BUSHCLUMP-GRASS INTERACTIONS IN A SOUTH-EAST AFRICAN SAVANNA: PROCESSES AND RESPONSES TO BUSH CONTROL

A dissertation
by
LEANDER CLEMENT JARVEL

Submitted in partial fulfilment of the requirements for the degree of

MASTER OF SCIENCE IN AGRICULTURE

in the
Department of Range and Forage Resources
University of Natal
Pietermaritzburg

December 1996

ABSTRACT

The objective of this study was to investigate woody-grass interactions and the initial response of vegetation to bush control in the mesic Eastern Cape bushclump savannas. The occurrence of multi-species bushclumps, rather than single-trees, presented an interesting variation to an otherwise well-studied interaction. The effect of bushclumps on their local environment was characterized. Since all woody-grass interactions involve competition for irradiance, nutrients and moisture, a factorial experiment was designed to discriminate these individual and interactive effects. Mechanical and chemical bush control measures were investigated in a formal, replicated experiment. The herbaceous, woody and soil responses to bush control treatments, for the first two seasons, are reported.

Bushclumps had a moderating effect on their microclimate when compared with the open grassland. Lower maximum and higher minimum temperatures, and higher humidity were the result of an 80-90% reduction in the irradiance regime. Soils beneath bushclumps were more fertile than grassland soils. The importance of bushclumps on sandier soils was discussed. Bushclumps were characterized by a sparse shade-tolerant herbaceous layer which contributed little to grazing capacity. An aspect effect increased grass production in the grassland on the south-facing side of bushclumps. Initial results suggest that the lateral spread of woody roots could be as far as 25 m.

The factorial experiment tested the individual and interactive effects of irradiance (normal sunlight, 40% and 80% shade), nutrients (normal nutrient level, low and high nutrient addition levels) and moisture (low, normal and additional moisture levels) on the herbaceous layer. The interaction of 80% shade and high nutrients had a detrimental effect on herbaceous production. Deep shade did not affect herbaceous production, but *Themeda* *triandra* showed etiolated growth, aerial tillering, an increase in the number of leaves, and an increase in the proportion of stem under deep shade. The root mass of the herbaceous layer also decreased. This suggested that below-ground biomass production was impaired at the expense of maintaining above-ground biomass. The addition of nutrients significantly increased herbaceous production and resulted in a change in sward composition. Moisture was not an important factor in this experiment.

Mechanical clearing in the bush control experiment resulted in a significant increase in herbaceous production. *Panicum maximum* colonized the ex-bushclump zone and contributed significantly to the increased production. Oversowing with *Chloris gayana* significantly increased grass yields. The two contrasting seasons revealed the importance of rainfall in affecting herbaceous production. The second season was characterized by lower soil fertility and a decline in grass quality. This was attributed to high grass production in the above-average rainfall season. A four-fold increase in woody stem density after two seasons demonstrated the coppicing ability of the woody layer once mechanically cleared. Most of the coppice occurred within the first season. Exceptional coppice growth characterized the second season. *Acacia karroo* recruitment was mainly from seed.

Woody plants showed their susceptibility to chemical poisoning by dropping their leaves within the first season. Many of these individuals succumbed during the second season. Mortality was greatest in woody plants with a smaller basal circumference. Owing to the difficulty of accessing all woody stems in a bushclump, mortality in bushclumps was lower than that in the open grassland. Grass production in the bushclump and its periphery were significantly increased in both seasons. This was attributed to the increased productivity of mainly *Panicum maximum* which took advantage of the increased irradiance regime.

Both the mechanical and chemical treatments displayed significantly greater grass production in the open grassland zone. This demonstrated the extent to which the woody layer had competitively dominated the herbaceous layer.

DECLARATION

I hereby certify that the research work reported in this dissertation is the result of my own original investigation, except where acknowledged.

Signed..

ACKNOWLEDGEMENTS

I wish to express my sincere appreciation to the following individuals and organizations for the valuable assistance and co-operation that was received during the study period:

My supervisor, Prof. Tim O'Connor, for his personal interest and guidance;

The Department of Agriculture, Eastern Cape, for funding this project and the use of material developed whilst in their employ;

Felix Hobson and other colleagues in the Pasture Section, at the Döhne Research Station, Stutterheim, for the support and enjoyable working conditions. Thanks to Messers Machlachlin, Witbooi, Khatshwa and Nyamakazi for their assistance in the establishment of the trial. Thanks to Xolani Nelani for his assistance with field and laboratory work, and data collection;

Ruelof Coetzer, Biometrics, Agricultural Research Council, for assisting me with many of the statistical analyses;

Estelle Brink of the Albany Museum, Rhodes University, Grahamstown, for her assistance in the identification of tree and forb species;

Brian Newey for making an area of his farm available for the purpose of this study;

My parents, for their support, which has allowed me the opportunities denied to so many;

My wife Leanne, for the sacrifices, love and support.

TABLE OF CONTENTS

CHAPTER PAGE

ABSTRACT (ii)

DECLARATION (v)

ACKNOWLEDGEMENTS (vi)

TABLE OF CONTENTS (vii)

1 INTRODUCTION 1

2 STUDY SITE 5
  2.1 LOCATION 5
  2.2 CLIMATE AND RAINFALL 5
  2.3 SOILS 7
  2.4 VEGETATION 8

3 INFLUENCE OF BUSHCLUMPS ON THEIR LOCAL ENVIRONMENT 10
  3.1 INTRODUCTION 10
  3.2 PROCEDURES 11
    3.2.1 Irradiance Regime 11
    3.2.2 Temperature and Humidity 12
    3.2.3 Soil Physical and Chemical Properties 13
    3.2.4 Herbaceous Production, Composition and Quality 14
    3.2.5 Seedbank and Seedlings 15
    3.2.6 Lateral Root Distribution 18
  3.3 RESULTS 21
    3.3.1 Irradiance Regime 21
    3.3.2 Temperature and Humidity 23
    3.3.3 Soil Physical and Chemical Properties 28

3.3.4 Herbaceous Production, Composition and Quality 30
3.3.5 Seedbank and Seedlings 33
3.3.6 Lateral Root Distribution 34
3.4 DISCUSSION 36

4 **INFLUENCE OF IRRADIANCE, NUTRIENTS AND WATER ON THE HERBACEOUS LAYER** 41
4.1 INTRODUCTION 41
4.2 PROCEDURES 42
4.2.1 Site Description 42
4.2.2 Treatments 43
4.2.3 Measurements 46
4.2.4 Statistical Analyses 48
4.3 RESULTS 49
4.3.1 Herbaceous Layer 49
4.3.2 *Themeda* Dynamics 51
4.3.3 Litter 53
4.3.4 Root Biomass 55
4.3.5 Soil Chemical Status 56
4.4 DISCUSSION 58
4.4.1 Effect On Herbaceous Production 58
4.4.2 Effect On Forage Quality 61

5 **RESPONSES TO BUSH CONTROL** 64
5.1 INTRODUCTION 64
5.2 MATERIALS AND METHODS 65
5.2.1 Site Description 65
5.2.2 Treatments 65
5.2.2.1 Mechanical treatment 65
5.2.2.2 Chemical treatment 66
5.2.3 Measurements 66
5.2.3.1 Herbaceous layer 66
5.2.3.2 Soil nutrient status 67
5.2.3.3 Woody layer 67

5.2.4 Data Analyses 69
    5.2.4.1 Herbaceous layer and soils 69
    5.2.4.2 Woody layer 70
5.3 RESULTS 72
  5.3.1 Herbaceous Responses 72
    5.3.1.1 Herbaceous production 72
    5.3.1.2 Herbaceous composition 74
    5.3.1.3 Grass quality 78
  5.3.2 Soil Response 80
  5.3.3 Woody Dynamics 82
    5.3.3.1 Chemical vs control: large individuals 82
    5.3.3.2 Chemical vs control: small individuals 85
    5.3.3.3 Mechanical clearing 88
    5.3.3.4 Mechanical vs oversown 94
5.4 DISCUSSION 94
  5.4.1 Mechanical Treatment 94
  5.4.2 Chemical Treatment 97

6 CONCLUSIONS 100

LITERATURE CITED 106

APPENDICES 115

CHAPTER 1

INTRODUCTION

The interaction between woody and herbaceous components has received considerable attention in savanna regions world-wide. In southern Africa the emphasis has been exclusively on single-tree savannas without any attention to multi-species bushclumps. Bush encroachment or densification, which in South Africa is reported to affect some 13 million ha (Trolloppe *et al.* 1989), has been the motive for many of these studies. Some reasons given for bush encroachment are incorrect grazing practices, a lack or misuse of fire and the absence of browsing animals. Bush encroachment occurs as a result of an altered woody/grass balance with the result that the woody component gains a competitive advantage over the herbaceous layer. This is of serious concern to pastoralists or ranchers. In the Eastern Cape, *Acacia karroo* is responsible for much of the encroachment, especially in the semi-arid areas (du Toit 1967; Aucamp *et al.* 1983). However, in the mesic coastal areas of the Eastern Cape the vegetation is not dominated by individual trees but by a species-rich woody component which occurs as bushclumps. Bush encroachment, in these areas, takes the form of an expansion of existing bushclumps into the adjacent grassland. These have the potential to form closed canopy woodlands which preclude grasses.

Modifications of the abiotic environment accompany the changes in vegetation associated with bush encroachment. Enhanced soil nutrient status with woody development has been demonstrated under *Prosopsis juliflora* (Tiedemann & Klemmedson 1973), *Acacia tortilis* and *Adansonia digitata* (Belsky *et al.* 1989), tree clumps (Mordelet *et al.* 1993) and bushclumps (Palmer *et al.* 1988). An altered microclimate is also a characteristic of woody development (Belsky *et al.* 1989; Vetaas 1992). Herbaceous changes are also associated with the development of the woody component. This depends on the balance between increased production potential (from greater available soil nutrients and ameliorated microclimate), and decreased production as a result of competition from woody plants. Trees in temperate and tropical savannas were thought to reduce the productivity of understorey plants through competition for light, moisture and nutrients (Walker & Noy-Meir 1982). A few recent studies, however, have documented that isolated trees may also improve understorey productivity (Stuart-Hill *et al.* 1987; Belsky *et al.* 1989, 1993).

Since grasses are generally excluded from bushclumps, the reduction in herbaceous production with increased bushclump development provides a compelling motivation on its own to control bush. The decision to control bush rests on the assumption that the increased herbaceous, and therefore livestock production, offsets the cost of bush control. Mechanical clearing (manual or bulldozing) and chemical poisoning (using soil- and plant-applied arboricides) are bush control methods often employed to improve the grazing capacity. These methods, however, are very expensive and usually need to be repeated since woody re-encroachment from coppice and seed is certain. Local articles (Glen-Leary 1992), however, report "quick-fix" solutions to bush encroachment, without considering the implications and financial soundness of such operations. Alternatives, such as the incorporation of a browser (Aucamp 1976) and the use of fire (Trolloppe 1974) in bushveld areas to control and curb bush encroachment have been recommended for many years. However, the utilization of such biological control agents has, in general, not been favourably received by farmers which run predominantly cattle and sheep enterprises.

It has been widely shown that the large scale removal of trees and shrubs by mechanical or chemical means does result in increased herbaceous production of up to 400% (Barnes 1979). Work done in *Eucalyptus* savanna demonstrated an immediate and substantial increase in herbage biomass, following tree thinning

(Walker *et al.* 1986), woody plant clearing (Harrington & Johns 1990), and chemical poisoning (Walker *et al.* 1972). Initial results in the Northern Cape show 220-740% increases in grass production following chemical bush control (Moore *et al.* 1985). However, most bush control experiments report their initial success in increasing herbage production, but few report the situation after several years when, presumably, woody re-encroachment may have significantly reduced grass production to previous levels. In the Eastern Transvaal lowveld it was reported that the recovery of cleared mopane thicket, to a level where its effect on grass production was similar to that in the pre-cleared state, occurred within fourteen years (Scholes 1990). It was also shown that the clearing exercise was uneconomic. Results gathered over 15-19 years in four veld types in the south-west of Zimbabwe showed that herbage response to bush clearing was also strongly influenced by rainfall regime and soil type (Dye & Spear 1982). Most bush control experiments report only the increased herbaceous production without investigating further ecosystem responses to bush clearing, such as changes in herbage quality, and changes in the soil nutrient status, woody re-establishment dynamics, and the long-term stability of the system. The inclusion of these response variables in an economic model would provide a valid assessment of the financial viability of such bush control operations (Moore & Odendaal 1987).

The above approach has formed the basis for the establishment of a programme addressing bush control in the mesic bushclump savannas of the Eastern Cape. A formal replicated field experiment has been initiated to test the efficacy of mechanical and chemical bush control. Since these methods are rarely 100% effective due to woody re-establishment from both coppice and seeds, the inclusion of follow-up treatments (fire, goats, fire and goats) have been included. Cognizance has been taken of the importance of measuring response variables vital for a valid economic assessment. Once woody re-encroachment has reached a level of relative stability the financial soundness of the treatments can be assessed.

The aims of this thesis were three fold. First, it was to characterise the bushclump and grassland environment (Chapter 3). This would provide insight into woody-grass interactions in the mesic Eastern Cape savannas. The bushclump physiognomy also provides an interesting variation to an otherwise well-studied interaction. Second, a factorial experiment was initiated to discriminate the individual and interactive effects of irradiance, nutrients and moisture (the three resources for which the woody and herbaceous layers compete) on a homogenous grassland. Since these factors are usually compounded their elicitation could provide further insight into woody-grass interactions (Chapter 4). Finally, herbaceous, woody and soil responses to mechanical and chemical treatments in a bush-control experiment were examined for the first two seasons following clearing (Chapter 5).

CHAPTER 2

STUDY SITE

2.1 LOCATION

The study area was located on the farm "Lily-Park" (32°41'S; 27°41'E) near Kei Road, in the magisterial district of King Williams Town, Eastern Cape. The farm is approximately 2 km from the Gonubie River valley. The farm is owned by Mr Brian J. Newey. It has been grazed by cattle and sheep for the past 46 years. Fire has generally not been used as a veld management tool. Although stocking rate could not be quantified, it was probably moderate as no obvious signs of over-utilization were evident, however, the north-facing slopes seemed to be more heavily grazed than the south-facing slopes. Previous signs of cultivation were not evident. The experimental area was 20 ha in extent and situated on the foot and middle portion of a relatively uniform and moderate (20%) north-facing slope. The study area was located on the bottom and mid-slope. Elevation was 560-610 m above-sea-level.

2.2 CLIMATE AND RAINFALL

The area is relatively mesic when compared with South African savannas and is frost-free, with an average seasonal rainfall of 646 mm, recorded 1 km away at the farm's homestead over a period of 46 years. The annual rainfall (July-June) is extremely variable, with an average CV of 26.9%. Dry spells are considered the norm (Jury & Levy 1993). The pattern of rainfall for "Lily-Park" exhibited a definite dry winter period as well as a slightly drier mid-summer period (Figure 2.1).

Rainfall during the experimental period was recorded with a standard weather bureau rain gauge, which was situated within the study site. The rain gauge was positioned in an open area of grassland clear of woody vegetation, at a height of 1.2 m above ground level. The monthly rainfall from July 1992 to June 1994 is presented in Figure 2.2.

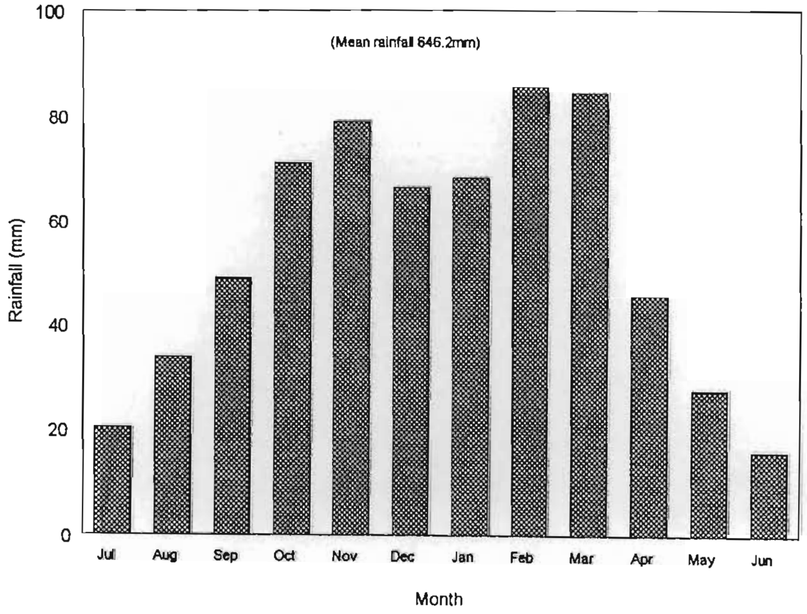

Figure 2.1 Mean monthly rainfall at "Lily-Park" for the period 1948 to 1994.

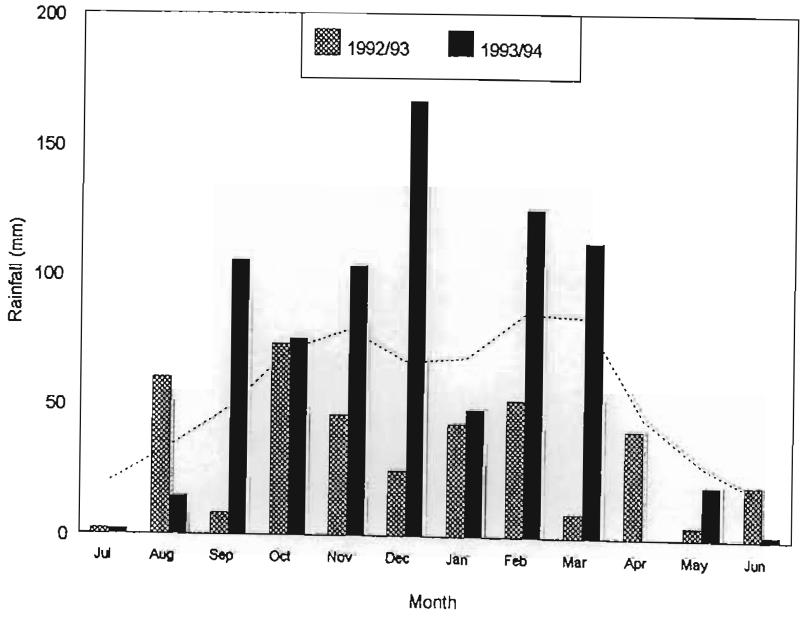

Figure 2.2 Monthly rainfall recorded during the experimental period. The broken line indicates the mean rainfall obtained over 46 years.

Rainfall during the experimental period was very variable. Extremely dry conditions were experienced during the 1992/93 season with a total rainfall of 384 mm, well below the long term average of 646 mm. However, the second season was characterised by above average rainfall with a total of 777 mm.

2.3 SOILS

Two soil types were identified in the study area, with the one soil type occurring upslope of the other. This effectively split the study area into an upper and lower portion (hereafter referred to as the upper and lower slope of the study area). The soil of the upper slope was classified as a Hutton 3100 according to the S.A. binomial soil classification system (Soil Classification Working Group, 1991). Underlying geology was dolerite. The orthic A horizon was approximately 400 mm deep, while the red apedal B horizon penetrated to at least 800 mm. According to the relative proportions of sand (46-56%), clay (33-43%) and silt (6-16%) in the orthic A horizon, the soil texture was described as sandy-clay. In the apedal B horizon the proportion of clay increased (39-53%) and the soil was described as a clay.

The lower slope of the study area was on soil classified as a Glenrosa 1211 according to the S.A. binomial soil classification system (Soil Classification Working Group, 1991). Geology was sandstone. The orthic A horizon was approximately 350 mm deep and the lithocutanic B horizon reached a depth of 800 mm. The relative percentages of sand (56%), clay (23%) and silt (20%) in the A-horizon resulted in the soil texture being described as sandy-clay-loam. Although the B horizon showed a slight increase in clay percentage, soil texture remained a sandy-clay-loam. There were no free stones or boulders embedded in the profiles of either soil types.

2.4 VEGETATION

Grass species nomenclature follow Gibbs-Russell *et al.* (1985), and dicotyledonous plant nomenclature follow Gibbs-Russell *et al.* (1987).

The study area falls into the mesic bush-grass communities of the Eastern Cape agricultural region. This vegetation-type occurs in the districts of Alexandria, East London, Bathurst, Komga, Albany and King Williams Town and comprise 3.7% (629 753 ha) of the region (O'Reagain & Hobson 1989). The vegetation consists of a structurally diverse mosaic of open grassland, scattered to dense *Acacia karroo* individuals, discrete multi-species bushclumps within a grassland matrix, and closed canopy woodland. The vegetation in the study area consisted of multi-species bushclumps which occurred in a grassland matrix.

Descriptive accounts of this vegetation-type by Dyer (1937), Story (1952) and Comins (1962) reported the invasion of *A. karroo* into grassland as early as the 1900's. This was linked to the deterioration of the grass layer due to incorrect veld management. *Acacia karroo* was also reported to be the precursor in the succession to scrub which eventually replaced grassland. Acocks (1953), classified this vegetation-type as Eastern Province Thornveld (7). It also resembles similarities of the False Thornveld of the Eastern Cape (21), where the vegetation is scrub forest, marginal to the high forest of the mountains, and separated from the Valley Bushveld (23) by a zone of grass, thorn and bushclump veld along the edges of the valleys. Acocks (1953) also postulated that the initial invasion of *A. karroo* into grassveld occurred where the dense *Themeda* sward was broken down by selective grazing. *Acacia karroo* individuals have been reported as providing microsites for bird-dispersed woody species (Bews 1917; Acocks 1953), notably *Scutia myrtina*, which establish and develop into bushclumps. This pattern resembles the autogenic succession of sub-tropical grassland to thorn woodlands in southern Texas (Archer *et al.* 1988; Archer 1989 & 1990), where discrete shrub clusters represent an intermediate stage in the conversion of grassland to woodland. As new shrub clusters initiate and existing clusters expand and coalesce, a gradual shift from grassland to savanna to woodland occurs.

Bushclumps in the study area, were dominated by *Scutia myrtina*. Other common species were *Maytenus heterophylla*, *Cussonia spicata*, *Canthium mundianum*, *Rhus undulata*, *Diospyros simii*, *Hippobromus paucifloris*, and *Grewia occidentalis*. (Appendix 1 contains a list of all woody species identified in the study area). Woody seedlings (generally less than 20 cm in height) were abundant in the understorey vegetation of bushclumps. *Coddia rudis* was a very common shrub species which dominated the peripheral regions of bushclumps and occurred in the grassland matrix. *Acacia karroo* and *S. myrtina* also occurred as individuals or in small woody clusters in the grassland. An investigation of 52 bushclumps in the study area showed that bushclump areas ranged from 32 to 1991 m^2, with a mean area of 326 m^2, and heights averaged 6 m, depending on species composition. The proportion of the study area covered by woody vegetation ranged from 31 to 89%, with a mean of 67%.

The herbaceous grassland layer was dominated by C_4 perennial grasses, in particular *Themeda triandra*, *Eragrostis curvula*, *Sporobolus africanus*, *Eragrostis plana*, *Panicum maximum*, *Aristida congesta* and *Digitaria eriantha*. The bushclump understorey was comprised of species such as *P. maximum* and *Helictotrichon capense* (C_3 grass), and dicotyledenous plants.

CHAPTER 3

INFLUENCE OF BUSHCLUMPS ON THEIR LOCAL ENVIRONMENT

3.1 INTRODUCTION

Savannas are characterized by a continuous herbaceous layer and a discontinuous tree layer (Huntley 1982). Both layers are considered to develop competitive interactions (Walker & Noy-Meir 1982; Knoop & Walker 1985). Competition for irradiance, nutrients and water characterize the interaction of the woody and herbaceous components in savannas. Many studies have focused on quantifying the effect of woody plants on their local environments by investigating the irradiance, nutrient and moisture regimes under trees and in open grassland (Tiedemann & Klemmedson 1973, 1977; Stuart-Hill *et al.* 1987; Belsky *et al.* 1989, 1993; Smit & Swart 1994; see Vetaas 1992 for a review). Such studies provide insight into the woody-grass interaction. However, the above-mentioned studies investigate single-tree savannas which hinders the transfer and applicability of results to a bushclump savanna. Although studies in the humid West African tree clump savannas seem relatively comparable (Mordelet *et al.* 1993; Mordelet & Menaut 1995) large climatic differences exist. Thus, information pertinent to the mesic Eastern Cape bushclump savannas remains lacking.

The vegetational differences between bushclumps and grassland are self-evident, but differences in irradiance, nutrients and moisture are not. In order to gain insight into woody-grass interactions in this savanna a study was initiated to quantify and describe the local environment associated with bushclumps and open grassland. The aim of this chapter is to determine the extent to which the irradiance regime and microclimate are altered by bushclumps which affects both evapotranspiration and the moisture regime, whether the soil physical and chemical characteristics beneath bushclumps are different from open grassland, and the extent to which woody roots spread into the adjacent grassland which would provide insight into the competitive nature of the woody layer. Herbaceous productivity, composition and quality under bushclumps and in the open grassland were compared as this would provide an indication of the degree of competition which exists between the woody and herbaceous layers. Seedbanks and seedling densities were also quantified since they play an important role in future vegetation dynamics.

3.2 PROCEDURES

3.2.1 Irradiance regime

Three random sites were selected on the lower slope of the study area (Section 2.3). The criterion for site selection was that a site should consist of a discrete bushclump surrounded by grassland. At each site three random but parallel transects were placed through the bushclump. Transects ran in a north-south direction, starting in the grassland on the north-facing side of the bushclump and ending in the south-facing grassland. Irradiance was measured at one metre intervals along each transect using a LiCor LI 1000 quantum sensor at a height of 0.2 m above the ground (herbaceous vegetation did not interfere with measurements). The irradiance regime was determined at midday on a single clear day in April 1992. Data were stratified according to vegetation zone and aspect (Figure 3.1). The peripheral bushclump zone (PBC) was defined as the two-metre-wide band extending from the grassland-bushclump interface inwards.

A split-plot design was used, with site the block or whole-plot factor, transect the main-plot factor and stratum, aspect and distance the various sub-plot factors. Data were analysed using PROC GLM (SAS Ins. 1982). Data were transformed using a Box-Cox transformation (Weisberg 1985) and residuals were examined for normality (PROC UNIVARIATE, SAS Ins. 1982). Data were normally

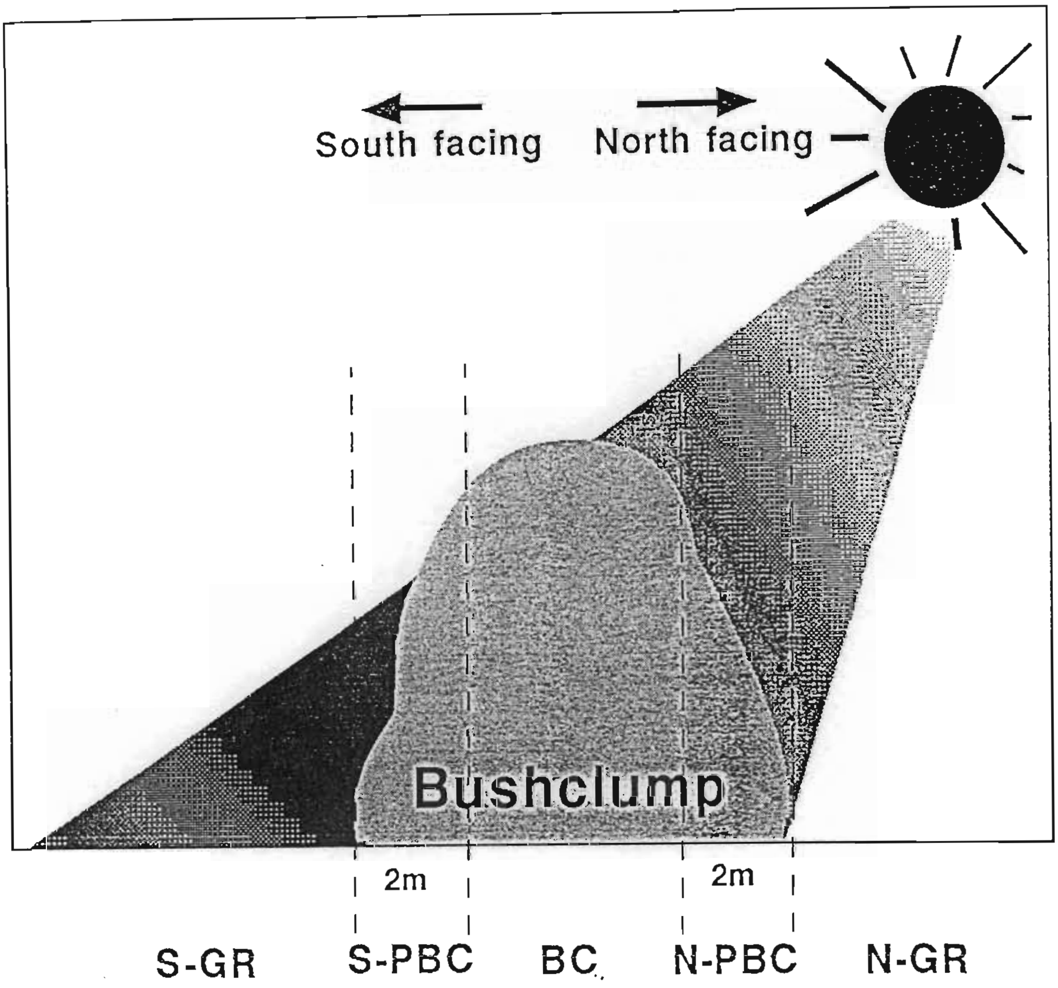

Figure 3.1 Stratification of the vegetation into a bushclump zone (BC), peripheral zone (PBC) and grassland zone (GR) each described according to its aspect (either north- (N) or south-facing (S)).

distributed. Tukey's studentized range test was used to compare main effects and CONTRAST statements were used to test the interactive effects. Means were back-transformed and reported with 95% confidence levels.

3.2.2 Temperature and Humidity

Three sites were randomly selected in the upper portion of the study area (section 2.3). The criterion for site selection was the same as in section 3.2.1. At each site a monitoring station was placed inside the bushclump interior and another in the adjacent open grassland. At each of the six monitoring stations thermohygrographs, housed in Stevenson-screens, recorded temperature and humidity.

Data were collected from 1 December 1992 to 30 November 1993. Daily maximum and minimum temperature and humidity were used as a measure of the microclimate. Maximum and minimum thermometers were placed in the Stevenson-screens during the period 17 August 1993 to 30 November 1993, as a secondary and more precise measure of the stations temperature profiles. Weekly maximum and minimum readings were recorded.

Polynomial regressions were fitted to the maximum and minimum temperature and humidity data collected from each monitoring station, using PROC REG (SAS Ins. 1982). Bonferroni multiple comparison tests (Groeneveld 1970) were performed for each site, to test for differences in temperature and humidity patterns between the bushclump and grassland stations. The maximum and minimum thermometer readings measured during the latter experimental period were analyzed using analysis of variance (PROC GLM, SAS Ins. 1982). Data were transformed prior to analysis using a Box-Cox transformation (Weisberg 1985) and residuals were tested for normality (PROC UNIVARIATE, SAS Ins. 1982). Data were normally distributed.

3.2.3 Soil Physical and Chemical Properties

Five sites were randomly selected on each of the two soil types occurring in the study area (section 2.3). The criterion for site selection was the same as in section 3.2.1. Soil samples were collected in February 1993. At each site, soil samples were collected from beneath the bushclump and from the adjacent grassland. Soil samples were collected from three depths (0-20 cm, 20-40 cm and 40-60 cm) within each bushclump and grassland zone. Within each vegetation zone a composite sample of three random soil samples was formed for each depth.

Soil characteristics analyzed were particle size distribution, soil density, pH, organic C, total N, extractable P, K, Ca, Mg, Na, Cl and electrical conductivity. Methods of soil analyses are reported in Appendix 2.

