.6	25.7	8.0	15.9	17.9	11.3	14.9	13.1	10.0	8.4	11.3	14.7		10.4	8.9	8.4	10.2	4.4		2.7
M	- Necromass	$\bar{x}$	311.7	359.7	373.3	373.6	311.7	248.0	348.5	240.0	371.2	182.2	270.4	389.1	442.7	363.5	313.1	-	198.0	121.0	193.5	180.7	151.0	-	185.1
I		SE	15.2	61.4	13.7	49.6	39.7	33.7	32.1	40.0	37.4	52.6	76.9	53.3	26.5	66.1	67.4		27.8	12.0	19.3	21.7	18.3		20.0
R	- Litter	$\bar{x}$	658.0	897.1	609.7	545.1	534.2	593.1	536.3	473.2	425.4	463.0	538.0	468.6	358.7	384.9	501.0	-	456.9	378.0	248.3	373.2	345.0	-	346.1
O		SE	70.9	79.9	50.5	37.8	45.8	49.0	35.0	77.2	39.0	33.9	14.8	39.1	24.4	45.7	28.3		55.7	26.2	19.5	35.8	31.0		21.3
L	Total	$\bar{x}$	1074.8	1358.9	1066.1	1024.5	988.4	958.0	1062.6	989.0	955.9	725.6	877.5	931.6	873.4	820.1	899.0	-	746.9	560.0	565.7	633.7	594.0	-	635.8
		SE	79.6	119.2	72.0	63.8	33.5	64.0	22.9	114.8	80.7	78.7	81.2	50.3	32.5	111.0	66.9		41.0	22.9	31.5	46.7	41.3		29.5

Appendix 4.2. Standing crop (g m^{-2}) at the C. validus - D. natalensis site

TREATMENT			DATE 1985 Aug	Sep	Oct	Nov	Dec	1986 Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	1987 Jan	Feb	Mar	Apr
	- Phytomass	$\bar{x}$	22.8	10.5	67.3	99.3	131.9	250.8	235.2	196.4	201.2	124.1	118.2	87.9	87.6	87.7	157.3	139.6	164.6	170.7	341.6	251.9	262.9
G		SE	3.7	1.0	8.9	14.5	17.0	29.9	30.8	42.1	21.3	7.3	8.4	10.1	19.3	8.9	11.4	19.9	15.9	32.6	64.6	8.6	19.9
R	- Necromass	$\bar{x}$	10.6	19.0	64.2	64.2	60.7	104.3	127.1	155.3	195.9	145.6	266.1	339.9	338.0	292.8	311.0	311.6	362.6	419.2	319.1	403.9	410.7
A		SE	7.3	7.7	16.6	10.0	6.8	10.0	17.3	21.8	16.2	9.1	12.2	27.3	26.7	27.4	30.5	47.3	57.2	56.5	49.1	46.0	48.9
Z	- Litter	$\bar{x}$	-	-	14.0	-	22.6	41.6	23.8	25.3	26.6	25.3	43.4	52.1	46.7	54.2	50.9	68.0	59.0	70.2	107.2	89.8	80.0
E		SE			3.5		2.8	9.9	4.8	6.0	5.0	2.7	4.0	7.9	5.8	7.5	8.3	8.6	8.1	14.7	11.2	16.3	6.6
D	- Total	$\bar{x}$	63.4	89.6	145.4	163.5	215.1	369.9	286.1	377.0	423.8	295.0	427.7	479.9	472.4	453.5	475.3	519.3	586.2	657.2	767.9	745.5	753.6
		SE	7.8	7.9	23.6	22.1	15.2	33.7	40.4	61.1	40.8	17.0	17.5	25.9	48.3	30.2	24.6	65.1	70.2	90.5	82.7	53.3	59.8
U	- Phytomass	$\bar{x}$	30.2	76.5	84.2	126.7	207.1	266.5	295.3	266.1	197.4	196.6	142.4	81.3	88.7	123.7	163.4	120.6	166.7	193.0	293.9	267.0	265.5
N		SE	3.8	7.3	5.1	13.0	8.9	21.5	19.6	33.9	36.7	11.7	13.9	9.2	5.1	5.4	24.4	11.3	22.3	40.7	76.1	42.0	16.3
G	- Necromass	$\bar{x}$	28.2	26.9	33.2	41.0	54.7	108.0	111.9	138.6	223.0	211.9	268.4	359.1	165.6	415.4	323.2	258.4	332.6	419.5	447.5	392.0	382.6
R		SE	6.3	5.7	6.7	3.1	5.9	14.2	9.0	17.6	8.6	21.2	21.8	22.8	18.4	16.4	35.0	18.4	46.6	75.2	66.4	85.1	38.5
A	- Litter	$\bar{x}$	-	-	13.4	-	16.9	17.6	18.2	28.0	26.3	33.4	64.5	54.9	33.2	58.5	29.4	54.2	58.6	72.6	62.8	105.8	109.0
Z		SE			3.5		7.5	1.7	4.1	10.2	11.0	7.6	15.2	11.1	5.2	7.0	7.4	8.1	7.2	13.5	3.3	17.6	11.7
E	- Total	$\bar{x}$	58.3	103.4	130.9	167.7	278.8	391.8	425.4	432.6	446.7	441.9	475.3	495.3	587.6	597.6	526.1	439.2	557.9	685.1	804.1	764.7	757.2
D		SE	8.1	8.9	6.9	13.7	12.5	20.8	25.8	55.8	51.7	12.2	49.0	28.8	22.4	21.1	62.8	20.8	72.4	125.7	136.7	136.8	47.9
C	- Phytomass	$\bar{x}$	163.6	132.4	124.9	-	280.7	220.7	290.7	243.8	266.6	176.8	168.3	114.1	94.7	151.4	184.4	240.4	237.6	214.2	441.8	448.4	288.4
O		SE	14.3	27.5	8.9		31.9	23.6	14.6	51.5	34.0	30.9	21.5	11.7	8.7	23.4	7.2	58.3	15.8	19.6	7.5	56.2	60.9
N	- Necromass	$\bar{x}$	622.0	550.8	686.6	-	633.5	473.1	373.4	568.8	461.8	438.6	413.4	624.9	728.1	780.6	755.2	722.6	730.4	629.5	555.7	707.2	458.5
T		SE	53.4	99.9	90.6		113.3	35.7	41.8	96.6	38.3	88.2	53.0	48.6	82.7	39.1	64.1	138.8	88.1	133.1	102.3	136.8	96.7
R	- Litter	$\bar{x}$	182.0	231.2	263.2	-	197.7	185.8	190.8	222.8	243.8	229.8	299.2	276.0	206.9	334.1	322.4	296.1	291.8	302.2	198.5	268.3	293.5
O		SE	27.2	19.5	45.7		18.4	20.3	27.1	50.8	20.3	5.8	17.9	36.7	17.0	11.5	15.9	20.9	23.9	16.7	64.7	38.6	35.0
L	- Total	$\bar{x}$	967.7	914.4	1074.7	-	1111.8	879.6	854.8	1035.4	972.2	845.2	880.9	1015.0	1029.7	1266.1	1262.0	1259.1	1259.9	1145.9	1196.0	1424.0	1040.4
		SE	53.5	138.2	63.1		118.2	69.1	56.7	147.6	59.9	98.7	83.0	41.2	88.0	55.4	82.8	209.0	111.6	146.7	152.5	223.5	132.6

