

**THE RESPONSES OF GRASSES
TO FIRE AND BUSH CLEARING IN
THE HLUHLUWE GAME RESERVE**

PHILIP MARK GRAHAM

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DECLARATION

This thesis is the result of the author's original work, unless specifically stated to the contrary in the text. It has not been submitted for any degree or examination at any other University.

P.M. Graham

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ABSTRACT

Contemporary and historical studies of the flora of the Hluhluwe Game Reserve (HGR), have emphasised the woody component whilst little work has been performed on the herbaceous vegetation. This is particularly true with regard to the responses of grasses to historical fire and bush clearing. This study attempted to elucidate some of these responses.

Of all the variables considered in this study, woody cover, altitude, the number of fire events, geological and soil parent material are the most important affecting the abundance of grasses in this reserve. Most of these variables are not independent in their effects on grass abundance, with varying degrees of correlation between each other. Certain species appear to be restricted to particular geological substrates.

Along with successional changes in the composition and cover of the woody community, due to seemingly inevitable bush encroachment, there is a parallel change in grassland communities in this reserve. In the absence of clearing, numerous fires, higher altitudes, igneous geology and soils derived from igneous parent material delays this succession, whilst sedimentary geology at lower altitudes and fire frequencies accelerates the trend to high woody cover and associated grass species.

The grass communities in HGR were shown to be significantly affected by bush clearing and fire. Specifically the number of clearings and fire events, physical bush clearing during 1957 - 1963 and chemical bush clearing during 1968 - 1978.

From the responses of species in relation to the various key environmental variables, viz. geological substrate, woody cover and burning and clearing, a model of species response to these variables was developed. With increased fire and bush clearing frequency, the grass communities shift from closed woodland,

shade tolerant species through to more open fire climax grassland. These are also more productive communities producing palatable grasses.

Validation of aspects of the model were successful - the model having a relatively high predictive capability. Further testing of the model over different substrates and under different clearing regimes is necessary.

With regular fires and re-clearing in some bush cleared areas, the vegetation of this reserve should be able to be maintained as productive and diverse grasslands. In the absence of this management, the grass communities will shift towards species associated with woodlands. Bush clearing activities would appear to be most effective over sites on igneous substrate, at higher altitudes, where successional rates are slowest. This is in comparison to sites at lower altitudes over sedimentary geology.

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CHAPTER 1

INTRODUCTION

Bush encroachment - the ecological process whereby a grass dominated community changes into one dominated by woody species (Strang 1973) - is widespread in southern Africa. This encroachment has been identified as a problem in many conservation areas (Wills and Whately 1983). The result is typically a decrease in grass cover, with a parallel reduction in grazer carrying capacity of an area (eg. Ward 1962). For wildlife managers and conservationists this represents a loss of habitats and species diversity. Where tourist utilization of these areas is important, the reduced visibility for game viewing, is also an undesirable feature.

Although there was no systematic vegetation monitoring after the proclamation of Hluhluwe Game Reserve in 1897, Bourquin and Hitchins (1979) after reviewing the available records and literature for the reserve, conclude that bush encroachment was taking place by 1949. By the early 1950's it was recognised as a major problem in the Hluhluwe Game Reserve (HGR) (Ward 1957, Brooks and MacDonald 1983), with control measures being implemented by 1957. Watson and MacDonald (1983) identified a progressive increase in tree canopy cover, over the period 1937 to 1975, of the order of 14% to 20%. King (1987) estimated that the pure grasslands in HGR had been reduced by 50% between 1937 and 1982.

This decrease in extent of grassland and its replacement in many areas by woody vegetation was initially described verbally. It has since been described quantitatively (Bourquin and Hitchins 1979; Downing 1980; Watson and MacDonald 1983; Wills and Whately 1983; King 1987). Ward (1962) views the open grassland in Hluhluwe as a seral stage of the vegetation that is climatically

and edaphically a potential forest climax. He feels, however, that it may be prevented from progressing to this stage by being subjected to periodic fires.

Bush encroachment appears to have taken place throughout the reserve, not being concentrated in any one habitat or vegetation type (Wills and Whately 1983). King (1987) states that there are no altitudinal or soil restrictions to all of HGR being woodland and forest.

At different times since 1959 stands of vegetation invaded by 'problem' encroaching species have been cleared of woody vegetation and subsequently burnt at various intervals. This, and previous work on vegetation changes in HGR, has emphasized the woody component (Ward 1957, Bourquin and Hitchins 1979; Downing 1980; Brooks and MacDonald 1983; Watson and MacDonald 1983; Wills and Whately 1983; King 1987). Herbaceous vegetation, on the other hand, has received little attention particularly with regard to its response to the historical fire and bush clearing regime. There was therefore a need to determine the effects of these practices on the community composition and structure of the herbaceous layer in this reserve.

CHAPTER 2

OBJECTIVES OF STUDY

Historically the woody component of vegetation in this reserve has received significant attention. The grass component on the other hand, has been poorly researched, particularly with regard to their response to bush clearing and fire regime. This study was designed to redress this situation.

The overall aim of this dissertation is to examine the responses of grasses to fire and bush clearing in different habitats in HGR.

Within this broad aim, specific objectives were to:

- 2.1 Establish which of a range of selected environmental variables (Table 2.1) are important in affecting the volume abundance of grasses in uncleared areas
- 2.2 Establish which of a range of selected environmental variables (Table 2.1) are important in affecting the volume abundance of grasses in bush cleared areas
- 2.3 Establish a model of species response to key environmental variables in bush cleared and uncleared areas
- 2.4 On a site of known clearing history, test the model developed in the previous objective
- 2.5 Infer the likely consequences of disturbance by fire and bush clearing on herbaceous vegetation in HGR.

**Table 2.1: List and explanation of all environmental variables considered as possibly important in bush cleared and uncleared areas
(Variables restricted to uncleared areas marked *)**

Name of variable	Description of variable
ALTIT *	Altitude as height above sea level (m)
ASPT_N *	Northern aspects
ASPT_E *	Eastern aspects
ASPT_S *	Southern aspects
ASPT_W *	Western aspects
MID *	Mid-slope topographic position
FOOT *	Foot-slope topographic position
DRAIN *	Distance to drainage line (m)
WD_COV *	% Woody cover
NO_FR	Number of fire events
CLEAR	Cleared or uncleared
NO_CL	Number of clearing events
TSLC	Time since last clearing
OLD	Old clearing (1957 - 1965)
MEDIM	Cleared in medium term (1968 - 1978)
RECNT	Cleared recently (1984 - 1989)
E_CHEM	Early chemical clearing
E_PHYS	Early physical clearing
M_CHEM	Medium term chemical clearing
M_PHYS	Medium term physical clearing
R_CHEM	Recent chemical clearing
R_PHYS	Recent physical clearing
G_IGN *	Igneous derived geology
G_SED *	Sedimentary derived geology
S_IGN *	Igneous derived soils
S_SED *	Sedimentary derived soils

CHAPTER 3

LITERATURE REVIEW

3.1 Successional theory and models

Central to an understanding of the community structure of all plant communities are the dynamics of succession (Huston and Smith 1987). Drury and Nisbet (1973) observed that although succession is a temporal phenomenon, most of the evidence for successional change comes from spatial sequences of vegetation on adjacent sites, and they argued that a general theory of succession should explain both temporal and spatial patterns.

Terrestrial plant succession, generally defined as "the dynamics of plant populations on an initially bare substrate" (Tilman 1988) has been the subject of ecological debate since the turn of the century (Cowles 1899; Cooper 1913; Clements 1916; Gleason 1917, 1927). Although recent work has clarified some of the patterns and mechanisms of succession (Drury and Nisbet 1973; Connell and Slatyer 1977; MacMahon 1981), the continuing generation of hypotheses suggests that this phenomenon is still not fully understood. Ecology has still yet to produce a general unifying theory based on all the underlying processes common to all successions (Finnegan 1984; Huston and Smith 1987).

Current ecological theory allows for alternative stable states, discontinuous and irreversible transitions, non-equilibrium communities and stochastic effects in succession (eg. Drury and Nisbet 1973; Connell and Slatyer 1977; May 1977; Noble and Slatyer 1980; Price *et al.* 1984; Strong *et al.* 1984).

The typical model of succession that had been applied to southern African savannas up until the early 1980's had been Clementsian-Tansleysian in origin.

Essentially this model states that systems possess stability and that when their state was shifted by disturbance, the equilibrium was then re-established. The contemporary view of savanna functioning is now interpreted in terms of both equilibrium and non-equilibrium theories (Mentis and Bailey 1990).

Non-equilibrium theory does not assume systems have stable properties. Rather there are a number of possible states that a system can exist in and which are dictated by primary determinants eg. plant available moisture (PAM) and available nutrients (AN). Within these possible states, secondary determinants eg. fire, herbivory and other forms of disturbance, are superimposed. These act as events over a range of spatio-temporal scales, to create patch diversity. The dynamics of savannas are seen to be driven by these events. Any given site will therefore occupy a 'home range' in the PAM/AN plane, but which may be moved about in this plane by variations in secondary determinants as well as short term variations in moisture and nutrient supply. This implies an event driven model of savanna functioning (Frost *et al.* 1986).

This contemporary view of savannas explains their characteristic spatio-temporal diversity better than the orthodox equilibrium model. Environmental conditions, except where artificially constrained, are never uniform for long enough for competitively superior species to oust competitively inferior ones. With temporal fluctuations in conditions then, variety is maintained. To maintain diversity driving variables must be kept diverse (Mentis and Bailey 1990).

3.2 Structure of savannas

The structure of savannas comprises woody vegetation, which may be divided into established mature trees, shrubs and saplings, and herbaceous vegetation. This latter type is dominated by perennial grasses and consists of two main types:

those grasses occurring in the open areas between trees and those occurring in the sub-canopy areas, (Tinley 1982).

Several authors have suggested that the inherent basic structure of 'climax' savanna vegetation has been extensively modified by fire (West 1971; Phillips 1974; Kruger 1984), man (Feely 1980; Hall 1984a) and herbivores (Vesey-Fitzgerald 1973; McNaughton 1976; Pratt and Gwynne 1977). Werger (1978) maintains that the greater proportion of open savannas are in fact derived grasslands which have been largely shaped and maintained by fire, man and large herbivores. But for these influences, most of these open formations receiving > 500 mm rainfall p.a. would be either forest or closed woodland.

3.3 Determinants of savannas

3.3.1 Climate

On the basis of Thornthwaite's (1948) classification, the major tropical savannas fall within the CA'w category ie. medium precipitation (c.300 mm/yr to c.1000 mm/yr), high temperatures (15° to 35° C), with wet summers and dry winters. Rainfall in these areas occurs over a short (4 to 5 month) period in summer, with the bulk of it coming as relatively heavy downpours.

The topsoil dries out soon after the end of the rains, although subsoil water is available for much longer (Tinley 1982). Walker and Noy-Meir (1982) feel that the most important feature affecting the ratio of grass and woody vegetation of a savanna is this alternating wet and dry soil phase. Cole (1982) and Tinley (1982) emphasize the importance of the soil water balance in determining savanna types and the fact that this balance is determined by rainfall, soil type (texture), soil depth and geomorphology. The high temperatures characteristic of savannas lead

to reduced rainfall efficiency (due to high evaporation) and laterization (Walker 1985).

3.3.2 Soils

Cole (1982) has reviewed the influence of physicochemical factors on the distribution of plant communities in savannas, and concludes that within climatic limits, the main control was exerted by edaphic factors. Bell (1982) too, states that for a given rainfall regime, a major ecological distinction is possible between dystrophic sandy soils and eutrophic clay soils.

Mott *et al.* (1985) conclude from work in Australian savannas that nutrients and light, as well as water, affect the grass:wood ratio. Frost *et al.* (1986) in an examination of several savanna ecosystems, consider plant available moisture (PAM) and available nutrients (AN), as the most important determinants of savannas. These may vary in both time and space and constitute a gradient along which the various savanna types, in terms of their grass:woody ratios, are positioned.

Soil particle size (texture) affects much of the nutrient, aeration and moisture relations in savanna soils (Tinley 1982) whilst dead organic matter has been shown to be important as nutrient reservoirs for intra-system cycling (Singh and Gupta 1977). Strain and Billings (1974) claim that over long time periods, vegetation is one of the main factors influencing soil properties. Anaerobic conditions limit root depth (Anderson and Herlocker 1973; Tinley 1982) and as a result grassland communities do better on heavily textured soils. Better drained soils with larger particle sizes, will support more woody species.

Bosch and van Wyk (1970) found that soils under trees in the western Transvaal were enriched in N, P, Ca, Mg and K compared to soils in the open. Whilst

Dyer (1983) found evidence of changes in the relative distribution of some soil cations (Ca, Mg and Na) in the soil profile as a result of changes in the woody-grass ratio in a range of savanna types in southern Africa.

In the southern African context there appears to be a recurring sequence of denser woodland savanna on coarse textured upper slopes, through scrubby mixed savanna on shallower soils in the mid-slope region, to taller trees in open savanna on the deeper, heavier soils in the illuvial zone of the catena (Walker 1985).

Fire and herbivores are the two most important forms of disturbance which modify the inherent structure imposed on savannas by climate and soil type (Walker 1982).

3.3.3 Fire

Fire climaxes or pyroseres are common in Africa (Booyesen and Tainton 1984). Regular fires are one of the characteristic features of tropical savannas, and while some are still caused by lightning (Komarek 1971; West 1972) the main source of ignition for the past tens of thousands of years has been man (West 1972; Phillips 1974). This influence has been so extensive that some authors suggest that current tropical savannas are anthropogenic systems derived from deforestation and repeated burning (Rawitscher 1948; Budowski 1956; Clayton 1961). It is only since the advent of the Europeans in southern Africa, leading to the protection from fires in extensive areas, that this trend has been altered to one which favours woody plants and harms grasses (Lamprechts 1974).

Savanna grasses have life cycle, morphological and physiological adaptations to fire which include: dormant buds, at or below ground level, that are largely protected from fire in the dry season during burns; a tillering habit in the face of

frequent burns; underground rhizomes, or stolons at or close to the surface, which possess tiller initials, able to develop after defoliation; the tendency of the meristematic apex of the grass stem to remain near the soil surface during vegetative growth to survive defoliation; the apex being completely surrounded by the old sheath bases of earlier formed leaves, which provides insulation against temperature extremes; and with crown or surface head fires they are able to tolerate the heat as the majority of the heat energy is released away from the shoot apices of these species (Tainton and Mentis 1984; Trollope 1984).

Woody savanna species also have adaptations to fire which include: very thick, well insulated bark which is highly resistant to intense fires eg. *Acacia sieberana* (West 1971); an ability to coppice from axillary buds, located in the collar region, after fires (Trollope 1984); and cryptogean germination which ensures that the root crown develops below the soil surface and therefore protects the dormant bud from fire (Jackson 1974).

Much attention has been given to the effect of fire on the grass:woody ratio in South African savannas (Scott 1947, 1971; Donaldson 1969; Roux 1969; West 1969; Trollope 1984). Generally fire favours the development and maintenance of a predominantly grassland vegetation by retarding young trees and shrubs and preventing the development of more mature plants to a taller fire resistant stage. Once woody species become dominant however, and are suppressing grass, fire no longer affects the former significantly because of insufficient grass fuel for intense fires.

Trollope (1984) feels that the 600 mm/yr isohyet for South African savannas is critical in affecting the grass:woody balance. Above this rainfall figure it is possible to maintain the grass:woody balance with fire alone, because despite coppicing by the woody species, rainfall is sufficient and reliable enough to accumulate enough grass material under grazing conditions to support frequent fires. These burn coppice growth and control bush seedlings. In drier areas

(<600 mm/yr) the rainfall is insufficient to accumulate enough fuel under grazing conditions for adequate fires.

Current theory suggests that fire is only one of a number of interacting factors affecting savanna structure and dynamics, (Huntley and Walker 1982; Bourliere 1983; Tothill and Mott 1985).

3.3.4 Herbivory

The major, direct influences of herbivores are of two main kinds. The first is the direct short term effects on vegetation structure, ie. the conversion of woodland to grassland by elephants, and the second are the effects which have developed over evolutionary time. For example the development of defences against herbivory - spines, thorns, silica bodies and chemical compounds, and by altering growth processes and responding positively to defoliation (Walker 1985).

Large herbivores encourage grassland at the expense of woody vegetation, (West 1971; Vesey-Fitzgerald 1973; Pratt and Gwynne 1977). Noy-Meir (1982) has indicated that this is probably an indirect effect resulting from competitive release of the grass species when woodland species are damaged or killed by large mammals. Verkaar (1987) maintains that herbivory affects plants not only in the vegetative and reproductive phases, but also in the pre- and post-dispersal phases of seeds. Chew (1974) and Mattson and Addy (1975) suggest that consumers, especially insects, regulate whole ecosystems through seed predation.

3.4 Dynamics and the competitive interaction between trees and the herbaceous layer

Tinley (1982) is of the opinion that the most important factor determining the spatial distribution of forest, savanna and grasslands in southern Africa, is soil moisture balance. This view is also supported by Walker (1980), Walker *et al.* (1981) and Walker and Noy-Meir (1982).

A model proposed by Knoop and Walker (1985) suggests that the proportion of grass to bush is determined by the proportion of water input into the top and subsoil layers. They argue that grasses use water only from the upper soil layers where it is the superior competitor. Woody vegetation on the other hand, although using some topsoil water, has exclusive use of subsoil water.

Severe or heavy utilization of the herbaceous layer, results in a reduction in water input into the topsoil as infiltration is reduced (van den Berg *et al.* 1976; Gifford 1984). This lowered infiltration does not affect the deep rooted tree component to the same extent as the relatively shallower rooted herbaceous layer. Hence the woody vegetation receives proportionally more water than the herbaceous layer and the open savanna structure tends to woody thicket where grass is insignificant (Knoop and Walker 1985).

Stuart-Hill (1985), working in a savanna in the eastern Cape, proposed an hypothesis which suggests that a sparse, degenerate herbaceous layer has a low evapotranspiration rate and therefore extracts water more slowly compared to an actively growing, dense herbaceous layer. This permits water from successive rains to accumulate in the profile, resulting in deeper infiltration under low grass cover than beneath a vigorous and active sward. Trees subsequently have a competitive advantage if the sward is damaged, because of an absolute increase in the amount of water reaching deep soil layers and not merely a proportional increase.

Stuart-Hill (op cit.) measured a consistent pattern of grass production around *A. karoo* trees, in which high yields occurred under the tree canopy, and lower yields immediately to the north of the canopy. He attributed the high yields to shade, tree leaf litter and favourable soil nitrogen relations; and low yields to rainfall redistribution around the trees. Trees of all sizes were observed influencing the grass up to at least 9m away from their stems. Even at low tree densities of 39 trees per ha, the entire grass sward in the area was under the competitive influence of the trees. Smith and Walker (1983) note that the larger the tree the larger will be its area of resource depletion and the greater the competitive effect on its neighbours.

Brown and Booysen (1967) noted that seedlings of *A. nilotica* and *A. tortilis* growing in competition with grass cover tended to be tall and spindly with relatively long internodes, whereas seedlings growing in the absence of grass, tended to be short and sturdy with short internodes. The seedlings growing in dense grass cover also tended to show the effects of moisture stress far sooner than those seedlings growing in the absence of grass. They hypothesized that the grass competed with the seedlings for light and moisture and also probably hindered the development of the seedling root system. This has been corroborated by subsequent work by Walker *et al.* (1981), Knoop and Walker (1983) and Stuart-Hill (1985).

CHAPTER 4

STUDY AREA

4.1 Location

The study area is the Hluhluwe Game Reserve (HGR) in central Zululand, Natal, South Africa, lying between 28°00' and 28°10' south and 32°00' and 32°10' east (Figs. 4.1 and 4.2). The area occupies the foothills of the first escarpment to the west of the coastal plain, and forms the north-eastern portion of the Hluhluwe-Corridor-Umfolozi Complex of the Natal Parks, Game and Fish Preservation Board.