The effect of vegetation zone and soil type on soil physical and chemical variables was analysed using analysis of variance. Spatial dependence between bushclump and grassland soils, and between depth classes were tested for each sampling site. This was done by obtaining residual errors (difference between the variable value and the replicate mean) for each depth of the bushclump and grassland zone within each sampling site, and testing whether the bushclump and grassland residuals were correlated using Pearson product-moment correlation (for normally distributed data) or Kendall's tau-b coefficient of rank correlation (for non-normally distributed data) (SAS Ins. 1982). The same procedure was followed for testing depth class correlation. Bushclump and grassland soil data were spatially independent. Depth classes were significantly correlated (spatially dependent), and so the analysis of variance was executed separately for each depth. The analysis of variance was also executed separately for soil type. Prior to analysis of variance, soil variables were transformed using the Box-Cox transformation (Weisberg 1985). Where data were normally distributed, analysis of variance (completely random design) using PROC ANOVA (SAS Ins. 1982) was executed. Where data were not normally distributed, non-parametric analyses were used (PROC NPAR1WAY, SAS Ins, 1982).

3.2.4 Herbaceous Production, Composition and Quality

Sixteen sites were randomly selected on the upper slope of the study area (Section 2.3). The vegetation at each site was stratified into three zones: the interior bushclump zone, the peripheral bushclump zone and the interclump grassland zone. Within each vegetation zone, five random quadrats were placed (quadrat dimensions were 0.5 m x 0.5 m). Frequency, cover-abundance and the dry-weight-rank method (Mannetje t' & Haydock,

1963) were used to describe the composition of the herbaceous layer in the three vegetation zones. All rooted, live herbaceous species (including forbs) occurring in a quadrat were identified. Braun-Blanquet cover-abundance scales, adapted by van der Maarel (1979), were assigned to each species identified in a quadrat, and the median of the cover class was used to derive a mean percent cover for each vegetation zone. For the dry-weight-rank method, the three herbaceous species (forbs were grouped) contributing most to the above-ground herbaceous biomass in a quadrat were noted. Herbaceous material in each quadrat was harvested at ground level. Harvested samples were separated into grass and forb components, weighed, and oven-dried at 60°C for 48 hours. Two seasons data were collected (1992/93 and 1993/94 seasons) during the months of April and May. For plant quality analyses, the five quadrat samples in each vegetation zone were pooled to give a composite sample. Methods of plant analyses are reported in Appendix 3. A compass direction was taken at each quadrat to determine whether aspect (north- or south-facing side of a bushclump) affected herbaceous production.

An analysis of variance was used to test the effect of vegetation zone on herbaceous production and quality (PROC GLM, SAS Ins. 1982). Data were transformed using a Box-Cox transformation (Weisberg 1985) and residuals were examined for normality (PROC UNIVARIATE, SAS Ins. 1982). Data were normally distributed. Tukey's studentized range test was used to compare main effects. Means were back-transformed and reported with 95% confidence levels.

3.2.5 Seedbank and Seedlings

Background

Seedbanks are generally defined as a collection of viable, dormant seeds in the soil of a defined area. The role dormant seeds play in plant ecology, be it in natural forests or deserts, has been studied by scientists in various ways (Roberts 1981).

Extracting seeds from soil samples is time-consuming and results are influenced by the time of year and methods used (Thompson & Grime 1979). Gross (1990) investigated different methods of determining seed numbers, such as germination, germination following cold-stratification, and washing using a modified elutriation system. Roberts (1981) noted that both sampling time and testing method could influence the species that germinated from samples.

A major problem with most seedbank studies is that estimates of seed numbers are very imprecise (Bigwood & Inouye 1988). As a result, most researchers have been able to make only a general, qualitative statement concerning the seedbank.

Most attempts to quantify seedbanks have relied on germination methods (Roberts 1981). The limitations of this approach have been readily acknowledged (e.g. Thompson & Grime 1979), but it is generally justified as providing an estimate of the germinable fraction of the seed bank.

Materials and methods

Thirty-six sample sites were randomly selected in the upper portion of the study area (section 2.3). The vegetation was stratified into three vegetation zones, namely: interior bushclump zone, peripheral bushclump zone and adjacent grassland zone. At each site seedbank samples from the litter layer and top-soil were taken. Top-soil cores of 16.5 cm diameter and 5 cm depth were extracted from each vegetation zone. In the bushclump and peripheral zones, litter layer samples (of the same soil core diameter) were taken prior to soil core removal. Samples were collected in October 1992.

Soil and litter samples were placed in germination trays in a glasshouse. Litter samples were mixed with sterile soil. Trays were watered regularly and germination assessments made weekly. The investigation was terminated on the 31 March 1993.

Germinated seedlings were given an identification code and enumerated. For each coded seedling a voucher specimen was removed and grown out in a larger pot for later identification. Although many seedlings died before positive species identification it was possible to classify them as grasses, sedges or dicotyledonous plants. At the end of the investigation, soil and litter samples were sieved and ungerminated seeds counted. Owing to the size of seeds, only larger woody seeds were counted.

Data were tested for normality but due to the large number of zero values in the dataset a non-parametric test was employed. A linear rank statistic (PROC NPAR1WAY, SAS Ins. 1982), based on Wilcoxon scores, was applied using the Kruskal-Wallis test for differences of location for the ranked dataset. The Mann-Whitney U statistic was used to perform unplanned multiple comparisons, increasing the probability of making a type I error (Sokal & Rohlf 1981). Seed density for litter and soil samples was expressed as individuals per m^2.

During the collection of the herbaceous composition data, the presence of woody seedlings was noted in each quadrat. An analysis of variance (PROC GLM, SAS Ins. 1982) was used to determine the effect of vegetation zone on woody seedling density. Data were transformed using a Box-Cox transformation (Weisberg 1985) and residuals were examined for normality (PROC UNIVARIATE, SAS Ins. 1982). Data were normally distributed. Tukey's studentized range test was used to compare main effects. Means were back-transformed and reported with 95% confidence levels.

3.2.6 Lateral Root Distribution

Background

The determination of the distribution of woody root systems has been met by some trepidation owing to their extensive branching and concealment by soil. Ecological studies such as Rutherford (1983) resorted to excavation to study the below-ground components of savanna systems. Isolating, tracing and measuring root systems by classical excavation methods is very laborious and labour intensive.

Radioactive-tracer techniques have been used in a number of investigations to determine the distribution and activity of plant roots (Bassett *et al.* 1970; Ellis & Barnes 1973; Coffin & Laurenroth 1991; Milchunas *et al.* 1992). However, radioactive-tracers suffer from a number of disadvantages. A short half-life makes repeated injection necessary in long-term experiments. Authority to make subsoil applications of long half-life radioactive-isotopes is not easily obtained, as unacceptable environmental risks exist. Careful handling is necessary to avoid radiation hazards when analyzing sampled material. These have led to the use of stable non-radioactive isotopes.

Non-radioactive isotopes require the following attributes: they must be taken up by plants similarly to a normal soil nutrient element, be non-toxic in concentrations that are easily detectable, not easily leached, and be of low natural concentration in the soil. Strontium (Sr) and Rb (rubidium) fulfil these requirements in many soils, behaving like Ca and K respectively. Strontium uptake was successfully used to estimate root activity in alfalfa (Fox & Lipps 1964) and barley seedlings (Soileau 1973), and root penetration in a number of crop plants (Pinkerton & Simpson 1979). Dye & Poulter (1991) investigated the use of Rb as a tracer to explore the lateral reach of *Eucalyptus grandis* roots. Rubidium was applied to a clearly defined region of the soil, and then plants in the vicinity were sampled for tracer uptake. This method is far less time consuming and less costly than the excavation of an entire root system. Although they were not successful in the detection of rubidium in *E. grandis* samples, cognizance was taken of their possible shortfalls. They suggested several improvements to enhance tracer detection when applying the tracer and sampling plant tissue.

Materials and methods

A pilot study was undertaken to study the lateral spread of woody root systems, using Rb as a non-radioactive tracer. Two experimental sites were selected. The first was situated on the lower slope of the study area (section 2.3) (Lily-Park site) and the second on the farm "Kentbury", near Kei Road (Kentbury site). The vegetation at both sites was comparable. The procedure followed at the 2 sites was different and therefore described separately.

Lily-Park site

The first assumption made was that the lateral reach of any woody individual was a maximum of 50 m. Thirteen Rb application sites were randomly selected. A selection criterion was that no two application sites were within 100 m of each other. This was to ensure that a woody individual sampled within a 50 m radius of a particular Rb application site could only take up Rb from that particular site. At each of the 13 application sites a pit 40 cm in diameter and 10 cm deep was dug. On 13 January 1993, 1 ℓ of water containing 6 g of $RbSO_4^-$ was poured into each hole. Holes were then flushed with 5 ℓ of water to promote tracer dispersion into a greater volume of soil.

The second assumption made was that any Rb taken up by woody plants would be concentrated in new growth (Dye & Poulter 1991), hence plant samples were taken from young leaves and twigs, as well as developing fruits.

Plant samples were collected after 4 months. At each of the 13 application sites, 10 to 13 woody individuals were sampled. *Scutia myrtina*, the most abundant woody species in this savanna, made up more than 50% of the plants sampled. Other species sampled included *Maytenus heterophylla*, *Canthium mundianum*, *Rhus undulata*, *Diospyros simii* and *Acacia karroo*.

Since the objective of the investigation was to assess the lateral reach of woody plants, individuals were sampled at various distances from the application sites so that a range of distances was covered. Woody plant size was quantified so that a relationship between tree size, distance and Rb concentration in plant samples could be investigated.

After plant samples had been collected, soil samples for 2 of the 13 application sites were taken at 0, 0.5, 1, 4 and 40 m from the respective application sites and at 2 depths (0-50 and 50-100 cm). This was to done to assess Rb dispersion through the soil and background Rb levels.

Kentbury site

The same assumptions were made in this investigation. Sampling procedure, however, differed from the Lily-Park site in a number of ways. Only 2 application sites were selected. Sampling was more intensive, and only *S. myrtina* was sampled. At each of the 2 application sites, 3 smaller holes (layed out in a triangle, 50 cm apart) were augered to a depth of 15 cm. This was to improve the dispersion of the $RbSO_4^-$ solution in the soil, and to cause less disturbance than the previous technique of excavation. A solution containing 9 g of $RbSO_4^-$ in 1 ℓ of water (more concentrated than that used at the Lily-Park site) was evenly divided between the 3 auger holes, and then flushed with 5 ℓ of water.

Tree and soil samples were taken prior to Rb application (2 November 1993) to account for possible background Rb levels. The same trees were re-sampled after 2 weeks from the application date (a shorter uptake period than that employed at the Lily-Park site). Both Rb and K concentrations in plant and soil samples were determined. Since Rb is an analog of K, a change in the ratio of these elements in sampled plant material may indicate tracer uptake. Methods for Rb and K determination in plant and soil samples are reported in Appendix 4.

3.3 RESULTS

3.3.1 Irradiance Regime

The irradiance regime associated with the bushclump and peripheral zones was 11% and 25%, respectively, of the irradiance regime in the grassland zone (Table 3.1). Aspect had an important effect on the irradiance regime. Shading was significantly greater in the south-facing peripheral zone than in the north-facing peripheral zone (Figure 3.2). Irradiance was also significantly higher in the first metre (from the bushclump-grassland interface inwards) of the north-facing peripheral zone than in the second metre ($P<0.003$), whilst no significant differences occurred within the south-facing peripheral zones.

Table 3.1 Mean (± SE) irradiance measured as photosynthetic photon flux density ($\mu molm^{-2}s^{-1}$), at 0.2 m above ground-level in the three vegetation zones.

Vegetation zone	**Irradiance (PPFD)** **mean ± SE**
Grassland	1547 ± 69
Peripheral	381 ± 88
Bushclump	174 ± 56

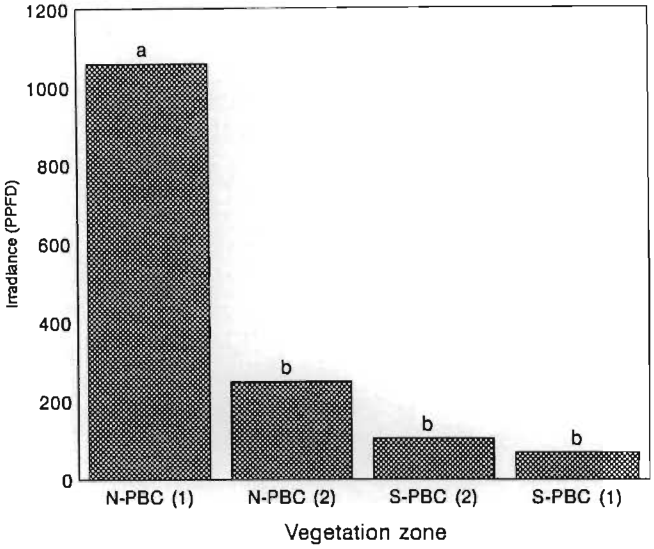

Figure 3.2 The effect of aspect on irradiance, measured as photosynthetic photon flux density (μmol.m^{-2}.s^{-1}), in the first and second metre of the peripheral zone (PBC) on both the north (N) and south (S) side of the bushclump. (Letters which differ indicate significance at the 5% level.)

Bushclumps had a major spatial effect on the irradiance regime in the south-facing grassland zone, but had no effect in the north-facing grassland (Figure 3.3).

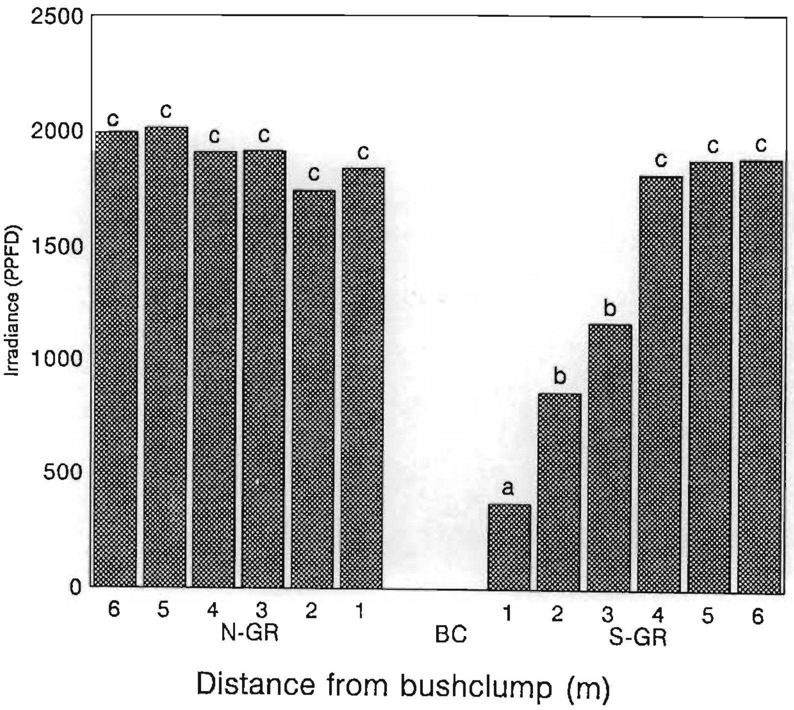

Figure 3.3 The effect of aspect on irradiance, measured as photosynthetic photon flux density (μmol.m^{-2}.s^{-1}) in the grassland zone (GR) on the north (N) and south (S) side of the bushclump (BC). Distance measures indicate the distance from the bushclump-grassland interface. (Letters which differ indicate significance at the 5% level.)

3.3.2 Temperature and Humidity

Although this investigation spanned a year, only 254 recording days were obtained due to various problems, of which most occurred in the initial stages of the investigation.

Temperature and humidity profiles exhibited a large variation within and between monitoring sites, possibly due to real site differences or instrumentation errors. Maximum temperature (Figure 3.4) varied greatly between the three monitoring sites. Although significant differences between the bushclump and grassland stations were only apparent during a portion of the year, in site (a) and (b), the maximum temperature within a bushclump was always lower than that in the adjacent grassland.

Minimum temperature (Figure 3.5) also showed an erratic pattern with conflicting trends between the bushclump and grassland stations. In Figure 3.4, site (c) was observed to have a consistently larger maximum temperature range for the grassland station than that of the bushclump station. In Figure 3.5, a similar trend was observed for the minimum temperature range. An incorrect temperature setting on the thermohygrograph would have affected both the maximum and minimum temperature ranges, with a setting too high resulting in high maximum and high minimum temperature profiles, which may explain the pattern observed in site (c). If this was the case, the real difference between the bushclump and grassland profiles would have been less.

The outcome of the secondary investigation, using maximum and minimum thermometers, was a significantly lower maximum temperature and significantly higher minimum temperature in the bushclump stations than in the grassland stations (Table 3.2). The difference between the maximum and minimum temperature profile at each station (temperature fluctuation) showed that bushclumps had a moderating effect on the temperature regime.

Table 3.2 The influence of bushclumps on maximum and minimum temperature, and temperature difference when compared to grassland (n=12). (Letters which differ within a column indicate significance at the 5% level.)

Vegetation zone	**Maximum temperature °C**		**Minimum temperature °C**		**Temperature difference °C**	
	mean	±SE	mean	±SE	mean	±SE
Bushclump	31.84^a	0.50	8.83^a	0.31	23.00^a	0.59
Grassland	33.08^b	0.51	8.16^b	0.36	24.90^b	0.63

Bushclumps were also shown to have a moderating effect on humidity profiles. Although significant differences between the bushclump and grassland stations were erratic and did not show a consistent trend, minimum humidity was in all cases higher in the bushclump stations than that in the grassland stations (Figure 3.6). There were no maximum humidity differences between the bushclump and grassland stations.

As expected, seasonal variation was obvious with lower maximum and minimum temperatures, and lower maximum and minimum humidity, characterizing late-autumn, winter and early-spring.

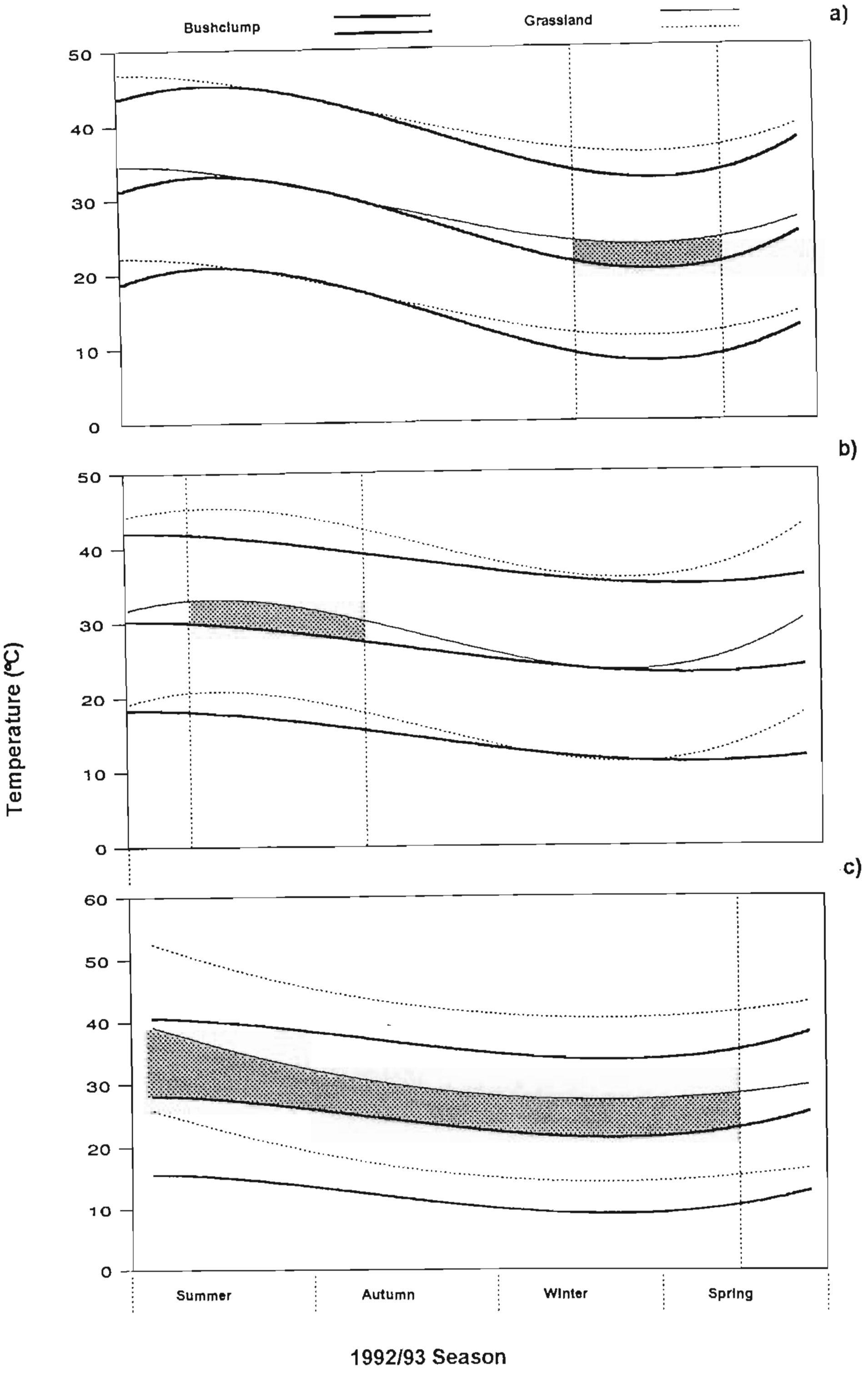

Figure 3.4 Mean maximum temperature profiles (with 95% confidence intervals) during the monitoring season for the three monitoring sites (a, b and c). The thick middle line represents the mean maximum temperature in the bushclump zone, the thick outer lines indicate the 95% confidence interval for the bushclump zone, the thin line represents mean maximum temperature in the grassland zone, and thin outer dotted line the 95% confidence interval for the grassland zone. The highlighted area denotes where significant differences between the bushclump and grassland zones existed. (Summer = 1 December-28 February, Autumn = 1 March-31 May, Winter = 1 June-31 August, Spring = 1 September-30 November.)

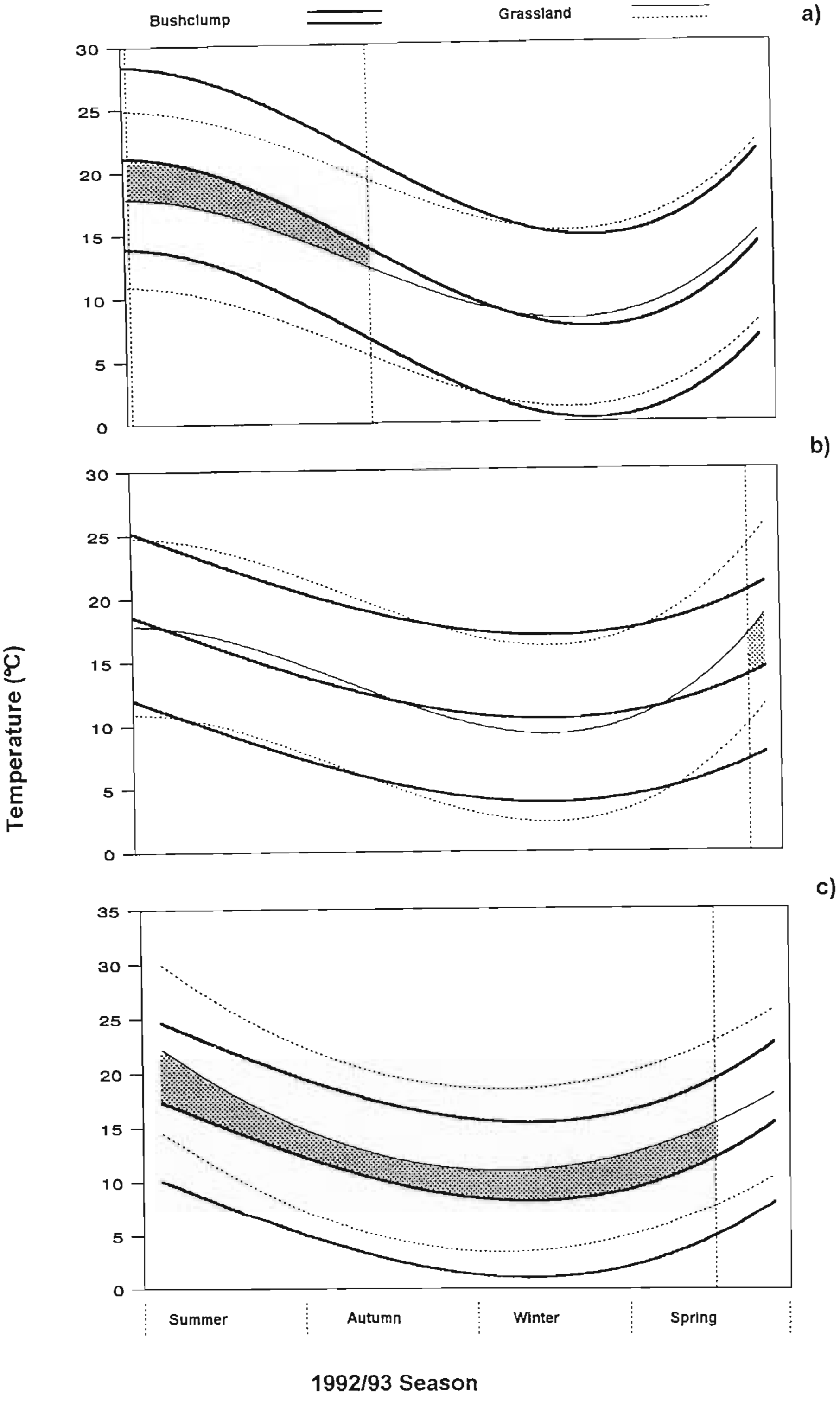

Figure 3.5 Mean minimum temperature profiles for the three monitoring sites (a, b and c) (with the 95% confidence intervals) during the monitoring season. The thick middle line represents the mean minimum temperature in the bushclump zone, the thick outer lines indicate the 95% confidence interval for the bushclump zone, the thin line represents mean minimum temperature in the grassland zone, and thin outer dotted lines the 95% confidence interval for the grassland zone. The highlighted area denotes where significant differences between the bushclump and grassland zones existed. (Summer = 1 December-28 February, Autumn = 1 March-31 May, Winter = 1 June-31 August, Spring = 1 September-30 November.)

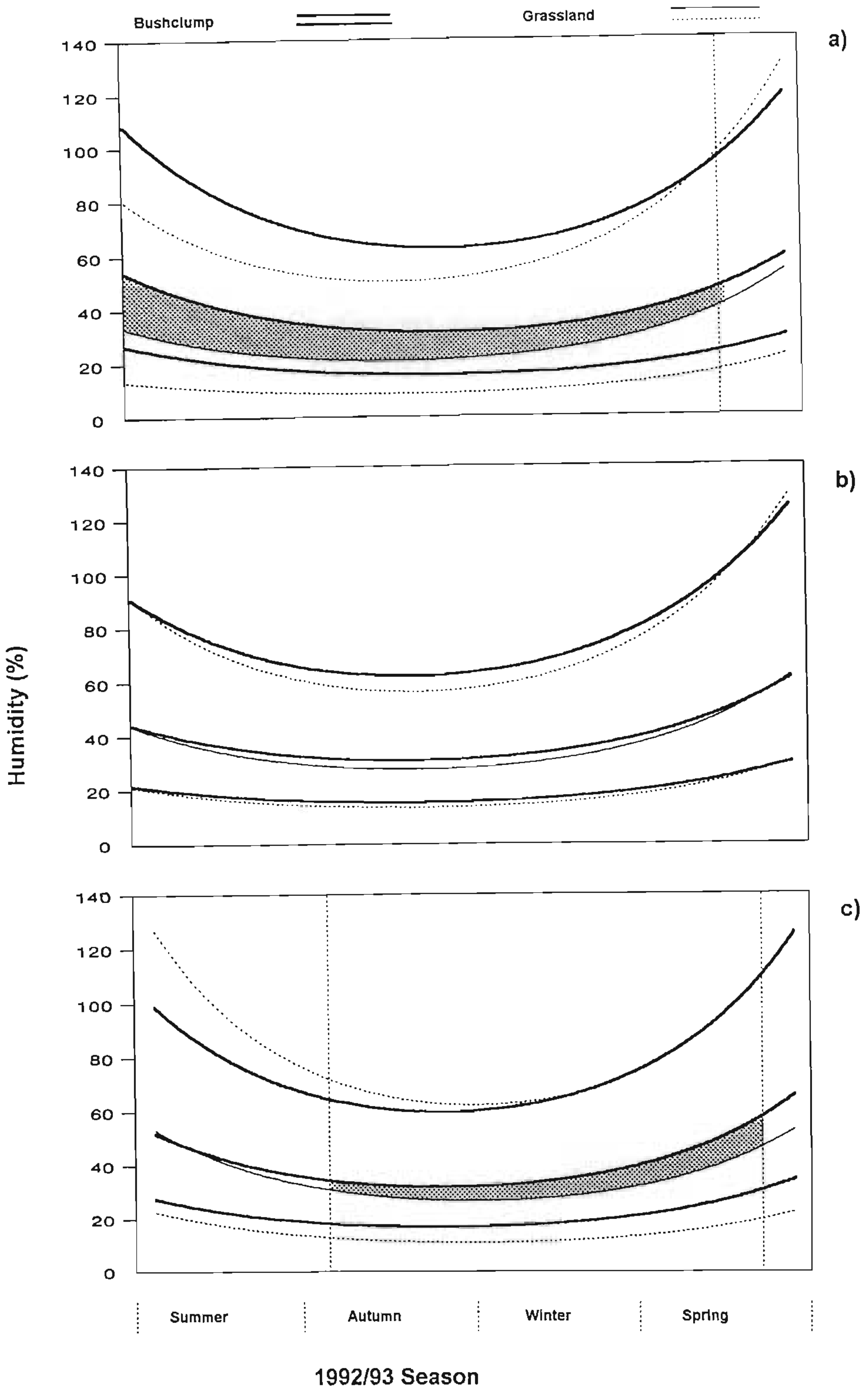

Figure 3.6 Mean minimum humidity profiles (with the 95% confidence intervals) during the monitoring season for the three monitoring sites (a, b and c). The thick middle line represents the mean minimum humidity in the bushclump zone, the thick outer lines indicate the 95% confidence interval for the bushclump zone, the thin line represents mean minimum humidity in the grassland zone, and thin outer dotted line the 95% confidence interval for the grassland zone. The highlighted area denotes where significant differences between the bushclump and grassland zones existed. (Summer = 1 December-28 February, Autumn = 1 March-31 May, Winter = 1 June-31 August, Spring = 1 September-30 November.)

3.3.3 Soil Physical and Chemical Properties

Many of the soil characteristics examined varied with depth and soil type (Table 3.3). Bushclumps played an important role in altering many of the soil variables investigated. Bushclump soils were not significantly different from grassland soils with respect to particle size distribution and Na content. Although no significant difference in soil density occurred between the bushclump and grassland soils, the density of the 0-20 cm layer under bushclump, for both the Hutton and Glenrosa soils, was noticeably lower than under grassland.

The fertility status of the grassland soils was poorer than the bushclump soils. Both the Hutton and Glenrosa bushclump soils had significantly higher organic C in all three depth classes (Figure 3.7a), significantly higher P and K in the 0-20 and 20-40 cm layers, and significantly higher CEC and Mg content in the 0-20 cm layer.

In the Glenrosa soil, bushclump soils were significantly higher in total N (Figure 3.7b), Ca, EC and Cl than grassland soils, for the 0-20 cm layer, with no significant effect occurring in the deeper layers. No significant bushclump effect was evident in the Hutton soil for the abovementioned soil variables.

The same trend in pH occurred in both soil types, with the bushclump topsoil having a greater pH than the grassland topsoil, whilst in the two deeper layers the trend was reversed with pH greater in the grassland than in the bushclump.

Table 3.3 Mean (± SE) soil physical and chemical properties of the bushclump (bclump) and grassland (grsland) soils for the two soil types sampled. (EC=electrical conductivity, CEC=cation exchange capacity) (Letters which differ between bushclump and grassland soils for a specific soil type and dep indicate significance at the 5% level.)

