



A synthesis of field experiments concerning the grass layer in the savanna regions of southern Africa

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PREFACE

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

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

This report provides an empirical catalogue of the long term experiments carried out in southern Africa concerning the grass layer of savannas. This information provides a basis for the investigation of the dynamical response of savanna systems to various management strategies, for a range of savanna types encountered in southern Africa. The study is therefore a keystone in Phase III of the Savanna Ecosystem Project - the study of management strategies for the optimal utilisation of savanna ecosystems.

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ABSTRACT

The purpose of this synthesis of long term experiments was to develop an account of how the principal determinants (rainfall, soil type, woody/grass ratio, herbivory, fire) influence the dynamics of the grass layer of southern African savannas.

The review covers bush clearing, fertilization, grazing, fire, reclamation and exclusion experiments, and appropriate monitoring sets. The 126 experiments included provide a poor data base because of defects in experimental design, a low intensity of sampling, inappropriate indices for assessing change, and inadequate presentation of data.

Fluctuations in species abundances are the norm in savannas, and are related to the degree of rainfall variability. Available soil moisture, determined by rainfall, soil type and the woody/grass ratio, is the primary determinant of compositional fluctuations across all climatic regimes, but its effect is more pronounced in semi-arid than in mesic savannas, and on heavier textured than sandy soils. Correspondingly, the influence of fluctuations in the availability of nutrients, principally nitrogen and phosphorus, is greatest in the sandy soils of mesic savannas which are nutrient rather than moisture limited. The processes underlying compositional fluctuations are the differential patterns between species of mortality of established tufts, germination and establishment, and growth in response to fluctuating environmental conditions, principally soil moisture. Grazing and fire exercise an indirect effect on the above processes through their influence on the abiotic environment. The direct relationship between grazing or fire and population processes is contingent upon the abiotic environment, and possibly non-linear.

Grassland composition does not display the classical pattern of static stability, but the same compositional state is recurrent for a given set of abiotic conditions. Changes in the abiotic environment rapidly effect a change in composition, as evidenced in fertilization experiments. An irreversible change in composition cannot take place without an associated irreversible change in abiotic state structure. The major recorded changes of savannas which are potentially irreversible in the short term are increases in the woody/grass ratio of heavy textured soils subjected to consistent overgrazing, effected through a change in the soil moisture regime.

The variability of herbaceous yield at a site is related to the variability of available soil moisture, as determined by rainfall and soil type. The woody component has a consistent depressive effect on yield through its utilisation of soil moisture. Therefore sandy soils of mesic savannas, particularly when debushed, exhibit more stable trends of herbaceous yield than heavy textured soils on mesic savannas or semi-arid savannas. There is little evidence to evaluate the long term effect of grazing or fire on yield. Irreversible changes in the yield potential of a site are associated with long term changes in available soil moisture and nutrients.

There is insufficient empirical data to derive predictive relationships between determinants and abiotic variables. Grazing and fire, which can significantly influence soil physical and chemical properties, need to

be evaluated in the context of other interacting processes affecting nutrient cycling.

Long term ecological experiments in southern African savannas will continue to be an impoverished source of insight into the functioning of savannas until experiments are conducted within the framework of formalized models from which explicit tests of key processes can be made, rather than as exercises which generate empirical data bases.

CONTENTS

Page

PREFACE.....	iii
ACKNOWLEDGEMENTS.....	iii
ABSTRACT.....	iv
INTRODUCTION.....	1
GENERAL APPROACH.....	2
Sources of data.....	2
Evaluation of data.....	2
DEFINITIONS AND CONCEPTS.....	4
Description of a system.....	4
Determinants of a system.....	4
Rainfall.....	4
Soil characteristics.....	5
Herbivory and fire.....	5
SHORTCOMINGS OF THE DATA BASE.....	6
Intensity of sampling.....	6
Time of sampling.....	8
Inadequate presentation of published data.....	9
Functional species groups.....	9
Mensuration.....	9
THE EFFECTS OF DETERMINANTS ON STATE VARIABLES.....	11
TRENDS IN HERBACEOUS COMPOSITION.....	11
The effects of rainfall.....	11
Long term experiments.....	11
Short term experiments.....	19
Discussion.....	21
The effects of grazing.....	23
Long term experiments: rainfall variability and grazing.....	23
Long term experiments: grazing alone.....	27
Short term experiments: rainfall variability and grazing.....	32
Short term experiments: grazing alone.....	36
Discussion.....	41
The effects of fire.....	44
Long term experiments: rainfall variability and fire.....	44
Long term experiments: fire only.....	46
Experiments including fire as a treatment.....	47
Discussion.....	49
The effects of fertilization.....	50
Discussion.....	53
The effects of ripping and reseeding.....	54
Effects of ripping.....	54
Effects of reseeding.....	56
Discussion.....	57
TRENDS IN HERBACEOUS YIELD AND BASAL COVER.....	59
The effects of rainfall.....	59
The influence of soil type.....	59
The influence of the woody component.....	62
The effects of grazing.....	64
Experiments.....	64
Discussion.....	67
The effects of fire.....	67
Frequency of burning.....	68
Season of burning.....	68
Type and intensity of fire.....	69
Discussion.....	69

The effects of fertilization.....	69
TRENDS IN SOIL VARIABLES.....	71
Soil moisture, infiltration and run-off.....	71
Soil loss and soil physical properties.....	73
Soil chemical properties.....	74
The influence of rainfall.....	74
The influence of grazing.....	74
The influence of fire.....	75
The influence of fertilization.....	78
The influence of the woody component.....	79
Discussion.....	81
GENERAL DISCUSSION.....	82
Determinants of herbaceous trends.....	82
Mechanisms of compositional trends.....	83
System dynamics: the effects of stress levels of determinants.....	87
Case studies of system change.....	89
System dynamics: concepts and key hypotheses.....	91
An approach toward predicting system response to stress.....	91
REFERENCES.....	94
APPENDICES.....	111
RECENT TITLES IN THIS SERIES.....	120

INTRODUCTION

The overall objective of this study is to review all long term experimental work which has been undertaken in the savanna regions of southern Africa, to synthesize the results and to develop an account of the understanding they have given of the determinants of savanna dynamics. The principal determinants considered are rainfall, soil type, herbivory and fire. The variables of interest are the composition and production of the herbaceous component, and the physico-chemical properties of the soil.

The following set of key questions were posed with respect to the herbaceous component:

1. What is the influence of rainfall, herbivory and fire on the trends in the variables of interest (composition, production and soil properties)?
2. What is the response of these variables to stress levels of these determinants ? Alternatively, what are the conditions associated with significant changes in these variables?
3. What is the long term dynamic behaviour of these variables with respect to stress levels of determinants ?
4. For questions 1, 2 and 3, how does soil type and component structure (principally the woody/grass ratio) mediate the response of the above state variables ?

With respect to long term dynamic behaviour, the aim was to examine systems which had been stressed and then left to recover, or systems which had been continuously stressed , and to detect whether such systems (from examination of individual species response) had exceeded their limits of resilience, and a) lost any components and established a new system, or b) crossed a threshold and moved to a new equilibrium (sensu Holling 1973). A third dynamic aspect considered was whether the system would display any non-linear effects (eg hysteresis) in the pattern of change when stressed and then when released from stress.

This empirical catalogue therefore seeks to identify dynamical patterns, but as with any set of empirical data, does not suppose to elucidate the processes underlying the perceived patterns.

The above set of questions were chosen because future utilisation of the savanna grazing resource requires knowledge suitable for predicting the effects of stress levels of determinants on the stability and resilience of savanna grasslands. The present study will identify what has been accomplished toward this end, and what are the remaining gaps. Such a synthesis would therefore provide a basis for the direction of future research.

GENERAL APPROACH

Sources of data

The region in southern Africa delimited as savanna is described by Huntley (1982). The following research bodies have undertaken long term research in this region: Agricultural and Technical Services of South Africa and South-West Africa (ATS), Animal Production and Research Unit of Botswana (APRU), Department of Research and Specialist Services of Zimbabwe, Natal Parks Board (NPB), National Parks Board of South Africa and various universities. The ATS research stations include Armoedsvlakte, Dohne, Estcourt, Koopmansfontein, Mara, Messina, Omatjenne and Towoomba. The NPB parks include the Hluhluwe/Umfolozzi Complex, Mkuze and Ndumu Game Reserves. The National Parks considered are the Kruger (KNP) and the Kalahari Gemsbok (KGNP). The Zimbabwe agricultural research stations include Grasslands (Marondera), Matopos, Nyamandhlovu, Nuanetsi and Tuli.

Connell and Sousa (1983) suggest an appropriate measure for long term experiments: the responses of the populations of a community must be judged according to the minimum time period of at least one complete turnover of all individuals. This synthesis indicates that few perennial grasses live in excess of 10 years, and the half life of most populations is well below this (Table 10). Therefore long term experiments are arbitrarily defined as greater than 10 years duration.

Long term experimental work relating to grazing, exclusion, bush clearing, fire, fertilization and reclamation (ripping and reseeding), together with long term monitoring sets relating to the above mentioned variables, are reviewed. Shorter term experiments have been incorporated when appropriate to the key questions considered.

In addition, information has been drawn from the savanna regions of East and West Africa, and from the non-savanna regions of southern Africa, where these are felt to highlight certain points. However, the research and review of this secondary data base is not as extensive as that of the savanna regions of southern Africa.

Evaluation of data

Each experiment reviewed was defined in terms of its experimental variables (determinants) and state variables, in addition noting the soil type and rainfall regime. The experiments were evaluated for

1. whether stress (or extreme) levels of determinants had been induced, and for what duration;
2. whether significant or critical changes had taken place in the state variables;
3. what the nature of these changes had been,

4. at what rate they had occurred, and
5. whether the changes had been reversible or not.

Each experiment was therefore examined for the variability and dynamics of the state variables of interest, and how these related to the influence of a single, or a set of, determinants. It has been necessary to describe the experiments in some detail, because the original presentation of results was not generally in a form suitable for direct reference. The data base evaluated is summarised in Appendix 1, in which each study is assigned a reference number, and which includes data on the locality and soil type of each experiment. For ease of reference, long term rainfall records for some of the more important stations are provided in Appendix 2 (referred to in text as Table A2).

DEFINITIONS AND CONCEPTS

For ease of later discussion, some elementary concepts are briefly discussed below.

Description of a system

A system is described at any one time by the amounts of the state variables representing that system. State variables can be abiotic or biotic. The abiotic state variables of interest are the soil physical and chemical properties, including soil moisture. Rainfall is an indirect estimate of soil moisture. The biotic state variables of interest are the components of the herbaceous layer. The smallest unit used to describe these components is generally a species, but species may be extended (by the original researcher) to form functional groups (eg perennial grasses). The dynamics of these components can be described by a number of attributes, including production, a size index (eg basal area), or population parameters. Production can be considered as a functional variable of the total herbaceous layer (eg MacNaughton 1979). Associated problems of production terminology have been discussed by Grossmann (1982).

Determinants of a system

The response of a biotic state variable to the effects of herbivory or fire needs to be assessed in relation to rainfall and soil type. Some relevant characteristics of rainfall and soil type are therefore briefly discussed below.

Rainfall

The amount of soil water available to plants for growth is principally determined by the rainfall. The total mean annual rainfall shows a broad relationship to the vegetation formations in southern Africa (Huntley 1982). Savanna systems in southern Africa lie within the 300 to 800 mm mean annual rainfall zone. These systems are further characterised by a large inter- and intra-seasonal variation in rainfall. Inter-seasonal variation in rainfall increases with decreasing mean annual rainfall, with a range in the coefficient of variation from around 10% at 1000 mm to >40% at 350 mm. There is evidence for a cyclical long term pattern of the summer rainfall region of South Africa, with a quasi-periodicity of 18 years (Tyson and Dyer 1978), and a similar pattern appears to exist in Zimbabwe (Ngara, McNaughton and Lineham 1983). The cycle consists of a nine year wet period in which the majority of years have above average rainfall, followed by a nine year dry period. Tyson and Dyer (op cit) required a regional analysis to elicit the 18 year cycle. Of greater importance for plant dynamics is whether such cycles occur on a point

scale. However no extensive analysis of single site records has been made, but the regional analysis of the KNP (Gertenbach 1980) indicates a similar pattern. Irrespective of whether true cycles take place or not, runs of wet or dry years occur with a higher than expected probability in savanna systems (MacDonald 1982).

Intra-seasonal variation in rainfall decreases with increasing mean annual rainfall, and the occurrence of mid-season droughts becomes less common. The effect of storm size and intensity compounds the effect of seasonal rainfall distribution on soil water recharge. The proportion of water infiltrating the soil and that lost to runoff is directly related to storm size and intensity.

Soil characteristics

Soil as a medium for plant growth principally affects the supply of water and nutrients to the plant. The soil water regime is determined by four factors other than the pattern and amount of rainfall; infiltration, percolation, root extraction and evaporation. Soil type exerts a marked influence on these factors. The distinction between coarser textured sandy soils and finer textured soils with a higher clay content is of particular ecological consequence. The sandier soils allow rapid infiltration and percolation through the profile and minimise evaporation through the soil surface. Although sandy soils have potentially a lower water holding capacity than clay enriched soils, most of the moisture that is present is available to plants. Sandy soils also show less fluctuation in plant available moisture between seasons because they maintain higher proportions of residual moisture than clay enriched soils. The development of caps on clay soils can markedly influence the rate of infiltration (Kelly and Walker 1976), and subsequent soil hydrology dynamics.

Soil nutrient content is primarily a function of soil parent material, the cation exchange capacity of the soil and the amount of leaching which occurs. A major ecological distinction, for a given rainfall regime, is between dystrophic sandy soils and eutrophic clay soils (Bell 1982).

Herbivory and fire

The majority of long term experimental work on the effects of grazing has been derived from man-managed pastoral systems. The concepts and terminology pertaining to grazing and grazing management are used as defined by Booysen (1967). Similar use is made of Trollope's (1981) terms, definitions and units of fire ecology.

SHORTCOMINGS OF THE DATA BASE

Intensity of sampling

The 72 experiments considered in this review are listed in Table A1. The list does not include a number of earlier experiments which were described in general terms, and which were of no value to the present synthesis. Table A1 provides the following summarised information for each experiment: the nature of the experiment, locality and soil type, duration, variables monitored, and the number of censuses for each variable. A number of the experiments listed (studies 1, 3, 15, 18, 22, 24, 27, 28, 43, 48, 49, 60, 61, 65) consist of a set of identical experiments conducted in different regions, or on different soil types in the same region; to provide a total of 126 discrete experiments.

The breakdown for the duration of the 126 experiments is shown in Figure 1. Only 44 of the experiments involve a time span greater than 10 years. The attention received by the different variables in these experiments is shown in Table 1. The order of variables in terms of experimental input, judged by both the number of experiments and the sum of years of experiments, is herbaceous composition, total basal cover, yield, soil properties and plant density. These variables differ in the intensity of sampling they have received (Table 1). Yield has generally been sampled

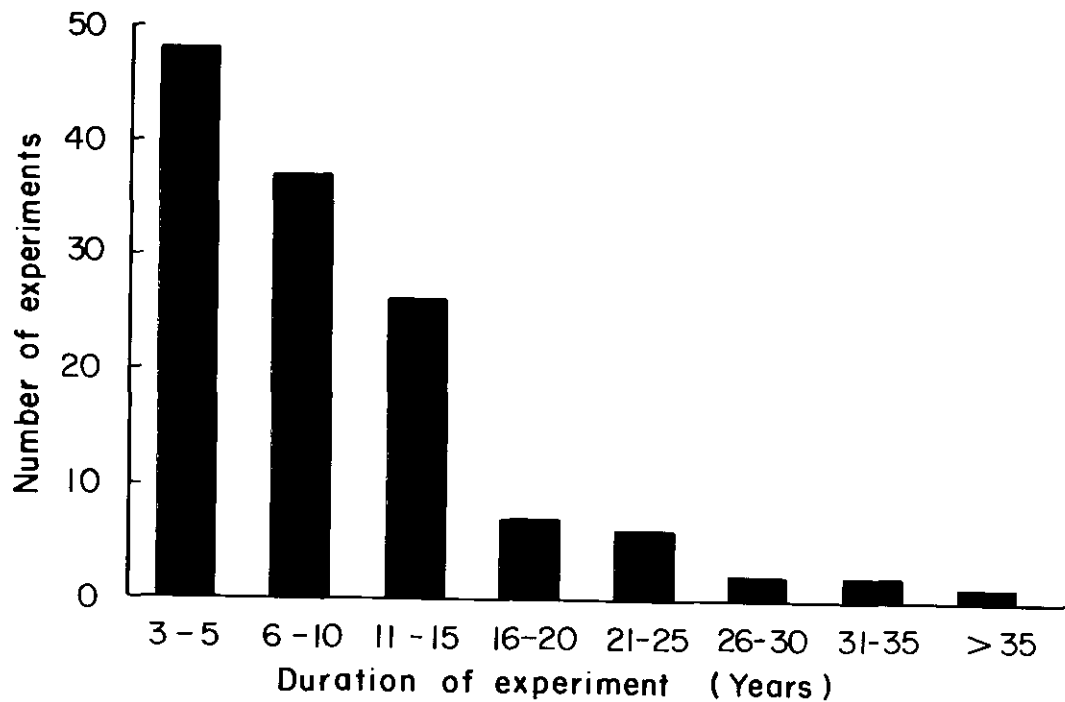


Figure 1. The duration of field experiments concerning the grass layer in the savanna regions of southern Africa.

Table 1. The intensity of long-term experimental input into variables of the grass layer and soils of southern African savannas.

	Number of experiments for each frequency of sampling (greater than 10 years duration)								Sum total number of experimental years		Years per census	
	1	2	3	4	5	>5	>5 as % of total	All experiments	Experiments > 10 years	All experiments	Experiments > 10 years	
Herbaceous composition	9	8	4	2	0	15	39	38	1 057	725	2,69	3,70
Total basal cover	6	6	2	2	2	9	27	33	721	533	2,57	3,86
Yield	1	0	0	0	0	6	7	86	283	130	1,33	1,11
Plant density	2	1	0	0	0	0	3	0	111	77	3,47	11,00
Soil properties	4	1	0	0	0	0	5	0	177	114	7,08	19,00

on an annual basis. Herbaceous composition and total basal cover show a similar proportion of frequently sampled long term data sets (35 and 30% respectively), and both variables are sampled on average every 3,5 to 4 years in long term experiments. In contrast plant density and soil properties are usually sampled only once in long term experiments.

A low intensity of sampling poses the following problems for interpretation. Experiments without baseline data assume homogeneous baseline conditions over all treatments at the commencement of the trial. Experiments sampled at their termination have only the differences between treatments and control to indicate the effect of treatments. However, differences between treatments detected at the end of the trial may on occasions be ascribed to factors other than the treatments. For example, the trends in herbaceous composition in the KNP fire trials are the result of an interaction between soil type, fire and grazing (Trollope 1984), and unfortunately these interactions were not taken into account in the experimental design. Controls (no treatment applied) are a misnomer because they are subject to extraneous influences. Savanna ecosystems have evolved with grazing and fire as agents of natural selection. Controls which exclude these agents are in effect a treatment, and often result in more marked changes than the treatments being investigated (egs studies 27, 48, 49, 52). These experiments report that perennial tufts develop a moribund condition, and subsequently die, with a sustained absence of defoliation. Controls cannot therefore be used to evaluate whether treatments have caused a significant change in experiments which are sampled at their termination only. Such experiments further provide no information on dynamic trends. Similarly, experiments which are sampled both at the beginning and the end cannot be used to evaluate the rate or variability of changes, although they do indicate whether significant changes have taken place.

The behaviour of a system can only be documented with an increased intensity of sampling. The intensity with which a state variable is sampled should ideally be related to the time span within which the variable can show a marked change, and therefore would intuitively be different for the herbaceous, woody and soil components. The herbaceous component can undergo marked changes in composition and production between two seasons, and should ideally be sampled on an annual basis. Unfortunately very few studies have attained this ideal.

Time of sampling

Total basal cover or basal cover of various components has been one of the most widely used indices for detecting long term changes. Total basal cover in a Pretoria grassland showed a statistically significant seasonal increase through summer and a corresponding decrease as rainfall began to decrease (Morris and Muller 1970). The seasonal changes in basal cover were the result of small changes in the basal cover of many species. In a seven year extension of this study the basal cover of an untreated control varied significantly on a seasonal basis in relation to rainfall (Le Roux and Morris 1977). The seasonal behaviour of basal cover illustrates that uniformity in the season of sampling is a strict prerequisite for the use of this index in experimental evaluation. Similarly, basal cover can show an immediate response to the resting of

veld (Edwards and Nel 1973), with obvious implications for experimental design and interpretation of results with experiments involving grazing or resting. The use of standing crop as an index would require similar considerations. A number of the long term trials had not made these considerations, thereby obscuring the trends in state variables of interest.

Uniformity in the time of sampling is also required on a longer time scale, particularly in experiments which have a low sampling intensity. Climatic conditions for two comparative sets of data need to be approximately equivalent because of the extreme effect of rainfall on all biotic state variables (this synthesis). A large proportion of the longer term experiments, particularly those only sampled twice, had been initiated and terminated in different rainfall periods, thereby obscuring treatment effects (studies 3, 16, 26, 27, 28, 31, 32, 36, 40, 41, 42, 43, 44, 48, 49, 65).

Inadequate presentation of published data

Functional species groups

Species composition data are often presented as groups of species rather than as individual species. Common groups are perennials, annuals and other seed plants; or climax, sub-climax and pioneer grasses; or tribes of grasses. It is suggested that such groups have little ecological meaning, or that such data are inferior to data pertaining to individual species. A tribe or group may contain ecologically very dissimilar species, for example palatable and unpalatable species (Themeda and Cymbopogon), or shade tolerant and shade inhibited species. There is a further implicit assumption when grouping species and then evaluating long term trends that the grouped species share similar demographic properties. There is limited information on the life history characteristics of any of the perennial species of southern Africa. Similarly the use of successional categories presupposes firstly that succession is a valid and applicable concept, and secondly that the process is well documented for the ecosystems to which it is applied. The first supposition is rejected because succession is still a theory requiring extensive testing (Connell and Slatyer 1977), and in southern Africa the second supposition has only been accomplished by fitting existing facts to a theory. It is therefore suggested that future published work should firstly present data pertaining to individual species.

Mensuration

Basal cover is one of the most commonly used indices for monitoring both compositional and functional trends of the grass sward. Mentis (1982) provides a detailed analysis of the theoretical and sampling problems associated with this index, and concludes basal cover is an inadequate

means of assessing herbaceous trends. It is an index which is subject to significant operator bias (Walker 1970), and this can therefore result in a Type 1 error in which significant changes are detected when they have not occurred, as has been admitted in some experiments (study 48). Basal cover is a poor means of assessing composition because of the large number of point samples needed, particularly in savanna types which are generally characterised by low basal cover. Species trends in diverse swards are further obscured because of the proportionately low number of samples of the less frequent species. The trends of individual species reported in the literature have also been obscured by presenting each species as a percentage of the total basal cover without detailing total basal cover. Such data do not reveal whether changes of a species percentage of total basal cover are primarily a result of changes in the basal cover of that species or of the rest of the sward.

Trends of herbaceous yield or basal cover are characteristically highly variable, but data pertaining to these trends are often presented as means without any measure of variability.

THE EFFECTS OF DETERMINANTS ON STATE VARIABLES

For ease of presentation the information concerning each variable is presented singly according to each determinant.

TRENDS IN HERBACEOUS COMPOSITION

This sections examines the influence of rainfall, grazing, fire, fertilization, ripping and reseeding on changes in composition. Compositional changes are a summation of the population changes of the component species, although species populations are usually indirectly estimated through basal cover or contribution to biomass, rather than directly estimated through changes in density.

The effects of rainfall

No studies were found which had experimentally manipulated the rainfall regime over a number of years. The data sets used to evaluate the effects of rainfall alone on trends in herbaceous composition include exclusion plots, bush clearing experiments, and controls of other experiments. Long term experiments and short term experiments are considered separately. The studies in each section are individually described in approximate accordance with a rainfall regime gradient from semi-arid to mesic savannas.

Long term experiments

1. Messina successional study

Secondary succession on formerly overgrazed areas in the mopane veld of the northern Transvaal was followed for 20 years (study 18). The experiment was initiated in 1964 at the height of the 1960's drought, and continued through a complete rainfall cycle until 1983 (Table A2). The perennial grass component of three sites was closely dependent on total annual rainfall over 20 years, irrespective of soil type (Figure 2). It was absent in 1964 and became established from 1970/71 onwards, the season which marked the beginning of a number of wet years. It was maintained throughout the wetter 1970's until 1981, but by 1983 had disappeared or considerably decreased. The wet 1966/67 season also produced perennials, which subsequently disappeared again until 1970/71. The same pattern occurred on 3 (of 4) other sites which were monitored from 1970. The major perennial grass species to appear were Brachiaria nigropedata, Bothriochloa sp, Digitaria eriantha, Enteropogon simplex, Eragrostis lehmanniana, Cenchrus ciliaris, Panicum maximum, Schmidtia pappophoroides, Stipagrostis uniplumis and Urochloa mosambicensis.

Soil type notably influenced the amount of perennial grass appearing during the wetter years. Perennial basal cover (total basal cover in parentheses) during the 1970's peaked at 1,9 (3,8), 1,3 (5,3) and 2,2% (3,3%) for a deep Portsmouth series, a gravelly red loam and an undescribed soil type, respectively. In contrast the maximum perennial cover during the same period on shallow soils of the Shorrocks series (with granite present), a gravelly shallow soil of the Mispah series, very sandy ground and a dark brown sandy loam was 0,3 (2,5), 0,1 (1,7), 0,3 (0,9) and 0,1% (2,9%) respectively. On all sites annual grasses, principally *Aristida adscensionis*, *Enneapogon cenchroides* and *Tragus berteronianus*, were the predominant components of the remainder of the sward. The annual grasses showed a pronounced variation in relation to annual rainfall, for example from 0 to 3,8% basal cover. Six of the seven sites also showed a notable increase in woody cover of mopane (*Colophospermum mopane*).

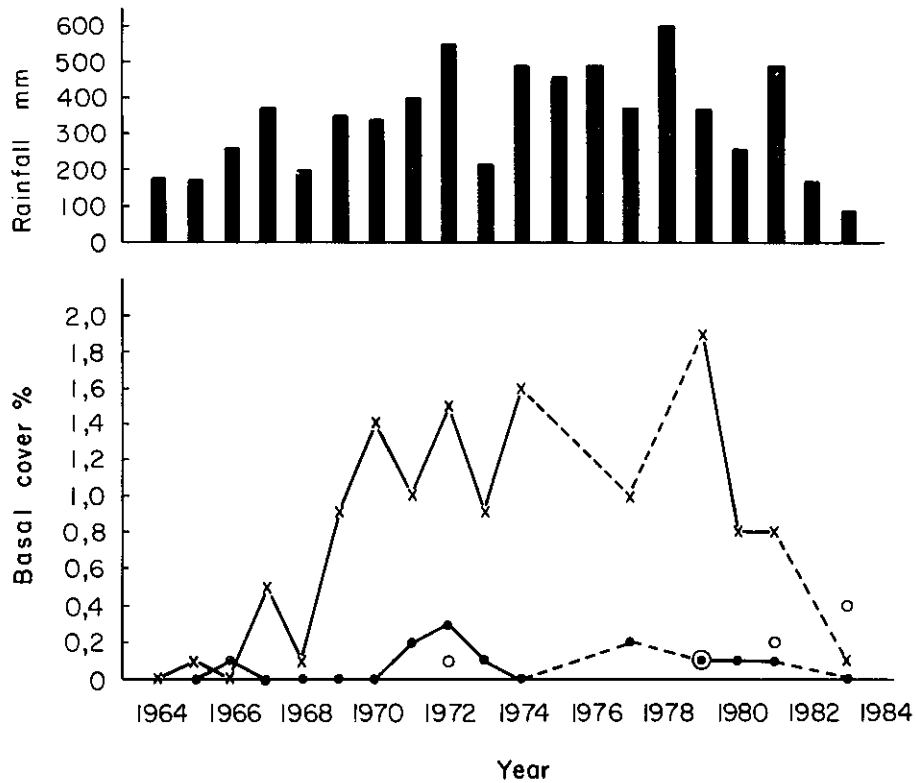


Figure 2. Trends in the percentage basal cover of perennial grasses on three soil types at Messina experimental station. Deep and fertile Portsmouth series (x—x); shallow Shorrocks series with granite present on surface (o—o); shallow gravel soil of Mispah series (o). Dotted lines indicate that data for the intervening years were not available. (Data from Donaldson, Rootman and van der Merwe 1983)

2. Tuli bush clearing trial

Similar trends in composition occurred in the semi-arid Tuli lowveld of Zimbabwe (study 1; Table 2). During the wetter years between 1967/68 and 1977/78 (Table A2) there was an increase in Digitaria pentzii and Eragrostis rigidior on bushed plots, and in Schmidtia pappophoroides on cleared plots, at the expense of Aristida barbicollis. Annuals comprised a relatively constant proportion of the sward on bushed plots, irrespective of rainfall.

3. West Transvaal bush clearing trial

The basal cover of the Mixed thornveld of the Crocodile river valley in the western Transvaal declined from 14 to practically 0% between 1954 and 1967 (study 20; Figure 3), as a result of the severe drought between 1962 and 1966 (Table A2). Subsequent rainfall in the region until 1969/70 was average, but all seasons between 1970/71 and 1979/80 were well above average or at least average except for 1979/80 (Table A2). A bush clearing experiment was undertaken between 1970 and 1980 on a farm in close proximity to the one van Wyk (1967) had monitored (study 2). In 1970/71 the sward had a total basal cover of 3,8%, and was dominated by Aristida congesta subsp barbicollis (1,53% cover) and Eragrostis rigidior (0,8% cover). Subsequently bush clearing treatments were implemented. Total basal cover increased dramatically to 27% (over all treatments) in 1979/80, and the sward was dominated by Eragrostis rigidior (8,07% cover), Panicum maximum (5,87% cover), P coloratum (5,68% cover), Digitaria eriantha (3,68% cover) and Schmidtia pappophoroides (1,87% cover).

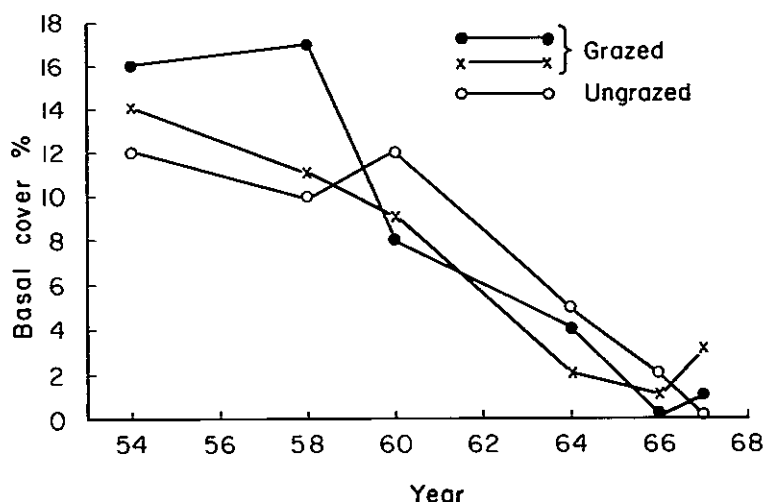


Figure 3. Changes in the percentage basal cover over 14 years in the mixed thornveld, West Transvaal. (Data from van Wyk 1967)

Table 2. Percentage contribution of species to mean grass yields from cleared and bushed plots.

