The influence of acacias on below canopy grass communities

Honours thesis

Anthony Roberts

University of Cape Town

Botany Department

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KD ROBE

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Contents

Abstract

1. The influence of acacia species through their varying life stages (seedlings, juveniles, adults and dead trees) on sub-canopy grass communities was investigated at various sites in the Hluhluwe-Umfolozi Park (HUP).
2. Their were significant differences between classes (at $p < 0.05$) to each other and to the open sites, but to differing extents at the different rainfall regions within the HUP. Significant differences occurred between young acacias and the open sites more frequently at the drier sites than at the wetter sites. Young acacias do not influence below canopy grass communities in the high rainfall regions.
3. In the low rainfall sites, the young acacias act as refugia for 'bunch' grass species in the sea of 'lawn'. A switch back to lawns occur below the adult acacias dominated by the 'lawn' grass *Dactyloctenium australe* which occurs at differing proportions to the 'bunch' grass *Panicum maximum* below the canopy depending on the extent of animal disturbance, measured as density of droppings.
4. Rainfall was responsible for separating communities out between the various sites in HUP. However, the impact of animals on the grass communities within each of the sites had more influence on the resulting grass communities in each of the classes.
5. The response of a variety of grass species to light levels failed to explain the presence of particular species below adult acacias and others away from the influence of these acacias.

6. Succession is occurring between grass communities as a result of establishment of acacias with the process being more evident in the dry areas of the HUP. The grass communities in the high rainfall areas revert back to early successional communities more rapidly once a tree dies than they do in the low rainfall areas. The influence of the adult acacias on the below canopy soils is greater and affects grass communities for a longer period of time in the low rainfall areas than it is in the high rainfall areas even after the tree has died.

Acknowledgements

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Introduction

Savannas include a wide range of vegetation types and can be characterised by a continuous herbaceous layer and a discontinuous cover of shrubs and trees (Huntley & Walker, 1982). The relative abundance of these two components are regulated by external determinants such as rainfall, soil, fire, and herbivory (Vetaas, 1992). In more arid environments it is believed that the importance of rainfall increases relative to disturbance factors such as fire and grazing (Vetaas, 1992). Rainfall and soil are thought to be the most important factors in controlling the distribution of species (Scholes & Archer, 1997). Competition between grass species is also a key factor in limiting species distribution and species influence within and between communities (Begon *et al*, 1996).

Disturbance in the form of herbivory is also recognised now as one of the major factors influencing grass species distribution. Coughenour (1985) states that "graminoid grazing tolerance and the nearly simultaneous increase of grasses in the fossil record (Stebbins, 1981, as cited in Coughenour, 1985) suggest that grasses are adapted to herbivory perhaps as a result of coevolution". Amongst grasses two growth forms have evolved: one a low growing grass, "lawn grass", with small shoots whose advantages are rapid response to ephemeral water availability, distribution of the risk of drought induced mortality and an increased rate of recovery after defoliation (Coughenour, 1985). The second form is that of the "bunch grass", with taller stature through increased activity of intercalary meristems (Stebbins, 1981) thereby increasing light competitive ability. The bunchgrass growth form is less resistant to herbivory than more rhizomatous or stoloniferous growth forms, possibly due to coevolution of the latter with large herbivores (Mack & Thompson, 1982).

Factors determining mixtures of bunch versus lawns are relatively unknown. Likely factors are rainfall and competitive interactions between species and growth forms as well as the influence of disturbance such as fire and herbivory.

Vegetative reproduction by tillering is an efficient method of lawn grasses for colonising sites and is adaptive for plants that compete for space in early successional stages or disturbance sites, a method Coughenour, (1985) dubs are "guerrilla-like tactics". The lawn grasses are able to colonise open areas through lateral growth relying on the resources from an already established plant for the growth of tillers. Bunch grass growth forms spread by the dispersal of seed and the subsequently established seedbanks. The young bunch grass seedlings are susceptible to herbivory and trampling and they require refugia for establishment in areas with high grazing levels. In order for the bunch grasses to recruit and establish two factors are advantageous: a good period of rainfall and a refuge from grazers. For example, below thorny shrubs, a phenomenon of 'nucleation' (Yarranton & Morris, 1974), in which individual plants take advantage of the favourable microhabitats induced by the larger plant. In this case it is not a process of competition that is occurring but one of facilitation (Roberts, 1987) and this often influences the overall species composition (Vetaas, 1992). Bunch grasses are likely to out-compete any lawn grass surviving below a shrub and dominate the micro-habitat. At the landscape level, the occurrence of canopy micro-habitats, interacting with other factors such as fire and herbivores, will increase habitat or community diversity in a savanna as compared to open grassland (McNaughton, 1983; Belsky, 1990).

Bond & van Wilgen (1996) coined the term 'gullivers' for the small, suppressed, but not necessarily young, individuals of resprouting savanna tree species that have not managed to escape the herbivore or fire layer. These 'gullivers' are generally plentiful in the apparent treeless or sparsely tree covered grasslands (Scholes &

Archer, 1997), however their effect on grass communities below them which are protected from herbivore impact have not been investigated in South African savannas.

The effect of adult trees in savannas on below canopy nutrients (Bate *et al*, 1982; Belsky *et al*, 1989; Roos & Allsopp, 1997), moisture content (Belsky *et al*, 1989), and soil organic matter (Garcia-Moya & Mckell, 1970; Belsky *et al*, 1989) and consequently their associated communities(McNaughton, 1983; Belsky, 1989; Carter & O'Connor, 1991) have been investigated. The association between certain grass species and tree canopies have been explained, for example that of *Panicum maximum* with acacia species, by enriched sub-canopy soil and the influence of mycorrhiza (Roos & Allsopp, 1997).

Aims

The aim of this study was to determine if the acacias influenced the grass communities growing below them through their various life-stages at different sites and to determine if there were significant differences between the various size classes. The next step was to determine how grass/tree interactions varied across a rainfall gradient and to determine the effect of rainfall and animals on the grass communities along these gradients. An explanation for the difference in communities in acacia sub-canopy to those away from the zone of influence would also be considered in terms of light response curves to determine if sub-canopy species were adapted to low light levels. Finally, the process of succession was investigated, to see whether there was a trend through the life-stages of the acacias resulting in what might be deemed a climax community and to investigate how dynamic the system was by determining how far back the grass communities would shift in the successional sequence once an adult acacia died.

Methods

STUDY SITE

The study was conducted in the Hluhluwe-Umfolozi Park (HUP), located in KwaZulu Natal, South Africa (28° 00 – 28°26 S, 31°43 – 32°09E; see Fig.1). There is a large altitudinal shift in the park, associated with variation in rainfall gradients, from 60m to 750m above sea level. The majority of the Umfolozi portion of the park is low lying and has low rainfall compared to Hluhluwe which has a greater portion in the higher rainfall region. The vegetation consists predominantly of the Lowveld subcategory of the Tropical Bush and Savanna Types of Acocks (Brooks and MacDonald, 1983). There is an abundance of large herbivores such as buffalo, rhino, zebra, and elephant including large herds of the smaller game such as impala and nyala.

Ten sites were chosen for the purpose of this study with an attempt made to chose sites over a range of altitudes. Seven sites were chosen in Hluhluwe and three in Umfolozi. Site information is given in Table 1 below. Rainfall data was attained by applying the formula: 1.164 (altitude) + 462.72 (Balfour *pers. comm.*).

Figure 1: Study Sites in the Hluhluwe-Umfolozi National Park, and the position of the Park in relation to South Africa (insert).

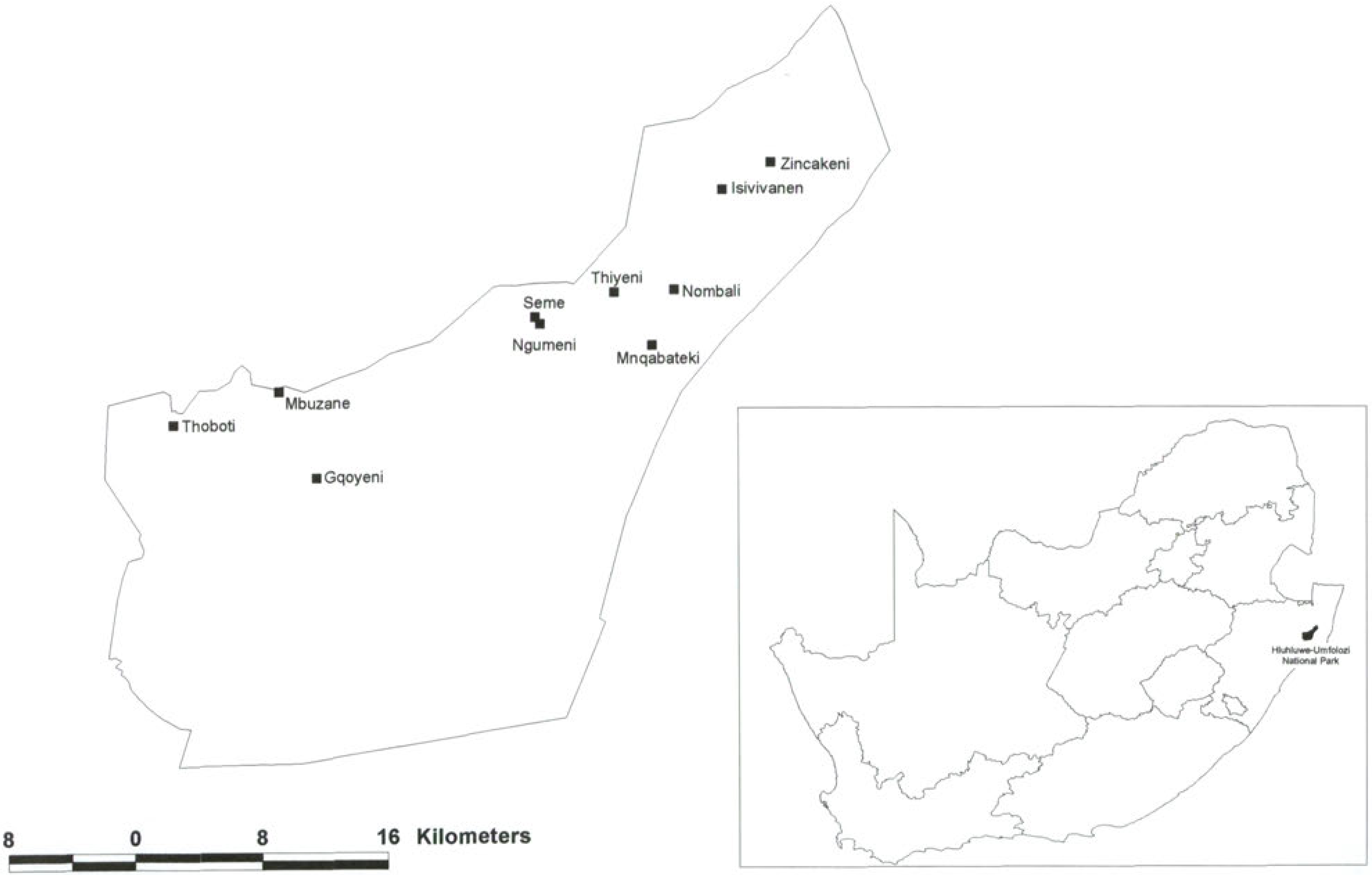


Figure 2.1: Topography of the Hluhluwe-Umfolozi National Park. Included with Site Names are Height and Rainfall respectively.