	Hutton soil						Glenrosa soil					
	0 - 20 cm		20 - 40 cm		40 - 60 cm		0 - 20 cm		20 - 40 cm		40 - 60 cm	
	Bclump	Grsland	Bclump	Grsland	Bclump	Grsland	Bclump	Grsland	Bclump	Grsland	Bclump	Grsla
Sand (%)	55.2^a (2.8)	48.6^a (2.3)	46.8^a (2.7)	44.8^b (2.2)	44.4^a (1.6)	42.6^a (1.8)	77.4^a (0.8)	78.0^a (1.1)	75.6^a (0.8)	74.0^a (1.2)	67.4^a (2.1)	67. (2
Silt (%)	14.8^a (2.0)	14.6^a (3.0)	15.2^a (1.4)	12.0^a (2.8)	14.4^a (0.4)	17.0^a (2.5)	12.8^a (1.2)	11.8^a (0.6)	12.4^a (0.5)	13.0^a (0.9)	11.6^a (1.6)	10. (1.
Clay (%)	30.0^a (1.7)	36.8^a (4.6)	38.0^a (2.6)	43.2^a (3.6)	41.2^a (1.7)	40.4^a (3.4)	9.8^a (0.7)	10.2^a (0.5)	12.0^a (0.6)	13.0^b (0.7)	21.0^a (2.6)	22. (2.
Density (g.cm^{-3})	1.088^a (0.019)	1.120^a (0.007)	1.130^a (0.007)	1.144^a (0.007)	1.144^a (0.014)	1.134^a (0.015)	1.182^a (0.026)	1.246^a (0.009)	1.248^a (0.012)	1.242^a (0.012)	1.240^a (0.026)	1.21 (0.02
pH	5.14^a (0.12)	4.84^a (0.07)	4.60^a (0.03)	4.76^b (0.02)	4.62^a (0.04)	4.80^b (0.03)	5.48^a (0.17)	4.86^b (0.05)	5.20^a (0.03)	5.48^a (0.12)	5.90^a (0.21)	6.6 (0.2
EC (mS.m^{-1})	58.2^a (9.7)	36.8^a (10.4)	41.4^a (4.2)	30.6^a (3.1)	32.8^a (2.4)	30.0^a (3.9)	76.2^a (6.7)	33.2^b (4.2)	53.4^a (8.2)	53.8^a (8.5)	106.4^a (36.8)	118. (18.
Cl (ppm)	107.1^a (16.1)	62.4^a (14.3)	77.3^a (3.4)	63.1^a (4.1)	71.6^a (6.7)	65.9^a (11.6)	159.5^a (15.8)	56.7^b (8.6)	120.6^a (20.3)	119.8^a (26.7)	299.2^a (114.6)	343. (76.
Organic C (%)	3.14^a (0.11)	2.44^b (0.11)	2.00^a (0.05)	1.76^b (0.06)	1.52^a (0.04)	1.38^b (0.06)	1.90^a (0.20)	1.00^b (0.09)	1.30^a (0.11)	0.90^b (0.09)	1.26^a (0.18)	0.7 (0.0
Total N (ppm)	211.4^a (18.9)	233.4^a (85.6)	154.8^a (15.1)	132.6^a (9.5)	121.0^a (7.7)	110.0^a (6.6)	253.8^a (40.9)	143.4^b (11.2)	146.4^a (8.8)	185.4^a (48.9)	132.6^a (10.7)	118. (5.
P (mg.ℓ$^{-1}$)	5.4^a (0.4)	3.2^b (0.2)	2.4^a (0.2)	1.6^a (0.4)	1.6^a (0.4)	1.2^a (0.5)	12.4^a (2.1)	5.0^b (0.3)	5.8^a (0.9)	2.0^b (0.6)	1.0^a (0.6)	0. (0.
K (mg.ℓ$^{-1}$)	509.8^a (60.3)	254.0^b (51.6)	257.4^a (58.2)	95.4^b (12.2)	100.4^a (17.4)	64.2^a (6.9)	261.4^a (50.9)	74.0^b (14.8)	144.8^a (30.1)	50.6^b (7.9)	124.6^a (21.7)	78. (8.
Ca (mg.ℓ$^{-1}$)	2605.6^a (179.6)	2187.8^a (176.9)	1697.6^a (102.7)	1743.8^a (106.3)	1469.4^a (72.7)	1443.6^a (61.5)	2226.2^a (376.1)	700.4^b (173.2)	1302.0^a (98.9)	1150.8^a (91.2)	2188.8^a (172.8)	2344. (188.
Mg (mg.ℓ$^{-1}$)	545.0^a (19.7)	422.6^b (27.1)	448.2^a (20.9)	414.2^a (13.7)	407.0^a (21.2)	395.4^a (19.6)	408.4^a (33.0)	231.0^b (12.4)	371.4^a (21.3)	409.2^a (36.7)	837.2^a (43.9)	907. (58.
Na (mg.ℓ$^{-1}$)	0.08^a (0.04)	0.06^a (0.02)	0.12^a (0.04)	0.12^a (0.05)	0.16^a (0.07)	0.08^a (0.02)	0.22^a (0.10)	0.26^a (0.10)	0.20^a (0.08)	0.54^b (0.11)	1.18^a (0.24)	1.6 (0.1
CEC (cmol$^+$.kg^{-1})	14.24^a (0.45)	12.00^b (0.18)	11.72^a (0.25)	10.92^a (0.31)	10.90^a (0.23)	9.48^b (0.25)	8.08^a (1.01)	4.24^b (0.74)	5.92^a (0.83)	6.20^a (1.31)	11.28^a (1.69)	14.6 (1.4

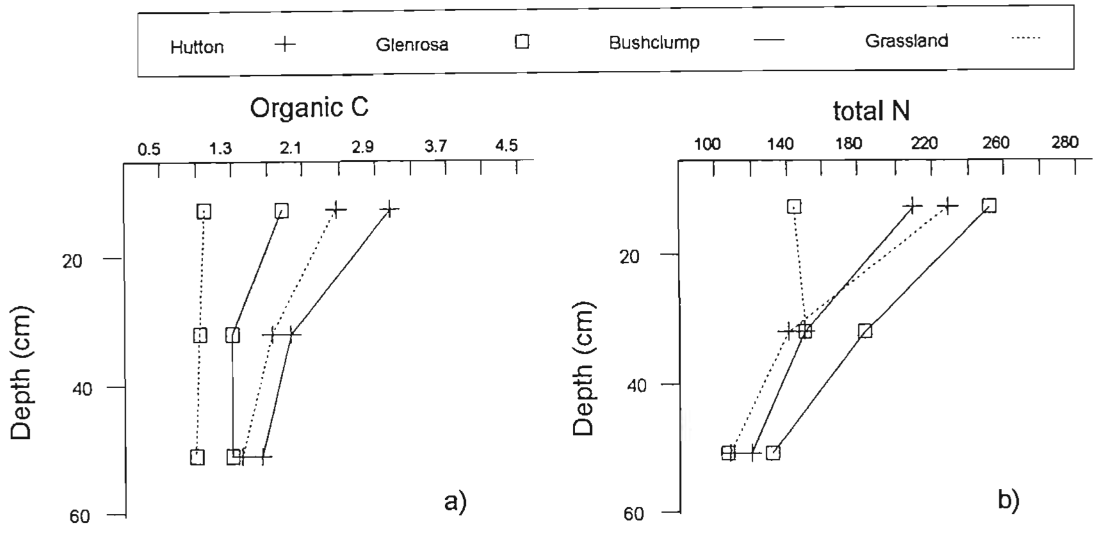

Figure 3.7 The influence of bushclumps on a) organic C, and b) total N, in the Hutton and Glenrosa soils for the three depth classes.

3.3.4 Herbaceous Production, Composition and Quality

Vegetation zone had a major effect on grass production in this savanna (Figure 3.8). Grass production at the end of both seasons was significantly lower in the interior bushclump zone than in the peripheral and grassland zones.

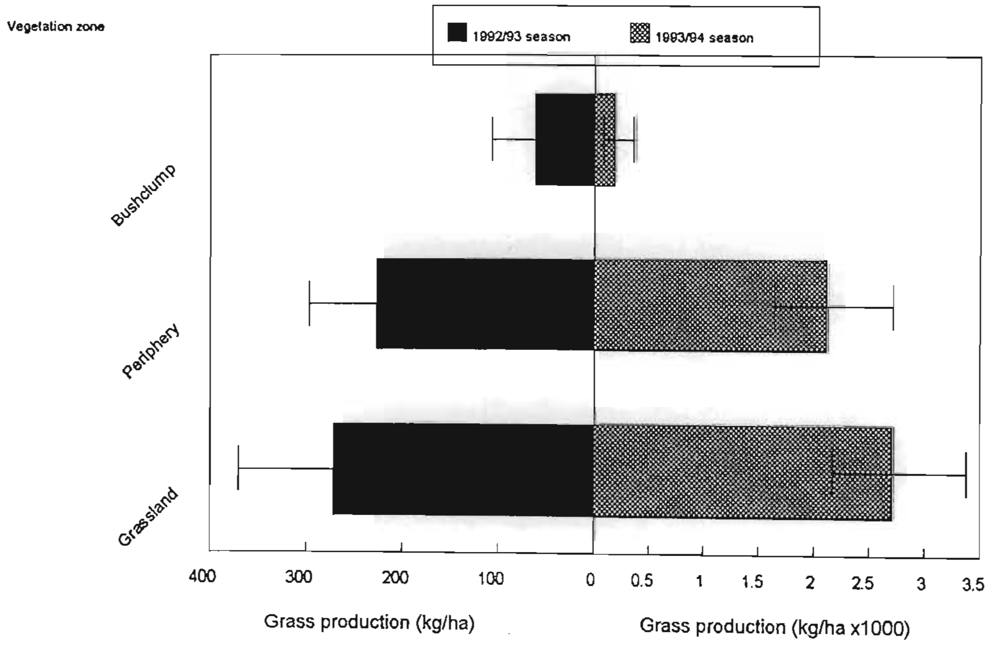

Figure 3.8 Grass production (kg.ha^{-1}) in the 1992/93 season, and grass production (kg.ha^{-1} x1000) in the 1993/94 season, in the three vegetation zones. (Bars indicate the 95% confidence interval.)

Aspect affected herbaceous production in the peripheral zone. Although no significant difference between the north and south-facing peripheral zones existed at the end of the first season, grass production was 25% greater in the south-facing side than in the north-facing side. At the end of the second season a significant difference between aspects was apparent ($P<0.05$), with 47% more grass produced in the south-facing peripheral zone than in the north-facing peripheral zone. Forb production at the end of both seasons seemed unaffected by both vegetation zone and aspect. Forb production at the end of the first season averaged 12 $kg.ha^{-1}$, whilst the higher rainfall in the second season resulted in an average production of 41 $kg.ha^{-1}$.

Herbaceous composition was notably different in the three vegetation zones (Table 3.4). Since herbaceous composition did not change over the two seasons, only results from the 1992/93 season are reported. The bushclump zone was characterized by *Panicum maximum* (C_4 grass), *Helictotrichon capense* (C_3 grass), *Galopina circaeoides* and *Priva meyeri* (both forbs). *Panicum maximum*, with the forbs, contributed significantly to the herbaceous biomass in the bushclump zone. The grassland zone was characterized by a suite of species, of which C_4 grasses *Sporobolus africanus*, *Eragrostis curvula*, *Cynodon dactylon*, *Aristida congesta* and *Themeda triandra*, and forbs *Selago corymbosa* and *Teucrium trifidum* were important. The peripheral zone contained both bushclump and grassland elements. Herbaceous cover in the bushclump zone was markedly reduced when compared with the peripheral and grassland zones.

Table 3.4 Herbaceous composition in the three vegetation zones expressed as a percentage of dry-weight, frequency (%), and cover (%). (BC - bushclump, PBC - periphery, GR - grassland.)

	Dry-weight rank (%)			Relative frequency (%)			Mean basal cover (%)		
	BC	PBC	GR	BC	PBC	GR	BC	PBC	GR
Total yield (kg.ha^{-1})	133	301	391						
Grass species									
Aristida congesta	0.0	4.8	7.7	3	26	43	0.0	1.4	2.3
Cynodon dactylon	2.0	8.0	11.7	11	54	61	0.2	3.4	3.9
Digitaria eriantha	0.9	3.6	5.9	1	10	14	0.1	0.5	2.1
Eragrostis chloromelas	0.0	0.9	6.2	0	1	13	0	0.5	1.6
Eragrostis curvula	12.7	12.9	21.9	24	60	53	1.1	2.9	5.8
Eragrostis plana	0.6	3.2	0.1	3	8	1	0.1	0.5	0.1
Helictotrichon capense	13.6	2.2	0.0	28	8	0	2.1	0.2	0.0
Panicum maximum	37.9	19.8	5.8	44	61	35	4.4	3.1	1.8
Sporobolus africanus	3.5	21.1	22.1	14	71	83	0.4	4.5	5.8
Themeda triandra	2.6	11.7	9.1	9	29	29	0.3	2.3	2.8
Sedges	5.8	2.1	0.1	33	26	18	0.9	0.7	0.3
Forbs	20.3	9.6	6.9						
Forb species									
Abutilon sonneratianum				3	5	0	0	0	0
Berkheya bipinnatifida				0	1	0	0	0	0
Chaetacanthus setiger				0	9	8	0	0	0
Clutia ericoides				1	4	4	0	0	0
Falkia repens				1	0	3	0	0	0
Galopina circaeoides				18	18	3	0	0	0
Hypoestes aristata				1	6	3	0	0	0
Melhania didyma				1	5	3	0	0	0
Priva meyeri				36	43	13	0.8	0.6	0.2
Rhynchosia ciliata				11	19	20	0	0	0
Rhynchosia hirsuta				4	8	0	0	0	0
Senecio erubescens				0	4	1	0	0	0
Senecio tamoides				3	3	1	0	0	0
Selago corymbosa				1	33	49	0	0.6	1.3
Sida rhombifolia				5	10	4	0		0
Teucrium trifidum				0	18	31	0	0.3	0.7
Total cover (%)							10.4	21.5	28.7

Data obtained in the 1992/93 season showed that vegetation zone had little influence on herbage quality. Herbage from the bushclump zone had greater concentrations of Mg ($P<0.0044$) and TKN ($P<0.0273$) than herbage in the peripheral and grassland zones. However, in the 1993/94 season differences in herbage quality were conspicuous with significantly greater concentrations of Ca, Na, Mg, K and total Kjeldahl nitrogen (TKN) in herbage from the bushclump zone than that in the peripheral and grassland zones (Table 3.5). Only P concentration in the herbage, did not vary between vegetation zones.

Table 3.5 The influence of vegetation zone on herbaceous quality. TKN = total Kjeldahl nitrogen. (Letters which differ within a column indicate significance at the 5% level.)

Vegetation zone	Ca (%)	Mg (%)	Na (%)	K (%)	P (%)	TKN (%)
Bushclump	0.89^a	0.17^a	0.24^a	1.77^a	0.30^a	1.05^a
Periphery	0.69^b	0.14^b	0.22^a	1.07^b	0.27^a	0.81^b
Grassland	0.69^c	0.11^c	0.12^b	0.87^c	0.26^a	0.75^b

3.3.5 Seedbank and Seedlings

Enumeration of residual woody seeds in soil and litter samples after the germination trial, showed that bushclump and peripheral zone samples had significantly greater woody seed counts than grassland zone samples (Table 3.6). The germination trial also showed that dicotyledonous seeds were most common in the bushclump and peripheral zone samples, whilst grass seeds were most common in grassland and peripheral zone samples. No significant difference in the distribution of the sedge seedbank was observed.

Some of the voucher species identified were grasses such as *Tragus berteronianus, Cynodon dactylon, Panicum maximum, Panicum deustem, Eragrostis curvula, Sporobolus africanus, Helicototrichon capense* and *Digitaria eriantha;* and dicotyledons such as *Jasminum* sp., *Acacia karroo, Cussonia spicata, Senecio* spp., and individuals from the *Mimosiaeae, Asteraceae* and *Amaranthaceae* families. *Acacia karroo* and *Diospyros* spp. were species identified during the woody seed count.

Table 3.6 Total seed and seedling densities (number.m^{-2}) from combined soil and litter samples, taken from the three vegetation zones, after germination and hand separation. (Letters which differ within a column indicate significance at the 5% level.)

Vegetation zone	Woody seed count	Grass seedlings	Dicot. seedlings	Sedge seedlings
Bushclump	81^a	158^a	702^a	83^a
Periphery	105^a	478^b	525^a	115^a
Grassland	3^b	1 015^b	261^b	101^a

Results from the woody seedling count confirmed that the bushclump zone had a significantly greater ($P<0.0001$) woody seedling population than the other two vegetation zones (Figure 3.9).

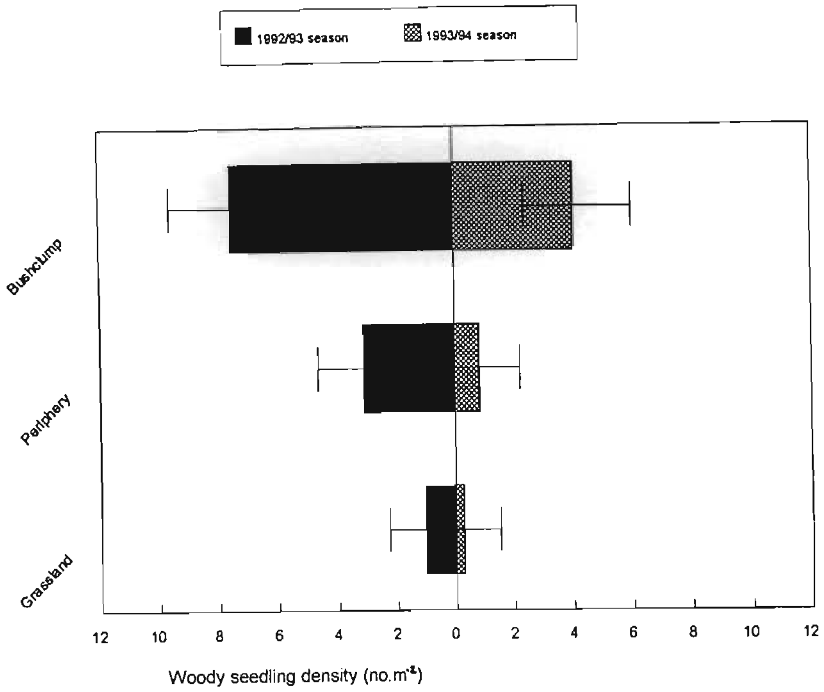

Figure 3.9 Woody seedling density (number.m^{-2}) in the three vegetation zones at the end of the two seasons. (Bars indicate the 95% confidence interval.)

3.3.6 Lateral Root Distribution

Lily-Park site

In all, 136 woody plants were sampled for Rb concentration over the thirteen application sites. Rubidium concentration in the leaves was never higher than 10 ppm in all the species sampled, and when tested on *S. myrtina* no trend was apparent (Figure 3.10a). There was no indication of any Rb concentration-by-distance relationship which may have indicated the possible extent of woody lateral root spread. A subsidiary investigation, from plants far enough from the application sites to be considered uncontaminated by the application sites, revealed background Rb levels of up to ± 8 ppm. Soil samples taken from two of the application sites demonstrated that background levels of 1 ppm Rb existed (Table 3.7). Soil samples taken from within the application pits showed that Rb remained present in the soil, and at fairly high concentrations. However, at 0.5 metres from the application site no increase in Rb concentration was measured (Table 3.7).

Table 3.7 Soil Rb concentration (ppm) at various distances from application sites 1 and 2 of the Rb application sites at the Lily-Park site. Soil samples were taken at two depths.

		Distance from application site (m)				
Site	Depth (cm)	0	0.5	1	4	40
1	0-50	26.93	0.28	0.13	0.19	0.19
	50-100	1.18	0.65	0.50	0.70	0.63
2	0-50	26.89	0.33	0.28	0.29	0.16
	50-100	4.13	0.55	0.65	0.79	0.70

Fruit samples collected from *S. myrtina* showed in some instances a 3-fold increase in Rb in relation to the leaf sample concentrations (Figure 3.10b). If these values were due to Rb uptake then it seems that the lateral root distribution of *S. myrtina* can be as far as 25 metres. Investigation of K concentration and Rb:K ratio failed to reveal any further information.

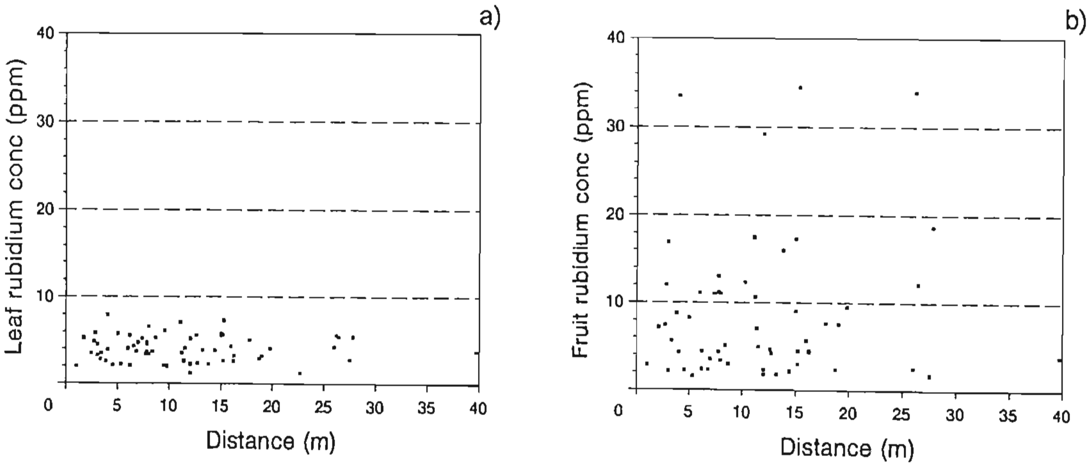

Figure 3.10 Rubidium concentration in a) the leaves, and b) the fruit, of *Scutia myrtina* trees at varying distances from the Rb application sites at the Lily-Park site.

Kentbury site

Prior to Rb application, leaf samples were collected from 29 *S. myrtina* trees at various distances from the two application sites. Rb concentration in these leaves revealed that background levels were present. A soil Rb analysis also showed Rb concentrations of less than 1 ppm. Two weeks after Rb had been applied to the application sites, the same plants were harvested. No nett increase in Rb was observed. Potassium levels in leaves were also examined prior to application and in the material collected after two weeks. No change in potassium, or Rb:K ratio over the two week-period was apparent. Distance effects were non-existent. Since *S. myrtina* was not in fruit at the time, fruit analyses could not be carried out.

3.4 DISCUSSION

Bushclumps had a marked effect on the local environment. The irradiance regime in the interior bushclump zone was reduced by 80-90% of that experienced in the open grassland. This high level of shade can be attributed to the dense foliage characteristic of the broadleaved evergreen species which constitute these bushclumps. The effect of aspect was also evident, owing to the Eastern Cape's southerly latitude. The south-facing peripheral zone and the first three metres of the grassland zone received significantly greater shade than the north-facing zones. Thus, bushclumps not only affected the irradiance regime directly beneath them but also had an effect on the irradiance regime in the adjacent grassland. Temperature and humidity profiles within bushclumps were also different to those in the adjacent grassland. Bushclumps had a moderating effect on both temperature and humidity, with lower maximum and higher minimum temperatures, and greater humidity than that experienced in the grassland. Thus, temperature and humidity fluctuations were lower than those in the grassland zone. The effect of shade, lower temperature fluctuations, and higher humidity was reported to reduce soil temperatures and increase soil moisture content (Belsky *et al.* 1989). However, interception of rainfall could counteract the effect of canopy shade on soil moisture. Although rainfall interception was not measured in this investigation, tree and shrub canopies are reported to intercept rainfall and redistribute the water to the atmosphere by evaporation, and to the ground by through-fall and stem-flow (Pressland 1973).

The herbaceous layer in the bushclump zone was markedly different from that in the grassland zone. Herbaceous cover was 60% lower and species composition altered, with many grassland species absent. The bushclump zone was characterized by shade-tolerant grasses such as *Panicum maximum* and *Helictotrichon capense*. The strong association of *P. maximum* with tree canopies has been widely reported (Bosch & van Wyk 1970; Kennard & Walker 1973).

Herbaceous production in the bushclump zone was 66% and 90% lower, in the first and second seasons respectively, than that of the grassland zone. Lower grass production under canopies was reported by Grossman *et al.* (1980) and Mordelet & Menaut (1995), whilst others reported greater grass production under isolated tree canopies (Stuart-Hill *et al.* 1987; Belsky *et al.* 1989). These conflicting results could be the effect of tree cover density and the leaf area index of trees. Compared with the open grassland situation, grass production under *Acacia karroo* (Stuart-Hill *et al.* 1987), *Acacia tortilis* and *Adansonia digitata* (Belsky *et al.* 1989) was reported to be greater. Kennard & Walker (1973) demonstrated the importance of the density of the tree canopy cover. They measured higher *P. maximum* biomass under open canopies and lower biomass under closed canopies as compared with open areas. Thus, the dense foliage and significantly reduced irradiance regime beneath bushclumps probably played an important role in reducing the herbaceous cover and production in the bushclump zone, as well as altering herbaceous species composition.

An effect of aspect was also apparent, with greater production in the south-facing peripheral zone than in the north-facing peripheral zone. The lower irradiance regime, which characterised the south-facing peripheral zone, may have been the causal factor. Stuart-Hill *et al.* (1987) also reported significantly greater grass production immediately south of the tree canopy. They attributed this to favourable influences by the tree (e.g. shade and litter), whilst the lower production in the north side of the canopy was attributed to lower water input associated with a physical redistribution of rainfall by the tree and competition from the tree for soil water.

Grass quality under bushclumps was greater than that in the grassland zone. In the first season, the crude protein content of the herbage was 5% greater than that in the grassland zone, whilst in the second season this was increased to 29%. Belsky (1992) reported that forage quality increased from open grassland to tree understorey, and since forage yield also increased from grassland to the canopy zone, total nutrient content per unit area increased towards the tree base. However, it was reported that this was offset by a slight drop in digestibility. The importance of the canopied environment, and the nutritional value of the forage associated with it, was highlighted by Grossman *et al.* (1980). In this mesic savanna grass production under bushclumps was dramatically reduced and although grass quality was higher in the bushclump zone than in the other two zones, on a per unit area basis the bushclump zone did not significantly contribute to the improvement of available forage. Although, grass production in the peripheral zone was greater than that of the bushclump zone, its nutritional quality was not unlike that of the grassland zone. Therefore, the proportion of the area occupied by bushclumps was equated with a proportional reduction in grazing capacity.

Bushclumps were also characterised by a large woody seedbank and high seedling density, affirming the perception that bushclumps are the foci of bush encroachment. The bushclump and peripheral zone contained a significantly greater woody seed density than the grassland zone. Coupled with this was a high density of established woody seedlings. The favourable microclimate and the available seed source associated with the bushclump zone was therefore conducive to the germination and establishment of woody seedlings. Since bushclumps act as 'nurseries' for woody recruitment, their management is essential if woody encroachment is to be contained.

Bushclump soils were significantly more fertile than grassland soils. Although soil physical differences were absent, a lower bulk density was apparent in the topsoil of bushclumps, probably due to a higher organic matter content and observed faunal activity. Bushclump soils were significantly richer in organic C, P, K and cations than grassland soils. Many studies ranging from the semi-desert shrub communities (Garcia-Moya & McKell 1970), arid grassland (Tiedemann & Klemmedson 1973), neotropical savanna (Kellman 1979), West Sahelian savanna (Bernhard-Reversat 1982), East African savanna (Belsky *et al.* 1989), West African humid savanna (Mordelet *et al.* 1993) and South African savannas (Bate & Gunton 1982; Palmer *et al.* 1988; Smit & Swart 1994) all reported that trees and shrubs improved the nutrient status of the soils beneath them. This was achieved by tree-root systems re-distributing nutrients from areas beyond their canopies to beneath their canopy. An interaction between soil type, vegetation zone and soil depth highlighted the important nutrient-cycling ability of bushclumps in this savanna. In the Glenrosa soil (sandier soil), bushclump topsoils had significantly greater total N, Ca, EC and Cl levels than the grassland topsoils. The susceptibility of sandy soils to leaching is well recognized. The low nutrient levels in the grassland zone of the Glenrosa soil were testament of this. Bushclumps on the Glenrosa soil, therefore, demonstrated their ability to hold topsoil nutrients to levels not dissimilar from the Hutton soil. Thus, bushclumps played an important role in maintaining and effectively recycling nutrients. With the threat of complete bush control in these mesic savannas cognizance should be taken of the importance of bushclumps, especially on sandier soils, in maintaining the nutrient richness of the ecosystem.

An attempt to determine the lateral root distribution of woody individuals and bushclumps in this mesic savanna was not very successful. However, the high levels of Rb recorded in the fruits of *Scutia myrtina* does show promise. Indications were that tree roots extended up to 25 metres into the grassland. Work done by Rutherford (1983) reported that woody plants in *Burkea africana-Ochna pulcra* savannas extended up to seven times the extent of the plant canopy cover. When one considers that bushclumps in this mesic savanna consist of many different woody species co-existing in close proximity to one another, the degree of overlap and level of competition probably results in many woody species extending into the open grassland. This has a negative implication from a grassland production point of view, since overlap between woody and herbaceous roots are inevitable.

CHAPTER 4

INFLUENCE OF IRRADIANCE, NUTRIENTS AND WATER ON THE HERBACACEOUS LAYER

4.1 INTRODUCTION

Competition for irradiance, nutrients and water form the basis of all woody-grass interactions. Contradictory results exist with respect to the productivity of the herbaceous layer in savanna systems. Traditionally, trees are perceived to reduce understorey productivity through competition for light, water, and nutrients (Walker & Noy-Meir 1982). However, it has also been documented that isolated trees may improve productivity (Stuart-Hill *et al.* 1987; Belsky *et al.* 1989).

Differences in productivity between below-canopy and open-grassland habitats have been attributed primarily to three factors: (1) improved fertility of soils beneath tree canopies (Tiedemann & Klemmedson 1973), (2) improved water relations of shaded plants (Kinyamario *et al.* 1995), and (3) competition between trees and grasses for light, soil moisture and nutrients (Walker & Noy-Meir, 1982).

The effect of trees on herbaceous productivity is not only a consequence of altered soil fertility, shade, and the competition for soil moisture and nutrients, but more importantly the interaction of these factors. In a semi-arid Eastern Cape savanna, trees at low densities were shown to have a positive effect on grass productivity whilst, at moderate to dense levels a negative effect occurred (Aucamp *et al.* 1983). Bosch & van Wyk (1970) reported a *Panicum maximum* - tree association and attributed its increased productivity to soil enrichment beneath tree canopies. Kennard & Walker (1973) showed that the highest grass yields were obtained under open tree canopies, whilst open grassland sites produced more than closed canopy sites. In

Chapter 3, herbaceous production was significantly lower under bushclumps than in the adjacent grasslands, despite bushclump soils being more fertile than adjacent grassland soils and irradiance levels significantly less than the adjacent grassland. Thus, tree competition under different circumstances yields different herbaceous responses. The determination of the causal factor(s) is difficult to ascertain since factors are naturally confounded.

In order to evaluate the relative effects of irradiance, water and nutrients on herbaceous layer productivity in this mesic Eastern Cape savanna an experimental approach was adopted. A factorial design was employed to elicit the individual and interactive effects of irradiance, water and nutrients on herbaceous layer dynamics.

4.2 PROCEDURES

4.2.1 Site Description

The site occurred on a gentle slope (12%), adjacent to the study area described in section 2.1. Elevation was 600 m a.s.l. and aspect was south-westerly. Three soil types were identified on the experimental site. One was a Swartland soil with an orthic A horizon 350 mm deep and pedocutanic B horizon extending to a depth of 500 mm. The second soil type was a Tukulu with an orthic A horizon 240 mm deep and a neocutanic B horizon extending to a depth of 470 mm. The third soil type was a Sterkspruit with an orthic A horizon 220 mm deep and a prismacutanic B horizon extending to a depth of 470 mm. All three soils had relatively deep orthic A horizons and were classified as sandy-loams with 77% sand, 10-13% clay and 10-13% silt. Soil physical and chemical characteristics were very similar with an accessible moisture of 106 mm.m^{-1}, pH(H_2O) between 6.1 and 7.1, electrical conductivity between 31-43 Ms.m^{-1}, base saturation was 73-84% and cation exchange capacity between 4.3-8.5 cmol(+). The site was selected in a portion of savanna grassland with homogenous botanical composition. The herbaceous sward was comprised primarily of tufted C_4 perennial grasses, with the following percentage contribution of the main species: *Themeda triandra* (28), *Heteropogon contortus* (20), *Hyparrhenia hirta* (14), *Sporobolus africanus* (8), *Digitaria eriantha* (7) and *Eragrostis plana* (6). The site had been grazed by cattle and sheep for the last 40 years (personal communication: Mr B.J. Newey - landowner).