Matopos thornveld

Year	71/72	72/73	73/74	74/75	75/76	76/77	77/78	78/79	79/80	80/81
Rainfall mm	771	302	935	949	707	785	995	611	559	674

Bushed

Annual spp	18,7	0,5	10,2	18,5	2,0	0,4	0,1	0,0	0,9	4,0
Eragrostis trichophora	25,0	13,6	18,3	9,1	6,9	7,6	6,0	2,1	3,3	2,4
Heteropogon contortus	1,2	5,5	3,4	4,7	6,9	9,0	6,7	9,0	10,6	9,9
Panicum maximum	51,2	73,0	62,6	60,9	81,9	80,4	81,0	86,2	82,2	82,6

Cleared

Annual spp	47,7	1,5	19,6	30,7	10,1	0,5	0,0	0,1	2,0	21,7
Heteropogon contortus	3,5	11,0	13,1	20,7	45,1	55,7	55,4	74,6	70,2	69,6
Urochloa mosambicensis	39,1	70,7	50,7	33,0	34,2	30,6	21,6	11,6	16,6	1,1

Matopos sandveld

Year	71/72	72/73	73/74	74/75	75/76	76/77	77/78	78/79	79/80	80/81
Rainfall mm	733	330	1032	888	802	722	1091	379	508	801

Bushed

Digitaria pentzii	15,9	22,1	45,4	40,6	36,2	24,1	14,5	9,9	14,8	15,8
Heteropogon contortus	16,5	23,3	15,6	8,8	7,5	6,8	5,0	7,6	4,8	5,8
Panicum maximum	6,2	4,4	6,1	5,4	3,8	8,4	6,7	8,6	8,3	8,3
Schizachyrium jeffreysii	26,1	20,0	7,6	14,0	18,1	26,1	28,0	20,9	25,8	22,6
Trachypogon spicatus	10,6	10,9	8,7	17,0	15,7	17,8	27,4	32,8	28,7	30,7

Cleared

Brachiaria nigropedata	6,5	3,9	6,1	6,3	10,2	10,5	9,3	9,5	9,6	14,4
Digitaria pentzii	0,9	5,4	11,5	15,9	14,1	10,4	5,2	5,9	4,2	3,8
Eragrostis rigidior	15,9	11,1	16,4	10,6	7,5	7,4	5,1	5,6	5,6	6,3
Heteropogon contortus	9,3	9,1	7,0	2,1	2,6	5,2	3,6	7,1	8,7	11,0
Rhynchelytrum repens	11,1	9,2	10,7	5,4	4,2	5,5	3,9	3,5	2,0	3,3
Schizachyrium jeffreysii	24,4	20,3	12,7	15,2	21,1	20,8	19,8	15,2	20,7	19,3
Trachypogon spicatus	15,7	23,9	26,4	36,9	31,2	31,8	45,4	44,1	40,6	33,2

Table 2. Continued

Nyuzamandhlovu Sandveld

Year	68/69	69/70	70/71	71/72	72/73	73/74	74/75	75/76	76/77	77/78
Rainfall mm	739	414	427	590	377	822	683	673	647	1133

Bushed

<i>Aristida pilgeri</i>				8,4	8,0	7,3		5,3	7,0	4,5
<i>Digitaria pentzii</i>					15,1	20,0		23,3	22,4	20,4
<i>Eragrostis rigidior</i>					36,0	31,2		31,2	30,2	22,1
<i>Hyperthelia dissoluta</i>	4,9*	4,0	0,0	0,0	0,3	0,1	3,5	5,1	6,8	8,6
<i>Schizachyrium jeffreysii</i>	12,8*			7,3	11,9	8,4		11,2	17,8	20,1
<i>Schmidtia pappophoroides</i>					11,9	17,0		8,8	1,1	0,6

Cleared

<i>Aristida pilgeri</i>				27,0	19,7	19,9		16,2	20,5	18,8
<i>Digitaria pentzii</i>					15,0	15,4		8,9	10,3	7,3
<i>Eragrostis rigidior</i>					16,7	14,9		6,3	7,2	6,8
<i>Hyperthelia dissoluta</i>	24,5*	28,4	2,9*	0,1	1,3	0,3	1,9	8,1	9,3	9,8
<i>Schizachyrium jeffreysii</i>	17,0*			9,5	14,0	14,5		27,9	31,5	31,5
<i>Schmidtia pappophoroides</i>					19,6	26,0		13,0	4,4	4,9

Tuli Sandveld

Year	67/68	68/69	71/72	72/73	73/74	74/75	75/76	76/77	77/78
Rainfall mm	232	317	688	132	548	550	668	578	704

Bushed

Annual spp				7,9	11,2	7,6	8,4	9,2	10,7	9,0
<i>Aristida barbicollis</i>		15,0*		34,4	14,9	9,4	11,3	9,4	9,3	8,5
<i>Digitaria pentzii</i>				4,1	6,8	8,2	7,6	9,6	7,8	13,1
<i>Eragrostis rigidior</i>		6,6*		5,9	10,6	10,3	11,4	17,3	17,8	20,1
<i>Schmidtia pappophoroides</i>		11,2*		29,3	28,5	31,1	24,8	33,3	34,9	27,0
<i>Urochloa mosambicensis</i>				10,9	16,3	12,6	22,1	9,6	12,2	4,1

Cleared

<i>Aristida barbicollis</i>	41,7*	10,3*		7,5	1,5	4,3	6,6	3,3	5,3	5,2
<i>Eragrostis rigidior</i>	19,2*	27,5*		21,0	21,7	14,9	14,5	12,9	18,2	20,9
<i>Schmidtia pappophoroides</i>	14,4*	34,8*		65,6	70,5	72,1	69,5	77,4	69,0	63,1

* of fresh mass

Aristida congesta declined significantly (0,9%) in all treatments over the same period. The same trends were revealed by the relative density and frequency of the species.

The different bush clearing treatments had no significant effect on the number of individual plants in any of the four seasons sampled. The number of individual plants recorded in the 1970/71 and 1971/72 seasons were each significantly different to the number recorded in the 1976/77 and 1979/80 seasons, but each pair of years was not significantly different. These changes suggest that a sustained run of wet years in this region leads to a continuous change in both the structure (density) and composition of the sward, and these changes are not affected by the woody component. The woody component influenced which species occurred, for example Digitaria eriantha increased notably under cleared bushes. Soil structure influenced the degree of change. Half of the plots had soils with a higher clay content, and the average basal cover of these in 1979/80 was 31,3% as compared with 19,5% for the sandier soils. The plot with the highest clay content showed the highest increase in basal cover.

There were significant differences between species in the extent of increase in the number of individuals. Panicum coloratum and P maximum showed the largest increase (in the order of 1000), whilst Eragrostis spp, Digitaria eriantha and Schmidtia pappophoroides showed a decreasing extent of increase respectively. Aristida spp decreased markedly.

4. Matopos and Nyamandhlovu bush clearing trials

A set of bush clearing experiments were conducted at four sites in south western Zimbabwe (study 1). The pattern of rainfall of the Matopos and Nyamandhlovu sites was similar; all seasons between 1971/72 and 1979/80 experienced above average annual rainfall, except for 1972/73 and 1979/80 (Table A2). Rainfall was below average between 1961/62 and 1970/71, except for the 1968/69 season at Nyamandhlovu. The data set indicates the trends in herbaceous composition relating to a cumulative number of wet years following an extended dry period, and of the effect of a dry year interspersed among a run of wet years. The composition of the grass sward was monitored from 1971/72, some 8 years after the experiment had commenced. Recorded changes in composition are therefore considered to be due to rainfall and not to the effects of bush clearing.

The contribution of annual species to mean grass yield varied dramatically on the Matopos thornveld, from 0 to 19% and 0 to 48% on bushed and cleared plots respectively. The annual component was particularly prolific in wet years following a dry year (eg 1972), and subsequently decreased with a continued number of wet years, until virtually eliminated. These changes suggest that the annual component proliferates when the perennial component is temporarily weakened by drought. In contrast the annual component was insignificant on either bushed or cleared sandveld plots.

The perennial component of the Matopos thornveld showed marked shifts in the relative contribution of the dominant species to mean grass yield (Table 2). The wet 1970's resulted in an increased contribution to yield of Heteropogon contortus at the expense of Urochloa mosambicensis on the

cleared sites, and increases in H contortus and Panicum maximum and a decrease in Eragrostis trichophora on the bushed sites. E trichophora and U mosambicensis are considered xeric species in comparison to H contortus and P maximum (Dye and Spear 1982). The compositional shifts during the 1970's on the Matopos sandveld were less pronounced (Table 2). During this period the relative contribution to yield of Trachypogon spicatus gradually increased on both bushed and cleared plots, whilst H contortus gradually decreased on bushed plots, but was relatively stable on cleared plots. P maximum is associated with bushed plots and contribution to yield varied from 4 to 9%. Digitaria pentzii exhibited no consistent long term trend but increased notably in response to particularly high rainfall years.

On the Nyamandhlovu sandveld, the above average rainfall subsequent to 1974 resulted in an increase in the contribution to yield of the more mesic species Hyperthelia dissoluta and Schizachyrium jeffreysii, and a decrease in the more xeric species Schmidtia pappophoroides and Eragrostis rigidior on both bushed and cleared plots. Similar trends occurred at Nyamandhlovu between 1946 and 1950 (study 24). During this period the region experienced above average early rains and an accentuated January - February drought, with below average total annual rainfall. The effect of this drought on herbaceous composition was most marked on heavy black basaltic soils, intermediate on red sandy loams, and least on the Kalahari sands. The perennial cover of the basaltic soils was replaced by annual herbaceous forbs and annual grasses. On the red sandy loams H contortus and Themeda triandra were depleted whilst Tragus racemosus and Schmidtia pappophoroides increased. On the Kalahari sands there was a decrease of the late flowering perennials such as Hyparrhenia spp, Schizachyrium semiberbe, Trachypogon plumosus, Andropogon spp and Digitaria spp, whilst Pogonarthria squarrosa, Perotis indica, Rhynchelytrum repens, Aristida spp and Urochloa spp increased.

5. Towoomba fertilization trial and protected plot

Similar trends are evident on another mesic savanna site at the Towoomba research station, Transvaal. The composition of a control plot of a 30 year fertilizer trial (study 59) was monitored at five yearly intervals from 1955/56. The region experienced a pronounced drought during the 1960's and wetter eras during the 1950's and 1970's (Table A2). It was concluded that there was no significant correlation between rainfall and composition (Donaldson, Rootman and Grossmann 1984), but it is suggested that this conclusion is an artefact of species having been lumped into tribes. A relationship between rainfall and the basal cover of individual perennial species is suggested by the data, although correlations are non-significant. Cymbopogon plurinodis declined between 1955/56 and 1970/71 (40 to 10% of total basal cover) with increasing aridity, but returned to former levels during the wetter 1970's (overall $r = 0,5438$; 4df; $p > 0,05$). Heteropogon contortus and Themeda triandra displayed the reciprocal pattern, with Heteropogon increasing from 8 to 46% of total basal cover between 1955/56 and 1970/71, and subsequently decreasing (overall $r = -0,3182$; 4df; $p > 0,05$). The changes in Digitaria argyrograpta were not obviously related to rainfall. Monitoring covered a complete rainfall cycle (Table A2), with the initial and final samples taken during periods of similar climatic conditions. The composition of the plot in

1980/81 is very similar to the composition in 1955/56, although marked shifts in composition occurred in the interim. The only major change over 25 years was a significant increase in Heteropogon. Similar stability in composition at Towoomba was recorded in a plot protected for 31 years

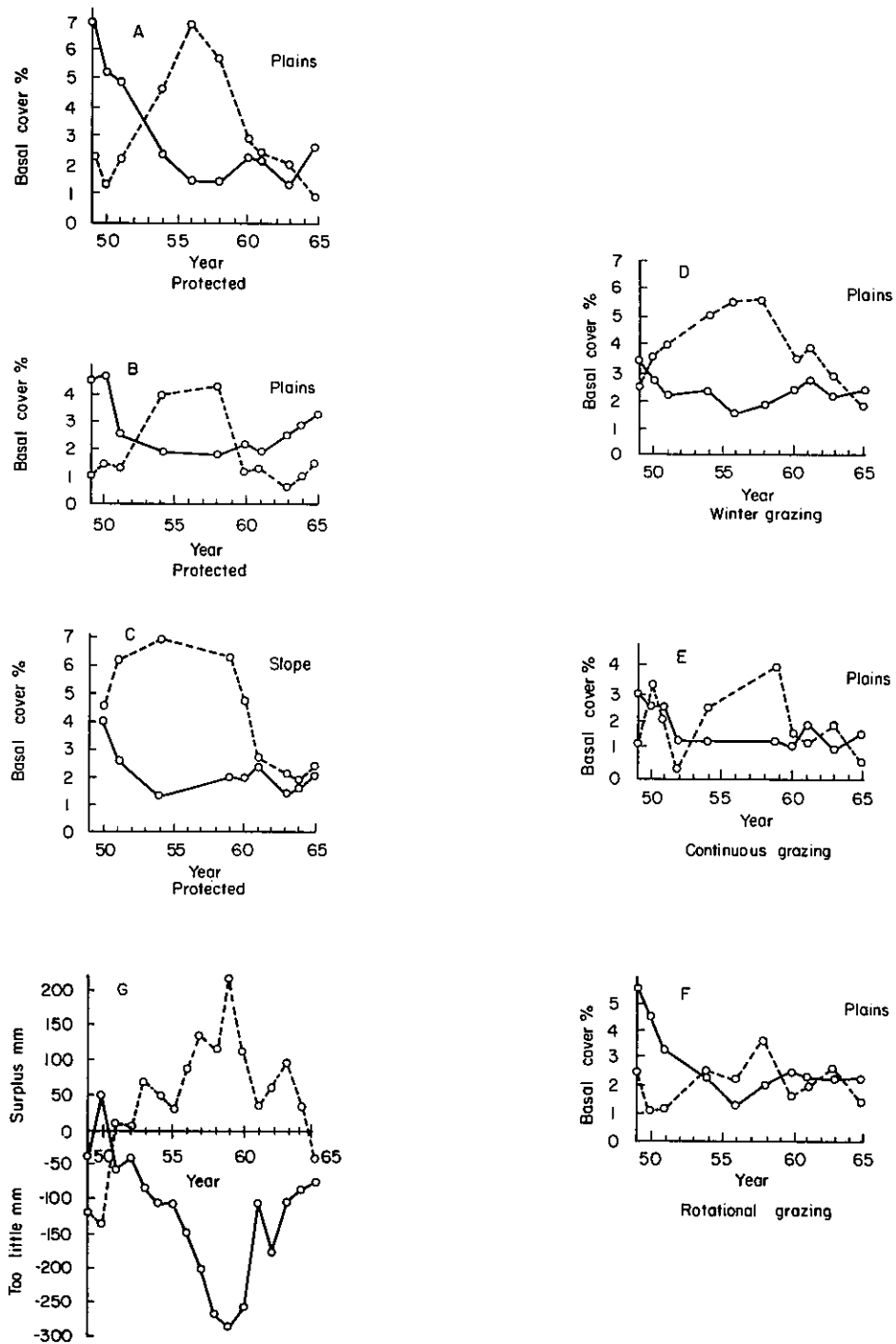


Figure 4. Changes in the percentage basal cover over 16 years of grass (o---o) and shrubs (o—o) in protected and grazed treatments (A to F) in the Karoo. Graph G indicates the accumulative deviation of the seasonal rainfall from the long term mean (mean September-February 216 mm (o---o); mean March-August 143 mm (o—o)).

(study 17). During this period the position of communities (which had been mapped) remained static, but the Enneapogon scoparius-Cenchrus ciliaris community increased in size by 20% at the expense of climax grassland. This change was probably due to the perennial tufts of the climax species becoming moribund.

6. Karoo grazing trial

The influence of long term patterns of rainfall on trends in composition has also been described for the semi-arid eastern mixed Karoo, which has an average rainfall of 400 mm. The vegetation of this region is principally composed of grass and shrubs. Eragrostis, Aristida, Cynodon and Tragus are the most important grasses, and Pentzia, Pteronia, Chrysocoma and Eriocephalum are the major shrubs. Grasses are favoured by spring and summer rains, falling between September and February, whilst shrubs are favoured by autumn and winter rains, falling between March and August. Roux (1966) reports on a 16 year grazing trial which included protected plots. The trial commenced in 1949, and "grass rains" became more favourable from 1950 till 1959, and then "shrub rains" were more favourable from 1960. Significant fluctuations occurred over this 16 year period in the basal cover of grass and bush (Figure 4), which were a result of seasonal rainfall (Roux 1966). The fluctuations in the basal cover of grass and bush were between 1 and 4% and 1 and 7%, respectively.

Short term experiments

1. Bush clearing trials: Namibia and northern Cape

Two sites of a six year bush clearing experiment in Namibia (study 3) experienced two years of severe drought before final monitoring in 1960, and a third site experienced only one year of drought before final monitoring. There was a dramatic decrease in the basal cover of all compositional groups (annual grasses, perennial grasses, other seed plants) and total basal cover on the first two sites after two years of drought, irrespective of treatment. This effect did not occur on cleared treatments of the third site, and most treatments showed an increase in the basal cover of all compositional groups and of total basal cover. The bush component exerted a significant effect; significantly more perennial grasses died in the uncleared than the cleared plots, and more grasses died in the area of thickest Acacia mellifera (the dominant woody species). The influence of the woody component on the survival of perennial grasses in semi-arid regions during drought years has also been described for the Molopo area of the northern Cape (Donaldson 1967). The mortality of perennial grasses in this area as a result of the 1964/66 drought differed between cleared and bushed plots (Acacia mellifera) by 10 to 80% respectively. In a subsequent bush clearing trial in the northern Cape commencing in 1982, grass density increased by between 73 and 136% within 22 to 25 months after applying Tebuthiuron, mainly due to increased density of Eragrostis lehmanniana (Moore, van Niekerk and

Knight 1985). The rainfall of the two seasons of this study were on average 22% below the long term mean.

2. Range monitoring: Botswana and Nylsvley

The marked effects of a drought year are further illustrated by the results of the range monitoring programme of Botswana (study 22). Eight of nine countrywide sites experienced a dry year between 1975 and 1980, usually the 1978/79 season. The major perennial species of all eight sites, irrespective of soil type or grazing regime, showed a conspicuous response to the advent of a dry year. Notable changes on the sandier soils were the marked decrease of Antheophora pubescens and the increase of Digitaria spp. A similar response to a drought year during a wetter period has been recorded for the Burkea savanna of Nylsvley (study 21). Three different sites within this vegetation type showed a slight to marked decrease in total basal cover attributable to the low rainfall of the 1978/79 season. The decrease in total cover was accompanied by a decrease in the cover of Rhynchelytrum villosum, Themeda triandra, Elionurus muticus, Panicum maximum and Setaria perennis, and an increase in the cover of forbs.

3. Matopos growth study

Grass shoot yields of an ungrazed area on siallitic red soils of Matopos were regularly recorded over five years, in order to observe patterns of growth in relation to the erratic rainfall characteristic of the region (study 23). The growth of the three dominant species (and total grass yield) differed in relation to the pattern of availability of soil moisture in the summer growing season. Heteropogon contortus displayed an opportunistic "stop-start" pattern of growth to cope with the unpredictable availability of soil moisture. Cymbopogon popischilii (C plurinodis) displayed a primary growth phase little affected by low levels of soil moisture, followed by a quiescent phase regardless of adequate soil moisture, and finally a further shoot growth phase if soil moisture was sufficient for growth. The pattern of development of this species was remarkably independent of the different weather conditions. Themeda triandra showed a similar sequence of growth to C popischilii, except that there was more scope for secondary growth following the quiescent period. From these differential patterns it was concluded (Dye 1985) that the timing of rainfall within a growing season could confer advantage to one or other species, which would account for observed differences in the proportion of species from year to year.

4. Degraded areas

Two areas of formerly different grazing history, one previously heavily grazed and one previously moderately grazed, were irrigated during a drought year (with no irrigation controls), and the effect on the

perennial component recorded (McKay 1968). On the site formerly moderately grazed, irrigation resulted in a significant improvement (of 28% by mass) of the perennial component, involving species such as Brachiaria nigropedata, Digitaria sp, Eragrostis rigidior and Schmidtia pappophoroides. Irrigation caused no improvement in the perennial component on the area formerly heavily grazed, although the annual Tragus racemosus increased markedly. This experiment was conducted at Morale in Botswana, on a heavier textured non-calcareous loam. The Matopos thornveld developed a mosaic of poor and good patches as a result of selective overgrazing (MacDonald 1978). These patches supported a different species composition, and responded differently to rainfall. Degraded patches accentuated the instability of the low rainfall years, because of their infiltration and run-off characteristics.

Discussion

The eight long term studies indicate that longer term patterns of rainfall cause an associated pattern of change in herbaceous composition. A continued run of wet or dry years generates a continued, if small, cumulative change in the composition of the sward. Cumulative compositional changes are overridden by the influence of a singularly dry or wet year. These patterns of change are most pronounced at the drier end of the savanna spectrum. In marginal semi-arid areas such as Messina the existence, let alone the composition, of the perennial component is directly dependent on the mean annual rainfall. This suggests that a mean annual rainfall equivalent to that experienced during the drier years at Messina, and on heavy textured soils with mopane, approaches the lower limit at which most perennial grasses can survive. In the more mesic savanna areas such as Matopos and Towoomba, rainfall variation causes compositional shifts, but not the elimination of the major components of the sward. These compositional changes are a result of perennial tuft mortality. Tuft mortality has not been investigated during average or above average rainfall conditions, but sparse data is available for mortality during drought years. Fourie and Roberts (1977) record that 90% of Eragrostis lehmanniana died during the 1972 midsummer drought in the northern Cape. Scholes (1984) monitored tuft mortality in the Klaserie Private Nature Reserve, Transvaal (mean annual rainfall 480 mm) during the 1982/3 season (219 mm), which followed the 1981/2 drought season (279 mm). Percentage mortalities in excess of 70%, and as high as 97%, were recorded for the dominant palatable species Panicum maximum, P coloratum, Digitaria eriantha and Schmidtia pappophoroides. The aromatic unpalatable Bothriochloa radicans experienced only 7% mortality. Mortality was increased by increased grazing intensity, increased clay content of the soils, and higher tree densities. In an intensive study of individually marked tillers in the False thornveld of the eastern Cape, 40% of tillers of Sporobolus fimbriatus senesced prematurely on an irrigated treatment as opposed to 94% of the tillers on a control treatment during a relatively dry year (Danckwerts, Aucamp and Du Toit 1985). In a similar experiment at the same general locality, 70 and 90% of the irrigated and non-irrigated tillers respectively of Themeda triandra senesced prematurely after one year (Danckwerts, Aucamp and Du Toit 1984).

Soil type has a pronounced influence on the patterns of compositional change. Trends are accentuated on heavier textured than sandier soils, but this is dependent on the general climatic regime. In the semi-arid mopaneveld of the northern Transvaal, drought causes an almost complete elimination of the perennial component, irrespective of soil type. However, the influence of soil type is apparent in the extent of response during the wetter years, with far higher levels of perennial species attained on the heavier textured soils (study 18). The relative compositional instability of the heavy textured as opposed to the sandy soils is apparent in less semi-arid and mesic savannas (studies 1, 2).

The influence of the woody component on the extent of compositional change can vary. The survival of perennial species on heavier textured soils in semi-arid regions during drought years is dependent on the extent of woody encroachment (study 3, Donaldson 1967). The woody component influenced the extent of compositional change on the Matopos sandveld, but not the thornveld, during the wet 1970's (study 1); but did not significantly affect the herbaceous trends of a semi-arid site in the western Transvaal during this period (study 2). Long term changes in the woody component can be expected to induce a corresponding change in herbaceous composition, because of the relation between a number of grass species and canopy cover (eg Panicum maximum - Bosch and van Wyk 1970, Kennard and Walker 1973, Theron, Morris and van Rooyen 1984).

The former grazing history of a site can further influence the effect of rainfall on compositional trends of heavier textured soils (MacDonald 1978, McKay 1968). In both these studies the perennial component was far slower to respond to increased rainfall, probably due to an increased xeric soil environment resulting from reduced infiltration.

Different perennial species at any one locality respond very differently to a given pattern of rainfall change. The response of an individual species to a specified climatic regime is also dependent on soil type, for example Heteropogon contortus increased on the Matopos thornveld but decreased on the sandveld during the wet 1970's (study 1). Fourie and Roberts (1977) also recorded significantly different yields on limeveld and dolomiteveld of a host of species (including Eragrostis lehmanniana and Themeda triandra) for three stages in the growing season. Similarly, the same species in two different localities may show a different response to the same pattern of climatic change, for example Eragrostis rigidior increased prolifically in the semi-arid western Transvaal during the wet 1970's (study 2) but decreased in the more mesic Matopos area over the same period (study 1), although a similar soil type was involved. MacDonald (1982) provides an intensive analysis of the rainfall induced changes of some individual species.

MacDonald (1982) prefers an explanation of the factors controlling the preponderance of forbs and annual grasses in the sward, which concurs with the experiments described above. During a period of below average rainfall bare patches develop as a result of mortality of perennial tufts. In the first high rainfall season following such a dry period the bare patches are invaded by annual grasses and forbs, and also by pioneer perennial grasses adapted to bare ground. In subsequent seasons of above average or average rainfall the proportions of forbs and annual grasses decrease as perennial grasses assume dominance. Additional evidence for this pattern in forbs is described by MacDonald (op cit) for the Hluhluwe-Umfolozzi monitoring from 1977/78 to 1981/82, over a variety of

vegetation types. MacDonald's explanation is applicable principally to heavy textured soils of mesic savannas, annual grasses always constitute a major component of the sward in semi-arid regions such as Messina (study 18) and Tuli (study 1). In contrast neither annual grasses or forbs are recorded as major components of the mesic sandveld areas (eg study 1).

There is no evidence that rainfall patterns alone have caused a major change in any system. The compositional changes discussed have been cyclic in accordance with rainfall cycles, that is composition for any particular climatic state is nearly constant. All species eliminations which have occurred due to drought have been of a temporary nature.

The effects of grazing

Experiments which allow for a direct evaluation of the effect of both grazing and the long term variability of rainfall are considered first. The second group of experiments considered are long term experiments dealing primarily with the effects of grazing only. The third and the fourth set of experiments reviewed are the short term experiments, including a few infrequently sampled long term experiments, dealing with the effects of grazing and rainfall variability, and with the effects of grazing alone, respectively. The effects of grazing are considered according to season of grazing, the system of grazing, and stocking rate.

Long term experiments: rainfall variability and grazing

1. The Towoomba trial

The longest running grazing experiment conducted in the savanna regions of southern Africa is the continuous versus fixed season rotational grazing trial at Towoomba, initiated in 1935 (Irvine 1940) and maintained until the present day (study 25). Each of the four grazing systems of 7,7 ha was grazed by two oxen, although the length of stay of the oxen was not kept constant because of variations in climatic conditions. All camps had a similar botanical composition in 1935, but by 1941 and 1948 there were differences between camps grazed during the non-growing season and camps grazed during the growing season (Louw 1973c). The former had increased in "climax" grasses at the expense of "successional" grassland, and the latter showed the opposite trend. Composition was monitored at five yearly intervals from 1962 (Donaldson and Rootman 1983), and confirmed the trends detected by Louw (op cit). It was concluded that the variability and trends in species composition were largely influenced by rainfall variability in addition to the differential effects of grazing treatments. The response of selected species in this trial are described.

Schmidtia pappophoroides closely tracked rainfall, virtually disappearing during drought years but becoming well established during wetter years. Schmidtia suffered from grazing during the growing period. Themeda triandra showed a similar response, declining markedly with the onset of

drought except in the winter grazed camp. The changes over the full length of the trial suggests that Themeda succumbs to continued grazing during the growing season. The species only attained pre-drought levels in 1982 on the winter grazed camp. Heteropogon contortus also showed a decline during the dry 1960's, which was accentuated in camps grazed during the growing season. The species recovered more slowly during the wetter 1970's on camps grazed during the growing season. Urochloa mosambicensis was most prolific during years of high rainfall on sites grazed during the growing season. Digitaria eriantha decreased during drought years but was stable during wet years, when grazed during the summer season. This species became prominent in drought years in treatments grazed during the non-growing season. Eragrostis rigidior consistently increased during the run of dry years, and subsequently decreased during the wetter years. Eragrostis appears to have been encouraged by grazing during the growing season. Aristida spp and forbs were most conspicuous during drought years, and the former was stimulated by grazing during the growing season. Panicum maximum increased over all treatments, ascribed to a general increase in the woody component. The wet period following 1972 resulted in a general increase of this species, but which was less pronounced on camps grazed during the growing season. Elionurus argenteus declined or was eliminated on all treatments over the full length of the experiment.

Summarising this experiment, the drought of the early 1960's resulted in a marked deterioration of the "climax" perennial species and an influx of Aristida species and Eragrostis rigidior. The subsequent above average rainfall of the 1970's promoted the recovery of the perennial component to predrought levels. The extent of deterioration of the perennial species, and their rate of recovery, depended on the grazing treatment. The different species exhibited notably different responses to both rainfall variability and grazing (and their interaction). Apart from the demise of Elionurus and the continued increase of Panicum, there is little evidence of a major change in composition. The data suggest an oscillation in composition dependent on cyclic rainfall characteristics. The grazing regime influenced the relative proportion of the major components, rather than dictating a long term trend. Treatments involving intense grazing during the growing season have had the most pronounced effect on composition. The main shifts in composition have occurred during the very wet or very dry years.

2. Continuous grazing trial on the Matopos red soils

A trial of continuous grazing by cattle (at a stocking rate of 4 ha/AU) has been conducted in an open Acacia/Colophospermum savanna at Matopos since 1950 (study 70). The frequencies of climax perennial grasses (8 species) in 1970 were not appreciably different from those recorded 13 to 15 years earlier, while the frequency of all pioneer perennial species (7 species) had increased. Between 1970 and 1972, the frequencies of four climax perennial species Cymbopogon plurinodis, Digitaria milanjiana, Heteropogon contortus and Themeda triandra, and the frequencies of all pioneer perennial species, had been significantly reduced. This was attributable to the cumulative effect of four consecutive seasons of below average rainfall from 1967/68 to 1970/71 (Table A2; mean 401 mm versus long term mean of 598 mm), which caused large scale mortality of perennial grass tufts in both the 1970 and 1971 dry seasons. During this period the

mesic perennial grass species virtually disappeared. A further die-off of perennial grass species occurred in 1973, following a very low rainfall season. The 1973/4 growing season experienced high and well distributed rainfall, resulting in good establishment, so that perennial grass frequencies had approximately returned to the 1973 levels. Climax perennial grasses continued to increase until 1976, with three consecutive seasons of above average rainfall, except for Cymbopogon plurinodis and Panicum coloratum (both considered marginal climax perennial species). Most of the pioneer perennial grass species had decreased by 1976, after reaching their maximum frequencies in 1973 or 1974.

The annual grasses (12 species) increased in frequency in response to the high rainfall of the 1971/72 season, but were significantly reduced following the 1972/73 below average rainfall season. Annual grasses were frequent in the following high rainfall year of 1974, but declined progressively to a low level in 1976 following the third consecutive high rainfall season.

3. Grazed Acacia savanna, Umfolozi Game Reserve

Three fixed line transects in the Umfolozi Game Reserve (mean annual rainfall 695 mm) were monitored five times in the 12 year period 1971 to 1982 (study 71). Climax perennial grasses increased in frequency during the period of above average rainfall between 1971 to 1979; Themeda triandra increased from 44 to 54%, and Panicum maximum increased from 2 to 10% (associated with a simultaneous increase in the woody plant canopy cover from 4% in 1971 to 25% in 1979). Large scale mortality of perennial tufts occurred following three consecutive seasons of below average rainfall, and the percentage frequency of most perennial grasses declined. The grazing resistant species Digitaria argyrograpta and Panicum coloratum increased in frequency from 1980 to 1981 through improved survival relative to the large tufted species Panicum maximum, Setaria spp and Themeda triandra. The bare ground annual Tragus berteronianus increased following the favorable, but below average, growing season of 1980/81. The second season of relatively high rainfall in 1981/82 resulted in an increase of the large tufted annual Diplachne eleusine, the biennial Urochloa mosambicensis, and some of the climax perennial species, notably Themeda triandra and Panicum species. However, other climax perennial species such as Digitaria and Setaria continued to decline.