4.2 Geology

The general structure of the HGR is a faulted monocline with the rock units dipping approximately 10 degrees to the east. The oldest formations, the granite-gneiss of the Archaean Complex, lie in the west, alongside which lie the medium to coarse grained quartzitic sandstones of the Natal Group. There are also areas of Dwyka tillite on this western boundary. The central Reserve is comprised mainly of sandstones and shales of the Volksrust, Vryheid and Pietermaritzburg Formation, all of the Ecca Group, whilst the eastern part is covered by shales and sandstones of the Beaufort Group. Dolerite has intruded extensively into these formations in the form of dykes and sills with Whatekys (pers. comm.) being of the opinion that these dolerite formations may be more extensive than is currently indicated in the literature (King 1970). Basalt lava of the Letaba Formation, Lebombo Group, also occurs on this eastern boundary. The general disposition is broken by roughly north-south parallel faults which complicate the geological pattern. Young alluvium has been deposited along the Nzimane and Hluhluwe

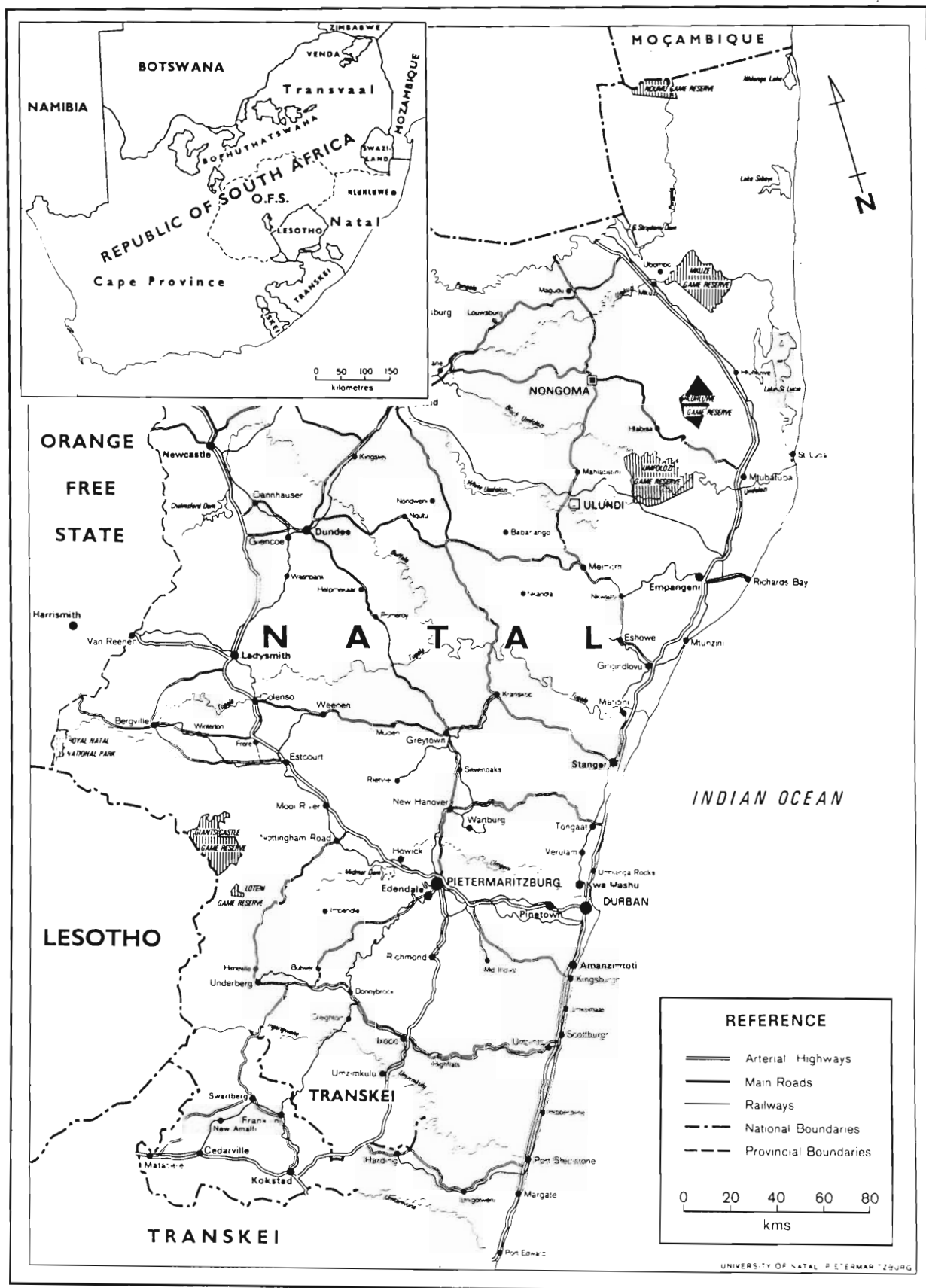


Figure 4.1 Location of the Hluhluwe Game Reserve within southern Africa and Natal.

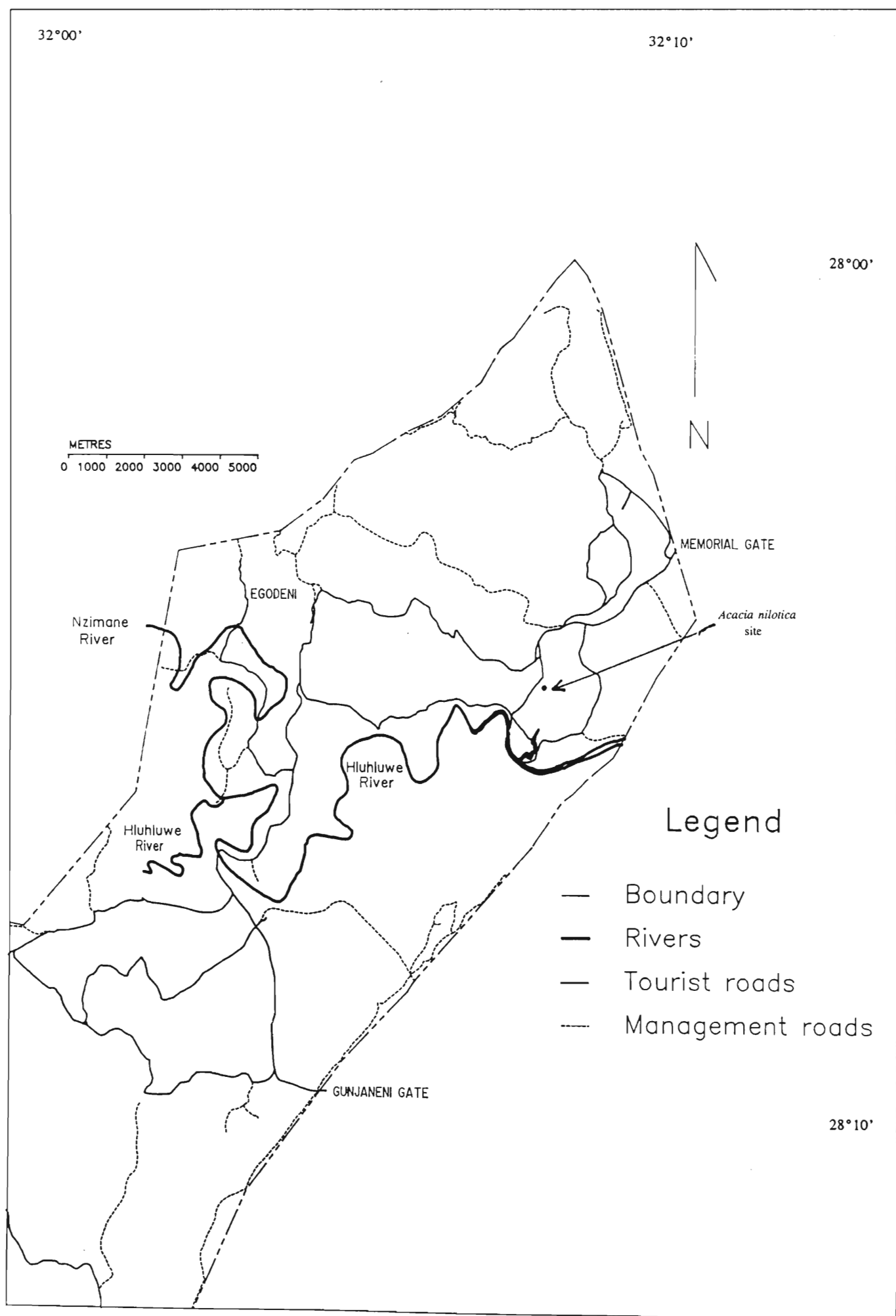


Figure 4.2 Base map of Hluhluwe Game Reserve showing the boundary, major rivers, tourist and management roads as well as the *Acacia nilotica* study site

Rivers (King op cit.; SACS 1980; Whately and Porter 1983; Barrow 1986). The geological map of the reserve is shown in Figure 4.3 (after King op cit.).

4.3 Soils

The soils found in this Reserve are largely "typical" in their occurrence with respect to geology, and terrain position. Barrow (1986) has recognised 19 soil forms and 38 soil series (McVicar *et al.* 1977) for the Reserve. Of these the predominant upland and midslope soils are Hutton and Shortlands (deep phase) and Glenrosa, Mispah, Mayo and Milkwood (shallow phase). The bottomland soils are Oakleaf, Valsrivier, Fernwood, Bonheim and Inhoek (all deep phase). Dolerite is thought to be the dominant pedogenic factor, giving rise to the high clay Hutton and Shortlands forms.

4.4 Topography

The area considered in this study centres on the two valleys of the Hluhluwe, and its tributary, the Nzimane River. (Fig. 4.2). Throughout the reserve the topography is bisected by essentially ephemeral water courses with only three main perennial rivers, namely the Hluhluwe, the Nzimane and the Mansiya converging in the south to continue as the Hluhluwe. The southern and south-eastern portions of the Reserve are undulating whilst in the west the slopes are steeper and the country more broken. The north and north-west have steep slopes, although not as broken as the west. Altitude ranges from ca. 90 m a.s.l., at the point where the Hluhluwe River leaves the Reserve, to ca. 580 m a.s.l. at the highest point on the northwest boundary.

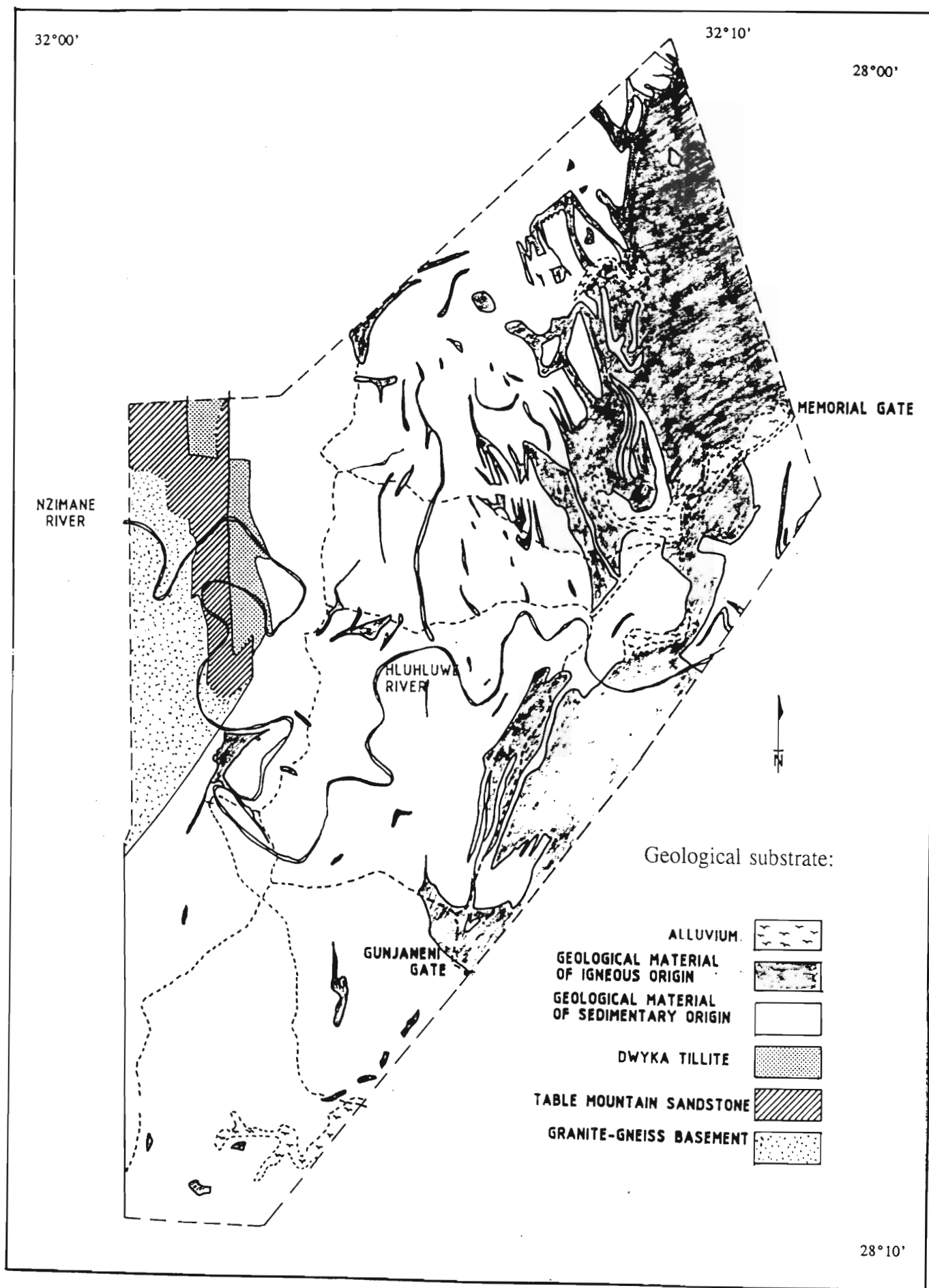


Figure 4.3 Geological map of the Hluhluwe Game Reserve.

4.5 Climate

Rainfall for the Reserve shows an annual mean of 978.2 mm (n=54) (measured at Egodeni on the north-western boundary), with a recognised precipitation gradient going from north to south and from west to east (Wills pers. comm.; King 1987). Annual means for HGR at Memorial Gate (in the northeast) and Gunjaneni Gate (in the southeast) being 771.3 mm (n=19) and 671.0 mm (n=26) respectively (Fig. 4.2). The wet season runs from October through to March with the highest monthly mean being February (148.7 mm) and the lowest June (26.5 mm) (King 1987).

Prevailing winds are generally from the north and south. The south tend to be the rain-bearing winds with thunderstorms occurring with the west, southwest and northwest winds. There are frequent mists in the summer months above 300m above sea level.

The mean annual temperature at Egodeni in the reserve is 18.5°C, with the highest and lowest mean monthly temperatures occurring in January (25.9°C) and September (11.5°C) respectively. The highest recorded summer temperature has been 40°C and the lowest winter temperature 4°C with frost undetected by the stations (Barrow 1986; King 1987).

4.6 Vegetation

The first attempt at mapping the vegetation in this region was made by Aitken and Gale (1921) which depicts the area covered by HGR as an *Acacia* dominated thornveld. Later Curzon (in Henkel 1937) published an account and map of the floral regions of Zululand in which he related the different plant communities to the distribution of the Tsetse fly (*Glossina* spp.). Henkel (1937) produced the earliest known descriptions, as well as the first vegetation map, specifically for

the reserve. In his work Henkel (op cit.) describes the vegetation then as comprising mainly woodlands and parkland savannas, with large expanses of open grasslands. In 1952, Acocks (1988) recognized two major veld types within HGR, namely the Zululand Thornveld (type 6), which is a Coastal Tropical Forest Type and the Lowveld Tropical Bush and Savanna (type 10). Of these, it is the former which is the major veld type in HGR and which may be further divided into two subtypes, a low and high altitude form. These areas correspond to Phillips (1973) bioclimatic regions nine and ten.

Ward (1961) was the first to compile a preliminary physiognomic map of HGR. In 1975 Whately improved upon this situation with a map at a scale 1:25 000, of the woody communities occurring in the Complex. The physiognomy of the vegetation in this area has been variously described as forest, savanna woodland, savanna (various types), woodland, wooded grassland, bushland thicket and induced types (Anon. 1956; Pratt *et al.* 1966; Greenway 1973). Whately and Porter (1983) provide the most comprehensive account of the vegetation in the reserve to date. They use the conventions of Phillips (1973) which gives the following vegetation types: forest, woodland, open woodland, bushland thicket and grassland, as well as an induced thicket category described by Pratt *et al.* (1966).

4.7 History of the area

Recent archaeological research has placed the known beginnings of Early Iron Age man's occupation of the Natal coast, and valley lowlands at A.D. 290 (Feely 1980) with continuous occupancy over the past 1600 years (Feely 1980). Penner (1970) puts man as occupying the area almost continuously, for the past half million years. The abundance of Late Iron Age and Early Iron Age sites in the Zululand game reserves, including Hluhluwe, testifies to these early human influences on the system. These people probably exploited the environment by

cutting down trees for iron smelting, domestic heating and home construction, as well as field clearance for cultivation, with probably only limited areas never used (Feely 1980). There is also evidence that suggests that these people often burnt the veld in winter to encourage a green flush, and so attract grazing game, as did the Zulu people when they moved into the area (Hall 1979a;b; Hall 1984a; Feely 1980). Thus the presence of fire, and these latest archaeological discoveries reveal that man was around for sufficient time to have been a cause of vegetation modification.

Indications are that the historical densities of grazing ungulates were low by comparison with the densities recorded in the 1950's and 1960's, with the Rinderpest in 1896 reducing the game numbers in Zululand generally (Bourquin and Hitchins 1979). Outbreaks of disease such as this probably occurred periodically in Africa. This, in combination with the natural migration patterns, ensured that no single area was severely overutilized for any great length of time. With the proclamation of Hluhluwe Game Reserve in 1896, and later fencing the boundaries, game densities increased within the reserve, although the Ngana campaign during the 1920's and 1930's kept the game densities relatively low. By 1954 there were areas in the reserve that were almost without grass (Bourquin and Hitchins 1979), although this did correspond with a period of low rainfall (1950 - 1954).

The reduced frequency of burning, attributable to the high ungulate densities over an extended period that has kept fuel loads down, and the removal of other human influences, following the reserves proclamation, are seen as fundamental factors responsible for the recent increases in woody plant communities in HGR (Watson and MacDonald 1983).

Direct physical control methods, over the period 1957 to 1977, which include digging, cutting, application of herbicides, combinations of cutting and herbicides, partial cutting, pulling with a tractor and cable and hydrastumping, have yielded poor results in the control of bush encroachment (Wills and Whately 1983).

CHAPTER 5

THE EFFECTS OF SELECTED ABIOTIC AND BIOTIC FACTORS ON THE GRASS LAYER

The study was carried out in two phases:

- (I) an hypothesis and model generation phase, and;
- (II) a model testing phase.

I Hypothesis and model generation

The objective in making quantitative estimates of vegetation in this study includes achieving an estimate of the composition of the herbaceous vegetation within certain treatment areas; and, a correlation of herbaceous vegetation differences with differences in habitat factors in that stratum. From these results a descriptive model of species response to key environmental variables identified for cleared and uncleared areas in HGR is hypothesized.

To achieve this the following key questions were addressed:

Which environmental variables are important in affecting grasses in uncleared areas ?

Is grass composition influenced by bush clearing and fire ?

Which environmental variables are important in affecting grasses in cleared areas ?

What grass species occur in different vegetation types associated with bush clearing in HGR ?

5.1. Methods

5.1.1 Sample site location

In order to determine the effects of bush clearing on the grass layer, historically bush cleared areas were sampled together with adjacent ‘uncleared’ stands of the ‘original woody community’ which occurred on similar geology, soil type, aspect, topographic position, altitude and rainfall regime. Sites selected were chosen to represent as far as possible contrasts in bush clearing history. This therefore represented a primary stratification of sites with respect to bush clearing.

A further consideration was that all sample sites be restricted to a similar, relatively narrow, range of altitude, 100m to 200m (mean 147m). This was to reduce the confounding effects of topographic rainfall on herbaceous vegetation variability. This phenomenon of rainfall increasing with altitude has been observed for this reserve (Wills pers. comm.).

5.1.2 Bush clearing treatments

All available historical records, related to bush clearing in HGR, from 1957 to 21989, were extracted. These primarily took the form of maps with supplementary notes. Most maps detailed areas cleared, species removed, method of removal and dates of the clearing exercise.

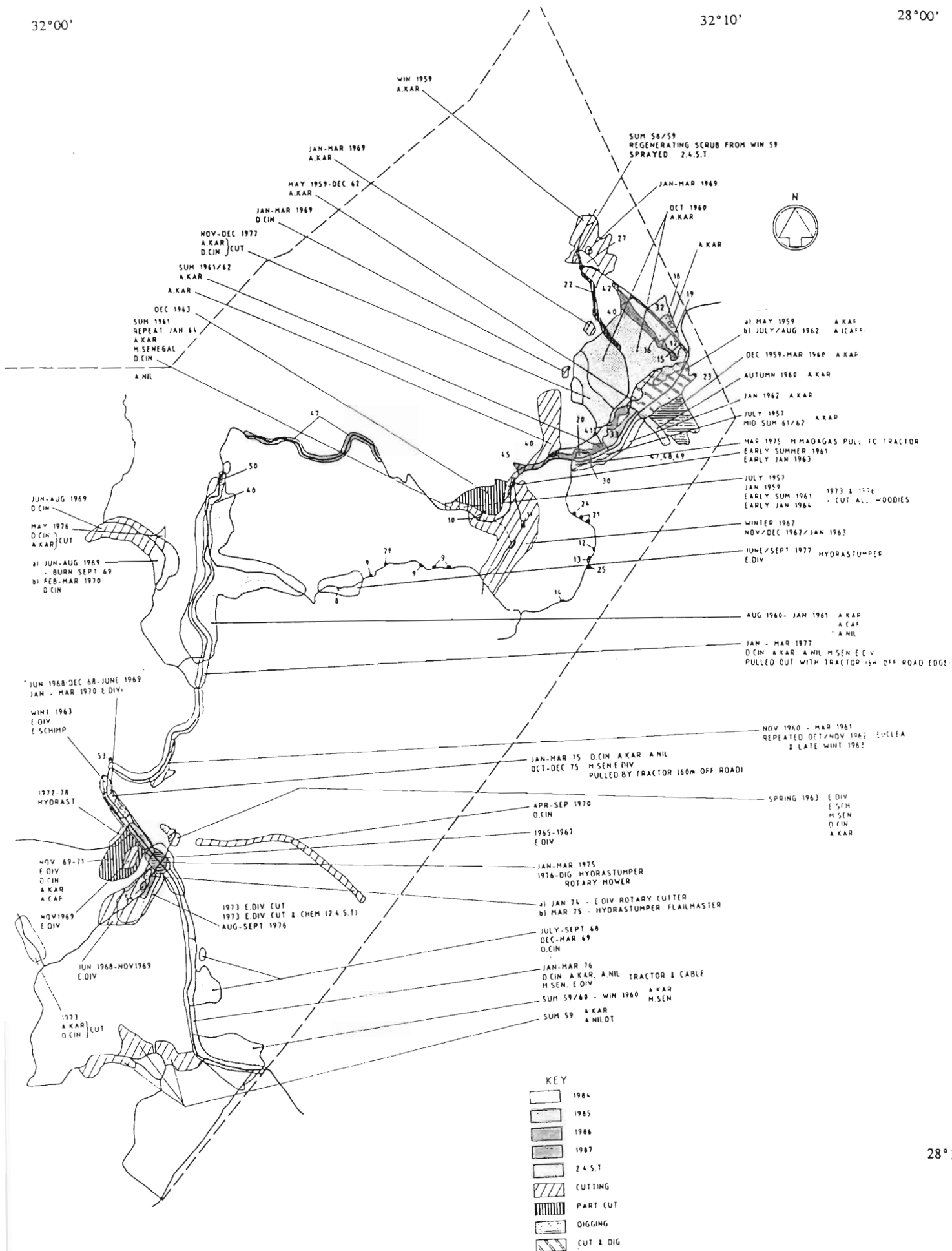


Figure 5.1 HGR Bush clearing summary map and history.
Annotation details year and species cleared.