4.2.2 Treatments

The study spanned 1½ growing seasons. It was initiated on 17 December 1992 and terminated on 23 May 1994. Experimental design was a 3^3 factorial set up as a single, completely randomised block. The three main effects were irradiance, nutrients and water. Each treatment combination had three replicates to provide a total of 81 experimental units. The randomised block constituted 81 plots of 3 x 3 m. A 2 x 2 m experimental unit was positioned at the centre of each plot and, to minimise edge effects, only the central 1 x 1 m was measured. Treatments were applied to the entire 2 x 2 m area. The site was fenced to exclude livestock.

Irradiance regime

The irradiance levels applied in this experiment simulated irradiance levels of 10-20% found beneath bushclumps (Chapter 3), 40-55% beneath single savanna trees (Belsky et al. 1989), and 100% in the open grassland. These levels were simulated using commercial shade cloth graded as 40% and 80% light reduction. The shade cloth was attached to posts located at the four corners of each plot. Shade cloth was positioned one metre above the ground. Photosynthetic photon flux density (PPFD, 400-700 nm) was measured at noon on a single clear day, above and below the shade cloth, using a Li-Cor Li-1000 quantum sensor. Irradiance was reduced by 83% and 42% by the 80% and 40% commercial shade cloth respectively. Irradiance treatments were maintained for the entire study period.

Nutrient regime

The intention of this treatment was to simulate the effect of increased soil fertility, as found beneath bushclumps (Chapter 3), on the herbaceous layer. Although it was not possible to replicate the nutrient regime characteristic of bushclump soils in a climax grassland soil, it was possible to achieve a higher soil nutrient status with fertilization. Three nutrient levels were employed, a high nutrient addition level which simulated the bushclump soil, a normal nutrient level which was the current nutrient regime under grassland, and an intermediate level (low nutrient addition level) which was intended to test whether a small quantity of nutrients would have an effect on the herbaceous layer. The high nutrient addition level consisted of 6 $g.m^{-2}$ N, 3 $g.m^{-2}$ P and 9 $g.m^{-2}$ K per season. The low nutrient addition level was set at the square-root of the large nutrient addition level. No fertilizer was added to the normal nutrient level. A combination of commercial fertilizers 2:3:0, KCl and LAN was used to attain the required nutrient regime. Fertilizer addition was split over three application periods during each season. In the first season (1992/93) fertilizer was added on 22 December 1992, 27 January 1993 and 25 February 1993. In the second season (1993/94) fertilizer was added on 8 September 1993, 3 November 1993 and 21 December 1993. In the first fertilizer application of the season all the P and K was applied and a third of the N. The balance of the N was evenly split between the two later applications.

Moisture regime

The intention of this treatment was to simulate three levels of rainfall: below-average, normal and above-average. Moisture levels were manipulated by irrigation and rainfall interception during the course of the two growing seasons. Irrigation was provided between rainfall events rather than on a regular basis.

Water was added using a watering-can and applied evenly to each experimental plot. Irrigation events equated to a 10 mm rainfall event. The interception of rainfall was achieved by placing plastic covers over steel frame cages, which were positioned on experimental plots, prior to rainfall. The steel frame cages were semi-permanent fixtures which did not affect the experimental units in any significant way. The frame was positioned over the experimental plot and measured 2 m in length and breadth, and had a height of 1 m in the front and 1.2 m at the back (difference in height provided a slope for run-off). Plastic covers were made from damp-proofing black plastic. After each rainfall interception event covers were removed. A network of channels were constructed at the front and rear of each rainfall-interception plot to re-direct run-off or run-on away from experimental plots and out of the experimental area. This ensured that experimental plots below interception plots did not receive extra moisture, and that interception plots did not receive any run-on from upslope.

Rainfall during the experimental period was below-average for the first season and above-average for the second season (L.T.A. 650 mm). Since greater than 50% of the rainfall in the first season occurred before the initiation of the experiment, differences between the moisture treatment levels at the end of the first season were limited (Figure 4.1a). In the second season (1 July 1993-23 May 1994) a greater degree of interception was achieved (Figure 4.1b). The above average rainfall, however, limited the opportunity for supplementation.

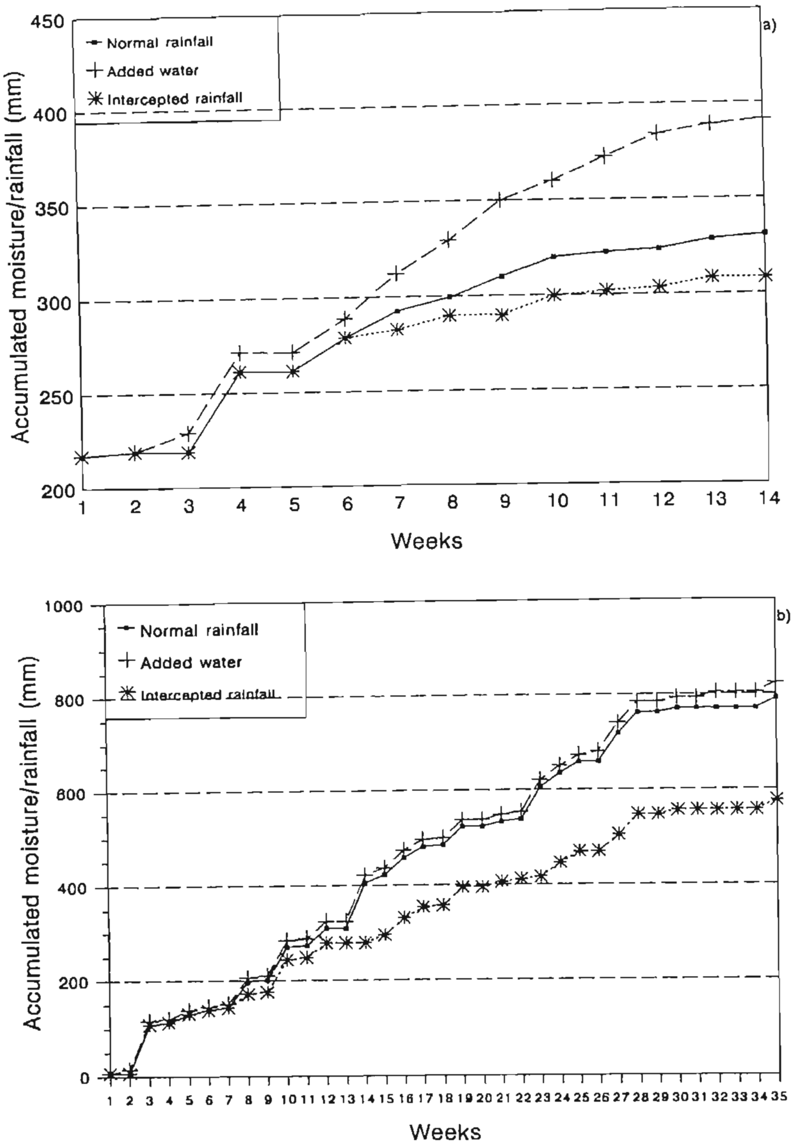

Figure 4.1 Accumulated rainfall (mm) for the moisture treatments in the factorial experiment during a) the 1992/93 season (starting 17 December 1992), and b) the 1993/94 season (starting August 1993).

4.2.3 Measurements

At the end of the first season all plots were clipped to ground level. Response variables quantified at the end of the second season were *Themeda triandra* (hereafter referred to as *Themeda*) tiller heights and tiller leaf number, tuft circumference and number of tillers, and the weight of green leaves, dead leaves and stems; herbaceous standing crop; litter biomass; and root biomass. Forage quality of *Themeda* and the grass component of the herbaceous layer (hereafter referred to as the sward), and the nutrient status of the litter and roots were determined. Soil chemical status was also quantified.

Themeda dynamics

Two *Themeda* tufts in each experimental unit were randomly selected. The circumference of each tuft was measured and the number of tillers per tuft counted. Two tillers per tuft were selected and the height and number of leaves on each tiller measured. (Aerial tillering was also noted.) The two *Themeda* tufts were then harvested and separated into green leaf, dead leaf and stem components, oven-dried at 60°C for 48 hours and weighed. *Themeda* components were then pooled and milled to pass through a 2 mm sieve and its forage quality determined.

Herbaceous layer

The herbaceous layer in each experimental unit was harvested, and separated into grass and forb components and oven-dried at 60°C for 48 hours, and weighed. (The mass of the two *Themeda* tufts removed from each experimental unit was included in the grass mass.) The grass component (sward) was milled to pass through a 2 mm sieve and its forage quality determined.

Litter

After the herbaceous layer was harvested all surface litter was collected from each experimental plot and bagged. Samples were oven-dried at 60°C for 48 hours and weighed. These samples were then milled to pass through a 2 mm sieve and the nutrient concentration was determined.

Root biomass

Two cores with dimensions 20 x 20 x 15 cm were removed from each experimental unit for the determination of root biomass. The cores were washed free of soil, oven-dried at 60°C for 48 hours and weighed. The two root samples from each experimental unit were pooled and milled to pass through a 2 mm sieve and root nutrient concentration was determined. Further cores were taken at 15-30 cm and 30-45 cm depths from five randomly selected experimental units to determine the proportion of root biomass which occurred further down the profile.

Soil chemical status

Soil samples were taken at three depths (0-20, 20-40, and 40-60 cm) in each experimental plot. Each sample consisted of a composite sample of two cores. Soils were prepared for soil chemical analyses following Döhne Agricultural Development Institute laboratory procedures (Appendix 2).

Forage quality and nutrient concentration determination

Total Kjeldahl N, P, K, Ca and Mg for *Themeda*, sward, litter and root components were analysed by the laboratory at the Döhne Agricultural Development Institute (Appendix 3). Plant fibre analyses (*in vitro* digestible organic matter, neutral detergent fibre (NDF), acid detergent fibre (ADF) and lignin) were done on *Themeda* and the sward by the Glen Agricultural Development Institute (Appendix 3).

4.2.4 Statistical Analyses

The effect of the treatments on the response variables was investigated using factorial analysis of variance using PROC GLM (SAS Ins., 1982) after the normality of the residuals were evaluated with the Shapiro-Wilk statistic (PROC UNIVARIATE, SAS Ins., 1982). The Box-Cox method (Weisberg 1985) was used to find the best transformation of the dependent variables, when the distribution of the residuals was non-normal. Independence of residuals was ensured by the completely randomised design. Tukeys comparison of means test was used to test main effects. In the case of a significant interaction data were analysed by the main effect and an LSD comparison of means test was employed. Means and standard errors were back transformed.

4.3 RESULTS

4.3.1 Herbaceous Layer

Irradiance and nutrients had a major effect on most responses of the herbaceous layer (Table 4.1). Sward mass was affected by an interaction between irradiance and nutrient addition with 80% shade negating the positive effect of fertilization (Figure 4.2a). Forb mass was also affected by an interaction between irradiance and nutrient addition (Figure 4.2b). Under normal irradiance only the high nutrient level significantly increased forb mass, whilst even the low nutrient level under both levels of shade significantly increased forb mass.

Table 4.1 Summary of *F*-ratios and significance levels for grass mass (Gwt) and forb mass (Fwt), and total Kjeldahl N (TKN), P, K, Ca, Mg, organic matter (OM), *in vitro* organic matter (IVOM), non-detergent fibre (NDF), acid-detergent fibre (ADF) and lignin contents of the sward in the 3^3 factorial experiment

	df	Gwt	Fwt	TKN	P	K	Ca	Mg	OM	IVOM	NDF	ADF	Lignin
I	2	8.29^{***}	4.40^{*}	29.76^{***}	15.33^{***}	62.11^{***}	1.59	27.96^{***}	18.87^{***}	17.72^{***}	1.13	7.23^{**}	35.12^{***}
N	2	12.09^{***}	46.84^{***}	1.88	112.75^{***}	7.13^{**}	2.36	17.03^{***}	26.44^{***}	0.82	15.21^{***}	13.83^{***}	6.35^{**}
W	2	0.40	0.63	1.03	0.02	0.97	2.43	1.07	3.38^{*}	0.22	3.05	0.40	3.34^{*}
IxN	4	3.49^{*}	4.18^{**}	0.81	2.81^{*}	2.94^{*}	1.99	3.43^{*}	2.67	0.66	2.05	0.24	0.71
IxW	4	2.13	2.62	0.63	0.53	2.60^{*}	1.94	1.23	2.07	0.32	1.74	1.27	0.27
NxW	4	1.74	1.41	0.52	0.99	1.81	2.03	2.48	1.88	0.82	0.51	1.44	1.23
IxNxW	8	0.85	1.58	0.95	0.23	2.66*	0.79	0.50	0.84	0.77	1.69	1.81	0.69

I = Irradiance, N = Nutrients, W = Water

* $P<0.05$, ** $P<0.01$, *** $P<0.001$

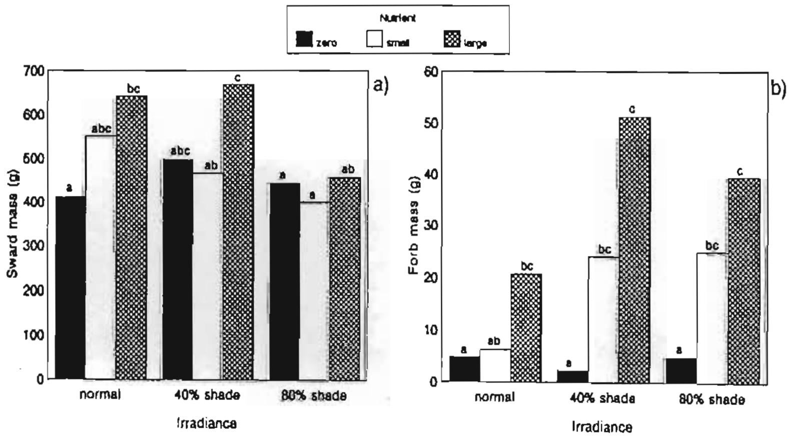

Figure 4.2 Interaction of irradiance and nutrients illustrating a) mean sward mass, b) mean forb mass for each treatment combination in the factorial experiment. (Letters which differ indicate significance at the 5% level.)

Nutrient concentration of the sward responded positively to both the irradiance and nutrient treatments. Shading significantly increased the N concentration (P<0.0001) of the sward from 0.328% to 0.543%. Although P concentration displayed a positive response to fertilization, it was also affected by an interaction between irradiance and nutrient addition (Figure 4.3a). Potassium levels were also affected by shading. A second order interaction between irradiance, nutrient addition and water showed that under the irrigated and normal moisture regimes shading significantly increased K levels. However, in the intercepted moisture treatment a significant interaction between irradiance and nutrient addition showed that the high nutrient level removed the positive effect of 80% shade (Figure 4.3b). Magnesium was also affected by an interaction between irradiance and nutrient addition (Figure 4.3c). Shading increased the Mg concentration under the zero and small nutrient levels but this was precluded under the large nutrient level.

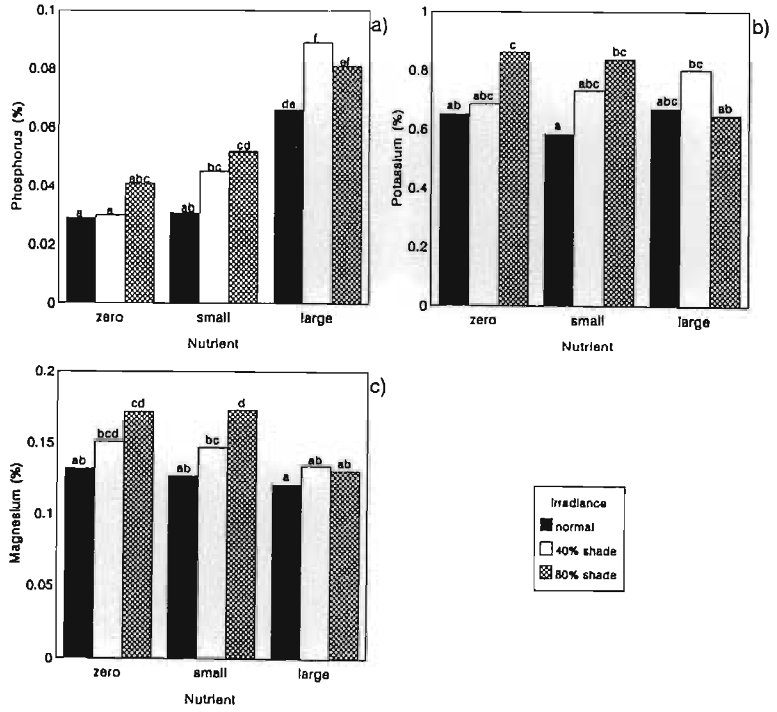

Figure 4.3 Interaction of irradiance and nutrients illustrating the swards a) mean P concentration, b) mean K concentration under the intercepted moisture level and, c) mean Mg concentration for each treatment combination in the factorial experiment. (Letters which differ indicate significance at the 5% level.)

Both irradiance and nutrients significantly affected the sward's forage quality. Minimum irradiance, provided by the 80% shade level, significantly reduced the digestible component (OM and IVOM) of the sward (Table 4.2). This was probably due to the significant increase in fibre components (ADF and lignin). Fertilization significantly increased the digestible component of the sward, with even the low nutrient level showing significance. *In vitro* organic matter content, however, was unaffected by fertilization. The high nutrient level was associated with a significant increase in the fibre components of the sward.

Table 4.2 Table of means illustrating the effect of the irradiance and nutrient treatments on organic matter (OM), *in vitro* organic matter (IVOM), non-detergent fibre (NDF), acid-detergent fibre (ADF) and lignin components of the sward in the 3^3 factorial experiment. (Letters which differ horizontally within either the irradiance or nutrient treatments indicate significance at the 5% level.)

	Irradiance			**Nutrient addition**		
	normal	**40% shade**	**80% shade**	**zero**	**small**	**large**
OM	90.61^{a}	90.14^{a}	89.44^{b}	89.33^{x}	90.07^{y}	90.81^{z}
IVOM	51.57^{a}	50.93^{a}	48.18^{b}	50.40^{x}	50.36^{x}	49.89^{x}
NDF	70.90^{a}	71.41^{a}	71.28^{a}	70.38^{x}	70.68^{x}	72.56^{y}
ADF	45.89^{a}	46.34^{ab}	47.16^{b}	45.68^{x}	46.29^{x}	47.45^{y}
Lignin	5.54^{a}	5.97^{b}	6.80^{c}	5.87^{x}	5.97^{x}	6.33^{y}

4.3.2 *Themeda* Dynamics

Shading resulted in etiolated growth in *Themeda* (Table 4.3). Both the 40% and 80% shade levels increased tiller length, number of tillers per tuft, and decreased tuft circumferences. Deep shade also increased the number of leaves per tiller. Aerial tillering was also increased ($P<0.0484$).

Table 4.3 The effect of shade on *Themeda* tiller length and number, tuft circumference, and number of leaves per tiller in the 3^3 factorial experiment. (Letters which differ within a column indicate significance at the 5% level.)

Shade (%)	**Tiller length (mm)**	**Tiller number**	**Tuft circumference (mm)**	**Number of leaves per tiller**
0	408^{a}	55^{a}	350^{a}	10.0^{a}
40	530^{b}	37^{b}	224^{b}	11.0^{a}
80	665^{c}	35^{b}	204^{b}	12.9^{b}

Tiller length was also affected by the nutrient treatment, with an increase from 468 mm to 632 mm occurring in the high nutrient addition level (P<0.0001). The nutrient treatment also increased the proportion of green leaf mass to total mass with a mean ratio of 0.251 for the high nutrient addition level, 0.214 for the low nutrient addition level and 0.154 for the normal nutrient level (P<0.0001). Shading increased the proportion of stem mass to total mass, from a ratio of 0.318 under zero shade to 0.393 under 80% shade (P<0.0103). Of interest was the significant reduction in the proportion of dead leaf to total mass under both levels of shade, with a ratio of 0.473 under zero shade and 0.411 and 0.402 under 40% and 80% shade respectively.

The variation in nutrient content of *Themeda* across treatments mirrored that of the sward. The irradiance and nutrient treatments again had the greatest effect (Table 4.4).

Table 4.4 Summary of *F*-ratios and significance levels for total Kjeldahl N (TKN), P, K, Ca, Mg, organic matter (OM), *in vitro* organic matter (IVOM), non-detergent fibre (NDF), acid-detergent fibre (ADF) and lignin contents of *Themeda* in the 3^3 factorial experiment

	df	TKN	P	K	Ca	Mg	OM	IVOM	NDF	ADF	Lignin
I	2	30.74***	15.02***	15.48***	0.46	5.44**	2.02	2.15	0.61	0.06	7.02**
N	2	0.89	43.25***	0.12	1.99	3.39*	4.38*	0.56	4.74*	1.20	2.00
W	2	0.65	3.33	4.74*	0.11	0.53	0.29	0.56	0.76	1.12	1.22
IxN	4	1.06	0.31	0.77	1.16	0.46	1.12	0.36	1.69	0.80	1.99
IxW	4	2.28	1.62	3.96**	1.37	1.36	0.38	0.96	1.04	1.40	0.64
NxW	4	2.24	1.24	2.29	2.00	0.81	1.91	1.04	0.74	0.82	0.59
IxNxW	8	0.82	1.61	1.31	0.54	1.00	1.07	0.88	0.70	0.56	0.70

I = Irradiance N = Nutrients W = Water
* P <= 0.05 ** P <= 0.01 *** P <= 0.001

Both levels of shade increased the N (P<0.0001) and P (P<0.0001) concentrations of *Themeda* from 0.396% to 0.570% and from 0.036% to 0.049%, respectively. The P concentration of *Themeda* was also increased by both levels of nutrient addition (P<0.0001), from 0.035% under the normal nutrient level to 0.040% and 0.064% for the low and high nutrient addition levels respectively. An interaction between irradiance and water significantly affected the K concentration of *Themeda*. Shading under irrigated conditions had no notable effect, whilst shading in the intercepted rainfall level significantly increased the K concentration of *Themeda* (Figure 4.4). Calcium concentration was again unaffected by treatments, whilst Mg concentration was significantly greater under 80% shade (0.139%) than under zero shade (0.119%).

The digestible component of *Themeda* did not show the same response to the treatments as did that of the sward. An increase in the organic matter concentration with fertilization did, however, occur with 89.4% under the normal nutrient level and 90.6% under the high nutrient addition level (P<0.0178). Fibre analysis showed that the NDF component, as in the sward, was also increased by the nutrient treatment (P<0.0030), from 71.3% under the normal nutrient level to 73.1% under the high nutrient addition level. The ADF component, however, was unaffected by treatments. Lignin content was also increased by shading (P<0.0027), from 7.0% under zero shade to 7.6% under 80% shade.

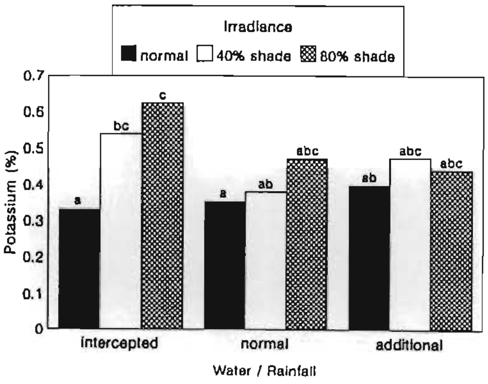

Figure 4.4 Interaction of irradiance and moisture illustrating mean *Themeda* K concentration (%) for each treatment combination in the factorial experiment. (Letters which differ indicate significance at the 5% level.)

4.3.3 Litter

The addition of nutrients increased litter production, from 4.95 g for the non-fertilized level to 9.43 g in the highest nutrient level (P<0.0007). The irradiance and nutrient treatments exercised the predominant effect on plant nutrient concentration of litter (Table 4.5).

Table 4.5 Summary of *F*-ratios and significance levels for litter mass (Mass), and total Kjeldahl N (TKN), P, K, Ca and Mg concentrations of the litter in the 3^3 factorial experiment

	df	Mass	TKN	P	K	Ca	Mg
I	2	3.35	52.23***	27.63***	11.54***	0.20	9.57***
N	2	8.68***	22.80***	93.25***	24.86***	7.77**	3.28
W	2	0.59	1.61	0.34	0.79	0.09	2.23
IxN	4	0.73	2.71*	2.01	2.43*	1.91	1.92
IxW	4	0.34	2.01	1.98	1.62	1.05	1.12
NxW	4	1.58	2.30	1.06	1.45	2.39	0.90
IxNxW	8	2.01	2.22*	1.66	0.88	1.53	0.84

I = Irradiance N = Nutrients W = Water
* P <= 0.05 ** P <= 0.01 *** P <= 0.001

A significant interaction among irradiance, nutrients and water influenced the N concentration of the litter. In both the irrigated and intercepted water treatment levels, a positive interactive effect between irradiance and nutrients resulted in the combination of 80% shade and the high nutrient level significantly increasing the N concentration of the litter (Figure 4.5a & b). In the normal moisture level an interactive effect was absent. The individual effects of irradiance and nutrients resulted in shading and nutrient addition increasing the N concentration of the litter (P<0.0001).

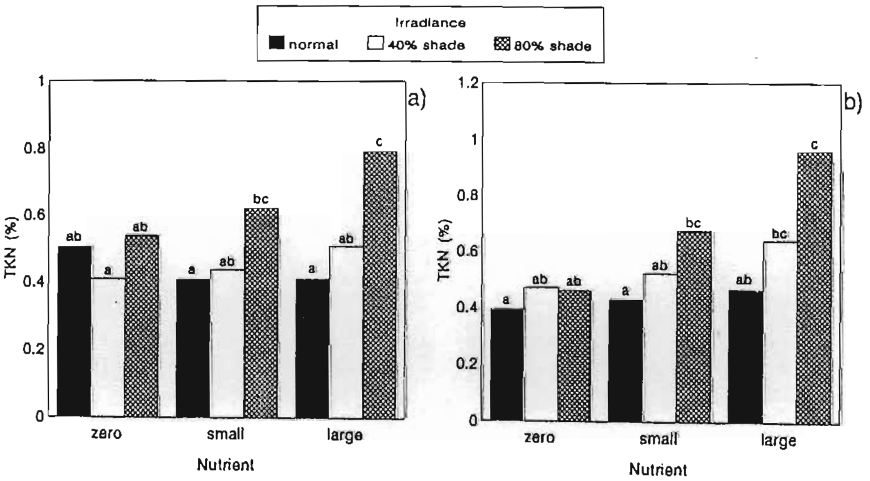

Figure 4.5 Interaction of irradiance and nutrients illustrating total Kjeldahl nitrogen concentration (TKN%) of the litter layer within a) the irrigated moisture level, and b) the intercepted rainfall level, in the factorial experiment. (Letters which differ indicate significance at the 5% level.)

The nutrient treatment had a major effect on the P concentration of the litter. Phosphorus concentration was significantly increased from 0.036% to 0.045% by the low nutrient addition level, and further increased to 0.071% by the large nutrient level. Irradiance also influenced P levels, with a significant increase from 0.043% under zero shade to 0.060% under 80% shade occurring. Potassium concentration of the litter was affected by an interaction between irradiance and nutrients. Nutrient addition under normal irradiance resulted in no positive effect, but the combination of shade and the high nutrient addition level significantly increased the K concentration of the litter (Figure 4.6). Calcium concentration of the litter was increased by both levels of nutrient addition (P<0.0028), whilst Mg concentration was influenced by the irradiance treatment (P<0.0005).

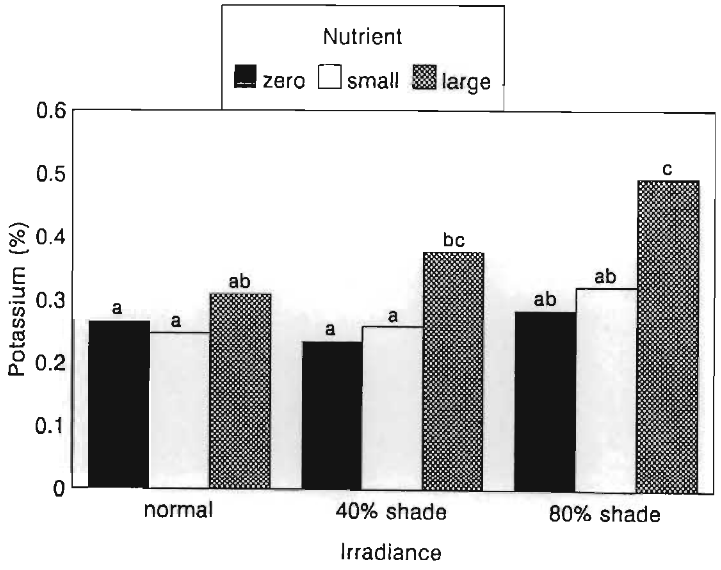

Figure 4.6 Interaction between irradiance and nutrients illustrating mean K concentration (%) of the litter layer for each treatment combination in the factorial experiment. (Letters which differ indicate significance at the 5% level.)

4.3.4 Root Biomass

As expected, roots were most abundant in the topsoil. In the five experimental units where deeper core samples were removed, 87% of the root mass occurred in the top 15 cm of soil, 12% in the 15-30 cm layer and 1% in the 30-45 cm layer. The response variables reported pertain to the top 0-15 cm of soil.

Shading had a detrimental effect on root biomass. Root biomass was reduced (P<0.0015) from 116.7 g (normal irradiance level) to 87.6 g under 80% shade. Nutrient addition at the low nutrient level increased root biomass from 94.4g to 117.5g (P<0.0161), but at the high nutrient addition level (99.4g) significant differences were not apparent. Both irradiance and nutrient treatments significantly affected the N concentration of the roots. Root N under 80% shade (0.58%) was greater than under 40% shade (0.42%) and normal irradiance levels (0.42%) (P<0.0001), whilst the high nutrient level had greater root N (0.53%) than the low and zero nutrient addition levels (0.44% and 0.43%, respectively) (P<0.0071). Root P was increased by the nutrient addition treatment, from 0.041% (normal nutrient level) to 0.053% (low nutrient addition level) to 0.074% (high nutrient addition level) (P<0.0001). Phosphorus, as with N, was also increased under 80% shade (P<0.0162). The addition of nutrients also had a positive effect on K levels, with root K increasing from 0.188% (normal nutrient level) to 0.229% in the high nutrient addition level (P<0.0305). The cations, Ca and Mg, were not influenced by treatments.

4.3.5 Soil Chemical Status

Results are reported for the 0-15 cm soil layer only, as treatment responses were limited to this layer. Nutrient addition was the treatment which most affected soil chemical status (Table 4.6).

Table 4.6 Summary of *F*-ratios and significance levels for soil variables: total nitrogen (N%), phosphorus (mg.ℓ^{-1} P), potassium (mg.ℓ^{-1} K), calcium (mg.ℓ^{-1} Ca), magnesium (mg.ℓ^{-1} Mg) and pH (KCl) in the 3^3 factorial experiment.

	df	N	P	K	Ca	Mg	pH
I	2	0.62	0.34	3.00	0.74	0.73	0.01
N	2	3.50^{*}	8.65^{***}	18.38^{***}	0.25	0.17	2.24
W	2	0.55	0.33	1.13	2.90	2.99	0.36
IxN	4	0.27	0.58	3.62^{*}	2.12	0.57	0.53
IxW	4	0.57	0.26	1.11	0.14	0.41	0.23
NxW	4	2.35	2.32	0.40	0.56	0.49	1.24
IxNxW	8	1.67	0.48	0.78	0.52	0.53	0.33

I = Irradiance N = Nutrients W = Water
* P <= 0.05 ** P <= 0.01 *** P <= 0.001

Treatments did not affect topsoil Ca and Mg levels with the result that pH levels were also unaffected. Total soil N was affected by nutrient addition (P<0.0372). Nitrogen in the high nutrient addition level (0.0361%) was notably less than the low (0.0595%) and zero nutrient addition levels (0.0518%). Soil K concentration was significantly affected by an interaction between shade and nutrients. Nutrient addition under 40% shade and normal irradiance did not result in any residual effect, whilst under 80% shade a residual effect was obvious in the high nutrient addition level (Figure 4.7). Soil P was affected by the nutrient treatment, and displayed a significant accumulation from 2.55 mg.ℓ^{-1} in the zero nutrient addition level, to 4.73 mg.ℓ^{-1} in the low nutrient addition level and 6.93 mg.ℓ^{-1} in the high nutrient addition level (P<0.0006).