As with the preceding experiment, there is no indication of how marked the trends attributed to rainfall might have been in the absence of grazing.

3. Tuli combined bush clearing and grazing trial

The dependence of perennial species on annual rainfall was recorded in a 23 year combined bush clearing and grazing trial conducted at Tuli, on a sandy soil derived from paragneiss (study 69). There were no replications

of treatments, and sampling frequency was low. In the first 13 years of the trial, four stocking rates were applied on uncleared veld (at 8,7; 11,1; 13,5 and 16,0 ha/AU) and three on cleared veld (at 4,9; 8,0 and 10,2 ha/AU), using a three paddock rotational resting system in each case. In the final 11 years of the trial, only 2 stocking rates were continued on each of the uncleared (12,8 and 16,0 ha/AU) and the cleared (4,8 and 4,3 ha/AU) sites, and a short duration grazing system with eight paddocks was added to each at 11,0 ha/AU on uncleared; 6,6 to 4,5 ha/AU on cleared). The uncleared veld in 1957, following three years of good rainfall, was dominated by perennials, but deteriorated to bare ground by 1964 after a number of years of very poor rainfall. Moderate rainfall was recorded from 1964 to 1967, and the cover (mainly of Aristida species) improved. In contrast, a good perennial cover was maintained on cleared veld until 1961, which then deteriorated by 1964 (156 mm), but a good cover of perennials recovered by 1967. In 1969, cleared areas were dominated by desirable perennials, whilst the uncleared areas were dominated by annuals and less desirable perennials. The desirable perennials include Brachiaria nigropedata, Digitaria pentzii, Eragrostis rigidior, E. superba, Bothriochloa insculpta, Heteropogon contortus, Urochloa bolbodes and Schmidtia pappophoroides. The annuals and less desirable perennials include Aristida spp, Eragrostis porosa and other annual Eragrostis species, Stipagrostis uniplumis, Enneapogon cenchroides, Brachiaria deflexa, Tragus berteronianus, Chloris virgata, Microchloa caffra, Pogonarthria fleckii, Urochloa mosambicensis and Rhynchelytrum repens.

By 1974, during a period of increased rainfall, the cleared areas showed a high percentage of desirable perennial species, and less undesirable perennials than the uncleared areas, in spite of higher stocking rates. There was in general no consistent effect of stocking rate on veld composition, and grazing system had no discernible effect. The marked changes in perennial species which took place in this semi-arid region could therefore be accounted for by rainfall variability, as influenced by the woody component.

5. Karoo grazing trials

A 16 year grazing trial in the Karoo (Roux 1966), described above, displays similar features to the above experiments. The proportion of grasses and bushes were dependent on the relative amounts of winter and summer rainfall, irrespective of grazing treatment, and followed a well defined climatic cycle. The different grazing treatments (winter, continuous, rotational grazing) affected the amplitude of changes in basal cover of these components (Figure 4). The extent of variation of these components during a 16 year cycle was not as great under grazing as protection. Grazing also altered the ratio of palatable to unpalatable shrubs in favour of the latter.

The influence of seasonal rainfall on the proportion of perennial grasses and Karoo bushes is also evident in the 11 year comparison between the effects of continuous grazing by Angora goats and Merino sheep, and complete protection (Skinner 1976). The trial was undertaken in the lower central Karoo near Graaf Reinet, from 1959 to 1969. The average rainfall for the first six years was exceptionally high (319 mm), compared to only 191 mm for the last five years, and was associated with a pattern of an

increasing amount of rain falling in the period March to August (more favorable for bushes - Roux 1966). Perennial grasses decreased markedly during the later years in all three treatments, whilst pioneer grasses fluctuated in accordance with annual rainfall. Palatable succulent shrubs significantly increased over the whole period under continuous grazing by goats, while palatable Karoo shrubs and Pentzia incana were significantly reduced under continuous sheep grazing. The perennial components other than grasses significantly increased under complete protection.

However, the importance of grazing for long term trends of perennial grasses in the Karoo is suggested from the casual observations made by Bedford and Roberts (1975) in the Hanover area over 35 years (1939 to 1974). In 1939 the area comprised pure Karoo bush; but Aristida species increased from 1948, concomitant with the commencement of systematic resting, and reached serious proportions in 1952. Aristida species decreased from 1954 to 1959 to become a minor component, associated with a gradual increase in other volunteer grass species such as Tragus racemosus, Enneapogon brachystachyus, and then Eragrostis obtusa and Cynodon incompletus. By 1964, after 16 years of systematic resting, cover had increased by 50%, and Panicum stapfianum had reappeared. These changes in the grass component could be explained in terms of rainfall patterns, grass rains (sensu Roux 1966) prevailed from 1949 to 1959, followed by bush rains from 1960 to 1965, that is, the commencement of systematic resting had coincided with favorable grass rains.

Long term experiments: grazing alone

Zimbabwe isolation transects and other grazing trials

A set of grazing experiments were set up in various areas in Zimbabwe in the mid-1940's. Isolation transects were established at Matopos, Nyamandhlovu, Tuli and the Zimbabwean highveld (study 27). The treatments implemented were

1. heavy grazing for from one to 15 years followed by 15 to one years protection;
2. protection for from one to 15 years followed by 15 to one years heavy grazing, and
3. complete protection.

1. Matopos thornveld isolation transect

Pronounced changes occurred on the Matopos thornveld, with very different responses by the different species to heavy grazing or resting (McKay 1956, Kennan 1969). Heteropogon contortus showed no decrease after two to five years of heavy grazing, but it decreased significantly after 8

years, and disappeared after 12 years. It reestablished after five years of rest. Bothriochloa insculpta was also initially very stable under heavy grazing, persisting or increasing under 8 years of heavy grazing, but disappeared after 10 years of grazing. It required 5 years of protection before it began to reappear. Cymbopogon plurinodis showed decreases from only one year of heavy grazing, and disappeared after 7 years of heavy grazing. The species required 13 years of rest before it reappeared. Hyparrhenia filipendula was eliminated by 8 years of heavy grazing, but reestablishment occurred after only 3 years of rest, although at a very slow rate. Protection favoured the species. Themeda triandra was stable under protection, but disappeared within 7 years of heavy grazing, and it required 8 years of rest before it reappeared. Rhynchelytrum repens was relatively sensitive to heavy grazing and disappeared quickly, but was reestablished after 5 years rest. In contrast, 4 and 2 years grazing promoted the appearance of Tragus berteronianus and Eragrostis patentipilosa, respectively, and each species disappeared after 9 and 13 years rest, respectively. Circumstantial evidence suggests the importance of rainfall variability for some of the recorded changes. The trial commenced with apparently well established perennial populations which experienced a severe drought during the first few years of the trial, and subsequently weakened. The high rainfall of the mid-1950's resulted in the proliferation of Eragrostis patentipilosa.

2. Matopos thornveld: other grazing experiments

A 15 year seasonal grazing experiment further illustrates the sensitivity of the perennial component of the Matopos thornveld to sustained grazing (study 28). The fixed seasons investigated included the first half of the growing season, the second half of the growing season, the complete growing season, the dry season, and complete protection. Grazing during the growing season rapidly eliminated most perennials and an annual sward developed. The perennial component maintained itself with grazing during the dry season, although slight changes in composition occurred. In a subsequent trial on thornveld conducted between 1967 and 1971, all years of below average rainfall (Table A2), the effects of grazing systems and stocking rates on botanical trends were examined (study 30). Two intensive rotational grazing systems involving 12 paddocks to one herd (at 3,4 ha/AU) were compared with a four paddocks to three herds rotational resting system (at 5,4 ha/AU). No significant differences between grazing treatments, or between the initial and final years of these treatments, were detected. There were also no significant differences in the trends in botanical composition between the different stocking rates, but notable species changes occurred between the beginning and the end of this trial. Digitaria milaniana and Hyparrhenia filipendula (plus Hyperthelia dissoluta) decreased markedly, Themeda triandra and Heteropogon contortus decreased to a lesser extent, whilst Bothriochloa insculpta, Rhynchelytrum repens, Eragrostis lehmanniana, E. superba and annuals increased substantially. There was an associated change in the structure of the sward, with an increase in the distance between tufts. The pattern of these changes does not appear to be a result of the grazing system or stocking rate alone, but partly a result of 4 years of sustained below average rainfall.

The grazing experiments conducted on the Matopos thornveld illustrate that the inherent instability of composition on this soil type due to rainfall variability (study 1) is accentuated by grazing. The major perennial species of this sward decrease, and are eventually eliminated, in the face of heavy grazing. Species differ notably in their ability to withstand, and recover from when rested, heavy grazing.

3. Matopos sandveld isolation transect

In contrast, the Matopos sandveld did not show such pronounced changes in the face of heavy grazing. In the 15 year isolation experiment the dominant species, Digitaria pentzii, persisted both under protection and heavy grazing, and even increased under heavy grazing for some years. Heteropogon contortus persisted well under heavy grazing and increased with protection. Pogonarthria squarrosa was stable for 8 years of heavy grazing, but was eventually eliminated from some of the plots when protection followed grazing. Heavy grazing caused the disappearance of Rhynchelytrum sp in some plots but not in others. Grazing promoted the appearance of Perotis patens and Setaria pallide-fusca. The number of annual forbs were proportional to the annual rainfall. The effects of the severe drought at the commencement of the trial were qualitatively not as marked as those on the thornveld (Kennan op cit).

4. Matopos sandveld: other grazing experiments

The 15 year seasonal grazing trial also illustrates the compositional stability of the Matopos sandveld under grazing (study 28). The seasonal grazing systems investigated are the same as those described for the Matopos thornveld (also study 28). All plots maintained a good perennial cover under six different grazing treatments. Grazing during the growing season eliminated Trachypogon spicatus but favoured Digitaria pentzii. Similar results were obtained in a short term (1971 to 1975) trial of six grazing procedures at two stocking rates on the Matopos sandveld (study 32). The six grazing procedures involved three periods of stay (5, 10, or 20 days) in either four or eight paddock units. Each procedure was applied at two stocking rates, the one rate double the other. The first three years of the trial experienced well below average rainfall, but the last years of the trial had well above average rainfall (Table A2). Although no major differential effects of the various grazing treatments were detected, conspicuous changes occurred in all treatments. Hyperthelia dissoluta, Diheteropogon amplexans, Rhynchelytrum repens, Pogonarthria squarrosa, Hyparrhenia filipendula and Loudetia simplex increased on all treatments, whilst Heteropogon contortus and Aristida species decreased on all treatments. These changes were associated with a marked increase in total basal cover and a decrease of rooted dead cover. The changes suggest that rainfall variability has an overriding effect on the perennial composition of sandveld, despite high stocking rates. Neither have any differential effects due to grazing treatments been reported for a presently ongoing comparison of continuous versus rotational grazing on the Matopos sandveld (study 33).

The grazing experiments conducted on the Matopos sandveld suggest that the perennial species are resistant to, and stable under, heavy grazing. The relative proportion of major species can be influenced by grazing, and some species can be eliminated by sustained heavy grazing. Circumstantial evidence suggests that rainfall variability is a prime influence on compositional changes on this soil type.

5. Nyamandhlovu isolation transect

The response of the Nyamandhlovu red soils to grazing was similar to that of the Matopos thornveld, although only qualitative impressions were recorded. The isolation trial at Nyamandhlovu commenced in 1948 after the area had been subjected to extreme drought for a number of years. At the commencement of the trial the original perennial cover dominated by Themeda triandra and Heteropogon contortus had been replaced by annuals (Aristida species). Subsequent grazing maintained the annual sward, but protection allowed the perennial component to reappear. Heteropogon was the first perennial to reestablish after rest, and the last to be eliminated with grazing. Themeda triandra, Eragrostis rigidior and Aristida pilgeri took longer to return after rest. A pilgeri was nearly as resistant to grazing as Heteropogon, because of its unpalatability. A conspicuous result of the trial was that the area changed from being relatively free of bush in 1948 to densely bushed at the cessation of the trial 16 years later. The rapid development of the woody component, principally Acacia species, possibly had a greater effect than grazing on the perennial grasses.

6. Nyamandhlovu: other grazing trials

The seasonal grazing study on the Nyamandhlovu red soils (no 28 - same treatments as described for Matopos thornveld) produced similar results to the isolation transects. Grazing during the growing season and continuous grazing resulted in a sward dominated by annuals, and with concomitant severe bush encroachment. Completely protected and winter grazed plots were dominated by the perennials Themeda triandra, Heteropogon contortus, Schmidtia pappophoroides, Eragrostis rigidior and Aristida pilgeri. The influence of rainfall on the compositional changes described for the grazing trials on the Nyamandhlovu red soils is suggested by a six year trial of two multi-paddock grazing systems on this soil type (study 31). The systems were a 16 paddocks to one herd system and a 4 paddocks to one herd system, at a rate varying from 4,9 ha/AU to 7,8 ha/AU. There was an increase in the percentage frequency of Rhynchelytrum repens, Sporobolus stapfianus, and a host of annual species, and a decrease in Aristida barbicollis, between 1970 and 1974, irrespective of treatment. The seasonal rainfall for 1970 (416 mm) was well below average (541 mm), and for 1974 was well above average (821 mm), indicating that rainfall was primarily responsible for the compositional changes. The density of perennial grasses increased in both systems between 1968 and 1972, but subsequently decreased in one system between 1972 and 1974. The changes in density suggest a relatively rapidly changing perennial tuft structure.

The long term grazing experiments on Nyamandhlovu red soils are conspicuous when contrasted with the Matopos trials because grazing has maintained a sward consisting of annual species, despite changes in rainfall. The trends documented on the Nyamandhlovu red soils nevertheless complement the changes observed on the Matopos thornveld, that of a pronounced instability of composition on heavier textured soils with this rainfall regime.

7. Tuli isolation transect

The 15 year isolation transect monitored at Tuli (Kennan 1969) displayed similar results to the Tuli bush clearing trial (study 1) and the Messina successional study (study 18). Rainfall had an overriding effect on the survival of perennial grasses, even in protected plots. Species particularly susceptible to drought were Eragrostis rigidior, Schmidtia pappophoroides and Bothriochloa insculpta, but these perennials maintained themselves during drought in the absence of grazing. Grazing caused a rapid deterioration of the perennial component within two years, and formed a sward of annuals consisting principally of Aristida spp, Eragrostis porosa and Tragus berteronianus. Tragus became the dominant annual with sustained grazing. The perennial component recovered fairly rapidly when rested. The rate of recovery was dependent on rainfall, for example Urochloa mosambicensis took from 2 to 6 years to recover depending on the pattern of rainfall. The sandy nature of the soil appeared to aid the rate of recovery (Kennan op cit).

8. Messina grazing trial

The overriding effect of rainfall on the survival of perennials in this climatic zone is also shown in a trial which compared the effects of different forms of grazing on trends in herbaceous composition in the mopane veld of the northern Transvaal (study 40). The trial compared grazing by cattle only, goats only, and cattle plus goats, each treatment being grazed according to a fixed rotational grazing system. The trial commenced in 1969 at the end of a dry spell, and was terminated in 1974 after a few years of above average rainfall (Table A2). There was a significant increase in the total cover of all three treatments over this period, but the only perennial grass which increased significantly was Oropetium capense. The perennial grasses Eragrostis lehmanniana, Stipagrostis uniplumis, Panicum maximum and Urochloa mosambicensis showed non-significant increases. The basal cover of annuals, principally Aristida adscensionis and Tragus racemosus, increased significantly by 2% over all treatments. The different grazing systems, which would have differed in their severity of defoliation of perennial grasses because goats consume a large proportion of browse, exerted little effect on trends in composition.

9. Grasslands grazing trials

Composition was generally stable under sustained heavy grazing in the isolation transect experiment on the high rainfall site at Grasslands (mean average rainfall 936 mm - study 27). Heteropogon contortus became dominant in continuously grazed stands, but decreased with protection. Sporobolus pyramadalis and Cynodon dactylon increased, whilst Hyparrhenia filipendula declined, under heavy grazing. Heavy grazing limited the development of the woody component. Different stocking rates (3,24; 5,26; 7,69 ha/AU with a 3 herds/ 4 paddocks system) had no effect on species composition of this vegetation type (study 29). The compositional changes which occurred between 1955 and 1963 were ascribed to seasonal variation. Barnes (1965) therefore concluded that the high altitude sandveld of Zimbabwe would remain unchanged under heavy grazing for periods of at least 15 years, provided the woody component did not become dominant. Severe seasonal cutting had little effect on the grass composition of a Brachystegia/Julbernardia woodland in the same high altitude region of Zimbabwe, but on heavier textured soils (study 34). The sward was dominated by Hyparrhenia species, Sporobolus pyramadalis and Chloris gayana. The slight changes in composition which occurred were restored after only one seasons rest from cutting.

Short term experiments: rainfall variability and grazing

1. Botswana trials

A trial of continuous versus rotational grazing (three paddock one herd, deferred rotational system) was conducted for 28 years at Morale, Botswana (study 36). The stocking rate for both grazing systems was 8,1 ha/AU for the first 11 years, and thereafter 5,38 ha/AU. There were no significant differences between the two grazing systems in the density of the major compositional components in 1965 or 1966. The components included Aristida species, Digitaria species, Eragrostis rigidior, E. superba, Schmidtia pappophoroides, Tragus racemosus, forbs and sedges (and total herbage cover). However, marked changes occurred in the density of the major perennial species of each grazing system between 1957 and 1966. The year 1957 was within a wetter era, and 1966 was within a pronounced series of drought years. The key perennial species Brachiaria nigropedata, Digitaria sp, Eragrostis superba and Schmidtia pappophoroides were either eliminated or markedly reduced over this period, resulting in a significant decrease in the total perennial cover of both treatments. At the same time the basal cover of Eragrostis rigidior, Tragus racemosus (an annual) and forbs increased.

Trials of both grazing systems and stocking rates have been conducted at Morapedi and Matlokgang, Botswana, since 1976 (studies 37, 38). The grazing systems include continuous grazing, 3 paddocks per herd, a four day graze and 32 day rest multicamp system, and a seven day graze and 56 day rest multicamp system. The two stocking rates employed were 8 ha/AU and 4 ha/AU. Both areas experienced above average rainfall between 1976 and 1978, but 1978/79 and 1979/80 were consecutively dry years (Table A2).

At Morapedi, basal cover of all grazing systems fluctuated between 1976 and 1978, and declined sharply by 1980. Basal cover decreased continuously on the sandveld at Matlokgang between 1976 and 1980, with a proportionately greater decrease at higher stocking rates. The key perennial species Stipagrostis uniplumis, Digitaria eriantha, Eragrostis lehmanniana, Schmidtia pappophoroides, Brachiaria nigropedata, Antheophora pubescens and Pogonarthria squarrosa decreased between 1976 and 1980 irrespective of treatment, suggesting an overriding effect of rainfall. However the severity of defoliation appeared to affect the degree of response of Stipagrostis, Digitaria and Eragrostis lehmanniana.

A stocking rate trial was conducted in the western Kalahari between 1976 and 1980 (study 39). The grazing systems employed were a simulated 3 paddock 2 herd system at both 8 ha/AU and 18 ha/AU, a multicamp system at 18 ha/AU, and an ungrazed paddock. The herbaceous vegetation was dominated by Schmidtia pappophoroides, Stipagrostis uniplumis and annuals. Total productivity and the productivity of individual components was dependent on total rainfall over these four years. However the proportion of each perennial species depended on the grazing regime. The productivity of the palatable Schmidtia pappophoroides decreased under heavy grazing but increased under moderate grazing. Total productivity decreased under continued overgrazing.

2. Namibian bush clearing and grazing trial

Grazing treatments were incorporated into a six year bush clearing trial in Namibia (study 3), and included light winter grazing, heavy summer grazing, and no grazing. The overriding effect of rainfall was apparent on all treatments which experienced two years of drought prior to final monitoring. The extent of the decrease of all compositional groups was influenced by both the woody component and the grazing regime. In an experiment in which baseline conditions were severely degraded and encroached by Acacia mellifera, the highest total cover and cover of individual components was on cleared treatments. The treatments grazed during winter and during the growing season showed the two highest values for cover of the various components. The differences with other treatments were due to annuals and other seed plants as perennials did not reestablish.

A sister experiment was conducted on the same soil type in which baseline conditions were comparatively good. The cover of perennials, other seed plants and total cover decreased under heavy grazing, but perennial cover was maintained under no grazing and light winter grazing. Annuals were maintained irrespective of grazing system. In a third experiment which was concluded in 1960 after only one year of drought, baseline conditions were heavy encroachment by A mellifera. The perennial cover was significantly higher on cleared than bushed areas in the drought year. There were no significant effects of grazing on either the perennial or annual component. These three experiments indicate that rainfall, in particular critical drought years, has an overriding effect on the perennial component. The instability of the perennials was accentuated on bushed areas, and especially those which had been severely degraded. The influence of grazing on the perennials and other components was not as marked as the influence of rainfall or the woody component, although

grazing significantly affected composition, especially the reestablishment of perennials on formerly heavily utilised sites.

3. Towoomba bush clearing trial

The primary influence of the woody component, as opposed to grazing, on herbaceous composition and total basal cover is further suggested by a bush clearing trial at Towoomba (study 4). Composition differed between the three treatments in 1959, which followed a number of wet years. The sward of the completely cleared treatment was dominated by Cymbopogon plurinodis, Themeda triandra, Heteropogon contortus and Digitaria argyrograpta, all of which are considered climax perennial species (Louw and van der Merwe 1973). These species were poorly represented on a control, which was dominated by Aloe spp, Cynodon dactylon and Panicum maximum. The selectively cleared treatment carried a mixture of these species, and was dominated by Digitaria argyrograpta, Cynodon dactylon and Sporobolus spp. Total clearing resulted in a 14% increase, and selective clearing a 41% increase in basal cover over the control. There is no indication of the influence of grazing on these differences.

4. Eastern Cape trials

Two identical studies (41, 42) were undertaken on the effect of goat or sheep grazing on herbaceous composition in the eastern Cape; in both the False thornveld and in grassland invaded by Acacia karroo. The treatments applied in each experiment were continuous and rotational grazing by both sheep and goats, and an ungrazed control. The stocking rates applied were 1 goat/ha and 1 to 1,5 sheep/ha. The first two seasons of these studies were characterised by below average rainfall (438 mm and 350 mm), but the 1970/71 season was particularly favourable (757 mm; Du Toit 1972c). The general results of the two trials differed. Basal cover of the False thornveld remained stable (5%) under both sheep grazing treatments, but increased significantly on the two goat treatments (5 to 8%). No data were presented for the control treatment. The major species responded differently to the grazing treatments. All grazing treatments eliminated Eustachys paspaloides. Eragrostis lehmanniana showed a greater decrease under sheep than goat grazing. Cymbopogon plurinodis, Digitaria eriantha and Sporobolus fimbriatus were relatively stable under sheep grazing but increased under goat grazing. Tragus koelerioides was stable under all treatments. Aristida diffusa was stable under all treatments except rotational sheep grazing, under which it increased. Heteropogon contortus increased for three of the treatments, but decreased significantly under rotational sheep grazing. Panicum stapfianum established in three of the treatments. The above pattern of changes suggest that the severity of defoliation, considered greater with sheep than with goats, influenced compositional trends. However the pattern of defoliation appeared to have little effect, as there were no major differences in herbaceous trends between continuous and rotational grazing for either goats or sheep.

In contrast, the basal cover of all treatments (including the control) increased significantly in grassveld invaded by Acacia karroo (Du Toit

1972b). The general increase was primarily due to increases in Digitaria eriantha and Sporobolus fimbriatus. Therefore although sheep and goats differed in their pattern of grazing (Du Toit op cit), grazing did not appear to influence the major trends. The observed trends appear to be a result of shorter term rainfall changes.

5. East African trials

Two sets of grazing experiments from East African savannas provide parallels to southern African experiments. A trial of grazing rates and systems was conducted over four years in Tanzania (O'Rourke 1978). The treatments were heavy, moderate and light grazing (1,2; 3,6 and 6,1 ha/AU respectively for the first three years, raised to 0,9; 2,6 and 4,3 ha/AU in the final year), each rate under continuous and rotational (biannual rotational for three years and seasonal grazing for final year) grazing systems. The soils were calcareous black clays derived from alkali rich volcanic rocks. The final two years of the trial experienced only 424 and 483 mm of precipitation, in contrast to the considerably wetter initial two years (728 and 561 mm). The two major species, Cynodon dactylon and Digitaria scalarum, showed no response to grazing systems. Cynodon showed no response to grazing rates, but Digitaria increased slightly more under light grazing than heavy or moderate grazing. The influence of rainfall is reflected in the changes of total plant frequency. There were no significant differences in total plant frequency between continuous and rotational grazing at the beginning of the trial (94 and 97% respectively) or at the termination of the trial (25 and 26% respectively). There were no significant difference in total plant frequency between the different grazing rates at the beginning of the trial (96, 95, 96% for heavy, moderate, light grazing respectively), but at the termination of the trial the plant frequency was significantly lower on heavily grazed than lightly grazed sites (20 and 31% respectively). Therefore, although grazing rate affected trends, the major changes appeared to be directly related to rainfall trends.

Similarly, in a further set of experiments at Ukuriguru, Tanzania, stocking rate had a greater influence on herbaceous trends than grazing systems. The experiments included a four year comparison of rotational (three weeks in and six weeks out; at 1,0 ha/AU) and continuous grazing systems (Walker 1968, Walker and Scott 1968a), followed by a comparison of three stocking rates (0,61; 1,21; 2,43 ha/AU) over four years (Walker and Scott 1968b). The trials were all on hardpan soils. All years of the experiment experienced rainfall equivalent to or above the average of 840 mm. The dominant species under continuous grazing was Bothriochloa insculpta, followed by Panicum infestum. There was little difference from this in the composition of two rotational grazing systems, except that the above two major species were codominant. However, although composition differed little between the two systems, the continuously grazed area developed a short grass sward and the rotationally grazed areas developed tall grass swards. In the stocking rate trial, Panicum increased under all treatments, whilst Bothriochloa decreased under the low stocking rate but was stable or increased under the high stocking rate. Heteropogon contortus and Sporobolus pyramadalis increased on all treatments. Hyparrhenia dissoluta and H. altissima decreased at high stocking rates but otherwise increased. The different grazing treatments

had little effect on dicotyledons. In these experiments stocking rate appeared to be a more important determinant of compositional change than grazing system. There were however no major changes in composition on any of the treatments, suggesting a relatively stable herbaceous layer on these hardpan soils during a wet four year period.

Short term experiments: grazing alone

1. Northern Cape trials

Pronounced effects of grazing were detected on the Tarchonanthus shrub savanna of the Ghaap plateau in the northern Cape (study 43). Six main experiments (ranging from 5 to 9 years) were conducted, each on limeveld and dolomiteveld, and included different grazing intensities and different grazing systems of cattle, or sheep, or cattle plus sheep. The composition of all treatments changed pronouncedly, irrespective of which years the treatment ran, suggesting that the changes were primarily due to grazing rather than rainfall variability. The general change recorded was an increase in what were termed the seral, weed, karroid and pioneer species, accompanied by a decrease of the "climax" perennial species (Ebersohn 1962).

The key species showed marked differences in their response to grazing. Two palatable species, Fingerhuthia africana and Eustachys paspaloides and the less palatable Tragus koelerioides, were dramatically reduced or eliminated under all grazing treatments. Themeda triandra occurred more frequently on limeveld than dolomiteveld, but decreased to a greater extent on limeveld. Susceptibility of this species to grazing was dependent on stocking rate, and it was concluded that Themeda was relatively tolerant of grazing (Ebersohn op cit). Digitaria eriantha was likewise tolerant of grazing, but was more susceptible to grazing on limeveld than dolomiteveld. Less palatable perennials such as Chrysopogon montanus, Cymbopogon plurinodis and Sporobolus fimbriatus were stable under the majority of grazing regimes, but could be eliminated when initially sparse. Heteropogon contortus occurred principally on dolomiteveld, and was stable under most grazing treatments except for those involving intensive use by sheep. The most marked change under all grazing treatments was the increase of Eragrostis lehmanniana, irrespective of soil type. The species was noted to rapidly colonise bare areas.

In summary, most changes in composition occurred independently of the system of grazing or the type of animal, although stocking rate exerted an influence on the degree of change. Ebersohn (op cit) recognized that the effect of either incidental or prolonged drought was important, and suggested that the moisture availability and the degree of defoliation, as against the season of leaf removal, were more important for the survival of perennials in this semi-arid environment.

2. Towoomba trial

Louw (1974a) reports on an evaluation of improved fixed seasonal grazing rotation systems on mixed sour veld at Towoomba, initiated in 1937 (study 26). Botanical analyses were undertaken in 1941, 1948 and 1950, a generally dry period (Table A2). Continuous summer grazing or continuous summer grazing together with grazing during any other period led to the most marked changes in composition, with the sward becoming dominated by perennials such as Bothriochloa insculpta, Digitaria argyrograpta, Elionurus argenteus and Cymbopogon plurinodis, and by annual species, particularly Aristida congesta subsp barbicollis. In comparison camps grazed during the winter or spring only became dominated by the taller perennials such as Heteropogon contortus, Themeda triandra, Brachiaria nigropedata, Digitaria argyrograpta, in addition to Cymbopogon plurinodis and Elionurus argenteus. Grazing during autumn had pronounced effects.

3. Charter Estate trial

A seven year trial on the Zimbabwe highveld compared the effects of four different systems of grazing management on botanical composition (study

Table 3. Changes in the percentage frequency of occurrence between 1969 and 1975 in the Charter Estate grazing trial. S1 and S2 represent two short duration grazing systems, and C1 and C2 their respective controls. Asterisks denote statistically significant changes. (Data from Clatworthy 1984)

Species	S1		C1		S2		C2	
	1969	1975	1969	1975	1969	1975	1969	1975
<u>Hyperthelia dissoluta</u>	23	39*	4	14	21	25	45	55
<u>Hyparrhenia filipendula</u>	18	33*	8	8	67	82*	63	88*
<u>Perotis patens</u>	--	--	96	82*	--	--	--	--
<u>Rhynchelytrum repens</u>	49	42	27	19*	91	50*	--	--
<u>Aristida congesta</u>	--	--	32	7*	--	--	--	--
<u>Brachiaria serrata</u>	53	59	33	47*	--	--	34	35
<u>Eragrostis racemosa</u>	17	32	9	15*	--	--	44	54
<u>Stereochlaena cameronii</u>	33	46	19	45*	5	15*	--	--
<u>Heteropogon contortus</u>	50	58	39	43	85	86	86	68
<u>Pogonarthria squarrosa</u>	50	55	54	43	40	55	--	--
<u>Brachiaria nigropedata</u>	16	24	45	35	25	26	--	--
<u>Eragrostis chapelierii</u>	5	12	2	11	--	--	--	--
<u>Sporobolus stapfianus</u> plus	55	55	23	30	91	87	67	79
<u>Michrochloa kunthii</u>								

68). The grazing systems were a Savory rotational system (S1) using 15 (initially 21) paddocks, a system (C1 and C2) comprising four paddocks in which several herds were run and moved at the discretion of the manager, and a system (S2) of five (enlarged to seven) paddocks grazed in rotation by a single herd. The stocking rates employed varied throughout the trial from 3,5 ha/AU (heavy) to 6 ha/AU (light). The S1 and C1 systems were sited on a fine grained sand derived from sandstone, while the S2 and C2 systems were sited on a sandy loam derived from the contact zone between basalt and sandstone. The composition and basal cover of each system were monitored annually, and the species which showed significant changes between the beginning and the end of the trial are shown in Table 3. The changes were of degree (approximately 20% frequency of occurrence) rather than of kind. Rapid rotational grazing had no specific effect on composition, and the rotational systems showed changes in common with the controls. Basal cover fluctuated and showed no consistent relationship to grazing treatment, nor was basal cover directly related to rainfall. Basal cover appeared to show a one year lag effect in relation to rainfall; for example there was a dramatic decrease in basal cover of all four systems from the 1973 (390 mm) to the 1974 (1311 mm) seasons, but a subsequent increase from 1974 to 1975.