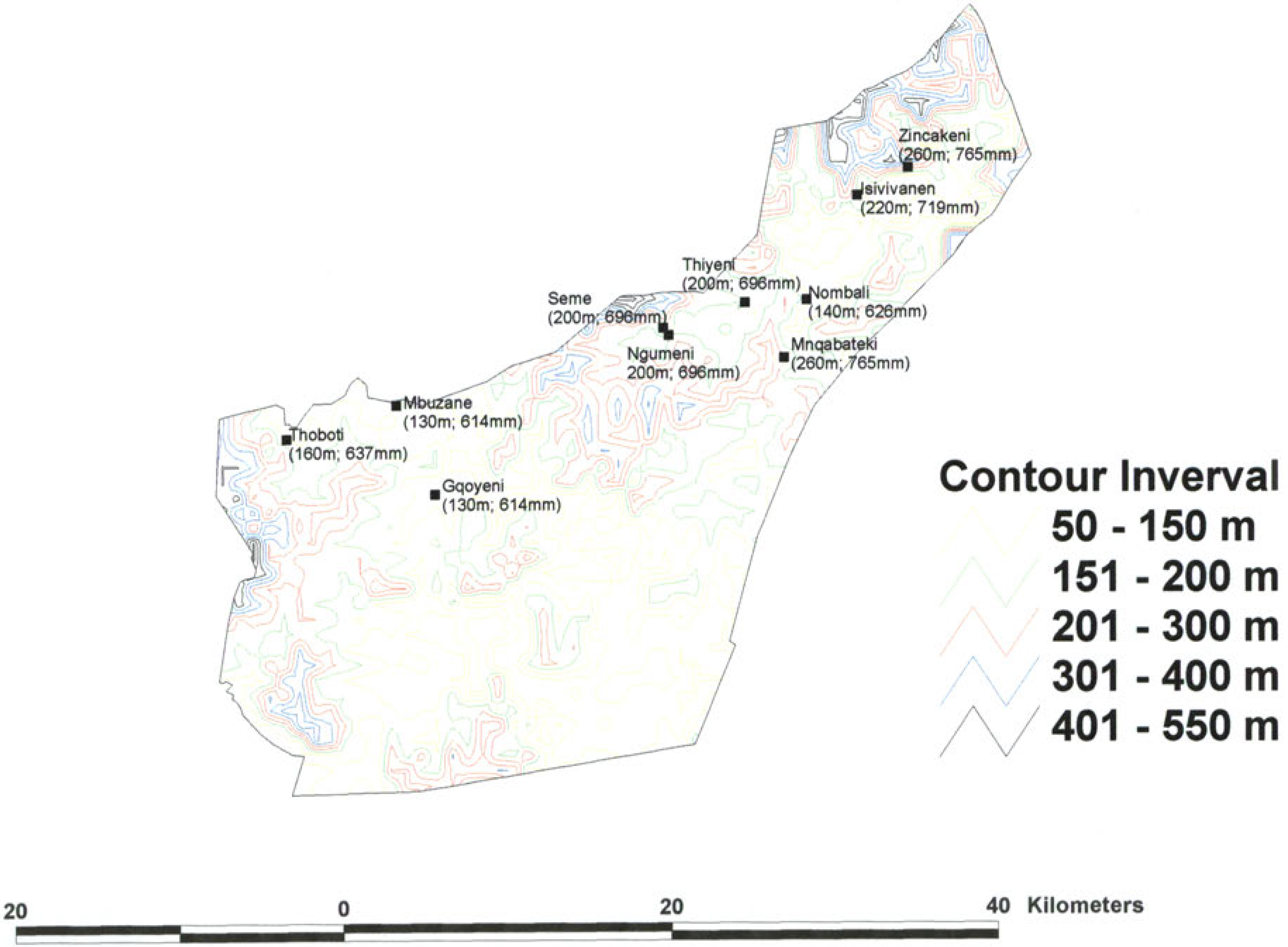


Figure 2.2: Annual Precipitation in the Hluhluwe-Umfolizi National Park. Isohyte Intervals are 10mm. Included with Site names are Height and Rainfall Respectively.

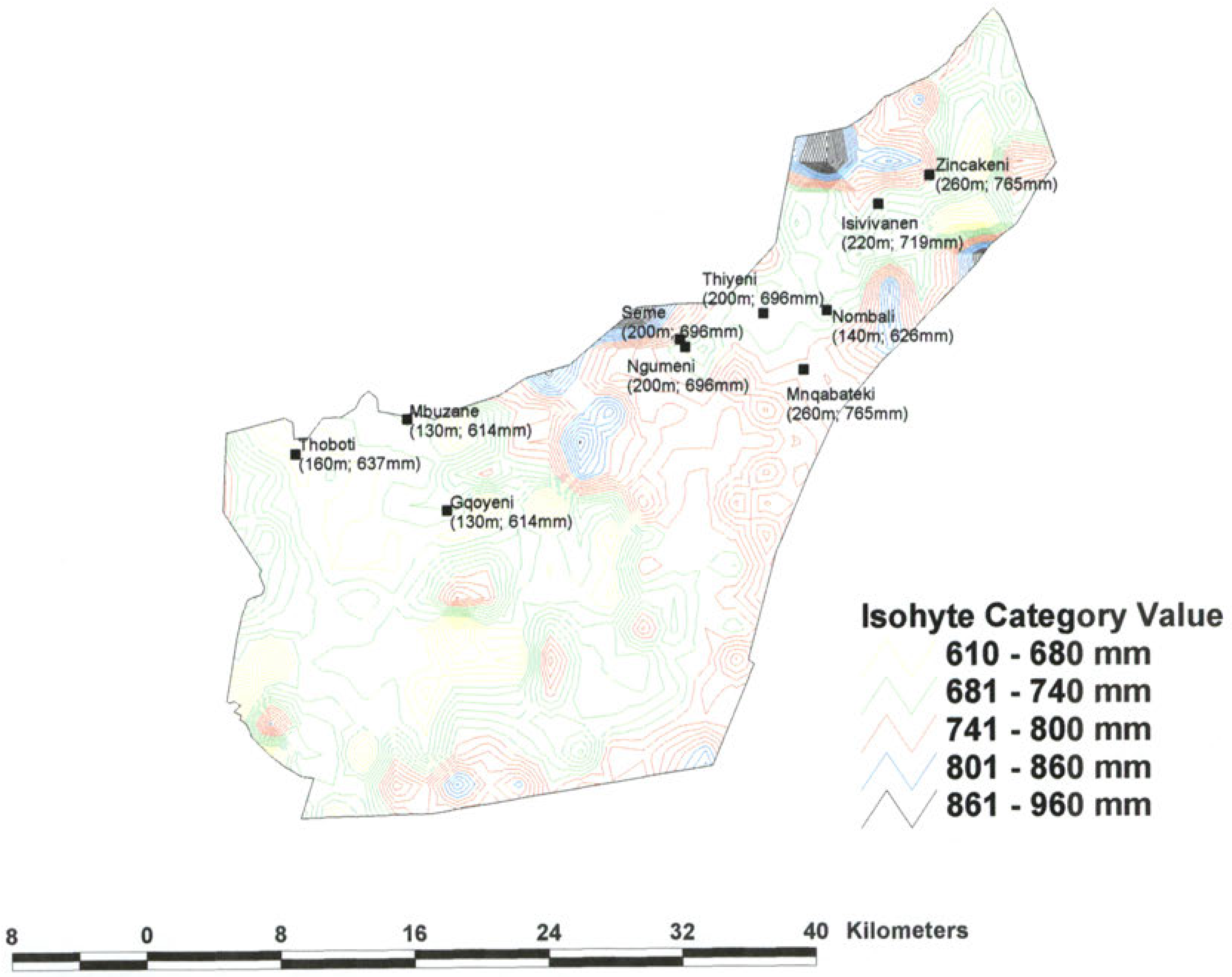


Table 1: Location and rainfall for the ten study sites located through the Hluhluwe-Umfolozi Park

Site	Location	Rainfall (mm)
Zincakeni (Hlu)	28°05' S, 32°05' E	765
Isivivaneni (Hlu)	28°06' S, 32°03' E	719
Nombali (Hlu)	28°10' S, 32°02' E	626
Ngumeni (Hlu)	28°12' S, 32°01' E	696
Seme (Hlu)	28°10' S, 31°58' E	696
Mnqabateki (Hlu)	28°11' S, 32°00' E	765
Thiyeni (Hlu)	28°09' S, 31°59' E	696
Mbuzane (Umf)	28°13' S, 31°47' E	614
Gqoyeni (Umf)	28°16' S, 31°46' E	614
Thoboti (Umf)	28°13' S, 31°50' E	637

SAMPLING

The sites in the low rainfall areas were chosen on the basis of the presence of "lawns". The reason for this is to compare the effect of acacias on the normal grass composition of open site i.e. that of lawns. In the high rainfall areas open woodlands of adult acacias of adult acacias, mainly those of *A. nilotica* were chosen. A number of tree size classes were selected and where possible a minimum of ten samples taken for each. These classes were "open" – those areas away from influence of acacias; "seedling" – multi-stemmed acacias below 50cm; 'gulliver' – single-stemmed acacia under 1m in height; "young adult" – acacia with stem < 10cm yet producing pods; "A1" – Adult acacia with spreading crown but whose crown does not touch that of another acacia; "A2" – Adult acacia with crown touching the crown of only one other acacia; "A3" – Adult acacia with crown in contact with those of other adults around entire crown; "dead" – Adult acacias that have died.

For each class the grass communities growing under or within what was deemed to be the zone of influence of the acacia were identified and their abundance recorded. For 'seedlings' and 'gullivers' this was the entire area below their protruding branches. For the "young adults" and those in the "A" classes the area sampled was below the canopy, representing an estimated two thirds of the canopy area, in a circle around the base of the tree. The "dead" category, having varying numbers of branches still intact, had an area of influence deemed to be two thirds of the canopy when the tree was alive. At each site a number of 'open' class grass communities were recorded equivalent to the area of the closest 'gulliver' or 'seedling'. Abundance was estimated along four levels of density: "0" – absent from the area; "1" – present but less than 10% of total area; "2" – 10-90% of total area and "3" - >90%.

The soil type and depth at each site were identified by taking auger samples from the surface to the bedrock and compared to a Munsell Colour Chart. The soil types found were in agreement with soil maps at the Hluhluwe Research Centre.

ANIMAL IMPACT

This was determined by taking dung densities as a surrogate for animal numbers in the area. Dung densities were determined by counting piles of droppings within or touching a 5mx5m quadrat randomly placed either below the canopy of an "A1"/ "A3" tree or out in the open. Dung was identified down to species where possible. There was no dung occurring below 'seedlings' and 'gullivers' except for occasional droppings of small rodents not deemed to be of importance to this study.

DATA ANALYSIS

To investigate whether there were significant differences in grass communities between tree size classes, PRIMER version 4.0 (Plymouth Marine Laboratory) was used. Using similarity matrices and applying the ANOSIM function the significant differences between sites were obtained for each site (Figure 3). The result is a numbers of matrices depicting the relationship of each size class to the others with regards to similarities in grass communities for each of the sites. This same method was then applied to the combined data for all sites to determine if there were meaningful groups over the entire park regardless of the differing environmental factors at each site.