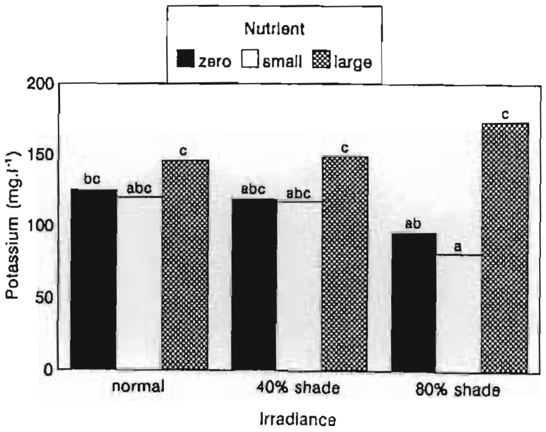

Figure 4.7 Interaction between irradiance and nutrients illustrating soil K (mg.ℓ^{-1}) for each treatment combination in the factorial experiment. (Letters which differ indicate significance at the 5% level.)

4.4 DISCUSSION

4.4.1 Effect On Herbaceous Production

In this experiment herbaceous yields were positively affected by the addition of nutrients. This response to fertilization has been reported in many studies (Weinmann 1938; Coughenour *et al.* 1985; Van Auken & Bush 1992; Belsky 1994). However, the significant interaction between irradiance and nutrients, revealed that the positive effect of nutrient addition was precluded under 80% shade (Figure 4.2), whilst moderate shade did not negate the positive effect of nutrient addition on herbaceous yields. Irradiance, on its own, had no significant effect on herbaceous production. Similar results were reported by Eriksen & Whitney (1981) with their positive yield response to fertilization under conditions of moderate to high solar irradiance. Blackman & Templeman (1938), also reported that shading at 61 and 44% did not affect yields under low N fertilization, but when N fertilizer was added yields increased dramatically under normal sunlight but not in shade. In order to discern the basis for this negative interaction between the high nutrient addition level and the 80% shade level, the individual effects of the nutrient addition and irradiance treatments on the sward are examined separately.

The effect of fertilization on sub-climax grasslands has been shown to significantly increase herbaceous yields, although it is accompanied by a change in species composition (Barnes *et al.* 1987; Hall *et al.* 1950). The dominance of Decreaser species such as *Themeda* and *H. contortus* in this densely tufted savanna grassland suggests that it was in a sub-climax state. Although herbaceous composition was not formally quantified in this experiment, notable changes were observed. Nutrient and irradiance treatments were observed to increase the proportion of *S. africanus*, *E. plana* and forbs and decrease the proportion of

Themeda and *H. contortus*. The susceptibility of *Themeda* to N fertilization is also well documented (Edwards & Nel 1973; Grossman & Cresswell 1974; Amory & Cresswell 1981). *Senecio pterophorus* (locally known as Nkanga) contributed most to forb production in this experiment. Its response to the fertilization and irradiance treatments was not surprising. This species often dominates nutrient-rich areas (e.g., animal resting points) in a paddock, and is often associated with *Acacia karroo* canopies where elevated nutrient levels and shading occur.

A further response to the high nutrient addition treatment was a marked reduction in total soil N. It is postulated that this occurrence was related to a change in species composition with fertilization. Since Increaser II and Invader species (e.g., *E. plana, S. africanus* and *S. pterophorus*) are able to outcompete climax species in fertilized situations, this suggests that they are able to take better advantage of elevated soil N levels than climax species. Hence it is hypothesized that the notable decrease in total soil N at the end of the experimental period was due to the efficient utilization of nutrients by species adapted to elevated nutrient levels. Under the low nutrient addition level, a species compositional change was not observed and the slight increase in total soil N was probably due to an accumulation of N not utilized by the climax grassland species.

Irradiance on its own had no effect on grass yield. Work done by Belsky (1994) and Kinyamario *et al.* (1995) ascribed this to sward composition and reported that unlike canopy-zone species, grassland-zone species are physiologically unable to take advantage of low light conditions and continue to loose water. Canopy-zone species, however, are able to conserve water by adjusting their stomatal conductance (Amundson *et al.* 1995) and respond positively to shade. Thus, the absence of canopy-zone species in this sward explains the lack of a positive yield response to low irradiance.

Cannell & Grace (1993) described how the photosynthetic rate of plants declined under shade, and that most plants responded to shade by increasing the allocation of assimilates to shoots so as to compensate for the poor availability of light. This would result in the plant having to draw on stored carbohydrate reserves in the roots and stubble. In this experiment, testament of this was the significant reduction in root biomass under 80% shade. Cannell & Grace (1993) also reported that plants responded to shading by an increase in extension growth and an increase in leaf area. These responses to shade were evident in *Themeda*. Etiolated growth under high shade occurred with a significant increase in tiller height, and an increase in the proportion of stem and a reduction in the proportion of dead leaf. Aerial tillering was also common. An increase in the number of leaves on tillers demonstrated an increase in leaf area. Further reaction of *Themeda* to shading was a significant decrease in tuft circumference and tiller number. These results emulate those of McNaughton (1992) on *Eustachys paspaloides* and *Themeda triandra* in the Serengeti National Park. These altered patterns of resource allocation provide evidence that *Themeda*, under low irradiance levels, could not function normally.

Separate examination of the effects of the high nutrient addition level and 80% shade on sward yield in this experiment provide insight to their negative interaction. Fertilization, although increasing sward yield, was detrimental to the climax species and resulted in a compositional change. Irradiance on its own, at the end of the experimental period, did not affect grass yield, but reduced photosynthetic rates and altered resource allocation patterns. This was detrimental to the functioning of *Themeda*, and provided gaps in the sward for opportunist species such as *S. pterophorus* and Increaser II species. It is speculated that it would be a matter of time before the negative effect of 80% shade would have translated into reduced grass production. The negative interaction of 80% shade and the high nutrient addition level in this experiment occurred mainly as a result of intensive shading. Fertilization, however, probably accelerated the time frame in which this occurred.

4.4.2 Effect On Forage Quality

The irradiance treatment had the greatest effect on plant mineral concentrations. Shading significantly increased the N, P, K and Mg concentrations of the sward, *Themeda* and the litter. These results mirror those of Eriksen & Whitney (1981). Root mineral content also displayed a significant increase in N and P concentrations. This may not be a direct treatment effect but rather a concentrating effect caused by the significant reduction in root biomass.

Nutrient addition also played an important role in affecting plant mineral concentrations. It has been well demonstrated that fertilization significantly increased the mineral content of herbage (Weinmann 1938; Weinmann 1943a; Weinmann 1943b; Ruess & McNaughton 1984; Coughenour *et al.* 1985). The results of this experiment show that fertilization, however, did not affect the N concentration of the sward or *Themeda*. Phosphorus and K concentrations in the sward and in *Themeda* were, however, increased with fertilization. Litter and root N, P and K concentrations were significantly greater with fertilization. The absence of an increase in the N concentration of the sward and of *Themeda* with fertilization was probably due to the lateness in the season in which samples were taken, as N withdrawal from aboveground components and relocation to storage, prior to the dormant period, may already have occurred. Another plausible reason for the absence of significantly higher N concentrations in aboveground vegetation is presented by Ruess & McNaughton (1984), where in the absence of grazers, NH_4NO_3 fertilization significantly stimulated investments to belowground production. Thus, ungrazed plants altered their biomass allocation to conserve producer resources, thereby enabling them to withstand defoliation more successfully. The presence of significantly greater N levels in the litter of the fertilized treatments, however, does provide evidence that leaf N concentrations were significantly increased in the sward during the season.

Belsky's (1992) work in Tsavo National Park, Kenya, reported that concentrations of N, P, K, and Ca in the graminous forage tended to increase from open grassland to tree understorey. In this experiment both the individual effects of shade and nutrients were responsible for significantly increasing grass mineral concentrations. However, the increased herbage quality in the shaded treatments occurred at the detriment of root reserves, essential for sustainable plant production. Fertilization also increased aboveground quality and plants were able to allocate surplus nutrients to storage. Thus, it was clear that shade and/or nutrients, generally associated with tree canopies, significantly increased the mineral content of the herbage.

Investigation of the treatment effects on forage quality also showed that the nutrient addition treatment significantly increased the OM content of both the sward and of *Themeda*. *In vitro* digestible organic matter was, however, not affected by fertilization. Fibre concentrations, NDF and ADF, as well as lignin were significantly increased by fertilization. Van Soest (1982), also reported an increase in lignin production with fertilization. Shading, however, significantly depressed the digestible components (OM and IVOM) of the sward and significantly increased the ADF and lignin concentrations. Trees in the savannas of Tsavo National Park also appeared to depress the digestibility of forage by increasing lignin production in grasses (Belsky 1992). Grossman *et al.* (1980) also reported decreased IVOM under *Ochna pulchra* clumps when compared with open grassland. *Themeda* responded to shading by increasing only its lignin concentration. This increase in lignin with shading can be attributed to an increase in the stem:leaf ratio, since stems tend to have greater lignin concentrations than leaves. The work of Belsky (1992) and Grossman *et al.* (1980) are difficult to compare with this study, since species composition differed. However, taking the results of this experiment into consideration, it appears that it is shade rather than nutrient addition which causes herbage under canopied zones to have lower digestibilities and greater fibre and lignin concentrations than herbage in open zones.

CHAPTER 5

RESPONSES TO BUSH CONTROL

5.1 INTRODUCTION

Bush encroachment in the mesic savannas of the Eastern Cape is characterized by the expansion of existing bushclumps into adjacent grassland, with eventual coalescence and the formation of woodland. The bushclump understorey is comprised of a sparse herbaceous layer (Chapter 3). Thus, associated with an increase in bushclump density is a decrease in grazing capacity. As grazing is paramount to commercial livestock (beef and sheep) production in these mesic savannas, bush control is a measure often considered.

Methods of bush control, such as mechanical clearing or chemical poisoning, are often employed to eliminate or lessen woody competitiveness, thus moving the woody-grass balance in favour of the grass component. The resultant increase in grass and animal production is considered to surpass the costs of control. Land managers justify the financial soundness of the bush control operation by the increased herbaceous production following clearing, without discounting the subsequent woody re-encroachment. Little attention has been payed to the potential effect of bush control on savanna ecology.

The bush control experiment which has been established was designed to test the efficacy of mechanical clearing (using a bulldozer) and chemical poisoning (using a plant-applied arboricide) the woody layer. The aim of this chapter is to investigate the initial responses to bush control in this experiment. The first two seasons herbaceous, woody and soil responses to bush control treatments are reported.

5.2 MATERIALS AND METHODS

5.2.1 Site Description

An area of relatively homogenous soil, slope, aspect and vegetation was selected in the upper slope of the study area (Chapter 2). An area of approximately 10 ha was deemed suitable and was characterized by a relatively homogenous soil of the Hutton form.

5.2.2 Treatments

The experimental design was a simple random design with three treatments: mechanical clearing, chemical poisoning and a control. Eight replicates per treatment were randomly assigned to 0.36 ha (60 m x 60 m) experimental plots. An extra mechanical treatment was added to the design and oversown with a dryland pasture grass. This treatment was included so as to hasten grass establishment and improve grass production, relative to the other mechanical treatment. This treatment was duplicated.

Pseudo-replication is a limitation, as the experiment is not replicated at other sites in this vegetation type. This makes results less transferable especially where soil type, for example, differs from this experiment. However, owing to cost, time and other logistical problems, site replication was not feasible. The experimental design does contain adequate replication (a feature seldom associated with large vegetation trials) to provide sufficient confidence in the results obtained.

5.2.2.1 Mechanical treatment

The above-ground woody component was completely cleared from the mechanical plots using a D6-bulldozer, and the debris removed from the experimental area. The bulldozer blade was used to push-over and uproot large individuals. In the bushclump areas the bulldozer operator used a ripper to sever the intact roots of large woody individuals. Soil disturbance was limited to the bushclump area. The removal of topsoil was also minimized, as the bulldozer blade was kept above the soil surface when pushing debris. Bulldozing took place on the 20-23 October 1992. A week later, without any further seedbed preparation, *Chloris gayana* seed was hand-broadcasted on the mechanical-oversown plots at 6 kg.ha^{-1}.

5.2.2.2 Chemical treatment

All woody material in the chemical plots was sprayed with a mixture of 1 % Tordon Super and diesel, using a red dye as a marker. The active ingredients of Tordon-Super are trichlopyr and picloram, these target plant photosynthesis, respiration and nucleic acid synthesis. The arboricide was applied to woody stems using a knap-sack sprayer. A band, from ground level up to 20 cm, was wetted. Plots were sprayed on the 14-18 December 1992.

5.2.3 Measurements

5.2.3.1 Herbaceous layer

The vegetation was stratified into three vegetation zones: the interior bushclump zone, the peripheral bushclump zone (defined as the two-metre-wide interface between the bushclump and the adjacent grassland), and the interclump grassland zone. Herbaceous composition, production and quality were obtained from samples taken from two random monitoring sites within each experimental plot. At each monitoring site 5 random quadrats (50 cm x 50 cm), per vegetation zone, were used for sampling. All herbaceous species (including forbs) occurring in a quadrat were identified for frequency determination. Braun-Blanquet cover-abundance classes were assigned to each species. The median percentage for each cover-abundance class was used to calculate percentage cover (van der Maarel 1979). The dry-weight-rank method (t'Mannetje & Haydock, 1963) was used to rank the three herbaceous species (forbs were grouped) contributing most to the aboveground herbaceous biomass. The documented multipliers were used to weight scores. Quadrat samples were harvested and taken back to the laboratory where they were stored in refrigeration for later separation into grass and forb components. After separation, grass and forb samples were oven-dried at 60°C for 48 hours and weighed. For plant nutrient analyses, quadrat samples were milled to pass through a 1 mm sieve and TKN, P, K, Ca, Mg and Na were determined (methods listed in Appendix 3).

Data were collected at the end of the 1992/1993 season (May-June 1993) and at the end of the 1993/94 season (April-May 1994). Experimental plots were grazed down by oxen after all herbaceous measurements had been collected.

5.2.3.2 Soil nutrient status

In each experimental plot soil samples were collected from two random sites. At each site topsoil (0-20 cm) samples were taken from two vegetation zones: the bushclump zone (or former bushclump zone, in the case of the mechanical treatments), and the adjacent grassland zone. Within each vegetation zone a composite sample of three random soil samples was formed. Soil samples at the end of the first season (14 June 1993) were collected from the mechanical treatments only, since a chemical treatment effect after the first season was not anticipated. All treatments were sampled at the end of the second season (14 April 1994). Soil samples were analyzed for soil density, pH, Ca, Mg, P, K and total N (methods listed in Appendix 2).

5.2.3.3 Woody layer

Baseline measures of the structure and composition of the woody vegetation were obtained prior to the implementation of the treatments. In each experimental plot two randomly located, permanent belt transects were marked out. Each belt transect was located by two permanent iron standards set 30 m apart, between which a three-metre-wide belt was measured.

The vegetation was stratified into three vegetation zones: the bushclump zone, the peripheral zone, and the interclump grassland zone.

Woody vegetation was separated into two size classes: the mature and established individuals which were greater than 0.5 m in height or with stem basal circumference greater than 5 cm (hereafter referred to as large individuals), and the smaller individuals which consisted of woody seedlings, saplings or shrubs smaller than the large individuals (hereafter referred to as small individuals).

All large individuals within each belt transect were monitored. Since the task of measuring all the small individuals was impracticable, an exercise was undertaken to determine the optimum sub-sample size that efficiently reflected the species richness and abundance of the small individuals within an experimental plot. The most efficient approach was found to be measuring all the small individuals in the grassland zone of a transect, a single quadrat of 4 m^2 in the bushclump zone, and two quadrats of 3 m^2 in the peripheral zone.

Since quadrats would be revisted in subsequent seasons, it was necessary to assign co-ordinates to all woody individuals in each belt transect for ease of relocation. Each individual in the large individuals class was assessed for genus and species, stem basal circumference(s) and height, vegetation zone, and state-of-health (to identify early signs of mortality in the chemical treatment). In the small individuals class, variables measured were an individuals' genus and species, height, vegetation zone and state-of-health.

A week after bulldozing, a complete re-assessment of the mechanical plots was carried out to provide a post-bulldozing baseline data set which would serve as a covariate in separating the remnant woody component from the following seasons coppice and seedling establishment. Annual re-assessments of all treatments were made during May-July of the first (1992/93) and second (1993/94) seasons.

5.2.4 Data Analyses

5.2.4.1 Herbaceous layer and soils

The data were analysed as a split-plot design, with vegetation zones split within experimental plots (replicates). The model was constructed as follows:

$Y_{ijk} = \mu + \alpha_i + \beta_{ij} + \gamma_k + (\beta\gamma)_{ik} + \varepsilon_{ijk}$

where μ = sample mean,

α_i = the effect of the i^{th} treatment,

β_{ij} = the effect of the j^{th} rep nested within the i^{th} treatment,

γ_k = the effect of the k^{th} vegetation zone,

$(\beta\gamma)_{ik}$ = the interaction of the i^{th} treatment and the k^{th} vegetation zone,

ε_{ijk} = measurement error,

Treatment was the whole-plot factor (tested using rep(treatment) as the error term) and vegetation zone the sub-plot factor (Steel & Torrie, 1981).

Data were transformed when necessary using the Box-Cox transformation (Weisberg 1985) and analyzed using PROC GLM (SAS Ins., 1982). *A posteriori* comparison of means tests were carried out using Bonferroni and Tukey tests, which accounted for experimentwise error rates (SAS Ins., 1982). Contrast statements were also employed. Means and variances were back-transformed.

5.2.4.2 Woody layer

Chemical versus control: large individuals

Large individuals were subjectively divided into three size classes according to basal circumference: ≤ 10 cm (class 1), larger than class 1 and ≤ 25 cm (class 2), and > 25 cm (class 3).

The effect of the arboricide was determined by investigating the large individuals' mortality at the end of each of the two growing seasons following treatment implementation. Mortality was determined from examination of the heartwood beneath the bark. Multi-stemmed woody individuals were classified dead when all stems had succumbed. Percent mortality was calculated as the number of individuals alive at the start of the growing season which were dead at the end of the same growing season, divided by the total number of live individuals at the start of the season. Deaths from the previous season and individuals which had recruited during the course of the current season were excluded. Mortality was calculated on the basis of species and size-class, separately for each of the three vegetation zones.

Chemical versus control: small individuals

The detailed monitoring of individuals in permanent quadrats enabled the population dynamic of each cohort to be tracked. This was described separately for the different vegetation zones. The grassland zone was separated into two zones: the 'under-canopy' zone and the 'open' zone (area not beneath a tree canopy). Because quadrat size and monitoring area in the various vegetation zones varied, data were expressed as the number of individuals per m^2. The status of small individuals at the end of each season was described as the total number of live individuals per unit area. Percent mortality of small individuals was calculated in the same way as for large individuals. Coppicing was described as those individuals initially classified as dead at the end of the first season, which had resprouted during the second season. Recruitment was described as the new cohort not present at the last assessment.

Analysis of variance was performed using PROC GLM (SAS Ins., 1982) to test the effect of the arboricide on small individual density at the end of each season. Recruitment and mortality in the chemical treatment at the end of each season, and coppicing at the end of the second season, was compared with the control. Boxcox transformations (Weisberg 1985) were employed to ensure data were normally and independently distributed. Bonferroni comparison of means test were performed to test the effects of treatment and vegetation zone.

Mechanical versus control

The removal of the woody component in the mechanical treatments completely transformed vegetation structure and thus obviously eliminated the possibility of comparing the mechanical treatment with the control.

An attempt was made to correlate subsequent coppice with pre-bulldozed baseline vegetation. However, considering that coppice occurs along the length of any exposed root or stem, it was clear that to relate coppice to post-clearing vegetation was practically impossible, except if tracers/markers had been used.

Investigation of mechanical treatment effects was therefore of a descriptive nature. Woody recruitment was sourced as being from either coppice or seedling establishment. Coppice was easily identified by its multi-stemmed nature or the presence of old woody material from which it had developed. In the case of

Acacia karroo, an exercise was undertaken to determine the precision in identifying its form of recruitment. One hundred *A. karroo* individuals which had recruited during the first season were randomly selected. Each individual was first classified as either having recruited from coppice or seed. Individuals were then excavated to confirm the form of recruitment. Species distribution and the location of woody recruitment were related to the pre-bulldozed vegetation zones.

The extent to which woody biomass re-establishes following clearing is a function of the density of woody individuals which have recruited, the height of these individuals, and the rate at which re-establishment occurs. Woody individual recruitment was, therefore, described on the basis of species and vegetation zone, and expressed on a stem density and height basis for the three periods of assessment. Oversown and mechanical treatment differences were also investigated. Owing to non-normal distribution, the Wilcoxon-Mann-Whitney two-sample test (SAS Ins., 1982) was employed to test for re-establishment differences between oversown and mechanical treatments.

5.3 RESULTS

5.3.1 Herbaceous Responses

5.3.1.1 Herbaceous production

Variable rainfall (1992/93 season = 384 mm and 1993/94 season = 777 mm) had a major effect on herbaceous production, and this was aptly reflected in the grass and forb yields of the two dissimilar seasons. As anticipated with mechanical clearing, a significant increase in grass production was evident in the two seasons post-clearing (Figure 5.1). Oversowing with *C. gayana* produced significantly greater grass yields than the non-oversown mechanical treatments. At the end of the first season, grass production was greatest in the grassland zone of the mechanical treatments. In the second season it was the bushclump zone which produced the greatest yields. Forb production was also significantly increased in the mechanical treatments (Figure 5.2). However, forb yields in the oversown treatment were significantly less than in the mechanical treatment. When compared with the control, the chemical treatment effect was only manifested in the second season, since no difference in grass yield was apparent in the 1992/93 season. In the 1993/94 season, grass yields were significantly greater in all three vegetation zones of the chemical treatment than in the control. Forb production was not affected by the chemical treatment.

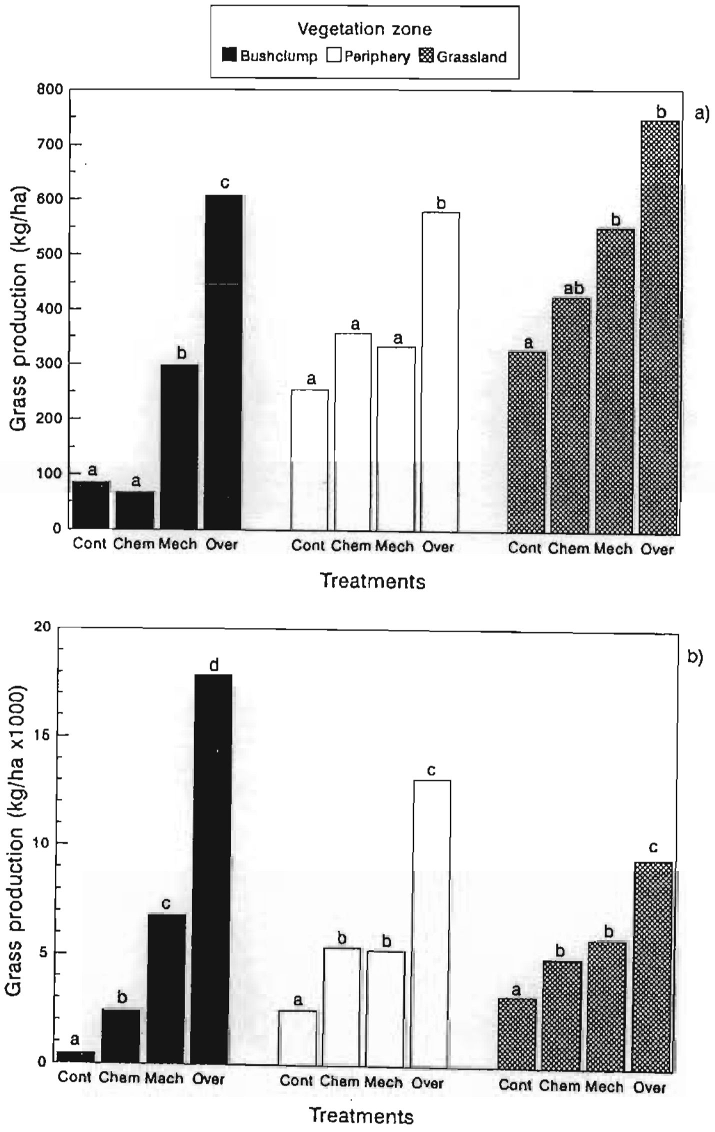

Figure 5.1 Grass production in response to bush control treatments (Cont=control, Chem=chemical, Mech=mechanical, Over=oversown) in a) the 1992/93 season, and b) the 1993/94 season. (Letters which differ within a vegetation zone indicate significance at the 5% level.)

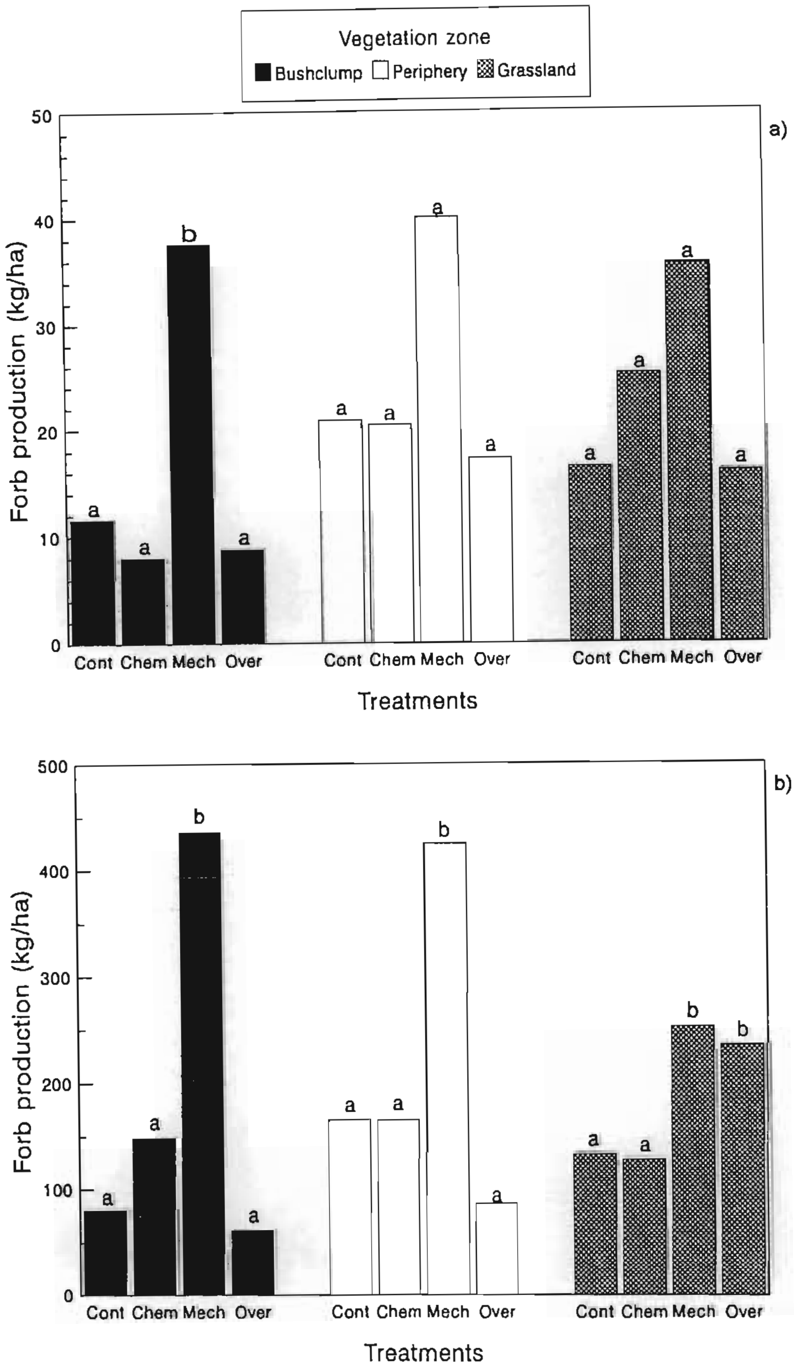

Figure 5.2 Forb production in response to bush control treatments (Cont=control, Chem=Chemical, Mech=mechanical, Over=Oversown) in a) the 1992/93 season, and b) the 1993/94 season. (Letters which differ within a vegetation zone indicate significance at the 5% level.)

5.3.1.2 Herbaceous composition

Mechanical clearing of the woody layer significantly modified herbaceous composition. Compared to the control treatment, where bushclumps did not accommodate a productive herbaceous layer, mechanical clearing certainly achieved increased production. This was mainly attributed to the domination of the ex-bushclump zone by *Panicum maximum*, with a contribution to biomass of 50.7% in the 1992/93 season and 70.4% in the 1993/94 season, and by forbs (Table 5.1 and 5.2). Herbaceous cover in the ex-bushclump zone displayed a two-fold increase at the end of the 1992/93 season, and a three-fold increase at the end of the second season (Appendix 5 & 6). The ex-bushclump zone was characterised by bushclump species with a marked increase in frequency, e.g. *P. maximum* and *Priva meyeri*, as well as species that were either not associated with bushclumps or normally occurred at lower frequencies, e.g. a creeping form of *Digitaria eriantha*, *Cynodon dactylon*, *Aristida congesta*, *Tragus berteronianus*, *Abutilon sonneratianum*, *Berkheya bipinnatifida*, *Clutia ericoides*, *Senecio pterophorus* and *Sida rhombifolia* (Appendix 7 & 8). Mechanical clearing also resulted in the loss of bushclump-associated species, e.g. *Helictotrichon capense* and sedges. The grassland zone of the mechanical treatment, although significantly more productive than the control treatment, remained very much intact with little difference in composition, e.g. *Themeda triandra* remained as frequent and productive as it formally was. In the grassland zone, *Panicum maximum*, was more productive in the mechanical plots than in the control plots in the 1993/94 season. The ex-peripheral zone simply consisted of a mix of bushclump and grassland species.

Oversowing with *C. gayana* was extremely successful. It provided an excellent early cover (a three-fold increase within the first season, and a five-fold increase at the end of the second season), significantly increased grass yields (especially in the 1993-1994 season), and significantly reduced undesirable dicotyledon colonizers such as *Berkheya bipinnatifida* and *Solanum incanum*.

Table 5.1 Herbaceous composition of the bush control treatments, expressed as a dry-weight percentage, illustrating the contribution of the species to total dry matter production for the 1992/1993 season, separately for the three vegetation zones. (Cont=control, Chem=chemical, Mech=mechanical, Over=oversown.)