The following Table 5.1 to be read in conjunction with this map, as it indexes the numbered cleared areas.

Table 5.1: Index for numbered cleared areas on bush control map, Fig. 5.1: HGR Bush clearing summary and history.

(Note: Table as complete as possible, within limitations of available records)

Area number	Method of control	Species cleared	Chemical used
1	Mech hydrostump/cut stump & chemical	A.caf/A.kar	Tordon
2	Cut stump & chemical	Dic.cinerea	Tordon
3			
4	Cut stump & chemical		Tordon
5	Cut stump & chemical		Tordon
6	Cut only	A.karoo	Nil
7	Cut stump	A.karoo	Tordon
8	Cut only (selective)	General	Nil
9	Cut only (selective)	General	Nil
10	Cut only (selective)	General	Nil
11	Cut only (selective)	General	Nil
12	Cut only (selective)	General	Nil
13	Cut only (selective)	General	Nil
14	Cut only (selective)	General	Nil
15	Cut stump	A.karoo	Diesel
16	Cut stump	A.karoo	Round-up
17	Cut stump (hydrostump)	General	Tordon
18	Cut only	A.karoo	Nil
19	Cut stump	A.karoo	Tordon
20	Cut stump	A.karoo	Round-up
21	Cut only	General	Nil
22	Cut stump	A.karoo	Tordon
23	Cut stump	General	Tordon
24	Basal bark spray/cut stump	Maytenus	Garlon
25	Basal bark spray/cut stump	Euclea	Garlon
26	Basal bark spray/cut stump	Maytenus	Garlon
27	Trial	Dic.cinerea	Nil Diesel Garlon

28	Trial	Euclea	Nil Diesel Garlon
29	Trial	A.nilotica	Nil Diesel Garlon
30	Trial	A.caffra	Nil Diesel Garlon
31	Frilling Foliar spray Frilling	Maytenus Maytenus Maytenus	XSA 1061 XSA 1061 Garlon
32	Cut stump		
33	Cut stump		
34	Cut stump		Tordon
35	Cut stump	A.nil/A.kar	Tordon
36	Cut stump	Acacia spp.	245 T
37	Cut stump	A.nilotica	Tordon
38	Cut stump	A.nilotica	245 T
39	Cut stump	A.nilotica	Tordon
40	Cut stump	A.karoo	Tordon
41	Cut stump	A.karoo	245 T
42	Cut stump	A.karoo	Tordon
43	Cut stump	A.karoo	245 T
44	Cut stump	Acacia spp.	245 T
45	Cut stump	A.nil/A.kar	Tordon
46	Cut stump		Tordon
47	Cut stump	A.karoo	245 T
48	Cut stump & spray	A.karoo	245 T
49	Cut stump	A.karoo	245 T
50	Cut stump	A.karoo	245 T
51	Cut stump	Acacia spp.	245 T
52	Cut stump	Acacia spp.	245 T
53	Spray	Euclea	Garlon
54	Spray	Euclea	Garlon

In several cases there was incomplete information on some aspects of the clearing activity. Wherever possible this information was traced and added to existing knowledge.

All clearing information from each map examined was then converted to the same scale (1:50 000) and transferred onto a composite transparency over a topocadastral map for the reserve. This then portrayed the total extent of areas cleared, methods of clearing, species cleared and time of clearing on one map (Fig. 5.1).

Several features are evident from this figure and the accompanying table (Table 5.1). One of them is the complexity of all permutations of species cleared, type, method and time of clearing. There were two main areas which have received clearing attention in the past. An area in the north of HGR and an area in the south (Fig. 5.1). This appears to be linked to the distribution of the roads in the reserve. Most clearing seems to have been determined by the requirement for visibility for game viewing and is therefore not evenly represented across all habitat types. The number of clearing events since 1957 and time since last clearing at any particular site are visible from Fig. 5.1.

Because of the seemingly unstructured approach to historical bush clearing (Fig. 5.1), a lumping exercise was necessary to find trends in the bush clearing history. A graphical representation of historical bush clearing events is presented in Figure 5.2. The data for this was derived from the composite map (Fig. 5.1) of all bush clearing events from 1957 to 1989. Any clearing episode, regardless of size, method, or species cleared, was considered a clearing event. This figure illustrates three distinct periods of bush clearing activity; viz. 1957 to 1964 (old clearing), 1968 to 1978 (medium interval clearing) and 1984 to 1989 (recent clearing). Within these broad time scale distinctions of clearing history, there was a possible further aggregating on the basis of whether a site was chemically or physically cleared.

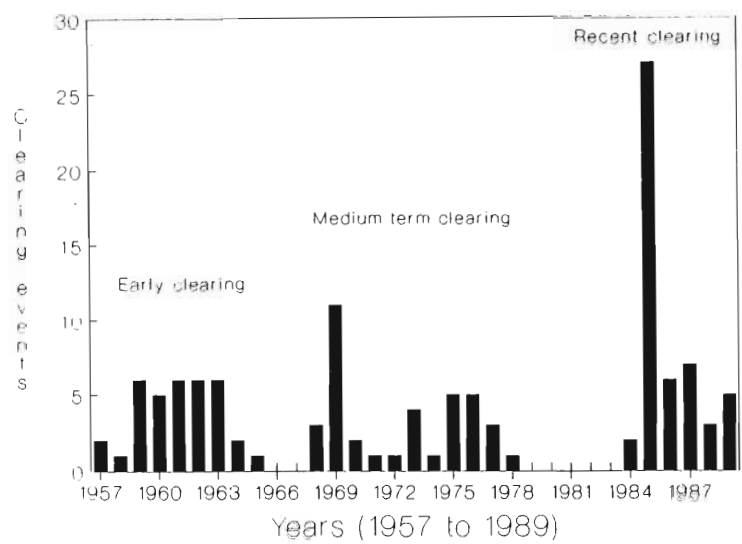


Figure 5.2 Number of historical bush clearing events.
From the composite bush clearing map, Fig. 5.1.

5.1.3 Fire history

Nott’s (1991) composite map of the fire history from 1955 - 1987 was used to locate areas with different burning histories (Fig. 5.3). For the purposes of this study the major concern was the fire history in bush cleared and adjacent areas.

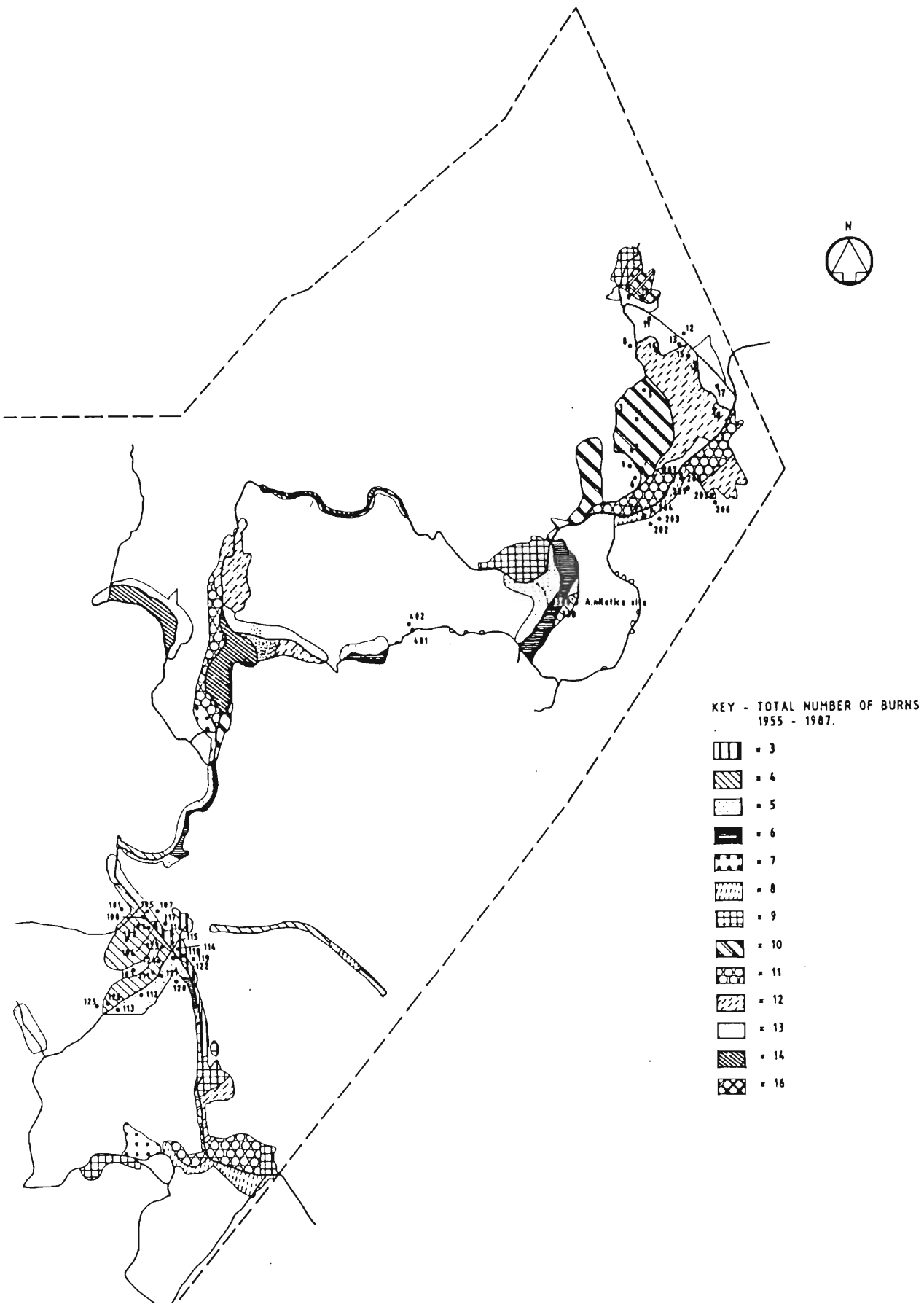
5.1.4 Combinations of clearing and burning events

From the large number of possible combinations of clearing and burning events, (due to the complexity of the bush clearing and fire history), fifty five were selected for sampling. These were over a range of clearing and fire regime and were thought to be sufficient to generate hypotheses and to model the responses of grasses to bush clearing and fire in this study.

32°00'

32°10'

28°00'



28°10'

Figure 5.3 HGR Fire history (number of fire events), and sample site distribution.

(Note: number of fire event boundaries are restricted only to bush cleared areas, from Fig. 5.1, for clarity).

5.1.5 Geological substrate and soil parent material

Geological substrate and soil parent material, as being either igneous or sedimentary in origin, were determined for all sites by using geological (Fig. 4.3 - adapted from King 1970) and soil (Barrow 1986) maps for the reserve. This produced nominal variables for these environmental parameters. A technique of fuzzy coding was used in cases where a site was located on a boundary between two possible substrates. This entailed giving equal weight to both of the options for the specific nominal environmental variable concerned eg. if a site fell on the boundary between an igneous and sedimentary geological substrate then it would receive a half point for each of the two geological substrate options.

5.1.6 Areal cover of woody plants

Woody cover was visually estimated as a percentage of the ground that the tree canopies were covering at each sample site. For example: woodland with a continuous canopy rated as 100%, whilst an open grassland with little or no woody canopy cover rated as 0.1% woody cover.

5.1.7 Topographic position

Three broad classes of topographic position were used - top, mid and foot of slope. The high altitude, ridge top grasslands in HGR have shallow soils and an historical record of high fire frequencies (Nott 1991; Wills pers. comm.). They consequently show little sign of bush encroachment (King 1987) and no clearing has taken place in these areas. There were therefore only two effective topographic classes in which sampling occurred: mid and foot slope positions.

5.1.8 Altitude, aspect and distance to drainage lines

Additional environmental variables that were felt may be affecting the herbaceous layer were altitude, aspect and distance to nearest drainage line. This information

was extracted from a 1:50 000 topo-cadastral map of the area (map number: 2832 AA) and recorded for each sample site.

All variables examined in this study, which were thought to affect herbaceous species composition, are listed in Table 5.2 along with their short form used in ordination diagrams and analyses tables.

Table 5.2: List and explanation of all environmental variables measured for each site sampled.

(* = The only variables measured in uncleared sites, as clearing related variables were not applicable)

Name of variable	Nominal or vector (N or V)	Description of variable
ALTTT *	V	Altitude as height above sea level (m)
ASPT N *	N	Northern aspects
ASPT E *	N	Eastern aspects
ASPT S *	N	Southern aspects
ASPT W *	N	Western aspects
MID *	N	Mid-slope topographic position
FOOT *	N	Foot-slope topographic position
DRAIN *	V	Distance to drainage line (m)
WD COV *	V	% Woody cover
NO FR *	V	Number of fire events
CLEAR	N	Cleared or uncleared
NO CL	V	Number of clearing events
TSLC	V	Time since last clearing
OLD	N	Old (early) clearing (1957 - 1965)
MEDIM	N	Cleared in medium term (1968 - 1978)
RECNT	N	Cleared recently (1984 - 1989)
E CHEM	N	Early chemical clearing
E PHYS	N	Early physical clearing
M CHEM	N	Medium term chemical clearing
M PHYS	N	Medium term physical clearing
R CHEM	N	Recent chemical clearing
R PHYS	N	Recent physical clearing
G IGN *	N	Igneous derived geology
G SED *	N	Sedimentary derived geology
S IGN *	N	Igneous derived soils
S SED *	N	Sedimentary derived soils

5.1.9 Sampling

Quadrats were used as the sampling unit as these were felt to be the most efficient means of capturing the data to describe community composition in each treatment. Within each quadrat presence/absence, modal height (in cm) and areal cover (as a percentage of the total area of the quadrat covered by that particular species), for each species was recorded. Cover was chosen as the measure of abundance as it is not biased by the size or distribution of individuals (Floyd and Anderson 1987). A further restriction in the sampling procedure was that quadrats with plants obviously grazed in them were discounted. This was to avoid possible bias from grazing effects.

Only plants of the family *Poaceae* (Gibbs Russell *et al.* 1990) were identified to species level. Five species encountered were unidentifiable due to the lack of an inflorescence. These were rare species with isolated distributions and often restricted to only one site. The full list of species encountered on sites sampled in this study are presented in Table 5.

From a random start at each particular site (performed by throwing a steel spike into the area), successive quadrats were placed regularly every three metres across the longest axis of a representative community at that site until the required sample number, or 'edge' of the community, was reached. If the 'edge' of the community was reached before the required sample number, sampling was continued as another 'transect' several metres parallel to the first, returning through the community to gain the required sample number. Placement of quadrats every three metres was to maintain independence of samples as at any lesser distance there may have been association between individual tufts of grasses (Mentis 1982). Greig-Smith (1983) is of the opinion that there may be a slight risk that equally spaced samples might give data from one phase only of a periodic variation in the vegetation. The random start of each transect in this survey was designed to counter that possibility.

Sampling for this phase of the study was conducted over as short a period as possible (approximately one and a half months) to reduce temporal effects as well as being at the end of the growing season when relative growth was low. This also allowed for the maximum expression of abundance. Sampling was performed only in dry weather to reduce possible data error due to lodging of herbaceous vegetation in the rain.

5.1.10 Quadrat size

In the field, plant populations depart more or less from randomness, tending to be more clumped or contagiously distributed (Ashby 1948; Greig-Smith 1983), so that the size of the quadrat used and even perhaps its shape, will affect the accuracy of the results obtained. The commonest result of quadrat size changes is that a reduced number of a larger size of quadrat, gives an increase in the standard error expressed as a proportion of the mean. The smallest quadrat that is practical, or desirable on other grounds, should therefore be used. This minimizing of variance in determining the size of the quadrat must be seen in the light of a trade-off with edge effects. The smaller the quadrat the greater the length of quadrat boundary per unit area and consequently the greater the chance of significant edge effects, due to the observer consistently including individuals that ought to be excluded or vice versa (Greig-Smith 1983). A balance must be struck between the lesser edge effects (and convenience of sampling) of larger quadrats and the greater efficiency per unit area of small quadrats.

Using a nested plot technique (Mueller-Dombois and Ellenberg 1974) in various communities, species/quadrat area curves (Rice and Kelting 1955) were derived (Fig. 5.4) in an effort to establish an optimum quadrat size. Examination of this figure reveals that the majority of the species being recorded are encountered in the first 0.2m^2 to 0.4m^2 . With the theoretical considerations and practical field limitations associated with the unwieldiness and placement of larger quadrats, a 0.25m^2 ($0.5\text{m} \times 0.5\text{m}$) quadrat was used in the determination of species abundance.

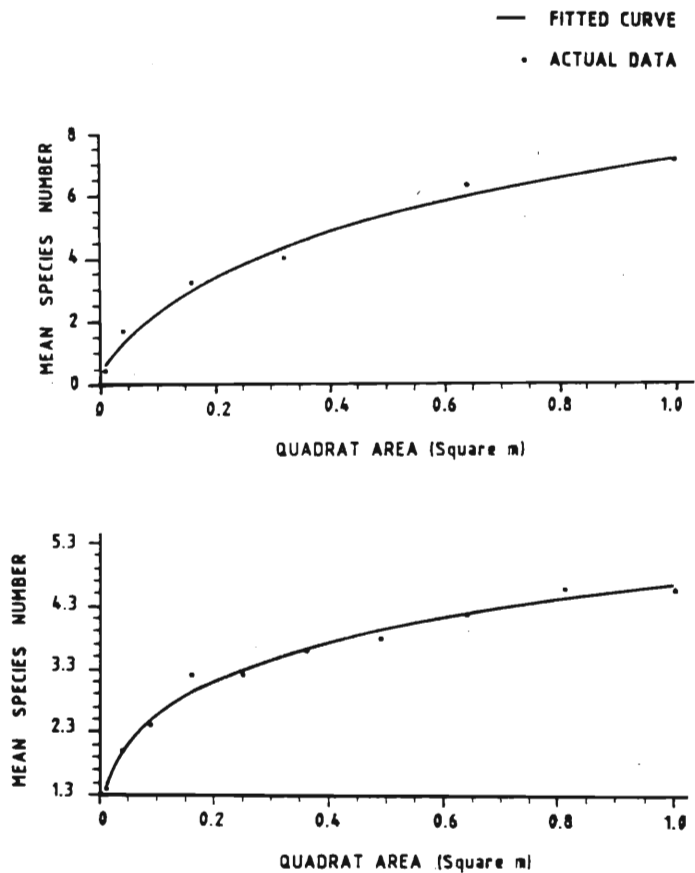


Figure 5.4 Species/quadrat area curves.
Examples derived from two visually diverse communities. (For optimum quadrat size determinations).

5.1.11 Sample size

Greig-Smith (1983) has emphasized that the accuracy of a count is not a function of the area sampled, but a function of the number of enumerations (sample size). Mentis (1984) recommends that the sample size should be determined empirically in each study area, as the appropriate number of sites is tied to the heterogeneity of that area. Daubenmire (1968) states that homogeneity is relative and suggests that one must sample at an intensity so as to reduce the error of the aggregate sample to an acceptable level.

A practical guide recommended by Mueller-Dombois and Ellenberg (1974) and others (Kershaw and Looney 1985), to estimating adequacy of sample size, is to stop sampling at the point at which additional quadrats do not significantly alter the mean of the more important (or abundant) species. This can be tested by calculating and plotting a cumulative or running mean during quadrat analysis (Kershaw and Looney 1985). It may also be satisfactory to set an arbitrary standard of sampling size by requiring that a sample be within five or ten percent of a more time consuming maximum sample (Mueller-Dombois and Ellenberg 1974).

Therefore a pilot survey was conducted in various communities, subjectively chosen to be relatively heterogenous, to determine the optimal sample number. This entailed sampling as detailed in section 5.1.9. The results from this exercise are shown in Figure 5.5, This figure demonstrates that a sample number around twenty five appears to reflect the population mean for the more abundant species in the communities examined. This sample number is also within 5% of the mean of a more time consuming larger sample of forty quadrats and was therefore deemed to be an efficient sample size.

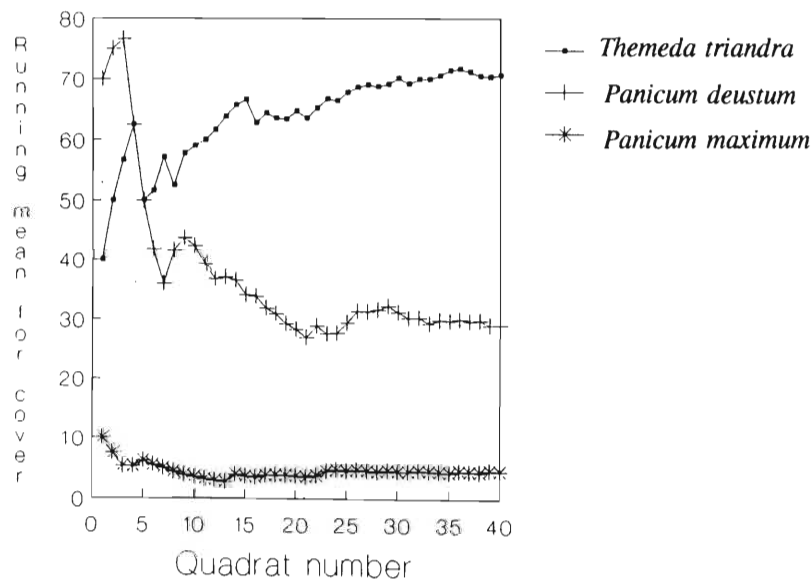


Figure 5.5 Plot of running mean for cover for optimal sample number determination.