Two ordination methods, detrended correspondence analysis (DCA) and detrended canonical correspondence analysis (DCCA), were applied to the site and species data using CANOCO version 4.0 (Centre for Biometry Wageningen, CPRO-DLO, Netherlands). This program is primarily for the study of plant communities and their associated environmental variables and is particularly good at handling data sets with large amounts of zero scores as is the case with the data sets in this study. In DCA the programme fits the best distribution of data points to theoretical axis according to a unimodal model. Species are scored according to their positions on these theoretical axes. Sites are then scored by multiplying species scores and abundances, and new species scores are derived from the site scores. This process is continued until species and site scores stabilise. With CA (correspondence analysis) a 'horse shoe affect' frequently occurs where the two ends of the axis are compressed relative to the middle. Here detrending is applied and the curve is flattened. For a more detailed explanation of these methods see Hill and Gauch, (1980). DCCA incorporates correlations between species abundance and given environmental variables before correspondence analysis is performed (ter Braak, 1996).

A total of 30 grass species was recorded from all of the ten sites. This data was used in both the DCA and the DCCA. The DCA explained differences within sites between the different acacia classes with regard to their associated grass species. The DCCA was applied to determine differences between classes for all sites. The environmental variables used in the DCCA, were rainfall and dung counts and the covariables were soil depth and soil type. A covariable is a concomitant or background variable corresponding to nuisance parameters (ter Braak & Smilauer, 1988). It was evident when sampling that soil type was affecting grass species composition and thus it was included in the analyses as covariables as this study was concerned more with the impact of animals and the effect of differing rainfall patterns. The abundance scores of species for each class was averaged at each of the sites so as to reduce the size of the data set when applying DCCA to the combined sites. Significance tests using Monte Carlo Permutations were applied to determine the significance of the environmental variables in explaining the respective canonical axes.

In order determine if rainfall correlated with the distances between open and adult acacia at the various sites on the primary axis, the positions for both the open and adult acacias were obtained from the CANOCO solution file. The distance along the primary axis between the two centroids was then plotted against rainfall at each of the respective sites using STATISTICA '99 edition (Statsoft Inc).

In investigating the question of a successional sequence at the different sites between the various classes the centroid points were plotted. These x and y values were obtained from the CANOCO solution file and were taken as the average for each of the first and second axis provided for the various classes. This was a means of simplifying the ordination diagrams to establish whether there was a successionary trajectory. What was also of concern here was whether the communities below the 'dead' class reverted back to those most similar to the early successional communities and to communities of which size class they were most similar. The reverting back of communities was became apparent with the centroid plots.

SHADE TOLERANCE

Several species of grass were transported back to Cape Town and grown in a phytotron lab at varying light intensities to determine their light saturation points. These species were four 'lawn' grasses: *Urochloa mosambicensis*, *Dactyloctenium australe*, *Digitaria longiflora* and *Eragrostis superba* and two 'bunch' grasses: *Themeda triandra* and *Panicum maximum*. Two individuals of each species were grown at a high light intensity (HLI) of 900 mol.m^{-2}.s^{-1} and another two at a low light intensity (LLI) of 120 mol.m^{-2}.s^{-1} for three weeks. Their photosynthetic rates (mg C gm.dw^{-1}.h^{-1}) were then plotted for varying light intensities between 0-1200 mol.m^{-2}.s^{-1}.

Results

ARE GRASS COMMUNITIES DISTINCT BELOW DIFFERENT ACACIA SIZE CLASSES

The average abundance of grass species for both the high and low rainfall areas are represented in Appendix 1 and 2. The abundance of the more dominant 'bunch' and 'lawn' species occurring at the high and low rainfall sites are represented in Figure 3.1-3.5. The two bunch grass species, *Themeda triandra* and *Panicum maximum* are resent at both high and low rainfall sites. *T. triandra* is absent or present in very low levels below adult acacias whereas *P. maximum* increases in abundance between the small acacia size classes and the adults.

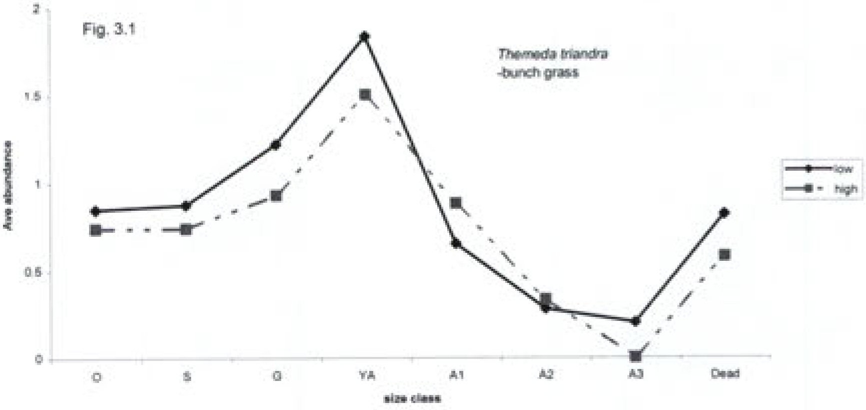


Fig. 3.1

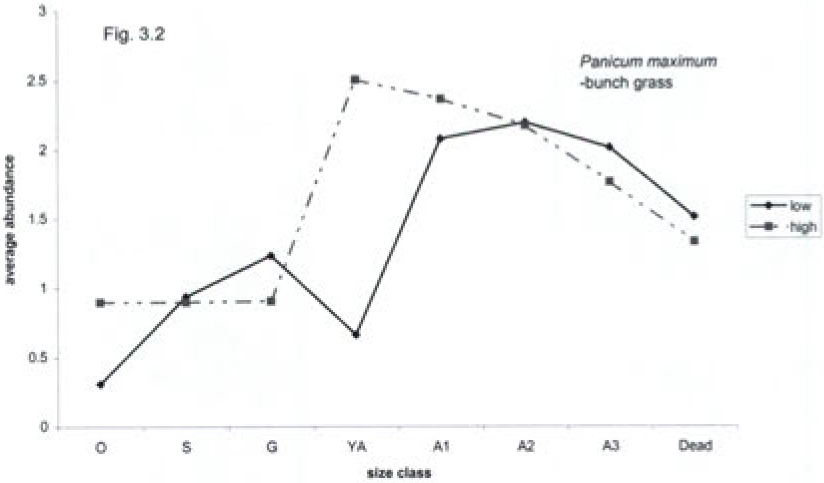


Fig. 3.2

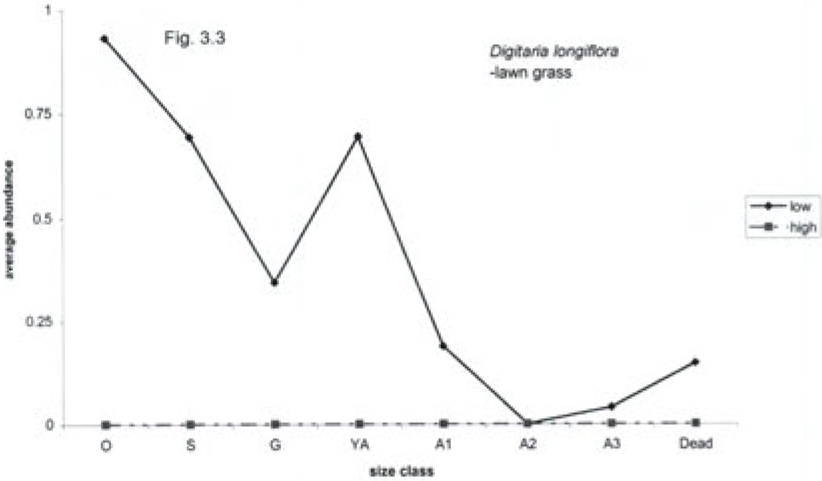
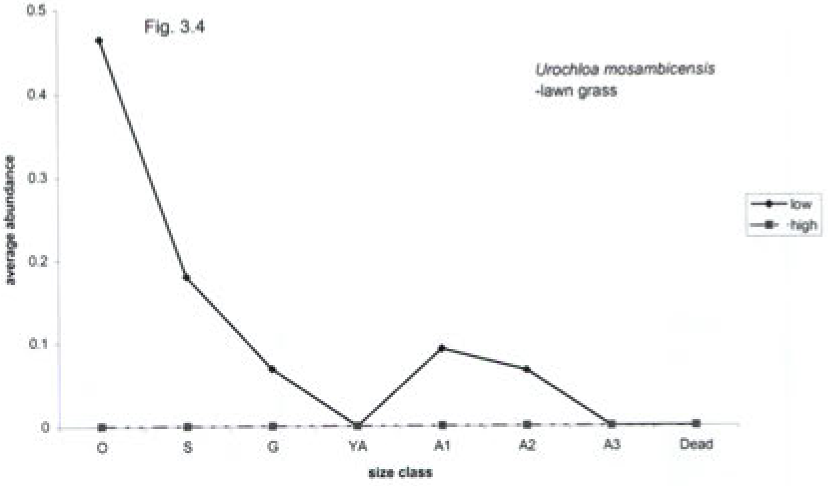


Fig. 3.3



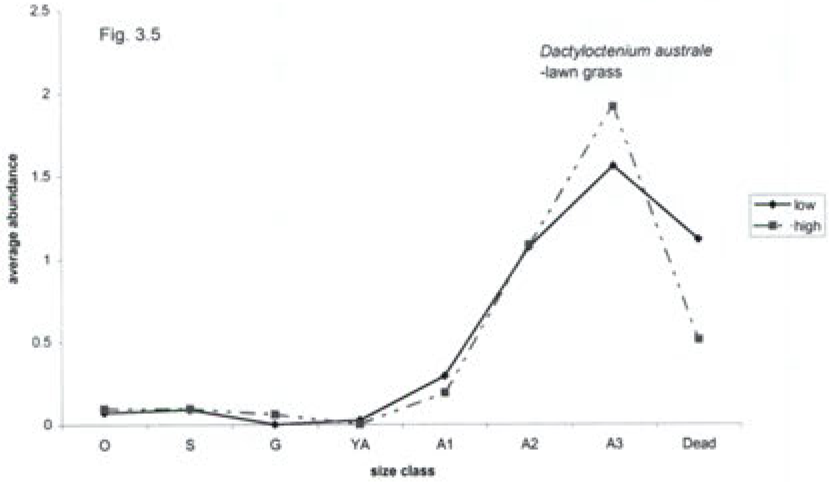


Fig. 3.1-3.5: Effects of different size classes on the abundance of five grass species. Size classes: O-open, S-seedling, gulliver, YA-young adult, 'A1', 'A2' and 'A3'-adult acacias, Dead-dead adult acacia.

In both the low and high rainfall areas the presence of acacias in the 'gulliver' and 'young adult' size classes results in the increase in abundance of *T. triandra* (Fig. 4). The 'lawn' grasses *Urochloa mosambicensis* and *Digitaria longiflora* are both absent in the high rainfall areas and have decreasing abundances with increasing size of the acacias coinciding with increase in *T. triandra* abundance.

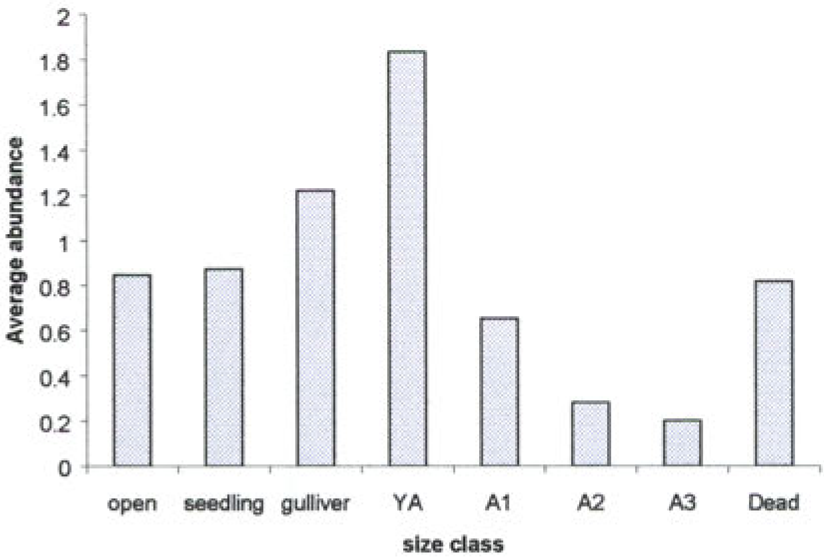


Fig. 4: The relative abundance of the dominant bunch grass species *Themeda triandra* occurring in HUP under the different size class acacias.