	Bushclump				Periphery				Grassland			
	Cont	Chem	Mech	Over	Cont	Chem	Mech	Over	Cont	Chem	Mech	Over
Total yield (kg/ha)	133	122	401	650	301	422	424	622	391	499	629	790
Grass species (%)												
Aristida congesta	0.0	1.0	2.6	0.7	4.8	7.4	4.5	6.3	7.7	13.8	10.5	2.3
Chloris gayana	0.0	0.0	0.0	69.2	0.0	0.0	0.0	29.0	0.0	0.0	0.0	31.9
Cynodon dactylon	2.0	8.8	3.0	3.6	8.0	21.3	28.1	16.0	11.7	13.9	24.8	13.6
Digitaria eriantha	0.9	0.0	10.6	1.9	3.6	0.2	4.1	1.5	5.9	0.1	0.6	1.2
Eragrostis chloromelas	0.0	0.0	0.0	0.0	0.9	1.0	0.0	0.0	6.2	2.4	2.8	0.0
Eragrostis curvula	12.7	3.7	1.1	0.7	12.9	7.8	6.5	4.1	21.9	19.0	11.1	7.2
Eragrostis plana	0.6	1.6	1.8	0.0	3.2	5.2	0.5	3.4	0.1	4.9	1.0	0.7
Helictotrichon capense	13.6	18.7	0.0	0.0	2.2	1.7	0.0	0.0	0.0	0.0	0.0	0.0
Heteropogon contortus	0.0	0.0	0.0	0.0	0.0	0.0	0.3	3.7	0.0	0.0	0.8	0.0
Hyparrhenia hirta	0.1	1.0	0.0	0.0	0.0	0.2	0.5	0.0	2.5	0.8	0.7	0.0
Panicum maximum	37.9	30.4	50.7	18.5	19.8	20.7	23.9	14.3	5.8	8.2	10.4	19.3
Sporobolus africanus	3.5	8.4	6.3	2.2	21.1	12.0	8.9	13.6	22.1	16.4	15.9	18.7
Themeda triandra	2.6	3.1	3.0	0.9	11.7	14.6	9.5	0.6	9.1	14.8	14.4	0.3
Tragus berteronianus	0.0	0.0	2.7	0.0	0.0	0.0	1.2	0.0	0.0	0.1	0.9	0.0
Sedges	5.8	4.3	0.1	0.0	2.1	0.6	0.0	2.7	0.1	0.1	0.0	0.0
Forbs	20.3	19.2	18.1	2.3	9.6	7.3	12.0	4.8	6.9	5.5	6.1	4.8
Total (%)	100	100	100	100	100	100	100	100	100	100	100	100

Table 5.2 Herbaceous composition of the bush control treatments, expressed as a dry-weight percentage, illustrating the contribution of the species to total dry matter production for the 1993/1994 season, separately for the three vegetation zones. (Cont=control, Chem=chemical, Mech=mechanical, Over=oversown.)

	Bushclump				**Periphery**				**Grassland**			
	Cont	**Chem**	**Mech**	**Over**	**Cont**	**Chem**	**Mech**	**Over**	**Cont**	**Chem**	**Mech**	**Over**
Total yield (kg/ha)	**814**	**3555**	**8324**	**18356**	**2834**	**5906**	**6373**	**13784**	**3572**	**5302**	**6544**	**11032**
Grass species (%)												
Aristida congesta	0.0	0.0	0.7	0.8	5.1	2.0	3.1	2.4	7.8	6.38	2.8	4.7
Chloris gayana	0.0	0.0	0.0	92.4	0.0	0.0	0.0	81.0	0.0	0.0	0.0	65.1
Cynodon dactylon	1.0	1.8	1.0	0.0	2.3	4.1	3.9	2.0	3.2	2.6	3.3	5.0
Digitaria eriantha	0.0	1.8	4.0	0.3	6.5	2.2	2.6	0.0	12.2	5.7	7.2	2.3
Eragrostis curvula	1.3	1.7	5.9	0.0	6.3	9.9	9.3	3.5	25.9	22.8	11.0	4.3
Eragrostis plana	0.0	0.0	0.4	0.0	0.9	0.5	0.0	0.0	0.0	1.4	0.0	0.0
Helictotrichon capense	5.7	15.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Heteropogon contortus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Hyparrhenia hirta	0.0	0.0	0.5	0.0	0.0	0.0	0.8	0.0	0.6	1.9	1.4	0.0
Panicum maximum	41.0	50.2	70.4	3.6	38.7	57.0	47.0	8.0	11.7	23.2	32.2	4.0
Sporobolus africanus	3.1	1.2	0.8	0.0	7.7	3.3	6.8	1.0	4.4	4.6	9.1	2.7
Themeda triandra	3.5	0.7	2.6	1.7	22.4	14.1	11.7	0.0	27.0	26.7	24.7	8.1
Tragus berteronianus	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sedges	8.0	3.2	0.0	0.0	1.2	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Forbs	36.4	24.0	13.7	1.2	8.8	6.4	14.3	2.1	6.7	4.8	8.3	3.8
Total (%)	100	100	100	100	100	100	100	100	100	100	100	100

The herbaceous composition of the chemical treatment was no different from the control at the end of the 1992/93 season. In the bushclump zone, however, common species such as *P. maximum, H. capense* and *P. meyeri* were slightly less frequent, possibly due to arboricide over-spray. The significant increase in herbaceous production in the second season can be attributed to *P. maximum* (in all three zones), *H. capense* and forbs (in the bushclump zone), and a proportional increase in productivity of the peripheral and grassland zone species. An increase in *Senecio pterophorus* in the bushclump zone after the second season was noted.

5.3.1.3 Grass quality

Mechanical removal of the woody component resulted in a significant increase in grass nitrogen concentration from ex-bushclump and ex-peripheral zones (Figure 5.3a) in the first year following clearing. In the second season, however, a significant decrease in grass nitrogen concentration occurred in the mechanically cleared plots (Figure 5.3b). Although this trend was only significant in the ex-bushclump zone of the mechanical treatment, it was significant in all three zones of the oversown plots.

An unexplainable and significant decrease in Ca (4130 $mg.kg^{-1}$ in the control to 2671 $mg.kg^{-1}$ in the chemical treatment), and Na (1892 $mg.kg^{-1}$ in the control and 847 $mg.kg^{-1}$ in the chemical treatment) characterized the first season. This did not occur in the second season.

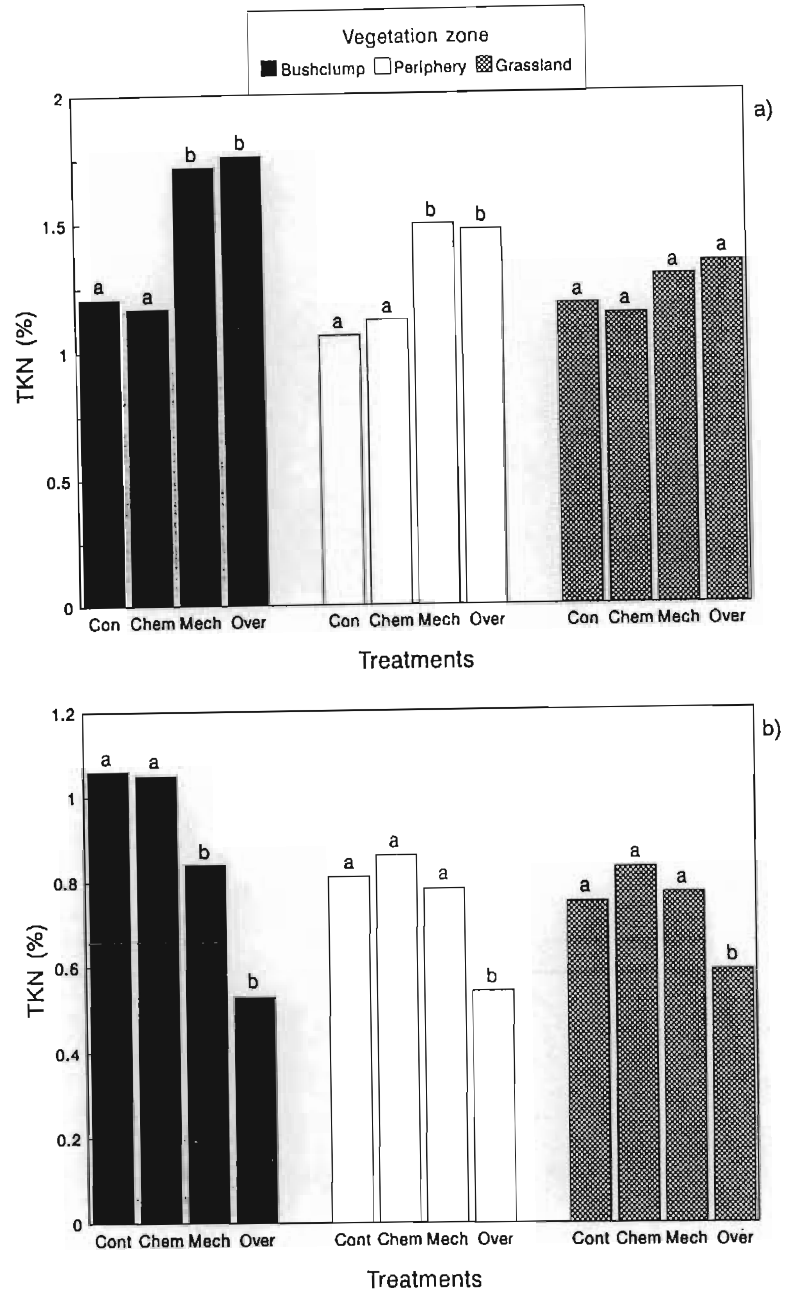

Figure 5.3 Nitrogen concentration (total Kjeldahl nitrogen %) of the grass layer for the treatments in the bush control experiment for a) end of the 1992/93 season, and b) end of the 1993/94 season. Letters which differ within a vegetation zone indicate significance at the 5% level. (Cont=control, Chem=chemical, Mech=mechanical, Over=oversown.)

Most of the variation in the treatments was explained by vegetation zone effects. Bushclump grass samples were significantly higher in Ca, Mg, Na, P than grassland samples in all treatments for both seasons. A significant interaction between treatment and vegetation zone occurred in the second season for the mechanical treatments, with K and TKN levels no higher in the ex-bushclump zone than in the grassland zone (Table 5.3).

Table 5.3 Grass quality analyses illustrating the vegetation zone effect on K and TKN for the respective bush control treatments at the end of the 1993/94 season. (Letters which differ within treatments indicate significance at the 5% level.)

Treatment	**Veg. Zone**	**K (ppm)**	**TKN (%)**
Control	Bushclump	17 296^{a}	1.06^{a}
	Periphery	10 499^{b}	0.81^{b}
	Grassland	8 525^{c}	0.75^{b}
Chemical	Bushclump	17 152^{a}	1.05^{a}
	Periphery	12 178^{b}	0.86^{b}
	Grassland	9 594^{c}	0.83^{b}
Mechanical	Bushclump	13 569^{a}	0.84^{a}
	Periphery	11 631^{a}	0.78^{a}
	Grassland	10 774^{a}	0.77^{a}
Oversown	Bushclump	15 296^{a}	0.53^{a}
	Periphery	13 917^{a}	0.54^{a}
	Grassland	13 239^{a}	0.59^{a}

5.3.2 Soil Response

As previously shown (Chapter 3), bushclump soils were significantly more fertile than grassland soils (Table 5.4). Chemical poisoning of the woody vegetation had no significant effect on soil chemistry at the end of the second season, although most soil variables were numerically lower than the control, particularly bushclump total N (Pr<0.1341).

Mechanical removal of the woody vegetation resulted in marginally higher soil densities at the end of the second season, probably due to the increase in organic matter (Table 5.4). Ex-bushclump soil pH was significantly lower in the mechanical and oversown treatments than in the control treatments. This was probably related to the significantly lower ex-bushclump Ca values in the mechanical and oversown treatment when tested against the control. Total soil N in the ex-bushclump zone was markedly lower in the mechanical ($Pr<0.0850$) and oversown ($Pr<0.0204$) treatments than in the control. Phosphorus, although not significant, was lower in the mechanically cleared treatments than in the control. Soil Mg and K values were unaffected by the bush control treatments.

Table 5.4 Mean soil variables for the respective vegetation zones, at the end of the 1993/94 season, for the bush control treatments. (Letters that differ along a row indicate significance at the 5 % level.)

	Vegetation	Bush control treatments			
Soil variable	zone	Control	Chemical	Mechanical	Oversown
Density (g.cm^{-3})	Bushclump	1.078^a	1.083^a	1.101^a	1.130^a
	Grassland	1.116^a	1.110^a	1.135^a	1.155^a
pH	Bushclump	5.75^a	5.66^a	5.43^b	5.15^b
	Grassland	4.91^a	5.00^a	5.02^a	5.15^a
Ca (mg.ℓ^{-1})	Bushclump	3408^a	3215^a	2791^b	2463^b
	Grassland	2132^a	2250^a	2200^a	2409^a
Mg (mg.ℓ^{-1})	Bushclump	554^a	543^a	555^a	624^a
	Grassland	494^a	502^a	526^a	516^a
K (mg.ℓ^{-1})	Bushclump	328^a	355^a	373^a	280^a
	Grassland	156^a	163^a	169^a	211^a
P (mg.ℓ^{-1})	Bushclump	6.61^a	6.22^a	5.40^a	3.74^a
	Grassland	3.18^a	4.18^a	3.83^a	4.61^a
total N (%)	Bushclump	0.127^a	0.095^a	0.091^a	0.055^b
	Grassland	0.073^a	0.067^a	0.076^a	0.116^a

The 1992/93 dataset permitted a direct seasonal comparison with the mechanical treatments' 1993/1994 dataset. Magnesium increased significantly in the second season for both vegetation zone and treatments (Table 5.5). A significant increase in K occurred in the ex-bushclump zone on the mechanical treatment, this however was not apparent in the oversown treatment. No marked differences in soil density, Ca and P were apparent. Total N for the 1993/1994 season was significantly lower than 1992/1993 season levels, for both mechanical and oversown treatments.

Table 5.5 Changes in bushclump and grassland soil properties in the 1992/93 and 1993/94 seasons following mechanical clearing. (Letters that differ within a row and treatment indicate significance at the 5 % level.)

		Treatments			
		Mechanical		**Oversown**	
Soil variable	**Vegetation zone**	**'92-93 season**	**'93-94 season**	**'92-93 season**	**'93-94 season**
Density (g.cm^{-3})	Bushclump	1.114^a	1.101^a	1.090^a	1.130^a
	Grassland	1.130^a	1.135^a	1.138^a	1.155^a
pH	Bushclump	5.46^a	5.43^a	5.50^a	5.15^a
	Grassland	5.18^a	5.02^a	5.38^a	5.15^a
Ca (mg.ℓ^{-1})	Bushclump	2814^a	2791^a	2968^a	2463^a
	Grassland	2358^a	2200^a	2461^a	2409^a
Mg (mg.ℓ^{-1})	Bushclump	408^a	555^b	382^a	624^b
	Grassland	350^a	526^b	364^a	516^b
K (mg.ℓ^{-1})	Bushclump	262^a	373^b	284^a	280^a
	Grassland	156^a	169^a	168^a	211^a
P (mg.ℓ^{-1})	Bushclump	4.39^a	5.40^a	4.02^a	3.74^a
	Grassland	3.26^a	3.83^a	1.91^a	4.61^a
total N (%)	Bushclump	0.1974^a	0.0905^b	0.1811^a	0.0550^b
	Grassland	0.1637^a	0.0762^b	0.1300^a	0.1160^b

5.3.3 Woody Dynamics

5.3.3.1 Chemical vs control: large individuals

Within a couple of months, signs of the effect of the arboricide were visible. Many woody individuals dropped their leaves. Arboricide had a marked effect ($P<0.0001$) on the mortality of large individuals in the chemical plots (Table 5.6). Mortality was highest in the first season, with a carry-over effect evident in the second season. Most of the individuals which succumbed at the end of the second season had previously shown signs of arboricide susceptibility. From the state-of-health observations made at the end of the first season, 86.7% of the individuals in the bushclump zone, 87.2% in the peripheral zone and 100% in the grassland zone, were identified as 'sick', (i.e., leaves had dropped but still had live heartwood), and had succumbed by the end of the second season.

Table 5.6 The effect of the arboricide on the mortality of large individuals at the end of the 1992/93 and 1993/94 seasons for the control (Cont) and chemical (Chem) treatments for the 3 vegetation zones (BC=bushclump, PBC=periphery, GR=grassland) and size classes (1=basal circumference ≤ 10 cm, 2=basal circumference 10 cm≤x ≤25 cm, 3=basal circumference > 25 cm).

		Mortality (%)							
Veg.		1992/93 season				1993/94 season			
Zone	Class	Cont	mean	Chem	mean	Cont	mean	Chem	mean
	1	0.8		27.4		2.8		11.1	
BC	2	3.9	1.7	32.7	25.5	3.2	2.7	11.5	12.0
	3	4.3		12.5		1.5		13.3	
	1	0		38.0		3.5		12.8	
PBC	2	0	0	17.5	33.4	0	2.3	18.6	16.4
	3	0		23.5		0		17.7	
	1	2.5		48.4		0		12.8	
GR	2	1.7	2.0	33.7	43.7	1.7	0.7	13.0	11.0
	3	0		14.3		0		7.1	
Grand Mean			1.7		32.9		2.4		13.1

Percent mortality at the end of the first season was generally least in the largest individuals. Herbicide companies advise that in the case of larger stems (e.g. ≥ 25 cm circumference), a greater dosage be applied or that stems be scarified to improve the efficacy of the arboricide. As this would have made what was an enormous task a lot more time consuming, it was accepted that arboricide efficacy with larger stems would be lessened. Greatest mortality occurred in the grassland zone (54.7%) and least in the bushclump zone (37.5%). This was attributed to the difficulty of gaining access to the bushclump interior relative to the open grassland, and was compounded by the high density of stems present in the bushclump zone.

Owing to the enormous task of applying the arboricide to every stem in each paddock, it could not be assumed that every individual had been treated. Interpretations of species responses to the arboricide therefore have to be viewed with caution. Some field observations of species responses to the arboricide were highlighted by the data. *Canthium mundianum* was observed to be less susceptible to the arboricide, this was most apparent for medium and large size individuals in the bushclump zone (Table 5.7).

Table 5.7 Mortality in response to arboricide treatment of the large individuals on a species basis, in the various size classes (1=basal circumference ≤ 10 cm, 2=basal circumference 10 ≤ x ≤ 25 cm, 3=basal circumference > 25 cm), for the 3 vegetation zones. (Missing values indicate a species size class consisting of less than 5 individuals, which makes interpretation difficult.)

	Mortality (%)								
	Bushclump zone			**Peripheral zone**			**Grassland zone**		
	Size class			**Size class**			**Size class**		
Species	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Canthium mundianum	44	8	11	45	-	-	57	-	-
Coddia rudis	26	13	-	45	22	-	77	37	-
Cussonia spicata	71	-	9	-	-	-	-	-	-
Diospyros simii	32	14	-	22	-	-	-	-	-
Grewia occidentalis	50	88	-	21	-	-	-	-	-
Hippobromus paucifloris	45	-	-	-	-	-	-	-	-
Maytenus heterophylla	56	73	44	58	69	-	58	57	-
Rhus undulata	57	-	-	89	-	-	100	-	-
Scutia myrtina	48	51	24	63	65	-	80	59	-
Trimeria trinervis	44	69	-	70	-	-	100	-	-

Coddia rudis (a multi-stemmed shrub) and *Diospyros simii* (a multi-stemmed shrub with a creeping habit) also showed less susceptibility to the arboricide, probably due to their growth habits which make complete and efficient application of the arboricide difficult. It should be noted that with multi-stemmed woody individuals, although many stems did succumb, mortality was only defined when all stems had succumbed. Within each species, greater mortality occurred in the grassland zone than in the bushclump zone. The two species which contributed most to woody biomass in this vegetation, *Scutia myrtina* and *Maytenus heterophylla*, were susceptible to the arboricide and therefore chemical control was able to impact seriously the woody component of this vegetation. However it must be stressed that a separate study would be required to test accurately the susceptibility of species and size classes to arboricide.

5.3.3.2 Chemical vs control: small individuals

The baseline dataset clearly indicated that the distribution of small individuals was strongly affected by vegetation zone (Figure 5.4). The application of arboricide had a major effect on small individuals. Percent mortality at the end of the first season was greater in the chemical plots than in the control plots with all vegetation zones having been severely impacted (Figure 5.5).

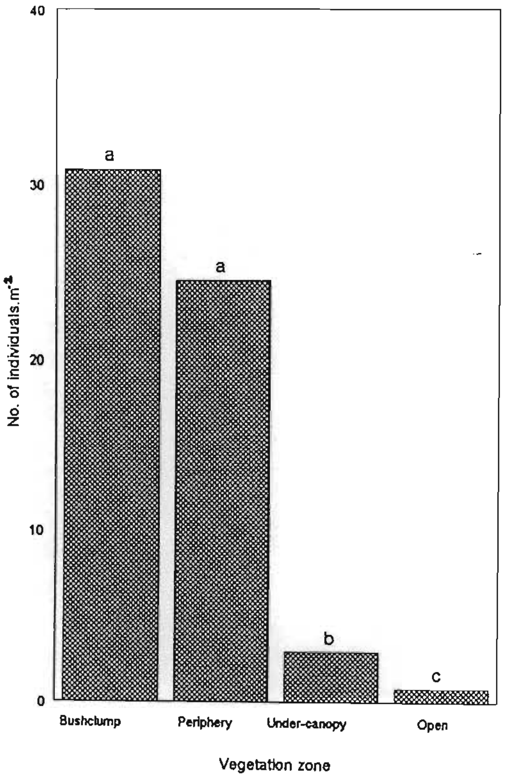

Figure 5.4 Density of small individuals in the four vegetation zones prior to treatment implementation in the bush control experiment. (Letters which differ indicate significance at the 5% level.)

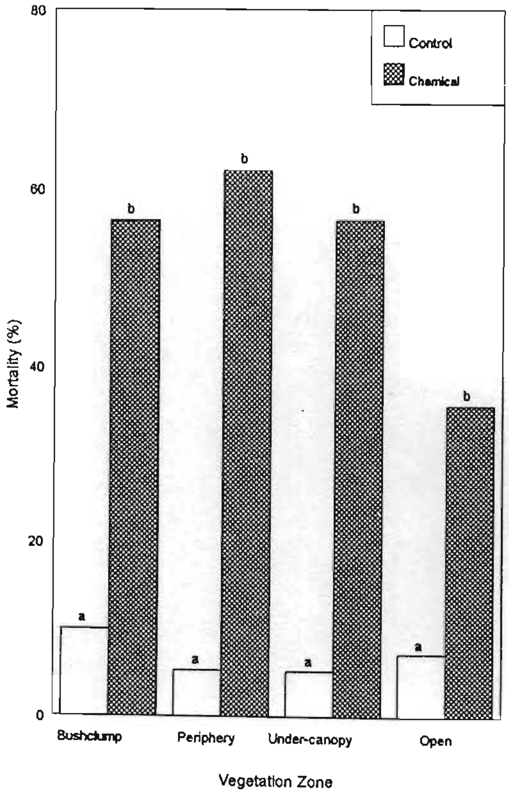

Figure 5.5 Mortality of small individuals in the chemical and control treatments in the four vegetation zones at the end of the 1992/93 season. (Letters which differ within a vegetation zone indicate significance at the 5% level.)

The arboricide did not, however, affect the recruitment of small individuals. The rate of recruitment was not significantly different between the chemical and control treatments, but differed between vegetation zones (Figure 5.6). The number of seedlings at the end of the first season, taking into account both mortality and recruitment, resulted in a reduction (P<0.0001) in the density of small individuals in the chemically treated plots (Figure 5.7).

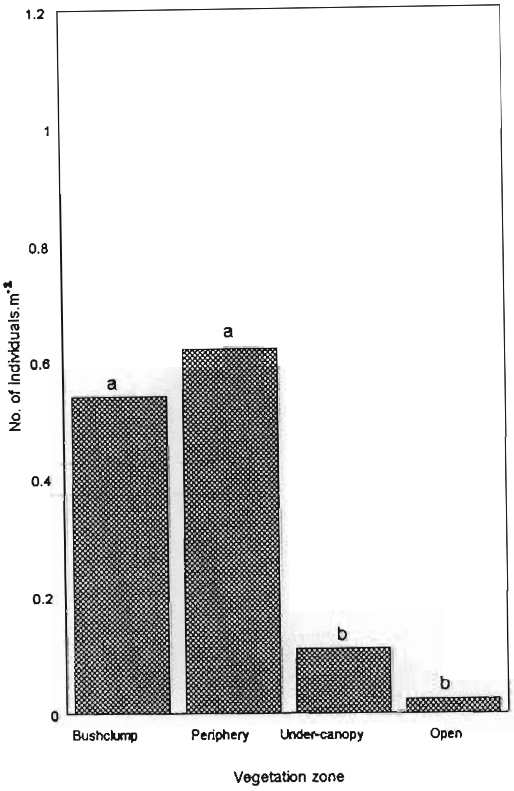

Figure 5.6 Density of recruiting small individuals in the four vegetation zones during the 1992/93 season. (Letters which differ indicate significance at the 5% level.)

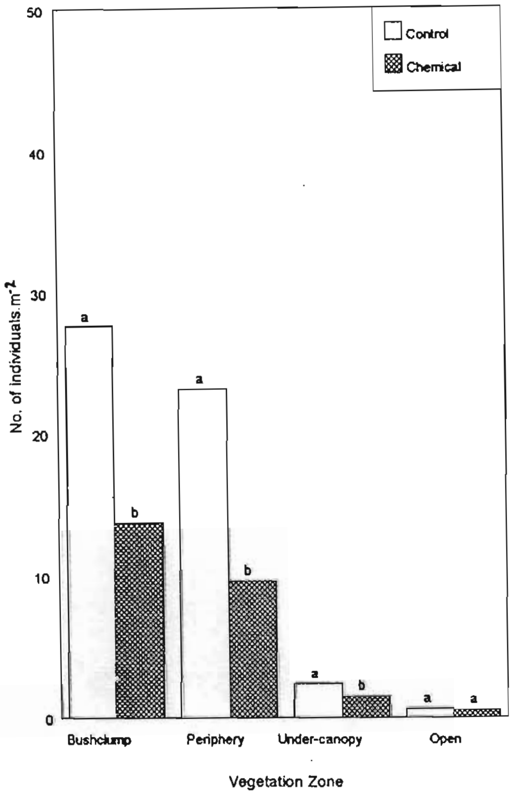

Figure 5.7 Density of small individuals in the control and chemical treatments in the four vegetation zones at the end of the 1992/93 season. (Letters which differ within a vegetation zone indicate significance at the 5% level.)

Percent mortality in the second season was again significantly greater in the chemically treated plots than in the control plots, but was less than in the first season (Figure 5.8). The second season was characterized by higher than average rainfall which provided favourable conditions for germination and establishment. Recruitment was therefore greater during the second season than during the first, but differed markedly between vegetation zones (Figure 5.9). Again, no treatment effect was apparent.

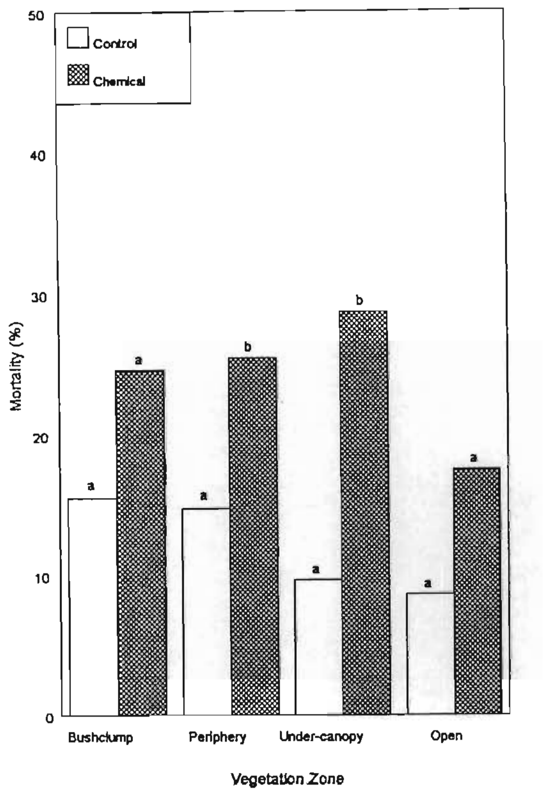

Figure 5.8 Mortality of small individuals in the chemical and control treatments in the four vegetation zones at the end of the 1993/94 season. (Letters which differ within a vegetation zone indicate significance at the 5% level.)

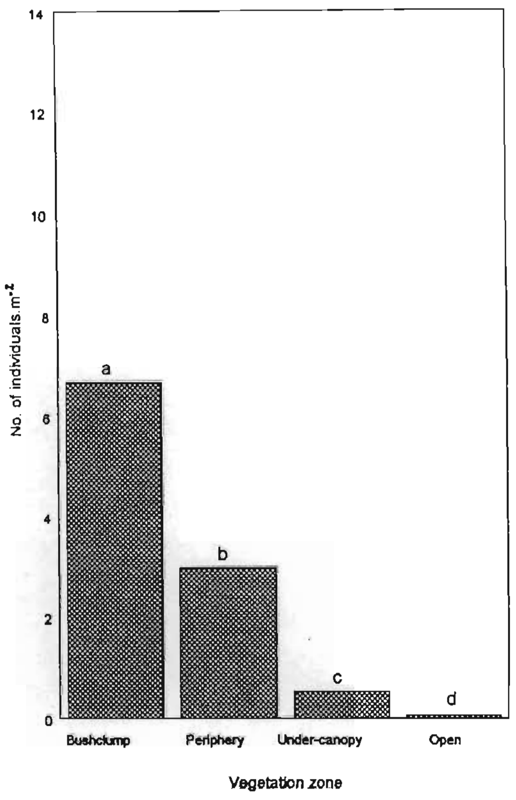

Figure 5.9 Density of recruiting small individuals in the four vegetation zones during the 1993/94 season. (Letters which differ indicate significance at the 5% level.)

Coppicing of small individuals was a characteristic of the bushclump and periphery zones in the chemically treated plots during the second season (Figure 5.10). At the end of the second season treatment differences were still obvious (P<0.0688), with the bushclump and periphery zones most affected (Figure 5.11). However these differences were smaller than at the end of the first season.

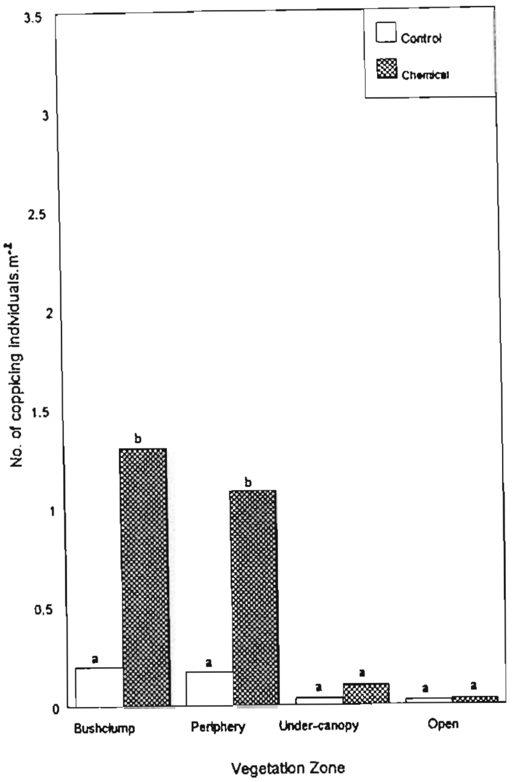

Figure 5.10 Density of coppicing small individuals in the control and chemical treatments in the four vegetation zones at the end of the 1993/94 season. (Letters which differ within a vegetation zone indicate significance at the 5% level.)

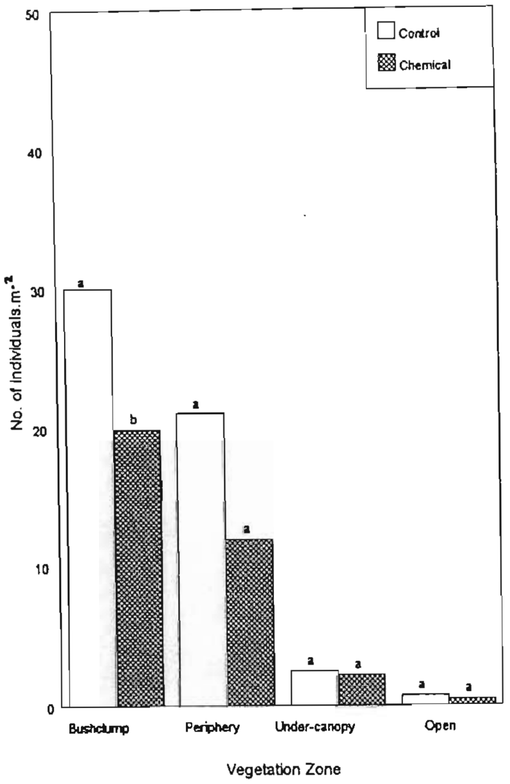

Figure 5.11 Density of small individuals in the control and chemical treatments in the four vegetation zones at the end of the 1993/94 season. (Letters which differ within a vegetation zone indicate significance at the 5% level.)