5.2 Data entry

From the species modal height and percentage areal cover data collected, a volume measure for each species occurring in a quadrat was estimated by finding the product of areal cover and modal height. The environmental data corresponding to each site and the species abundance estimates were then processed to create data in a suitable format for further statistical analysis, ie. into Cornell condensed format (Gauch 1982).

Greig-Smith (1983) advises that a subjective decision has to be made of which criteria to be used in the characterization and comparison of different stands of vegetation. This has to be done in the light of the kind of information required. Trial ordinations were run using cover and then volume measures of species abundance. These ordinations showed similar distributions of species and sites in the ordination diagrams. Volume was selected as the abundance measure for use in further analyses as it probably represents a biologically more meaningful measure of relative species performance. Accordingly, herbaceous species composition was assessed in terms of volume abundance.

5.3 Analysis

5.3.1 Introduction

Over the past 25 years the problems of analyzing the large amount of data generated by the floristic description of vegetation to examine plant and community distributions in relation to environmental factors and gradients have resulted in the development of numerous techniques for data reduction - usually grouped under the two headings of classification and ordination. (Kent and Ballard 1988).

All species occur in a characteristic, limited range of habitats and within their range tend to be most abundant around their particular environmental optimum.

The composition of biotic communities thus changes along environmental gradients (ter Braak and Prentice 1988). Successive species replacements occur as a function of variation in the environment, or (analogously) with successional time (Peet and Loucks 1977; Pickett 1980).

Problems in community ecology often require the inferring of species-environment relationships from community composition data and associated habitat (environmental) measurements (ter Braak 1986). Gauch and Wentworth (1976) and Gittins (1985) have shown that when the data are collected over a sufficient habitat range for species to show non-linear, non-monotonic relationships with environmental variables it is inappropriate to infer species - environment relationships by correlation coefficients or to analyze the data by techniques that are based on correlation coefficients, such as canonical correlation analysis. An alternative two step approach has been to extract from the species data the dominant pattern of variation in community composition by an ordination technique and then to attempt to relate this pattern (ie. the first few ordination axes) to the environmental variables (Gauch 1982). This two-step approach is essentially Whittaker's (1967) indirect gradient analysis.

The theoretical foundation for gradient analysis lies in the species individualistic concept as originally proposed by Gleason (1926) and more recently by others eg. Curtis and McIntosh (1951) and Curtis (1959). This concept suggests that communities are groupings of species whose abundances change in sympathy with environmental factors.

Recently regression and ordination have been integrated into techniques of multivariate direct gradient analysis (ter Braak 1986, 1988). One of these techniques, Canonical Correspondence Analysis, escapes the assumption of linearity, common in other direct gradient analysis models, and is able to detect unimodal relationships between species and external variables.

5.3.2 Ordination

Ordination is the collective term used to describe multivariate techniques that arrange sites along axes on the basis of data on species composition (Jongman *et al.* 1987). The objective of ordination is in generating hypotheses about the relationships between composition of vegetation and the environmental, or other factors which determine it (Greig-Smith 1983).

5.3.3 Canonical Correspondence Analysis (CCA)

Correspondence analysis (CA) is an extension of the method of Weighted Averaging used in the Direct Gradient Analysis of Whittaker (1967). Whittaker, among others, observed that species commonly show bell-shaped response curves with respect to environmental gradients where each species has an optimal response (abundance) and is largely confined to a specific interval of that environmental variable (Fig. 5.6).

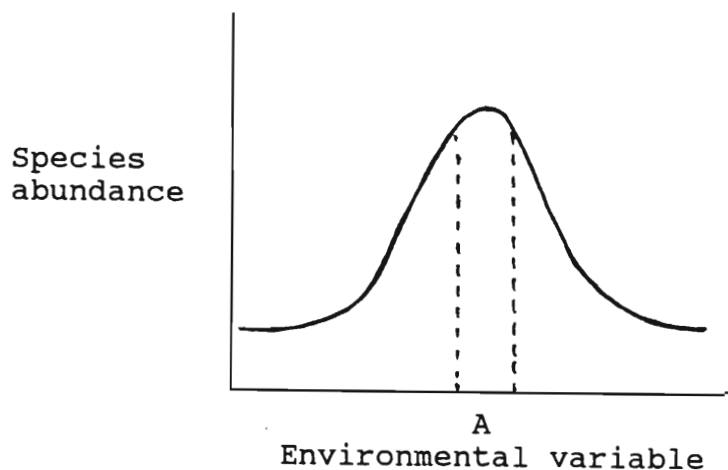


Figure 5.6 Gaussian or unimodal response model of species abundance to an environmental variable
A = optimal response or abundance

For each species it is possible to obtain a first indication of where it occurs along an environmental gradient by taking the weighted average of the environmental variable at each site at which the species occurs. This average is an estimate of the optimum of the species along the specified gradient and is called the species score. The dispersion ('spread') of the scores for different species is a measure of the usefulness of the particular environmental variable in explaining differences in species composition at different sites. If the dispersion is large, the variable neatly separates the response curves of different species and therefore explains differences in species composition at different sites well. By calculating the dispersion for each variable it is possible to select the 'best' variable. To compare the 'explanatory power' of different environmental variables, each environmental variable must be standardized to mean 0 and variance 1 (ter Braak 1987).

Hill and Gauch (1980) developed detrended correspondence analysis (DCA) as a modification of CA, designed to correct its two major 'faults'. Namely, that the ends of the axes are often compressed relative to the axes middle and that the second axis frequently shows a systematic relation with the first axis ie. the 'arch effect.' Pielou (1984) and Minchin (1987) advise that DCA, as available in the programme DECORANA (Hill 1979), may be 'overzealous' in correcting some of the faults of CA and result in distorted ordinations.

The length of the ordination axes are, by definition, the range of the sample scores in Standard Deviation (SD) units. Use of a linear response model (Fig 5.7) method eg. Principal Components Analysis (PCA) is advised by ter Braak (1988) if in ordinations by CA or DCA the range of sample scores is less than 1.5 SD.

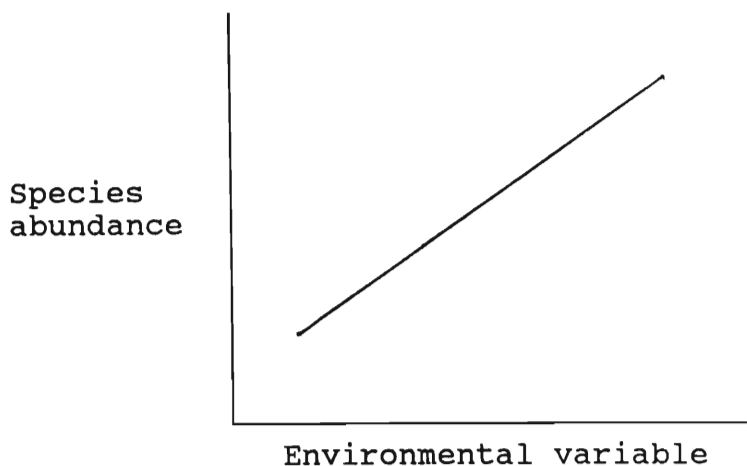


Figure 5.7 Linear response model of species abundance to an environmental variable

CA and DCA are indirect gradient analysis techniques, ie. ordination followed by environmental gradient identification and interpretation. If the ordination of the species data can be readily interpreted with these variables, the environmental variables are apparently sufficient to explain the main variation in the species composition or abundance (Jongman *et al.* 1987).

Canonical ordination techniques, on the other hand, are designed to detect the patterns of variation in the abundance of species at different sites that can be explained 'best' by the environmental variables. The ordination diagram developed expresses not only a pattern of variation in species data but also the main relations between the species and each of the environmental variables. It thus combines aspects of regular ordination with aspects of regression (ter Braak 1987). Again the assumption is that the response model is unimodal or Gaussian (Fig. 5.6).

In the same way as CA constructs a theoretical variable which maximizes the dispersion of species scores along the first and subsequent axes, canonical correspondence analysis (CCA) developed by ter Braak (1988) selects the linear combination of environmental variables that maximizes the dispersion of the

species scores ie. it chooses the best weights for the environmental variables which gives the first CCA axis. CCA is a 'restricted CA' in the sense that the site scores are restricted to be a linear combination of measured environmental variables. The eigenvalues in CCA are usually smaller than those in CA because of the restriction imposed on the site scores in CCA.

CCA provides a measure of the association between species and the environmental variables, which is the correlation between site scores that are weighted averages of the species scores and the sites scores that are a linear combination of the environmental variables. As with CA, the importance of the association between species and environmental variables is expressed by the eigenvalue (Jongman et. al. 1987).

Species and sites are positioned as points in the CCA diagram and their joint interpretation is also as in CA. Sites with a high abundance value of a species tend to be close to the point for that species. The environmental variables are represented by arrows which point in the direction of maximum change of that variable across the diagram. Their length is proportional to the degree of change in this direction ie. long arrows change more rapidly and are more important in separating species. The species points may be projected perpendicularly onto the axes defined by arrows and the order of the projection points corresponds approximately to the ranking of the weighted averages of the species scores, with respect to the specified environmental variable. The weighted average indicates the 'position' of a species distribution along an environmental gradient. The ordination diagram therefore expresses:

- (i) the pattern of community composition ie. association between species;
and
- (ii) the distributions of species along the environmental gradients.

This joint plot of species points and environmental arrows is a 'biplot' (ter Braak 1986) that approximates the weighted averages of each of the species with respect to each of the environmental variables. Environmental variables with long arrows are more strongly correlated with the ordination axes than those with short

arrows and therefore more closely related to the pattern of variation in species composition shown in the ordination diagram (Jongman *et al.* 1987).

5.3.4 Sequence of analyses

Initially all the herbaceous volume data, from all sites sampled, was analyzed and ordinated using DCA and CCA. This was to check for anomalous sites and outlier species. These sites and species were then removed from subsequent analyses.

To help generate hypotheses about the influence of abiotic and biotic factors on the herbaceous layer, the complete data set was split on the basis of those sites which had never been cleared with those which had. Only sites occurring on uncleared areas were then analyzed by CCA using only the 'pure' environmental variables associated with those sites eg. altitude, geology etc. Clearing in this sense was considered in terms of historical management ie. since the proclamation of the reserve in 1897. The effects of fire were statistically removed from the species data in this analysis by making the number of fire events a covariable. This was then a 'partial analysis,' in which the effects of a particular covariable is eliminated from the analysis and ordination.

Such a partial analysis allows the residual variation in the species data, (after covariable effects are statistically removed), to be displayed. This enables the residual variation to be related to the variables of specific interest: in this case pure environmental variables. Constrained ordination axes will, therefore, represent the effect that is 'uniquely' attributable to the environmental variables and not to covariables (Jongman *et al.* 1987; ter Braak 1988).

The complete set of environmental variables were then split into those strictly related to the environment and those related to management in the form of fire and bush clearing. The complete data set of species from all sites was then reanalysed with the effects of the management variables removed from the analysis as covariables. The effective number of samples examining the response

of grasses to 'pure' environmental variables was therefore increased over the examination of this response on only uncleared sites. It also served to validate the results of the analysis of species responses on uncleared sites.

The next step was an analysis of all the sites from both cleared and uncleared areas, considering all the environmental variables measured at those sites. This was to establish how the grass communities were reacting to all the measured environmental variables.

The full data set was again reanalysed but this time with the 'masking' effects of 'pure' environmental variables on species response removed as covariables. This allowed the response of grasses to the various clearing and fire treatments to be determined.

By plotting sites in relation to environmental variables for the various analyses and then reference to the sites environmental data, the range of environmental variables experienced by species at those sites in the biplots could be determined.

To test the relationship of particular environmental variables to the variability in the species data, a Monte Carlo permutation test (Hope 1968) was used. If the species react to the supplied environmental variables, then the test statistic calculated from the data-as-observed will be larger than most of the test statistics calculated from the random data set created to run the test. For a test at the 5% significance level, minimally 19 permutations are required with the power of the test being increased with increasing numbers of permutations (Hope 1968; ter Braak 1987).

In some instances in the analyses certain variables were shown to be of negligible variance. In these cases the analyses were run without these variables. They were however represented in correlation matrices to maintain variable naming continuity (only being represented as 00 in the matrix).

Due to the fuzzy coding technique (section 5.1.4), used on certain sites where there was no clear distinction between nominal variables eg. geological substrate, there were sometimes apparently anomalous results in some of the correlation matrices. This produced outputs which intuitively may have been expected to be different to those valid results generated in the analyses.

5.4 Results and discussion

5.4.1 Detection of outlier sites and species

Visual examination revealed site 16 as an extreme outlier in an ordination of all sites and all herbaceous species data. This site was subsequently removed as inspection of the data showed this site to be dominated by *Panicum aequinerve* with few other common species. As noted by Hill (1979) "in some applications individual samples with rare species may distort the analysis." ter Braak (1988) states that rare species may distort an analysis only if they appear in samples with few other more common species. He defines these as deviant samples and advises the removal of these samples from further analysis.

The complete data set was then reanalysed using CCA. Examination of species scores and the species ordination (Fig. 5.8), reveals certain 'outlier' species. These species points on the edge of the ordination diagram are often rare species, lying there either because they prefer extreme (environmental) conditions or because their few occurrences by chance happen to be at sites with extreme conditions (ter Braak 1987). These species viz. UN1 and UN7, were dropped from the data set and further analyses to allow a better dispersion of the majority of species and hence interpretation of response to environmental gradients. Intuitively this feels a more elegant approach than a form of weighting of these species.

Ordination axes data from the DCA analysis (Table 5.3) showed ordination axes in excess of 1.5 SD units. This indicates that a unimodal model would be the most appropriate method for further analysis (ter Braak 1987). CCA (based on a

unimodal model of species response to environmental variables, Fig. 5.6), is also a direct gradient analysis technique and was therefore used for further analyses with all environmental variables (Table 5.2). For weighted averaging methods, eg. CA and CCA, Jongman *et al.* (1987) advise the downweighting of rare species to minimize their influence. This is because techniques like CA are sensitive to species that occur in only a few species-poor sites. The first ordination axis is adversely affected by this situation. Rare species were therefore downweighted in the analyses.

Table 5.3: Axis statistics for preliminary analysis of complete data set.

Axis	Axes length (SD) from DCA	Eigen-value from DCA	Eigen-value from CCA	Spp-environ't correlation (CCA)	Cumulat-ive % variance accounted for (CCA)	Fraction variance explained (CCA)
1	3.88	0.546	0.494	0.95	42.6	0.426
2	4.07	0.330	0.210	0.81	60.7	0.181
3	4.45	0.204	0.132	0.79	72.1	0.114
4	2.26	0.109	0.107	0.77	81.3	0.092

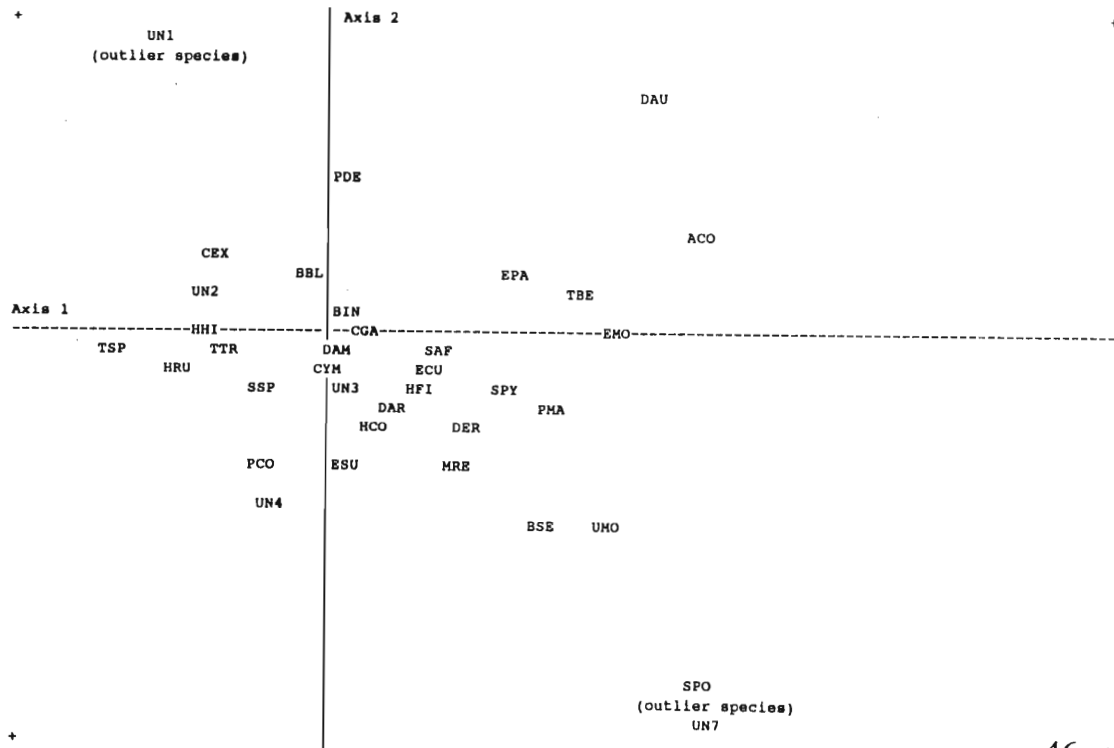


Figure 5.8 Preliminary species ordinations by CCA for detection of outlier species.

(Note: Full list of species acronyms and their full form in Table 5 on the opposite page).

5.4.2 Effects of environmental variables in uncleared areas

The results of the initial analysis on uncleared sites are presented in Table 5.4 and Fig. 5.9. Only ‘pure’ environmental variables, unrelated to clearing, are considered in this analysis with the covariable effects of fire statistically removed.

Table 5.4: Ordination axes, corresponding eigenvalues, species-environment correlations, percentage variance accounted for and fraction of variance explained by CCA on all sites with no clearing history. (Note: covariable effects of fire removed from analysis).

Axis	Eigen-value	Species - environment correlation	Cumulative % Variance accounted for by axis	Fraction of variance explained
1	0.385	0.98	33.7	0.337
2	0.374	0.99	66.4	0.327
3	0.149	0.81	79.4	0.130
4	0.103	0.89	88.4	0.090

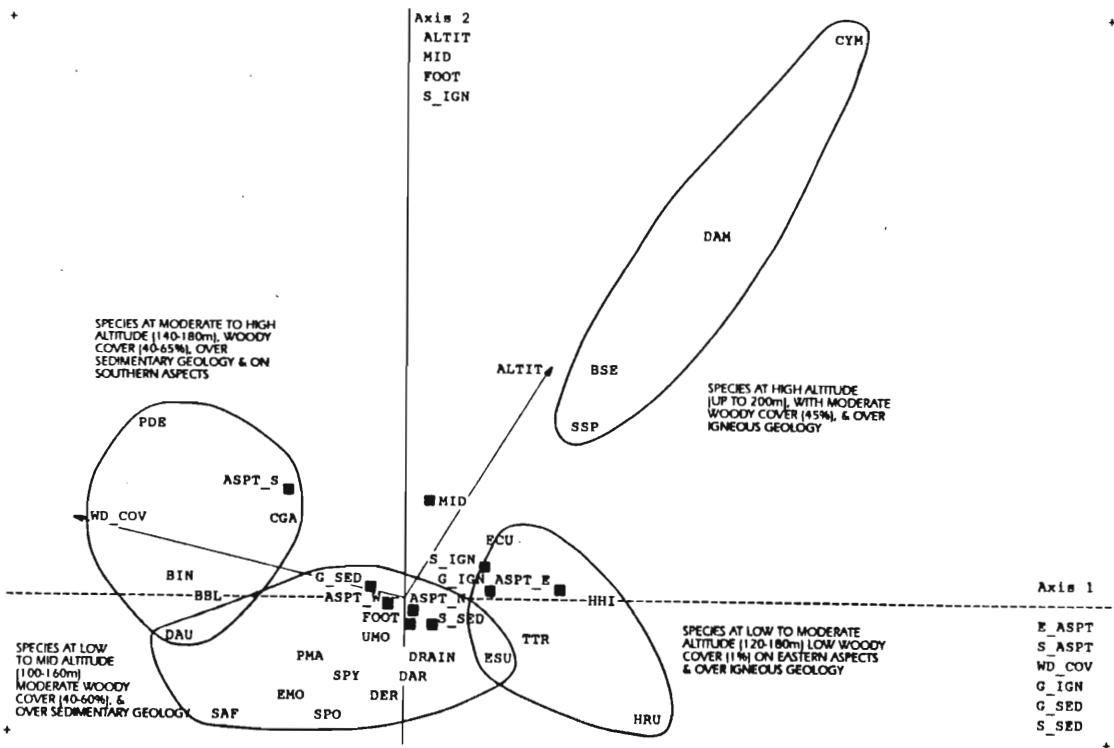


Figure 5.9 Biplot of species and environmental variables on uncleared sites. Covariable effects of fire removed in analysis.

Variable acronyms and explanation as per Table 5.2. Vector variables as arrows and nominal variables as centroids. Variables significantly correlated with axes, listed under respective axes.

The correlation matrix of all environmental variables with each other, on uncleared sites, is shown in Table 5.5.

Table 5.5: Weighted correlation matrix for all environmental variables with each other, on all uncleared sites.

Note: Covariable effects of fire removed from this analysis. Variables significantly correlated with each other, highlighted in bold.