4. Wildlife studies

Further information on the effects of grazing in savanna regions is limited to wildlife communities. Compositional changes over 14 years (1962 to 1976) in the Ndumu Game Reserve, Natal, have been assessed (study 47). Grazing pressure is considered to have continually increased over this period, due to population increases of hippopotamus and impala. At the same time Panicum species have been replaced by Urochloa mosambicensis, despite a two fold increase in woody cover. There has been an apparent increase in species richness with the establishment of Eragrostis rigidior, Aristida congesta and Cyperus esculentus. The long term exclusion of grazing on the Mweya peninsula, Queen Elizabeth National Park, Uganda, has led to a marked decrease in species richness (Yoaciél 1981). Sporobolus pyramidalis is the dominant species in grazed areas, while Hyparrhenia filipendula, Heteropogon contortus and Cenchrus ciliaris are the dominant species in enclosures. Themeda triandra is present in enclosures but absent from grazed areas, and Bothriochloa insculpta, Cynodon dactylon and Panicum maximum are more common in enclosed areas. In one vegetation type four species are found in the enclosure as opposed to 23 species in the grazed area, the respective figures in a second vegetation type are 3 and 14 species.

Long term vegetation changes have also been monitored in the Umfolozi Game Reserve, Natal, through the use of enclosure plots established in 1966 (study 19). Subsequently a cull/non-cull experiment was established in 1978, thereby creating two grazing regimes (study 46). Species composition of the enclosure plots and of sites on both cull and non-cull areas was monitored in 1982. Sites on the cull/non-cull area were paired for the two major soil types, the swartland (derived from Ecca shales) and the shortland (derived from dolerite) soils. Preliminary analysis suggests that the two soil types differ markedly in their response to the relaxation of grazing pressure. Swartland soils showed a lower grass basal cover and a lower grass seedling establishment than shortland soils

(Emslie 1983). Species differences on the enclosure plots resemble those of the cull versus non-cull sites.

5. East African studies

There is circumstantial evidence to suggest that the Ankole pastures of Uganda have been irreversibly invaded by the unpalatable Cymbopogon afronardus between 1920 and 1960, concomitant with the demise of cattle farming resulting from tsetse fly invasion (Harrington 1974). The Ankole pastures lie within the Dry Acacia Savanna (mean annual rainfall of 750 to 1000 mm), with a grass sward dominated by Themeda triandra, Cymbopogon afronardus, and Loudetia kagarensis. The area was extensively chain cleared for tsetse control, and was then regularly burnt. A two and a half year study investigated the control of C afronardus in this region (Harrington and Thornton 1969). Three treatments were applied, all of which involved initial burning. Two of these treatments were first rested, and then periodically stocked to maintain C afronardus at stubble height. The second of these had nitrogen applied (at 158 kg N/ha/annum). The third treatment had C afronardus hoed out after burning and was then periodically stocked to maintain the grass in a short condition. The changes in foliar cover and the number of tussocks of C afronardus between the beginning and end of the trial are shown in Table 4. The periodic very heavy stocking (treatment 1) converted hillslope pasture with 47% cover of C afronardus to a mixed sward dominated by Brachiaria decumbens. The addition of N strongly favored B decumbens over all other species. Although the reduction within each treatment was highly significant (Table 4), there were no significant differences between the treatments.

Table 4. Percentage foliar cover by Cymbopogon afronardus and number of C afronardus tussocks over 2,54 cm basal diameter per 21 m² before and after treatment. (Data from Harrington and Thornton 1969)

Treatment	Foliar cover		Tussock number	
	July 1965	April 1968	July 1965	April 1968
1	47	12	31	14
2	47	10	25	14
3	51	10	33	11

The reduction within treatments 1 and 2 was a result of the exceptionally severe dry season of 1967, causing tussock death. Treatments 1 and 2 reduced tussock size rather than completely killing the plants. Hoeing was initially effective in eliminating C afronardus from treatment 3. The recovery of the species from seed was attributed to the type of rotational grazing management applied. The performance of this unpalatable species is therefore influenced by rainfall variability, grazing pressure, fire,

nutrient levels and seed reserves. There was however little evidence that grazing alone could initiate major changes in the occurrence of this species.

In contrast, grazing pressure has been postulated as the major factor causing change in the composition of a grassland in the high rainfall (annual mean 1140 mm) Buganda region of Uganda (Thornton 1970). Three grazing treatments were applied in a four year trial on this grassland: 1. 0,3 ha/AU (4 weeks on and 8 weeks off) plus sulphate of ammonia and superphosphate; 2. 0,4 ha/AU (6 weeks on and 6 weeks off) plus fertilizer (as above); 3. 0,81 ha/AU (continuous grazing) with no fertilizer. In treatment 1 the original sward of the unpalatable species Pennisetum purpureum and Imperata cylindrica was transformed after two years to a sward dominated by Cynodon dactylon, Panicum maximum, Setaria sphacelata and Brachiaria spp. Treatment 2 showed a similar response except the reduction of Imperata cylindrica was not as pronounced. The botanical changes on treatment 3 were the least marked. The changes in botanical composition were considered proportional to grazing pressure (Thornton 1970), but no cognisance was taken of the profound effect fertilization can have on composition in a short space of time (see this synthesis). A similar study over five years in a high rainfall grassland at Kitale (mean annual rainfall 1140 mm), Kenya, revealed no differences in composition between a four paddock rotational grazing system (eight week cycles), a three paddock deferred grazing system, and continuous grazing (Bogdan and Kidner 1967).

6. Highveld grassland trials

A large number of grazing trials have been conducted in the highveld grasslands of South Africa which illustrate that grazing can have pronounced effects on compositional trends. Two of these studies are described here because they illustrate trends not revealed by studies in the savanna regions.

The first study is a sheep grazing trial conducted at the Glen Research Station in the central OFS from 1937. Four systems of sheep grazing were compared; 1 month graze and 3 month rest (camp 1), 2 month graze and 2 month rest (camp 2), 3 month graze and 1 month rest (camp 3), continuous grazing (camp 4); for each of the seasons early summer, late summer and winter. After 6 years the systems were subjectively assessed (Morris 1944). Themeda triandra and Eragrostis lehmanniana decreased with increased summer grazing, whilst Aristida congesta and Tragus koelerioides increased most under camps 3 and 4. These four systems were closed and rested for a further nine years to evaluate whether the differences induced by the different grazing treatments would persist. The composition of the four camps was sampled at the end of this period using basal cover (Mostert 1958). Total basal cover and the basal cover of perennial grasses decreased along the gradient of camps 1 to 4, but the cover of shrubs and herbs increased along this gradient. Themeda triandra, Heteropogon contortus, Sporobolus fimbriatus and Eragrostis chloremelas reflected the trend of total basal cover. Aristida congesta had disappeared from camp 1, but was still present on the remaining camps being most prolific on camp 4. Eragrostis lehmanniana had also become most prolific on the formerly most heavily grazed camp 4, on which it had

originally shown the greatest decrease. Digitaria eriantha was most prolific on camps 1 and 2 but absent on camp 4.

Therefore the differential effects induced by four grazing systems of different severity had persisted in this veld type for nine years of rest. Similar influences of heavy grazing on this veld type are described for a plot rested for 7 years and one heavily grazed by cattle over the same period of time (Mostert op cit), for a well managed camp and one which had been heavily overgrazed by cattle and sheep for 30 years (Mostert op cit); as well as for a number of different seasonal grazing systems (van den Berg, Roberts and Vorster 1975). Very similar results of grazing trials have also been described for the Cymbopogon-Themedata veld type of the Potchefstroom district (Coetsee and Benadie 1975, Coetsee and van Rensburg 1975a, Coetsee and van Rensburg 1975b, Edwards and Nel 1973). A conspicuous feature of the above mentioned grazing trials on highveld grasslands is that heavy grazing, although capable of markedly altering the composition, has not eliminated any of the major components. The most dramatic changes were recorded on protected plots, for example a Themeda-Elionurus vegetation type changed to a Cymbopogon-Setaria type with 20 years of protection (Coetsee and van Rensburg 1975b).

The Tall grassveld of Natal is the only case recorded in the literature where grazing had caused a major change in composition, and which appeared to be potentially irreversible in the short term (Tainton 1972). The sward comprised Themeda triandra, Tristachya hispida, Andropogon amplexans and Hyparrhenia hirta at the commencement of the trial in 1958. This vegetation type is considered to be stable under a moderate degree of overgrazing (Tainton op cit), but the sward showed well defined changes with sustained overgrazing. There was little botanical change in the first 4 years under continuous overgrazing, but a change in growth form accompanied by a decrease in production of 50% was recorded. Patches then began to die out and were invaded by weeds. After six years of treatment there was further invasion by pioneers, principally Sporobolus capensis, accompanied by a further decrease in production. Aristida junciformis then began to invade and to establish as the dominant component of the sward. A three paddock seasonal resting system allowed Aristida to invade after only the first few years, so that the sward was dominated by Aristida and Sporobolus after only 12 years.

Discussion

Limited data illustrate that long term rainfall variability, independent of grazing regime, has an overriding effect on compositional trends (studies 25, 69, 70, 71, Bedford and Roberts 1975, Roux 1966, Skinner 1976), which is further suggested by a number of long and short term studies (studies 3, 27, 29, 30, 31, 32, 36, 37, 38, 39, 40, 41, 68, O'Rourke 1978). This effect of long term rainfall variability on compositional trends has also been reported for grazed ranges in the semi-arid south west of New Mexico, USA (Paulsen and Ares 1961, Wright and van Dyne 1976), and for the prairie grasslands of USA (Coupland 1974). Because of the influence of rainfall, the influence of grazing varies from the semi-arid to the more mesic savannas. The most pronounced effects of grazing have been recorded in the semi-arid regions such as the Ghaap plateau of the northern Cape (study 43) and the Tuli area of Zimbabwe

(study 27). In contrast grazing appears to exert little influence in the high rainfall savanna areas of Zimbabwe (studies 27, 29).

The effect of grazing in the mesic savannas is dependent on soil type, best illustrated by a comparison of the responses of the Matopos thornveld and sandveld to heavy grazing (study 27). The inherent compositional instability of the thornveld (study 1) is exacerbated by the effects of heavy grazing. Little work has been done on the interaction between woody density and grazing on compositional change. The combined bush clearing and grazing trials in Namibia (study 3) and Tuli (study 69) suggest, for both a heavier textured and a sandy soil in a semi-arid environment, that the woody component exerts a far greater effect than grazing on perennial grasses during critical drought years.

The effects of grazing on compositional trends need to be considered in relation to the season of grazing, stocking rate, and the system of grazing, and probably the spectrum of grazing herbivores. These parameters are further considered within a framework of key questions:

1. Does the influence of these parameters vary with climatic regime and/or soil type?
2. Within a given climatic regime and soil type, is the influence of a parameter dependent on certain conditions, for example a critical wet or dry year?
3. What is the interactive effect of these parameters on compositional trends?

The season in which the most intense defoliation takes place has a marked effect on composition (studies 25, 26, 28, van den Berg, Roberts and Vorster 1975) dependent on the physiological state of the plant. In mesic savannas, the influence of seasonal grazing was most marked on the heavier textured soils, and least marked on sandy soils. Continuous grazing during the growing season can lead to pronounced compositional changes.

Stocking rate rather than the system of grazing has a far greater influence on compositional trends (studies 37, 42, 43, O'Rourke 1978, Walker 1968, Walker and Scott 1968a, 1968b). Persistent heavy grazing inevitably leads to some scale of change in composition (studies 27, 42, 43, Yoaciel 1981), but this scale of difference, although significant, has not been as marked in trials comparing different stocking rates (studies 3, 30, 37, 39, 41, 42, 43, O'Rourke 1978, Walker 1968, Walker and Scott 1968b). Notably stocking rate trials have shown no significant effects on compositional trends in the mesic sandveld or high rainfall regions (studies 29, 32, 33), but have shown significant effects in the semi-arid savannas and on the heavier textured soils of mesic savannas (studies 3, 30, 37, 39, 41, 42, 43, O'Rourke 1978, Walker and Scott 1968b). It is also notable that grazing system trials have shown no significant effects on composition over a wide range of savanna types (studies 30, 31, 32, 33, 36, 37, 38, 41, 42, 68, Bogdan and Kidner 1967, O'Rourke 1978, Walker 1968, Walker and Scott 1968a, b), even though many of these studies compared continuous grazing and some form of rotational grazing. Furthermore, there is no evidence that controlled selective grazing has any influence on botanical trends.

The above listed studies do not provide sufficient evidence to evaluate whether the significant effects of season of grazing or stocking rate were dependent on specific conditions such as a drought year, or whether these effects were independent of rainfall amount. There is also no available data set to examine whether increases in stocking rate might interact with grazing system or the spectrum of herbivores. Stocking rate increases during the growing season would be expected to be the grazing variable with the most pronounced effects on composition, but this has never been investigated. Different species respond in a markedly different manner to the same treatment under the same set of conditions. The response of a species is also very dependent on soil type and climatic regime, illustrated for example by the responses of Heteropogon contortus on the Matopos thornveld, Matopos sandveld and high altitude sandveld of Zimbabwe (study 27). It was eliminated on the Matopos thornveld after 12 years of heavy grazing, but persisted on the sandveld, and became the dominant species on the highveld.

There is no information on the effect of grazing on tuft mortality to assist the interpretation of compositional changes. There is a critical need to separate out the effects of drought and grazing on tuft mortality, for example the dramatic perennial grass mortality recorded in Klaserie (Scholes 1984) was under conditions of both severe drought and overgrazing.

Vesey-Fitzgerald (1970) has illustrated the necessity of investigating vegetation dynamics in relation to the operative forces, which can be of a controlling or a modifying nature. For example, he postulates that the controlling force of the valley grasslands of East Africa is drainage, with fire only a modifying force. In contrast fire is the controlling force of secondary grasslands, with grazing a modifying force. In adopting this approach for the savanna grasslands of southern Africa, it is suggested that rainfall, as affected by soil type and the grass/woody ratio, is the controlling force, and grazing a modifying force. A corollary is therefore that grazing would not cause an irreversible change in the composition of savanna grasslands, as has been recorded for the Tall grassveld of Natal (Tainton 1972). It is notable that 45 years of continuous grazing on a heavy textured soil at Towoomba has not caused a major change in composition (study 25). Sustained overgrazing in the isolation transects in Zimbabwe (study 27) eventually led to a complete change in composition. However, these changes were not irreversible and with rest recovery took place on both the Matopos thornveld and sandveld and in the Tuli area. A potentially irreversible change appears to have occurred on the Nyamandhlovu red soils, but this was primarily a change in the woody/grass ratio. Similarly the composition of the high altitude sandveld of Zimbabwe appears to be stable under severe grazing unless there is a change in the woody/grass ratio (study 29).

The cumulative effects of grazing do however influence the rate of rainfall induced compositional change. This is apparent in the differential response of areas previously heavily and moderately grazed, and then irrigated, in Botswana (McKay 1968), and in the mosaic of veld types in the Matopos thornveld (MacDonald 1978). This is also suggested by the residual effects of grazing in the Glen sheep trial (Mostert 1958). Similarly, some individual species at Towoomba, (eg Heteropogon contortus), responded more slowly to improved rainfall conditions under grazing during the growing season than under grazing during the winter.

The effects of fire

The effects of the fire regime have to be considered according to the season of burning, the frequency of burning and the type and intensity of fire (Trollope 1984). This section evaluates the influence of these parameters on compositional trends, and also as affected by rainfall variability and soil type. The long term trials which allow for an assessment of the effect of both rainfall variability and fire regime parameters are considered first, followed by those experiments concerned with the effects of fire parameters only.

Long term experiments: rainfall variability and fire

1. Matopos trials

Burning trials have been conducted on the Matopos thornveld and sandveld since 1947 (study 48). The effect of fire, under conditions of no grazing, was greatest on the Matopos thornveld. Annual burning at the end of the dry season caused the most marked compositional changes. The sward in 1949 was comprised principally of the perennials Themeda triandra, Cymbopogon plurinodis, Bothriochloa insculpta and Hyparrhenia filipendula. In 1963 Cymbopogon was the dominant species, Themeda had almost disappeared, and 28% of the cover consisted of annuals or pioneering species such as Aristida scabrivalvis, Brachiaria eruciformis, Digitaria ternata and Sporobolus sp, most of which were not recorded in 1949. However this change was gradual, for some 8 years after the commencement of the trial cover was dense. The change was precipitated by the poor rainfall of 1955/56 (Table A2) during which a large proportion of the perennials succumbed and were replaced by annuals. A progressive deterioration occurred subsequent to the 1955/56 season and by 1971 all plots were dominated by annuals. In 1971 Cymbopogon was the main surviving perennial, whilst Rhynchelytrum repens, Eragrostis trichophora and Themeda triandra were present in far smaller amounts.

A similar composition was present in 1971 on plots burnt bi-, tri- and quintennially at the end of the dry season, and on plots burnt annually or triennially in spring just before the first rains. However the frequency of burning had a pronounced effect on composition prior to the years of drought before 1971. In contrast, up until 1963 (under triennial burning at the end of the dry season), Themeda triandra, Eragrostis trichophora and Hyparrhenia filipendula increased, whilst Cymbopogon plurinodis and Bothriochloa insculpta decreased, and no annuals established. Plots burnt quintennially at the end of the dry season showed a similar pattern. The deterioration subsequent to 1963 under quintennial burning was less marked, and Cymbopogon and Themeda remained predominant. In contrast 14 years of protection resulted in a change from a Themeda-Cymbopogon type, with Bothriochloa insculpta and Hyparrhenia filipendula well represented, to a Themeda-Setaria porphyrantha sward accompanied by the disappearance of Bothriochloa and Hyparrhenia and the virtual elimination of Cymbopogon. Themeda had largely disappeared by

1971 due to drought, and Cymbopogon became the most prominent perennial (Kennan 1972).

The Matopos sandveld showed less response to treatments and to the drought of the 1960's (Kennan 1972). On plots burnt annually or biennially in autumn, Heteropogon contortus increased twofold in cover between 1949 and 1963 to become the dominant species, whilst Hyperthelia dissoluta, Pogonarthria squarrosa and Rhynchelytrum repens decreased markedly over the same period. Digitaria pentzii showed little change. Aristida barbicollis and Eragrostis rigidior became more conspicuous during the drier years of the 1960's. In contrast Hyperthelia dissoluta increased threefold in cover, and Heteropogon contortus decreased by half, between 1949 and 1963 on plots burnt annually or biennially at the end of the dry season. However, in the latter treatment, Hyperthelia had largely disappeared, and Heteropogon and Aristida barbicollis had become more conspicuous by 1971, ostensibly due to the 1960's drought. The differences between plots burnt annually or biennially in either autumn or at the end of the dry season illustrate the effect season of burning can have on composition. Frequency of burning was also an important variable, plots burnt triennially or quintennially at the end of the dry season differed from those burnt annually or biennially. Little change in total basal cover was recorded on a protected plot between 1949 and 1963, but composition changed. The main changes over this period were that Digitaria pentzii, dominant in 1949, decreased fourfold, whilst Hyperthelia dissoluta doubled in cover to become dominant, Pogonarthria squarrosa decreased, Rhynchelytrum repens increased, and Heteropogon contortus remained stable. By 1971 R repens had decreased and H dissoluta, although still common, was not as dominant.

2. Kruger National Park

Rainfall variability rather than the fire regime appears to be a more powerful dictate of compositional trends on the Sclerocarya caffra-Acacia nigrescens vegetation type of the KNP (Gertenbach and Potgieter 1975). Composition was monitored in 1966 and 1975, the former year within a stretch of below average rainfall years and the latter followed three years of high rainfall (Gertenbach 1980). There were no significant differences between treatments in 1975, after 21 years of treatment, which was attributed to the high rainfall and a reduction in grazing pressure (Gertenbach and Potgieter op cit). There were however significant differences between treatments in 1966. There were also major species changes between 1966 and 1975, attributed to the changing pattern of rainfall; Bothriochloa radicans and Urochloa mosambicensis were stable or increased, Themeda triandra and Panicum coloratum were stable, Tragus berteronianus was eliminated, annuals decreased, and total basal cover tended to increase. In contrast, a protected plot showed no change for total basal cover over this period, but B radicans decreased significantly whilst Digitaria pentzii and U mosambicensis increased significantly. The general conclusion was that the grass layer responded positively to any fire treatment under good rainfall (Gertenbach and Potgieter op cit).

A similar conclusion was reached for the mopaneveld of the KNP which had been subjected to fire treatments for 25 years (Gertenbach and Potgieter 1979). There were no significant differences in total cover between

treatments in 1977/78, a peak rainfall season of a number of very wet years (Gertenbach 1980). Fire treatments had however affected composition; Aristida barbicollis and Urochloa mosambicensis were more prolific on annually and biennially burnt plots, especially if burnt in August, October or December, Bothriochloa radicans was most prolific on plots burnt biennially or triennially in October, and Digitaria pentzii showed the opposite trend to Bothriochloa.

The effect of rainfall variability was not as marked on the Terminalia-Dichrostachys type of the KNP, which is a sandveld area of higher rainfall than other parts of the park (van Wyk 1972). There were no significant changes in the total basal cover of any treatment between 1954 and 1968, the former survey within a wetter era and the latter survey following a number of dry years (Gertenbach 1980). However, all treatments showed a decrease in basal cover, albeit not significant, accompanied by compositional change. Hyperthelia dissoluta, originally the dominant species, decreased over all treatments but remained a dominant species on the control. Elionurus argenteus and Loudetia simplex, initially subdominant species, decreased generally over all treatments, and particularly on the control. The trends on the control were partly the result of the sward developing a moribund condition. The frequency of burning influenced composition; Digitaria pentzii, D. longiflora, Pogonarthria squarrosa and Heteropogon contortus increased on annually burned plots. Despite these changes, the results led to the conclusion (van Wyk *op cit*) that the effect of the treatments on the grass stratum had been negligible.

Long term experiments: fire only

1. Frequency of burning

A 22 year burning trial was conducted in an Acacia nigrescens/Combretum apiculatum vegetation type in Botswana (study 50). There were no consistent differences between treatments in grass basal cover. Brachiaria nigropedata and Eragrostis rigidior declined in frequency with an increased interval between burning, whilst Schmidtia pappophoroides displayed the opposite trend. Digitaria eriantha was the dominant species in all treatment plots, but was less frequent on the control.

Robinson *et al* (study 56) found that more frequent burning over five years had significant effects on composition in the False thornveld of the eastern Cape. More frequent burning favoured grasses in general and Themeda triandra in particular, while less frequent burning favoured Cymbopogon plurinodis, Sporobolus fimbriatus and forbs. Similar results have been obtained from another experiment in the eastern Cape (study 57). Annual spring burning resulted in a 42% increase over nine years in the proportion of Themeda, while Cymbopogon decreased over the same period. Digitaria eriantha and Sporobolus fimbriatus appeared indifferent to fire treatment, and Panicum stapfianum showed no initial response, but eventually decreased.

In contrast, frequency of burning was found to have no significant effects on the total basal cover or on the composition of the Brachystegia/Julbernardia veld of the high altitude area of Zimbabwe (study 52). The basal cover of protected plots was however lower than treated plots, and there was an insignificant tendency for cover to be lower on plots burnt less frequently. The basal cover of Digitaria diagonalis, Themeda triandra and Heteropogon contortus increased between 1961 and 1975, irrespective of fire treatment. The basal cover of these three species and total basal cover decreased in protected plots over the same period, due to the sward becoming moribund. Barnes (study 53) also found no significant changes in the basal cover of individual species following two years of burning on the heavy textured Tataguru series soils of this high altitude region.

2. Season of burning

Burning at different months almost every year for 14 years had little effect on the grass sward of the sour mixed bushveld (study 51). The lowest total basal cover was recorded on the control (10,8%) and the February burns, and the highest basal cover was recorded on the April burns (14,2%). Elionurus argenteus was dominant on treatments burnt in February, April and November, and the codominant species, together with Heteropogon contortus, Schizachyrium semiberbe and Diheteropogon amplexans, of the treatments burnt in August and October, and the control. Themeda triandra was the dominant species of the treatment burnt in August, and was only a minor component of the control and the treatment burnt in February. Similarly, there was no effect of different month of annual burning over 37 years on the abundance of the dominant species of a Trachypogon- other species grassland at Frankenwald, but the control changed considerably over the same period of time (van Wijk Verkerk 1972). Pronounced effects on composition resulting from annual seasonal burning over only four years have been recorded in an induced savanna in Nigeria, West Africa (Afolayan 1978), where annual rainfall is in excess of 1000 mm. Late dry season burning promoted the growth and development of perennial grasses while early burning reduced perennial grasses and encouraged annual grasses. In contrast, five years of annual seasonal burning in the Kidepo National Park, Uganda, had no effect on composition (Harrington and Ross 1974), although the area had previously been burnt annually in a "natural" fire regime. Themeda triandra was however significantly reduced on plots protected from fire for only one year.

Experiments including fire as a treatment

MacDonald and Bisset (in MacDonald 1982) monitored the compositional response of both degraded and sound veld sites to a September burn versus no burn treatment over four seasons at Matopos (study 72). The first season (1973) experienced very low rainfall (Table A2), but was followed by three consecutive high rainfall seasons. The annual species Aristida scabrivalvis and Brachiaria eruciformis were scarcely represented on the unburnt degraded site in 1973, but reached their highest densities on this site after two seasons of above average rainfall, and declined following

the third high rainfall season. In contrast, the density of these two species continued to increase on the burnt degraded site throughout all three seasons. The two pioneer perennial species Rhynchelytrum repens and Bothriochloa insculpta both increased on the unburnt and burnt degraded patches during the higher rainfall period, but the increments were lower on the burnt degraded patches. Rhynchelytrum repens increased on unburnt sound veld over this period, but declined on burnt sound veld. The climax perennial species Themeda triandra (virtually restricted to sound veld) and Heteropogon contortus both increased on burnt veld but decreased when top hamper and litter accumulated. Heteropogon contortus therefore also increased on unburnt degraded veld. The mesic perennial Digitaria milaniana (restricted to sound veld) showed a dramatic increase with successive years of high rainfall which was unaffected by fire regime. In summary, the different species were responding to rainfall, but this response was dependent on the condition of the site, and fire had a further modifying influence on both the magnitude and direction of changes.

The effects of two individual fires on the composition of the Burkea savanna of Nylsvley have been monitored (study 21). Both fires resulted in a significant decrease in total basal cover, accompanied by a decrease in the basal cover of the dominant species Eragrostis pallens, and a less marked decrease of the second most prolific species Digitaria eriantha. A number of formerly unrecorded grasses and forbs appeared. The dry matter production of the different species following one of these fires was monitored (Grossmann and Grunow 1981). This back fire resulted in significantly less dry matter production over the following year, compared to an unburnt area. This was largely due to the significant reduction in dry matter and basal cover of the non-forage species group (including Eragrostis pallens) which had, prior to the fire, exhibited a notable accumulation of dead material. In contrast, basal cover and dry matter production of the leafier forage species group were not significantly affected by the backfire.

Joubert (1966) reports on the effects of spring burning on the grass sward for two experiments in Namibia. Perennial cover and total cover of a spring burning treatment on an unbushed plot increased over a two year drought period, while perennial cover and total cover declined on all other treatments over the same period. Similar trends were recorded on both bushed and cleared sites which had experienced only one years drought. These improvements relative to the other treatments were attributed to the increased mortality (up to 32%) of encroaching Acacia mellifera, and a reduced vigour of remaining trees, which had resulted from fire. Similarly, Pratt (1966b) describes the manifest effect of a single very hot fire on the mortality of a desert shrub Disperma on the El Barta plains of northern Kenya. A complete alteration in the flora followed the fire. The burnt area was recolonised mainly by shrubs and woody herbs such as Heliotropium, Solanum and Sericocomopsis. with some regrowth of Disperma, while grass increased within the shrub mosaic. In time these species were largely replaced by a tall dense growth of Aspilia sp (Compositae). After three years little Disperma had reestablished.

Discussion

The effects of fire on compositional trends are dependent on the general climatic regime, successful fire regimes are not maintained in semi-arid regions such as Tuli (Kennan 1972). Circumstantial evidence suggests that rainfall variability is a more powerful dictate of compositional trends in mesic savannas than the fire regime (studies 48, 49), and that the effect of both is dependent on soil type (study 48).

The parameters of the fire regime which exert a significant effect on composition of the grass sward of mesic savannas are the season of burning (studies 48, 49, 51, Afolayan 1978, Trollope 1984), and the frequency of burning (studies 48, 49, 50, 56). There is no comparative information available on the effects of the type and intensity of fire on herbaceous composition, although these parameters are known to affect the woody vegetation (Trollope 1982). The most pronounced compositional changes have resulted from annual dry season burning on heavy textured soils. The brief data available further suggest that marked compositional changes are not independent of rainfall variability, but are an interactive effect of fire and soil moisture deficits on population responses (study 48). The indirect effects of fire on herbaceous composition through the suppression of the woody component may be more important than the direct effects of fire on composition, at least on heavier textured soils in semi arid regions during critical drought years (study 3).

West (1965) has highlighted the rapid compositional changes which can ensue from protection from fire (or grazing), with some species (eg Themeda triandra) tending to die out very quickly. West (op cit) proposes that the effects of protection are an accumulation of moribund material, which eventually kills grasses. The speed at which moribund material and litter accumulate will vary greatly according to the general rainfall; in regions of high to medium rainfall accumulation of litter is very rapid. Similarly litter accumulation will be more rapid in semi-arid savannas during periods of high rainfall. However, the effects of moribund material on tuft mortality are inadequate to account for the marked compositional changes which occur under annual burning in the dry season (study 48). It is suggested that the major factor influencing such compositional changes is the indirect effect of fire on soil moisture patterns. San Jose and Medina (1975) illustrate that a single fire can result in a lowered availability of soil moisture throughout the following growing season.

There is a similar marked variation in the response of individual species to the same fire treatment as there is to the same grazing treatment. The response of any individual species is dependent on the general climatic regime, well illustrated by the stability of Themeda under an annual burning regime in high rainfall areas (eg Harrington and Ross 1974), and the species decline on the Matopos thornveld under annual burning (study 48). There is, however, a lack of population based approaches to assist interpretation of compositional changes under fire in savanna regions.

The evidence suggests that, in terms of direct effects, fire, like grazing, is a modifying rather than a controlling force on savanna grasslands. However, the role of fire varies over the savanna spectrum, and in the higher rainfall savannas the indirect effects of fire on herbaceous composition, through its suppression of the woody component

(eg Trapnell 1959), render fire a controlling force of these grasslands. Other than the effect on the woody component, there is no evidence that fire alone has caused a major change in the composition of any system. Fire and drought have caused major compositional changes on the Matopos thornveld (Kennan 1972), but there is no indication of how irreversible these changes might be, or of the residual effects sustained burning has had. The critical question is raised of whether the compositional changes under annual burning occurred as a result of the effects of fires during the drought years themselves or in the higher rainfall years of recovery following drought. It is noteworthy that the compositional changes on the controls of fire trials have usually been as pronounced as those on the treatments (Kennan 1972, van Wyk 1972).

The effects of fertilization

A limited number of fertilization experiments have been carried out in savanna regions of southern Africa, because fertilization is not considered to be economically feasible for this region.

1. Towoomba fertilization trial

The fertilizer trial at Towoomba is the longest running fertilization experiment in southern African savannas (study 59). The trial commenced in 1949, and the different species had shown pronounced differential responses to the various treatments by 1956 and 1962 (Louw 1966). The differences between species in 1962 for the four nitrogen levels applied (ammonium sulphate at N1-38, N2-76, N3-151 and N4-303 kg N/ha) and a control (N0), and for two phosphate levels (P1-19 and P2-38 kg P/ha, as superphosphate), and a control (P0) are described (Table 5). The basal cover of Cymbopogon plurinodis, Heteropogon contortus, Themeda triandra, Elionurus argenteus, Hyparrhenia hirta and Aristida bipartita decreased, whilst that of Panicum maximum, Urochloa mosambicensis, Eragrostis rigidior and Brachiaria serrata increased with increasing levels of nitrogen. Eragrostis superba, E chloromelas, Digitaria argyrograpta and Sporobolus stapfianus increased at lower levels of nitrogen but decreased markedly at the highest levels of nitrogen. The basal cover of Cymbopogon plurinodis, Heteropogon contortus, Themeda triandra, Elionurus argenteus, Brachiaria serrata, Aristida bipartita and Rhynchelytrum repens decreased, while the basal cover of Hyparrhennia hirta, Panicum maximum, P coloratum, Urochloa mosambicensis and Sporobolus stapfianus increased, with increasing application of phosphate. With the NP interaction the basal cover of Cymbopogon plurinodis decreased from 4,3 to 0,13% for the P2N0 and P0N4 levels respectively, whilst the basal cover of Urochloa mosambicensis increased from 0,05 to 3%.