Appendix 4.3. Standing crop (g m^{-2}) at the T. triandra - C. asiatica site

TREATMENT			DATE 1986 Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan 1987	Feb	Mar	Apr	May
C	- Phytomass	$\bar{x}$	84.6	123.8	133.1	88.1	-	152.4	112.2	-	221.1	190.8	175.4	187.0
O		SE	9.4	15.3	20.1	15.9		25.7	27.0		21.4	33.0	28.6	18.6
N	- Necromass	$\bar{x}$	306.1	282.7	364.0	275.5	-	306.1	363.8	-	301.2	305.2	338.7	503.5
T		SE	17.4	38.9	41.2	24.7		22.6	37.3		28.2	37.0	40.2	27.4
R	- Litter	$\bar{x}$	187.5	289.2	195.6	375.9	-	262.6	421.8	-	326.5	364.7	327.2	458.2
O		SE	33.4	15.0	21.1	13.5		14.8	24.9		22.1	25.7	7.5	48.1
L	- Total	$\bar{x}$	578.2	695.7	692.7	739.5	-	721.0	897.9	-	848.8	860.7	841.4	1148.7
		SE	49.5	65.0	44.5	23.9		35.6	69.0		43.8	77.8	61.0	87.0

Appendix 5. Absolute mass, and percentage loss from the litter bags at all three sites

SITE	SPECIES		DATE 04.09.85 Initial mass	08.01.86 mass (g)	08.01.86 loss (%)	05.04.86 mass (g)	05.04.86 loss (%)	21.06.86 mass (g)	21.06.86 loss (%)	12.09.86 mass (g)	12.09.86 loss (%)	19.12.86 mass (g)	19.12.86 loss (%)	28.04.87 mass (g)	28.04.87 loss (%)
T. leucothrix - L. simplex	C. validus	$\bar{x}$	10.00	4.70	53.00	4.43	55.67	4.07	59.30	4.00	60.00	3.50	65.00	2.53	76.00
		SE		0.15	1.53	0.03	0.33	0.03	0.33	0.15	1.53	0.10	1.00	0.52	5.29
	D. natalensis	$\bar{x}$	10.00	4.70	53.00	4.03	59.67	3.70	63.00	3.90	61.00	3.63	64.00	3.30	67.00
		SE		0.12	1.15	0.12	1.20	0.55	5.57	0.12	1.15	0.15	1.45	0.40	4.04
	E. villosa	$\bar{x}$	10.00	4.93	50.67	4.83	51.67	4.43	55.67	3.93	60.67	4.43	56.00	3.20	68.00
		SE		0.09	0.88	0.12	1.20	0.19	1.86	0.18	1.76	0.18	1.76	0.46	4.62
	L. simplex	$\bar{x}$	10.00	4.83	51.67	4.20	58.00	4.03	59.67	3.93	60.67	4.03	60.00	3.53	65.00
		SE		0.13	1.33	0.21	2.08	0.09	0.88	0.12	1.20	0.09	0.72	0.22	2.19
	T. triandra	$\bar{x}$	4.50	2.03	55.00	1.97	56.30	1.53	65.67	1.50	66.67	1.23	73.00	0.73	84.00
		SE		0.03	1.00	0.12	2.73	0.07	1.67	0.06	1.45	0.12	2.73	0.07	1.67
	T. leucothrix	$\bar{x}$	10.00	4.97	50.30	4.53	54.67	4.23	57.67	4.63	53.67	4.43	56.00	3.83	62.00
		SE		0.03	0.33	0.18	1.76	0.09	0.88	0.03	0.33	0.07	0.67	0.07	0.67
	Wire grasses	$\bar{x}$	5.00	3.53	29.30	3.33	33.30	3.33	33.30	3.33	33.30	3.10	38.00	2.57	49.00
		SE		0.17	3.33	0.23	4.67	0.03	0.67	0.07	1.33	0.23	4.62	0.29	5.81
C. validus - D. natalensis	C. validus	$\bar{x}$	10.00	4.56	54.30	4.23	57.67	3.70	63.30	3.76	62.30	3.67	63.30	3.40	66.00
		SE		0.07	0.67	0.12	1.20	0.30	0.33	0.07	0.67	0.07	0.67	0.12	1.15
	D. natalensis	$\bar{x}$	10.00	4.37	56.30	4.03	59.67	3.47	65.30	3.90	61.00	3.40	66.00	2.40	76.00
		SE		0.07	0.67	0.09	0.88	0.13	1.33	0.00	0.00	0.25	2.52	0.21	2.08
	E. villosa	$\bar{x}$	10.00	4.60	54.00	4.47	55.30	3.40	66.00	3.90	61.00	4.20	58.00	2.90	71.00
		SE		0.00	0.00	0.09	0.89	0.75	7.55	0.36	3.61	0.12	1.15	0.30	3.00
	L. simplex	$\bar{x}$	10.00	4.67	52.30	4.27	57.30	3.77	62.30	4.20	58.00	3.73	64.00	2.27	77.30
		SE		0.12	1.20	0.03	0.33	3.52	3.52	0.00	0.00	0.29	2.65	0.41	4.06
	T. triandra	$\bar{x}$	4.50	1.80	60.00	1.53	66.00	1.20	73.30	0.97	78.67	1.30	71.00	0.57	87.30
		SE		0.06	1.15	0.03	1.00	0.06	1.45	0.24	5.36	0.06	1.15	0.12	2.72
	T. leucothrix	$\bar{x}$	10.00	4.73	53.67	4.70	53.00	4.23	57.67	4.20	58.00	4.27	57.30	1.87	81.30
		SE		0.03	0.33	0.06	0.58	0.03	0.33	0.15	1.53	0.33	3.03	0.15	1.45
	Wire grasses	$\bar{x}$	5.00	3.60	28.00	3.43	31.30	2.93	41.30	3.20	36.00	2.43	51.30	2.00	58.67
		SE		0.00	0.00	0.09	1.76	0.07	1.33	0.23	4.62	0.58	4.06	0.21	2.91
T. triandra - C. asiatica	C. validus	$\bar{x}$	10.00	4.57	54.30	4.60	54.00	3.93	60.67	4.00	60.00	3.57	64.00	2.77	72.30
		SE		0.07	0.67	0.15	1.53	0.17	1.67	0.06	0.58	0.07	0.67	0.39	3.93
	D. natalensis	$\bar{x}$	10.00	4.33	56.67	3.90	61.00	2.90	71.00	3.30	67.00	3.33	67.00	1.67	83.30
		SE		0.12	1.20	0.21	2.08	0.51	5.13	0.10	1.00	0.22	2.19	0.28	2.85
	E. villosa	$\bar{x}$	10.00	4.90	51.00	4.63	53.67	4.20	58.00	4.10	59.00	3.60	64.00	0.40	96.00
		SE		0.06	0.58	0.03	0.33	0.12	1.15	0.12	1.15	0.17	1.73	0.25	2.52
	L. simplex	$\bar{x}$	10.00	4.87	51.30	4.47	55.30	3.77	62.30	3.87	61.30	3.70	63.00	2.47	75.30
		SE		0.23	2.33	0.03	0.33	0.09	0.88	0.12	1.20	0.12	0.89	0.03	0.33
	T. triandra	$\bar{x}$	4.50	2.03	54.70	1.63	63.57	1.60	64.00	1.20	73.30	0.77	83.67	0.47	90.67
		SE		0.07	1.67	0.07	1.67	0.00	0.00	0.06	0.58	0.03	0.67	0.15	3.48
	T. leucothrix	$\bar{x}$	10.00	4.87	51.30	4.57	54.30	4.27	57.30	4.40	56.00	3.83	62.30	3.80	62.00
		SE		0.03	0.33	0.12	1.20	0.13	1.33	0.10	1.00	0.20	2.60	0.25	2.52
	Wire grasses	$\bar{x}$	5.00	3.67	26.67	3.33	33.30	3.23	35.30	3.10	41.30	2.93	41.30	2.87	42.67
		SE		0.09	1.76	0.03	0.67	0.29	5.70	0.15	5.81	0.07	1.33	0.71	14.11