ALTIT	1.00							
ASPT_N	.00	.00						
ASPT_E	.11	.00	1.00					
ASPT_S	.16	.00	.09	1.00				
ASPT_W	.00	.00	.00	.00	.00			
MID	.67	.00	.41	.50	.00	1.00		
FOOT	-.67	.00	-.41	-.50	.00	-1.00	1.00	
DRAIN	.20	.00	-.63	-.16	.00	-.34	.34	1.00
WD_COV	-.08	.00	-.45	.54	.00	-.03	.03	-.10
G_IGN	.56	.00	.68	.21	.00	.48	-.48	.06
G_SED	-.03	.00	-.42	.77	.00	.21	-.21	-.09
S_IGN	.44	.00	.48	.11	.00	.38	-.39	-.31
S_SED	-.02	.00	.27	-.64	.00	-.24	.24	.29
ALTIT ASPT_N ASPT_E ASPT_S ASPT_W MID FOOT DRAIN								
WD_COV	1.00							
G_IGN	-.55	1.00						
G_SED	.79	.49	1.00					
S_IGN	-.05	.49	-.11	1.00				
S_SED	-.78	.47	-.85	-.25	1.00			
WD_COV G_IGN G_SED S_IGN S_SED								

The geology of the reserve is such that igneous formations have intruded extensively into the sedimentary geology which covers most of the reserve (Whatekys pers comm; King 1970). These intrusive igneous formations, in the form of dykes and sills, tend to be at higher altitudes, hence explaining the positive correlation between this geology and altitude.

Woody cover is negatively correlated with igneous geology. This may be due to geological formations tending to be at higher altitudes, as outlined above, and as noted by King (1987) grasslands tend to occupy the higher, flat ridge tops of the reserve. With the dominance of grasslands at higher altitudes fires are more likely to burn vigorously through this vegetation type and therefore adversely

affect woody species. Another explanation for this result may be King’s (op cit.) observation that scrub encroachment rates are lower over igneous geology compared with sedimentary geology. Woody cover, positively correlated with sedimentary geology, further supports this observation. The higher rates of bush encroachment over sedimentary geology has resulted in a higher woody cover at those sites.

Woody cover was also observed to be positively correlated with southern aspects (ASPT_S). This is not an unusual phenomena in savannas where south and east facing slopes are generally found to be cooler and therefore moister due to their lower radiation load. This higher moisture regime leads them to being generally more heavily wooded than north and west facing slopes.

There are several environmental variables significantly correlated with species axes on uncleared sites (shown in Table 5.6). Of primary interest are the variables correlated with the first two axes, as they account for 66.4 % of the variability in the herbaceous data on uncleared areas.

Table 5.6: Correlation matrix for all environmental variables with species axes, on all uncleared sites with the covariable effects of fire removed.
(Note: Variables with large correlation with species axes are highlighted in bold. Variable names and explanation as per Table 5.2).

SPEC AX1	1.0000			
SPEC AX2	.0068	1.0000		
SPEC AX3	-.0411	-.0398	1.0000	
SPEC AX4	.0536	.0150	-.1552	1.0000
ALTIT	.2775	.6821	-.0896	.0294
ASPT_N	.0000	.0000	.0000	.0000
ASPT_E	.5989	.2297	.0502	.0023
ASPT_S	-.5528	.4965	-.4120	.0011
ASPT_W	.0000	.0000	.0000	.0000
MID	.0908	.6594	-.0472	.2543
FOOT	-.0908	-.6594	.0472	-.2543
DRAIN	-.0099	-.1393	-.2349	-.1883
WD_COV	-.8732	.2571	.1092	-.1978
G_IGN	.7893	.4083	-.1826	-.2012
G_SED	-.8140	.4959	-.0639	.1244
S_IGN	.3147	.5845	.3521	-.3657
S_SED	.7927	-.4345	-.1102	.0984
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4

The major environmental variables affecting species distributions on uncleared sites are those most strongly correlated with the species axes in this analysis. In this case the first axis is primarily a woody cover, geological and soil substrate axis. Eastern and southern aspects also have some effect on this axis although they are also correlated with geology and soil substrate. The second axis is one related to altitude, topographic position and igneous soil substrate.

Figure 5.9 exhibits distinct herbaceous communities and their distribution in relation to these various environmental variables. Groupings of 'similar' species are near each other, whilst 'dissimilar' species are further apart in the ordination diagram (Gauch 1982).

At low to mid altitudes (120m - 180m) and with very low woody cover (1%), sites over igneous geology and soils derived from that material are dominated by *Hyparrhenia hirta*, *H. rufa* and *Themeda triandra*, with some *Eragrostis superba*. These species also appear to favour eastern aspects. At generally lower altitudes (100m - 160m), on foot slopes, with increasing woody cover (40 - 60%) and over sedimentary geology, *Urochloa mossambicensis*, *Panicum maximum*, *Digitaria argyrograpta*, *D. eriantha*, *Sporobolus* sp., *S. pyramidalis*, *S. africanus*, *Enteropogon monostachyus*, *Eragrostis superba*, and *Dactyloctenium australe* dominate. On southern aspects and mid-slopes at mid altitudes (140m - 180m) and generally high woody cover (40 - 65%), the communities are dominated by *Chloris gayana*, *Bothriochloa insculpta*, *B. bladhii* and *Panicum deustum*. *Dactyloctenium australe* may also occur under these conditions where the geological substrate is of sedimentary origin. At still higher altitudes (up to 200m) but decreasing woody cover (45%), over igneous geological material the dominant species are *Setaria sphacelata*, *Brachiaria serrata*, *Diheteropogon amplectens* and *Cymbopogon* sp.

5.4.3 Effects of pure environmental variables on all sites - covariable effects of management removed

The environmental data, split into 'pure' and 'management' related variables, was now used in this analysis. The management related variables were made covariables and thus had their effects on grasses statistically removed from the following analysis on all sites.

The results of this analysis are presented in Table 5.7 and correlation matrix Table 5.8.

Table 5.7: Ordination axes, corresponding eigenvalues, species-environment correlations, percentage variance accounted for and fraction of variance explained for partial CCA on all sites. Covariable effects of management removed.

Axis	Eigen-value	Species - environment correlation	Cumulative % Variance accounted for by axis	Fraction of variance explained
1	0.26	0.94	33.3	0.333
2	0.15	0.90	52.3	0.190
3	0.08	0.75	62.7	0.104
4	0.07	0.83	72.1	0.094

As with the preceding analysis, woody cover is the environmental variable most strongly correlated with the first ordination axis of an analysis by CCA. This axis accounts for a third of the variance in the data (Table 5.7), so once again woody cover appears to be the environmental variable explaining most of the variability in the species data. Geology and soils are the only other environmental variables accounting for any significant variability in the species data. These results were similar to those obtained for the previous analysis of sites on uncleared areas.

Table 5.8: Partial correlations of environmental variables with species axes for partial CCA. Covariable effects of management removed. Data from all sites - cleared and uncleared.

Variables strongly correlated with axes highlighted in bold.

SPEC AX1	1.00			
SPEC AX2	-.02	1.00		
SPEC AX3	.09	-.04	1.00	
SPEC AX4	.06	.06	.11	1.00
ALTIT	-.20	.36	-.20	.05
ASPT_N	-.04	-.07	.04	-.08
ASPT_E	-.36	.39	.00	.17
ASPT_S	-.01	.08	-.13	.14
ASPT_W	.37	.08	.01	.13
MID	-.11	.31	-.04	.16
FOOT	.17	-.32	.06	-.18
DRAIN	-.06	-.07	-.03	.23
WD_COV	.79	-.09	.10	.06
G_IGN	-.56	.52	.09	.15
G_SED	.45	.04	-.12	-.06
S_IGN	.26	.63	.06	-.22
S_SED	-.50	-.11	.28	.15
	AX1	AX2	AX3	AX4

The major environmental variables examined, (not directly associated with fire or bush clearing), affecting the distribution of species in this reserve are then primarily woody cover and geological and soil substrate. To a lesser degree altitude and topographic position are important.

A trial biplot of species and environmental variables for this analysis (Fig. 5.10) did not reveal much new information about how species are responding to environmental variables, with species such as *Dactyloctenium australe*, *Panicum deustum*, *Bothriochloa bladhii*, *B. insculpta* and *Chloris gayana* again dominating sites at moderate to high woody cover over geology of sedimentary origin. At the other extreme ie. in open grassland (1% woody cover) and over igneous geology, species such as *Themeda triandra*, *Hyparrhenia rufa*, *Diheteropogon amplexens*, *Trachypogon spicatus* and *Cymbopogon* sp., are

dominant. The first three of these species were also dominant under similar conditions in the previous analysis.

These distributions of species in relation to key environmental variables are similar to those obtained in the analysis of species over uncleared sites (Fig. 5.9). This latest ordination however does reveal some new species not encountered on purely uncleared sites.

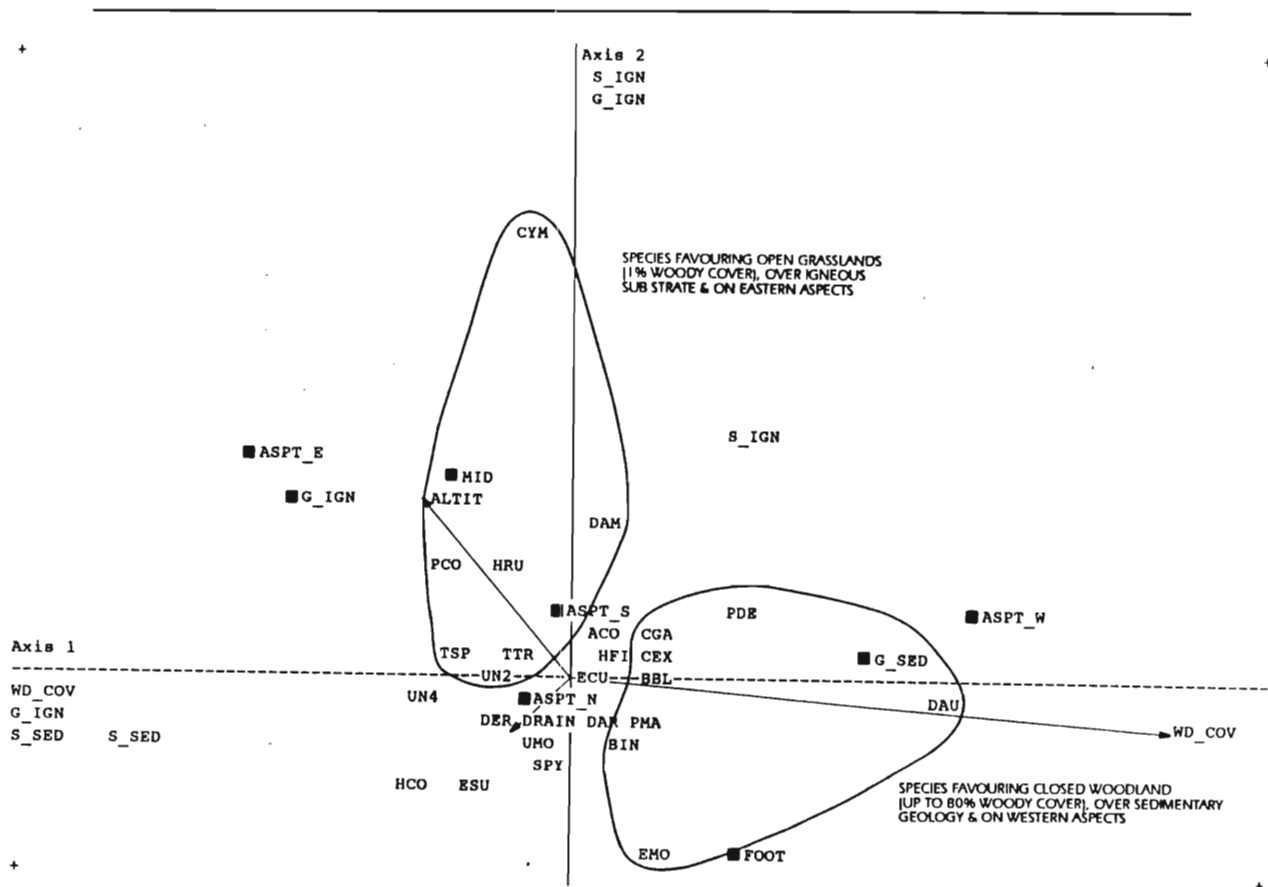


Figure 5.10 CCA Biplot of species and 'pure' environmental variables for all sites. Bush clearing and fire effects removed as covariables. Variable acronyms and explanation as per Table 5.2. Vector variables as arrows and nominal variables as centroids. Variables significantly correlated with axes, listed under respective axes.

5.4.4 Effects of all environmental variables on cleared and uncleared sites

The complete data set consisting of sites from both cleared and uncleared areas was now analyzed. All environmental variables were considered in this analysis and these results presented in Table 5.9.

Table 5.9: Correlation matrix of all environmental variables with species axes, for all sites

Environmental variables with high correlation with species axes highlighted in bold.

SPEC AX1	1.0000			
SPEC AX2	-.0062	1.0000		
SPEC AX3	.0094	-.0256	1.0000	
SPEC AX4	.0555	-.1080	-.0066	1.0000
ALTIT	-.5524	.1087	.1324	-.3276
ASPT_N	-.1146	.0318	-.1013	-.0495
ASPT_E	-.4537	-.0300	.0827	-.2720
ASPT_S	-.1931	.1354	-.0432	-.1083
ASPT_W	.0460	.3373	-.1140	-.0450
MID	-.3520	.1220	.0720	-.2489
FOOT	.3792	-.0805	-.0559	.2655
DRAIN	.0049	-.0853	-.0962	.2239
WD_COV	.8000	.2488	-.2004	-.1780
NO_FR	-.6677	.2729	.0495	-.2463
CLEAR	-.2345	-.0070	.0054	.2096
NO_CL	-.0112	-.1792	-.1254	.4298
TSLC	-.1672	.0974	-.1472	-.1375
EARLY	-.2433	-.0017	-.4213	-.0142
MEDIM	.1891	-.1041	.0281	.3331
RECNT	-.0137	-.1519	.1500	.2784
E_CHEM	-.1464	-.0997	-.3155	-.2518
E_PHYS	-.2167	.0857	-.2025	.2272
M_CHEM	.4514	-.3341	-.3130	-.2082
M_PHYS	.1891	-.1041	.0281	.3331
R_CHEM	-.0341	-.1196	.0379	.3179
R_PHYS	.0682	-.1456	.2324	.1528
G_IGN	-.7259	.0646	.0000	-.4394
G_SED	.6640	.0054	.0853	.2970
S_IGN	-.5823	.4435	.2969	-.3491
S_SED	-.0541	-.3710	-.2820	.0445
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4
Eigenvalue :	0.49	0.21	0.13	0.11
Spp/envIRON. correlation :	0.95	0.81	0.79	0.77
Cumulative % variance accounted for by axes :	42.6	60.7	72.1	81.3

The first two axes of the species-environment biplot account for 60.7% of the variance in the data set, whilst the first and second eigenvalues were 0.49 and 0.21 respectively. A multiple regression of the site scores of the first axis on the environmental variables gave a species-environment correlation of $r = 0.95$. The conclusion from this is that the measured environmental variables (Table 5.2) account for the majority of the variation in the species data.

Examination of the correlations between environmental variables and the first 2 species axes reveals that the first axis is a woody cover/altitudinal/fire event/geological axis, whilst the second is a weak, soil parent material axis (Table 5.9). This relationship is also seen in the CCA biplot of species and environmental variables (Fig. 5.11).

From this figure (Fig. 5.11) the response of grasses to significant environmental variables is as follows. At lower altitudes (120m - 140m), in areas of high woody cover (60 - 80%), relatively infrequent fires (4 - 8) and few clearing events (1 - 2 clearings), species dominating the grass communities are *Dactyloctenium australe*, *Panicum maximum*, *Sporobolus pyramidalis*, *S. africanus*, *Enteropogon monostachyus* and *Digitaria eriantha*. These areas also tend to be underlain by sedimentary geology.

With increasing altitude (140m - 180m), fire (8 - 12 burns) and clearing frequency (1 - 5 clearings), there is a decrease in woody cover (0.1 - 20%) and the species dominating here are *Cymbopogon excavatus*, *Hyparrhenia hirta*, *H. rufa*, *Themeda triandra*, *Setaria sphacelata* and *Trachypogon spicatus*. Between these extremes of important environmental variables ie. at mid altitudes (120m), moderate burning frequency (8 - 12 burns) and intermediate levels of woody cover (25 - 40%), species dominant are *Panicum deustum*, *Bothriochloa bladhii*, *B. insculpta* and *Chloris gayana*. Also occurring under these conditions but tending to favour more frequently cleared and hence disturbed sites, are: *Eragrostis curvula*, *E. superba*, *Digitaria argyrograpta*, *Heteropogon contortus*

and *Panicum coloratum*. These last two groupings of species at higher and mid altitude, tend to be underlain by igneous geology and hence soils derived from this material.

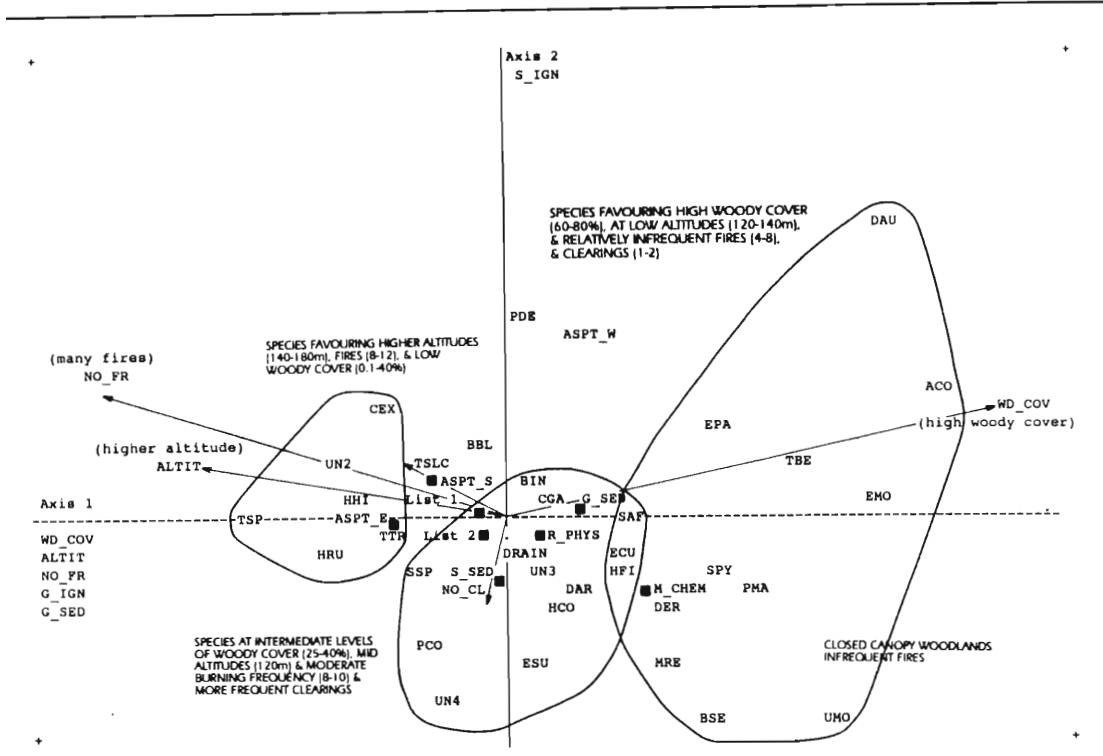


Figure 5.11 CCA Biplot of species and all environmental variables.

Variable acronyms and explanation as per Table 5.2. Vector variables as arrows and nominal variables as centroids. Variables significantly correlated with axes, listed under respective axes.

Lists of variables necessary to represent all information in the diagram.

List 1: ASPT_N, S_IGN, G_IGN, MID, E_PHYS.

List 2: EARLY, CLEAR, FOOT, E_CHEM, R_CHEM, M_PHYS, MEDIM, RECNT.

What is evident from Fig. 5.11 is that the majority of the key variables associated with the first axis (ALTIT, WD_COV, NO_FR, G_IGN, G_SED and S_IGN), are not fully independent. Independent effects of environmental variables on community composition are indicated by the environmental axes or arrows being at right angles to each other (ter Braak 1988). Figure 5.11 clearly shows most of the variables associated with the first ordination axis are in the same plane as this axis, thereby indicating some degree of association. This relationship is also seen in the correlation matrix of environmental variables with each other (Table 5.10).

Table 5.10: Correlation matrix of all environmental variables with each other for all cleared and uncleared sites.

Environmental variables with high correlation highlighted in bold.