5.3.3.3 Mechanical clearing

Bulldozing obviously resulted in a radical reduction in both the structure and height of the woody component. Although bulldozing was non-selective, a few individuals were either missed or incompletely removed. It seemed that some individuals may have survived bulldozing owing to flexible stems. *Coddia rudis* seemed the least affected by the clearing process, with *Lippia javanica* also quite numerous in the grassland zone (Table 5.8). Species such as *Scutia myrtina* and *Maytenus heterophylla* also featured among the post-bulldozing survivors, but their occurrence was most likely a function of their original abundance in the vegetation prior to clearing.

By the end of the first growing season, it was clear that extensive woody recruitment had occurred since the post-bulldozing assessment (Table 5.8). It was observed that post-bulldozing recruitment was in the form of coppice for all species, except in the case of *Acacia karroo* where seedling establishment also occurred. Woody recruitment was most common in the bushclump and peripheral zones, except for *L. javanica* which was abundant in the grassland zone.

Acacia karroo recruitment was mainly attributed to seed germination and establishment. Four incorrect classifications were made in the form of recruitment exercise. Thus, an acceptable precision of 96% in recruitment classification was obtained. Recruiting *A. karroo* individuals sourced from the seedbank was 83.2% for the bushclump zone, 68.9% for the peripheral zone, and 67% for the grassland zone. The reduced *A. karroo* density in the second season can probably be attributed to seedling mortality in response to competition from grass.

The above average rainfall in the second growing season was accompanied by a notable increase in dicotyledonous species such as *Berkheya bipinnatifida* and *Solanum incanum*. A further increase in coppicing woody individuals in the second season generally did not occur, the exception being *Scutia myrtina*, *Trimeria grandifolia* and *Trimeria trinervis*.

Although a general increase in the density of woody individuals from the first to the second season did not occur, an increase in their number of stems was apparent (Table 5.9). Species such as *Canthium ciliatum*, *Canthium mundianum*, *Coddia rudis*, *Trimeria grandifolia*, *Trimeria trinervis* and especially *Scutia myrtina* showed a marked increase. The decline in stem density of *Cussonia spicata* and *Hippobromus paucifloris* was attributed to browsing by indigenous herbivores.

Table 5.8 Mean density of woody individuals on a species-basis for large individuals pre-bulldozing (Pre-B) and all woody individuals post-bulldozing (Po-B), at the end of the 1992/93 and 1993/94 seasons, in the previous 3 vegetation zones of the mechanical treatment in the bush control experiment.

	Density of woody individuals (mean no.ha^{-1})											
	Bushclump				**Periphery**				**Grassland**			
Species	**Pre-B**	**Pos-B**	**92/93**	**93/94**	**Pre-B**	**Pos-B**	**92/93**	**93/94**	**Pre-B**	**Pos-B**	**92/93**	**93/94**
Acacia karroo	17	107	6370	5473	11	269	9737	8180	33	368	3940	3453
Berkheya bipinnatifida	0	0	527	1531	0	0	1051	3288	0	11	421	1491
Canthium ciliatum	33	0	101	371	11	0	67	324	0	0	48	115
Canthium mundianum	389	86	1879	1622	106	226	2396	2616	50	122	736	835
Coddia rudis	994	2497	5041	4885	972	4877	8763	9145	406	2768	5298	5532
Cussonia spicata	89	0	448	441	0	0	74	220	0	0	9	25
Diospyros lyciodes	39	0	176	175	17	0	67	67	0	0	34	34
Diospyros simii	139	77	1491	1402	67	291	1266	1157	6	18	400	397
Dovyalis caffra	0	20	442	575	0	0	94	206	6	19	231	281
Grewia occidentalis	144	207	1762	1675	39	304	2687	3003	17	265	957	977
Hippobromus paucifloris	138	92	4485	4730	61	19	2150	2520	6	18	553	617
Jasminum angulare	444	130	4238	3760	22	325	3010	2360	0	18	811	626
Lippia javanica	0	69	412	375	22	478	1541	1607	311	1366	3260	3397
Maytenus heterophylla	522	806	2178	1954	261	1333	2704	2626	250	530	1196	1214
Rhus refracta	0	0	199	193	6	0	306	306	0	18	267	340
Rhus undulata	78	31	270	283	89	146	826	759	72	81	357	363
Scutia myrtina	1006	487	930	2499	300	453	372	1703	311	138	255	694
Solanum incanum	0	0	1321	2267	17	0	1199	2188	83	9	351	1283
Trimeria grandifolia	78	27	831	1375	11	56	599	810	0	0	113	219
Trimeria trinervis	211	33	5072	6205	61	91	2860	2855	28	41	1045	1143
Other	167	49	1180	1295	83	152	987	1142	61	166	750	791
Total	4488	4718	39353	43086	2156	9020	42756	39720	1640	5974	21032	23827

Recruitment following mechanical clearing was phenomenal, as illustrated by the density of woody stems in the two seasons following the post-bulldozing assessment (Table 5.9). When compared with a mean of 24853 woody stems per hectare prior to bulldozing, stem-density after two seasons had increased almost four-fold.

Table 5.9 Mean density of woody stems on a species-basis for large individuals pre-bulldozing (Pre-B) and all woody individuals post-bulldozing (Po-B), at the end of 1992/93 and 1993/94 seasons, in the mechanical treatment of the bush control experiment.

	Mean stem density (no.ha^{-1})			
Woody species	**Pre-B**	**Pos-B**	**1992/93**	**1993/94**
Acacia karroo	72	278	8322	7422
Canthium ciliatum	139	0	383	2472
Canthium mundianum	983	139	3956	4767
Coddia rudis	8333	2956	17733	18806
Cussonia spicata	89	0	806	306
Diospyros simii	617	61	2644	2994
Dovyalis caffra	22	17	928	1161
Grewia occidentalis	389	250	5483	5678
Hippobromus paucifloris	339	44	8556	8083
Maytenus heterophylla	4106	678	4222	4306
Rhus refracta	6	11	1094	1278
Rhus undulata	489	72	1533	1589
Scutia myrtina	5472	272	1367	4906
Trimeria grandifolia	111	17	1372	2044
Trimeria trinervis	578	56	9917	12939
Others	2839	89	3006	3461
Total	24583	5023	77878	87251

The incremental height growth of some of the common woody species over the first two seasons illustrates the rapidity and zeal of woody coppice (Figure 5.12). Growth was most rapid in *Scutia myrtina*, *Trimeria trinervis*, *Grewia occidentalis* and *Canthium mundianum* as illustrated by the sharp increase in frequency from the lowest height class in the first season, to a dominance in the higher height classes. Other species such as *Acacia karroo*, *Diospyros simii*, *Hippobromus paucifloris* and *Maytenus* *heterophylla* exhibited a more even distribution within the height classes at the end of the second season.

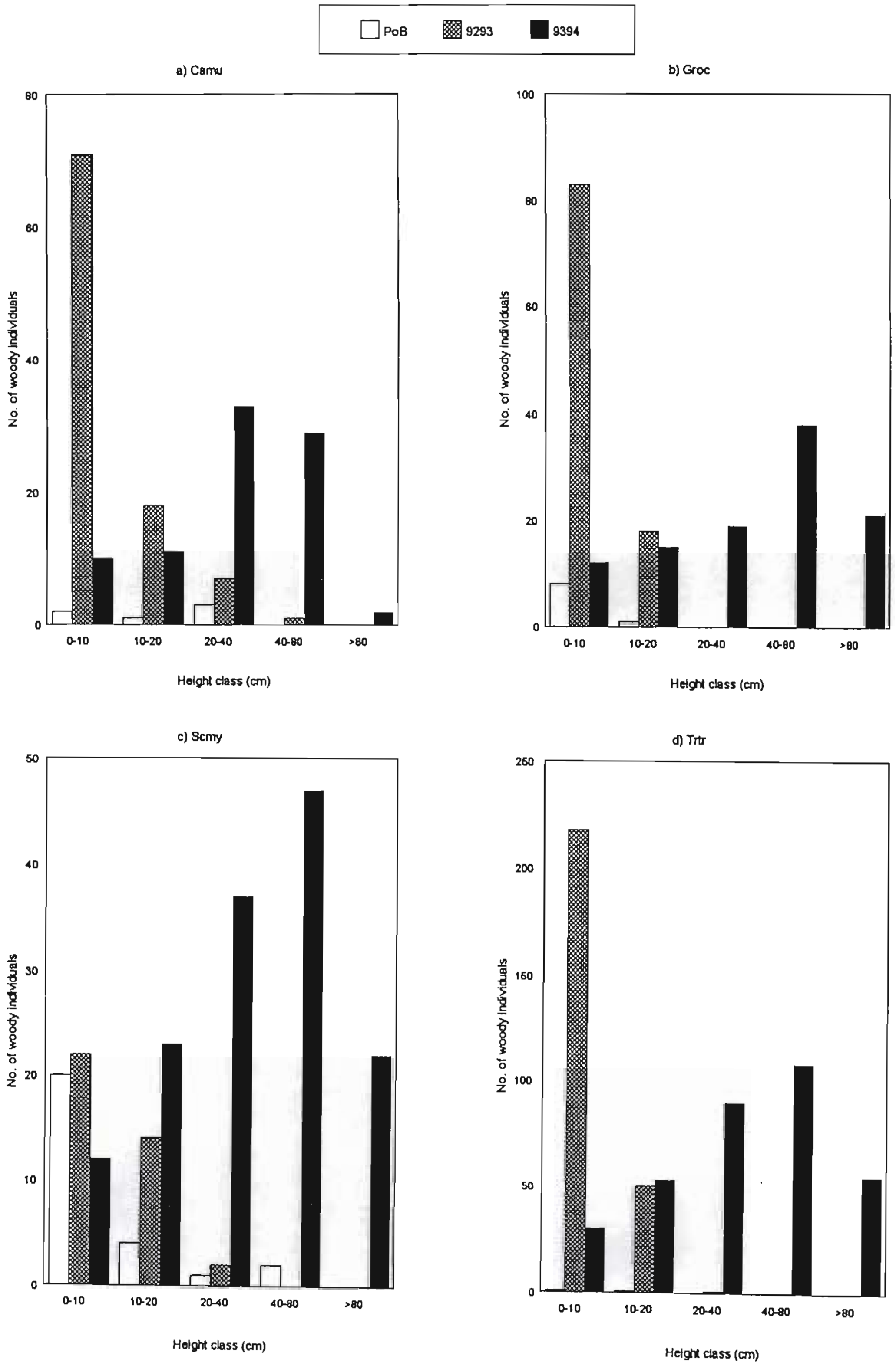

Figure 5.12 Frequency of a) *Canthium mundianum* (Camu), b) *Grewia occidentalis* (Groc), c) *Scutia myrtina* (Scmy), and d) *Trimeria trinervis* (Trtr), in the five height classes for the three measuring periods (PoB=post-bulldozing, 9293=1992/93 season, 9394=1993/94 season), in the mechanical treatment of the bush control experiment.

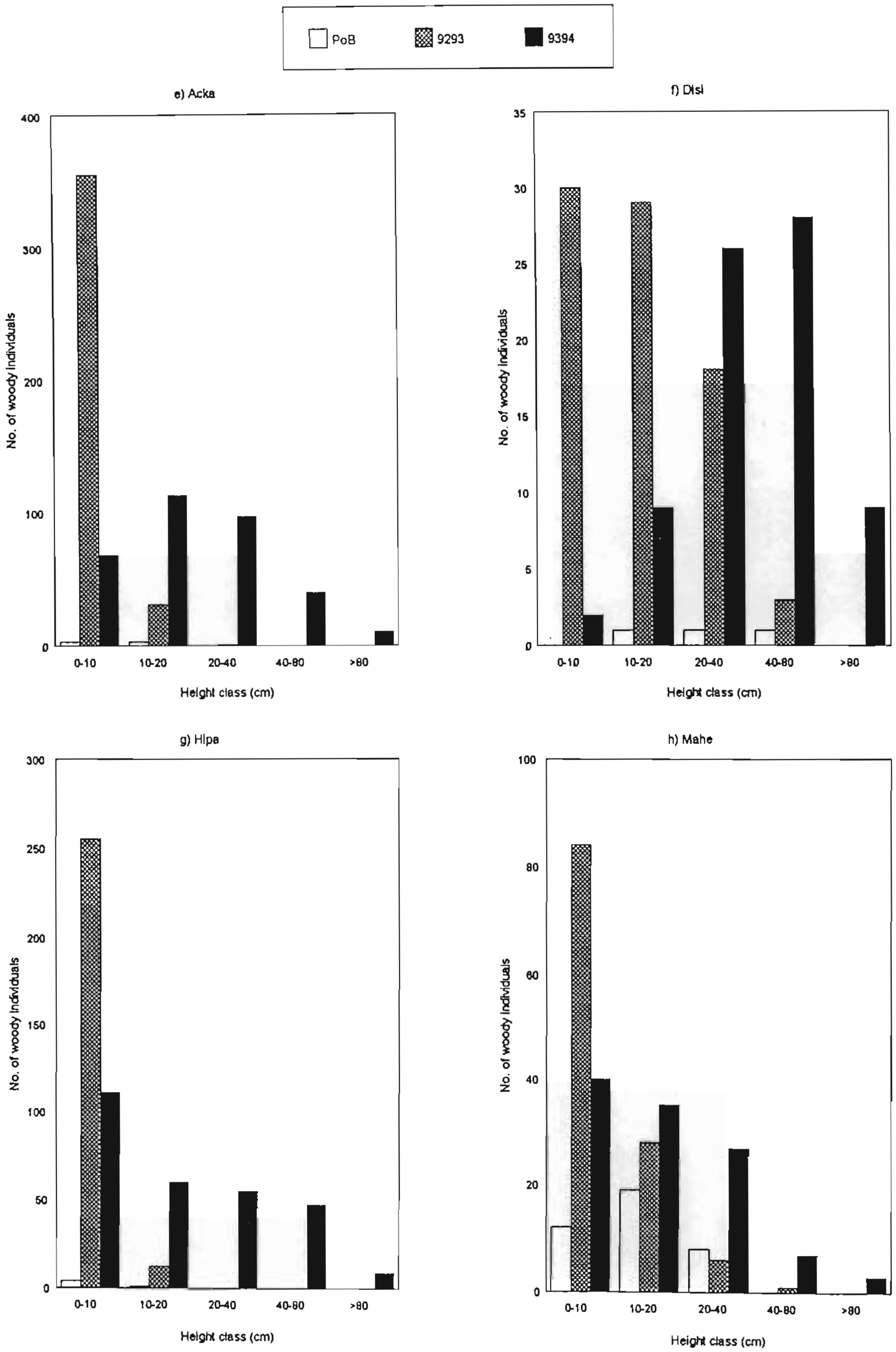

Figure 5.12 (continued) Frequency of e) *Acacia karroo* (Acka), f) *Diospyros simii* (Disi), g) *Hippobromus pauciflorus* (Hipa), and h) *Maytenus heterophylla* (Mahe), in the five height classes for the three measuring periods (PoB=post-bulldozing, 9293=1992/93 season, 9394=1993/94 season), in the mechanical treatment of the bush control experiment.

5.3.3.4 Mechanical vs oversown

Oversowing with *Chloris gayana* improved grass production and played an important role in woody-tree and dicotyledonous plant dynamics. The oversown plots experienced less *Berkheya bipinnatifida* and *Solanum incanum* recruitment than the mechanical plots during both the first ($P<0.0318$) and second ($P<0.0107$) growing seasons.

Woody-tree dynamics were not influenced to the extent that the undesirable dictoyledonous plants had been. Woody mortality in the oversown treatment was greater in the first ($P<0.0718$) and second ($P<0.0415$) growing seasons. This, however, did not impact the woody-tree population at the end of either seasons. Further investigation revealed that *A. karroo* densities were reduced ($P<0.0258$) in the oversown plots in comparison with the non-oversown mechanical plots. No further species differences were detectable.

5.4 DISCUSSION

5.4.1 Mechanical Treatment

The significant increase in herbage production following mechanical removal of the woody vegetation clearly demonstrated the dominance of the woody layer in this savanna system. The significant increase in herbaceous production in the grassland zone, with its relatively unaltered herbaceous composition, demonstrated the competitive release of moisture and nutrients to the herbaceous layer following mechanical clearing. This, however, was probably confounded by the release of nutrients from decomposing woody roots.

The grazing capacity of the mechanical plots showed a marked improvement within the first two seasons, mainly due to the colonization of *Panicum maximum* (a productive and preferred grazing species) into the ex-bushclump zones. The relatively undamaged herbaceous layer of the grassland zone increased its productivity and further contributed to this improvement. Colonization of the ex-bushclump zone by indigenous herbaceous species was relatively slow in the first season, when compared to the oversown treatment. Oversowing with *Chloris gayana* was, therefore, very successful in that it provided an excellent cover and was very productive. Rainfall had a large influence on the potential productivity of the herbaceous layer as demonstrated by the two dissimilar seasons. The relatively high rainfall recorded in the second season accompanied by the increased soil fertility following mechanical clearing provided the resources for phenomenal grass production, as illustrated by the oversown plots.

Investigation of the soil nutrient status in the mechanical and oversown plots, at the end of the second season, revealed a marked depletion of total N. This was probably due to the depletion of the available nutrient reserve by the high level of herbaceous production or leaching due to the high rainfall recorded during the second season. Whether this decline is temporary remains unknown. A decline may indicate the start of the system run-down, thus questioning the sustainability of mechanical bush control. On the other hand the soil nutrient status may well be replenished by the mineralization of organic matter during the following season. However, both of these theories are speculative and can only be resolved with further monitoring.

The marked increase in the soil nutrient status of the mechanical treatment, at the end of the first season, was associated with a significant increase in grass quality. However, in the 1993/1994 season, soil nutrient status of the mechanically cleared plots was significantly reduced. A marked decline in grass quality was also observed. This could be indicative of a decline in soil nutrient status, or could equally be attributed to the high level of grass production. Grass in the mechanically cleared plots at the end of the second season was very tall (*P. maximum* was approximately 1.5 m tall and *C. gayana* approximately 2 m tall), stemmy and mature, and probably had a high C:N ratio. This would explain the lowered grass TKN concentration. When one considers that in the 1992/93 season total grass nitrogen content in the standing crop of the mechanical treatment was 5.1 $kg.ha^{-1}$, and in the second season this was increased to 57.1 $kg.ha^{-1}$, then it is obvious that the herbaceous quality did not deteriorate due to a reduction in soil nitrogen, but rather due to a diluting effect caused by the increase in grass structure and stemminess, especially with the absence of grazing. Thus, the decline in grass quality was probably a function of plant structure rather than soil nutrient status, and the decline in soil nutrients was attributed to the high level of grass production sustained in the second season.

Bulldozing obviously resulted in the complete removal of the woody component, except for a few smaller individuals which "escaped". Woody re-encroachment during the first season was remarkable. Coppicing was the principal means of re-establishment, with all species exhibiting an ability to coppice. The belated ability of *Scutia myrtina* to coppice and the further increase in stem density displayed by *Canthium ciliatum*, *Trimeria trinervis* and *Hippobromus paucifloris* were a feature of the second season.

The highlight however, was the germination and establishment of *Acacia karroo* seeds following bulldozing, especially since *A. karroo* was considered a minor component in this mesic savanna. Acocks (1953) considered *A. karroo* a pioneer species in this veld type and a precursor to the broadleaved species characteristic of this savanna. Its prolific germination following disturbance reinforces the premise that *A. karroo* is capable of producing a dormant seedbank. This is illustrated by the dominance of *A. karroo* on old cultivated lands.

With an almost four-fold increase in stem density and cognizance taken of the height increment of coppice at the end of each season, it is obvious that woody re-encroachment within the next couple of seasons will result in a situation which probably will be worse than that before clearing. This would negate the financial feasibility of the bush clearing operation as the woody layer would again compete with the herbaceous layer for light, nutrients and water.

Oversowing with *C. gayana* also had the added benefit of significantly reducing the abundance of undesirable woody dicotyledonous plants. Woody re-establishment in the oversown treatment was not different from the mechanical treatment. *Acacia karroo* mortality was, however, greater in the oversown plots. The susceptibility of the seedlings, when compared with coppice, to excessive and prolonged shading and competition provided by the high levels of grass production can possibly be attributed to the absence of a large root reserve, which probably exists with coppice. Whether these high levels of grass production can be sustained is questionable as the persistence of *C. gayana* pasture is perceived to be relatively short-lived. However, this sward is only grazed on an annual basis and has set seed each year which may increase its longevity. If the grass cover in the oversown treatment remains, greater coppice mortality may possibly occur in subsequent seasons.

5.4.2 Chemical Treatment

Chemical control using a plant-applied arboricide resulted in rapid mortality of the woody vegetation. Leaf-drop in the large individual class was observed within a couple of months and mortality at the end of the first season was high. The effect of the arboricide persisted into the second season with further mortality. As anticipated individuals with stem circumferences of less than 25 cm were most vulnerable. Individuals in the bushclump zone were least affected owing to the difficulty in accessing and spraying stems. More importantly individuals in the grassland and peripheral zones (vegetation zones where woody encroachment is active) were effectively controlled. The susceptibility of *Scutia myrtina* and *Maytenus heterophylla*, the two species contributing most to woody biomass in this savanna, to the arboricide bodes well for the efficacy of initial chemical bush control. This however, can only be determined with further monitoring.

The susceptibility of the small individuals to the arboricide initially decreased its population size. Coppicing of individuals in the second season, previously classified as 'dead' at the end of the first season, partly ameliorated this reduction. The effect of the arboricide on small individuals was, therefore, seen as temporary.

The significant increase in grass production in the bushclump and peripheral zones in the chemical plots was attributed to the increase in the irradiance regime, due to leaf drop and woody mortality, the subsequent release of nutrients from these decomposing sources, and the higher rainfall recorded in the second season. Increased grass production was mainly attributed to the increased production of *P. maximum*. The significant increase in the frequency of *Senecio pterophorus* and increase in the contribution to biomass of forbs in the second season was not surprising, since this species was found to colonize the low shade and nutrient rich treatments in the factorial experiment (Chapter 4). The significant increase in grass production in the grassland zone was attributed to a change in the woody-grass balance, with an increase in the availability of resources to the herbaceous layer due to woody mortality. Herbaceous composition and quality were no different from the control treatment. The lowered soil nutrient status in the chemical treatment may also be ascribed to the higher level of production experienced in the second season, which may have had a reducing effect on soil nutrient levels.

CHAPTER 6

CONCLUSIONS

The bushclump physiognomy provided an interesting variation to woody/grass interaction studies conducted predominantly in single-tree savannas. The bushclump environment was characterized by a major reduction in irradiance. This was attributed to the dense evergreen foliage which characterizes most bushclump species. Associated with this low-irradiance habitat was a sparse herbaceous layer which consisted of mainly shade tolerant species such as *Panicum maximum* and *Helictotrichon capense*. Tree clumps, in the humid savannas of West Africa, were also characterized by a sparse herbaceous cover (Mordelet & Menaut 1995). This was mainly attributed to the level of shading which had been shown to limit grass photosynthesis (Mordelet 1993). Single-tree savannas, on the other-hand, are characterized by a relatively continuous herbaceous layer. Thus, the significantly lower irradiance regime and sparse herbaceous layer which distinguishes the bushclump environment highlighted a fundamental difference between single-tree savannas and this bushclump savanna.

Bushclumps, not unlike single-trees, were shown to have a moderating effect on their local environment with lower maximum temperatures, higher minimum temperatures and greater humidity levels than that experienced in the open grassland. This has the potential to lower rates of evapotranspiration and increase levels of moisture under bushclumps. The bushclump environment was also characterized by an abundance of woody seedlings. Investigation of the seedbank confirmed the importance of bushclumps as woody seedling "nurseries" and sites for sustained woody encroachment. As in most savanna studies, soils beneath woody vegetation were more fertile than the soils of the open grassland. On the sandier soil the difference between the bushclump and grassland soil was large.

Bushclumps, on sandier soils, therefore have the ability to play an important role in nutrient recycling since these soils are more prone to leaching. Bush control on sandier soils should, therefore, receive serious review. A similar recommendation was made by Barnes (1979). It was suggested that where a choice existed, trees be cleared on high quality soil and be left on soils of poorer quality. An increase in the mineral concentration of grasses in the bushclump environment, when compared with the open grassland, was also a characteristic. A similar trend was reported by Belsky (1992), under single-trees. However, unlike single-tree savannas where an increase in herbage quality under trees translates to increased grazing capacity, an increase in herbage quality under bushclumps has little effect since herbaceous production in the bushclump environment is almost negligible. Bushclumps not only influenced their under-canopy environment but also affected the adjacent grassland, as depicted by an aspect effect which had a positive influence on herbaceous production in the immediate south-facing grassland. This mirrored the results of Stuart-Hill *et al.* (1987). The investigation into the lateral reach of woody roots revealed that *Scutia myrtina*, the dominant woody species, could possibly be competing with the herbaceous layer as far as 25 metres from bushclumps.

The factorial experiment (Chapter 4) was successful in addressing the complex interaction of irradiance, nutrients and moisture. Moisture in this experiment was not an important factor. The importance accorded to moisture as a crucial factor involved in woody/grass interactions is not discounted. However, rainfall in this mesic bushclump savanna is relatively high compared to that of other savannas, and thus where rainfall is limited, moisture would form an integral component of woody/grass interactions. This was demonstrated by Belsky *et al.* (1993) in a low and high rainfall savanna.

Fertilization, in this experiment, had a significant and positive effect on herbaceous production. However, a change in composition was also apparent. Climax species such as *Themeda triandra* and *Heteropogon contortus*, which had dominated the sward, were replaced by species such as *Eragrostis plana* and *Sporobolus africanus*. The irradiance treatment also had a significant effect on the herbaceous layer. Although shade had no significant effect on herbaceous production during the experimental period, it seemed apparent that with time herbaceous production, composition and cover would deteriorate. This was seen in the response of *T. triandra* to 80% shade. Etiolated growth, aerial tillering, and an increase in the number of leaves suggested that *T. triandra* was not functioning normally under high shade. Further evidence of a deteriorating sward was the significant decrease in root mass which possibly indicated that below-ground resources were being used to support above-ground production. The highlight, however, was the interaction of irradiance and nutrients which had a detrimental effect on herbaceous production. The combination of 80% shade and high nutrients resulted in a significant decrease in herbaceous production. It was hypothesized that it was high shade rather than high nutrients which was responsible for the reduction in herbaceous production, and that the high level of nutrients probably accelerated the time frame in which it occurred.

The combination of a high shade and a nutrient rich environment, therefore, elucidates the sparse herbaceous layer characteristic of the bushclump interior. The experiment also demonstrated that lower levels of shade had no detrimental effect on the herbaceous layer, and that with the addition of nutrients increased herbaceous production occurred. This explains the reason for greater grass production reported under individual savanna trees. However, the contrasting results of several savanna studies can possibly be attributed to differing herbaceous species composition, tree canopy densities and widely different climatic conditions.

Both the irradiance and nutrient treatments significantly increased the grass mineral content of the herbaceous layer. This explains the increase in nutrient concentration of the grass layer under bushclumps (Chapter 3) and corroborates the results of other studies (Belsky 1992; Grossman *et al.* 1980). However, this increase in mineral concentration under shade and with higher nutrient levels was negated by a decrease in digestibility due to an increase in fibre and lignin concentrations. This was also reported by Belsky (1992).

The bush control experiment revealed that the short-term responses to both mechanical and chemical control are attractive with respect to herbaceous production. Mechanical clearing of the woody vegetation in the bush control experiment resulted in a significant increase in grass production in all three vegetation zones. A further benefit was the colonization of *Panicum maximum*, a productive and preferred grazing species, in the ex-bushclump zones. Barnes (1979) reported that the colonization of generally undesirable grasses often occurs after mechanical clearing. The increase in grazing capacity following mechanical clearing was also due to an increase in the productivity of the generally unchanged herbaceous layer of the grassland zone. This was probably due to the removal of competition from the previously dominating woody vegetation and the mineralization of decomposing tree roots. Oversowing with *Chloris gayana* was very successful. Its rate of establishment, on the disturbed areas of the mechanically cleared plots, was quicker than that of the indigenous grasses in the non-oversown plots. It was also very productive. Rainfall played a large role in affecting herbaceous productivity in this experiment, as demonstrated by the two contrasting seasons. The importance of rainfall in affecting herbaceous production in seasons subsequent to bush clearing was reported by Barnes (1979) and

Dye & Spear (1982). At the end of the second season a decrease in soil fertility occurred. This decline was attributed to the high level of grass production sustained during the second season. Grass quality mirrored the trend in soil fertility. The decline in quality at the end of the second season was attributed to the tall and stemmy nature of grasses in the mechanical treatments. This would have had a diluting effect on the mineral concentration of grass, which would explain its decrease in nutrient quality.

Woody re-establishment was pronounced at the end of the first season. Coppicing was the major form of re-establishment. Species differences, with respect to their ability to coppice, were unapparent. The highlight of the first season was the germination and establishment of *Acacia karroo* seeds. This lends weight to the premise that this species is a pioneer species and the precursor of the bushclump savanna (Acocks 1953). The potential role of seedbanks as sources for re-establishment following major disturbances such as mechanical clearing was also confirmed. The second season was characterized by a significant increase in coppice height growth. Oversowing with *C. gayana* not only produced significantly greater grass yields than non-oversown plots, but also caused higher *A. karroo* seedling mortality. Coppice was, however, unaffected.

Chemical poisoning of the woody vegetation in the bush control experiment was also successful. Leaf-drop occurred within the first season which demonstrated the susceptibility of the woody layer to the arboricide. Most of the individuals which had displayed signs of susceptibility in the first season succumbed at the end of the second season. Susceptibility was, as expected, greatest in the small circumference size class and lowest in the large circumference size class. Mortality was also greatest in the grassland zone and lowest in the bushclump zone. This was a function of accessibility and stem density, which resulted in the proportion of woody stems missed in the bushclump zone being much greater than that missed in the more open grassland zone. Small recruiting individuals, although not targeted, were affected by the over-spray of the arboricide. Significant mortality occurred at the end of the first season. However, in the second season these individuals coppiced with the result that the population of small individuals in the chemical treatment was not significantly lower than that of the control.

Grass production in the bushclump and peripheral zones of the chemical treatment was significantly greater than that of the control. This was attributed to leaf-drop and the subsequent increase in the irradiance regime. *Panicum maximum* capitalized on the increased irradiance regime. In the second season grass production in the grassland zone of the chemical plots was significantly greater than that in the control plots. This, as in the mechanical treatment, demonstrated the herbaceous layers release from the previously competitively dominant woody vegetation.

LITERATURE CITED

Acocks J.P.H. 1953. The Veld Types of South Africa. Memoirs of the Botanical Society of South Africa. No. 28.

Amory A.M. & Cresswell C.F. 1981. A stimulation of an alternative photorespiratory CO_2 pathway by nitrogen in *Themeda triandra* - a possible explanation for its sensitivity to nitrogen. Proceedings of the Grassland Society of southern Africa 16: 145-149.

Amundson R.G., Ali A.R. & Belsky A.J. 1995. Stomatal responsiveness to changing light intensity increases rain-use efficiency of below-crown vegetation in tropical savannas. Journal of Arid Environments 29: 139-153.

Archer S., Scifres C.J., Bassham C.R., & Maggio R. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological Monographs 58: 111-127.

Archer S. 1989. Have Southern Texas savannas been converted to woodlands in recent history? The American Naturalist 134: 545-561.

Archer S. 1990. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A. Journal of Biogeography 17: 453-462.

Aucamp A.J. 1976. The role of the browser in the bushveld of the eastern Cape. Proceedings of the Grassland Society of Southern Africa 11: 135-138.

Aucamp A.J., Danckwerts J.E., Teague W.R. & Venter J.J. 1983. The role of *Acacia karroo* in the False Thornveld of the eastern Cape. Proceedings of the Grassland Society of Southern Africa 18: 151-154.

Barnes D.L. 1979. Cattle ranching in the semi-arid savannas of east and southern Africa. In: Management of Semi-Arid Ecosystems, editor B.H. Walker, Elsevier, Amsterdam.