Appendix 6.1. Herbivory and species preference ratios for the T. leucothrix - L. simplex community (all values other than PR are percentages). Continued over the page.

	AREA BURNT 1985																			
SAMPLING DATE	SEPTEMBER 1985				DECEMBER 1985				APRIL 1986				June 1986				September 1986			
SPECIES	PRESENT	GRAZED	DIET	PR	PRESENT	GRAZED	DIET	PR	PRESENT	GRAZED	DIET	PR	PRESENT	GRAZED	DIET	PR	PRESENT	GRAZED	DIET	PR
Alloteropsis semialata	18.34	0.59	3.30	0.18	19.50	1.16	19.66	1.01	20.87	0.68	12.11	0.58	19.67	0.82	10.85	0.55	18.01	0.57	10.85	0.60
Aristida junciformis									0.17	18.00	2.61	15.35								
Ctenium concinnum	0.44	8.16	1.10	1.54	1.81	2.22	3.49	1.93	1.82	0.04	0.05	0.03	1.62	-	-	-	2.32	0.38	0.93	0.40
Cyperus obtusiflorus	0.23	1.91	0.13	0.57	2.08	-	-	-	1.20	-	-	-	0.86	-	-	-	1.03	0.34	0.37	0.36
Digiatria littoralis					0.06	0.08	-	-	0.08	1.45	0.10	1.25								
Digitaria natalensis																	0.04	6.05	0.25	6.25
Diheteropogon amplectans	5.92	0.66	1.20	0.20	0.93	3.75	3.38	3.63	2.04	0.32	0.55	0.27	3.27	0.81	1.78	0.54	2.39	0.22	0.56	0.23
Elionurus muticus (broad-leaved variant)																				
Eragrostis capensis	1.57	2.60	1.47	0.94																
Eragrostis innomaena					0.15	4.42	0.57	3.80	0.19	16.86	2.73	14.37	0.70	5.87	2.76	3.94	0.39	40.92	16.87	43.26
Eragrostis plana																				
Eulalia villosa	1.95	5.49	3.27	1.68	2.35	0.69	1.41	0.60	3.30	0.62	1.74	0.53	2.29	0.27	0.42	0.18	2.12	0.18	0.40	0.19
Festuca costata													0.23	0.77	0.12	0.52				
Fimbristylis sp					0.20	0.37	0.06	0.30												
Harpechloa falx	0.20	-	-	-																
Heteropogon contortus	1.89	15.50	8.96	4.74	2.98	2.21	5.73	1.92	3.54	1.41	4.25	1.20	3.57	5.59	13.42	3.76	4.74	1.19	5.96	1.26
Loudetia simplex	1.13	15.21	5.25	4.65	4.26	0.19	0.70	0.16	5.63	0.26	1.24	0.22	4.51	0.71	2.15	0.48	4.36	0.01	0.04	0.01
Monocymbium ceresiforme																				
Panicum ecklonii	2.03	3.51	2.18	1.07	0.25	1.44	0.32	1.28	0.78	0.41	0.27	0.35	1.09	0.20	0.15	0.14	0.46	0.04	0.02	0.04
Panicum natalensis																				
Paspalum scorbiculum	0.42	4.90	0.79	1.88	0.20	0.26	0.04	0.20	0.21	5.33	0.92	4.52	0.30	19.05	3.85	12.83	0.09	6.25	0.59	6.56
Scleria bulbifera	0.50	3.23	0.50	1.00	5.48	0.19	0.90	0.16	0.66	2.30	1.30	1.97	0.79	0.05	0.03	0.04	1.23	-	-	-
Scleria melanomphylla					0.37	2.57	0.83	2.24	0.48	-	-	-	0.52	0.53	0.18	0.35	0.63	2.93	1.97	3.13
Setaria sphacelata					0.24	0.80	0.17	0.71	0.52	14.58	6.47	12.44	0.39	34.47	9.04	23.18	0.21	14.53	3.22	15.33
Sporobolus centrifugus	0.74	7.47	1.69	2.28	0.27	9.44	2.22	8.22												
Sporobolus africanus																				
Themeda triandra	7.78	5.32	12.65	1.63	3.00	1.50	3.91	1.30	1.77	0.62	1.02	0.58	3.31	1.95	4.34	1.31	2.98	0.77	2.42	0.81
Trachypogon spicatus	0.79	8.80	2.12	2.68	4.38	0.42	1.60	0.37	5.74	0.76	3.73	0.65	7.21	3.29	15.95	2.21	6.82	1.77	12.75	1.87
Tristachya leucothrix	26.24	3.20	25.67	0.98	28.16	2.04	48.94	1.77	27.92	2.22	52.85	1.89	21.43	1.94	27.95	1.30	24.79	0.85	22.27	0.90
Ureyletrum agropyroides	1.00	0.50	0.15	0.15	2.88	1.03	2.58	0.90	4.00	0.31	1.06	0.27	5.08	0.39	1.33	0.26	5.08	0.51	3.08	0.61
Wire grasses	28.20	3.43	29.57	1.05	20.42	0.14	2.49	0.12	19.04	0.43	6.97	0.37	23.46	0.36	5.68	0.24	22.31	0.74	17.45	0.78
Others	0.63	-	-	-	0.30	-	-	-	0.18	-	-	-	0.09	-	-	-	0.02	-	-	-