The 'lawn' grass *Dactyloctenium australe* is absent from both low and high rainfall sites away from the adult acacias with peaking abundances under the 'A3' class. These figures show the effect of the different size class acacias on relative abundances of a few 'bunch' and 'lawn' grass species but what is of more importance is how the different size classes of acacias alter grass community composition below them along the rainfall gradients.

Trends in the data are apparent in Tables 3.1-3.10 two sets of changes of grass under trees emerge. In one grass communities below small acacias differed significantly from open sites (Table 3.1 – 3.6). In the other group, grass communities were similar in open sites and under the small acacias (Table 3.7-3.10) The former occur in areas of lawn or mixed grass communities where 'gullivers' provided a refuge for 'bunch' grasses. The latter occurred in the high rainfall areas where the grass below in the open and under the small acacias were all bunch grasses and there were no significant differences between 'open' classes and 'seedling', 'gulliver' or even 'YA' classes (at

	open	seedling	gulliver	A1	A2	A3
open	-					
seedling	*	-				
gulliver	**	**	-			
A1		**		-		
A2	*	**			-	
A3						-

Table 3.1: Gqoyeni

	open	seedling	gulliver	YA	A1	A2	A3
open	-						
seedling		-					
gulliver	**	*	-				
YA	**	*		-			
A1	**	**	*	*	-		
A2	**	**	**	**	*	-	
A3	**	**	**	*			-

Table 3.2: Nombali

	open	seedling	gulliver	A1	A2	A3
open	-					
seedling	**	-				
gulliver	**		-			
A1	**	**		-		
A2	**	*			-	
A3						-

Table 3.3: Thoboti

	open	seedling	gulliver	A1	A2
open	-				
seedling	*	-			
gulliver	**		-		
A1	**	*		-	
A2					-

Table 3.4: Mbuzane

	open	seedling	gulliver	YA
open	-			
seedling	**	-		
gulliver	**	*	-	
YA	**	**		-

Table 3.5: Seme

	open	seedling	gulliver	YA	A1	A2	A3	dead
open	-							
seedling		-						
gulliver			-					
YA			*	-				
A1	**	**	**		-			
A2	**	**	**	**		-		
A3	**	**	**	**			-	
dead	**	**	**					-

Table 3.6: Ngumeni

	open	seedling	gulliver	YA	A1	A2	A3	dead
open	-							
seedling	*	-						
gulliver	**	**	-					
YA	**	*		-				
A1	**	**	**	*	-			
A2	**	**	**	**	**	-		
A3	*	*					-	
dead	**	**	**	**				-

Table 3.7: Thiyeni

	open	gulliver	A1	A2	A3	dead
open	-					
gulliver		-				
A1			-			
A2				-		
A3	**	*	**		-	
dead		**	*			-

Table 3.8: Isivivaneni

	open	gulliver	YA	A1	A2	A3	dead
open	-						
gulliver		-					
YA			-				
A1				-			
A2	*	**		**	-		
A3	*	*		*		-	
dead				*	**	*	-

Table 3.9: Zincakeni

	open	gulliver	YA	A1	A2	A3	dead
open	-						
gulliver		-					
YA			-				
A1				-			
A2	*	**		**	-		
A3	*	*		*		-	
dead				*	**	*	-

Table 3.10: Mnqabateki

Table 3.1-3.10: Similarity matrices for size classes at the ten sites with regard to their grass species composition. Significant differences: $p < 0.05$ (*), $p < 0.01$ (**)

$p < 0.05$). At no sites did 'gullivers' and 'young adults' differ significantly and the separation of these classes seems redundant.

The effect of large trees on below canopy grass communities was more apparent at both high and low rainfall sites than were the smaller acacia size classes. The differences between 'A1', 'A2' and 'A3' classes are less clear and no pattern of similarity or dissimilarity is evident from these matrices. However, it seems that 'A2' and 'A3' differ more frequently from the 'A1' class than the 'A1' class does from the smaller size classes in the higher rainfall areas and a closed canopy alters below canopy grass composition to a greater extent than do individual trees. Table 5 sums up the number of occurrences of the significance difference of one class with its proceeding class.

Table 4: The numbers of times an acacia size class is significantly different to the proceeding class in the successional sequence over the number of available comparisons.

class – class relationships	number of times with significant difference ($p< 0.05$)
open-seedling	5/7
seedling-gulliver	4/7
gulliver-young adult	1/5
young adult-A1	2/3
A1-A2	3/9
A2-A3	1/8
A3-dead	2/4

No significant difference exists between grass communities in 'open', 'seedling', 'gulliver' and 'young adults' when considering the park as a whole (Table 5). The 'A1' and 'A2' class seem to group together yet the 'A3' group is significantly different to ‘A1’ so as to be considered separate from the ‘A1’/’A2’ group. The dead class supports different communities to the ‘A3’ class thus once the acacia dies the community structure is changed again. The change in communities below the dead class will be explored later.

Table 5: Similarity matrix for the size classes for all sites along the rainfall gradient considered. Significant differences: $p < 0.05$ (*), $p < 0.01$ (**).

	open	seedling	gulliver	YA	A1	A2	A3	dead
open	-							
seedling		-						
gulliver			-					
YA				-				
A1		**			-			
A2	**	**	*	*		-		
A3	**	**	**	**	**		-	
dead		*		*			**	-

The relationships between the different classes with regard to their associated grass communities is represented by an ordination (Fig. 5). The classes can be seen to separate out to a greater extent along the first axis than they do along the second axis. The cumulative percentage of variance explained by the first two axis is 28.8% with the first axis explaining 16.9% of the variance. In this ordination the ‘open’, ‘seedling’, ‘gulliver’ and ‘young adult’ classes were grouped together as were the ‘A1’ and ‘A2’ classes, based on the similarities between the classes in Table 5. Classes do not separate out well in the ordination and there are possibly factors obscuring the patterns and hence the need to take into account environmental factors.

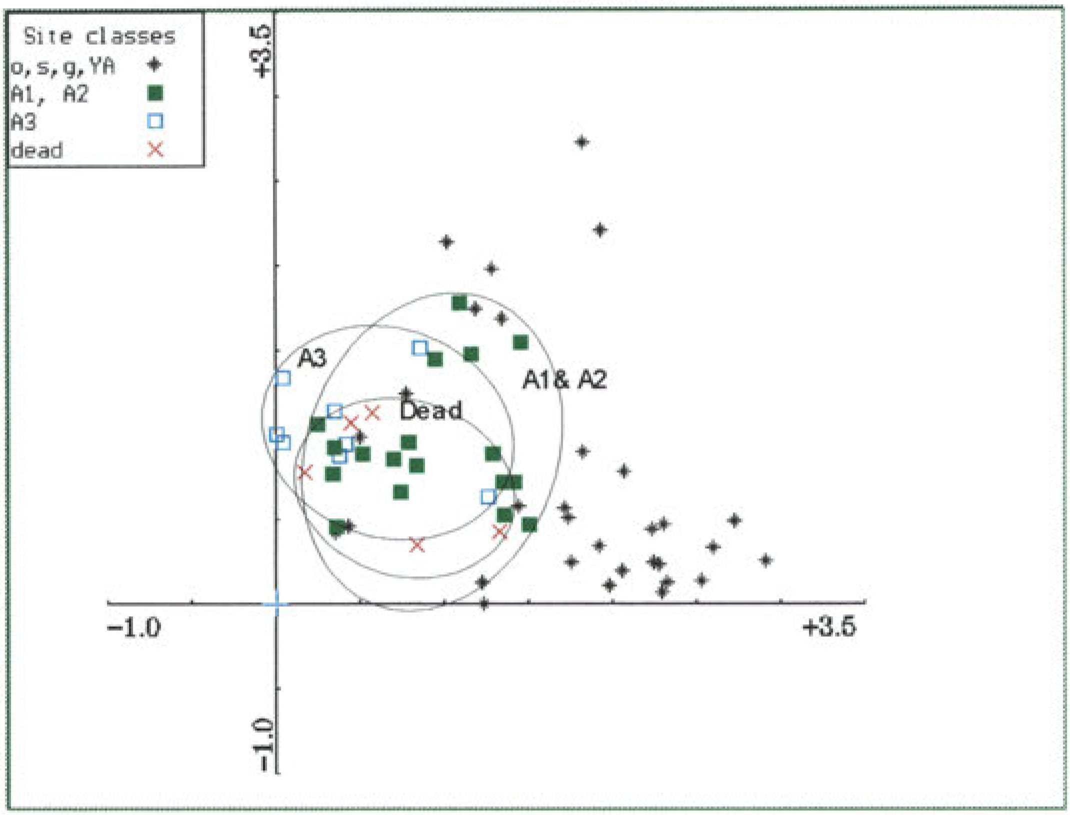


Fig. 5: Ordination, using DCA, of acacia size classes from all sites within the HUP. Grouping of classes based on similarity matrix (Table 5), grouped together if they were not significantly different ($p < 0.05$)

EFFECT OF ENVIRONMENTAL VARIABLES ON THE ORDINATION

Three classes were dropped when doing the DCCA, these being the 'young adult', 'A2' and 'Dead' classes thus the analyses concerned only the remaining five classes. Figure 6.1 shows the results of the DCA where theoretical axes are applied to the ordination. The 'A3' and 'A1' class group together well, with a reasonable distance along the primary axis between the two groups. However, the 'seedling', 'gulliver' and 'open' classes do not show any trends and are spread out in the ordination. There