The trends evident in 1962 had become accentuated by 1982 (Donaldson, Rootman and Grossman 1984). The treatments with high levels of nitrogen (N3, N4) had eliminated the members of the Andropogoneae, Digitaria argyrograpta, Eragrostis chloromelas and the Sporoboleae, and formed a sward dominated by Digitaria eriantha, Panicum maximum, Brachiaria nigropedata, Eragrostis rigidior and Cynodon dactylon. Increased

phosphate levels had little effect on their own, but compounded the effect caused by increased levels of nitrogen.

Table 5. The percentage basal cover of the grass species which reacted significantly to fertilization with sulphate of ammonia, in 1962 at Towoomba. (Data from Louw 1966)

Species	Basal cover				
	N0	N1	N2	N3	N4
<i>Cymbopogon plurinodis</i>	13,0	11,5	10,6	5,3	3,7
<i>Heteropogon contortus</i>	11,4	11,6	10,4	5,2	2,4
<i>Themeda triandra</i>	11,2	9,4	8,4	4,8	2,7
<i>Elionurus argenteus</i>	6,6	3,9	2,4	1,0	0,7
<i>Hyparrhenia hirta</i>	3,8	2,8	1,6	0,3	0,3
<i>Aristida bipartita</i>	4,5	2,7	2,1	1,8	1,2
<i>Panicum maximum</i>	0,3	0,3	2,9	4,8	4,9
<i>Urochloa mosambicensis</i>	1,2	2,5	4,9	10,1	7,6
<i>Eragrostis rigidior</i>	0,5	3,2	4,9	7,1	9,2
<i>Brachiaria serrata</i>	0,3	0,5	0,9	1,6	2,7

2. Matopos trials

The effects of nine years of nitrogen fertilization on three soil types of the Matopos region have been described (study 60). The effects of nitrogen (first applied as ammonium sulphate, then as calcium ammonium nitrate) were greatest on the Matopos sandveld, less on the red soils and least on heavy textured black clay soils (Table 6). Nitrogen applied to the sandveld at more than 135 kg/ha/annum had caused the majority of the species found on the control plot to disappear, and the yield of the remainder to decrease. *Eragrostis rigidior* had become the dominant, and virtually the only, of a total of three species; but was only a minor component on the control plot on which 18 species were found, dominated by *Hyparrhenia* spp, *Brachiaria serrata*, *Chloridion cameronii*, *Heteropogon contortus* and *Rhynchelytrum repens*. Nitrogen fertilization of red soils increased the yield of *Setaria porphyrantha* and decreased the yields of *Cymbopogon* spp, *Hyparrhenia* spp and *Rhynchelytrum repens*. Yields of an *Eragrostis* sp and *E. superba* were highest at the intermediate amounts of N applied. Annual species also showed a marked response to nitrogen fertilization, *Chloris virgata* and *Panicum astrosanguinem* increased and *Digitaria ternata* decreased at higher levels of N application. Species richness also decreased from 15 species on the control to 11 species found on the highest N application treatment. The yield of *Setaria porphyrantha* on the black soils increased as the amount of N applied increased. *Setaria* was the dominant species only at the highest level of N application, the annual *Brachiaria eruciformis* was dominant at intermediate levels of N application. *Ischmaeum brachyatherum* and

Dichanthium papillosum decreased with increasing levels of N application. Eight species were found on the control compared to five species at the highest levels of N application. The pattern of change in composition varied between soil type, according to visual records. Eragrostis rigidior took 5 or 6 years to become dominant on treated sandveld plots. In contrast, Setaria porphyrantha increased steadily to become dominant on treated plots of both the red and black soils.

Table 6. Dry matter yields of major grass species on three soil types at Matopos after nine years of fertilization. (Data from Mills 1964)

Species	Yield (kg) Kg N/ha/annum				
	0	67	134	202	269
Sandveld					
<i>Eragrostis rigidior</i>	47	859	3657	4605	4889
<i>Rhynchelytrum repens</i>	153	449	16	1	1
<i>Hyparrhenia</i> sp	318	68	0	0	0
<i>Chloridion cameronii</i>	243	0	0	0	0
<i>Heteropogon contortus</i>	198	0	0	0	0
<i>Brachiaria serrata</i>	253	1	0	0	0
<i>Eleusine indica</i>	0	0	16	74	111
Red soil					
<i>Setaria porphyrantha</i>	950	2499	3308	3265	2673
<i>Cymbopogon</i> sp	381	71	72	7	8
<i>Hyparrhenia</i> sp	457	0	32	4	48
<i>Rhynchelytrum repens</i>	124	20	0	0	0
<i>Digitaria ternata</i>	114	106	25	57	11
<i>Panicum astrosanguinem</i>	0	1	45	50	142
Heavy black soil					
<i>Setaria porphyrantha</i>	825	1077	1579	2659	2692
<i>Ischaemum brachyatherum</i>	897	208	466	564	540
<i>Brachiaria eruciformis</i>	85	728	1312	760	152
<i>Eragrostis</i> sp	155	1121	729	474	417
<i>Dichanthium papillosum</i>	101	19	17	0	0

3. Ukulinga trial

The compositional response of veld at Ukulinga, Natal, to 30 years of application of nitrogen, phosphate and lime has been reported (le Roux and Mentis 1985). Nitrogen was applied as ammonium nitrate or ammonium

sulphate (different treatments), each at three levels of application (70,5; 141 and 212 kg/ha/annum). Nitrogen had a stronger effect than lime or phosphate or both, and accounted for most of the botanical variation among the treatments. The application of nitrogen resulted in a complete replacement of the usually common species Themeda triandra and Tristachya leucothrix by other grasses, in particular Eragrostis curvula, E plana and Paspalum dilitatum. There was evidence for an interaction effect between nitrogen and phosphate; Themeda and Tristachya appeared to have a higher tolerance of nitrogen in the presence of lime and the absence of phosphate.

4. Zimbabwe highveld trials

Fertilization of the Tataguru soils of the Zimbabwe highveld with N, P and K resulted in a pronounced change in composition after only two years (study 63). The sward of this site was originally dominated by Hyparrhenia filipendula, Alloteropsis semialata, Sporobolus pyramidalis, Setaria sphacelata and Andropogon schinzii, and after fertilization was dominated by Setaria sphacelata and Sporobolus pyramadalis. The basal cover of Setaria increased threefold with increasing levels of N application, and also increased with increasing levels of P application. There was a significant N-P interaction effect on the basal cover of this species. Sporobolus pyramidalis showed the highest basal cover at low levels of N application when P was also applied. The remaining former dominant species decreased with increased levels of N application. Potassium was not found to have an effect on composition. In a sister experiment at the same location six years of N and P fertilization (N as sulphate of ammonia plus nitrolime at 168 and 504 kg N/ha/annum; P as superphosphate at 168 and 336 kg P/ha/annum) resulted in a decrease of the former dominant species Hyparrhenia vulpina and Andropogon schinzii, and an increase of Sporobolus pyramidalis (study 62). In contrast only very minor changes in composition were recorded with 5 seasons of N and P fertilization (N first as urea then calcium ammonium nitrate, P as superphosphate) of heavy textured soils on the Zimbabwean highveld (study 34).

Theron (1949) describes how the application of N completely replaced the "climax" community consisting of Elionurus, Hyparrhenia and Themeda species with Eragrostis species of a highveld grassland near Pretoria. The cover of the climax species was 28 to 30% on virgin veld, and was reduced to less than 1% on fertilized veld. Conversely the cover of Eragrostis and Cynodon species was 2 to 3% on virgin veld and increased to 30 to 32% on fertilized veld. These changes in composition became apparent within the first season of fertilization.

Discussion

Application of nitrogen based fertilizers in the mesic savanna regions of southern Africa can cause rapid and marked changes in species composition of the grass sward, which has also been noted for the highveld grasslands of South Africa (Grunow, Pienaar and Breytenbach 1970).

Application of phosphate fertilizers alone has far less effect on composition, but phosphate has an important effect through its interaction with nitrogen (study 59, 63, le Roux and Mentis 1985). There is no evidence that potassium fertilization has an effect on composition. The extent of compositional change due to nitrogen fertilization is dependent on soil type, heavy textured soils show less response to nitrogen fertilization than sandier soils (study 60). The information available is inadequate to determine which form of N applied has the greatest effect on composition, but Grunow, Pienaar and Breytenbach (1970) report for 13 fertilizer experiments in South Africa that ammonium sulphate displaced climax grasses most rapidly, and urea most slowly, when compared with ammonium nitrate and sodium nitrate. The Towoomba fertilization trial (study 59) illustrates that the response of individual species is highly dependent on the concentration of soil nutrients such as N and P. There is however no information on the effect of rainfall variability on these changes. Neither are there studies by which to compare the effect of fertilization under different climatic regimes, as fertilization studies have been restricted to the more mesic savannas. Fertilization trials in savanna regions have also always been cleared of bush before their commencement, and there is therefore no information on the influence of the woody component on grass swards which have been fertilized.

There is also no information on the persistence of compositional change resulting from fertilization once the fertilization is removed. All long term fertilization experiments resulted in the elimination of most species of the sward, illustrating the extreme sensitivity of individual species to abiotic factors.

The effects of ripping and reseedling

The effects of ripping and reseedling on composition are considered together because experiments have generally addressed the effects of both together. Ripping and reseedling form treatments of reclamation experiments, which in turn have only been conducted on areas subjectively judged to be severely degraded. Ripping attempts to principally modify the infiltration rate and soil moisture status, and thereby create a soil environment suitable for the germination and establishment of naturally available seed reserves. A second objective of ripping is to prepare a substrate suitable for reseedling. Reseeding (and replanting) is the only experimental treatment which attempts to directly manipulate the dynamics of the plant populations, and is undertaken to evaluate whether degraded areas have lost their natural seed reserves. A multitude of factors influence the success of both ripping and reseedling treatments. These are first considered below before an evaluation is made of the longer term influences of these treatments on compositional trends.

The effects of ripping

Ripping experiments have yielded variable results, and individual experiments are briefly described to illustrate the factors upon which the effect of ripping is contingent. There is firstly a paucity of

quantitative data to test the assumption that ripping exerts a direct influence on the soil moisture status. In an East African study ripping depleted soil moisture, ostensibly because of an increased surface area available for evaporation (Perreira and Beckley 1953). This suggests the possibility that negative results in ripping experiments may not always be due to a lack of seed reserves.

In a trial at Estcourt, Natal, on a red loam soil described as hard baked, ripping produced an initial improvement in the sward by promoting annuals and ruderals. The effect of the treatment soon disappeared, and at the end of the nine year trial the ripping treatment resembled the control which showed an increase in the proportion of bare ground and of an unpalatable Cymbopogon species (study 64). In contrast, ripping on the red soils of the Matopos, Zimbabwe, resulted in the establishment of a perennial grass cover including "climax" species after only four years (study 66). These changes took place during a period of average rainfall. In comparison a control showed only very minor changes over the same period.

Pratt (1962a, 1962b) reports on three year ripping experiments on three different soil types in East Africa. On a deeply gullied, calcareous clayey murram in which the upper horizon had been lost, ripping had no significant effect on the perennial cover. The annual cover was however maintained on a control. Ripping of a capped and gullied red loam soil did not improve the natural cover of annual grasses and an unpalatable perennial. Ripping of an alluvial soil type described as degraded but with substantial soil reserves did however promote a dramatic improvement in the germination, but not the establishment, of perennial grasses. There was a negligible change in the natural grass cover over the same period of time. There were significant differences between different cultivation treatments during a year of high rainfall, but these differences disappeared during a year of low rainfall (Pratt 1962b). In a further experiment in East Africa, ripping of a red sandy loam derived from gneisses and schists of the basement complex and described as severely capped, produced a slight improvement, particularly during the wet years (Perreira and Beckley 1953). In comparison there was no natural improvement in a control treatment over three years. Wilson (1962) reports on a six year ripping and reseeding experiment on the red soils of the Karamoja district, Uganda. Clearing plus ploughing promoted an increase in grass cover within a year, which later spread to surrounding cleared areas which had not been ploughed. Clearing alone had however encouraged a grass cover of perennial grasses after one year. Burning assisted the recovery of perennials on cleared areas through its control of regenerating Acacia mellifera.

The above experiments suggest that the efficacy of ripping is dependent on seasonal rainfall; low rainfall years do not promote sufficient germination and/or establishment of residual seed reserves (Perreira and Beckley 1953, Pratt 1962b). This effect appears confounded by soil type, illustrated by the comparative work in East Africa, which is also compounded by the extent to which the site had become degraded (Pratt 1962a). The extent of degradation reported in this study has obviously influenced intrinsic soil properties, on the gullied murram soil the entire upper horizon had been lost.

The effects of reseedling

Although there is a lack of direct evidence, germination and initial establishment appear highly dependent on the mean annual rainfall. Donaldson and Kelk (1970) conducted reseedling experiments with Antheophora pubescens in the Molopo area of the northern Cape during four years of drought. Germination was dependent on seeding rate. The only treatment to cause an increase in plant density was the highest seeding rate, and only on areas cleared of bush. Pratt (1962a) records for a site on alluvial soils that reseedling resulted in successful germination but that the seedlings were killed by subsequent drought. In a follow up trial (Pratt 1962b) seeding treatments were found to have a significant effect during a high rainfall year but not in the following low rainfall year.

The nature of the prevailing edaphic environment plays a definitive role in controlling successful germination and establishment. This is shown by experiments in which there is a significant interaction between reseedling and the type of cultivation (Pratt 1962b), and is supported by a number of incidental observations. In a non-statistical reseedling experiment of one year on red sandy loam soils derived from granitic parent material, differences in germination were apparent depending on how the seed bed was prepared (DuPlessis and van Wyk 1969). Donaldson and Kelk (1970) observed that awnless seeds germinated more prolifically when in cattle hoofprints and when covered with a layer of soil. Similarly, Themeda triandra germinated where loose silt had collected on the baked red soils of Estcourt (Scott 1951). An obvious corollary to the importance of the edaphic environment for germination and establishment is that the grass species chosen for reseedling must be suited to the particular edaphic environment, and is illustrated as a practical reality by a number of studies. Themeda triandra was the most successful of all species tested at Estcourt (Scott 1951). Themeda was also the only species suitable for revegetating abandoned fields on the highveld grasslands of the OFS (Smit 1972). Donaldson and Kelk (1970) found that recovery on experimental treatments was principally due to Eragrostis lehmanniana, a species adapted to the local region. Other species introduced by seed were not successful. Pratt (1962a) on each of three soil types, and Louw (1974b) on each of two soil types, similarly found that certain species were inferior to others for reseedling, even when all species could be expected to be found at the locality.

Fertilization treatments incorporated into reseedling trials illustrate that the availability of certain soil nutrients can have a marked effect on germination and establishment. Phosphate fertilization promoted the recovery of formerly abandoned fields which had been reseeded (Donaldson and Kelk 1970). Perreira and Beckley (1953) report that fertilization with dung had a significantly beneficial effect on a reseedling treatment. Louw (1974b) found that the effects of phosphate fertilization on the establishment of seed were still evident four years later.

The microenvironment can significantly influence germination and establishment. Louw (1974b) reports that cut branch cover had a significant effect on recovery in the northern Transvaal, but this effect was dependent on soil type. Responses were greater on the Shorrocks minus series of the Hutton form soils which support a Combretum apiculatum vegetation type, than on the Shorrocks plus series of the Hutton form which support an Acacia tortilis type. Pratt (1962a) found that branch

cover benefitted annual grasses on alluvial soils, but had no effect on two other soil types. In a follow up experiment on the alluvial soils (Pratt 1962b) branch cover had no effect on germination but assisted establishment. The importance of thorn cover is to both create a microclimate more amenable for germination (by shading) and to protect established grasses from grazing. The importance of shading is shown by the temperatures recorded on open areas of basalt derived soils in south-eastern Zimbabwe, which were lethal for germination (Kelly and Walker 1976). The importance of protection from grazing in areas where wild herbivores occur is emphasized by Du Plessis and van Wyk (1969) and Louw (1974b).

The amount of seed available has been found to have a significant effect on the extent of germination and establishment in both East Africa (Pratt 1962b) and in the Molopo area (Donaldson and Kelk 1970).

The woody/grass ratio has been observed to have a major effect on the outcome of reseeding trials, which has already been described for the Molopo area (Donaldson and Kelk op cit). Joubert (1966) compared the effects of a three camp grazing system with and without reseeding on composition over four years in Namibia. Each treatment was further split into bushed and cleared areas. Baseline conditions of the trial were described as severely degraded and encroached by Acacia mellifera. Reseeding was not found to have a significant effect on the recovery of the perennial component in either bushed or grazed plots, but cleared plots resulted in a threefold increase in the cover of perennials. In comparison, Pratt (1966) found that seeding was highly successful on cleared areas after three years, but had no effect on non-cleared areas. Seeding was not found to have a significant effect on yield after three seasons, but the unseeded sections were comprised principally of annuals as opposed to the perennial composition of the seeded areas.

Discussion

Having recognized some of the major influences affecting ripping and reseeding, the question remains of how important are residual seed reserves for long term trends in herbaceous composition. The present set of experiments provide little insight into this question because the majority of these experiments were short term. It is however notable that the controls of most of these experiments showed no substantial change in perennial cover (studies 3, 64, 65, 66, Perreira and Beckley 1953; Pratt 1962a, 1962b), and this effect persisted for nine years on the Estcourt site (study 64). There were two exceptions to this pattern. The first were the trends observed in the western Transvaal (Du Plessis and van Wyk 1969). This reseeding experiment was prompted because the available seed reserves in this area had been reduced by 95%, to a low of 110 seeds/m². Although seeding appeared to give an initial benefit to reestablishment (Du Plessis and van Wyk op cit), subsequent years of good rainfall promoted as good a recovery on untreated areas (study 2), and the reseeding experiment was therefore abandoned. Rainfall alone was similarly responsible for an increase in the density of desirable perennial species on both a Combretum apiculatum and an Acacia tortilis vegetation type in a reclamation experiment in the northern Transvaal (study 65). The increase was more pronounced on the Combretum vegetation

type, on which there was a significant increase in yield over four years. In contrast the Acacia vegetation type showed a significant decrease in yield over the same four years. This difference in response is accounted for by the Combretum type occurring on far sandier soils than the Acacia type.

A successional study on the Zimbabwean highveld (Strang 1974) is a further example of where seed reserves do not appear to have been depleted, or were rapidly reintroduced. The composition of known aged rested fields which had been formerly cleared and cultivated were examined. There was immediate and consistent recovery of the woody layer comprising Brachystegia and Julbernardia species. Cynodon dactylon became well established three to four years after abandonment, at which stage the fields showed a high density of shoots. The density of shoots decreased with time as composition changed from a pioneer community to a Hyparrhenia tufted community. However the grass sward began to deteriorate after ten years because of the increasing effect of the woody component.

However, a nine year study of Stylosanthes hamata in grazed pastures in Queensland, Australia (Gardener 1981), illustrates the importance of seed reserves for the stability of certain components. Individual plants proved short lived, with a half life of only three months. The majority died in their seedling year, and only 0,03% survived to the end of the third year. In most years, S hamata had to reestablish almost entirely from seed, but was a highly persistent legume in the long term owing to its consistently high seed reserves and ready regeneration from seed.

TRENDS IN HERBACEOUS YIELD AND BASAL COVER

The long term influence of the major determinants on trends in yield or basal cover of the grass sward are described below. Yield and total basal cover are the two main variables which have been used as estimates of functional patterns (McNaughton 1979) of change of grass swards in southern African savannas. It is not assumed that changes in basal cover reflect changes in total yield. The discussion places emphasis on long term trends in yield.

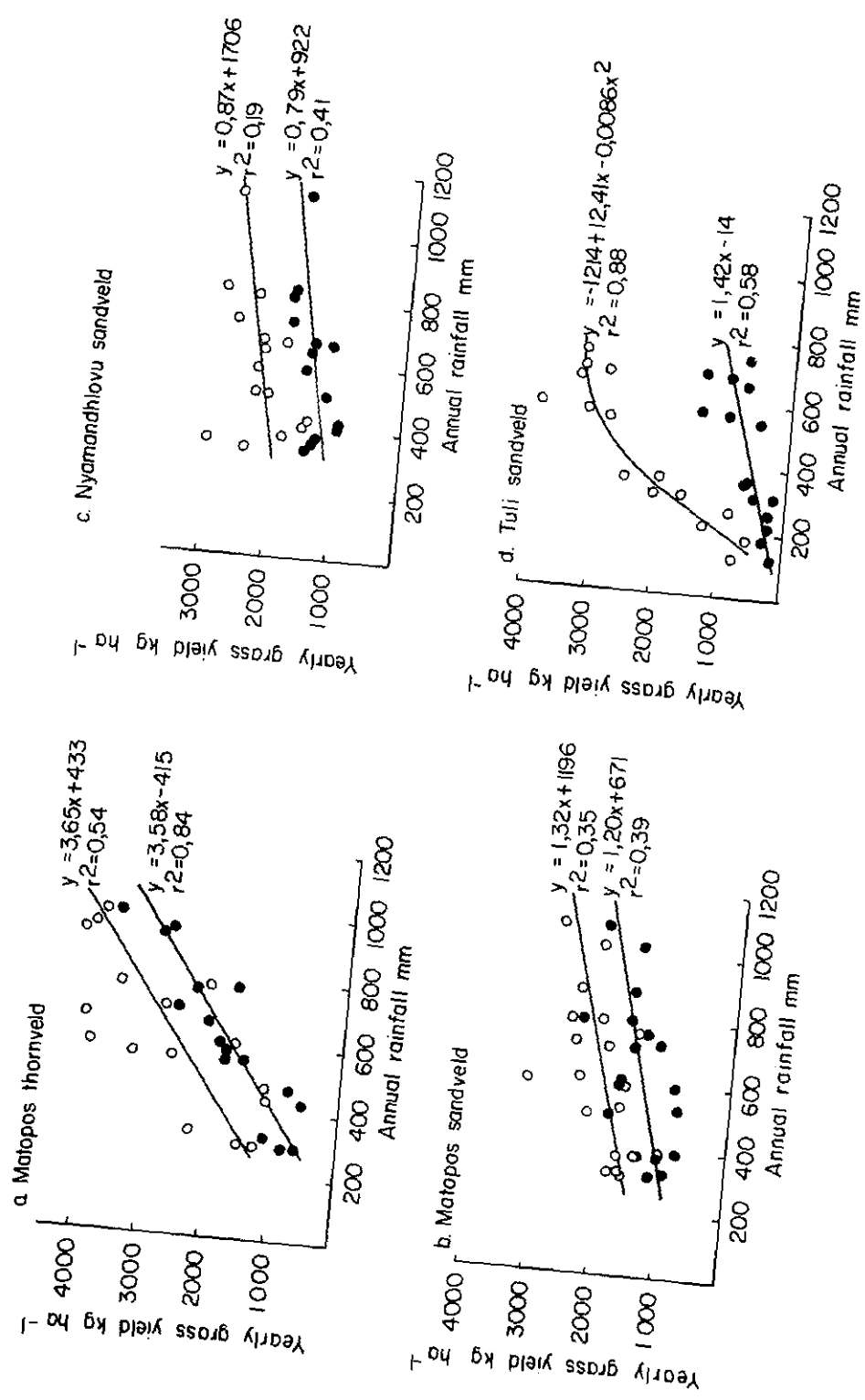
The effects of rainfall

A general positive correlation exists over Africa between annual rainfall and above ground primary production (Coe, Cumming and Philipson 1976, Deshmukh 1984). These relationships were derived from data on a regional scale. This section reviews the relationship between rainfall and yield on a site basis, and how this relationship is affected by inter- and intraseasonal rainfall variability, soil type and the woody component.

The influence of soil type

Dye and Spear (1982) have proposed a general concept of how rainfall variability, soil type and the woody component influence grass production in south western Zimbabwe, which provides a basis for evaluating additional experiments. They established correlations between annual rainfall and yield on both bushed and cleared plots at four sites, illustrating the effect of rainfall variability on yield (Figure 5). The fertile red soils of the Matopos thornveld showed a relatively high correlation of yearly grass yield with annual rainfall, and large year to year variations in these yields. In contrast, there was a poorer correlation between annual grass yield and annual rainfall, and less annual variations in these yields, on two sandveld sites. The effect of soil type on yield was further evident when comparing the grass yields of the Matopos thornveld and Matopos sandveld sites. In years of low rainfall production on sandveld is higher than production on thornveld, which Dye and Spear account for in terms of soil moisture availability. Coarse textured sandy soils allow for a greater infiltration and deeper percolation of rainwater than the heavier textured red soils, with a consequent increased moisture storage in the subsoil of the sandveld. Sandy soils enhance capillary movement of moisture less than the red soils. Sandy soils therefore have a lower opportunity for evaporative loss, thereby buffering the soil moisture available for plant growth against the effects of erratic rainfall. For a given absolute amount of water, clays have less available plant moisture because of high matric potentials (although a higher water holding capacity) than sandy soils. Therefore in low rainfall conditions there is potentially a greater amount of soil water available for growth in sandveld than in thornveld. However, thornveld produces markedly higher grass yields than sandveld in years of high rainfall, illustrating the effect of soil fertility.

Figure 5. The relation between annual rainfall and yearly grass yield in four veld types. (Data from Dye and Spear 1982)



Subsequently, Dye (1984) has successfully modelled the production dynamics of the grass sward of the Matopos red soils. Based on five years of data, weekly cumulative transpiration was related to an increment of net growth, and these increments were summed to simulate the pattern of growth through the season. Data input into the model included runoff, infiltration, storage within the soil profile, evaporation from the soil surface, uptake and transpiration by plants, and the relation between transpiration and growth. On the basis of these data, the weekly soil moisture content and the growth and development of the grassland could be realistically simulated for 32 growing seasons using only daily rainfall, weekly pan evaporation and weekly mean relative humidity data. Similarly McCown, Gillard and Edye (1974) illustrate for an Australian grassland that rainfall alone is not a good long term predictor of yield because of extreme runoff events. A simple model was developed to predict total annual yield using a relationship between potential evapotranspiration and actual evapotranspiration, soil water storage capacity and rainfall on a weekly basis.

The importance of annual carry over of soil moisture to a production model is suggested by the results of the fertilizer experiment at Towoomba (study 59). The control treatment (P0N0) of this experiment exhibited a significant correlation between annual rainfall and yield ($r = 0,532$; 28df; $p < 0,01$). This correlation was more significant if the combined rainfall of the present and preceding year of each yield figure was used ($r = 0,619$; 28df; $p < 0,01$). Dye and Spear (op cit) suggest the importance of a soil moisture carry over effect by a comparison between the Tuli sandveld site and the Matopos sandveld site of the relationship between yield and annual rainfall. The correlation between yield and rainfall for Tuli is high, indicating the efficient use of soil moisture by plants and the absence of a marked carry over of this moisture from one year to the next. In comparison the correlation between yield and rainfall for the Matopos sandveld is far lower.

There is however no direct evidence for judging whether seasonal carry over of soil moisture is the mechanism producing a significant effect. Work in the California chaparral provides negative evidence; soil drought occurred in nine continuous years regardless of vegetation cover or annual precipitation, which ranged from 300 to 800 mm (Miller, Poole and Miller 1983). The production of perennial grasses in the semi-desert southwest of America was dependent primarily on current summer rainfall and previous summer rainfall, but the influence of previous summer rainfall was an interaction effect, not a direct effect (Cable 1975). Specifically, correlations between rainfall and production were improved by including precipitation for one month at the end of the previous growing season, even though active growth had largely stopped; which was interpreted (Cable op cit) to indicate that the physiological processes occurring during this period (carbohydrate storage and bud enlargement) are important to the growth of plants the following summer. Winter and spring rainfall had little influence on the current summers perennial grass production, suggesting that seasonal transfer of moisture is not the mechanism involved. It is therefore suggested that the correlation between the previous seasons rainfall and yield in the Towoomba experiment (study 59) may in part be due to the effect of the previous seasons rainfall on stored products and tuft size.

The general effect of soil type for a given climatic regime, as evidenced by the comparison between the Matopos thornveld and the Matopos sandveld,

is also evident in the trends in total basal cover recorded in enclosure plots at Messina (study 18). The highest r values between annual rainfall and the basal cover of all grasses occurred on the more fertile soil types; a dark brown sandy loam ($r = 0,9518$; 7df; $p < 0,001$), a deep and fertile Portsmouth series soil ($r = 0,8287$; 14df; $p < 0,01$), a gravelly red loam ($r = 0,7208$; 7df; $p < 0,05$) and an undescribed soil type. There was a lower correlation between these two variables on the less fertile soils; a very sandy soil ($r = 0,4457$, 7df; $p > 0,01$), a gravelly shallow soil of the Mispah series ($r = 0,5422$; 14df; $p > 0,01$) and a shallow rocky soil of the Shorrocks series ($r = 0,6760$; 14df; $p < 0,05$). The interaction of soil nutrient availability and rainfall on herbaceous production is also indicated by the differences between treatments of the Towomba fertilization trial (Donaldson, Rootman and Grossman 1984). There were weaker correlations between rainfall and yield at the extreme lower levels of fertilizer application (NOPO and N1P1), and stronger correlations at the intermediate levels (N1P2, N2P1, N3P1). The extremely high N level (N4P0) showed a weak correlation.

The influence of the woody component

The relation between tree basal area and herbage yield is markedly hyperbolic (eg Beale 1973, Walker, Moore and Robertson 1971). Therefore removal of a proportion of woody material at low tree basal areas will have a far greater effect on herbage yield than at high tree basal areas (Figure 6). Experiments discussed below, which are generally the clearing of all woody material versus an untreated control, have to be evaluated in the light of this.

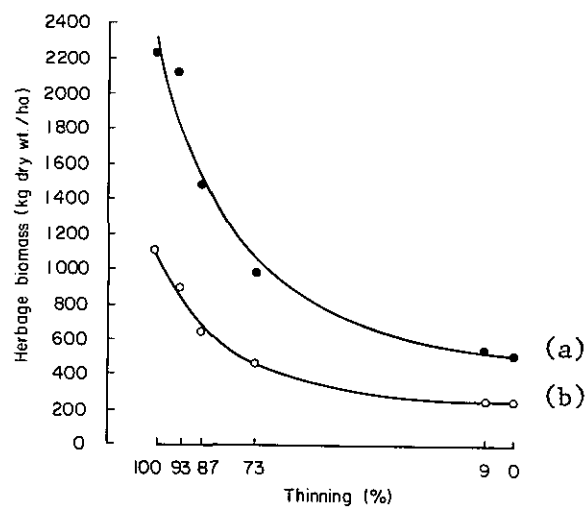


Figure 6. Relationship between mean dry weight of herbage (y) and percentage reduction of trees and shrubs (x), Wycanna, for (a) summer of 127 mm rainfall, and (b) the mean of harvests from summers and winters of differing rainfall. (Data from Walker, Moore and Robertson 1971)

Dye and Spear (op cit) further record that clearing bush consistently resulted in increased grass yields on all four sites. At the Matopos and Nyamandhlovu sites, the suppressive effect of the woody species on grass yields, due to soil moisture competition, was constant over the range of rainfall totals experienced. It was suggested that the soil moisture requirements (and use) of woody species on these sites is nearly constant from year to year, irrespective of annual rainfall. In years of high rainfall there is therefore a large surplus of moisture available to be utilized by grass. Hence, the relative increase in grass yield on cleared veld, as opposed to bushed veld, declines with increasing rainfall. In contrast at the Tuli site, the suppressive effect of the woody component on grass yields was not constant over the range of annual rainfall totals experienced, but increased with increasing rainfall. It was proposed that in such a semi-arid environment the water utilization of woody species increased when more moisture was available in years of high rainfall, leaving relatively little moisture for increased grass growth.