Appendix 6.1. Continued

SAMPLING DATE	BURNT 1985 December 1986				AREA	BURNT 1985 April 1987				AREA	BURNT 1986 SEPTEMBER 1986				AREA	BURNT 1986 DECEMBER 1986				AREA	BURNT 1986 APRIL 1987			
SPECIES	PRESENT	GRAZED	DIET	PR	PRESENT	GRAZED	DIET	PR		PRESENT	GRAZED	DIET	PR		PRESENT	GRAZED	DIET	PR		PRESENT	GRAZED	DIET	PR
Alloteropsis semialata	14.29	0.20	16.47	1.15	15.47	1.96	24.62	1.59		37.17	9.32	41.89	1.13		24.31	9.92	32.37	1.33		24.01	2.96	40.11	1.67
Aristida junciformis																							
Ctenium concinnum	1.75	-	-	-	1.78	-	-	-		0.89	2.08	0.22	0.25		4.71	3.22	2.04	0.43		3.11	0.75	1.31	0.42
Cyperus obtusiflorus	0.80	-	-	-	0.53	-	-	-		0.43	1.54	0.08	0.19		3.29	0.20	0.09	0.03		1.95	0.52	0.57	0.29
Digiatria littoralis																				0.02	4.94	0.06	3.00
Digitaria natalensis										2.02	10.53	2.57	1.27							0.06	21.68	0.73	12.17
Diheteropogon amplectans	2.71	-	-	-	3.71	0.16	0.48	0.13		3.68	0.83	0.37	0.10		2.53	0.52	0.18	0.07		2.22	0.80	1.00	0.45
Elionurus muticus					0.02	3.00	0.05	2.50		1.91	4.18	0.96	0.50		1.01	-	-	-		0.36	-	-	-
(broad-leaved variant)																							
Eragrostis capensis	0.05	-	-	-	0.10	38.00	3.09	30.90		0.76	6.19	0.57	0.75		0.12	9.95	0.16	1.33		0.04	3.88	0.09	2.25
Eragrostis innomaena	0.36	0.29	0.58	1.61	0.19	40.30	6.22	32.74															
Eragrostis plana					0.01	63.00	0.51	51.00							0.12	0.87	0.01	0.08		0.23	11.27	1.46	6.35
Eulalia villosa	1.46	-	-	-	2.02	1.28	2.10	1.04		2.44	3.72	1.10	0.45		5.75	1.56	1.20	0.21		7.51	0.31	1.31	0.17
Festuca costata										2.65	34.36	11.01	4.15		0.06	7.84	0.06	1.00					
Fimbristylis sp																				0.34	-	-	-
Harpechloa falx																				0.03	83.00	1.41	47.00
Heteropogon contortus	3.15	0.09	1.60	0.51	0.82	6.84	4.55	5.55		1.79	3.57	0.77	0.43		5.74	6.90	5.32	0.93		6.29	0.48	1.81	0.29
Loudetia simplex	4.33	0.02	0.52	0.12	6.56	0.02	0.11	0.02		0.34	3.26	0.13	0.38		2.96	1.24	0.49	0.17		2.86	-	-	-
Monocymbium ceressiforme					0.12	31.66	3.09	25.75															
Panicum ecklonii	1.30	0.02	0.17	0.13	0.65	0.87	0.46	0.71		0.08	0.43	-	-		0.98	1.53	0.20	0.20					
Panicum natalensis															0.21	52.20	1.47	7.00					
Paspalum scorbiculum	0.05	-	-	-	0.29	26.76	6.30	21.72		0.19	3.34	0.08	0.42		0.45	1.57	0.10	0.22		0.97	2.94	1.61	1.66
Scleria bulbifera	2.20	0.03	0.40	0.18	1.77	-	-	-							3.23	0.53	0.23	0.07		0.47	-	-	-
Scleria melanomphylla	0.59	1.02	3.45	5.85	1.40	0.01	-	-							0.64	0.81	0.07	0.11		1.04	-	-	-
Setaria sphacelata	0.21	4.19	5.07	24.14	0.08	1.90	0.12	1.50		1.00	38.00	4.59	4.59							0.03	4.85	1.39	46.33
Sporobolus centrifugus	0.11	-	-	-						0.55	7.58	0.50	0.91		0.17	12.92	0.30	1.76					
Sporobolus africanus																				0.13	16.23	1.59	12.23
Themeda triandra	1.89	0.18	1.96	1.04	1.67	0.46	0.63	0.38		2.60	7.27	2.29	0.88		0.60	14.77	1.19	1.98		1.90	2.55	2.74	1.44
Trachypogon spicatus	15.83	0.06	5.47	0.35	15.16	0.61	7.51	0.50							3.99	3.54	1.90	0.48		6.30	1.80	6.40	1.02
Tristachya leucothrix	27.93	0.40	63.31	2.30	28.57	1.61	37.35	1.31		25.65	5.32	16.51	0.64		23.95	14.54	46.75	1.95		19.93	3.16	33.76	1.78
Ureyletrum agropyroides	5.34	-	-	-	5.77	0.53	2.48	0.43		4.38	4.25	2.25	0.51		5.17	5.24	3.64	0.70		7.38	0.43	1.79	0.24
Wire grasses	14.46	-	-	-	10.22	0.04	0.33	0.03		12.30	9.24	13.74	1.12		9.44	1.77	2.24	0.24		11.73	0.13	0.86	0.07
Others	1.57	-	-	-	3.09	-	-	-		0.06	-	-	-		0.57	-	-	-		1.58	-	-	-

Appendix 6.2. Herbivory (%) and species preference ratios for the C. validus - D. natalensis community (all values other than PR are percentages). Continued over the page.