ALTIT	1.00								
ASPT_N	.05	1.00							
ASPT_E	.38	.14	1.00						
ASPT_S	.26	-.06	.04	1.00					
ASPT_W	.11	-.02	-.06	.22	1.00				
MID	.62	-.10	.40	.60	.19	1.00			
FOOT	-.63	.10	-.41	-.61	-.19	-.98	1.00		
DRAIN	.04	-.01	-.30	-.13	-.05	-.20	.20	1.00	
WD_COV	-.29	-.11	-.27	-.00	.21	-.05	.08	-.02	
NO_FR	.65	.09	.26	.21	.05	.32	-.32	-.12	
CLEAR	.05	.08	-.00	-.28	.04	-.14	.11	.12	
NO_CL	-.37	-.10	-.22	-.23	-.05	-.28	.26	.19	
TSLC	.31	.44	.17	.11	.25	.12	-.14	-.12	
EARLY	-.04	.21	.12	.05	.12	.04	-.05	-.16	
MEDIM	-.31	-.17	-.01	-.13	-.09	-.10	.09	.07	
RECNT	-.26	-.19	-.31	-.35	-.11	-.33	.32	.22	
E_CHEM	.25	.31	.35	.18	.18	.26	-.27	-.26	
E_PHYS	-.23	-.09	-.28	-.17	-.05	-.28	.27	.00	
M_CHEM	-.30	-.04	-.13	-.08	-.02	-.13	.13	-.04	
M_PHYS	-.31	-.17	-.01	-.13	-.09	-.10	.09	.07	
R_CHEM	-.23	-.18	-.28	-.33	-.10	-.30	.29	.22	
R_PHYS	-.10	-.04	-.12	-.07	-.02	-.12	.12	.20	
G_IGN	.79	.18	.53	.31	.10	.49	-.51	-.14	
G_SED	-.64	-.20	-.40	-.17	-.11	-.29	.31	.10	
S_IGN	.59	.11	.35	.21	.06	.35	-.34	-.27	
S_SED	.05	.16	.38	-.16	.09	.09	-.11	.19	
ALTIT	ASPT_N	ASPT_E	ASPT_S	ASPT_W	MID	FOOT	DRAIN		
WD_COV	1.00								
NO_FR	-.49	1.00							
CLEAR	-.30	.02	1.00						
NO_CL	-.20	-.37	.55	1.00					
TSLC	.00	.03	.36	-.08	1.00				
EARLY	-.10	-.07	.39	.55	.46	1.00			
MEDIM	-.04	-.49	.41	.71	-.01	.31	1.00		
RECNT	-.27	.02	.47	.54	-.53	-.11	.16	1.00	
E_CHEM	.00	.04	.27	.15	.66	.68	.16	-.38	
E_PHYS	-.20	-.12	.22	.53	.06	.57	.12	.18	
M_CHEM	.39	-.38	.10	.37	-.07	.27	.26	.23	
M_PHYS	-.04	-.49	.41	.71	-.01	.31	.99	.16	
R_CHEM	.25	-.01	.44	.56	-.53	-.06	.18	.94	
R_PHYS	-.07	-.03	.10	.10	-.05	-.19	.06	.21	
G_IGN	-.43	.81	-.04	-.45	.25	.02	-.51	-.25	
G_SED	.46	-.77	-.02	.36	-.14	-.02	.44	.14	
S_IGN	-.45	.78	.10	-.27	.10	-.05	-.22	-.01	
S_SED	.03	-.25	-.08	-.06	.05	.07	.05	-.25	
WD_COV	NO_FR	CLEAR	NO_CL	TSLC	EARLY	MEDIM	RECNT		
E_CHEM	1.00								
E_PHYS	-.10	1.00							
M_CHEM	.40	-.12	1.00						
M_PHYS	.16	.12	.26	1.00					
R_CHEM	-.34	.20	.24	.18	1.00				
R_PHYS	-.13	-.11	-.05	.06	-.03	1.00			
G_IGN	.31	-.23	-.25	-.51	-.27	-.05	1.00		
G_SED	-.27	.17	.22	.44	.16	.03	-.89	1.00	
S_IGN	.10	-.12	-.38	-.22	-.01	-.15	.66	-.59	
S_SED	.15	-.18	.05	.05	-.22	.01	.07	-.13	
E_CHEM	E_PHYS	M_CHEM	M_PHYS	R_CHEM	R_PHYS	G_IGN	G_SED		
S_IGN	1.00								
S_SED	-.40	1.0000							
S_IGN		S_SED							

This analysis, using the complete environmental data set, shows similar relationships between environmental variables as for the previous analysis of sites on uncleared areas. Igneous geology and soils derived from that material, occurring at higher altitudes, corresponding to those areas of the highest fire frequencies. These variables are all positively correlated with each other.

The first species axis identified in Fig. 5.11 may be interpreted as an indicator of the general trend of secondary succession in bush cleared areas. Results of King's (1987) work reveals that bush-encroachment is probably inevitable in this reserve. This mechanism is a 'natural' one and in HGR there appear to be no physical limitations to the process. As woody plant density, and hence woody cover increases, changes in species composition occur. Microphyllous, shade intolerant, fire tolerant, 'pioneer,' woody species eg. *Dichrostachys cinerea* and *Acacia* species, establish first in open grassland areas. These are followed by broadleaved, shade-tolerant, fire intolerant species eg. *Euclea* species, establishing beneath the canopies of the pioneers (King 1987).

Along with the changes in the composition and cover of the woody community there is a change in the composition of the grass community. The community therefore changes from an open grassland/shrubland to closed woodland and forest (Wills and Whately 1983; King 1987). This parallel change in grassland community composition with changes in woody cover are clearly visible in this last ordination (Fig. 5.11) and will be developed further in the model (section 5.5).

The direction of the other environmental arrows (for non-nominal) and centroids (for nominal environmental variables) in relation to axis 1, indicates that numerous fires, high altitude, igneous geology and soils derived from igneous parent material delays this succession. Sedimentary geology at lower altitudes and lower fire frequencies, on the other hand, accelerates the succession through to closed canopy woodland.

The higher soil nutrient status in areas on igneous derived geology or soil types, (as well as possible higher soil moisture), probably affects fire fuel loads here, through increased grass production. This in turn may be affecting the woody layer. The effects of fire on savanna trees depends on flame length and fireline intensity. These in turn are affected by the fuel loads, their architecture, and climatic conditions at the time of burning (Trollope 1978; van Wilgen and Wills 1988).

Savanna herbaceous communities are less susceptible to fire than are the woody communities with the most obvious changes occurring at the extremes of the number of fire events. For example regular burning favours species such as *Themeda triandra*, *Trachypogon spicatus* and *Hyparrhenia hirta* (this study), whereas less frequent burning favours species such as *Panicum maximum*, *Sporobolus pyramidalis* (this study) and *Cymbopogon plurinoides* and certain forbs (Davidson 1953; Harrington and Ross 1974; Robinson *et al.* 1979; Edroma 1984). Rainfall is a confounding factor however, with *T. triandra* being susceptible to drought. Although it (*T. triandra*), increases under frequent burning and decreases if fire is excluded, this only happens under average or above-average rainfall. The combination of frequent burning and low rainfall causes *T. triandra* to decline (Kennan 1972; O'Connor 1985).

There is evidence that in the absence of fire, the grass sward degenerates through lodging of senescent material and death of tillers (Menaut 1977). Protection from fire results in an increase in mesic shade-loving grasses such as *Panicum maximum* (Kennard and Walker 1973; Harrington and Ross 1974) and *Dactyloctenium australe*.

These species are clearly grouped around the end of the first axis, corresponding to high woody cover and low fire frequency, in the ordination of species and all environmental variables (Fig. 5.11). Other species observed favouring these conditions in this study are: *Enteropogon monostachyus*, *Tragus berteronianus*,

and *Aristida congesta*. These species may however be responding more to changes in tree density and associated microclimate, than directly to the absence of fire, since the removal of woody plants is known to influence herbaceous composition and production (Dye and Spear 1982; O'Connor 1985).

With longer intervals between fires, woody plant cover (and hence density) increases to a point where there is insufficient grass to fuel a fire intense enough to affect woody plants. Beyond this point it would appear that other factors such as edaphic variables become key determinants of grass:woody biomass ratios and hence structure of savannas (Frost *et al.* 1986).

5.4.5 Effects of environmental variables on grass communities over different geological substrates

Previous analyses on uncleared and cleared sites have consistently identified geological substrate as being an important variable influencing species distributions. The influence of these two variables was shown by their strong correlation with the first axis in the ordination diagram Fig. 5.11 ($r = -0.73$ and 0.66 for igneous and sedimentary geology respectively, Table 5.9). To examine the effects of environmental variables over the different substrates the data set was split into those sites over igneous and those sites over sedimentary geology.

Previous analyses have shown the variables EARLY, MEDIM and RECNT, to have limited explanatory power and so were removed from further analyses.

5.4.5.1 Sedimentary geology

The results of analysis by CCA on all sites over sedimentary geology are presented in Table 5.11 and correlation matrix Table 5.12.

Table 5.11: Ordination axes, corresponding eigenvalues, species-environment correlations, percentage variance accounted for and fraction of variance explained by CCA on all sites over sedimentary geology.

Axis	Eigen-value	Species - environment correlation	Cumulative % Variance accounted for by axis	Fraction of variance explained
1	0.451	0.94	41.1	0.411
2	0.247	0.85	63.5	0.225
3	0.142	0.85	76.5	0.130
4	0.103	0.62	85.8	0.093

Table 5.12: Correlation matrix for all environmental variables with species axes on all sites over sedimentary geology.

Variables with large correlation with species axes highlighted in bold.
Variable names and explanation as per Table 5.2.

SPEC AX1	1.0000			
SPEC AX2	.0105	1.0000		
SPEC AX3	-.0305	.0078	1.0000	
SPEC AX4	.0113	-.0607	.0247	1.0000
ALTIT	.2714	.2682	.4047	.1881
ASPT N	.0000	.0000	.0000	.0000
ASPT E	.4337	.1331	.6517	-.0020
ASPT S	.3747	.1754	.0381	-.1441
ASPT W	.0000	.0000	.0000	.0000
MID -	.4071	.2258	.4252	-.0834
FOOT	-.4582	-.1666	-.4629	.0633
DRAIN	.0886	-.3324	-.1047	-.0903
WD COV	-.7065	.2452	.1996	-.2821
NO FR	.5027	.4909	-.1913	.0346
NO CL	.3196	-.3981	-.2719	.0202
TSIC	.1554	-.0618	.0804	.0312
E CHEM	-.1993	-.2518	.1834	-.2116
E PHYS	.5794	-.1653	-.2389	-.1878
M CHEM	-.4635	-.2735	.1607	-.2062
M PHYS	.1048	-.1398	-.2320	.2698
R CHEM	.2046	-.2036	-.2860	.1196
R PHYS	-.0023	-.2206	-.0846	.0484
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4
% Variability : 41.1 and cumulative		22.5	13.0	9.3
% variability : 41.1 accounted for by axes		63.5	76.5	85.8

The correlation matrix (Table 5.12) indicates that woody cover is strongly correlated with the first species axis ($r = -0.71$). Because of this and as this axis accounts for most of the variability in the herbaceous data on sites over sedimentary geology (41.1 %), woody cover was statistically removed from the data set as a covariable. Results of this partial CCA are presented in the following tables.

Table 5.13: Ordination axes, corresponding eigenvalues, species-environment correlations, percentage variance accounted for and fraction of variance explained for partial CCA (with woody cover effects removed as a covariable), on all sites over sedimentary geology.

Axis	Eigen-value	Species - environment correlation	Cumulative % Variance accounted for by axis	Fraction of variance explained
1	0.294	0.88	37.0	0.370
2	0.195	0.86	61.6	0.246
3	0.132	0.78	78.3	0.167
4	0.061	0.56	86.0	0.077

Table 5.14: Partial correlation matrix for all environmental variables with species axes on all sites over sedimentary geology. (Covariable effects of woody cover removed).

Variables with large correlation with species axes highlighted in bold.
Variable names and explanation as per Table 5.2.

SPEC AX1	1.0000			
SPEC AX2	-.0428	1.0000		
SPEC AX3	-.0518	-.0811	1.0000	
SPEC AX4	.0619	.0017	-.1303	1.0000
ALTIT	.4001	.0390	.4074	-.0523
ASPT N	.0000	.0000	.0000	.0000
ASPT E	.4783	.3876	.4573	-.0472
ASPT S	.4317	.1700	-.1047	-.1340
ASPT W	.0000	.0000	.0000	.0000
MID	.5258	.2752	.2389	.0352
FOOT	-.5133	-.3386	-.2682	.0900
DRAIN	-.1829	.2563	-.1802	.1562
NO FR	.6215	-.2897	-.1161	.0406
NO CL	-.2364	.2038	-.2786	-.0504
TSIC	.1332	.2297	.0038	-.2015
E CHEM	-.1904	.3465	-.0193	-.2913
E PHYS	.2350	.3234	-.4096	-.0171
M CHEM	-.4081	.2255	.0063	-.2781
M PHYS	-.2044	-.1858	-.0190	-.1959
R CHEM	-.2256	-.1216	-.1544	.0692
R PHYS	-.2097	.0523	-.0436	.1814
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4
% Variability and cumulative	37.0	24.6	16.7	7.7
% variability accounted for by axes	37.0	61.6	78.3	86.0

The previous two analyses indicate that the number of fire events (NO_FR) is strongly correlated with the first species axis. This indicates that this fire variable is consistently affecting the species volume abundance on sites over sedimentary geology. Whether this is as a direct influence on the grasses, or through an indirect effect on the woody vegetation, which in turn affects grasses, is uncertain.

Of the management variables considered (ie. fire and bush clearing), the number of fires appears to be the most important affecting grass abundance over sedimentary geology. Topographic position (MID and FOOT) also appears to be significantly affecting species volume abundance on these sedimentary geological sites, although this is only evident when the effects of woody cover are removed as a covariable. Figure 5.12 provides an ordination of species and all environmental variables as they occur on sites over sedimentary geology.

Interpretation of this ordination diagram, which accounts for 63.5 % of the variability in the species data, is as follows. From the correlation matrix (Table 5.12) woody cover is the primary variable accounting for species variability on these sites over sedimentary geology ($r = -0.71$). Species dominating the open grasslands (0.1 - 40% woody cover), at moderate altitude (120m - 140m) are *Themeda triandra*, *Panicum coloratum*, *Eragrostis superba*, *Heteropogon contortus*, *Bothriochloa insculpta*, *Digitaria argyrograpta* and *Eustachys paspaloides*. These areas have been frequently cleared (1 - 5) and are relatively far from drainage lines (DRAIN). The early (1957 - 1965) physical removal of bush (E_PHYS), also appears to have favoured these species on these sites. Under similar conditions of woody cover, but with increased altitude (120m - 200m) and fire frequency (4 - 12 burns), species dominating are *Hyparrhenia hirta*, *Bothriochloa bladhii*, *Panicum deustum*, *Setaria sphacelata* and *Cymbopogon* sp.

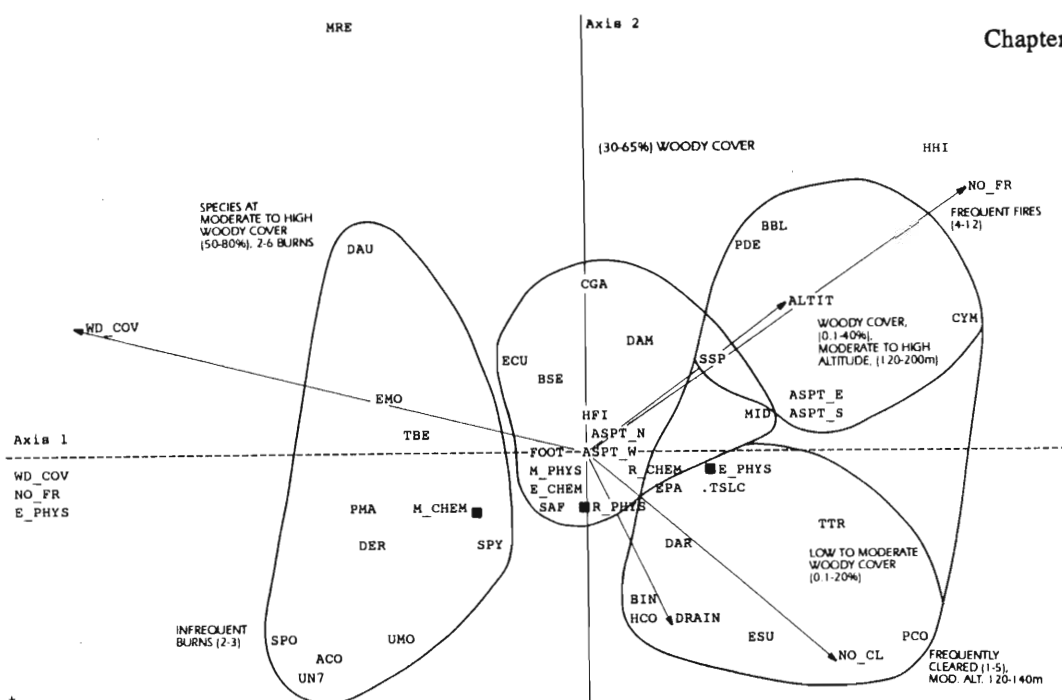


Figure 5.12 CCA Biplot of species and environmental variables on all sites over sedimentary geology.

Variable acronyms and explanation as per Table 5.2. Vector variables as arrows and nominal variables as centroids. Variables significantly correlated with axes, listed under respective axes.

With increasing woody cover (50 - 80%) on foot slopes, *Enteropogon monostachyus*, *Panicum maximum*, *Digitaria eriantha*, *Dactyloctenium australe* and *Melinis repens* dominate. Fire frequency is also lower on these sites (2 - 6 burns). Intermediate along this axis of woody cover and number of fire and clearing events, are species such as *Sporobolus africanus*, *S. pyramidalis*, *Hyparrhenia filipendula*, *Brachiaria serrata*, *Chloris gayana* and *Eragrostis curvula*.

At lower altitudes (120m - 160m), in areas which tend to have been chemically cleared in the medium term (1968 - 1978) and experienced fewer fires (2 - 4 burns), *Sporobolus pyramidalis*, *Panicum maximum*, *Digitaria eriantha*, *Urochloa mossambicensis*, *Aristida congesta*, and *Sporobolus* sp. predominate.

From these and previous analyses, the following species appear to be restricted to sites over sedimentary geology: *Enteropogon monostachyus*, *Eustachys paspaloides*, *Eragrostis superba*, *Melinis repens*, *Sporobolus africanus* and *Tragus berteronianus*.

5.4.5.2 Igneous geology

An initial analysis of the sites over igneous geology and examination of species scores, revealed that certain species were extreme outliers and were removed from further analyses. These species were *Brachiaria serrata*, *Enteropogon monostachyus* and *Eustachys paspaloides*. Reference to Fig. 5.11 showed these species tend to favour sites over sedimentary geology and therefore explains their outlier behaviour.

Analysis by CCA of all sites over igneous geology produced the following results.

Table 5.15: Ordination axes, corresponding eigenvalues, species-environment correlations, percentage variance accounted for and fraction of variance explained for CCA on all sites over igneous geology.

Axis	Eigen-value	Species - environment correlation	Cumulative % Variance accounted for by axis	Fraction of variance explained
1	0.262	0.94	35.7	0.357
2	0.188	0.92	61.3	0.255
3	0.114	0.92	76.8	0.156
4	0.069	0.81	86.2	0.094

Table 5.16: Correlation matrix for all environmental variables with species axes on all sites over igneous geology.

Variables with large correlation with species axes highlighted in bold.
Variable names and explanation as per Table 5.2.

SPEC AX1	1.0000			
SPEC AX2	-.0338	1.0000		
SPEC AX3	.0659	.0003	1.0000	
SPEC AX4	-.0031	.1321	-.0221	1.0000
ALTIT	.0817	-.0964	.4939	.0224
ASPT_N	.0662	-.1130	-.0411	-.0516
ASPT_E	-.1923	.0070	.4747	.1302
ASPT_S	.2107	-.1046	.1635	-.0547
ASPT_W	.6581	-.1489	-.0063	-.0359
MID	.0916	-.0230	.4392	.1382
FOOT	-.0916	.0230	-.4392	-.1382
DRAIN	.0066	.0165	-.0480	-.3150
WD_COV	.8513	.0826	.1784	.1326
NO_FR	.1068	-.1683	-.5289	-.3430
NO_CL	-.2875	-.2438	.1026	-.3439
TSLC	.1426	-.2508	.0989	.0452
E_CHEM	.0141	-.3560	.1486	.0029
E_PHYS	-.0006	-.1505	-.0403	.0082
M_CHEM	.0000	.0000	.0000	.0000
M_PHYS	-.2347	-.1714	.2003	.0261
R_CHEM	-.1752	-.0996	.0594	-.2584
R_PHYS	-.0004	.6648	-.4770	-.2226
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4
% Variability	35.7	25.5	15.6	9.4
and cumulative				
% variability	35.7	61.3	76.8	86.2
accounted for				
by axes				

As in previous analyses, woody cover is the dominant variable accounting for variability in the species data ($r = 0.85$, with the first species axis). Accordingly, its effects were statistically removed by making it a covariable, to determine if there were any other more subtle environmental effects which may otherwise have been obscured by this variable. The results are presented in the following tables.

Table 5.17: Ordination axes, corresponding eigenvalues, species-environment correlations, percentage variance accounted for and fraction of variance explained for partial CCA (with woody cover effects removed as a covariable), on all sites over igneous geology.

Axis	Eigen-value	Species - environment correlation	Cumulative % Variance accounted for by axis	Fraction of variance explained
1	0.188	0.92	37.0	0.370
2	0.122	0.95	61.1	0.241
3	0.076	0.82	76.1	0.149
4	0.051	0.69	86.1	0.100

Table 5.18: Partial correlation matrix for all environmental variables with species axes on all sites over igneous geology. (Covariable effects of woody cover removed).

Variables with large correlation with species axes highlighted in bold.
Variable names and explanation as per Table 5.2.

SPEC AX1	1.0000			
SPEC AX2	.0234	1.0000		
SPEC AX3	.1509	-.0405	1.0000	
SPEC AX4	-.0811	.0679	-.0200	1.0000
ALTIT	-.0936	.4833	-.1047	.2181
ASPT_N	-.1271	-.1061	-.1314	.1806
ASPT_E	.0384	.5190	.0300	.1334
ASPT_S	-.1244	.1537	-.0370	-.2098
ASPT_W	-.2773	-.2178	-.1551	-.0817
MID	-.0134	.5262	.1305	-.0490
FOOT	.0134	-.5262	-.1305	.0490
DRAIN	.0070	-.1189	-.3223	-.0647
NO_FR	-.1927	-.5693	-.2035	-.1671
NO_CL	-.2283	.1401	-.3388	.0469
TSLC	-.2653	.0415	-.0834	.3633
E_CHEM	-.3514	.1445	-.0699	.2486
E_PHYS	-.1521	-.0511	-.0308	.2006
M_CHEM	.0000	.0000	.0000	.0000
M_PHYS	-.1424	.2704	.0080	.1170
R_CHEM	-.0849	.0721	-.2218	-.1538
R_PHYS	.6440	-.5405	-.1478	.0085
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4
% Variability and cumulative	35.7	25.5	15.6	9.4
% variability accounted for by axes	35.7	61.3	76.8	86.2

With the statistical removal of woody cover as a covariable, recent (1984 - 1989) physical bush clearing becomes the dominant variable influencing the distribution of species. This variable had been strongly correlated with the second species axis when woody cover was still in the analysis. With the removal of woody cover effects, the influence of this clearing are more pronounced and it becomes the variable most strongly correlated with the first species axis ($r = 0.64$). Topographic position, east and western aspects and the number of fire events are also strongly correlated with the species axes (Table 5.16 and Table 5.18).