The general suppressive effect of woody vegetation on herbaceous production has been recorded for a number of sites (studies 6, 7, 10, 11, 12, 13, 14, 15, 16,). Pratchett (1978) has shown for one season in eastern Botswana, on heavier textured soils, that plants on cleared areas had sufficient water in the soil for growth from January through to June, while on uncleared and partially cleared areas the plants suffered from a water deficit for much of this time. Kelly, Schwimm and Barnes (1978a, 1978b) illustrate that the effect of the woody component on yield is dependent on the size structure of the woody individuals. In a selective bush clearing trial on a woodland on gneissic derived soils in the south east of Zimbabwe, the removal of larger trees only did not result in a significantly greater herbaceous yield than an uncleared area. However the removal of shrubs and small trees, and the removal of all trees and shrubs, resulted in a significantly greater yield than either an uncleared area or the area which had only the large trees removed. In comparison, the removal of varying densities of bush on a similar sandy textured soil in the Transvaal, resulted in no significant differences in plant population parameters between treatments (study 2).

The r values quoted by Dye and Spear (op cit) for regressions indicate that clearing has had an effect on the stability of yield. The relationship between rainfall and yield is stronger on bushed than cleared thornveld, suggesting that after clearing yield is not as closely linked to annual rainfall. A similar but less conspicuous trend is evident on both the Matopos sandveld and Nyamandhlovu sites. However the cleared sandveld sites show greater stability of yields than the cleared thornveld. Cleared thornveld still remains vulnerable to soil moisture deficits, although these are not as marked as the deficits on the bushed thornveld. In contrast the cleared sites at Tuli have a more variable yield than the bushed sites, and yield on this cleared site is the least stable of all the cleared sites.

The pronounced effect of the woody component on the stability of grass yield during drought years has been described for a high rainfall area in Zimbabwe (study 16). A ring barking trial was conducted over four years on soils derived from granite, which were medium grained sands over sandy loams and of fair depth and good permeability. There was on average a fourfold increase in yield on ringbarked plots as opposed to a contiguous woodland. During a season of low rainfall grass yield for the ringbarked treatment was eleven times the yield of the woodland, but only slightly

less than the yield recorded from the treatment in the previous exceptionally wet season. These results suggest an increased stability of grass yield on cleared areas of this sandveld site similar to the results observed on the Matopos and Nyamandhlovu sites.

Similar pronounced effects of the woody component on grass yield during critical drought years have also been reported for semi-arid areas. Donaldson (1967) recorded a tenfold difference in yield between cleared and bushed areas (of Acacia mellifera) in the Molopo area of the northern Cape, which was correlated with a similar order of magnitude of mortality of perennials. Moore, van Niekerk and Knight (1985) similarly report for the Molopo area that the dry mass of standing crop 22 months after bush eradication (via application of Tebuthiuron) was between 220 and 740% higher than a single non-cleared control. Likewise Joubert (1966) provides comparative data on the trends in total basal cover of two sites on the same heavy textured soil but differing in their degree of encroachment by Acacia mellifera. Two years of drought resulted in a 7 to 8 fold decrease in the basal cover of the heavily encroached site (from 11,6 to 1,6%), but only a decrease from 14,2 to 10,2% cover on a moderately encroached site. In a separate trial on a second area which was heavily encroached by Acacia mellifera, basal cover increased from 2,4 to 3,2% over four years on a bushed site, but increased from 3,2 to 11,4% on a cleared site.

The effects of grazing

There is limited detailed information on long term trends in yield or total basal cover on grazed areas. The effects of grazing are considered according to season of grazing, grazing system and stocking rate, and how these variables are influenced by climatic regime, rainfall variability, soil type and the woody component. Experiments are described along a gradient of rainfall regime.

Experiments

The effects of seven years of grazing practices on herbaceous yield of the high rainfall sandveld of Zimbabwe were investigated (study 35). All treatments were initially cleared of bush, which brought about a four to five fold increase in yield. Grazing by goats only resulted in the highest yield during the first two years after clearing, but the yields on this treatment declined markedly in the following years due to the failure of goats to contain the woody regrowth. In contrast the four cattle grazing treatments contained the woody regrowth, and showed significantly higher yields than the goat grazing treatment. Although there were initially significant differences in yield between the cattle grazing treatments, these were not apparent in a test of the residual effects of treatments, which took place after only one years rest and during a drought year.

In contrast, there were consistent differences between treatments of sheep in and out of a paddock for different periods on the moist Tall Grassveld at Ukulinga (Tainton, Booysen and Nash 1977). All combinations

of three periods in (2, 10 and 20 days) and three periods out (20, 40 and 60 days) were continued for two grazing cycles of three years, each cycle followed by a rest of all camps in the fourth year. The residual effects of the grazing treatments were examined in both of the rest years. Although differences were non-significant, there was increased yield as the period of presence was reduced from 20 to 2 days, and the period of absence increased from 20 to 60 days.

The 15 year isolation transect experiments at Matopos (study 27) illustrate the dependence on soil type of the effects of severe grazing on trends in basal cover. There was initial poor basal cover on the thornveld in 1949, due to the effects of drought. In plots grazed and then protected, total cover was lower in all those grazed for more than eleven years. In plots protected and then grazed there was a decrease in total cover in all plots protected for nine years or less. Total cover increased in plots protected for 16 years. Therefore grazing had a significant effect on trends in basal cover of the thornveld, and this effect was more pronounced on plots rested and then grazed. In contrast protection on the sandveld caused a decrease in total basal cover, and basal cover was stable or tended to increase under sustained grazing on this vegetation type. Similarly Denny and Barnes (1977) and Denny and Steyn (1978) report no significant effects of either grazing system or stocking rate on the total basal cover of the Matopos sandveld, but recorded changes in basal cover which could be related to rainfall (studies 32, 33).

The only experiment which has investigated the effects of season of grazing on trends in total basal cover is the Irvine trial at Towoomba (study 25), although total basal cover has only been reported for three seasons over 10 years (1962 to 1972). The data for the eight camps suggest a general correlation between total basal cover and annual rainfall (Table 7).

Table 7. The changes in total basal cover of the Irvine trial at Towoomba between 1962 and 1972. Rainfall figures in Table A2. (Data from Louw 1973c)

Season of grazing	1962	1967	1972
Continuous	5,77	5,71	9,46
Winter	6,00	6,30	10,65
Spring, summer and autumn	5,10	4,05	6,85
Late winter to late summer	6,70	6,60	9,20
Late summer to late winter	4,80	5,50	5,90
Spring and winter	5,15	10,30	10,00
Summer	4,10	5,30	9,19
Autumn and winter	4,05	8,80	10,07

The autumn plus winter and spring plus winter grazing treatments doubled in basal cover between 1962 and 1967, the latter a year of exceptionally high rainfall following a sustained drought, and retained high cover until 1972, over a period of moderate rainfall. The winter, midwinter to

midsummer, and summer plus winter grazing treatments had similarly increased in cover by 1972. The spring plus summer plus autumn, and the midsummer to midwinter camps showed a negligible increase between 1962 and 1972, and had the lowest basal cover of all camps. The effects of fixed seasons of grazing, and combinations thereof, on the Cymbopogon-Themeda veld of the central OFS have been described (Vorster 1975). Two experiments were run using cattle or sheep for ten and seven years respectively; and the residual effects of the treatments on yield were measured in the year following termination of the experiment, a high rainfall year. Grazing in the late summer had a depressive effect on yield, whereas spring or late winter grazing resulted in higher residual yields (although the differences were not significant). In contrast Coetsee (1975) found that grazing of the Cymbopogon-Themeda veld at Potchefstroom during autumn, winter and early summer had no effect on the yield of this summer rested veld.

Trollope (1982) provides one of the few analyses of the effects of grazing versus no grazing on yield (study 57). A multiple regression analysis of nine years of yield data showed that rainfall, the mean daily maximum temperature and goat stocking rate had a significant effect on yield, accounting for 43, 26 and 10% of the variance respectively. Bush density and veld composition score had no significant effect on yield. Goats decreased the standing crop of grass by 24%.

The results of shorter term studies on the effects of grazing and rainfall variability on yield or basal cover have been described previously. Two further long term studies illustrate that stocking rate can have a significant effect on basal cover in semi-arid regions. The effects of two cattle stocking rate and one goat stocking rate on trends in basal cover of the thornbushveld of Namibia were compared (study 45). All three treatments showed a marked decrease in basal cover over the 12 years of the trial, with the decrease most marked between 1963 and 1967 (Table 8).

Table 8. The effect of three stocking systems on the percentage rooted basal cover. (Data from van Niekerk 1980)

Year	Cattle: 5 ha/AU Total Perennial grasses		Cattle: 10 ha/AU Total Perennial grasses		Goats: 7 ha/AU Total Perennial grasses	
1963	3,88	0,95	5,13	1,35	7,18	1,95
1967	2,10	0,65	2,15	1,00	2,43	1,17
1972	1,07	0,41	1,77	1,32	3,05	2,78
1975	1,72	0,46	1,70	1,43	2,61	2,35
1977	1,96	0,65	2,68	1,83	2,96	2,75

Although basal cover of both cattle treatments increased consistently between 1972 and 1977, the increase was less pronounced under the heavier cattle stocking rate. Goat grazing in comparison resulted in the highest basal cover throughout the trial. The major effect of the heavy cattle stocking rate was that it resulted in a long term decrease of the perennial grasses in comparison to a long term increase of perennials on

the other two treatments. Fourie, Redelinghuys and Opperman (1984) report on the effects of both grazing systems and stocking rates on the basal cover of the limeveld of the northern Cape (study 44). Basal cover over all treatments increased from 5% in 1974 to 8% in 1977 due to favourable rainfall conditions, but subsequently decreased by 1979 due to the effect of the single very dry 1978/9 season. In 1982 the basal cover of a heavy continuous and a heavy rotational grazing treatment were both significantly lower than a benchmark value, while the basal cover of the other grazing treatments were not significantly different to the benchmark value. The effects of heavy continuous grazing were slightly more pronounced than the effects of heavy rotational grazing.

Discussion

The evidence suggests that rainfall variability has a primary effect on trends in basal cover or yield, irrespective of grazing treatment (studies 3, 25, 32, 33, 37, 38, 39, 40, 41, 42, 44). The relative influence of rainfall variability and grazing is dependent on the rainfall regime, soil type and woody/grass ratio. Grazing exerts little effect on trends in yield or basal cover in the higher rainfall savanna areas, but the woody grass ratio is of paramount importance in this region, particularly on sandveld areas (study 35). Grazing has a relatively weak effect on cover or yield in the sandveld areas of the more mesic savannas (studies 27, 32, 33), but exerts a more significant influence on the heavier textured soils of these areas (studies 25, 27). The relative significance of grazing to trends in yield or basal cover increases as the aridity of the environment increases, but stocking rate rather than the system of grazing has the greatest influence (studies 37, 38, 39, 41, 42, 44, 45). The woody component can exert a more profound effect than grazing on trends in basal cover or yield in semi-arid areas, particularly on heavier textured soils (studies 3, 4).

The above studies have relied on a single measurement of yield at the end of the growing season, which takes no cognisance of compensatory production in response to grazing (McNaughton 1979). Although such yield of a grazed plot may be lower than the yield of a protected plot, together with yield taken by consumers the final yield of a grazed plot may exceed that of a protected plot. A further shortcoming of the above studies is that, with the exception of study 57, none of the data sets have been analysed for a rainfall-grazing interaction.

The residual effects of grazing on yield or basal cover (Mostert 1958, Tainton, Booysen and Nash 1977, Vorster 1975) suggest that severe grazing may have a long term effect, but the persistence of this effect still needs to be investigated.

The effects of fire

The effects of fire on trends in yield or basal cover are considered according to frequency of burning, season of burning, and fire intensity, as influenced by rainfall variability and soil type.

Frequency of burning

Frequency of burning had no significant effect on basal cover or yield in the high altitude region of Zimbabwe (study 52). Basal cover of protected plots was significantly lower than that of treated plots, but yield of treated plots tended to be (not significantly) lower than that of protected plots. Annual burning for 14 years, irrespective of season, tended to reduce the basal cover of the Matopos thornveld (study 48), while plots burnt at a decreased frequency (biennially, triennially, quinquennially) tended to increase basal cover. In contrast the basal cover of the Matopos sandveld was relatively stable over all treatments for the same period. There was a non-significant tendency for basal cover of the Terminalia sandveld of the KNP to decrease as frequency of burning decreased, after 15 years of burning (study 49). The decrease in basal cover was in part related to drought. The effect of rainfall rather than frequency of burning on trends in basal cover of the mopaneveld and the Sclerocarya caffra-Acacia nigrescens veld of the KNP has been described. In these vegetation types the effects of fire were more apparent during the dry years (study 49). Annual and biennial burning had the most marked effect on the basal cover of the mopaneveld, while there were no significant differences between treatments in the Sclerocarya-Acacia type. Sweet (1982) found no consistent relationship between basal cover and frequency of burning in a Combretum apiculatum-Acacia nigrescens vegetation type in eastern Botswana, after 22 years of burning (study 50).

Season of burning

Season of burning has not been found to have as pronounced an effect as frequency of burning on long term trends in basal cover in either the Matopos sandveld or thornveld (study 48), or the Terminalia sandveld of the KNP (study 49). However the effects of annual or biennial burning on the basal cover of the mopaneveld of the KNP were most pronounced with burning in August, October and December (study 49). Season of burning had an effect on the yield of the mixed sour bushveld north of Pretoria (study 51). Treatments burnt annually in October, February and November gave significantly higher yields than treatments burnt in April or August. In contrast the February burns had the lowest basal cover and the April burns had the highest basal cover of all treatments. Trollope (1984) describes the short term effects of the season of burning on a Themeda triandra dominated grass sward in the eastern Cape. There was no significant difference in grass yield between an area burnt in midwinter and an area burnt immediately after the first spring rains. In comparison burning in midsummer caused a 37% reduction in grass yield during the first growing season. The standing biomass of grass at the end of the second growing season was still 31% lower than the areas burnt during spring and midwinter (Trollope 1980). In contrast a midsummer burn when the grass was dormant during a drought period had no deleterious effect on grass yield when compared with burning immediately after the first spring rains, indicating that the effect of a burn is dependent on the physiological state of the plants.

Type and intensity of fire

There is limited information on the type or intensity of fire on long term trends in basal cover or yield. Trollope (1982) performed a multiple linear regression on nine years of yield data from the False thornveld of the eastern Cape, using fire intensity, annual rainfall and the mean maximum daily temperature as the independent variables. Fire intensity had no significant effect on grass yield, while annual rainfall accounted for 40% of the variance and mean maximum daily temperature accounted for 20% of the variance. Trollope (1984) also found that backfires significantly reduced the yield of grass by 10% during the first growing season when compared with headfires, because backfires maintained critical temperatures for a longer period.

Discussion

Despite the paucity of data, certain general trends of the influence of fire on long term trends in basal cover or yield are evident. Fire appears to exert a weak long term effect on cover or yield in the higher rainfall savanna regions (study 52). Similar results have been reported for the relatively high rainfall Tall grassveld of Natal. Different frequencies of burning for 20 years at Thabamhlope did not result in significant differences (Edwards 1968). The basal cover of a control was however significantly less than the basal cover of treatments. A 25 year burning trial at Ukulinga in Natal produced similar results (Tainton *et al* 1978). Fire also has a weak effect on basal cover and yields in the sandveld areas of the more mesic savannas, but a more pronounced effect on cover and yields of the heavier textured soils of these areas. This pattern is evident in the Matopos (study 48) and in the KNP (study 49). However, even on the heavier textured soils, the effects of rainfall variability can overrule the effects of fire (Gertenbach and Potgieter 1975, study 48). Evidence suggests that the most important effects of fire on the basal cover of heavier textured soils in the semi-arid regions is through the indirect effects of fire on the woody component (study 3).

The effects of fertilization

The importance of soil nutrient limitation for the production of southern African savannas is demonstrated by the pronounced effects fertilization experiments have on yield. The effects of fertilization are dependent on both the general rainfall regime and on rainfall variability. In the 30 year fertilization trial at Towoomba (study 59) the average yield over all treatments was significantly correlated with annual rainfall ($r = 0,757$). The efficacy of fertilization was dependent on annual rainfall, as no significant treatment effects occurred in two of the years which were both relatively dry years compared to preceding years. The yield response curves constructed by Donaldson, Rootman and Grossmann (1984) also demonstrate the markedly different response to fertilization between wet and dry years. Grunow, Pienaar and Breytenbach (1970) reviewed 13 N

fertilizer experiments in South Africa, and found a fairly consistent correlation between summer rainfall and yield.

There was a significant difference in mean hay yields over 30 years between the N, P, and NP treatments (Donaldson, Rootman and Grossmann 1984), and a highly significant NP interaction (Louw 1968). Both N and P fertilization increased yields. For N fertilized veld only, the yield peaked at the N2 level in the long term, but yield peaked at the N3 level when P was added. During dry years the yield peaked at the P0N1, P1N1 and P2N3 levels. Barnes (1956) and Mills (1968) respectively recorded similar effects of three years of N, P and NP fertilization on the yield of the Tataguru series soils of the Zimbabwean highveld, and on three soil types at Matopos. Barnes (op cit) found that there was a limit to the increase in yield which could accrue from increasing N, and that potassium had no significant effect on yield either directly or through interaction with other nutrients.

The dependence on soil type of the effect of fertilization on yield is illustrated by a nine year trial at Matopos, on sandveld soils, red soils and black clay soils (Mills 1966). Yields at first increased and then declined along a gradient of increasing application of nitrogen. The greatest yield resulting from N application, irrespective of the amount of N applied, was recorded from sandveld, which also gave the greatest increase in yield over N0 in all years except 1962, when the composition changed to Eragrostis rigidior. The general response to fertilization was less on the red soils and least on the black clay soils. The sensitivity of sandveld to fertilization is further suggested by the residual effects of fertilization after two years at Morapedi in Botswana (Anon 1980).

TRENDS IN SOIL VARIABLES

Three main sets of soil variables are considered, soil water including infiltration and runoff, the soil physical environment including soil losses, and the soil chemical environment. Because of the paucity of information available for each of these, the effects of each determinant are generally considered together.

Soil moisture, infiltration and run-off

1. Soil moisture and infiltration

Kelly and Walker (1976) report for a study in the south-east of Zimbabwe that the infiltration of water into a basaltic derived heavy textured soil completely covered by litter was nine times faster than that for a bare soil. The amount of litter was in turn found to be related to the pattern of land use, and it was estimated that the litter cover of intensely utilized areas (23%) was significantly less than moderately or lightly utilized areas (45 and 68% respectively). van den Berg, Roberts and Vorster (1976) similarly recorded for a Cymbopogon-Themeda highveld grassland, that the rate of infiltration is highly correlated with the basal cover of perennial grasses. The basal cover of perennial grasses was in turn influenced by the long term effects of grazing during fixed seasons and combinations of seasons. The effect of sustained overgrazing on infiltration rate has also been described for the red soils of Matopos (MacDonald 1978). This soil type exhibits a mosaic of degraded patches in a matrix of sound vegetation dominated by Heteropogon contortus. Soil moisture at the end of a growing season during a drought year was lower on degraded patches than on the sound veld. Correlated with this was a reduced infiltration capacity (< 50 mm/hr) on degraded veld as opposed to 100 to 200 mm/hr on soundveld, which was measured in the following dry season.

Fire has been observed to affect the soil moisture status. Cook (1939) recorded that a plot unburnt for several years had a higher soil moisture content in a single dry season measured than a plot burnt, but there was little difference between the two in summer. The protected plot also had a water retaining capacity of 90% as opposed to 75% on the burnt plot. Webber (1979) recorded for duplex soils derived from granite in the KNP, that increased frequency of burning dramatically decreased soil moisture. Sweet (1982) recorded for a soil derived from acid-igneous and granitic parent material that the moisture holding capacity increased slightly with increased burning frequency. San Jose and Medina (1975) found in the central llanos of Venezuela (mean annual rainfall 1334 mm) that a single fire in the dry season resulted in a lowered soil moisture status of a burned area, compared with an adjacent protected area, throughout the entire following growing season (Figure 7).

Some inexplicable effects of fertilizer treatments on infiltration rate have been recorded in the Towomba trial (study 59). The highest infiltration rate in the first 5 to 15 minutes was recorded on the control

rather than on the N and N+P treatments. However, the fertilizer plots showed higher infiltration rates than the control over the first hour as a whole. Donaldson, Rootman and Grossman (1984) suggest that this effect is a result of fertilizer causing marked increases in compaction of the soil.

There has been no long term experimental work or monitoring in savannas of the amount of water lost through deep percolation, but this process was monitored for 16 years in the Pretoria region (Theron 1964). Lysimeters were installed to estimate percolation to 62 and 122 cm under natural grassland, 122 cm under maize crops, and 168 cm under fallow fields, although the soil type is not described. Leaching took place every year in the fallow lysimeter, with an average of 22% of the annual rainfall leached (of a mean rainfall over the 16 years of 688 mm). In the cropped lysimeters an average of 11% of the annual rainfall percolated through. Under natural grassland only 4% of the annual rainfall percolated through to 122 cm, although 6% and 11% percolated to 91 and 61 cm respectively. The amount of water percolating through to each of the three layers under natural grassland in any year is significantly linearly correlated with the annual rainfall ($r = 0,79$ for 61 cm; $r = 0,78$ for 91 cm; $r = 0,82$ for 122 cm; all 14df; all $p < 0,001$). During dry years there was effectively no percolation to 122 cm under natural grassland.

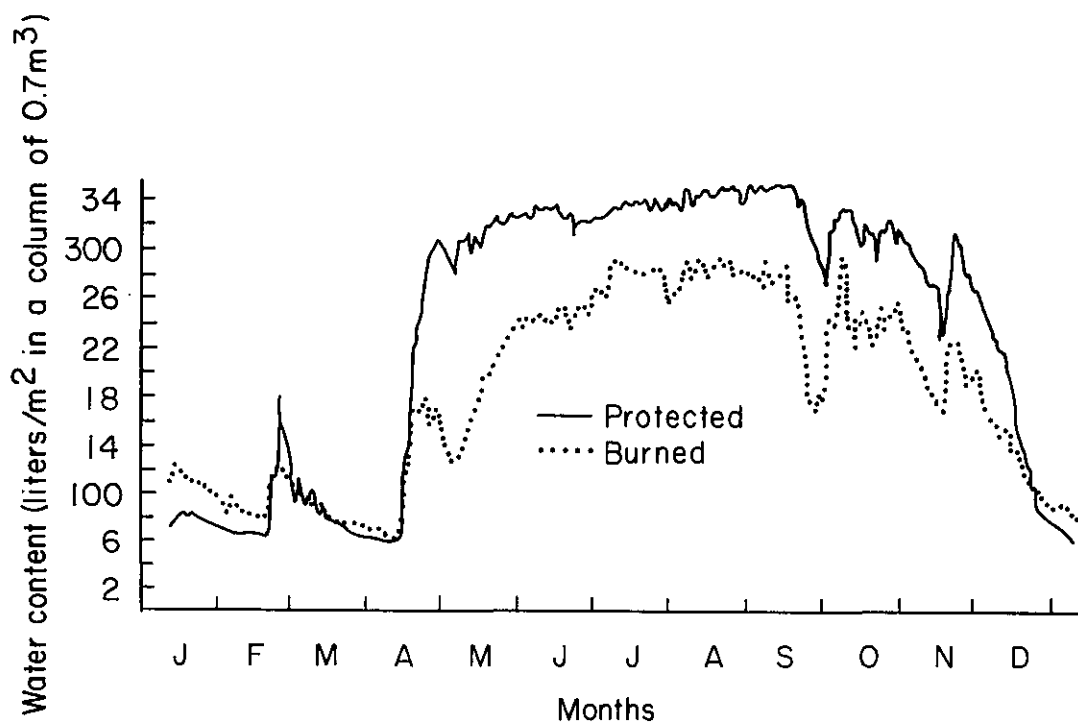


Figure 7. Trends of total soil-water content in protected and burned plots at Calabozo, Venezuela. (Data from San Jose and Medina 1975)

2. Run-off

The results of runoff experiments corroborate the findings of experiments on infiltration rate. In three separate long term experiments, the highest runoff consistently resulted from areas kept bare, and the least runoff from areas protected by natural vegetation (Barnes and Franklin 1970, Du Plessis and Mostert 1965, Haylett 1960). These three experiments included the Matopos sandveld (study 67), and two different red sandy loam soils supporting highveld grassland (Du Plessis and Mostert *op cit*, Haylett *op cit*). Runoff from the Matopos sandveld from areas clipped periodically during the growing season was significantly higher than protected vegetation (Barnes and Franklin *op cit*), but moderate utilization of a Pretoria highveld grassland by grazing and winter burning did not materially increase runoff (Haylett *op cit*). A study in the Themeda-Cymbopogon grassland of the OFS using a rainfall simulator found that basal cover had a marked influence on run-off, while slope had no significant effect (Snyman, van Rensburg and Opperman 1985).

Burning in general, and season and frequency of burning, can significantly influence the rate of runoff. On the Matopos sandveld annual burning in the mid-dry season resulted in the second highest rate of runoff after areas kept bare, and which was a significantly higher rate of runoff than on areas burnt annually just before the rains (Barnes and Franklin *op cit*). Quadriennial burning resulted in a significantly lower rate of runoff than annual burning on this soil type. An important contrast was recorded on the Tall grassveld of Natal (Scott 1972), where the highest runoff occurred on completely protected areas, due to the sward becoming moribund, and the lowest runoff occurred on annual rather than biennial or triennial burning treatments. On managed areas of a highveld grassland in the OFS, the highest runoff and soil loss occurred when veld was burnt and grazed, and was nearly three times that on veld moderately grazed but not burnt (Du Plessis and Mostert 1965).

Soil loss and soil physical properties

The patterns of runoff recorded in the above experiments tend to reflect the patterns of soil loss. On the Matopos sandveld, the rates of soil loss from areas kept bare were tenfold those of areas protected (study 67). There were no significant differences in rates of soil loss between areas protected and the other treatments, although annual burning in the mid-dry season had the second highest rate of soil loss following areas kept bare. Similarly the highest rates of soil loss recorded on the highveld grassland regions were from areas kept bare, and the lowest from protected areas (Du Plessis and Mostert 1965, Haylett 1960). A rainfall simulation study in the Themeda-Cymbopogon grassland of the OFS found that soil loss was highly significantly related to basal cover, but slope showed no significant relationship (Snyman, van Rensburg and Opperman 1985). In the KNP, 25 years of annual August burning has caused the loss of 33% of the orthic and perched gley horizons of a duplex soil through erosion, when compared with a control (Webber 1979).

The soil losses which have occurred on grazed areas also appear to have affected particle size structure. Strang (1974) compared three pairs of

adjacent grazed and protected sites on sandveld of the Zimbabwean highveld. Examination of soils on these sites indicated a strong tendency for the coarse sand fraction to be greater where grazing pressure was severe than in protected sites. These differences occurred to a depth of 30 cm, and were thought to be due to the removal of finer particles by runoff during heavy rainstorms combined with the activity of termites. Ebersohn (1962) concluded that heavy grazing on the dolomiteveld and limeveld of the northern Cape had diminished the percentage clay in soils and increased the percentage of sand and silt. On the grasslands of the Acacia woodlands at Talegaon, India, consistently overgrazed areas have a clay content of 8 to 36% as compared with 50 to 69% on adjacent cut and grazed areas (Bharucha and Shankarnarayan 1958), with a corresponding difference in the coarse sand fraction of 22 to 49% versus 2 to 3% respectively. Webber (1979) did not record any consistent effects of fire on particle size distribution of soils in the KNP. Burning in the KNP did however tend to influence compaction, resulting in surface crusting and a higher surface bulk density. Trapnell et al (1976) also noted that late season as opposed to early season annual burning of coppice plots in Zambia resulted in the compaction of the surface soil and a liability to surface soil wash (study 55). Similarly Brookman-Amissah et al (1980) found that bulk density was highest under late burning, and least under complete protection, after 27 years of annual burning in northern Guinea savanna in West Africa.

Soil chemical properties

The influence of rainfall

No information could be found in the literature pertaining to the effects of rainfall on soil chemical properties in savannas. However, the cation and nitrate loss in leachate of fallow land, cultivated fields and natural grassland near Pretoria was recorded for 16 years (Theron 1964). The nitrate content of the percolate from the fallow lysimeter was maintained at about 60 ppm for the first 25 years of the experiment (recordings on the fallow lysimeter were initiated in 1930), but after this suddenly decreased to an average of only 14 ppm. Theron (op cit) concluded that the point of exhaustion of the humus present in the virgin soil had been suddenly reached. Under natural grassland effectively no nitrogen was lost. Considerably more Ca and Mg ions and considerably less Na and K ions were lost from the soil under cultivation than from the soil under its natural grass flora.

The influence of grazing

No information is available for African savannas. Bharucha and Shankarnarayan (1958) found that consistent overgrazing affected the chemical properties of the soils of Acacia woodlands at Talegaon, India. Organic matter content was low on overgrazed soils (1,14 to 1,20%) compared with cut and grazed soils (2,06 to 2,67%). The base exchange

capacity ranged from 47,3 to 53,0 me % on cut and grazed soils, but only ranged from 28,7 to 31,0 me % on overgrazed soils. Likewise, the total exchangeable bases were consistently low in the overgrazed soils (range 27,2 to 28,0 me %) as compared to the cut and grazed soils (range 41,2 to 48,8 me %); as was also exchangeable Ca (range 12,0 to 14,3 versus 31,0 to 31,8 me % respectively).

A possible major mechanism accounting for extensive nutrient loss following overgrazing has been proposed by Charley and Cowling (1968), based on their experience of the semi-arid regions of Australia. Australian arid zone soils are notable for their weak organic development, low content of nitrogen, and the extent to which nutrients in organic form are concentrated near the surface (upper 10 cm). Erosional loss of the upper section of the profile following overgrazing could remove 35% of the total circulating pool of nitrogen and 45% of the organic matter, and probably a similar amount of phosphorus. Charley and Cowling (*op cit*) describe that perennial saltbush *Atriplex* communities which were previously heavily overgrazed and eroded did not reestablish even after 13 years of rest and with reclamation measures, although areas which had been heavily overgrazed, but where the soil had not been disturbed, quickly returned to the original condition. The difference in response is attributed to the irreplaceable loss of nutrients following overgrazing.

The influence of fire

Daubenmire (1968) has proposed that nitrogen and sulphur are volatilized to some extent during a fire, while the other macronutrients are transformed into simple salts that are water soluble and hence immediately available at the soil surface. This suggests that the long term effects of burning would be to decrease soil N and S, and to increase the pH, the availability of exchangeable bases, and soil P content. However the studies reported from savanna regions indicate a variable long term response of soil chemistry to burning.

1. pH, exchangeable bases, base saturation and P content

The pattern described above with respect to exchangeable bases, pH, and P content has been observed on soils derived from acid igneous parent material in eastern Botswana (study 50). After 22 years of burning, there was a tendency for pH to increase with increased burning frequency owing to the concomitant increase in exchangeable bases, notably Ca, Mg and K. Phosphorus levels also showed a marked increase with increasing burning frequency in the surface 2 cm. Both early and late season annual burning of a miombo woodland in a high rainfall area of Zambia markedly increased the pH, exchangeable Ca and Mg, and phosphorus status of these sandy soils, when compared with a protected area (study 55). Burning in the late season had a greater effect than burning in the early season. There was however no effect on exchangeable K or on the cation exchange capacity. Comparable results were obtained in a three year annual burning experiment in West Africa, which took place in a *Burkea/Detarium* vegetation type on

moderately deep, brown sandy loam soils (Afolayan 1978). Both early and late season burning increased the pH, P status, and exchangeable Ca, Mg and K content of the upper 0-10 cm layer, but had no effect on the 10-20 cm layer. Similar results were observed in a three and a half year burning trial conducted on an Acacia savanna pasture in Uganda (Harrington 1974). Both early and late annual burning increased the available Ca and P when compared with unburnt plots, and caused a tendency for an increase in exchangeable K. There were no differences between early and late burns. There was an increase in pH >0,3 due to burning.