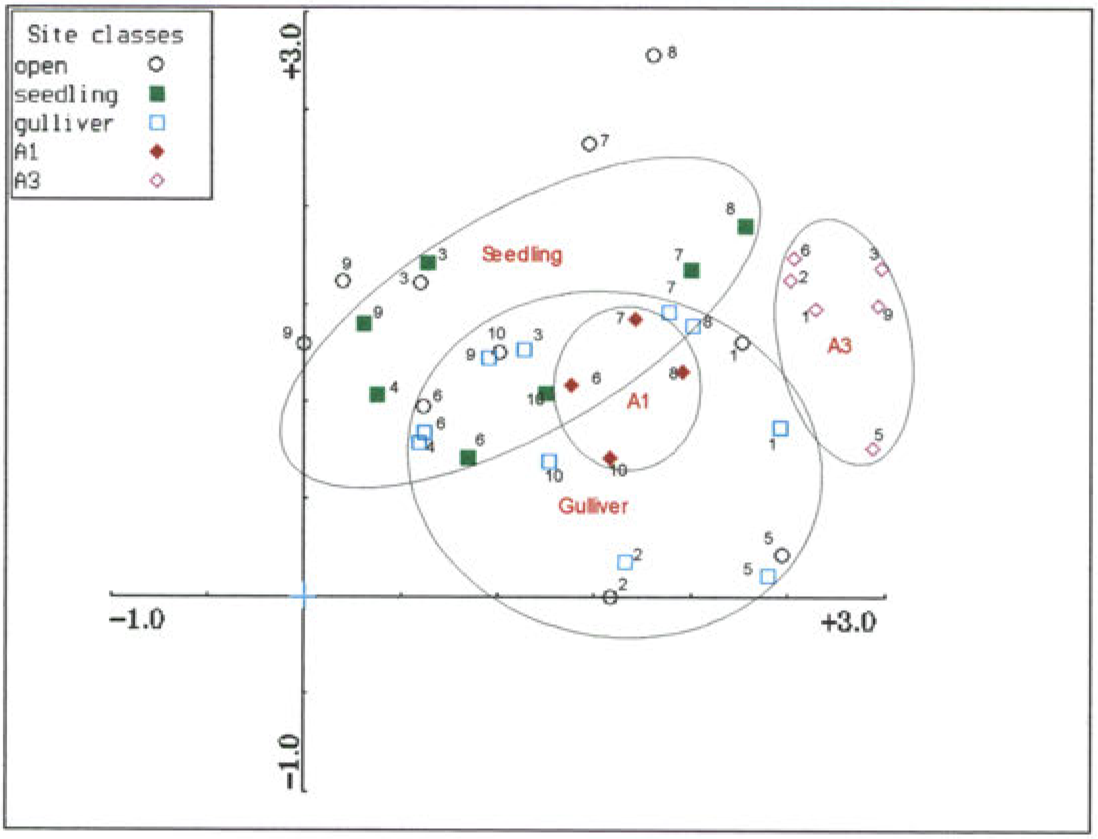


Fig. 6.1: Ordination, using DCA, of sites with 'YA', 'A2' and 'dead' classes missing. Numbers reflect sites: 1- Mnqabateki, 2 – Zincakeni, 3 – Thiyeni, 4 – Seme, 5 – Isivivaneni, 6 – Ngumeni, 7 – Mbuzane, 8 – Thoboti, 9 – Nombali, 10 – Gqoyeni.

is similar vertical and lateral spread between classes for all sites. Figure 6.2 shows the resulting ordination for the DCCA and the vectors representing the strengths of the environmental variables are shown on the figure. Classes separate to a greater extent along the animal impact axis than along the rainfall axis. However, rainfall explains differences in grass communities between site more so than animal impact. The Monte Carlo test of significance of the first canonical axis was $p = 0.01$. Hence there is a significant difference in grass communities between sites in relation to rainfall. However, in investigating the effect of rainfall on distance between 'open' and adult acacia centroids (Fig 7) it is apparent that rainfall does not significantly affect the separation of these classes to differing extents along the rainfall gradient ($R^2 = 0.241$, $p = 0.18$).

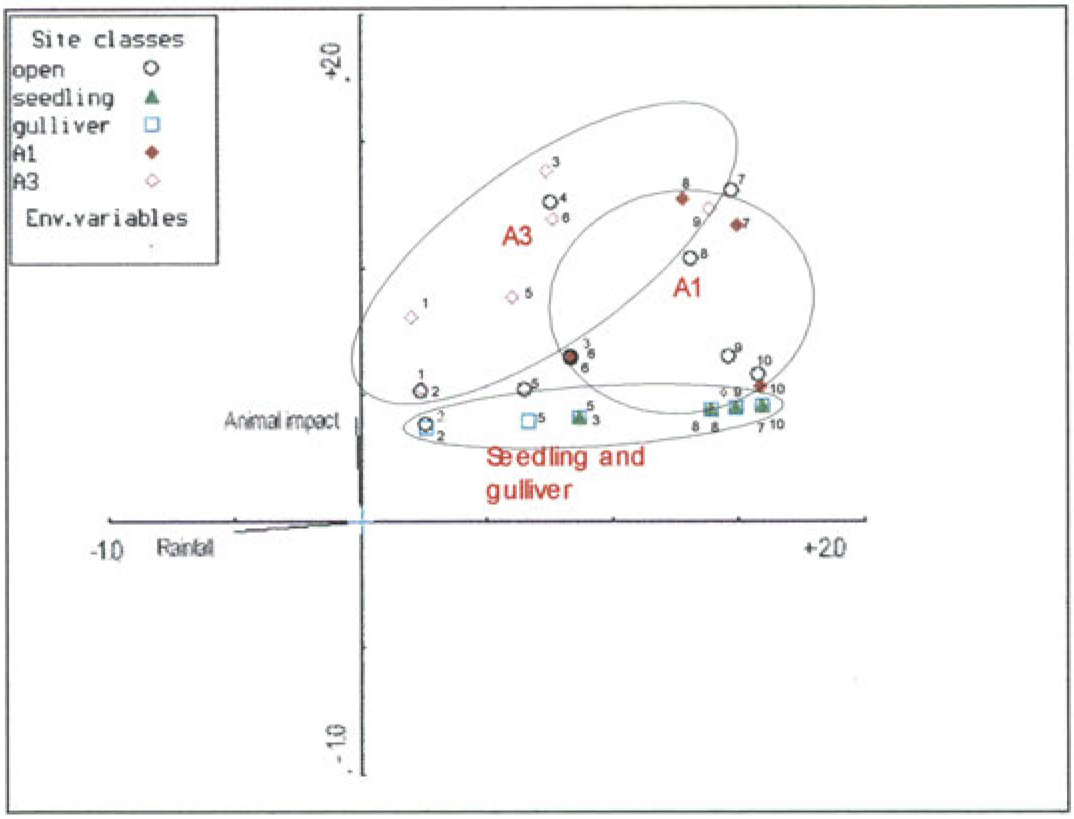


Fig. 6.2: Ordination, using DCCA, of size classes with regard to grass species composition showing environmental vectors. Refer to Fig. 6.1 for explanation of numbers alongside data points.

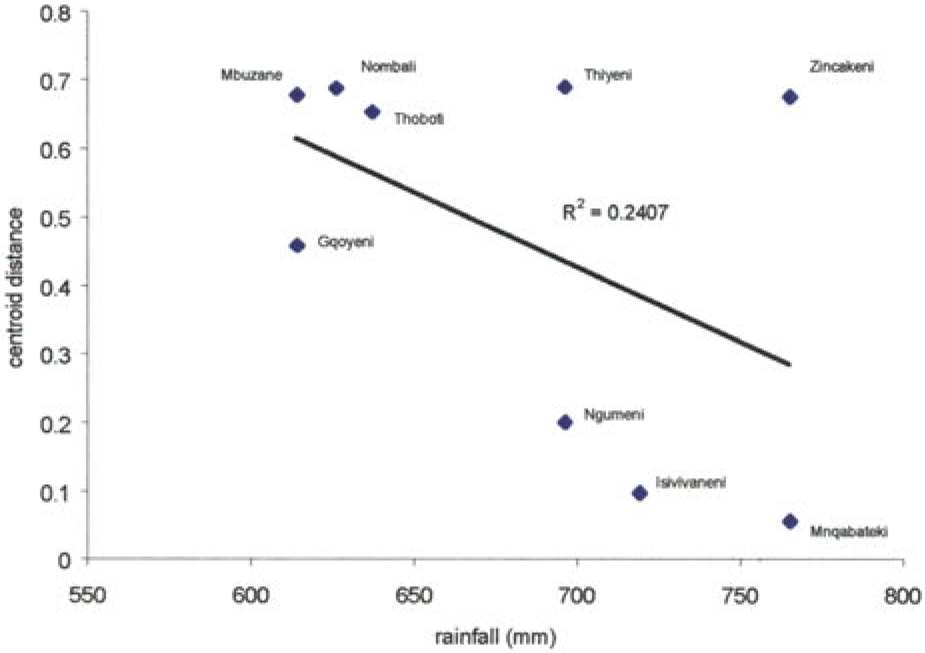


Fig.7: Centroid distances between 'open' and 'A1' classes vs. rainfall for study sites through HUP

The 'open' class is spread out and it is difficult to infer much from the site positioning (Fig. 6.2). There is greater separation out along the 'animal impact' axis at the dry to medium rainfall areas whereas there is not much separation between classes at the high rainfall areas.

The dominant grass community below 'A3' class is represented primarily by two species: *Dactyloctenium australe* and *Panicum Maximum*. The proportional shifts in the two species was were compared to different levels of animal impact i.e. densities of animal droppings (Fig. 8). As animal impact increases so the proportion *P. maximum* decreases and that of *D. australe* increases.

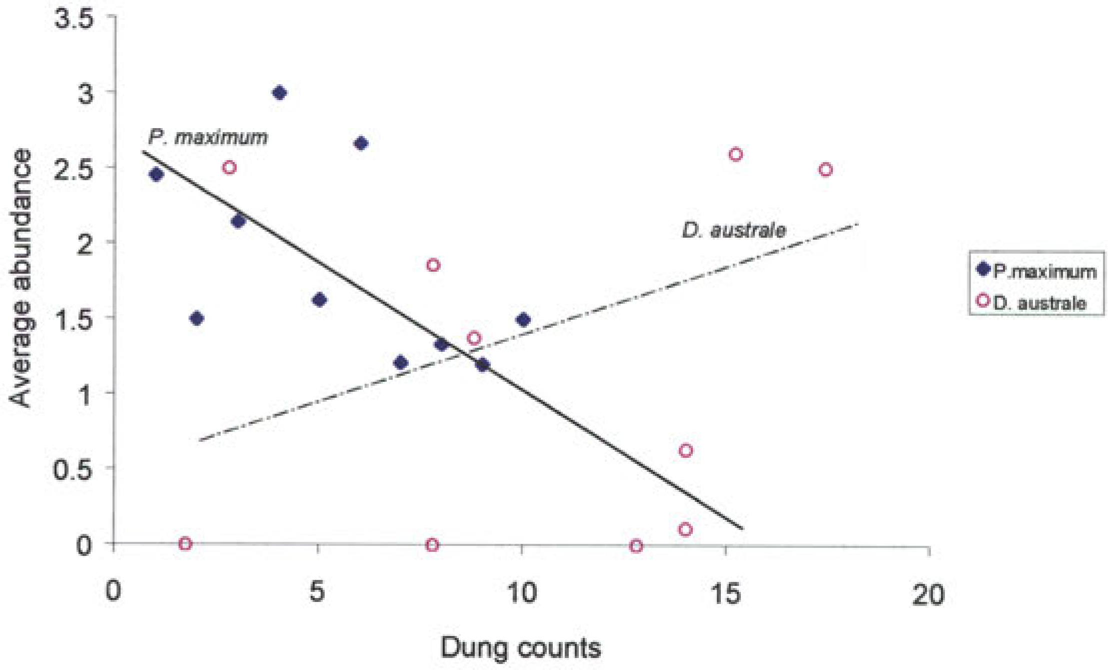


Fig. 8: The abundance of *P. maximum* and *D. australe* vs. dung counts at the various sites through HUP.

LIGHT RESPONSE CURVES FOR SEVERAL GRASS SPECIES

The light response curves for the low light treatment were used and those of the high light treatment ignored because of poor results. Figure 9.1 – 9.6 show the light response curves for the six species involved in the experiment. The two 'bunch' grasses *Panicum maximum* and *T. triandra* and the two 'lawn' grass species, *E. superba* and *D. longiflora* saturated at a low light intensity (100 mol.m^{-2}.s^{-1}) but the other lawn grasses *U. mosambicensis* and *D. australe* saturated at a much higher light intensity of approximately 600 mol.m^{-2}.s^{-1}.