SAMPLING DATE	BURNT 1985 DECEMBER 1986				AREA	BURNT 1985 APRIL 1987				SEPTEMBER 1986			AREA	BURNT 1986 DECEMBER 1986				AREA	BURNT 1986 APRIL 1987		
SPECIES	PRESENT	GRAZED	DIET	PR	PRESENT	GRAZED	DIET	PR	PRESENT	GRAZED	DIET	PR	PRESENT	GRAZED	DIET	PR	PRESENT	GRAZED	DIET	PR
Alloteropsis semialata	5.09	0.64	3.62	0.71	4.42	1.54	12.03	2.72	12.47	11.04	19.74	1.58	8.19	8.53	9.60	1.17	8.17	6.34	10.15	1.24
Ctenium concinnum	0.32	-	-	-					2.11	5.09	1.54	0.73	1.39	13.08	2.50	1.80	0.49	1.89	0.18	0.37
Cymbopogon validus	49.52	0.18	9.89	0.20	45.87	0.13	9.95	0.22	15.21	0.52	1.13	0.07	31.36	0.51	2.20	0.07	34.16	0.70	4.69	0.14
Cyperus obtusiflorus	0.32	-	-	-									1.35	-	-	-	0.51	-	-	-
Digiatria littoralis	0.47	-	-	-	0.12	0.21	0.05	0.42					0.45	-	-	-				
Digitaria natalensis	13.12	5.29	77.03	5.87	14.35	1.62	41.43	2.89	42.02	9.65	58.14	1.38	20.12	16.42	45.39	2.26	20.44	16.12	64.58	3.16
Diheteropogon amplectans	0.95	-	-	-	0.53	-	-	-	2.27	0.06	0.02	-	1.50	0.35	0.07	0.05	0.74	1.35	0.20	0.27
Elionurus muticus (broad-leaved variant)													0.44	-	-	-	0.19	-	-	-
Eragrostis capensis	0.15	-	-	-					0.51	7.97	0.58	1.14	0.38	12.54	0.66	1.74	0.03	42.00	0.25	8.33
Eragrostis curvula	0.01	38.00	0.42	42.00					0.13	3.00	0.06	0.46	0.26	23.67	0.84	3.23				
Eragrostis plana	0.04	1.64	0.08	2.00	0.15	8.00	2.12	14.10									0.06	17.39	0.20	3.33
Eulalia villosa	0.43	-	-	-	0.48	-	-	-					0.68	1.87	0.17	0.25	1.03	0.93	0.19	0.18
Festuca costata	3.13	-	-	-	4.05	-	-	-	2.17	11.64	3.62	1.67	1.72	7.77	1.84	1.07	2.60	0.21	0.10	0.04
Fimbristylis sp																	0.10	-	-	-
Harpechloa falx													0.24	67.05	2.21	9.21	0.07	51.14	0.70	10.00
Helictotrichon elongatum													0.24	66.20	2.18	9.08	0.48	27.69	2.60	5.42
Heteropogon contortus	0.31	0.23	0.08	0.26	0.27	0.20	0.08	0.30					1.24	15.55	2.65	2.14	1.07	6.75	1.41	1.32
Panicum aequinerve	0.30	-	-	-													0.06	3.00	0.03	0.50
Panicum deustum					0.22	0.89	0.33	1.50									0.07	-	-	-
Panicum ecklonii	0.21	-	-	-	0.17	1.77	0.53	3.12									0.15	0.07	-	-
Panicum natalensis																				
Paspalum scrobiculum	1.57	0.67	1.17	0.75	2.48	0.45	1.98	0.80	1.21	1.30	0.23	0.19	2.76	0.74	0.28	0.10	4.17	4.90	4.00	0.96
Scleria bulbifera													0.26	-	-	-				
Scleria melanophylla	3.77	0.06	0.24	0.06	7.16	0.18	2.28	0.32									1.00	-	-	-
Sedge	0.40	-	-	-	0.24	2.36	1.01	4.21					0.40	1.26	0.07	0.18	0.41	-	-	-
Setaria sphacelata	0.17	8.71	1.64	9.65	0.22	8.49	3.30	15.00	0.19	6.50	0.18	0.95	0.13	25.04	0.45	3.46	0.57	4.39	0.49	0.86
Sporobolus centrifugus	0.44	-	-	-					2.38	3.79	1.29	0.54	0.82	5.32	0.60	0.73	0.47	0.70	0.06	0.13
Sporobolus africanus					0.02	38.00	1.34	67.00									0.25	3.00	0.15	0.60
Themeda triandra	5.63	-	-	-	5.43	-	-	-					0.54	38.30	2.84	5.26	0.36	6.90	0.49	1.36
Trachypogon spicatus	3.96	0.25	1.10	0.28	3.05	0.19	1.02	0.33					1.85	0.41	0.10	0.05	3.32	6.88	4.48	1.35
Tristachya leucothrix	6.46	0.66	4.73	0.73	8.07	1.58	22.53	2.79	11.88	7.66	13.05	1.09	14.10	4.31	8.35	0.59	10.68	1.26	2.66	0.25
Urelytrum agropyroides					0.29	-	-	-	2.11	0.42	0.13	0.06	3.26	36.98	16.56	5.08	4.77	2.49	2.33	0.49
Wire grasses	2.17	-	-	-	2.03	-	-	-	3.68	0.57	0.30	0.08	3.17	0.19	0.08	0.03	2.57	0.13	0.06	0.02
Others	1.21				0.38	-	-	-	1.66	-	-	-	2.19	-	-	-	1.38	-	-	-