Figure 5.13, an ordination of all species and environmental variables on sites over igneous geological material, represents how the grass communities are responding to the measured environmental variables.

Interpretation of this ordination diagram, which accounts for 61.3 % of the variability in the species data, in sites over igneous geology, is as follows. From the correlation matrix (Table 5.16) woody cover is the primary variable accounting for species variability on these sites ($r = 0.85$). As woody cover increases from open grassland situations, to closed canopy woodland, the species shift in dominance accordingly. Species dominating the open grasslands (2 - 5% woody cover) are *Hyparrhenia rufa*, *H. hirta*, *Digitaria argyrograpta*, *D. eriantha*, *Themeda triandra*, *Cymbopogon excavatus* and *Bothriochloa insculpta*. Under similar conditions of low woody cover, but on more frequently cleared sites, *Trachypogon spicatus*, *Hyparrhenia filipendula* and *Urochloa mossambicensis* predominate.

At the other end of this woody cover gradient, in more closed woodland canopy situations (40 - 70%) and on more western aspects, the following species tend to dominate: *Dactyloctenium australe* and *Panicum deustum*. Intermediate along this axis (5 - 45% woody cover) and in areas that have recently (1984 -1989) been physically cleared of bush, species such as *Panicum maximum*, *Eragrostis*

curvula, *Panicum coloratum*, *Heteropogon contortus*, *Sporobolus pyramidalis*, *Chloris gayana*, *Diheteropogon amplexens*, *Bothriochloa bladhii*, and *Setaria sphacelata*, dominate.

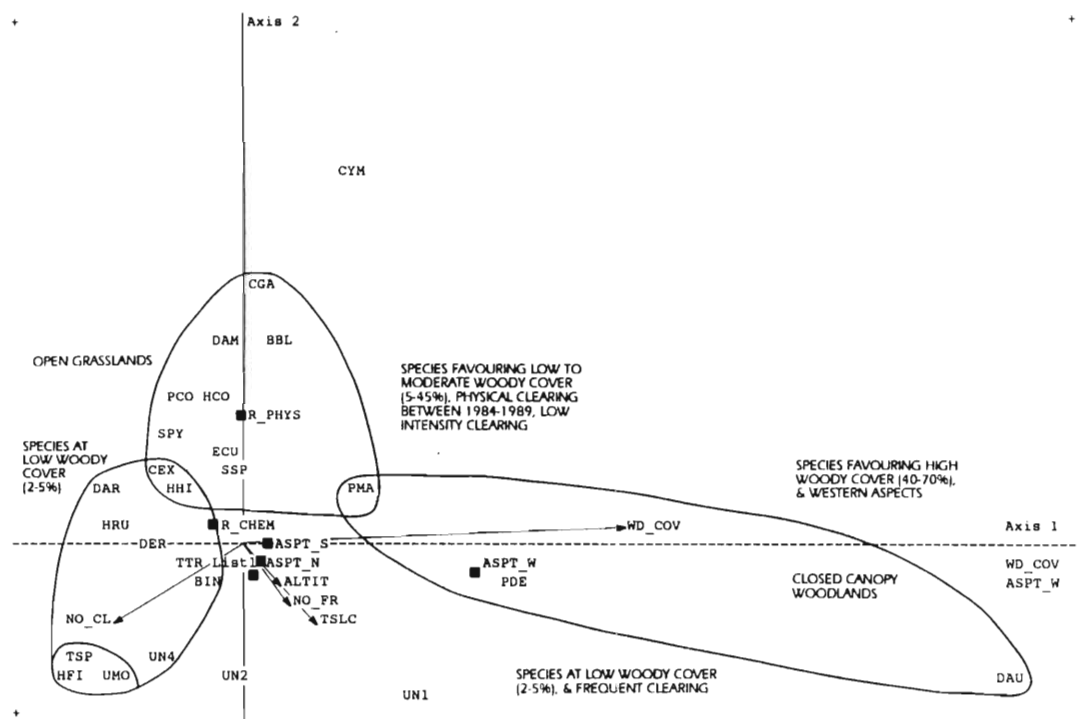


Figure 5.13 CCA Biplot of species and environmental variables on all sites over igneous geology.

Variable acronyms and explanation as per Table 5.2. Vector variables as arrows and nominal variables as centroids. Variables significantly correlated with axes, listed under respective axes.
List of variables necessary to represent all information in the diagram.
List 1: DRAIN, MID, FOOT, E_CHEM, E_PHYS, M_CHEM, ASPT_E, R_CHEM.

From these and previous analyses, the following species appear to be restricted to sites over igneous geology: *Cymbopogon excavatus*, *Hyparrhenia hirta*, *H. rufa*, and *Trachypogon spicatus*.

5.4.6 Effects of fire and clearing on grass communities

The preceding analyses, in uncleared areas, considering the complete species data set and on the different geological substrates, have consistently established certain environmental variables as affecting the herbaceous layer. Of all the environmental variables examined (Table 5.2) it is woody cover, the number of fire events, altitude, geological substrate and type of soil parent material, which appear to be the primary determinants of the herbaceous layer in HGR.

The fact that the cleared/uncleared variable (CLEAR) does not appear to be accounting for much of the variation in the species data needs some explanation. This variable only records if a site was cleared and therefore does not account for re-encroachment of an area after a clearing event. This process invariably takes place after clearing, with King (1987) stating that there is no altitudinal or soil restriction to woodland or forest in this reserve. Therefore, with time, woody cover in bush cleared areas is likely to increase in the absence of follow-up treatments.

Other variables (eg. aspect, topographic position and time since last clearing) which may have been thought to affect species more strongly than is at first apparent, do have some influence. These influences are only evident however when other more strongly correlated variables have had their effects statistically removed in the analyses.

As this study essentially focuses on the effect that bush clearing and fire have had on the herbaceous composition, the split of environmental variables, into those related to management (fire and clearing) and those strictly related to the 'environment,' (altitude, aspect, topographic position and soil type etc.), was again used. These latter variables were treated as 'covariables,' whilst those associated with bush clearing and fire were treated as the environmental variables of interest.

Table 5.19: List and explanation of environmental variables. Split on the basis of being either 'pure' environmental, or associated with fire and bush clearing.

Name of variable examined	Nominal or vector	Description of variable
Environmental covariables (or 'pure' environmental variables)		
ALTIT	V	Height above sea level (m)
ASPT N	N	Northern aspects
ASPT E	N	Eastern aspects
ASPT S	N	Southern aspects
ASPT W	N	Western aspects
MID	N	Mid-slope topographic position
FOOT	N	Foot-slope topographic position
DRAIN	V	Distance to drainage line (m)
G IGN	N	Igneous derived geology
G SED	N	Sedimentary derived geology
S IGN	N	Igneous derived soils
S SED	N	Sedimentary derived soils
Environmental variables associated with bush clearing or fire		
WD COV	V	% Woody cover
NO FR	V	Number of fire events
CLEAR	N	Cleared or uncleared
NO CL	V	Number of clearing events
TSLC	V	Time since last clearing
EARLY	N	Cleared early (1957 - 1965)
MEDIM	N	Cleared in medium term (1968 - 1978)
RECNT	N	Cleared recently (1984 - 1989)
E CHEM	N	Early chemical clearing
E PHYS	N	Early physical clearing
M CHEM	N	Medium term chemical clearing
M PHYS	N	Medium term physical clearing
R CHEM	N	Recent chemical clearing
R PHYS	N	Recent physical clearing

In this way the question of whether the differences in vegetation can be fully accounted for by the 'pure' environmental variables (covariables), or whether the variation that remains after fitting these covariables is systematically related to bush clearing and fire regime, may be answered.

Another question to be answered in this analysis was which aspects of fire and clearing are the most important in affecting grass communities, if in fact these variables are shown to be important. To answer these questions the complete data set was analyzed by CCA with pure environmental effects removed as covariables and the variables associated with bush clearing and fire, the variables of interest. This division shown in Table 5.19.

Results of this analysis of the split data set reveal that the first two axes account for 65.9% of the remaining variance in the data set (Table 5.20). The first eigenvalue of this analysis (0.15) was subjected to the Monte Carlo permutation test (99 permutations) leading to a P-value of 0.01 (Hope 1968). The variation in the vegetation that remains after fitting environmental covariables is therefore significantly related to the bush clearing and fire variables. There is thus evidence for a statistical relationship between species composition and the bush clearing and fire regime.

Table 5.20: Ordination axes, corresponding eigenvalues, species-environment correlations, percentage variance accounted for and fraction of variance explained for partial CCA.
Covariable effects of 'pure' environmental variables removed.

Axis	Eigen-value	Species - environment correlation	Cumulative % Variance accounted for by axis	Fraction of variance explained
1	0.152	0.92	36.5	0.365
2	0.123	0.77	65.9	0.294
3	0.055	0.72	79.0	0.131
4	0.030	0.61	86.3	0.073

Having established that bush clearing and fire are affecting grasses, it remains to be seen which of these management variables account for what proportion of the variation.

Examination of the correlation matrix (Table 5.21) reveals woody cover, the number of times an area is cleared and the early physical removal of bush as the variables most strongly correlated with the first species axis.

Table 5.21: Partial correlations of environmental variables with species axes for partial CCA.

**Covariable effects of ‘pure’ environmental variables removed.
Variables strongly correlated with axes highlighted in bold.**

SPEC AX1	1.0000			
SPEC AX2	-.0298	1.0000		
SPEC AX3	.0995	-.0333	1.0000	
SPEC AX4	.1737	-.0647	.2072	1.0000
WD_COV	-.7254	.4422	.0275	-.0494
NO_FR	.0965	.0323	-.1154	.1392
CLEAR	.4327	-.0411	-.0834	-.0935
NO_CL	.6396	-.0354	.0435	.1293
TSLC	.2505	.1213	.1270	-.2664
EARLY	.4786	.2400	.3670	.1028
MEDIM	.4163	-.0543	.0357	.1738
RECNT	.2336	-.3368	-.1610	.0308
E_CHEM	.1903	.0009	.2848	-.1787
E_PHYS	.5712	.3582	.2424	.2052
M_CHEM	-.0956	-.1688	.3950	-.0037
M_PHYS	.4163	-.0543	.0357	.1738
R_CHEM	.3652	-.1859	-.0660	-.0100
R_PHYS	-.0698	-.2541	-.3722	.0646
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4
% Variability	36.5	29.4	13.1	7.3
and cumulative				
% variability	36.5	65.9	79.0	86.3
accounted for				
by axes				

A biplot of species and the fire and bush clearing variables (Fig. 5.14) showed some change in the distribution of species and variables when compared to the biplot of species and all environmental variables (Fig 5.11). The relative positions

of species have altered and environmental variables have also changed in their influence on the species distributions. Woody cover consistently affects the species distributions in both biplots. In this last analysis the number of clearing events (NO_CL) significantly affects species distributions. This was not the case in the analysis using all environmental variables however ie. the number of clearing events only becomes relatively significant with the removal of pure environmental variables as covariables.

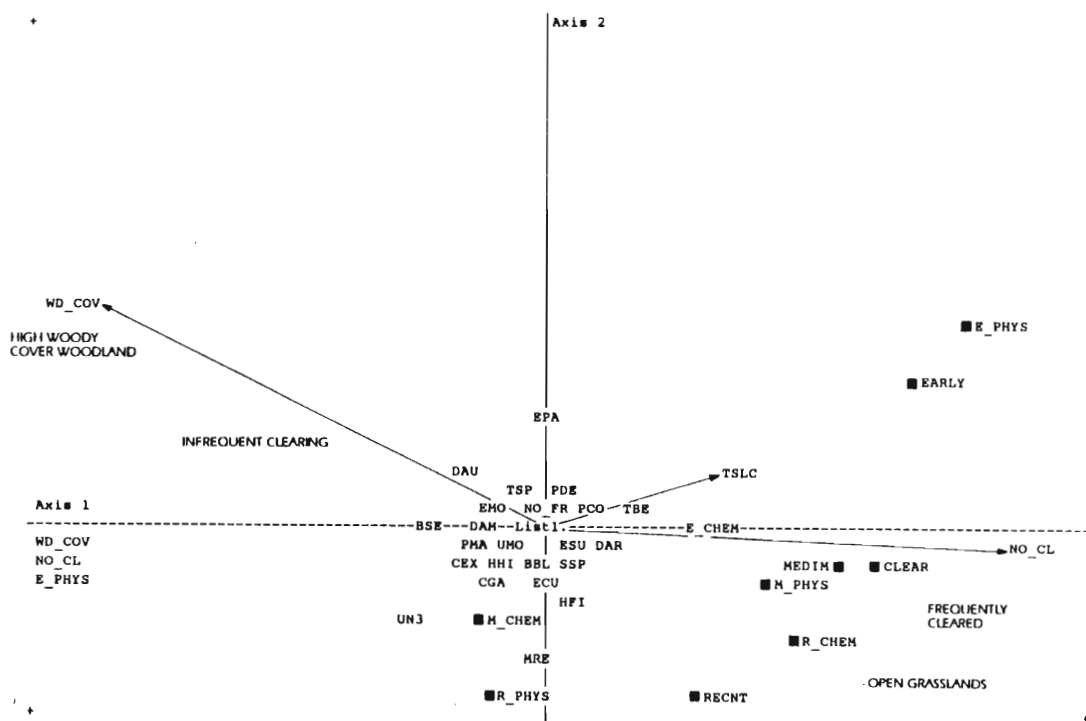


Figure 5.14 CCA Biplot of species with fire and bush clearing variables. Covariable effects of 'pure' environmental variables removed.

Variable acronyms and explanation as per Table 5.2. Vector variables as arrows and nominal variables as centroids. Variables significantly correlated with axes, listed under respective axes.
Species unable to be plotted on diagram represented as a list.
List 1: SPY, DER, BIN, TTR, HRU, UN4, ACO, HCO, SAF, CYM.

The high correlation with the first axis (Table 5.21) indicates that woody cover accounts for most of the variation extracted. Thus this variable, which depends in a complex way on both clearing frequency and intensity, fire and vegetation

dynamics, may be masking the more subtle effects the other clearing and fire related variables have on herbaceous species composition. To investigate this assumption, woody cover was made a covariable, along with the other 'pure' environmental variables and the data reanalysed.

Table 5.22: Ordination axes, corresponding eigenvalues, species-environment correlations, percentage variance accounted for and fraction of variance explained for partial CCA with bush clearing/fire variables (excluding woody cover) and pure environmental variables (including woody cover), as covariables.

Axis	Eigen-value	Species - environment correlation	Cumulative % variance accounted for by axis	Fraction of variance explained by axis
1	0.133	0.83	47.7	0.477
2	0.054	0.72	67.2	0.195
3	0.031	0.65	78.4	0.112
4	0.019	0.44	85.1	0.067

The first two axes account for 67.2% of the remaining variation in the data set (after the removal of pure environmental and woody cover effects) (Table 5.22). Once again the resulting first eigenvalue of this analysis was subjected to the Monte Carlo permutation test (99 permutations). The P-value of 0.01 indicates that this first canonical axis is still significantly related to the bush clearing and fire regime: - more specifically to physical bush removal during the period 1957 - 1965 ($r = -0.64$). Even with re-encroachment of cleared areas, this early physical removal of bush still appears to be affecting the composition of the herbaceous layer. This indicates that the physical clearing techniques used during that period (ie. cutting and partial cutting) had sufficient impact on the woody layer to still

be affecting grasses in these cleared areas. No other variables show significant correlations with this first or subsequent axes (Table 5.23).

Table 5.23: Partial correlations of environmental variables with species axes for partial CCA. Covariable effects of 'pure' environmental variables and woody cover removed.

Variables strongly correlated with axes are highlighted in bold.

SPEC AX1	1.0000			
SPEC AX2	-.0197	1.0000		
SPEC AX3	-.1073	.1957	1.0000	
SPEC AX4	-.0647	-.0723	-.0045	1.0000
NO_FR	-.0736	-.1189	.1597	.0777
CLEAR	-.2166	-.0703	-.1423	.0307
NO_CL	-.3777	.0723	.0955	.2973
TSLC	-.2447	.1338	-.2742	-.0452
EARLY	-.4832	.3779	.1011	.1452
MEDIM	-.1943	.0504	.1902	.1317
RECNT	.1715	-.1501	-.0356	.1723
E_CHEM	-.1078	.2909	-.1925	.1496
E_PHYS	-.6383	.2497	.2082	.0148
M_CHEM	.1898	.3973	-.0298	.2474
M_PHYS	-.1943	.0504	.1902	.1317
R_CHEM	-.0468	-.0518	-.0761	.0833
R_PHYS	.2641	-.3635	.0447	.2108
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4
% Variability	47.7	19.5	11.2	6.7
and cumulative				
% variability	47.7	67.2	78.4	85.1
accounted for				
by axes				

In the absence of pure environmental and woody cover effects on species distribution, *Sporobolus africanus*, *Panicum coloratum*, *P. deustum*, *Trachypogon spicatus*, *Themeda triandra*, *Heteropogon contortus* and *Bothriochloa insculpta* dominate on sites physically bush cleared during the period 1957 to 1965. From interpretations of previous analyses, these species are also those generally favouring areas of low woody cover ie. open grasslands.

This relationship is shown in the biplot of species and environmental variables (Fig. 5.15) for this latest analysis.

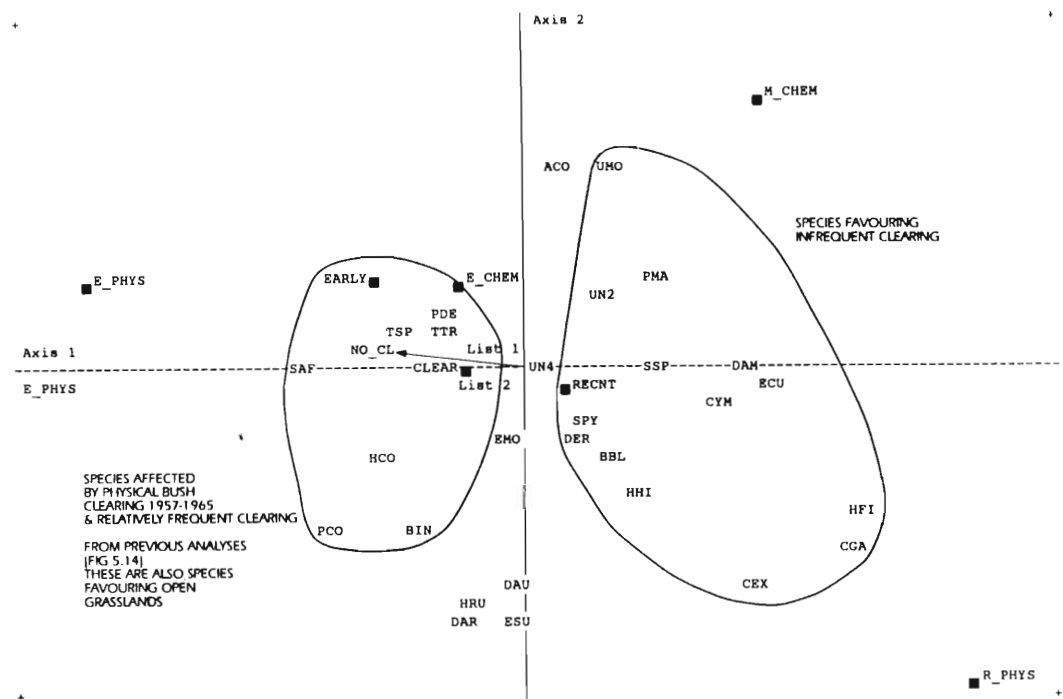


Figure 5.15 CCA Biplot of species and bush clearing/fire variables (excluding woody cover). Pure environmental variables and woody cover effects removed as covariables.

Variable acronyms and explanation as per Table 5.2. Vector variables as arrows and nominal variables as centroids. Variables significantly correlated with axes, listed under respective axes.
List of variables necessary to represent all information in the diagram.
List 1: TSLC, MEDIM, M_PHYS.
List 2: NO_FR, R_CHEM.

Although the Student t-test is not appropriate for tests of significance of canonical coefficients the t-values may still have exploratory use. When the t-value of a variable is less than 2.1 in absolute value, then the variable does not contribute much to the fit of the species data in addition to the contributions of the other variables in the analysis. This variable then does not have an effect that is uniquely attributable to itself and may be removed from further analysis without much affecting the canonical eigenvalues (ter Braak 1988).

An examination of t-values (Table 5.24) revealed that only recent clearing, particularly with chemical agents, number of fire events and early physical clearing, contributed significantly to the fit of the species data on the first axis of this last analysis, whilst number of clearing events and medium term chemical removal were the only variables significantly contributing to the second axis. (Note: In this analysis collinearity was detected when fitting the variable M_PHYS. It was therefore removed from further analysis).

Table 5.24: t-Values of canonical coefficients for environmental variables used in the fitting of species data to the first two species axes in the partial CCA. Covariable effects of pure environmental and woody cover variables removed from analysis.

Environmental variables which contribute significantly to the multiple regression fit of the species data, ie. where $t > 2.1$, highlighted in bold.

Variable name	t Values of canonical coefficients for environmental variables used in fitting of species data	
	Axis 1	Axis 2
NO_FR	-3.36	-0.76
CLEAR	-0.24	-1.06
NO_CL	-0.75	-2.41
TSLC	-0.51	0.66
EARLY	1.83	1.21
MEDIM	-1.71	1.08
RECNT	3.30	0.33
E_CHEM	-1.28	-0.31
E_PHYS	-2.20	0.18
M_CHEM	1.72	2.73
R_CHEM	-3.71	0.64
R_PHYS	-0.81	-0.33

To test the significance of the second canonical axis and variables associated with it, a separate analysis was carried out in which the first ordination axis derived from the previous analysis is made a covariable (ter Braak 1988). The statistics associated with this latest analysis are summarized in Table 5.25.