Barnes G.R., Bransby D.I. & Tainton N.M. 1987. Fertilization of southern tall grassveld of Natal: effects on botanical composition and utilization under grazing. Journal of the Grassland Society of southern Africa 4: 63-67.

Bassett D.M., Stockton J.R., & Dickens W.L. 1970. Root growth as measured by P^{32} uptake. Agronomy Journal 62: 200-203.

Bate G.C. & Gunton C. 1982. Nitrogen in the *Burkea* savanna. In: Ecology of Tropical Savannas. Ecological Studies 42. Eds: B.J. Huntley & B.H. Walker, Springer, Berlin, pp 498-513.

Belsky A.J., Amundson R.G., Duxbury J.M., Riham S.J., Ali A.R. & Mwonga S.M. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology 26: 1005-1024.

Belsky A.J. 1992. Effects of trees on nutritional quality of understorey gramineous forage in tropical savannas. Tropical Grasslands 26: 12-20.

Belsky A.J., Mwonga S.M., Amundson R.G., Duxbury J.M. & Ali A.R. 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. Journal of Applied Ecology 30: 145-155.

Belsky A.J. 1994. Influences of trees on savanna productivity: Tests of shade, nutrients, and tree-grass competition. Ecology 75: 922-932.

Bernhard-Reversat F. 1982. Biogeochemical cycle of nitrogen in a semi-arid savanna. Oikos 38: 321-332.

Bews J.W. 1917. Plant succession in the thorn-veld. South African Journal of Science 14: 153-173.

Bigwood D.W. & Inouye D.W. 1988. Spatial pattern analysis of seedbanks: an improved method and optimized sampling. Ecology 69: 497-507.

Blackman G.E. & Templeman W.G. 1938. The interaction of light intensity and nitrogen supply on the growth and metabolism of grasses and clover (*Trifolium repens*). Annals of the Botanical N. S. 7: 765-791.

Bosch O.J.H. & van Wyk J.J.P. 1970. The influence of bushveld trees on the productivity of *Panicum maximum*: A preliminary report. Proceedings of the Grassland Society of Southern Africa 5: 69-74.

Cannell M.G.R & Grace J. 1993. Competition for light: detection, measurement, and quantification. Canadian Journal of Forestry Research 23: 1969-1979.

Coffin D.P. & Laurenroth W.K. 1991. Effects of competition on spatial distribution of roots of blue grama. Journal of Range Management 44: 68-71.

Comins D.M. 1962. The vegetation of the districts of East London and King Williams Town, Cape Province. Memoirs of the Botanical Survey of South Africa no. 33.

Coughenour M.B., McNaughton S.J. & Wallace L.L. 1985. Responses of an African tall-grass (*Hyparrhenia filipendula* stapf.) to defoliation and limitations of water and nitrogen. Oecologia 68: 80-86.

✓ * Du Toit P.F. 1967. Bush encroachment with specific reference to *Acacia karroo* encroachment. Proceedings of the Grassland Society of Southern Africa 2: 119-167.

* Dye P.J. & Spear P.T. 1982. The effects of bush clearing and rainfall variability on grass yield and composition in south-west Zimbabwe. Zimbabwe Journal of Agricultural Research 20: 103-118.

Dye P.J. & Poulter A.G. 1991. An exploratory investigation into the use of rubidium as a tracer for determining the lateral spread of tree roots. Unpublished report, Land-use Hydrology Programme, Division of Forest Science and Technology, CSIR.

Dyer R.A. 1937. The vegetation of the divisions of Albany and Bathurst. Memoirs of the Botanical Survey of South Africa no. 17.

Edwards P.J. & Nel S.P. 1973. Short-term effects of fertilizer and stocking rates on the Bankenveld. I. Vegetational changes. Proceedings of the Grassland Society of southern Africa 8: 83-88.

Ellis F.B. & Barnes B.T. 1973. Estimation of the distribution of living roots of plants under field conditions. Plant and Soil 39: 81-91.

Engels E.A.N. & Van Der Merwe F.J. 1967. Application of an in vitro technique to South African forages with special reference to the effect of certain factors on the results. South African Journal of Agricultural Science 10: 983-995.

Engels E.A.N., De Waal H.O., Biel L.C. & Malan A. 1981. Practical implications of the effect of drying and treatment on nitrogen content and *in vitro* digestibility of samples collected by oesophageally fistulated animals. South African Journal of Animal Science 11: 247-254.

Eriksen F.I. & Whitney A.S. 1981. Effects of light intensity on growth of some tropical forage species. I. Interaction of light intensity and nitrogen fertilization on six forage grasses. Agronomy Journal 73: 427-433.

Fox R.L. & Lipps R.C. 1964. A comparison of stable strontium and P*32* as tracers for estimating alfalfa root activity. Plant and Soil 20: 337-350.

FSSA 1974. Manual of soil analysis methods. Fertilizer Society of South Africa publication no. 37.

Garcia-Moya E. & McKell C.M. 1970. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. Ecology 51: 81-88.

Gibbs-Russell G.E., Reid C., Van Rooy J. & Smook L. 1985. List of species of southern African plants. Memoirs of the Botanical Survey of South Africa, No. 51.

Gibbs-Russell G.E., Welman W.G., Retief E., Immelman K.L., Germishuizen G., Pienaar B.J., Van Wyk M. & Nicholas A. 1987. List of species of southern African plants. Memoirs of the Botanical Survey of South Africa, No. 56.

Glen-Leary J. 1992. Beating bush encroachment - with a bulldozer. Farmers Weekly: March 20, pages 29-30.

Goering H.K. & Van Soest P.J. 1970. Forage fibre analysis. U.S.D.A. Agricultural Handbook, No. 379.

Groeneveld H.T. 1970. Method for testing constrasts among polynomials. Agrochemophysica 2: 47-52.

Gross K.L. 1990. A comparison of methods for estimating seed numbers in the soil. Journal of Ecology 78: 1079-1093.

Grossman D. & Cresswell C.F. 1974. The influence of nitrate and ammonia nitrogen on the photosynthetic and photorespiratory activity of selected highveld grasses exhibiting C_4 photosynthesis. Proceedings of the Grassland Society of southern Africa 9: 89-94.

Grossman D., Grunow J.O. & Theron G.K. 1980. Biomass cycles, accumulation rates and nutritional characteristics of grass layer plants in canopied and uncanopied subhabitats of Burkea savanna. Proceedings of the Grassland Society of southern Africa 15: 157-161.

Hall T.D., Meredith D. & Altona R.E. 1950. Production from grassland in South Africa. Empire Journal of Experimental Agriculture 18: 8-18.

Harrington G.N. & Johns G.G. 1990. Herbaceous biomass in a *Eucalyptus* savanna woodland after removing trees and/or shrubs. Journal of Applied Ecology 17: 775-787.

Huntley B.J. 1982. Southern African savannas. In: Huntley B.J. and Walker B.H. (eds). Ecology of Tropical Savannas. Springer-Verlag, Berlin.

Jury M.R. & Levey K. 1993. The Eastern Cape drought. Water South Africa 19: 133-137.

Kellman M. 1979. Soil enrichment by neotropical savanna trees. Journal of Ecology 67: 565-577.

Kennard D.G. & Walker B.H. 1973. Relationships between tree canopy cover and *Panicum maximum* in the vicinity of Fort Victoria. Rhodesian Journal of Agricultural Research 11: 145-153.

Kinyamario J.I., Trlica M.J. & Njoka T.J. 1995. Influence of tree shade on plant water status, gas exchange, and water use efficiency of *Panicum maximum* Jacq. and *Themeda triandra* in a Kenya savanna. African Journal of Ecology 33: 114-123.

Knoop W.T. & Walker B.H. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. Journal of Ecology 73: 235-253.

Mannetje 't L. & Haydock K.P. 1963. The dry-weight-rank method for the botanical analysis of pasture. Journal of the British Grassland Society 18: 268-275.

McNaughton S.J. 1992. Laboratory-stimulated grazing: interactive effects of defoliation and canopy closure on Serengeti grasses. Ecology 73: 170-182.

Milchunas D.G., Lee C.A., Laurenroth W.K. & Coffin D.P. 1992. A comparison of ^{14}C, ^{86}Rb, and total excavation for determination of root distributions of individual plants. Plant and Soil 144: 125-132.

Moore A., van Niekerk J.P. & Knight I.W. 1985. The effect of Tebuthiuron on the vegetation of the thorn bushveld of the Northern Cape - A preliminary report. Journal of the Grassland Society of Southern Africa 2: 1-15.

Moore A. & Odendaal A. 1987. Die economiese implikasies van bosverdigting en bosbeheer soos van toepassing op 'n speenkalf-produksiestelsel in die doringbosveld van die Molopo-gebied. Tydskrif van die Weidingsvereniging van Suider Afrika 4: 139-142.

Mordelet P. 1993. Influence of tree shading on carbon assimilation of grass leaves in Lamto savanna, Côte d'Ivoire. Acta Ecologica 14: 119-127.

Mordelet P., Abbadie L. & Menaut J-C. 1993. Effects of tree clumps on soil characteristics in a humid savanna of West Africa (Lamto, Côte d'Ivoire). Plant and Soil 153: 103-111.

Mordelet P. & Menaut J-C. 1995. Influence of trees on above-ground production dynamics of grasses in a humid savanna. Journal of Vegetation Science 6: 223-228.

O'Reagain P.J. & Hobson F.O. 1989. Major veld types of the Eastern Cape. Döhne Information System, Döhne Agricultural Development Institute, P/Bag X15, Stutterheim, 4930.

Palmer A.R., Crook B.J.S. & Lubke R.A. 1988. Aspects of the vegetation and soil relationships in the Andries Vosloo Kudu Reserve, Cape Province. South African Journal of Botany 54: 309-314.

Pinkerton A. & Simpson J.R. 1979. The use of stable strotium as a chemical tracer for root penetration. Australian Journal of Agricultural Research 30: 239-250.

Pressland A.J., 1973. Rainfall partitioning by arid woodland (*Acacia anerua*) in south-western Queensland. Australian Journal of Botany 21: 235-245.

Roberts H.A. 1981. Seed banks in soils. Advances in Applied Biolgy 6: 1-55.

Robertson J.B. & Van Soest P.J. 1981. The detergent system of analysis and its application to human foods. In: The analysis of dietary fibre. Eds. James W.P.T. & Dekker O.T., New York.

Ruess R.W. & McNaughton S.J. 1984. Urea as a promotive coupler of plant-herbivore interactions. Oecologia 63: 331-337.

Rutherford M.C. 1983. Growth rates, biomass and distribution of selected plant roots in *Burkea africana-Ochna pulchra* savanna. Vegetatio 52: 45-63.

SAS Institute 1982. SAS users guide: statistics. SAS Institute Inc., Cary, NC, USA.

Scholes R.J. 1990. The regrowth of *Colophospermum mopane* following clearing. Journal of the Grassland Society of Southern Africa 7: 147-151.

Smit G.N. & Swart J.S. 1994. Influence of leguminous and non-leguminous woody plants on the herbaceous layer and soil under varying competition regimes in Mixed Bushveld. African Journal of Range & Forage Science 11: 27-33.

Soileau J.M. 1973. Activity of barley seedling roots as measured by strontium uptake. Agronomy Journal 65: 625-628.

Soil Classification Working Group, 1991. Soil classification: A taxonomic system for South Africa. Memoirs on the Agricultural Natural Resources of South Africa no. 15.

Sokal R.R., & Rohlf F.J. 1981. Biometry. W.H. Freeman and Company, New York.

Steel R.G. & Torrie J.H. 1981. Principles and procedures of statistics: A biometrical approach, 2nd Edition, McGraw-Hill Book Company, Singapore.

Story R. 1952. A botanical survey of the Keiskammahoek district. Memoirs of the Botanical Survey of South Africa no. 27.

Stuart-Hill G.C., Tainton N.M. & Barnard H.J. 1987. The influence of an *Acacia karroo* tree on grass production in its vicinity. Journal of the Grassland Society of Southern Africa 4: 18-24.

Thompson K. & Grime J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology 67: 893-921.

Tiedemann A.R. & Klemmedson J.O. 1973. Effect of mesquite on physical and chemical properties of the soil. Journal of Range Management 26: 27-29.

Tiedemann A.R. & Klemmedson J.O. 1977. Effect of mesquite trees on vegetation and soils in the desert grassland. Journal of Range Management 30: 361-367.

Tilley J.M.A. & Terry R.A. 1963. A two-stage technique for the *in vitro* digestion of forage crops. Journal of the British Grassland Society 18: 104-111.

Trolloppe W.S.W. 1974. The role of fire in preventing bush encroachment in the eastern Cape. Proceedings of the Grassland Society of Southern Africa 9: 67-72.

✓ Trolloppe W.S.W., Hobson F.O., Danckwerts J.E. & van Niekerk J.P. 1989. Bush encroachment and control. In: Grazing Management: A strategy for the future. Department of Agriculture & Water Supply, Agriforum '89, 23-32.

Van Auken O.W. & Bush J.K. 1992. Changes in species biomass in the Coastal Prairie of Texas when light and nutrients are altered. Canadian Journal of Botany 70: 1777-1783.

Van der Maarel H. 1979. Transformation of cover-abundance values in phyosociology, and its effects on community similarity. Vegetatio 39: 97-114.

Van Soest P.J. 1982. Nutritional Ecology of the Ruminant. O & B Books, Corvallis, Oregon.

Venter K. 1993. Döhne laboratory methods. Döhne Agricultural Development Institute, Department of Agricultural Development, Stutterheim.

Vetaas O.R. 1992. Micro-site effects of trees and shrubs in dry savannas. Journal of Vegetation Science 3: 337-344.

Walker J., Moore R.M., & Robertson J.A. 1972. Herbaceous response to tree and shrub thinning in *Eucalyptus populnea* shrub woodlands. Australian Journal of agricultural Research 23: 405-410.

Walker B.H. & Noy-Meir I. 1982. Aspects of the stability and resilience of savanna ecosystem. In: B.J. Huntley & B.H. Walker, editors. Ecology of tropical savannas, Springer-Verlag, Berlin, pp. 556-590.

Walker J., Robertson J.A. & Penridge L.K. 1986. Herbage response to tree thinning in a *Eucalyptus crebra* woodland. Australian Journal of Ecology 11: 135-140.

Weinmann H. 1938. Effect of fertilizer treatment on Transvaal highveld. South African Journal of Science 35: 246-249.

Weinmann H. 1943a. Effects of defoliation intensity and fertilizer treatment on Transvaal highveld. Empire Journal of Experimental Agriculture 11: 113-124.

Weinmann H. 1943b. Yields and chemical composition of pasture herbage as influenced by fertilising and frequent clipping. South African Journal of Science 15: 127-134.

Weisberg S. 1985. Applied linear regression. Chapter 6. 2nd Edition. John Wiley & Sons Inc.

APPENDICES

Appendix 1 List of all woody species identified in the experimental area on the farm "Lily-Park".

Acacia karroo
Allophylus decipiens
Aloe ferox
Buddelja dysophylla
Burchellia bubalina
Canthium ciliatum
Canthium inerme
Canthium mundianum
Carissa bispinosa
Cassine aethiopica
Clausena anisata
Clerodendrum glabrum
Coddia rudis
Commiphora harveyi
Cussonia spicata
Diospyros simii
Diospyros villosa
Diospyros whyteana
Dovyalis caffra
Ehretia rigida
Euclea crispa
Euclea natalensis
Euclea undulata
Grewia occidentalis
Hippobromus pauciflorus
Jasminum angulare
Maytenus heterophylla
Maytenus nemerosa
Ochna natalitia
Olea europaea
Rhoicissus tridentata
Rhus chirindensis
Rhus refracta
Rhus undulata
Scolopia zeyheri
Scutia myrtina
Sideroxylon inerme
Tecomaria capensis
Trimeria grandifolia
Trimeria trinervis
Vepris undulata
Zanthoxylum capense
Ziziphus mucronata

Appendix 2 Methods for soil analyses (FSSA 1974)

Particle size distribution:
Soil sample was treated with HCl solution, H_2O_2 solution and citrate/bicarbonate buffer solution with 3 g sodium dithionite powder added to remove carbonates, organic material and iron sesquioxides. The treated sample was then dispersed with Calgon solution.

pH: was determined in a KCL solution

Soil density:
An apparatus of constant volume was used to determine soil density.

EC and Cl:
A saturated soil-water paste was filtered under vacuum, and Cl and the EC was determined in the extract.

CEC and Na:
These were determined using an ammonium acetate exchange solution and after displacement, with a KCl solution, the NH_4^+ ions were determined by the Kjeldahl method.

Organic C
This was analyzed using the Walkley-Black method (potassium dichromate oxidation and titration of excess dichromate with ferrous ammonium sulphate).

Total N:
This was measured by the Kjeldahl method (extraction with 1 M KCl, liberation of ammonia by steam distillation in the presence of excess NaOH and Devarda's alloy, and titration with HCl using a mixed indicator).

Extractable P:
This was determined using an AMBIC extractant and the absorbance noted on a spectrophotometer.

Extractable K, Ca and Mg:
These were measured by atomic absorption spectrophotometry after extracting with an AMBIC solution and using a strontium solution as an ionic buffer.

Appendix 3 Methods for plant analyses (Venter 1993) and forage quality analyses.

Ca, Mg, K, Na and P:

These were digested with HNO_3 and $HClO_4$ at 150°C. The Ca, Mg, K and Na in the digest was determined by atomic absorption spectrophotometry, while P was determined by colorimetry using the spectrophotometer.

Total Kjeldahl nitrogen (TKN):

This was determined by converting the N in the sample to NH_4^+ in the presence of H_2SO_4 and a catalyst. The NH_4^+ was determined colorimetrically on an auto-analyzer at 660 nm.

In vitro digestible organic matter (IVOM):

The technique of Tilley & Terry (1963) was used, as modified by Engels & Van der Merwe (1967). Values were transformed into a value of digestible organic matter by an equation which was arrived at by the inclusion of standard samples in the analytical procedure (Engels *et al.* 1981).

Fibre Analysis (NDF, ADF, ADL)

Neutral and acid detergent fibre (NDF and ADF) and lignin (ADL) were determined according to the procedures described by Goering & Van Soest (1970) and Robertson & Van Soest (1981).

Appendix 4 Methods for plant and soil Rb and K determination (Venter 1993)

Plant Rb determination

Samples were milled to pass trough a 1 mm sieve. 10 g samples were weighed into crucibles. Samples were ashed for 3 hours in a muffle furnace at 550°C and allowed to cool *in situ*. The ash was dissolved in 5 cm^3 1:1 HCl, and 5 cm^3 conc. HNO_3 was added and heated on a hotplate until the sample was digested and the mixture had evaporated. The residue was dissolved in 5 cm^3 HCl and filtered in a 100 cm^3 plastic beaker. The crucible was washed with three 5 cm^3 aliquots of 5.085 g KCl/l solution, which acted as the ionization buffer, and then the solution was filtered. The filtrates were transfered to test tubes and rubidium concentration was determined by flame emission spectrophotometry.

Plant K determination

0.5 g samples were measured into digestion tubes. 5 cm^3 conc. HNO_3 was added to each of the tubes and left overnight in a fume cupboard. 3 cm^3 conc. $HClO_4$ was added and digestion was started at 70°C. After 1 hour the temperature was increased to 150°C. When the digest was clear and/or white vapour was visible, digestion was terminated and the tube was made up to 25 cm^3 with water. When cool, the tube was made up to 50 cm^3 with water, stoppered and shaken. A portion of the digest was diluted using an auto-diluter and potassium determined using the atomic absorption spectrophotometer.

Soil Rb determination

10 g of soil and 1 scoop of charcoal was measured into a 250 cm^3 Erlenmeyer flask. 50 cm^3 AMBIC extractant was added to the flasks, which were stoppered and shaken for 30 minutes. Two drops of Superfloc solution was added and the flask swirled. 10 cm^3 0.3069 M KCl solution was added and the extracts filtered through Whattman 41 paper into a 250 cm^3 Erlenmeyer flask. The rubidium in the extracts was determined by flame emission spectrophotometry.

Soil K determination

2.5 cm^3 of soil was measured, and placed into a stirrer cup and 2.5 cm^3 of the AMBIC extractant was added. 5 cm^3 of the extract was pipetted into a 100 cm^3 volumetric flask, 2 cm^3 of a Sr ionization buffer was added and the flask was filled up with water. The potassium concentration was read on an atomic absorption spectrophotometer.

Appendix 5 Mean cover (%) of herbaceous species occurring in the three vegetation zones, for the bush control treatments at the end of the 1992/93 season. (Cont=control, Chem=Chemical, Mech=Mechanical, Over=Overown)

	Bushclump				**Periphery**				**Grassland**			
	Cont	**Chem**	**Mech**	**Over**	**Cont**	**Chem**	**Mech**	**Over**	**Cont**	**Chem**	**Mech**	**Over**
Grass species												
Aristida congesta	0.0	0.2	0.7	0.3	1.4	2.0	1.0	1.5	2.3	5.5	3.4	1.0
Chloris gayana	0.0	0.0	0.0	31.6	0.0	0.0	0.0	15.6	0.0	0.0	0.0	22.0
Cynodon dactylon	0.2	1.2	1.1	0.7	3.4	7.6	8.3	7.2	3.9	6.0	11.7	6.1
Digitaria eriantha	0.1	0.0	2.3	0.5	0.5	0.3	0.8	0.3	2.1	0.2	0.3	0.3
Eragrostis chloromelas	0.0	0.0	0.0	0.0	0.5	0.3	0.2	0.0	1.6	0.6	2.0	0.0
Eragrostis curvula	1.1	0.3	0.3	0.2	2.9	2.5	1.8	1.7	5.8	6.3	3.9	2.0
Eragrostis plana	0.1	0.0	0.2	0.0	0.5	1.1	0.2	0.4	0.1	1.5	0.3	0.1
Helictotrichon capense	2.1	1.5	0.0	0.0	0.2	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Panicum maximum	4.4	2.4	8.7	3.3	3.1	5.7	4.4	3.7	1.8	2.8	2.6	4.2
Sporobolus africanus	0.4	0.8	1.1	0.6	4.5	2.5	1.8	2.9	5.8	5.6	4.0	4.0
Themeda triandra	0.3	0.2	0.8	0.1	2.3	3.2	2.7	0.2	2.8	6.3	5.6	0.1
Forb species												
Abutilon sonneratianum	0.0	0.0	0.7	0.3	0.1	0.2	0.6	0.2	0.0	0.0	0.2	0.4
Priva meyeri	0.8	0.2	2.0	0.4	0.6	0.5	1.1	0.9	0.2	0.2	0.4	0.5
Selago corymbosa	0.0	0.0	0.2	0.0	0.6	1.2	0.1	0.1	1.3	1.4	0.8	0.3
Teucrium trifidum	0.0	0.1	0.1	0.0	0.3	0.3	0.4	0.4	0.7	0.8	0.9	0.6
Sedges	0.9	0.6	0.0	0.0	0.7	0.5	0.0	0.6	0.3	0.3	0.0	0.0
Total cover %	11.5	8.4	20.2	38.3	23.3	29.6	25.5	37.4	30.0	38.7	38.3	42.2

Appendix 6 Mean cover (%) of herbaceous species occurring in the three vegetation zones, for the bush control treatments at the end of the 1993/94 season. (Cont=control, Chem=Chemical, Mech=Mechanical, Over=Oversown)

	Bushclump				**Periphery**				**Grassland**			
	Cont	**Chem**	**Mech**	**Over**	**Cont**	**Chem**	**Mech**	**Over**	**Cont**	**Chem**	**Mech**	**Over**
Grass species												
Aristida congesta	0.0	0.0	0.5	0.3	2.2	1.4	2.6	1.4	3.6	6.4	2.6	5.0
Chloris gayana	0.0	0.0	0.0	48.6	0.0	0.0	0.1	35.2	0.0	0.0	0.0	25.5
Cynodon dactylon	0.1	0.4	1.2	0.3	1.4	2.5	4.1	1.9	2.1	2.0	4.0	6.6
Digitaria eriantha	0.0	0.4	1.3	0.5	1.8	0.9	1.9	0.0	4.3	2.7	3.7	1.9
Eragrostis curvula	0.2	0.5	2.7	0.0	2.3	4.4	4.2	2.8	8.1	10.7	4.6	2.1
Eragrostis plana	0.0	0.0	0.1	0.0	0.4	0.3	0.0	0.0	0.0	0.6	0.0	0.0
Helictotrichon capense	0.6	1.8	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Panicum maximum	4.7	9.5	19.0	1.4	7.4	17.2	11.3	2.6	3.3	6.5	10.1	1.6
Sporobolus africanus	0.1	0.4	0.4	0.0	2.7	2.0	2.7	0.9	2.4	1.9	3.4	2.3
Themeda triandra	0.2	0.2	0.7	1.0	7.3	5.7	3.5	0.0	9.1	9.8	9.7	2.4
Forb species												
Abutilon sonneratianum	0.2	0.2	1.3	0.5	0.2	0.3	1.2	0.5	0.1	0.0	1.2	0.3
Conostomium natalense	0.6	1.0	0.0	0.0	0.2	0.5	0.6	0.0	0.0	0.0	0.2	0.1
Peristrophe cernua	0.3	0.2	0.8	0.0	0.5	0.3	0.1	0.0	0.1	0.1	0.1	0.0
Polygala hispida	0.2	0.2	0.2	0.2	0.5	0.2	0.4	0.6	0.8	0.4	0.3	0.6
Priva meyeri	0.3	0.4	1.1	0.2	0.8	0.6	0.8	0.3	0.4	0.3	0.5	0.2
Selago corymbosa	0.0	0.0	0.1	0.1	1.6	0.6	0.5	0.5	1.8	2.0	1.2	1.8
Senecio pterophorus	0.3	0.3	0.4	0.0	0.1	0.1	0.3	0.1	0.0	0.1	0.1	0.2
Teucrium trifidum	0.0	0.1	0.5	0.1	1.1	0.6	0.9	0.6	1.2	1.5	0.8	0.6
Sedges	1.5	2.0	0.0	0.0	0.1	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Total cover %	11.2	19.4	31.9	53.5	32.6	39.5	36.9	48.0	39.0	47.5	45.1	52.4

Appendix 7 The frequency (%) of herbaceous species occurring in the three vegetation zones, for the bush control treatments at the end of the 1992/93 season. (Cont=control, Chem=Chemical, Mech=Mechanical, Over=Oversown)

	Bushclump				Periphery				Grassland			
	Cont	Chem	Mech	Over	Cont	Chem	Mech	Over	Cont	Chem	Mech	Over
Grasses												
Aristida congesta	3	5	21	20	26	31	28	35	43	55	43	5
Chloris gayana	0	0	0	95	0	0	0	75	0	0	0	70
Cynodon dactylon	11	18	20	15	54	83	63	60	61	86	83	65
Digitaria eriantha	1	0	29	35	10	4	15	20	14	6	10	15
Eragrostis chloromelas	0	0	0	0	1	6	3	0	13	5	6	0
Eragrostis curvula	24	15	14	15	60	35	30	20	53	54	48	25
Eragrostis plana	3	3	6	0	8	11	6	20	1	13	9	5
Helictotrichon capense	28	13	0	0	8	6	0	0	0	0	0	0
Panicum maximum	44	35	71	55	61	65	50	75	35	35	48	45
Sporobolus africanus	14	23	19	10	71	66	43	30	83	74	69	45
Themeda triandra	9	8	6	5	29	31	20	10	29	35	33	10
Tragus berteronianus	0	0	11	0	0	0	9	20	0	8	8	0
Forbs												
Abutilon sonneratianum	3	0	23	20	5	6	19	10	0	1	9	20
Berkheya bipinnatifida	0	1	13	5	1	0	9	0	0	0	5	0
Chaetacanthus setiger	0	0	8	0	9	1	0	0	8	4	9	20
Clutia ericoides	1	3	14	10	4	4	10	25	4	5	6	5
Falkia repens	1	4	6	0	0	4	1	0	3	10	1	0
Galopina circaeoides	18	14	3	0	18	19	1	0	3	1	8	0
Helichrysum spp.	0	0	0	0	0	1	3	0	0	0	1	0
Hypoestes aristata	1	3	3	0	6	10	0	0	3	0	1	10
Melhania didyma	1	0	3	0	5	1	4	0	3	1	5	
Priva meyeri	36	10	59	35	43	30	41	55	13	16	26	30
Rhynchosia ciliata	11	1	10	20	19	18	11	20	20	13	16	10
Rhynchosia hirsuta	4	0	0	0	8	1	0	0	0	0	0	0
Senecio erubescens	0	0	0	0	4	4	3	15	1	1	1	0
Senecio tamoides	3	3	0	0	3	16	1	0	1	0	0	0
Selago corymbosa	1	3	5	0	33	33	11	5	49	53	29	15
Sida rhombifolia	5	0	9	10	10	4	8	5	4	10	4	5
Teucrium trifidum	0	3	5	0	18	21	25	15	31	41	35	30
Sedges	33	16	3	0	26	23	0	10	18	19	4	0

Appendix 8 The frequency (%) of herbaceous species occurring in the three vegetation zones, for the bush control treatments at the end of the 1993/94 season. (Cont=control, Chem=Chemical, Mech=Mechanical, Over=Oversown)

	Bushclump				**Periphery**				**Grassland**			
	Cont	**Chem**	**Mech**	**Over**	**Cont**	**Chem**	**Mech**	**Over**	**Cont**	**Chem**	**Mech**	**Over**
Grasses												
Aristida congesta	0	0	15	15	39	19	33	20	53	51	40	50
Chloris gayana	0	0	1	100	0	0	3	95	0	0	0	80
Cynodon dactylon	5	9	14	10	25	41	35	40	39	38	41	50
Digitaria eriantha	0	3	24	5	28	14	33	0	54	31	33	35
Ehrharta erecta	3	6	0	0	0	0	0	0	0	0	0	0
Eragrostis curvula	8	3	24	0	41	49	39	15	70	80	45	35
Eragrostis plana	1	1	1	0	6	5	0	0	1	5	0	0
Helictotrichon capense	21	18	0	0	3	3	0	0	0	0	0	0
Panicum maximum	49	50	95	35	73	90	78	35	49	55	60	20
Sporobolus africanus	6	8	14	0	43	28	28	25	39	39	44	35
Themeda triandra	1	4	6	5	30	26	15	0	38	36	31	10
Forbs												
Abutilon sonneratianum	10	14	38	35	15	18	36	20	6	3	33	25
Achyranthes aspera	15	11	3	10	8	4	5	25	3	0	4	25
Aptenia spp.	0	0	0	0	5	0	3	0	8	1	5	0
Berkheya bipinnatifida	5	4	4	0	4	1	5	0	1	4	3	5
Chaetacanthus setiger	11	1	9	0	14	5	3	0	8	0	1	0
Cheilanthes viridus	6	4	1	0	8	14	1	0	0	4	1	0
Clutia ericoides	0	0	3	0	1	0	1	0	8	4	0	0
Conostomium natalense	33	20	0	0	10	14	15	5	0	0	6	0
Falkia repens	3	1	4	0	14	14	8	0	14	15	10	5
Galopina circaeoides	0	11	9	0	6	11	4	0	3	0	6	10
Pelargonium alchemilloides	3	5	5	0	4	4	1	0	0	1	1	5
Peristrophe cernua	9	10	15	0	14	13	6	0	8	5	6	0
Polygala hispida	8	10	11	10	24	9	19	20	29	16	19	20
Priva meyeri	20	13	43	10	36	23	24	15	26	23	28	15
Rhynchosia ciliata	5	1	4	5	13	3	10	10	14	6	3	5
Rhynchosia hirsuta	0	1	0	0	5	1	8	5	0	3	4	0
Senecio pterophorus	16	26	26	0	9	6	28	10	0	6	11	5
Senecio tamoides	13	5	4	0	6	1	1	0	5	0	1	0
Selago corymbosa	3	0	3	5	45	23	29	25	64	56	48	40
Sida rhombifolia	3	6	13	0	6	15	9	5	9	6	16	5
Solanum incanum	8	8	5	5	9	8	5	0	4	1	6	0
Teucrium trifidum	1	6	18	5	29	29	29	35	41	50	30	35
Thunbergia capensis	6	4	5	5	11	4	4	0	4	8	10	5
Sedges	41	39	3	0	3	8	0	0	1	0	0	0