Appendix 6.2. Continued

SAMPLING DATE	SEPTEMBER 1985			AREA	BURNT 1985 DECEMBER 1985				APRIL 1986			AREA	BURNT 1985 JUNE 1986				SEPTEMBER 1986			
SPECIES	PRESENT	GRAZED	DIET	PR	PRESENT	GRAZED	DIET	PR	PRESENT	GRAZED	DIET	PR	PRESENT	GRAZED	DIET	PR	PRESENT	GRAZED	DIET	PR
Alloteropsis semialata	7.09	-	-	-	7.34	0.51	1.39	0.19	6.48	1.77	2.22	0.34	7.29	2.44	5.16	0.71	7.82	0.44	1.25	0.16
Ctenium concinnum	0.82	-	-	-													0.78	-	-	-
Cymbopogon validus	41.39	0.86	9.35	0.23	45.80	0.28	4.76	0.10	44.06	2.77	23.66	0.54	44.53	3.01	38.85	0.87	48.54	3.45	60.68	1.25
Cyperus obtusiflorus	0.53	-	-	-	0.20	1.23	0.09	0.45	0.27	-	-	-	0.29	8.24	0.69	3.28	0.30	-	-	-
Digiatria littoralis	1.08	1.11	0.26	0.24													0.03	2.91	0.03	1.00
Digitaria natalensis	18.69	16.49	80.02	4.28	13.44	3.50	17.48	1.30	16.00	21.86	67.82	4.24	17.32	8.56	42.97	2.48	13.02	6.37	30.05	2.31
Diheteropogon amplectans	0.39	0.02	-	-	1.73	0.05	0.03	0.02	0.39	0.30	0.02	0.05	0.60	-	-	-	0.70	-	-	-
Elionurus muticus (broad-leaved variant)																				
Eragrostis capensis					0.39	4.07	0.59	1.51					0.12	10.26	0.36	3.00				
Eragrostis curvula									0.07	1.57	0.02	0.29								
Eragrostis plana																	0.02	18.00	0.13	6.50
Eulalia villosa	0.73	0.21	0.05	0.07					1.18	0.50	0.11	0.09	0.61	2.49	0.44	0.72	0.92	1.26	0.42	0.46
Festuca costata	1.64	0.01	-	-	1.15	49.88	21.34	18.55	1.07	-	-	-	2.88	0.08	0.07	0.02	3.62	-	-	-
Fimbristylis sp																				
Harpechloa falx																				
Helictotrichon elongatum																				
Heteropogon contortus	0.39	20.86	2.08	5.30	0.30	19.27	2.15	7.17	0.12	11.09	0.26	2.17	0.38	-	-	-	0.31	2.97	0.33	1.06
Panicum aequinerve	0.41	2.33	0.26	0.63					0.25	6.59	0.32	1.28	0.02	39.55	0.23	11.50				
Panicum deustum																				
Panicum ecklonii					0.44	1.06	0.17	0.39												
Panicum natalensis	0.23	-	-	-																
Paspalum scorbiculum	3.29	2.85	2.33	0.71	1.60	1.77	1.05	0.66	3.64	4.71	3.32	0.91	2.42	2.21	1.55	0.64	1.88	1.33	0.91	0.48
Scleria bulbifera	0.58	0.74	0.10	0.17	1.19	1.56	0.69	0.58												
Scleria melanomphylla	1.12	0.39	0.10	0.09					5.42	0.52	0.55	0.10	2.79	-	-	-	1.88	0.14	0.09	0.05
Sedge																				
Setaria sphacelata									1.09	1.00	0.21	0.19	0.10	22.80	0.66	6.60	0.25	0.19	0.02	0.08
Sporobolus centrifugus	2.05	1.76	1.04	0.51	1.21	4.55	2.89	1.69	0.43	-	-	-	0.23	-	-	-	0.72	2.26	0.59	0.82
Sporobolus africanus																				
Themeda triandra	5.60	2.04	2.86	0.51	7.66	12.80	36.44	4.76	5.10	0.46	0.46	0.09	5.60	1.49	2.42	0.43	5.34	0.21	0.41	0.08
Trachypogon spicatus	1.22	0.71	0.23	0.19					2.10	0.12	0.05	0.02	1.23	5.47	1.95	1.58	2.72	2.68	2.64	0.97
Tristachya leucothrix	7.79	0.67	1.29	0.17	8.45	2.78	8.73	1.03	8.88	0.58	0.98	0.11	9.85	1.63	4.66	0.47	7.68	0.88	2.45	0.32
Urelytrum agropyroides					2.40	-	-	-					0.34	-	-	-				
Wire grasses	2.52	-	-	-	3.42	1.73	2.20	0.64	3.10	-	-	-	3.28	-	-	-	3.45	-	-	-
Others	2.00	-	-	-	2.78	-	-	-	0.35	-	-	-	0.12	-	-	-	0.02	-	-	-

Appendix 7.1. Nutrient content (%) of grass phytomass at the T. leucothrix - L. simplex site

NUTRIENT	TREATMENT	DAIF																					
		1985										1986								1987			
		Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
CP	Grazed	17.30	11.89	9.57	8.75	7.74	7.98	4.99	4.35	5.02	5.08	4.06	4.57	3.79	6.52	6.50	-	6.22	5.11	4.35	4.84	4.17	-	4.71
	Ungrazed	18.65	11.56	8.57	7.91	6.73	4.82	4.34	4.14	3.73	4.12	3.77	3.36	3.29	6.09	6.17	-	5.26	5.25	4.92	4.75	5.07	-	3.44
	Control	5.50	4.61	5.85	5.52	5.50	5.42	5.21	4.41	4.41	4.70	4.14	3.52	3.93	5.78	6.89	-	5.88	5.72	5.54	4.82	5.01	-	4.58
P	Grazed	0.24	0.13	0.09	0.09	0.07	0.06	0.04	0.04	0.04	0.04	0.03	0.03	0.03	0.07	0.07	-	0.05	0.05	0.05	0.05	0.04	-	0.03
	Ungrazed	0.26	0.12	0.09	0.08	0.06	0.04	0.04	0.04	0.03	0.04	0.04	0.03	0.03	0.07	0.06	-	0.05	0.05	0.04	0.04	0.03	-	0.03
	Control	0.05	0.04	0.05	0.05	0.05	0.06	0.05	0.04	0.04	0.04	0.04	0.03	0.03	0.07	0.07	-	0.05	0.06	0.05	0.05	0.05	-	0.04
K	Grazed	2.74	1.70	1.63	1.34	1.13	1.06	0.92	0.87	0.84	0.84	0.84	0.71	0.62	1.06	1.18	-	1.06	1.02	0.93	1.06	0.96	-	0.86
	Ungrazed	2.88	1.85	1.57	1.49	1.19	1.06	0.93	0.94	0.83	0.85	0.77	0.61	0.64	0.99	1.10	-	1.06	1.05	0.99	0.93	1.03	-	0.84
	Control	1.01	0.92	0.99	1.05	1.02	1.20	1.02	1.08	0.90	0.93	0.93	0.87	0.85	1.10	1.21	-	1.11	1.15	1.11	1.17	1.03	-	1.03
S	Grazed	0.22	0.21	0.21	0.18	0.16	0.15	0.13	0.14	0.14	0.14	0.16	0.13	0.14	0.17	-	-	-	-	-	0.16	0.13	-	0.11
	Ungrazed	0.21	0.21	0.17	0.17	0.15	0.14	0.13	0.13	0.14	0.17	0.15	0.13	0.14	0.17	-	-	-	-	-	0.14	0.16	-	0.15
	Control	0.16	0.18	0.16	0.18	0.17	0.15	0.15	0.14	0.16	0.15	0.16	0.16	0.15	0.16	-	-	-	-	-	0.14	0.12	-	0.13
Ca	Grazed	0.33	0.36	0.39	0.45	0.27	0.35	0.35	0.36	0.31	0.37	0.29	0.31	0.42	0.29	0.30	-	0.39	0.29	0.32	0.40	0.44	-	0.40
	Ungrazed	0.33	0.40	0.43	0.56	0.38	0.39	0.43	0.38	0.35	0.45	0.40	0.47	0.41	0.43	0.42	-	0.49	0.39	0.37	0.36	0.52	-	0.37
	Control	0.31	0.30	0.32	0.31	0.29	0.34	0.29	0.32	0.28	0.31	0.29	0.26	0.32	0.30	0.34	-	0.28	0.33	0.31	0.27	0.30	-	0.35
Mg	Grazed	0.25	0.26	0.27	0.25	0.18	0.22	0.22	0.25	0.24	0.22	0.22	0.26	0.28	0.24	0.21	-	0.25	0.21	0.21	0.18	0.22	-	0.23
	Ungrazed	0.26	0.26	0.25	0.27	0.26	0.27	0.24	0.21	0.22	0.26	0.21	0.20	0.22	0.22	0.22	-	0.20	0.20	0.20	0.19	0.21	-	0.17
	Control	0.19	0.20	0.21	0.20	0.19	0.18	0.17	0.18	0.18	0.22	0.18	0.19	0.19	0.20	0.19	-	0.20	0.22	0.19	0.15	0.17	-	0.19
Digest-ibility	Grazed	61.14	50.15	39.31	39.34	29.38	33.01	30.47	37.38	28.37	26.94	25.18	30.31	32.12	32.38	31.06	-	31.63	26.37	28.90	23.32	22.94	-	29.03
	Ungrazed	62.49	47.82	50.11	44.72	30.47	23.25	37.06	39.63	16.95	36.89	29.88	28.85	30.61	28.68	30.12	-	29.37	24.25	29.18	22.86	28.39	-	23.48
	Control	29.62	30.32	31.37	31.73	25.35	26.58	27.11	26.98	24.79	13.99	23.40	27.35	29.17	32.47	27.57	-	27.74	26.35	27.98	19.94	24.12	-	24.77