SUCCESSIONAL SEQUENCES AT THE DIFFERENT SITES

Plotting the centroid values for the classes at each of the sites resulted in a number of graphs depicting successional sequences (Figure 10.1-10.10). Some sites separate out along the axes more than others, for example Isivivaneni (Fig. 10.2) shows minimal distances between the centroids whereas Nombali shows large separations between centroids in the primary axis. Almost all sites (7/10) show a successional sequence from 'open' – 'gulliver' – 'adult acacia' (Table 6). At the high rainfall sites the separation of 'open' and 'gulliver' is not large and this reflects the significance of the various classes (Table 3.1-3.10).

Table 6: Successional sequences based on the similarity matrices (Table 3.1-3.10); Classes in brackets are considered not to be significantly different ($p < 0.05$).

Site	Successional order
Gqoyeni	O - S - G - A1 - A2 - A3
Isivivaneni	(O,G,A1) - (A2,A3,DEAD)
Nombali	O - S - G - A1 - (A2,A3)
Thiyeni	(O,S) - (G,YA) - (A1,A2,A3,DEAD)
Thoboti	0 - S - G - A1 - (A2,A3)
Zincakeni	(O,G,YA,A1) - A2 - A3
Mbuzane	O - S - (G,A1) - A2
Mnqabateki	(O,G) - A1 - A2 - A3
Ngumeni	(O,S,G) - YA - A1 - A2 - A3
Seme	O - S - (G,YA)

The question of whether the grass communities reverts back to that of one earlier in the successional path after an acacia has died is reflected in Figures 10.2, 10.4, 10.6, 10.8 and 10.9, that each have some representatives of the 'dead' class at the site. It is in the high rainfall areas where the greatest shift occurs, where communities revert back to those similar to early successional communities. At Thiyeni and Mnqabateki (10.7 and 10.10) the grass community below 'dead' acacias resembles that of the 'A1' class whilst that at Zincakeni resembles the community of the 'open' class. At Thiyeni and Isivivaneni the grass communities do not revert back to those communities earlier in the succession but stay remain with grass communities similar to the 'A3' class.

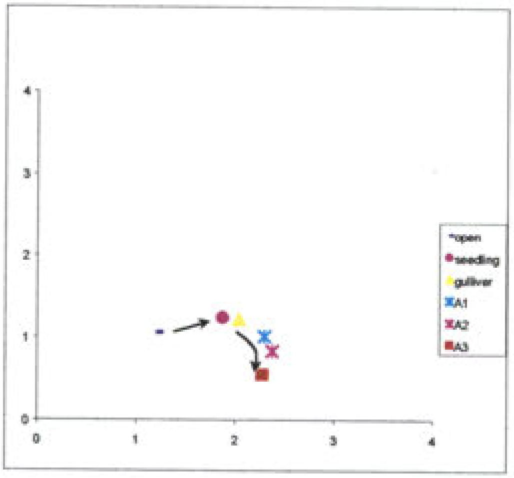


Fig. 10.1: Centroid plot for Gqoyeni

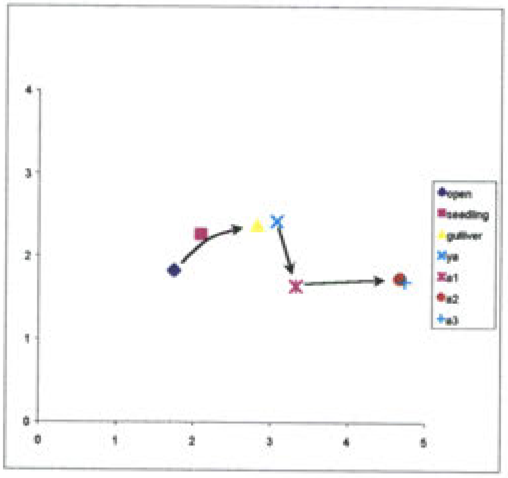


Fig. 10.2: Centroid plot for Nombali

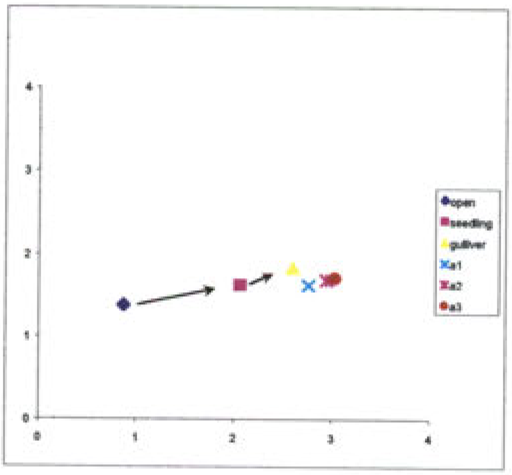


Fig. 10.3: Centroid plot for Thoboti

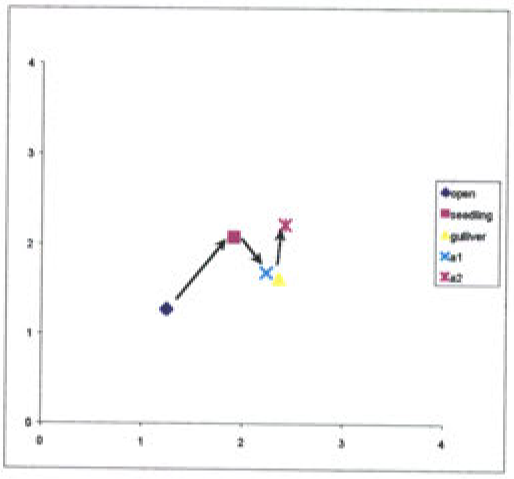


Fig. 10.4: Centroid plot for Mbuzane

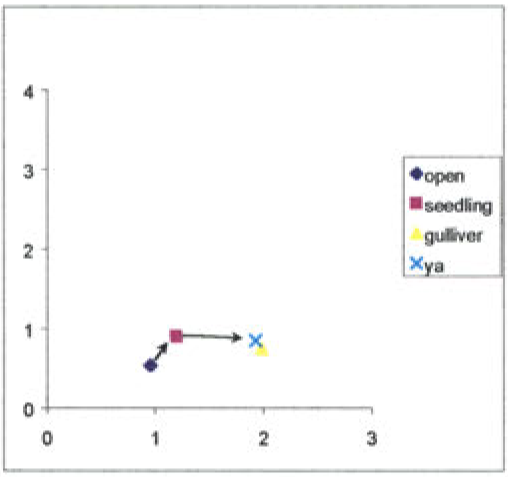


Fig.10.5: Centroid plot for Seme

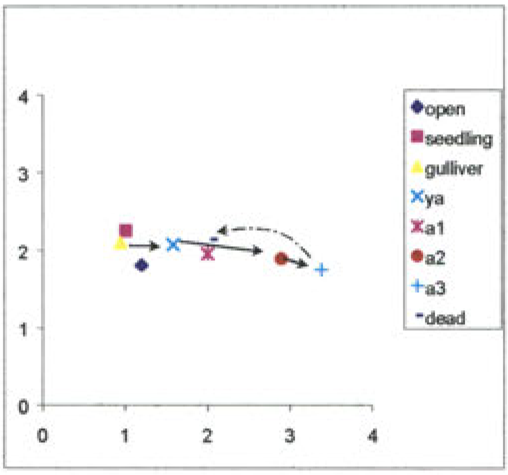


Fig. 10.6: Centroid plot for Ngumeni

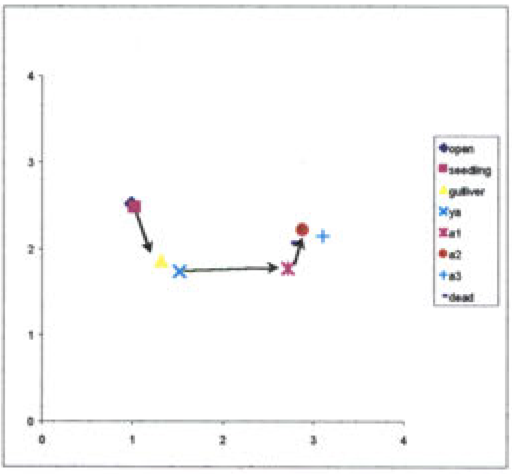


Fig.10.7: Centroid plot for Thiyeni

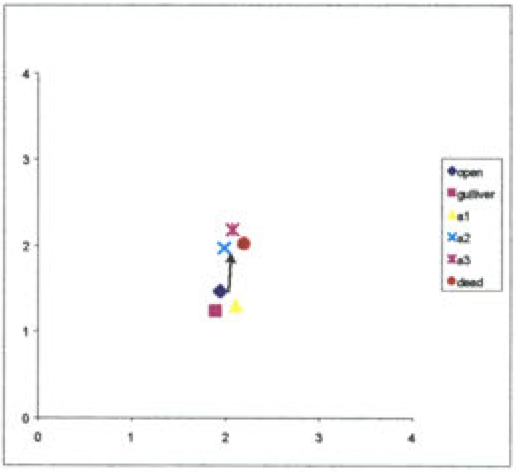


Fig. 10.8: Centroid plot for Isivivaneni

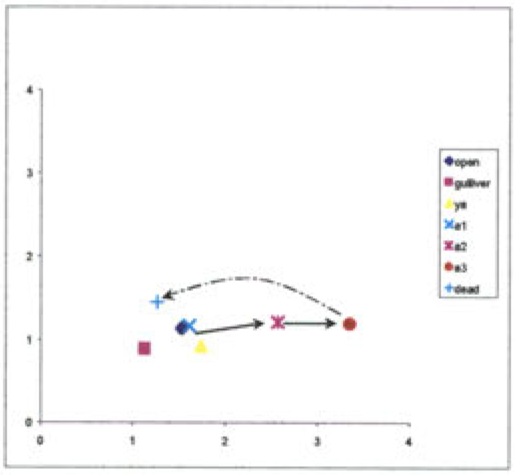


Fig.10.9: Centroid plot for Zincakeni

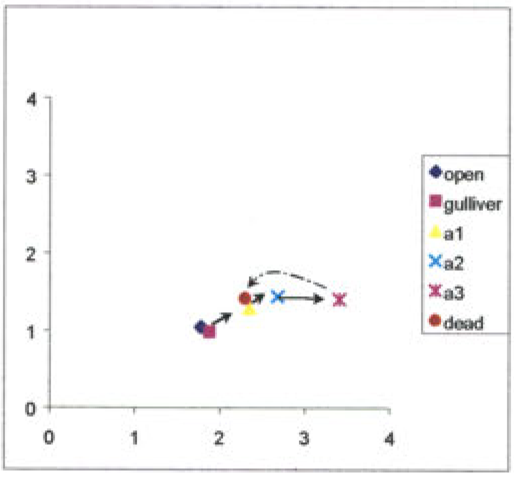


Fig 10.10: Centroid plot for Mnqabateki

Fig. 10.1 - 10.10: Centroid plots of class for each site. Solid arrows show successional sequences, broken lines reflect reverting back of communities below dead class.

Discussion

LANDSCAPE PATTERNS

Differences in species composition under and away from savanna trees are more distinct in low than in high rainfall areas (Belsky *et al*, 1993)and as one moves through the HUP it is evident that the high lying areas associated with higher rainfall are dominated by the taller swards of grass than are the lower, drier regions. Although bunch grasses are not absent from these lower areas they are reduced in density and seem isolated to small clumps within a sea of grazing lawn. These clumps are in turn associated with acacia plants in differing life stages and which, it seems, act as refugia for these bunch grasses (Fig's 3.1, 3.2, 4). However, The direct effect of trees on grasses may not be apparent until the trees reach a critical age or size (Scholes & Archer, 1997).