In comparison a number of studies have recorded the converse. Strang (1974) found that 30 years of annual burning of a grassland firebreak on the Zimbabwean highveld had lowered the pH and exchangeable bases of the upper 10 cm of the soil compared to an adjacent woodland. The pH of the firebreak and woodland were 4,6 and 5,0 respectively while the exchangeable bases were 1,36 and 2,27 me % respectively. Strang concluded that leaching and surface washing in the unprotected firebreak soil had increased acidity and lowered exchangeable bases in comparison with the soil under woodland. This effect was not detected in a comparison of a second firebreak, burnt in excess of 30 years, and an adjacent woodland (Strang op cit). White and Grossmann (1972) report on the chemical fertility of a soil under a Trachypogon-other species grassland at Frankenwald, after 38 years of seasonal burning, compared with that of an unburned control. Burning caused a significant decrease in the concentrations of individual cations (Ca, Mg, K, Na), and in the percent base saturation of the soil, irrespective of the month of burning. There was however no significant change in pH. The decrease in base saturation of the soil was greater after a spring burn, when rain fell in greater amounts and more intensely, than after a winter burn. White and Grossmann (op cit) concluded that these changes were the result of accelerated removal of plant ash by surface runoff. In contrast Cook (1939) found that annual burning increased the pH of a soil in close proximity to Frankenwald.

Long term burning trials from West Africa suggest similar patterns to those reported by White and Grossman (op cit). Meaningful comparisons of the effects of fire in West African trials can only be made between the early and late burnt plots, because of the radical vegetation changes which have occurred on protected plots. Early burns are far less fierce than late burns, and late burns would therefore be expected to have a greater long term effect on soil chemistry if the hypothesis of Daubenmire held. There were only slight differences in soil chemical properties of an early burnt, a late burnt, and a protected plot, after 28 years of seasonal burning in a north eastern Ghana savanna (Brookman-Amissah et al 1980). Soils are described as savanna ochrosols, and are fine sandy soils and fairly nutrient rich. With one exception, significant differences were only apparent in the topsoil sample (0-5 cm). Soil pH was slightly higher under early burning than in the other treatments. Available phosphorus was marginally significantly higher only in early burnt as opposed to protected plots. Exchangeable potassium was lowest in the late burnt plots at all depths, but this did not appear to be a treatment effect (Brookman-Amissah et al 1980). Higher bulk densities of late burnt plots suggested these were subject to increased runoff.

Moore (1960) and Oguntala (1980) both report on the effects of 30 and 50 years respectively of an annual burning trial in the derived savanna zone of Olokomeji, Nigeria. Moore found that available P (but not total P) was

50% higher in the early burnt plot than in the late burnt or protected plots. Cation exchange capacity (closely correlated with organic matter content) was higher in the early burnt than the late burnt plot, and intermediate in the protected plot; exchangeable cations (Ca, Mg and K) showed the same trend as exchange capacity. pH values, which were closely correlated with saturation percentages, were lowest in the protected plot. Oguntala (1980) , who inexplicably does not refer to Moore's results, found that available P in the top 10 cm was highest in the late burnt, least in the early burnt, and intermediate in the protected plot. Cation exchange capacity was highest in the late burnt plot, but the exchangeable cations Ca, Mg and K were higher in the early than the late burnt plot. There were no differences in pH between early and late burnt plots. No attempt is made here to explain the differences between the two sets of results for the same trial.

A number of studies have recorded no real changes in pH, exchangeable bases and P status of soils under burning. Fifteen years of different frequencies of burning and a control had no significant effect on the exchangeable bases of soils of the Zimbabwean highveld, but different subplot treatments of slashed versus not slashed had a highly significant effect on exchangeable bases (Strang 1974). Barnes (1956) also recorded no significant effect of two years of burning on the pH of the Tataguru series soils of the Zimbabwean highveld. Harrington and Ross (1974) found that five years of fire treatment had no significant effects on the pH, exchangeable Ca and K, or the P status of soils of the Kidepo National Park in East Africa, although P content tended to be depressed by protection. Coutts (1945) concluded from experiments using soil samples from the Estcourt station in Natal, that the influence of veld burning on base exchange capacity is very small and probably transitory, although the effects of burning on exchangeable bases themselves are not reported.

2. Nitrogen, carbon and organic matter

The effects of burning on soil nitrogen and organic matter status have been as variable as the effects on pH and exchangeable bases. Sweet (1982) reports an increase in organic carbon in the more frequently burned plots in eastern Botswana. Similarly Strang (1974) found a higher carbon content in the upper stratum of a firebreak soil burnt for 30 years than in an adjacent soil supporting woodland, on the Zimbabwean highveld. Strang also recorded a significantly higher nitrogen content in an unslashed plot burnt every four years, than in any other treatment of a 15 year burning trial. It was concluded that with slashed material on the ground there was probably a hotter fire causing increased volatilization of nitrogen (Strang op cit). Twenty three years of protection from burning had no effect on the nitrogen or organic matter content of a sandy soil in Zambia (study 55). This was attributed to the disposal of litter by large populations of both humus feeding and of wood and litter feeding termites. Trapnell et al (1976) suggested that fire promoted the return of material (and bases) from the woodland canopy, while the termites depleted this return by consuming unburnt litter, the derived bases gradually becoming concentrated in the large termite mounds, thereby maintaining a low level of organic content in the soil.

Harrington and Ross (1974) similarly recorded no effects of five years of burning on the percentage organic matter or nitrogen index of a soil in the Kidepo National Park, East Africa. Harrington (1974) also reports that three years of burning had no effect on the percentage organic matter of a soil supporting *Acacia* shrub savanna in Uganda, but that soil nitrogen content was reduced slightly but significantly with increased frequency of burning. There was however no difference between early and late burning. Four years of early season annual burning had little effect on the nitrogen content of a soil in West Africa, but late season annual burning reduced the nitrogen content of these soils (Afolayan 1978). Significant losses of organic carbon and total nitrogen from a highveld grassland soil were recorded after 28 years of seasonal burning (White and Grossmann 1972), and a slight loss of nitrogen from the same type of grassland soil after 6 years of annual burning was reported (Cook 1939).

The long term burning trials in the derived savannas of West Africa provide similar results. Brookman-Amissah *et al* (1980) report that the percentage organic matter and the percentage total nitrogen in the topsoil (0-5 cm) were both highest without burning, lower with early burning and least under late burning. Moore (1960) recorded similar trends for the percentage total nitrogen; but organic matter content of the upper 20 cm of the early burnt plot was 30% higher than that of the late burnt plot, with intermediate values for the protected plot. Similar differences in the percentage organic matter and the percentage total nitrogen between plots in this experiment were obtained by Oguntala (1980) 20 years later.

Isichei and Sanford (1980) estimated that 12 to 15 kg/ha/year of nitrogen are lost by burning through volatilization in a derived savanna in western Nigeria, and comment that it is difficult to reconcile an annual loss of this magnitude with the lack of change reported in long term experiments. They suggest that the nitrogen lost may be almost replaced by fixation by blue green algal crusts and by input with rain.

The influence of fertilization

Fertilization quite expectedly has a pronounced effect on soil chemical properties. Grunow, Pienaar and Breytenbach (1970) report that a decrease in pH with increasing application of N, but not with increasing application of P, has been a general result of fertilizer trials in South Africa. Changes of as large as three units pH have been recorded for depths up to 45 cm. The only detailed study in savanna regions of the effect of fertilizers on soil properties is the trial at Towoomba (study 59). Thirty years of fertilization significantly reduced pH from 6,1 (mean of NO treatments) to 3,5 (mean of N4 treatments). Application of phosphate had no effect on pH. Increasing application of N resulted in a significant reduction of the exchangeable cations Ca, Mg, K and Na. The order of magnitude of the difference between the control and the highest application of N treatment on the concentrations of these cations is sevenfold for Ca, fivefold for Mg, and twofold for K. In comparison increasing application of phosphate resulted in a significant increase in the concentration of Ca, K and Na, but not of Mg. Phosphate fertilization produced an expected significant increase in the P content of the soil, from a mean of 0,6 ppm on the control to 197 ppm on the

highest phosphate application treatment. Increasing application of nitrogen increased the total nitrogen content of the soil during the first 13 years of the trial (Louw 1969), but the nitrogen content of the soil was relatively constant throughout all treatments after 30 years of fertilization (Donaldson, Rootman and Grossmann 1984).

Increasing application of N also increased the carbon content of the soil. There was also a tendency for an increase in the carbon level as a result of phosphate fertilization, particularly at the lower levels of N fertilization. The C/N ratio decreased significantly from the lowest to highest level of N fertilization.

The speed with which fertilization can induce changes in soil chemical properties is shown by changes on the Tataguru series soils of the Zimbabwean highveld after two years of fertilization, in which pH dropped by 0,3 units. In a separate experiment on the same soils three years of fertilization significantly lowered the pH by 1,5 units (Barnes 1956).

The influence of the woody component

There is evidence that a primary influence on soil nutrient fluxes is the vegetation component itself (Strang 1974). The effect of individual trees on soil nutrient status has been reported for a wide variety of circumstances. Bosch and van Wyk (1970) found that soils under trees in the western Transvaal were enriched in N, P, Ca, Mg and K compared to soils in the open. Donaldson (1969) noted a similar effect of Acacia mellifera on heavy loam soils of the Molopo region of the northern Cape. Dyer (1983) provides correlative evidence of a change in the relative distribution of some soil cations (Ca, Mg and Na) in the soil profile as a result of changes in the woody/grass ratio, for both coarse and fine textured soils across a spectrum of the savanna types of southern Africa. In the sand sheet (Goz) soils of Sudan, 12 years of Acacia senegal fallow on soils previously cultivated influenced soil fertility (Gerakis and Tsangarakis 1970). Acacia senegal increased total nitrogen in the 0-20 cm layer, and organic carbon to a depth of 130 cm, but had no effect on soil texture, pH, available P and available K. The higher nitrogen content in the topsoil may have been partly caused by symbiotic fixation. Similarly, Acacia albida has promoted nutrient enrichment of mantle soils (loamy sands to clay loams) (Radwanski and Wickens 1967). The uppermost horizons of the profiles under A albida contain more organic carbon, nitrogen and phosphorus than soils without A albida. However, concentrations of available Ca, K and Mg were lower in soils under A albida than in soils without.

Similar effects have been recorded in both desert communities and neotropical savannas. Soil nitrogen content decreased significantly as a function of radial distance from the centre of the shrub canopy in a desert wash plant community on a gravelly sandy loam granitic alluvium in the Mojave desert (Garcia-Moya and McKell 1970). Soil nitrogen content also decreased significantly with depth, and was closely related to shrub species and their root distribution patterns. Legume shrubs were not significantly greater in nitrogen than non-legume shrubs, and both types served as a reservoir for soil fertility rather than in any significant participation in symbiotic nitrogen fixation. In a protected desert

grassland at the Santa Rita experimental range, Arizona, there was increased availability and increased total amounts of N and S under mesquite trees than in the open (Tiedemann and Klemmedson 1973). Phosphorus showed a slight, although significant, difference in availability between soils, but total P was the same. A threefold higher level of organic matter in soil under mesquite probably contributes to increased availability of P. Differences in total K and its supply to the test plants were not detected between the two soils. Five species of neotropical savanna trees growing on infertile ultisols derived from granite and metasedimentary parent materials in Belize, North America, showed preferential enrichment of Ca, Mg, K, Na, P and N of the superficial soil layers beneath their canopies when compared with adjacent open savanna (Kellman 1979). The species differed in the extent of their effect. Enrichment has been achieved without deep rooting by trees, indicating that the capture of precipitation inputs has been the major mineral nutrient source.

One system scale case has been monitored of a change in soil nutrient status following a change in vegetation in the Murchison Falls National Park, Uganda (Hatton and Smart 1984). The exclusion of large herbivores from a *Sporobolus-Setaria* grassland for 24 years resulted in a pulse of regeneration of *Acacia sieberiana* (Smart, Hatton and Spence 1983), and a build up of soil organic matter and a release of major nutrients into the soil (Table 9; Hatton and Smart 1984). There was an associated dramatic increase in extractable Ca, Mg and K, although Mn levels declined. Potassium showed approximately a 5-fold increase, and Ca and Mg a 2- to 3-fold increase. The increase in extractable cations was associated with an increase in pH of about 1,5 units. Soil organic matter content and organic carbon both increased by 20 to 30%, and nitrogen increased by 50%. Labile fractions of organic and inorganic P showed a 7-fold and 4-fold increase respectively, although a slight decline in total P was detected. The red brown loam soils had developed a darker brown humus layer, and the humic substances had diffused up to 1m down the profile. With the recent disappearance of large herbivores from this park, the vegetation

Table 9. Analytical data of soils from grazed and ungrazed grassland plots, Murchison Falls National Park, Uganda. Each value is a mean of three replicates. (Data from Hatton and Smart 1984)

Analysis	Grazed	Ungrazed
pH	6,0	7,4
Ca (mg 100g)	73	203
K (mg 100g)	8,9	44
Mg (mg 100g)	23	56
Mn (mg 100g)	3,4	0,4
Organic matter (%)	6,4	7,6
Total P (mg 100g)	46	41
Extractable organic P (mg 100g)	0,33	1,35
Extractable inorganic P (mg 100g)	0,43	2,93
Total N (%)	0,18	0,27

changes, and thereby ultimately the soil changes, are beginning to occur on a system scale. It is notable that the extent of these changes parallel those described for fertilizer experiments.

The ubiquitous feature of the above quoted studies is that woody individuals have resulted in an increase in the amount of nitrogen, and generally of organic matter, beneath trees on a range of soil types, but the response of available P and available bases has varied due to no obvious factor. Furthermore there is no substantiated mechanism to account for these changes. The critical question which arises is whether the nutrient enriched areas remain once the tree disappears, or at what rate concentrations decline.

Discussion

The foregoing synthesis on soil physico-chemical properties indicates that at present we lack any predictive ability of the effects of determinants on these properties. The available information suggests that the soil environment can be highly variable on a management time scale.

Soil nutrient changes on a system scale have also been recorded from the Amboseli National Park, East Africa (Western and van Praet 1973). A rainfall increase post 1960 resulted in an increment in the ground water of the Amboseli basin, which increased the salinity of the soil moisture available to plants up to 10-fold in certain places. The increased salinity caused the demise of the Acacia woodland the basin supported.

The major gaps in our knowledge of soil properties include measures of the dynamic variability of the soil environment. Grazing and fire are known to have a potentially significant effect on soil properties, but the conditions which determine the direction of the effects are not clearly understood. The potential irreversibility of changes in soil properties resulting from treatments, in particular fertilization, have not been examined. These and similar questions can only be resolved through holistic models of nutrient cycling, in which the influence of a single process (eg fire) can be gauged in the context of other interacting processes.

GENERAL DISCUSSION

Determinants of herbaceous trends

This synthesis sought to review the relative strength of each determinant on compositional trends and how this varies as conditions vary.

The total set of herbaceous species encountered at a site is determined by the general climatic regime and soil type. Changes in the presence/absence or relative abundance of a component are the norm in savannas, and the following hypothesis accounts for the pattern of these changes.

Hypothesis. Compositional changes in savanna grasslands are an adjustment of the fitness response of individual species (sensu Maguire 1973) to changing states of abiotic variables. Available soil moisture regime has the greatest effect on trends, except when there are dramatic changes in soil properties (as with fertilization experiments). Because of the influence of soil type and the woody/grass ratio on the availability of soil moisture and soil nutrients, these two variables will have a primary influence on herbaceous trends. The direct effects of grazing and fire are generally weak, and contingent upon the abiotic structure and on the population structure of the species. Grazing and fire indirectly affect species changes through their effect on the abiotic variables, principally soil moisture. Further corollaries to this hypothesis are elaborated below.

1. Rainfall and soil moisture

Stable conditions of soil moisture promote stable trends of the grass sward. These are dependent on mean rainfall conditions and rainfall variability, which are correlated. The most stable herbaceous trends are expected in the high rainfall regions (see studies 29, 52) and the most variable trends are expected in the semi-arid regions (see studies 1, 18, 27). Soil texture regulates the stability of the soil moisture regime on both an intra- and interseasonal scale. Differences in soil texture have a more profound effect on interseasonal trends in soil moisture in the mesic rather than the semi-arid or high rainfall savannas.

2. Soil nutrients

The general importance of soil nutrient supply to herbaceous trends is recognized from differences between soil types (studies 1, 2), and from fertilization experiments. Rainfall variability can induce marked changes in soil nutrient availability (Charley 1972), illustrated by the dependence of fertilization experiments on annual rainfall (study 59). There is however a dearth of information on natural fluxes in available soil nutrients, and how these fluxes might proportionally vary between

different soil types and between different rainfall regimes. There is limited evidence of systems experiencing major soil changes (Hatton and Smart 1983, Western and van Praet 1973). The importance of available nutrient supply will differ between the semi-arid and the high rainfall savannas. Semi-arid systems, even on sandy soils, are not nutrient limited because of the lack of leaching through the profile, but high rainfall areas are severely nutrient limited because of extensive leaching. Soil nutrient fluxes are therefore expected to have more pronounced effects in the high rainfall regions, particularly on sandy soils. No comparative data exists on nutrient losses or movements within the profile to substantiate this suggestion. One of the major causes of nutrient flux in savanna systems is the development of the woody component (see Hatton and Smart 1984, Strang 1974).

3. Grazing and fire

Grazing and fire are both interactive agents of defoliation, but the two differ in their temporal pattern of defoliation. In man managed pastoral systems grazing is no longer an interactive system, because high grazing pressures can be artificially maintained by the provision of additional fodder. Fire and grazing both exaggerate the instability of herbaceous trends resulting from rainfall variability. They have a negligible effect on herbaceous trends in high rainfall regions with a low soil moisture variability and relatively high soil moisture availability (studies 27, 29, 34, 35, 52), and on the sandy soils of mesic savannas (studies 27, 48, 49); but a pronounced effect on the heavier textured soils of mesic savannas (studies 25, 26, 27, 48, 49) and in the semi-arid regions (studies 43, 44). There is no information on the effects of fires on herbaceous trends in low rainfall areas, because erratic fuel production does not support a sustained fire regime. This pattern of influence of grazing and fire is considered a result of exacerbation of the variability of the available soil moisture regime.

Changes in the woody/grass ratio will override the effects of fire or grazing, because of the primary influence of the woody component on soil moisture relations. This pattern has been witnessed in both the semi-arid regions (study 3) and in the high rainfall regions (study 35), but similar data is lacking for the mesic savannas. This review has not considered the effects of fire or herbivory on the woody component, but it is suggested that the major importance of fire for herbaceous trends is through its effect on the woody component. Norton-Griffiths (1979) reached a similar conclusion for the Serengeti.

Mechanisms of compositional trends

The above key hypothesis needs to be investigated at the population level of the key component species of the major functional herbaceous groups of forbs, annual grasses and perennial grasses. This discussion will focus primarily on perennial grasses, as these are the primary constituents of southern African savanna swards.

Table 10. Demographic parameters of some perennial grass species; half life of all individuals, half life of individuals greater than one year old, and maximum recorded longevity. A range of greater than 1 year indicates significant differences between cohorts. Treatments: G = grazed plots, U = ungrazed plots.

Locality	Species	Condition	½ life (years)	½ life > 1 yr (years)	Maximum longevity (years)	Source
Arizona, USA	<i>Lycurus phleoides</i>	G	<1	1	4	Canfield 1957
		U	<1	2	7	
	<i>Bouteloua hirsuta</i>	G	<1	1	4	
		U	1-2	>2	6	
	<i>Heteropogon contortus</i>	G	<1	1-2	4	
		U	<1	1-2	6	
	<i>Aristida hamulosa</i>	G	<1	1-2	11	
		U	<1	1-2	13	
	<i>B eriopoda</i>	G	<1	1-3	10	
		U	<1	2-3	14	
	<i>Tricachne californica</i>	G	<1	3-4	11	
		U	<1	3-4	8	
	<i>B curtispindula</i>	G	<1	1-2	3	
		U	<1	<1	7	
	<i>B rothrockii</i>	G	<1	<1	5	
		U	<1	<1	3	
<i>Hilaria belangeri</i>	G	<1	<1	8		
	U	<1	<1	4		
<i>B filiformis</i>	G	<1	1	8		
	U	<1	<1	7		
<i>B chondrosioides</i>	G	<1	3-4	10		
	U	<1	3-4	8		
New Mexico, USA	<i>Bouteloua eriopoda</i>		2,20	3,85	27,5	Wright and Van Dyne 1976
	<i>Aristida longiseta</i>		1,89	3,60	9	
	<i>Sporobolus flexuosus</i>		1,70	3,40	18,9	
	<i>Aristida divaricata</i>		1,81	3,14	9,5	
	<i>Muhlenbergia arenacea</i>		1,80	2,79	9	
	<i>Scleropogon brevifolius</i>		1,80	3,00	12	
	<i>Hilaria mutica</i>		2,00	3,04	6,9	
Idaho, USA	<i>Agropyron spicatum</i>	G	2,8	7,1	43	West, Rea and Harniss 1979
		U	2,6	6,4	42	
	<i>Poa spp</i>	G	2,3	5,8	37	
		U	2,7	6,4	41	
	<i>Koeleria cristata</i>	G	3,7	7,2	29	
		U	2,8	6,2	27	
	<i>Oryzopsis hymenoides</i>	G	3,6	8,8	36	
		U	2,8	5,1	19	
	<i>Stipa comata</i>	G	3,3	10,0	41	
		U	3,2	9,6	43	
Utah, USA*	<i>Oryzopsis hymenoides</i>	G	<<2	-	>34	West 1979
		U	2	-	>34	
	<i>Sporobolus cryptandrus</i>	G	<<2	-	>34	
		U	2	-	>34	
NSW, Australia	<i>Danthonia caespitosa</i>	G	<1	1-3	-	Williams 1970
		U	+1	1-3	-	
NSW, Australia	<i>Danthonia caespitosa</i>	G	<1	<1	>18	Williams and Roe 1975
	<i>Enteropogon acicularis</i>	G	<1	1-5	>21	
	<i>Stipa variabilis</i>	G	<1	<1	11	
Queensland, Australia	<i>Astrebala spp</i>	U	<1	<1-7	23	
	<i>Eragrostis setifolia</i>	U	<1-3	<1-4	21	
	<i>Dichanthium sericeum</i>	U	<1-2	<1-5	7	

*Inadequate records for detailed calculations

An appreciation of the population processes of any species requires knowledge of mortality, regeneration and onward growth. Although extreme mortality events are well known to occur (eg Fourie and Roberts 1977, Scholes 1984), there is no data for southern African savannas on the rate of turnover of individual tufts in populations of perennial grasses, with such information as the mean and maximum life spans. Table 10 lists such data for perennial grasses from areas worldwide, although the table is not exhaustive (but there is a paucity of data (Harper 1977)). Two important points emerge. The first is that there are usually some individuals of a species that are extremely long lived. The second is that the majority of individuals of any species do not survive for a long period. Circumstantial evidence from compositional changes in the semi-arid and mesic savannas on heavier textured soils in southern Africa support this. These studies are reviewed to question the importance of soil moisture, grazing and fire, and their interaction, on tuft mortality.

Williams and Roe (1975) describe the demography of six species in relation to climate and grazing at two localities in Australia (Table 10). Data from 27 years in Queensland showed that grazing had no effect on the survivorship of Astrebla spp - this was overridden by rainfall. In an experiment lasting 19 years at Deniliquin, New South Wales (a winter rainfall area), the mortality of both Astrebla spp and Danthonia caespitosa was related to special climatic circumstances. Individuals of the former species were depleted by a series of dry summers, while individuals in a mature stand of the latter species succumbed to a sequence of a dry summer and delayed opening rains in the following autumn. Harper (1977) contests this conclusion; when the survivorship data are plotted on an approximate logarithmic scale, there is remarkably little difference in the mortality risk between years, suggesting climate has a negligible effect. A similar study at Deniliquin (Williams 1970) showed a tendency for grazing to favour survival of Danthonia, but grazed crops of Chloris acicularis exhibited heavy mortality in the juvenile stage. Hodgkinson (1976) undertook a detailed study of Danthonia caespitosa at Deniliquin, although on a different soil type to that reported by Williams and Roe (op cit). The rate of mortality of Danthonia was related to the frequency of defoliation and the time of the year. Complete defoliation every four weeks killed 100% of tufts, whereas complete defoliation every 12 weeks resulted in no appreciable tuft mortality. A higher death rate of plants defoliated every four weeks was recorded during the summer, suggesting that one cause of mortality was water stress. The difference in the response to grazing of Danthonia reported by Hodgkinson (1976) and Williams and Roe (1975) is most probably because the plants in the latter experiment were never completely defoliated. This work on Danthonia suggests that there is an interactive effect of grazing and the soil moisture regime on tuft mortality, and also that the effect of defoliation on mortality is non-linear - extreme and not moderate levels of grazing are important.

Chartography records of permanent quadrats on the Santa Rita experimental range, Arizona, were maintained for 17 years (Canfield 1957). Six of eleven species of grass were longer lived where protected than where grazed, while five species showed the opposite (Table 10). The former group of species predominate on lands that have been protected from grazing or that have been maintained in good condition, the latter group predominate on the ranges. Wright and van Dyne (1976) analysed demographic data for seven species over 28 years on the Jornada experimental range, south western New Mexico (Table 10). The level of

grazing had little effect on plant survival; plant survival was most readily interpreted by a water budget model, specifically the relationship between the number of days of effective soil moisture in a given time period and the age specific survival rate. Similarly West, Rea and Harniss (1979) used 20 years of long term records from Dubois, Idaho, to test the hypothesis that autumn grazing decreases plant longevity. Mean longevities of the grazed plants differed significantly from the ungrazed populations (Table 10). Grazing in the fall enhanced the average longevities of the major grasses Agropyron spicatum, Oryzopsis hymenoides and Stipa comata. The same hypothesis was tested with a similar data set from Utah covering 33 years (West 1979). The grasses Oryzopsis hymenoides and Sporobolus cryptandrus showed better survival on grazed plots than ungrazed plots (Table 10). The available direct estimates of tuft mortality highlight the influence on trends of climatic oscillations and lessen the role of grazing, except at very high intensities.

There is a lack of population based approaches to assist interpretation of compositional changes under fire, although fire has been recorded as a major mortality agent on the Santa Rita range (Cable 1965). A single fire killed 90% of Bouteloua eriopoda plants and more than 98% of Eragrostis lehmanniana plants. Everson, Everson and Tainton (1985) found that burning in winter or spring had no adverse effect on the tiller survival of Themeda triandra in the highland sourveld of Natal, whereas burning in summer had a catastrophic effect on tiller survival (only 6% of tillers survived).

Mortality of an established perennial tuft creates a gap for subsequent colonisation. The species capable of germinating and establishing within such a gap will dictate the long term compositional trend of the site. Grubb (1977) has formalized the regeneration niche as the requirements for a high chance of success in the replacement of one mature individual by a new mature individual of the next generation, involving the following processes: production of viable seed, dispersal of seed, germination, establishment and onward growth. Grubb (op cit) reviews the factors affecting germination, principally the physico-chemical environment, although little work has been undertaken on grasses. The factors known to influence germination of savanna grasses include initial precipitation regime (Cox 1984, Mott 1974) and subsequent limiting water potentials (Watt 1982), long term seed viability (Winkworth 1963), temperature and seed depth (Cox 1984), with some species known to be light obligate germinators (Mott 1974). The important point is that many of the differences between species are effective in ensuring that their seeds germinate in sites that differ in time and space.

Factors and processes controlling the onward growth of newly established tufts further influence compositional trends. Westoby's (1980) model of vegetation dynamics of arid rangelands concentrates on this phase, and is appropriate to savannas. Different growth forms can coexist stably in arid regions because they use different growth opportunities in complex weather sequences. A given climate can best be characterised by the growth opportunities it offers plants, not in terms of the climates average dryness or its variability, but in terms of the probability distribution of types of time of soil moisture available for plant growth (related to the frequency and duration of wetting and drying cycles). The pattern of rainfall which is never constant from year to year, would provide different mixtures of growth opportunities to different growth

forms. Thus a particular weather sequence may result in some species being present only as seeds or seedlings, while others are present as adults. Soil type and the grass/woody ratio, through their influence on soil moisture, would influence the growth opportunities during complex weather patterns. Competition may be a fundamental process during the period of onward growth of a plant, but there is little information on the role of competition in savanna grasslands, although competition is a keystone of community structure theory (Tilman 1982), and is important for savanna woody species (Smith and Walker 1983). In savanna grasses the outcome of competition between individuals is likely to be dependent on which is an adult and which is a seedling, rather than which species or growth forms are involved (Westoby 1980). The critical question is whether competition has enough time to operate in swards with a rapid turnover of individuals. In addition, competition may be most important at the seedling establishment phase in determining which individual occupies an available microsite.

It is suggested that the key to a predictive basis of compositional trends in savannas lies in unravelling the patterns of tuft mortality and regeneration and the processes influencing them, recognising that compositional change occurs on the size scale of an individual tuft.

System dynamics: the effects of stress levels of determinants

The second consideration is the effects of stress levels of determinants on herbaceous trends, and what insight this provides to concepts of system dynamics.

1. Rainfall

All savanna systems experience stress periods of rainfall which are more severe and generally longer sustained in the semi-arid regions. Pronounced changes in herbaceous trends occur during these stress periods, but there is no evidence that these changes endure in the long term. Savanna systems return to essentially the same set of state variables with a return to previous rainfall conditions, and this occurs independently of the grazing or fire regime (studies 3 plus 20, 18, 25, Roux 1966). The lack of long term changes due to rainfall variability are expected because semi-arid systems have evolved with a highly variable selective environment with respect to rainfall, and would possess the appropriate life history features and physiological attributes needed to meet the demands of such an environment. The herbaceous sward of semi-arid savannas and mesic savannas with heavier textured soils are therefore inherently unstable under stress levels of available soil moisture, but these systems show a high degree of resilience to drought. Resistance to change is weak, as changes rapidly follow drought, which involve dramatic population changes of the key component species.

In contrast the herbaceous trends of the high rainfall savannas and the sandveld areas of mesic savannas are relatively stable irrespective of grazing or fire regime (studies 27, 29, 48), but there is no evidence to

suggest that there is a slower response to drought stress in these systems than in semi-arid systems. It is suggested that far less change in population structure of grasses occurs in these regions, thereby promoting a rapid response to drought stress.

2. Soil nutrients

Stress levels of nutrient availability (eg fertilization) leads to a rapid and complete change of herbaceous composition in savanna systems. Two forms of experimental manipulation appear to influence the availability of soil nutrients to the extent that they possibly influence herbaceous trends. The first is complete protection from either fire or herbivory. The most extreme example of soil changes resulting from protection is the 24 year old exclusion plot in the Murchison Falls National Park, Uganda (Hatton and Smart 1984). In this time the original Sporobolus-Setaria grassland has been completely replaced by a closed canopy Acacia sieberiana woodland, with a concomitant transformation of the composition of the grass sward (Smart, Hatton and Spence 1985). Changes in the light regime have also influenced compositional changes. Similar soil data are lacking for other protected plots, but it is conspicuous that protected plots in the sandveld areas of mesic savannas and in the high rainfall savannas have shown pronounced changes in composition, often within a short period of time (studies 27, 48, 52). Similar pronounced changes in composition have occurred in the highveld grassland regions of South Africa (Coetsee and van Rensburg 1975b). However, the extent of vegetation change under protection is dependent on the general climatic regime (West 1965). Protection from herbivory has little effect in arid or semi-arid regions. For example, 50 years of protection from livestock grazing in the Sonoran desert (mean annual rainfall 250 mm) caused no significant change in composition, or any appreciable invasion of new species on the unprotected area (Blydenstein et al 1957). The most notable change on the protected area was an overall increase in plant density (of perennial grasses and a palatable shrub). It is suggested that these compositional changes are in part due to a change in the flux of nutrient cycling because of an increasing amount of nutrients stored in standing moribund and living vegetation. The effect of a stored pool of nutrients might be expected to be more pronounced on dystrophic sandy soils rather than heavier textured soils, and might account for the differences in compositional trends between the Matopos sandveld and thornveld when protected (studies 27, 48). Grazing and fire markedly affect the rate of nutrient cycling, but the effects of both on the spatial uniformity and temporal stability of available nutrients needs to be determined.