Appendix 7.2. Nutrient content (%) of grass phytomass at the C. validus - D. natalensis site

NUTRIENT	TREATMENT	DATE																			
		1985					1986											1987			
		Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
CP	Grazed	5.53	11.51	9.56	7.57	8.28	5.94	5.37	4.82	3.82	4.33	3.76	3.46	2.92	3.27	5.14	5.52	5.26	4.15	3.53	4.55	3.61
	Ungrazed	11.95	10.50	7.36	7.63	6.48	4.96	4.77	4.29	3.26	3.72	3.34	2.48	2.64	4.68	6.05	5.25	4.50	3.38	3.51	3.55	3.98
	Control	2.81	4.18	3.99	-	5.59	3.27	4.09	3.19	2.96	3.11	2.84	2.60	2.64	3.02	4.95	4.11	4.02	3.71	3.50	3.33	3.20
P	Grazed	0.07	0.12	0.09	0.07	0.08	0.07	0.05	0.04	0.04	0.05	0.04	0.04	0.03	0.03	0.07	0.07	0.05	0.05	0.04	0.05	0.05
	Ungrazed	0.14	0.11	0.07	0.07	0.06	0.05	0.04	0.04	0.04	0.04	0.03	0.03	0.03	0.06	0.07	0.06	0.05	0.06	0.05	0.04	0.04
	Control	0.02	0.05	0.04	-	0.08	0.04	0.05	0.04	0.04	0.04	0.03	0.03	0.04	0.04	0.06	0.06	0.05	0.06	0.06	0.05	0.04
K	Grazed	0.93	1.95	1.59	1.43	1.32	1.36	1.29	1.20	1.11	1.24	1.11	1.05	1.08	0.96	1.31	1.40	1.31	1.38	1.19	1.23	1.27
	Ungrazed	1.92	1.38	1.27	1.11	1.03	1.02	1.09	0.93	0.86	1.05	0.97	0.77	0.74	1.06	1.15	1.15	1.18	1.21	1.16	1.04	1.16
	Control	1.10	1.18	1.11	-	1.88	1.28	1.24	1.28	1.20	0.51	1.24	1.15	1.24	1.21	1.30	1.20	1.26	1.35	1.36	1.18	1.26
S	Grazed	-	0.18	0.21	0.17	0.19	0.15	0.14	0.15	0.13	0.18	0.17	0.14	0.13	0.11	0.16	-	-	-	-	-	-
	Ungrazed	0.17	0.17	0.15	0.19	0.14	0.13	0.13	0.13	0.15	0.15	0.15	0.12	0.11	0.17	-	-	-	-	-	-	0.13
	Control	0.13	0.14	0.18	-	0.15	0.12	0.13	0.13	0.14	0.15	0.14	0.12	0.12	0.13	-	-	-	-	-	-	0.13
Ca	Grazed	0.07	0.33	0.43	0.41	0.37	0.31	0.37	0.33	0.27	0.34	0.29	0.27	0.33	0.30	0.29	0.60	0.30	0.69	0.23	0.34	0.39
	Ungrazed	0.40	0.42	0.36	0.41	0.37	0.39	0.29	0.37	0.30	0.40	0.33	0.23	0.29	0.27	0.38	0.45	0.41	0.51	0.48	0.35	0.27
	Control	0.20	0.31	0.24	-	0.37	0.25	0.37	0.29	0.31	0.29	0.22	0.26	0.24	0.22	0.24	0.19	0.24	0.18	0.23	0.60	0.23
Mg	Grazed	0.08	0.22	0.23	0.23	0.25	0.20	0.16	0.17	0.16	0.19	0.16	0.16	0.16	0.17	0.18	0.19	0.18	0.16	0.15	0.18	0.15
	Ungrazed	0.30	0.29	0.27	0.28	0.26	0.22	0.22	0.24	0.18	0.22	0.21	0.18	0.17	0.20	0.20	0.22	0.17	0.16	0.15	0.16	0.18
	Control	0.17	0.22	0.21	-	0.21	0.16	0.20	0.15	0.18	0.17	0.14	0.17	0.16	0.18	0.19	0.14	0.18	0.14	0.14	0.15	0.18
Digest-ibility	Grazed	16.05	51.43	48.32	45.01	39.63	32.18	30.52	31.01	27.65	16.87	27.36	26.28	27.71	26.34	26.85	28.63	27.34	19.12	18.92	20.28	21.88
	Ungrazed	51.04	48.72	44.06	36.37	31.61	29.08	31.40	27.34	27.33	30.42	26.21	21.86	23.52	26.35	25.70	28.83	22.01	19.29	18.25	16.87	18.12
	Control	25.18	30.26	28.90	-	32.33	26.72	24.15	22.68	23.59	24.74	22.45	24.63	24.39	18.49	22.02	19.58	18.73	17.43	16.05	16.43	14.30