RELEVANCE OF CLASSES

The critical stage proposed by Scholes and Archer (1997) at which trees affect the grass communities below them varies from site to site and seems to be a product of rainfall. It is apparent from Table 3.8, 3.9, and 3.10 that in the high rainfall areas, small acacias have little influence on the grass community below them. These small acacias, or 'gullivers', may be decades old but are yet to escape the grass layer due to disturbance such as fire and grazing (Hara, 1987). In the high rainfall areas the first compositional shift seems not to have been under these 'gullivers' but under the adult acacias and only under those that had a partial or fully closed canopy, hence the smaller size classes in the high rainfall areas are redundant.

In the drier regions, the establishment of a seedling results in a compositional shift with bunch grass species such as *T. triandra* taking refuge in these microhabitats (Fig. 3.1-3.7 and Fig. 4). Often an acacia seedling provides enough protection to enable the establishment of 'bunch' grass to take refuge from grazers but is not tall enough to protect the 'bunch' grass reproductive parts from the grazers which the 'gullivers' are able to do. The taller bunch grasses dominate the refugia and out-compete and shade the low growing lawn grasses. It is not sure of how long these refugia last into the dry season, before the game brave the thorns to access the taller grasses, because of the shortness of this study. It is however long enough for the bunch grasses to produce seed that is vitally important for their colonizing strategies.

There is a again a compositional shift in below canopy grass communities from below the small acacia size classes to those below adult acacias. The effect of the adult acacias on grass communities is stronger in the high rainfall areas particularly with the 'A2' and 'A3' classes as a result of the closed canopies that allows for establishment of the 'lawn' grass *D. australe* that does not seem to establish particularly well under individual trees and even less so in the open.

In ignoring rainfall gradients and combining the data from all the study sites there does not seem to be an effect of acacias in the smaller size classes on below canopy grass communities and it is only the adult acacias that are responsible for the main shift in grass community structure (Table 4). However, it is clear from Table 3.1-3.7 that there are changes in grass communities associated with the these small acacias in the lower rainfall regions but these are likely to be the result of other factors and not merely be the direct influence of rainfall.

EFFECT OF ENVIRONMENTAL VARIABLES ON THE ORDINATION

The more distinct variation in species communities at low rainfall sites over those of high rainfall sites (Belsky *et al*, 1993) is reflected by the large ordination distance (Fig. 6.2). However, this may not be as much a moisture effect as it is a variation in impact due to animals, which separates out classes more so than does rainfall (Fig. 6.2). Higher numbers of game were associated with the low lying areas on lawns, than the higher areas, with taller swards, at the time of year of this study (June/July). These grazing lawns are a product of animal grazing and their production is accentuated by grazing intensity (McNaughton, 1984). McNaughton (1984) expresses the advantage to herbivores of keeping the grass short in order to increase their chances of seeing predators, but also that "grazing lawns increase the quality of food available to herbivores, particularly through enhanced nitrogen content". McNaughton (1984) also states that by keeping the grass low, grazers increase their harvesting rate dramatically – the reward per bite is increased substantially.

Animal impact in the higher rainfall regions is not as great as in the low rainfall regions because grass productivity is so much higher because water is not limiting and hence the dominance by 'bunch' grasses such as *T. triandra*. However, below acacia canopies, higher grazing intensities do shift the community from one dominated by a 'bunch' grass, *P. maximum* which is associated with below canopy communities, to one dominated by the 'lawn grass', *D. australe* (Fig. 8). In the absence of herbivores *P. maximum* is likely to dominate the environment below the canopy however the herbivores, through grazing and trampling, keep the area maintained as lawns of *D. australe*. In the high rainfall areas the proportion of *P. maximum* is higher because of increased productivity and the impact of animals is not as severe as in the low rainfall regions. As the dry season progresses there may be migration of animals into the higher rainfall areas in search of food. However, the dry season is not long enough for the grazers to have a high enough impact so as to shift the vegetation from a community dominated by 'bunch' grasses to one of 'lawn' grasses, a process that is likely to take decades , if at all. The dynamics of the high rainfall systems are driven by fire whereas those of the lower rainfall regions are driven by animals because high grazing levels reduce the fuel load and hence affects fire frequency, intensity and continuity of spread (Savage & Swetnam, 1990). Fires do play a role in the 'lawn' grass systems when animal impact is low or periods of increased rainfall result in increased grass productivity.

Swemmer (1998, unpublished) found no variations in soil nitrogen associated with lawns and bunch grass areas in the HUP. This is in contrast with findings by Ruess and McNaughton (1987) who found that soil total N was higher in short grass sites than in medium to tall grass sites in the Serengeti. Because of Swemmer (1998) findings in HUP, we propose that in the low rainfall areas the grass communities are a result of grazing and trampling by animals, rather than differing nutrient levels, and refugia in the form of small acacias enable the persistence of 'bunch' grasses through reduction in animal impact.

It was hypothesised that 'open' vs adult acacia classes would be more different (ie. greater centroid distance) in the low rainfall than in the high rainfall areas because of the dramatic change in grass productivity caused by adult acacias in the more arid regions (up to 95%, Belsky *et al*, 1993). This was not the case as rainfall did not correlate with 'open' to adult acacia centroid distances ($R^2 = 0.241$, $p = 0.18$) (Fig. 7), hence species compositions below 'open' and adult acacias are equally different in ordination space in low and high rainfall areas.

EFFECT OF SHADE ON BELOW CANOPY SPECIES

A question that arose out of lawn and bunch grass distributions and presence of some species under the acacia canopies and not others was that of shade tolerance. Belsky et al (1989) found that in Kenya, the savanna tree canopy reduces direct and indirect solar radiation reaching the shaded area by 25-90%. The hypothesis here was that some species were associated with the below canopy environment because of their ability to perform well in the shade. It was expected that the two species associated with the below canopy environment, *P. maximum* and *D. australe*, would saturate at a lower light intensity than those associated with the 'open' areas, also that lawn grass would tolerate low light intensities better than bunch grasses because of the likelihood of being shaded. The light response curves showed this not to be the case, with *D. australe* (Fig. 9.6) only saturating at a high light intensity as did those plants associated with open environments (Fig. 9.2, 9.3, 9.4 and 9.5). *Panicum maximum* (Fig 9.1) saturated at a low light intensity as did the other bunch grass considered, *T. triandra* (Fig. 9.2). The results were therefore inconclusive and it is likely other factors such as higher nutrient levels influencing below canopy species. Roos & Allsopp (1997) found increases in N and P in sub-canopy soils below *Acacia sieberana* and a positive influence of isolated trees on soil fertility and mineralisation causing increased plant growth in *P. maximum* independent of microclimate between open and sub-canopy positions. In addition to this, mycorrhizas enhanced growth and phosphorous uptake of *P. maximum*. Belsky *et al* (1993) also found increased nutrient contents below acacias but propose that increased herbaceous production below the canopy was the result of the greater importance of shade in reducing temperatures and evapotranspiration in the more arid environments. However, because we are getting similar 'climax' communities in both high and low rainfall areas below acacia canopies, *P. maximum* and *D. australe*, it is likely to not be only moisture resulting in these 'climax' grass communities.

If it were merely a nutrient or moisture factor then *D. australe* would be found in abundance in areas away from the shade and with high levels of nutrients or moisture associated with them, such as rhino middens or wallows. This is not the case and it is therefore likely to be a combination of factors such as shade, nutrients and moisture resulting in species distribution below acacia canopies.

SUCCESSIONAL SEQUENCES

Low to medium rainfall areas

Succession does seem to be occurring in the HUP with more successional steps evident in the low rainfall than the high rainfall sites as a result of the influence of the 'gullivers' on the grass communities in the low rainfall areas that is not evident in the higher rainfall areas (Fig. 10.1-10.6). The assumption here is that at the low to medium rainfall areas, lawn grass is the dominant state, although a natural mosaic is likely to exist with lawn grasses interspersed with bunch grasses. However, these bunch grass patches exist only because of the refuge from grazers offered by small acacias. Once acacia seedlings have established on a 'lawn' they are particularly resilient and are able to tolerate continual disturbance. The 'seedlings' act as a refuge for the 'bunch' grasses facilitating their establishment (Roberts, 1987), but which are often unable to set seed as the acacia seedlings are low and the flower heads of the 'bunch' grasses are susceptible to grazing. The 'gullivers' are however tall enough to enable grasses to take refuge below them and at the same time set seed. This is vital to prevent local extinction of the bunch grasses (O'Connor, 1994). The percentage of each functional grass type (see Scholes & Archer, 1997), 'bunch' and 'lawn', is likely to vary with varying periods of rainfall (Vetaas, 1992). Droughts will result in the areas being driven more towards 'lawns' through intense grazing and periods of higher rainfall will result in the system tending toward one being dominated by 'bunch' grasses. It is however the direct impact of herbivores, through grazing,

browsing and trampling, that keeps the system in the state it is. Lawn grasses would likely be outcompeted by the 'bunch' grasses in the medium rainfall areas in the absence of grazers (Coughenour, 1985) and the system would shift from one driven by animals to one driven by fire, as is the case in the higher rainfall areas.
When the 'gullivers' escape the grass layer, the fire zone, and become 'young adults' there is little change in the associated grass communities. But when these 'young adults' mature they influence the below canopy grass community and to varying extents depending on whether they are in close proximity to other adult acacias. The difference is more pronounced in the medium rainfall areas than in the low rainfall areas because of increased productivity resulting from adult acacias. The medium rainfall areas allow for the existence of a greater number of species to that of the low rainfall areas in both the open and sub-canopy sites, with different 'lawn' grasses dominating in the different areas.

High rainfall areas

The dominant grass community in the open is that of 'bunch' grass, mainly *T. triandra* with other bunch grass elements such as *Hyparrhenia* and *Cymbopogon* species being present. The presence of 'seedling', 'gulliver' and 'young adult' acacias does not influence the below canopy grass community (Fig. 10.8-10.10) and neither does the 'A1' class to any extent. This is the result of high productivity which results dominance by bunch grass species causing animal impact to be negligible. There is a dramatic compositional shift below the 'A3' class with islands of 'lawn' grass in a 'sea' of 'bunch' grass. In the absence of adult acacias from the system, *D. australe* would go extinct from the area

How dynamic is the system

The changes in the grass communities below dead acacias were more apparent in the high rainfall areas than in the lower rainfall areas (Fig. 10.9, 10.10). The effect of the adult acacias on the below canopy grass communities is longer lasting in the low rainfall areas than in the high rainfall areas (Fig. 10.6, 10.7). The increased soil nutrients, as a result of the adult acacia, are not likely leach out of the area as quickly in the low rainfall areas as they would in the high rainfall areas and this results in the grass communities not shifting back in the successional sequence right away. The grass community below the dead acacias at Thiyeni did not change much once the tree had died (Fig 10.7). This is because the majority of the dead trees were within a woodland of acacias and were not individual trees. Roos and Allsopp (1997) state, "increased tree density results in a reduction of soil nutrient heterogeneity associated with widely spaced trees in savanna landscapes" as well as organic matter content of the soil. Thus, when a tree within a woodland dies, there is less chance of the microhabitat around the tree changing and the grass community reverting to one earlier in the successional sequence.