Bush clearing is a severe perturbation because it effects the availability of soil moisture and soil nutrients, and the light regime. There is no information on the relative importance of these three variables to the trends subsequent to clearing, but complete bush clearing always has a marked effect on compositional trends and usually on functional trends (studies 1 to 16). The effects of bush clearing are generally impermanent, because of the ability of savanna woody species to regenerate from rootstocks. Extensive recovery of cleared woodland within 10 years has been noted in both high rainfall and semi-arid savanna regions (studies 2, 16, Strang 1974).

3. Grazing and fire

The changes in the Tall grassveld of Natal under sustained overgrazing (Tainton 1972) is the only potential example of the limits of resilience of a system having been exceeded and a new system established. No similar potential examples were found for savanna regions. The only system change under grazing which was irreversible in the short term is the major shift in the grass woody balance recorded in the 15 year isolation transect and seasonal grazing trials undertaken on the Nyamandhlovu red soils (studies 27, 28). Although sustained overgrazing led to pronounced compositional changes of both the Matopos thornveld and sandveld sites, these changes were not irreversible, although the Matopos is in a similar climatic region to Nyamandhlovu.

The recorded changes in the isolation transects of four sites (study 27) illustrate differences in the rate of response of a species to a stress and relaxation from that stress, which is evidence for hysteresis effects in compositional changes in savanna systems. Individual perennial species take longer to reestablish with complete rest than to disappear with sustained overgrazing. This differential rate of response will obviously be dependent on the extent of population change, but oscillations in soil properties may be involved. The sheep grazing experiment at Glen (Morris 1944, Mostert 1958) provides indirect evidence of an hysteresis effect. The areas which had been the most severely stressed by grazing showed the slowest reversion to the original composition.

There are no adequate data sets to judge whether sustained burning has potentially induced system changes which are irreversible in the short term, because of a lack of intensely sampled data sets. There is also no evidence on the residual effects of burning on vegetation or soil properties, which could suggest irreversible changes in herbaceous trends.

There are no experiments which give indications of the effects of extreme events on herbaceous trends, for example burning followed by severe grazing. McNaughton (1983) hypothesises that such extreme events are one of the major occasions in which fire and grazing can induce major changes in herbaceous trends. Observations in the KNP (study 47) and in the Hluhluwe/Umfolozzi complex (MacDonald 1980) lend support to this hypothesis.

Species losses have been recorded in a number of grazing and fire experiments, but the permanency of these losses is difficult to judge. Long term data sets suggest that most species losses are temporary in nature, depending on prevailing environmental conditions. Observed species losses are not therefore evidence of the internal structure of any of these systems having been changed by stress.

Case studies of system change

A second approach towards gaining an insight into the system dynamics of savannas was to search for case studies in which system changes had been recorded, and for which there was some evidence of the agents responsible.

Only five examples of apparently irreversible changes in savanna systems were located, two of which have been introduced. The demise of the Acacia xanthophloea woodlands in the Amboseli basin (Western and van Praet 1973) to a more arid habitat was initially ascribed to overgrazing by Masai cattle and elephant damage. Subsequent correlative data suggested the agents described earlier, with elephants only a catalytic agent affecting the rate of change. Strikingly the change took two decades to become apparent, and further evidence suggests that similar patterns may have occurred in the last century. This suggests a relative time scale which needs to be adopted when viewing system oscillations in a semi-arid habitat.

The second example is the transformation of a grassland to an Acacia woodland in the Murchison Falls National Park, Uganda (Hatton and Smart 1984, Smart, Hatton and Spence 1985). The pattern observed on protected plots is now occurring on a system scale because of the demise of the large mammal populations, particularly elephant, from poaching. The Masol plain in north west Kenya displayed a similar pattern when the area was abandoned by Pokot naturalists in 1974 because of warfare (Conant 1982). In the absence of regular burning and grazing by goats, the vegetation changed from a grassy open savanna to a dense thorny bushland.

The Hluhluwe/Umfolozzi complex in Natal has shown a gradual decrease in the extent of grassland and its replacement in many areas by woody categories over the last 40 years (Brooks and MacDonald 1983, Downing 1980, Watson and MacDonald 1983). It was concluded from the records available that sustained overgrazing by a multispecies herbivore assemblage had led to a deterioration of the tall grass cover, which appeared to have been precipitated by drought years.

Two further anecdotal examples are available from East Africa. The first is the invasion of the semi-arid El Barta plains of north Kenya by the dwarf shrub Disperma (Pratt 1966b). Historical records from 1888 make no mention of the plant, and available evidence indicates that before 1939 it was confined largely to the water courses and occurred on the open plains in scattered stands only. The plains were then only intermittently grazed and occasionally burnt. The region was heavily settled by the Samburu in 1936, with a concomitant increase in the livestock population until 1960. Over the same period, and particularly between 1942 and 1950, Disperma increased to over 2000 clumps per acre, which was attributed to the increased grazing pressure lessening grass competition and preventing fire.

The second anecdotal example is the apparent invasion of the Ankole pastures of Uganda by Cymbopogon afronardus (Harrington and Thornton 1969). Local pastoralists claim the species was uncommon in 1920. The spread of tsetse fly drove cattle and pastoralists from many parts of the Ankole during the period 1907-1960. By 1960, after a successful anti-tsetse campaign, C afronardus had increased to 40% of ground cover. This increase was attributed to the change in grazing and fire induced by the depopulation of the area.

System dynamics: concepts and key hypotheses

This empirical catalogue illustrates that the herbaceous component can vary markedly in response to variation in rainfall, nutrients, grazing, fire and the woody component. Two key hypotheses are presented to describe the dynamics of these systems.

Hypothesis 1. Savannas are not statically stable in that they possess an equilibrium state to which they return subsequent to an intrinsic or extrinsic perturbation. Rather, savannas display recurrence of states that have previously existed within a domain of attraction (Botkin and Sobel 1975). That is, for a given abiotic state (which is naturally variable), the system possesses a globally stable domain of both structural and functional properties, but the system may be highly mobile within this domain.

Hypothesis 2. There can be no irreversible change in composition or production of savanna grasslands without an associated irreversible change in the abiotic state structure (which affects the availability of soil moisture or nutrients). Grazing or fire can induce an alternate state through their indirect effect on the abiotic environment, rather than through any direct effect on species populations.

The few studies which suggest potentially short term irreversible changes in herbaceous trends are associated with a change in the grass/woody balance, initiated either by sustained overgrazing or sustained protection from fire or grazing. The grass/woody relationship has been formalised (Walker and Noy-Meir 1982, Walker *et al* 1981). The model is based on competition between woody vegetation and grass for soil moisture, and is therefore a corollary to hypothesis 2. Woody vegetation and grass compete for available surface soil water, whilst the woody vegetation has exclusive access to deeper soil water. On heavier textured soils in semi-arid regions the reduction of herbaceous biomass by sustained overgrazing leads to a relatively impermeable soil surface, and, in these conditions, the model shows that two different steady states may develop: with a lot of woody vegetation alone, or with a relatively large biomass of grass and rather little woody vegetation (Walker *et al* 1981). The model concurs with the observed changes reported in this review. The validity of the model has yet to be established for different rainfall regimes and for different soil types. Future modelling efforts would have to pay more attention to soil nutrient availability and changes thereof, and the effects of fire and herbivory on the woody vegetation (eg Pellew 1983), particularly in the higher rainfall regions.

An approach toward predicting system response to stress

A predictive basis of herbaceous trends of savanna grasslands is some time away, due to a number of interrelated reasons. Long term research in southern Africa has concentrated on investigating single components and single processes. Previous studies have been largely descriptive; these studies have not set out to test a suite of hypotheses but merely to describe the effects of a specific form of treatment on individual components. Results have occasionally been adapted to neo-Clementsian

successional theory, despite the criticisms (Drury and Nisbet 1973) and the poor falsifiability of the theory (Mentis 1982). There have been few attempts to unify the available information into a coherent conceptual model which is potentially falsifiable. A substantial amount of information has accumulated on single components and single processes, but an insight into the dynamical interrelationships of components, and the contingency of processes upon one another, is lacking.

The solution to this dilemma requires two major directions in future research. Individual experiments need to be defined in the context of an overall explicit set of hypotheses of the interrelationships of a system. One such approach is the development of theoretical models which attempt to impose a quantitative coherence to the different components, the processes affecting them, and the relationships between processes and between components. Such models serve as explicit statements not only of the major components and processes involved, but also of the strength of the relationship between different determinants. So stated the model becomes potentially falsifiable if evidence can be found of further components or processes of primary significance. This approach has rarely been adopted in southern Africa. Specific examples of such models are the production dynamics of heavier textured soils in a mesic savanna (study 23), the grass/woody balance in semi-arid savannas (Walker *et al* 1981, Walker and Noy-Meir 1982), and the dynamics of a highveld grassland under grazing (Mentis 1982).

Dye's (1984) production model can serve as an example of how such a model might be corroborated and improved. The model was corroborated against data from a bush clearing experiment (study 1), and successfully simulated herbaceous production of the red soils of Matopos without the influence of grazing or fire, although these driving variables can have a marked effect on the trends of this soil type (studies 27, 48). The model also needs to recognise the differential response of degraded portions of this soil type (MacDonald 1978).

Whatever conceptual models are generated to account for herbaceous dynamics of savanna grasslands, appropriate long term data sets are required to corroborate these models. There is a scarcity of appropriate data sets from southern Africa, with the exception of the well devised monitoring sets of Botswana (Anon 1980). Long term monitoring has only recently commenced in the wildlife areas of South Africa (Joubert 1983, MacDonald and Brooks 1983, van Rooyen *et al* 1984), although such monitoring tends to sacrifice detail for the expediency of extensive coverage. Monitoring procedures should be oriented toward testing hypotheses or answering questions of ecosystem structure and function (Callahan 1984), although quite substantial design difficulties need to be overcome (Hinds 1984). This synthesis suggests that the abiotic variables require greater monitoring input, because of the primary role these variables play in regulating biotic components. The appropriate time scale for monitoring needs to be related to the times over which components are known to change. Consideration of climatic oscillations suggests a minimum of 20 years, whilst consideration of the woody component suggests a time span far in excess of 20 years. A monitoring approach is also eminently appropriate to evaluate the role played by major disturbances - be they intrinsic disturbances deriving from conditions within the system (eg accumulation of fuel) or extrinsic disturbances coming from sources outside the system (eg drought) - in maintaining or changing the character of ecosystems (Callahan 1984).

Without detailed data sets of the changes of system components over time, covering a range of conditions, a risk of formulating incorrect models of the functioning of savanna systems is maintained.

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Appendix 1. Long-term experiments concerned with the herbaceous component and/or soil variables conducted in the savanna regions of southern Africa.

Study No	Details of locality*	Soil type/s	Nature of experiment	Duration of experiment	Variables	No of censuses	Source
BUSH CLEARING EXPERIMENTS							
1.	Zimbabwe: Matopos thornveld (615 mm)	Red sandy clay loams derived from basement schists	Complete clearing of bush and a control	19	Herb comp** Yield	10 19	Dye and Spear 1982 Barnee 1972
	Matopos sandveld (615 mm)	Sandy soil derived from felspathic-rich gneissic granite		19	Herb comp Yield	10 19	
	Nyamandhlovu (569 mm)	Deep sands derived from Triassic sandstone		15	Herb comp Yield	10 15	
	Tull (450 mm)	Shallow, sandy soils		15	Herb comp Yield	9 15	
2.	Mixed thornveld community of Crocodile river valley, western Transvaal (473 mm)	Shorrockes series, Hutton form	Complete clearing, and 33% and 66% clearing of bush, and a control	10	Herb comp Plant density Tbc***	4 4 2	Morris 1980
3.	Thornveld community, Demaraland, Namibia (200 - 500 mm)	Rocky loam soils	3 experiments: complete clearing of bush and no clearing; grazing and no grazing; burning and no burning; sowing of seed	6 (1 experiment 4)	Herb comp Tbc	4 4	Joubert 1966
4.	Thickly wooded mixed veld at Towoomba, Transvaal (622 mm)	Red clay soil of Makatini series	Control, complete clearing and selective clearing of shrubs. All treatments grazed midsummer to the start of autumn	20	Herb comp Tbc	1 1	Louw and van der Merwe 1973
5.	Molopo area, northern Cape	Not given	Complete clearing of bush and a control. All plots grazed in winter	8	Herb comp - by density Total density	2 2	Donaldson and Kelk 1970
6.	Molopo area, northern Cape	Not given	Complete clearing of bush and a control. All camps grazed	8	Yield	1	Donaldson and Kelk 1974a
7.	Molopo area, northern Cape (345 mm)	Red brown to greyish brown sand	Complete clearing of bush and a control	6	Herb comp Tbc Yield	2 2 1	Donaldson and Kelk 1974b
8.	Molopo area, northern Cape	Shallow, heavy textured soils	Complete clearing of bush and a control. All plots grazed by sheep or goats	5	Tbc	1	Donaldson and Kelk 1974c

Appendix 1. Continued.

Study No	Details of locality*	Soil type/s	Nature of experiment	Duration of experiment	Variables	No of censuses	Source
BUSH CLEARING EXPERIMENTS (continued)							
9.	Molopo area, northern Cape	Not given	Complete clearing of bush and a control. All plots grazed	8	Plant density	2	Donaldson and Kelk 1974d
10.	Molopo area, northern Cape (350 mm)	Sandy	Complete and partial clearing of bush	7	Yield	1	Donaldson and Kelk 1974e
11.	Molopo area, northern Cape (300 mm)	Red Kalahari sands	Complete clearing of bush and a control	6	Yield	1	Donaldson and Kelk 1974f
12.	Molopo area, northern Cape	Kalahari sands	Complete clearing of bush and a control	3	Yield Perennial mortality	1 2	Donaldson 1967
13.	Nuanetsi, south-east Zimbabwe lowveld	Shallow stiallitic loamy sand and sandy loam soil derived from gneiss	Ringbarking of all trees >2.5m height and a control. Plots grazed	6	Herb comp Yield	3 2	Kelly et al 1978a
14.	Nuanetsi, south-east Zimbabwe lowveld	As for study No 13	Complete and selective clearing of bush, and a control. Plots grazed	4	Yield Herb comp	4 2	Kelly et al 1978b
15.	5 sites representing the major vegetation zones of Botswana	Not given	Complete and partial clearing of bush, and a control. Sub treatments of grazing and exclusion	3	Yield Tbc Radiation Air temp Soil moisture	3 2 5 months 6 months 6 months	Pratchett 1978
16.	Brachystegia woodland, Makaholi, Zimbabwe (660 mm)	Medium grained sand over sandy loam, deep, permeable derived from granite	Ringbarking of larger trees and a control	4	Yield Herb comp	4 1	Ward and Cleghorn 1964
EXCLUSION STUDIES							
17.	Tsoomba, Transvaal (622 mm)	Red clay ground, Makatini series	Protected plot	31	Herb comp	2	Louw 1973b
18.	7 sites in mopane veld, Messina, Transvaal (367 mm)	Shorlocks,) Portsmouth) Mispah) Undescribed) Gravelly red loam) Sandy soil) Dark brown sandy loam)	Protected plots: protected for 20 years protected for 14 years	20 14	Herb comp Tbc	16 16	Donaldson et al 1983 Louw 1973a

Appendix 1. Continued.

Study No	Details of locality*	Soil type/s	Nature of experiment	Duration of experiment	Variables	No of censuses	Source
EXCLUSION STUDIES (continued)							
19.	Umfolozu Game Reserve, Natal (700 mm)	Not given	Protected plots	16	Herb comp Tbc	2 2	Bourquin 1967 Emslie 1983
MONITORING							
20.	Mixed thornveld of the Crocodile valley, West Transvaal (473 mm)	Not given	Monitoring cover of savanna	14	Tbc	6	Van Wyk 1967
21.	5 sites in Burkea africana savanna, Nylsvley, Transvaal (630 mm)	Sands derived from Waterberg sandstone	Monitoring of savanna supporting indigenous herbivores (low density), occasionally burnt	5	Herb comp Tbc	3 3	Van Rooyen and Theron 1982
22.	11 sites covering the major vegetation zones of Botswana, representing rainfall regimes from 200-300 mm to >600 mm	Non calcareous loams, non calcareous sandy soils, cracking soils and clays, alluvial soils	Monitoring of grazed savanna stocking rates known	6	Herb comp Tbc	6 6	Anon 1980
23.	Matopos, Zimbabwe (615 mm)	Red sandy clay loams derived from basement schists	Monitoring of savanna with trees removed	5	Yield Herb comp Tbc Density	5 5 5 5	Dye 1984 Dye 1985
24.	Nyamandhlovu, Zimbabwe (569 mm)	Heavy black basaltic soils, red sandy loams, Kalahari sands	Monitoring of grazed savanna (descriptive)	5	Herb comp	5	Addison 1950
GRAZING EXPERIMENTS							
25.	Towoomba, Transvaal (622 mm)	Heavy red loam of Shorrocks series	Continuous versus fixed seasonal grazing systems	47	Herb comp Tbc	9 5	Donaldson and Rootman 1983 Louw 1973c Irvine 1940
26.	Mixed sour veld at Towoomba, Transvaal (622 mm)	Heterogeneous heavy loam, principally Malkatini series	Fixed seasonal grazing rotation systems	13	Herb comp Tbc	3 1	Louw 1974a

Appendix 1. Continued.

Study No	Details of locality*	Soil type/s	Nature of experiment	Duration of experiment	Variables	No of censuses	Source
GRAZING EXPERIMENTS (continued)							
27.	5 sites in Zimbabwe: (1) Matopos thornveld (2) Matopos sandveld (3) Nyamandhlovu (4) Tuli (5) Marondera (Grasslands: 914 mm) See study No 1 for rainfall of other sites	Marondera: sands derived from granite. Refer to study No 1 for a description of the soils of the other sites	Isolation transects; rest following heavy grazing, rest preceding heavy grazing, and complete protection	15	Herb comp Tbc	4 for (1) & (2) 2 for (5) 1 for (3) otherwise visual assess- ments	Kennan 1969 McKay 1956 Strang 1974 West 1948
28.	3 sites in Zimbabwe: Matopos thornveld Matopos sandveld and Nyamandhlovu Descriptive only	See study No 1	Seasonal grazing experi- ments	15	Herb comp	Not given	Kennan 1969
29.	Zimbabwe highveld, Grass- lands, Marondera (914 mm)	See study No 27	Trial of 3 stocking rates	15	Herb comp Tbc	2 2	Barnes 1965
30.	Matopos thornveld, Zimbabwe (615 mm)	See study No 1	Trial of 3 multipaddock grazing systems on an area cleared of bush	5	Herb comp Plant density	2 2	Denny et al 1977
31.	Nyamandhlovu, Zimbabwe (569 mm)	Reddish brown, sandy soils derived from basalt and sand stone; varying from lithosols to deep fersial- litic sandy loams	Trial of 2 multipaddock grazing systems, on an area cleared of bush	6	Herb comp Plant density	2 3	Denny and Steyn 1977a
32.	Matopos sandveld, Zimbabwe (615 mm)	Fersiallitic sandy soils derived from granite	Trial of 6 multipaddock grazing systems, each at 2 stocking rates	5	Herb comp Tbc	2 2	Denny and Barnes 1977
33.	Matopos sandveld, Zimbabwe (615 mm)	See study No 2	Trial of continuous grazing and 2 rotational grazing systems, each system at two stocking rates	5	Herb comp Tbc	3 3	Denny and Steyn 1976, 1977, 1978 Denny and Yuba 1979, 1980
34.	Brachystegia/Julbernardia woodland on Zimbabwe high- veld (900 mm)	Brown to reddish brown silty clay derived mainly from argillaceous meta- sediments	15 treatments of 5 cutting frequencies and 2 levels of N & P application	5	Yield Herb comp Tbc	5 5 6	Boulwood 1969
35.	Brachystegia/Julbernardia woodland at Makaholi, Zimbabwe (660 mm)	Granite derived sand of low fertility (Makaholi G1 series)	6 grazing treatments on areas cleared of bush, and one grazing treatment on a bushed control	8	Yield	8	Ward and Cleghorn 1970

Appendix 1. Continued.

Study No	Details of locality*	Soil type/s	Nature of experiment	Duration of experiment	Variables	No of censuses	Source
GRAZING EXPERIMENTS (continued)							
36.	Morale, east Botswana (457 mm)	Coarse reddish brown sandy loam derived from granitic gneiss	Continuous grazing versus a 3 paddock, 1 herd deferred rotational system	28	Herb comp Plant density	3 2	McKay 1968
37.	Morapedi, Botswana (500 - 600 mm)	Not given	Continuous grazing, a 3 paddock, 1 herd and 2 multicamp systems: each system at 2 stocking rates	5	Herb comp Tbc	5 5	Anon 1980
38.	Matlakang, Botswana (400 - 500 mm)	Kalahari sands	3 paddocks, 1 herd and 2 multipaddock grazing systems	5	Herb comp Tbc	5 5	Anon 1980
39.	Western Kalahari, Botswana (300 mm)	Kalahari sands	2 stocking rates and a control of no grazing	4	Herb comp Yield	4 4	Anon 1980 Skarpe 1981 Skarpe and Bergstrom 1983
40.	Mopane veld, Messina, Transvaal (367 mm)	Not given	Trial of steers alone, goats alone, and steers with goats	6	Herb comp Tbc Grass height	2 2 1	Donaldson 1979
41.	False thornveld, eastern Cape (435 mm)	Not given	Continuous and rotational grazing by both sheep and goats, and a control	3	Herb comp Tbc	2 2	Du Toit 1972c
42.	Grassveld invaded by Acacia karoo, eastern Cape (503 mm)	Not given	As for study No 41	3	Herb comp Tbc	2 2	Du Toit 1972b
43.	Tarchonanthus shrub savanna Ghaap plateau, northern Cape (370 mm)	Limeveld and Dolomiteveld	35 treatments for 6 experiments of grazing systems and stocking rates for cattle only, sheep only, and cattle with sheep	5-9	Herb comp Soil properties	2 1	Ebersohn 1962 Ebersohn 1956
44.	Tarchonanthus savanna, Arnoedevlakte, northern Cape (476 mm)	Limeveld	Continuous and rotational grazing, each at 4 stocking rates	5	Herb comp	3	Fourie et al 1984
45.	Thornbushveld, Otjiwarongo, Namibia	Not given	2 stocking rates of cattle 1 stocking rate of goats	12	Tbc Perennial cover	5 5	Van Niekerk 1980
46.	Umfolozi Game Reserve, Natal (700 mm)	Swartland and shortland	Comparison of cull/non cull blocks	5	Tbc Herb comp Yield Seedling establishment	1 1 1 1	Emalie 1983

Appendix 1. Continued.

Study No	Details of locality*	Soil type/s	Nature of experiment	Duration of experiment	Variables	No of censuses	Source
GRAZING EXPERIMENTS (continued)							
47.	Ndumu Game Reserve, Natal		Monitoring of area grazed by indigenous herbivores	14	Herb comp	2	Hancock 1978
FIRE EXPERIMENTS							
48.	Matopos thornveld and Macopos sandveld, Zimbabwe (615 mm)	See study No 1	10 treatments of the season and frequency of burning, 2 mowing treatments, and a control	15	Herb comp Tbc	3 3	Kennan 1972 West 1948
49.	4 vegetation types in the KNP. Terminalia-Dichrostrachys	Brown, sandy loam soils of granitic origin	11 treatments of the season and frequency of burning, and a control, for each vegetation type	15	Herb comp Tbc Plant density	2 2 1	Van Wyk 1972
	Sclerocarya-Acacia	Basaltic soils		21	Herb comp Tbc	2 2	Gertenbach and Potgieter 1975
	Mopane	Basaltic soils, (flat areas)		25	Herb comp Tbc	1 1	Gertenbach and Potgieter 1979
	Combretum woodland	Brown-red granitic soils		25	Soil properties	1	Webber 1979
50.	Acacia nigrescens/Combretum apiculatum savanna in eastern Botswana (450 mm)	Non calcareous ferric luvisol of acid igneous or granitic parent material	5 frequencies of burning and a control	22	Herb comp Tbc Soil properties	1 1 1	Sweet 1982
51.	Sour mixed bushveld, Transvaal (635 mm)	Brown, sandy loam	5 treatments of season of annual burning, and a control	14	Herb comp Tbc Yield	1 1 1	Davidson 1953
52.	Brachystegia-Julbernardia woodland on the Zimbabwe highveld	Not given	Originally cleared of bush 3 treatments of frequency of burning, all grazed, and a control	15	Herb comp Tbc Yield	2 2 15	Boulwood and Rodel 1981
53.	Gwebi, Zimbabwe highveld (813 mm)	Grey/yellow brown Silty clays/clays	Annual burn in late dry season	2	Herb comp Tbc Soil pH	2 1 1	Barnes 1956
54.	Brachystegia-Julbernardia woodland on the Zimbabwe highveld (914 mm)	Granite derived sands	Frequency of burning and a control	11	Plant density Soil properties	1 1	Strang 1974

Appendix 1. Continued.

Study No	Details of locality*	Soil type/s	Nature of experiment	Duration of experiment	Variables	No of censuses	Source
FIRE EXPERIMENTS (continued)							
55.	Brachystegia-Julbernardia woodlands, Ndola, Zambia (1200 mm)	Infertile sandy soils	Different seasons of annual burning and a control	23	Soil properties	1	Trapnell et al 1976
56.	False thornveld eastern Cape	Not given	Initially cleared of burn 9 treatments of frequency and season of burning, and a control	5	Herb comp Aerial cover No species Rooted frequency	1 1 1 1	Robinson et al 1979
57.	False thornveld eastern Cape (510 mm)	Sandy loam of the Glentosa form	Annual spring burning, grazing by goats and a control	10	Herb comp Yield Tbc	4 9 4	Trollope 1982
58.	Eastern Cape (435 mm)	Not given	Initially cleared of bush. Frequency of burning, extended sparing, controlled grazing, and a control	6	Yield	6	Du Toit 1972a
59.	Towomba, Transvaal (622 mm)	Red loamy soil of Hutton form, Makatini series	4 levels of N and 2 levels of P application, and a control	33	Herb comp Tbc Yield Soil properties	6 6 33 2	Donaldson et al 1984 Louw 1966 Louw 1968 Louw 1969
60.	3 sites at Matopos, Zimbabwe (615 mm)	Coarse to loamy sands derived from granite: heavy red to brown clays derived from basement schists: heavy, grey to black clays derived from basement schists:	4 levels of N application, and a control	9	Herb comp Yield	1 9	Mills 1964 Mills 1966
61.	3 sites at Matopos, Zimbabwe (615 mm)	As for study No 60	3 levels of N application 2 levels of P application, and a control	3	Yield	3	Mills 1968
62.	Gwebi, Zimbabwe highveld (813 mm)	Tatagura series soils (see study No 53), and a black/grey black calcareous clay	2 levels of N and P application, 1 level of K application, and a control	6	Herb comp	3	Barnes 1956 Bate 1962
63.	Gwebi, Zimbabwe highveld (813 mm)	Tatagura series (see study No 53)	3 levels of N application 1 level of P and K application, and a control	3	Herb comp Yield Soil pH	2 3 1	Barnes 1956

Appendix 1. Continued.

Study No	Details of locality*	Soil type/s	Nature of experiment	Duration of experiment	Variables	No of censuses	Source
RECLAMATION EXPERIMENTS							
64.	Thornveld, Estcourt, Natal (635 mm)	Brown/red brown ferruginous lateritic soils, derived from shales and dolerite	3 ripping and reseeded treatments, and a control	9	Herb comp	2	Scott 1951
65.	Acacia tortilis and Combretum apiculatum vegetation types at Mara, Transvaal (425 mm)	Shorrocks + and Shorrocks - series of the Hutton form	Shallow and deep cultivation, follow on cultivation branch cover, fertilization and a control	4	Yield Herb comp Plant density	2 2 2	Louw 1974b
66.	Matopos thornveld, Zimbabwe (615 mm)	Red sandy clay loams derived from basement schists	Ripping and a control	4	Herb comp Tbc	3 3	Oates 1956
RUN OFF AND SOIL LOSS EXPERIMENTS							
67.	Matopos sandveld Zimbabwe (615 mm)	Moderately shallow medium grained fersiallitic sand derived from granite	Manipulation of vegetal cover by mowing and burning and a control	10	Run off Soil loss	10 10	Barnes and Franklin 1970
ADDITIONAL EXPERIMENTS							
68.	Charter Estate, Zimbabwe highveld (733 mm)	Fine grained sands from sandstone, sandy loams derived from basalt and sandstone	Trial of 4 grazing systems	7	Herb comp Tbc	7 7	Ciatworthy 1984
69.	Tuli lowveld, Zimbabwe (450 mm)	Sandy soil derived from paragneiss	4 stocking rates on un-cleared veld, 3 stocking rates on cleared veld Two grazing systems	23	Herb comp by density	3	Gannon 1983
70.	Matopos thornveld, Zimbabwe (615 mm)	Partly on red sandy clay loams derived from basement schists	Continuous grazing	27	Herb comp	7	MacDonald 1982
71.	Umfolozi Game Reserve, Natal (695 mm)	Not given	Wildlife grazing regime	12	Herb comp	5	MacDonald and Owen-Smith, in MacDonald 1982
72.	Matopos thornveld, Zimbabwe (615 mm)	Red sandy clay loams derived from basement schists	Different burning treatments on degraded and sound cleared veld	4	Herb comp by density	4	MacDonald and Bisset, in MacDonald 1982.

* Mean annual rainfall of locality in parentheses

** Herb comp = herbaceous composition

** Tbc = total basal cover

Appendix 2. Seasonal rainfall totals (mm) for various savanna sites.

	Towoomba	Messina	Matopos thornveld	Matopos sandveld	Nyamand- hlovu	Tuli	(W-Tvl) Welgevonden	Morapedi	Matlolak- gang
1982/83	547								
1981/82	569	239							
1980/81	648	525	674	801					
1979/80	613	237	559	508			567	320	432
1978/79	573	370	611	379			265	297	314
1977/78	717	482	995	1091	1133	704	830	767	521
1976/77	708	430	785	722	647	578	556	676	614
1975/76	818	398	707	802	673	668	582	699	543
1974/75	951	516	949	888	683	550	672	904	584
1973/74	758	365	935	1032	822	548	662	646	471
1972/73	414	212	302	330	377	132	271	266	250
1971/72	592	455	771	733	590	688	597	680	491
1970/71	796	415	439	530	427	363	715	460	463
1969/70	462	288	284	329	414	366	280		
1968/69	611	346	523	622	739	317	440		
1967/68	536	191	352	402	512	232	459		
1966/67	1020	291	576	604	838	753	684		
1965/66	371		482	599	508	322	183		
1964/65	563		301	382	339	269	324		
1963/64	553		310	340	360	191	322		
1962/63	440		577	681			300		
1961/62	454		478	437					
1960/61	700			842					
1959/60	477			425					
1958/59	635			611					
1957/58	583			627					
1956/57	768			661					
1955/56	792			509					
1954/55	738			1229					
1953/54	572			554					
1952/53	766			876					
1951/52	444								
1950/51	522								
1949/50	594								
1948/49	612								
1947/48	639								
1946/47	363								
1945/46	552								
1944/45	529								
1943/44	774								
1942/43	723								
1941/42	488								
1940/41	657								
1939/40	815								
1938/39	592								
1937/38	751								

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