Appendix 7.3. Nutrient content (%) of grass phytomass at the T. triandra - C. asiatica site

NUTRIENT	TREATMENT	1986							1987			
		Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
CP	Control	5.52	4.72	3.98	5.50	-	6.14	4.87	-	5.00	6.29	5.46	7.55
P	Control	0.04	0.03	0.01	0.04	-	0.05	0.05	-	0.05	0.06	0.06	0.07
K	Control	0.85	0.61	0.39	0.84	-	0.86	0.85	-	0.91	0.89	0.83	1.01
S	Control	0.23	0.17	0.16	0.20	-	0.15	0.17	-	0.17	0.17	0.17	0.26
Ca	Control	0.49	0.27	0.37	0.25	-	0.29	0.28	-	0.31	0.31	0.31	0.64
Mg	Control	0.33	0.24	0.25	0.19	-	0.23	0.21	-	0.27	0.25	0.23	0.37
Digest-	Control	30.11	20.15	19.61	21.10	-	22.40	18.96	-	24.04	29.54	21.86	35.12

KEY

Roads
Gates
Fences
Buildings
Guard huts
Dams
Monitoring sites
Block boundaries

31°15'
29°57'
31°18'
29°57'
30°00'
30°00'
31°18'
30°03'
31°15'

KWADLAMBU

A BLOCK
B BLOCK
C BLOCK
D BLOCK
E BLOCK
F BLOCK

1
2
3
4
5
6
A
B
C
D

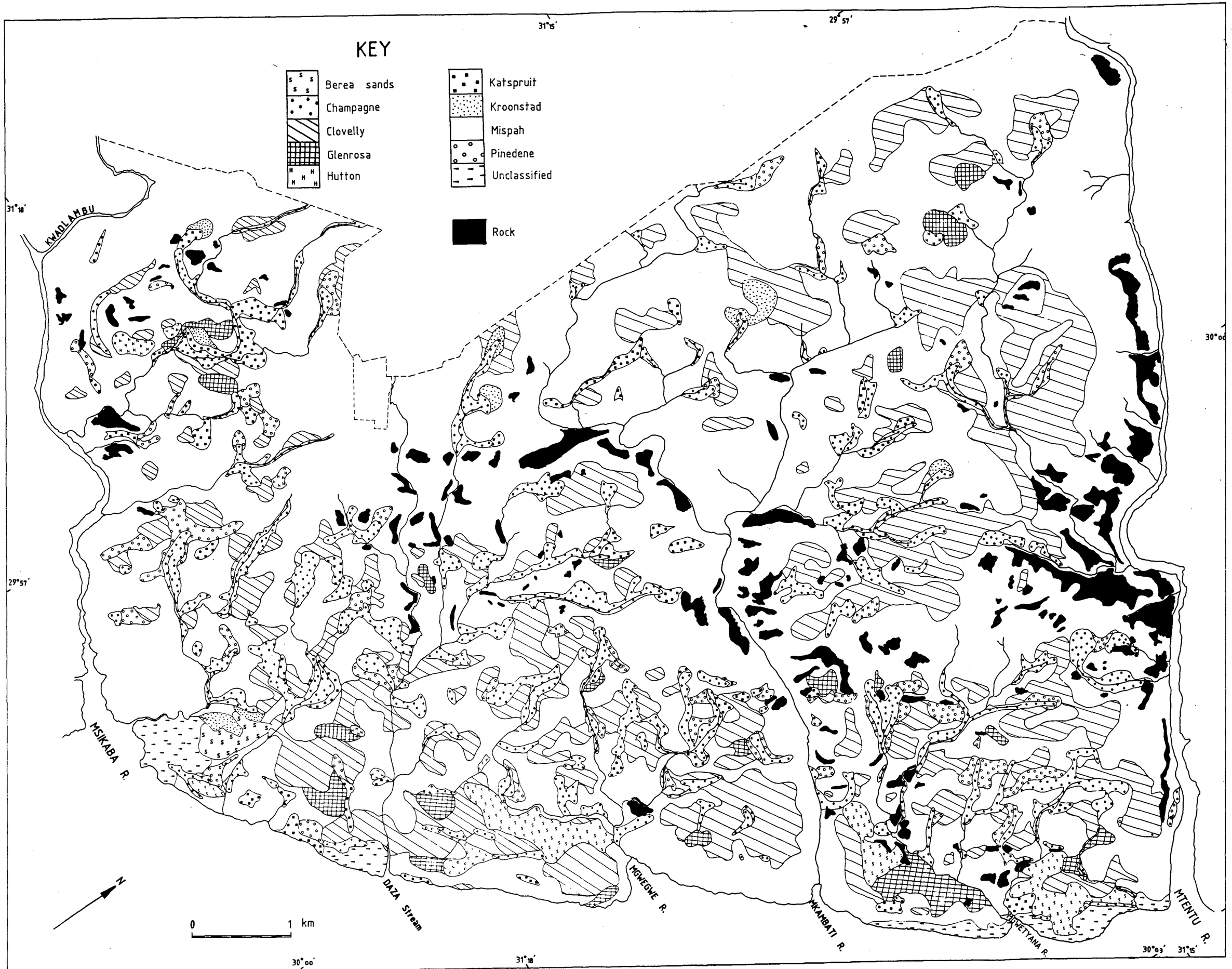
AIRSTRIP

MSIKABA R.
DAZA Stream
MGWEGWE R.
MKAMBATI R.
MDWETYANA R.
MTENTU R.
LUKEBENI R.

N

0 1 km

MAP 1. ADMINISTRATIVE MAP OF MKAMBATI GAME RESERVE



MAP 2. SOIL MAP OF MKAMBATI GAME RESERVE

KEY

- Forest (indigenous)
- Forest (exotic)
- Wetland
- Grassland
  - *Aristida junciformis - Helichrysum mixtum*
  - *Cymbopogon validus - Digitaria natalensis*
  - *Festuca costata - Albuca setosa*
  - *Themeda triandra - Centella asiatica*
  - *Tristachya leucothrix - Loudetia simplex*
  - *Stoebe vulgaris - Athanasia calva*
  - *Watsonia sp.*
- Rock

31°15'
29°57'
31°18'
30°00'
29°57'
30°00'
30°03'
31°15'
31°18'

KWADLAMBU

MSIKABA R.

DAZA Stream

MGWEGWE R.

MKAMBATI R.

QWETYANA R.

MTENTU R.

N

0 1 km

MAP 3. VEGETATION MAP OF MKAMBATI GAME RESERVE