It is difficult to apply a rate of reversal to the system because of the unsureity of the time since death of the tree. The dead trees were judged to be of similar age because of the amounts of small branches still maintained in the canopy which will likely vary between rainfall sites. For a better idea of the dynamics of the system it would help to know the exact amount of time since the trees death, also including the trees proximity to other adult trees. This however was beyond the scope of this project and will require more time and improved experimental procedures to determine correctly.

Conclusion

The concept of carrying capacity in southern Africa with regard to livestock and wildlife management has placed emphasis on the presence of particular species such as *Themeda triandra* as being important for high productivity. However current views are that lawn grass species are more nutritious and rewarding per unit effort of feeding (McNaughton, 1984) than are the bunch grasses and the previous notions of communal areas being overgrazed are false.

Lawns are favoured by game and their persistence in the lawn grass areas maintains them and decreases both the proportions of bunch grass and the ability for the bunch grasses to establish. In the low rainfall areas the establishment of acacia seedlings on the 'lawns' creates a refuge for the bunch grasses which persist below the small acacias. However, when the acacias break through the fire zone and attain their full stature their influence on below canopy grass communities shifts from one of protection to one associated with differing nutrients, shade and moisture levels as well as allowing for increased disturbance by animals through grazing and trampling. The extent and effect of animal disturbance varies along the rainfall gradient and between closed canopy environments and individual trees, with 'A3' canopies often supporting different communities to those below the 'A1' class. Succession is more evident in the medium to low rainfall areas where there seems to be a sequence of:

open gulliver adult
lawn → bunch → lawn

However, the lawn grass species below the adult acacias, *D. australe*, is different to the 'lawn' grass species associated with open areas.

It is evident that establishment of acacias in the low to medium rainfall areas results in a shift in community structure from 'lawn' to 'bunch' grass and a decrease in productivity associated with 'bunch' grass (McNaughton, 1984). This may have a cascading effect if game move out of the area because of the decreasing productivity resulting in the system shifting to one dominated by 'bunch' grass species. The negative effect of bush encroachment might be part of a natural cycle whereby lawn makes way for eventual acacia woodland which in time senesces and reverts back to a state of lawn. Lawn grasses are likely to persist in isolated areas where disturbance prevents bunch grasses from establishing such as termitaria and water points, until they are 'released' through disturbance events such as increased animal activity or drought periods, at which time they are again able to dominate the environment.

References

Bate, G.C. & Gunton, C., 1982. Nitrogen in *Burkea* savanna. In: Huntley, B.J. & Walker, B.H. (eds), *Ecology of tropical savannas*. Spriger-Verlag, Berlin: 498-513

Begon M., Harper, J.L. & Townsend, C.R., 1996. *Ecology. Individuals, populations and communities*. (ed) Blackwell Science, Oxford, pp 1068.

Belsky, A.J., Amundson, R.G., Duxberry, R.M., Riha, S.J., Ali, A.R. & Mwonga, S.M., 1989. The effects of trees on their physical, chemical and biological environment in a semi-arid savanna in Kenya. *J. Appl. Ecol.*, **26**: 1005-1024.

Belsky, A.J., 1990. Tree/grass ratios in East African savannas: a comparison of existing models. *J. Biogeogr.*, **17**: 483-489.

Belsky, A.J., Mwonga, S.M., Amundson, R.G., Duxbury, J.M. & Ali, A.R., 1993. Comparative effects of isolated trees on their under-canopy environments in high- and low-rainfall savannas. *J. Appl. Ecol.*, **30**: 143-55.

Bond, W.J. & van Wilgen, B.W., (1996). Fire and plants. *Population and Community Biology Series*, 14, Chapman and Hall, London.

Brooks. P.M. & MacDonald, I.A.W., 1983. The Hluhluwe-Umfolozi Reserve: an ecological case history. In: *Management of large mammals in African conservation areas*, (ed) N.R. Owen-Smith: 51-78, Haum Educational Publishers, Pretoria

Carter, A.J & O'Connor, T.G., 1991. A two-phase mosaic in a savanna grassland. *J. Veg. Sci.*, **2**: 231-236.

Coughenour, M.B., 1985. Graminoid responses to grazing by large herbivores: Adaptations, exaptations and interacting processes. *Ann. Missouri Bot. Gard.*, **72**: 852-863.

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

Hara, M., 1987. Analysis of seedling banks of a climax beech forest: ecological importance of seedling sprouts. *Vegetatio*, **71**: 67-74.

Hill, M.O. & Gauch, H.G., 1980. Detrended Correspondence analysis, an improved ordination technique. *Vegetatio*, **42**: 47-58.

Huntley, B.J. & Walker, B.H., 1982. In: *Ecology of tropical savannas*. Springer-Verlag, Berlin.

Mack, R.N. & Thompson, J.N., 1982. Evolution in steppe with few large, hooved mammals. *Amer. Nat.*, **119**: 757-773.

McNaughton, S.J., 1983. Serengeti grassland ecology: The role of composite environmental factors and contingency in community organisation. *Ecol. Monogr.*, **53**: 291-320.

McNaughton, S.J., 1984. Grazing lawns: Animals in herds, plant form, and coevolution. *Am. Nat.*, **124** (6): 863-886.

O'Connor, T.G., 1994. Composition and population responses of an African grassland to rainfall and grazing. *Journal of Applied Ecology*, **31**: 155-171.

Roberts, D.W., 1987. A dynamical system perspective on vegetation theory. *Vegetatio*, **69**: 27-33

Roos, P.C. & Allsopp, N., 1997. Soil nutrient ecology associated with *Acacia sieberana* at different tree densities in a South African savanna. *African Journal of Range & Forage Science*, **14** (2): 39-44.

Ruess, R.W. & McNaughton, S.J., 1987. Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. *Oikos*, **49**: 101-110

Savage, M. & Swetnam, T.W., 1990. Early 19th-century fire decline following sheep pasturing in a Navajo ponderosa pine forest. *Ecology*, **71**: 2374-78.

Scholes, R.J. & Archer, S.R., 1997. Tree-grass interactions in Savanna. *Annu. Rev. Ecol. Syst.*, **28**: 517-44.

Scholes, R.J., Pickett, W.N., Ellery, W.N. & Blackmore, A.C., 1997. Plant functional types in African savannas and grasslands. In Plant functional types: their relevance to ecosystem properties and global change, International Geosphere-Biosphere Programme Book Series 1, (eds) Smith, T.M., Shugart, H.H. and Woodward, F.I., Cambridge University Press, Ch 13.

Stebbins,G.L., 1981. Coevolution of grasses and herbivores. *Ann. Missouri Bot. Gard.*, **68**: 75-86.

Swemmer, T., 1998. The distribution and ecology of grazing lawns in a South African savanna ecosystem. Honours Thesis, University of Cape Town

Ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**: 1167-1179.

Ter Braak, C.J.F. & Smilauer, P., 1988. CANOCO Reference Manual and Users Guide to Canoco for Windows: Software for Canonical Community Ordination(version 4). Microcomputer Power, Ithaca, New York, 325pp.

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

Yarranton, G.A. & Morris, R.G., 1974. Spatial dynamics of primary succession: nucleation. *J. Ecol.*, **62**: 417-428.

	open	seedling	gulliver	YA	A1	A2	A3	Dead
A.con	0.19	0.11	0.12	-	-	-	-	-
A.diffusa	0.10	0.04	0.08	-	0.02	-	-	-
A.e	-	-	0.03	-	-	-	-	-
B. pelthof	0.02	-	-	-	0.02	0.05	0.20	-
B.bladii	-	-	-	-	-	-	-	-
B.ins	0.45	0.30	0.34	0.67	0.37	0.13	-	0.14
C.falc.	-	-	-	-	-	-	-	-
C.gay	0.18	0.26	0.17	0.13	0.17	0.10	0.10	0.36
Cymbo s	0.01	0.03	0.03	0.25	0.04	-	-	-
D.aust	0.07	0.09	-	0.03	0.29	1.07	1.55	1.11
D.erian	0.07	0.07	0.08	0.13	-	0.01	-	0.10
D.long	0.93	0.69	0.35	0.69	0.19	-	0.04	0.15
E.curv	0.11	0.14	0.19	0.70	0.39	0.33	0.29	0.79
E.p	0.11	0.08	0.08	0.03	0.01	0.03	-	-
E.pannicl	0.04	-	-	-	-	-	-	-
E.pasp	0.03	0.03	0.03	-	-	-	-	-
E.sup	0.53	0.52	0.30	0.18	0.24	0.05	-	0.09
H.cont	0.04	-	0.03	0.03	0.02	-	-	0.03
H.fili	0.01	0.01	0.07	-	0.05	-	-	0.06
H.hecta	-	-	-	-	-	-	-	-
M.repens	0.01	-	-	-	-	-	-	-
P.col.	0.32	0.03	0.02	0.03	0.05	-	-	-
P.deust	0.01	-	0.01	0.05	0.11	-	0.13	0.13
P.max	0.31	0.94	1.23	0.66	2.07	2.19	2.01	1.51
S. nigro	-	-	-	-	0.01	0.03	-	0.09
S. woodii	-	-	-	-	-	-	-	-
S.nit	0.08	0.04	-	-	-	-	-	-
S.pyr.	0.23	0.26	0.24	0.62	0.48	0.46	0.41	0.55
Setaria sp	0.06	0.04	0.06	0.08	0.20	0.04	-	0.13
T.triandra	0.85	0.87	1.22	1.83	0.65	0.28	0.20	0.81
U. mos	0.46	0.18	0.07	-	0.09	0.07	-	-

Appendix 1: Average abundance of grass species below the representative acacia size classes for the low rainfall sites.

	open	gulliver	YA	A1	A2	A3	Dead
A.con	-	-	-	-	-	-	-
A.diffusa	-	-	-	-	-	-	-
A.e	-	-	-	-	-	-	-
B. pelthof	-	-	-	-	-	-	-
B.bladii	0.12	0.03	-	-	-	-	0.10
B.ins	0.09	0.03	0.50	0.29	0.15	0.17	0.10
C.falc.	0.15	0.07	-	-	0.23	-	0.10
C.gay	0.62	0.52	-	0.38	0.18	0.09	0.71
Cymbo	0.54	0.57	0.50	0.75	0.50	0.26	0.89
D.aust	0.09	0.06	-	0.19	1.08	1.91	0.51
D.erian	-	-	-	-	-	-	-
D.long	-	-	-	-	-	-	-
E.curv	0.94	0.60	-	0.68	0.40	0.42	0.38
E.p	-	-	-	-	-	-	-
E.pannicle	-	-	-	-	-	-	-
E.pasp	-	-	-	-	-	-	-
E.sup	-	-	-	0.08	-	0.05	-
H.cont	-	0.07	-	-	-	-	-
H.fili	0.08	0.23	-	0.21	0.08	-	0.07
H.hecta	0.14	0.13	-	0.13	0.08	0.04	0.07
M.repens	-	0.03	-	-	-	-	-
P.col.	0.16	-	-	-	-	0.04	0.05
P.deust	0.39	0.72	-	0.75	0.50	0.64	0.94
P.max	0.90	0.91	2.50	1.64	2.17	1.76	1.33
S. nigro	-	-	-	-	-	-	-
S. woodii	0.11	0.10	-	-	-	-	0.03
S.nit	-	-	-	-	-	-	-
S.pyr.	0.11	0.06	-	0.26	0.33	0.61	0.24
Setaria sp.	0.03	0.10	-	0.16	0.17	0.04	-
T.triandra	0.74	0.93	1.50	0.88	0.33	-	0.58
U. mos	-	-	-	-	-	-	-

Appendix 2: Average abundance of grass species below the representative acacia size classes for the high rainfall sites.