Table 5.25: Ordination axes, corresponding eigenvalues, species-environment correlations, percentage variance accounted for and fraction of variance explained for partial CCA with the first ordination axis (primarily representing early physical bush removal) and pure environmental variable effects, including woody cover, removed as covariables.

Axis	Eigen-value	Species - environment correlation	Cumulative % variance accounted for by axis	Fraction of variance explained by axis
1	0.36	0.87	57.5	0.575
2	0.12	0.80	76.6	0.191
3	0.06	0.52	86.1	0.095
4	0.03	0.54	91.5	0.054

The most dominant variable now affecting grasses is the number of fire events (NO_FR) and medium term (1968-1978) chemical clearing (M_CHEM) on the first axis and number of clearing events (NO_CL) on the second axis (Table 5.26). A Monte Carlo test of significance for this new first axis reveals that the environment, specifically the variables NO_FR and M_CHEM, are still having a significant impact on herbaceous composition ($P < 0.01$). This relationship is visible in the ordination diagram (Fig. 5.16). Significantly all these variables (including early physical bush removal, E_PHYS) are linked in their affect on woody cover - the major environmental variable affecting grass species composition.

With the removal of the effects of pure environmental variables, woody cover and physical bush clearing during 1957 - 1965, the number of fire events, chemical clearing during 1968 - 1978 and the number of clearing events are now shown to be significantly affecting species distributions.

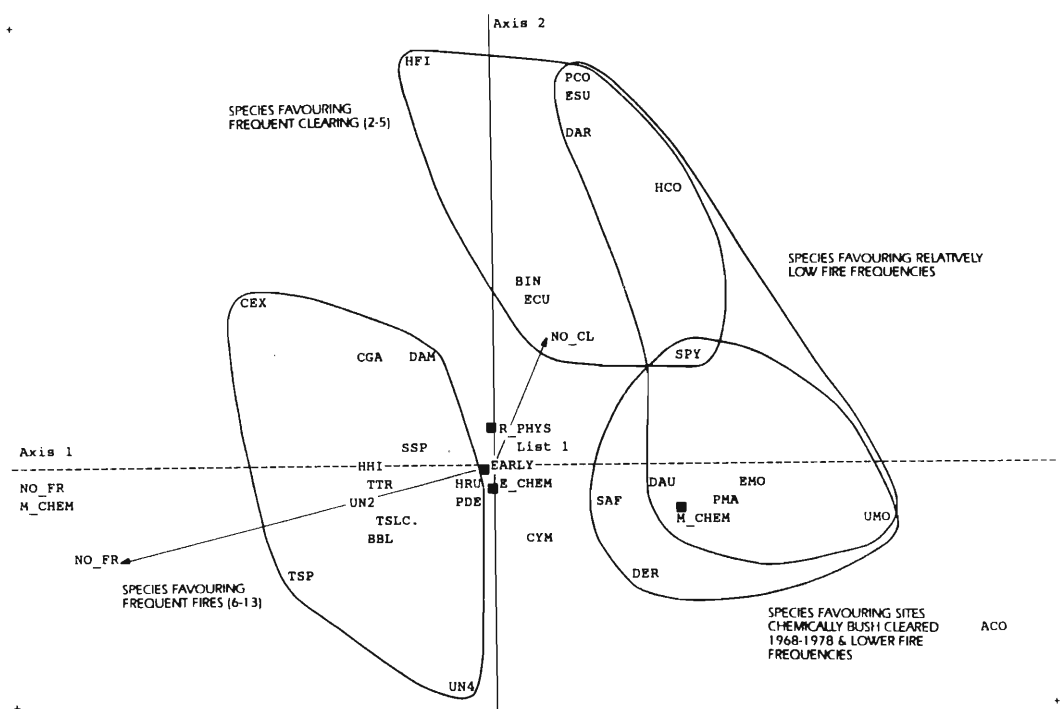


Figure 5.16 CCA Biplot of species and bush clearing/fire variables. Pure environmental variables, woody cover and first ordination axis effects from previous figure (Fig. 5.15), removed as covariables.

Variable acronyms and explanation as per Table 5.2. Vector variables as arrows and nominal variables as centroids. Variables significantly correlated with axes, listed under respective axes.
List of variables necessary to represent all information in the diagram.
List 1: CLEAR, RECENT, E_PHYS, R_CHEM, MEDIM, M_PHYS.

From Figure 5.16, *Sporobolus pyramidalis*, *Eragrostis curvula*, *E. superba*, *Bothriochloa insculpta*, *Heteropogon contortus*, *Hyparrhenia filipendula*, *Digitaria argyrograpta* and *Panicum coloratum* favour areas that are frequently cleared. This indicates these species are probably disturbance tolerant. Gibbs

Russell *et al.* (1990) also identifies several of these species eg. *Eragrostis curvula*, *E. superba*, *Bothriochloa insculpta* and *Hyparrhenia filipendula*, as occurring in disturbed areas. On sites less frequently cleared but more frequently burnt, *Trachypogon spicatus*, *Bothriochloa bladhii*, *Themeda triandra*, *Hyparrhenia hirta*, *Cymbopogon excavatus* and *Setaria sphacelata*, tend to dominate. These species therefore appear to favour less disturbed sites with Gibbs Russell *et al.* (op cit.) noting *Themeda triandra* preferring undisturbed sites.

Areas infrequently burnt and chemically bush cleared in the period 1968 to 1978, favour species such as *Panicum maximum*, *Urochloa mosambicensis*, *Enteropogon monostachyus*, *Dactyloctenium australe* and *Digitaria eriantha*. Areas of infrequent burning also correspond with woodlands where there is a low fuel mass. Hence these latter species favouring low burning frequency are also those species generally tolerant of high woody cover. Another conclusion from this observation is that this clearing method, in conjunction with low burning frequency, appears to have been rather ineffective in controlling bush encroachment as there are now generally shade tolerant grass species (associated with high woody cover) dominant on these sites.

Table 5.26: Partial correlations of environmental variables with species axes for partial CCA. Covariable effects of ‘pure’ environmental variables, woody cover, and the first ordination axis of the previous analysis, (primarily representing early physical bush clearing), removed.

Variables strongly correlated with axes are highlighted in bold.

SPEC AX1	1.0000			
SPEC AX2	.0697	1.0000		
SPEC AX3	-.1055	.0109	1.0000	
SPEC AX4	.0303	-.0575	-.0970	1.0000
NO_FR	-.7388	-.3223	-.0327	.0721
CLEAR	-.2160	.2309	.2305	-.0591
NO_CL	.1051	.4282	.4027	.0822
TSLC	-.1278	-.1805	.0461	-.1588
EARLY	-.0882	-.1559	.3714	-.0680
MEDIM	.2196	.4211	.1643	-.0432
RECNT	-.0343	.3387	.2045	.1679
E_CHEM	-.0617	-.3597	.2594	-.2108
E_PHYS	-.0919	.2122	.1956	.1032
M_CHEM	.5376	-.2691	.3398	.0066
M_PHYS	.2196	.4211	.1643	-.0432
R_CHEM	-.0111	.3577	.2296	.0355
R_PHYS	.0185	.1820	.0080	.3737
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4
% Variability	57.4	19.1	9.5	5.4
and cumulative				
% variability	57.4	76.6	86.1	91.5
accounted for				
by axes				

Successive analyses have removed the ‘masking’ influences of pure environmental and dominant bush clearing variables on grass species abundances. This allowed more detailed elucidation of the effects of bush removal and burning on the composition and abundance of grassland associations encroached by invasive woody species.

5.5 Model development

From the results obtained so far a model of grass species response to key environmental variables, in primarily cleared but also uncleared areas of HGR, is hypothesized.

The major environmental variables affecting species distributions were identified from analyses. Species were then grouped according to their distribution in relation to these variables. Within the groupings of species (responding to the major environmental variables) subgroups of species could sometimes be identified which were responding to other, less significant environmental variables (both pure and management related). This resulted in a hierarchy of species responses to the most important environmental variables. Variables significantly affecting species distributions were used to distinguish between groups at each level of species grouping in the model.

Analysis of species data on uncleared and cleared sites showed two broad groups of grasses in this reserve. Identified on the basis of their occurrence and response to either sedimentary or igneous substrates (geology and soils). This division was used to initially divide and group species (Level 1 of the model, Fig. 5.17). Certain species are present over both substrates whilst others are restricted to a particular substrate.

On the different substrates, species appear to respond primarily to differences in woody cover. This is a complex variable in that it co-varies and is correlated with other variables such as altitude, fire and clearing frequency, topographic position and aspect. Woody cover then provides the basis for the next grouping of species (Level 2 of Fig. 5.17).

On sites over sedimentary substrate there is a sufficient distinction in species response to woody cover to have three major groupings of species ie. at low (0.1

- 40%), moderate (30 - 65%) and high (50 - 80%) woody cover. Over igneous substrate there were only two major groupings of species in response to woody cover ie. at low to moderate (0.1 - 40%) and at high (40 - 70%) woody cover.

The results from the analysis and interpretation of the effects of bush clearing and fire on grass species gave further groupings of species according to management related variables, over the different substrates and in the various woody cover classes (Level 3 of Fig. 5.17).

The various groupings of grasses over the different substrates, in the various woody cover classes and in response to the extremes of bush clearing and fire regime, are portrayed in Figure 5.17.

Over the sedimentary substrate at medium levels of woody cover (30-65%) species only appeared to be responding to high fire and high clearing. At high woody cover over the same substrate there were only low fire and clearing effects on the grasses. This is understandable given that high woody cover has probably arisen due to low clearing and fire frequencies, as well as there being low fuel loads and consequently low incidences of fire associated with high woody cover.

Over igneous substrates, as well as responding to the extremes of fire and clearing, a further grouping of species appeared to favour the combination of high fire and clearing in habitats with low woody cover.

This model shows that as fire and clearing frequency increases in woodland there is a shift to open grassland (with its associated species). Conversely, when fire and clearing frequency decrease in grasslands there is a shift to woodland, with its associated grass species.

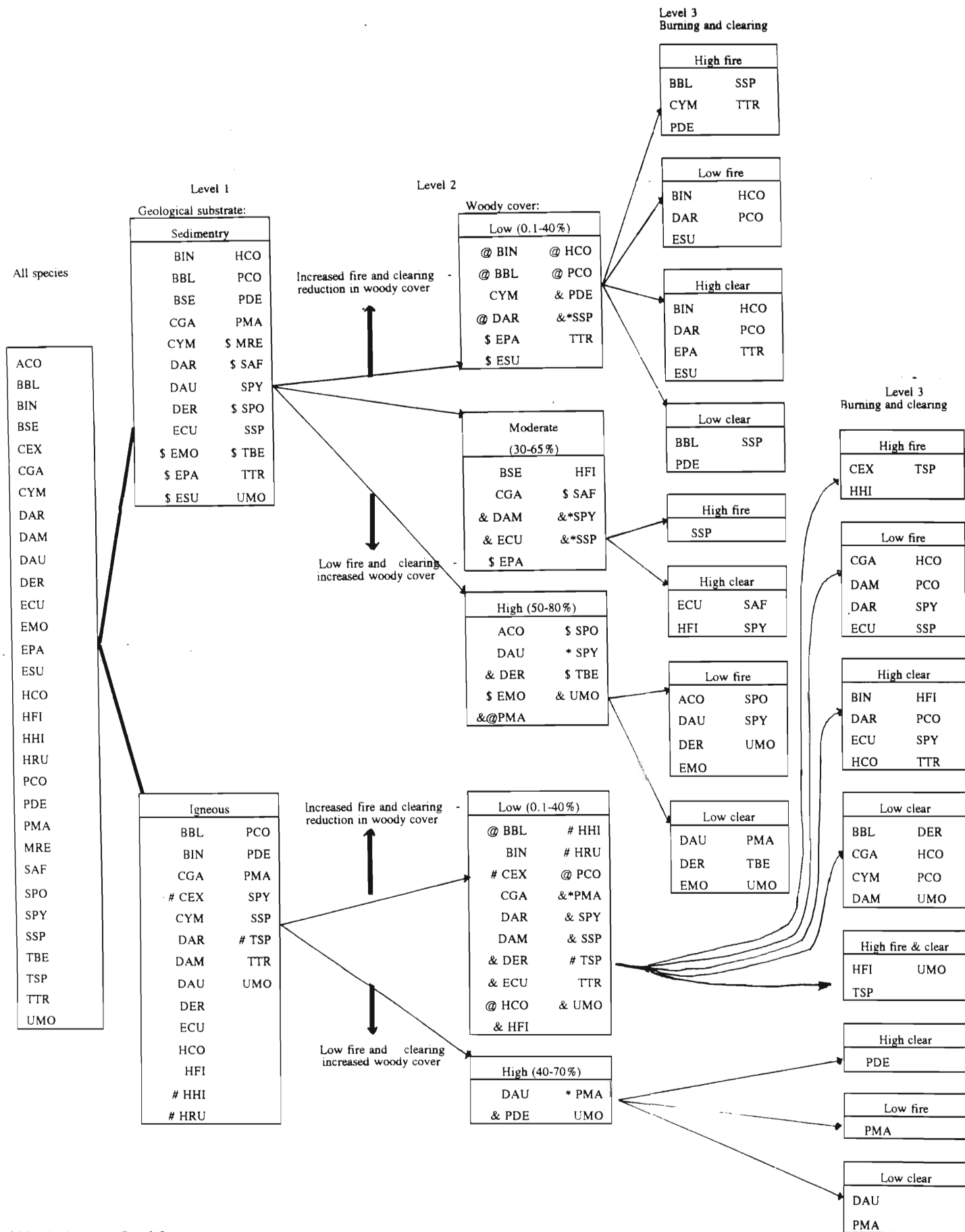


Figure 5.17 Model of species responses to key environmental variables in HGR

Legend:

Level 1 of model: species groups distinguished on the basis of geological substrate - sedimentary and igneous;
 Level 2: on the response to woody cover; and
 Level 3: on the response to extremes in burning and clearing
 Species codes in Table 5 on the opposite page.

With increased levels of fire and clearing, grasses tend towards communities at low woody cover, whilst decreased levels of fire and clearing favour communities at high woody cover.

II Model Testing

5.6 Experimental investigation of the effects of particular burning and clearing treatments on herbaceous species

5.6.1 Introduction

In previous analyses fire and clearing were shown to be important determinants of the species composition of the herbaceous layer in HGR (section 5.4.6). King (1987) proposed that a successional pathway in many areas of HGR was from *Themeda triandra* grassland (5.8% of the reserve), through *Dichrostachys cinerea* / *Acacia karroo* thicket (9.9%) and then to *A. nilotica* woodland (11.9%). Wills and Whately (1983) have also identified *A. nilotica* woodland as a key type in the bush encroachment process in HGR.

King (op cit.) initiated controlled bush clearing experiments in several vegetation types in 1985 to investigate the effect of arboricides on reversing successional trends. Included in that study was an *A. nilotica* woodland. This provided an area of detailed and known clearing history, as well as being in an 'important' vegetation type covering more than 10% of the reserve (King op cit.) in which to test the model developed in section 5.5. The location of this study site in relation to the whole reserve was shown on Fig. 4.2.

5.7 Methods

A two way, split plot design was used (Fig. 5.18) in which the effects of geology, altitude, aspect, distance to the closest drainage line and soil type were assumed to be uniform over the site. Another key assumption in the selection of

Acacia nilotica woodland

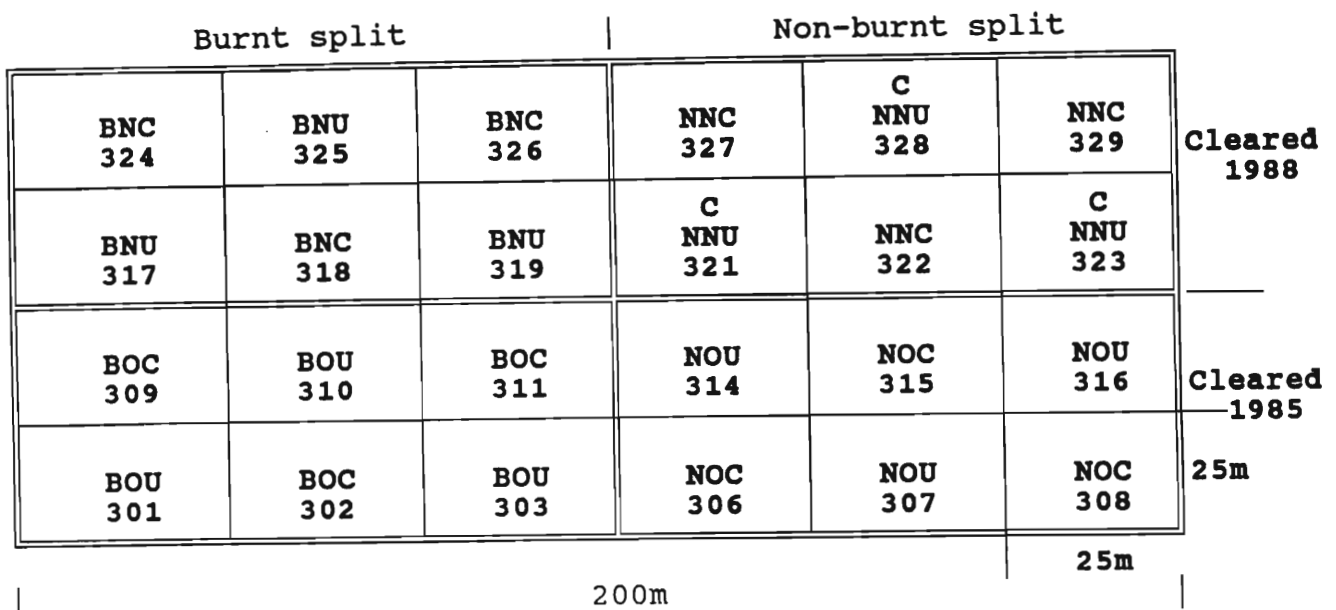


Figure 5.18 Experimental design for *Acacia nilotica* site.
Split plot with randomised blocks.
Treatment codes as per Table 5.27 below.
Site numbers corresponding to ordination diagram Fig. 5.20. *A. nilotica* site location shown on Fig. 5.5
Note: treatment NNU ie. non-burnt, new area and uncleared since 1962, constitutes the control, marked C.

Table 5.27: Treatment codes used in Fig. 5.18 and their explanation

Treatment codes	Explanation of treatment codes
BOC	Burnt 1988 and 1989, Old clearing area (1985), and recently reCleared (1988)
BOU	Burnt 1988 and 1989, Old clearing area (1985), and recently Uncleared (1988)
NOC	Non-burnt, Old clearing area (1985), and recently reCleared (1988)
NOU	Non-burnt, Old clearing area (1985), and recently Uncleared (1988)
BNC	Burnt 1988 and 1989, New clearing area (1988), reCleared (1988)
BNU	Burnt 1988 and 1989, New clearing area (1988), Uncleared (1988)
NNC	Non-burnt, New clearing area (1988), reCleared (1988)
NNU	Non-burnt, New clearing area (1988), Uncleared (1988), ie. Control - Unburnt and uncleared 1985 and 1988.

this site, and the analysis of data, was that grazing effects on species volume abundance would be uniform over all treatments.

Initially King (1987) cleared an area of 50m × 200m in 1985. Adjacent to this area cleared in 1985, a further 50m × 200m block of *A. nilotica* woodland was incorporated in the design in 1988. Both blocks then received clearing treatments in 1988, as detailed in Fig. 5.18. These clearing treatments (both in the old (1985) and new (1988) areas) were treated by cutting all woody species in the blocks designated by the experimental design. Cut stumps or stems were then treated with a 2% Garlon arboricide mix in a diesel carrier. This treatment was in accordance with current reserve management techniques for the control of encroaching woody species.

Superimposed on this whole bush cleared area was a split plot burning treatment. This involved splitting the whole experimental area (now 100m × 200m) in half and then burning the one half (Fig. 5.18). Burning was performed in conjunction with the reserves management, whose current objectives include the control of bush encroachment with fire. Accordingly, fires were applied in August (late winter, early spring) and under conditions which allowed for relatively hot fires, viz. low humidity, high ambient temperatures and high wind speeds. The non-burnt split was protected by fire breaks, as was the whole of the experimental area.

The split to be burnt had fires applied in 1988 and 1989. Burning history for the whole area, is six burns in the period 1955 to 1987. This is broken down to: burnt twice between 1965 and 1971; burnt twice between 1972 and 1979; and burnt twice between 1980 and 1987 (Nott 1991).

Clearing was implemented by King (1987) in 1985 and again for this work in 1988. Prior to any of this experimental work, the whole area was bush cleared by cutting once in 1962. However, there is no record of extent of clearing, or of

species removed, during this operation. It is assumed that this bush clearing treatment in 1962 was uniform over the whole area.

Woody cover was measured the same way as in the previous section ie. as a percentage estimate of ground covered by the tree canopies. The other environmental variables measured were determined from the fire and bush clearing maps of the area as well as the known clearing and fire treatments imposed on the site.

Table 5.28: List and explanation of environmental variables associated with bush clearing and fire on the *Acacia nilotica* site.

Name of variable examined	Description of variable
WD_COV	% Woody cover
NO_FR	Number of fire events
NO_CL	Number of clearing events
TSLC	Time since last clearing

Each of the eight treatments was pseudo-replicated (Hurlbert 1984) three times. Replicates were assigned systematically to blocks from a random start.

The grass volume abundance data was collected by placing twenty 0.5m^2 ($0.71\text{m} \times 0.71\text{m}$) quadrats in each of the three replicates of each treatment (Fig. 5.18). Because the treatment areas were smaller than those used in the broad hypotheses generating survey, twenty quadrats per replicate were deemed sufficient to characterize the species in each replicate (Fig. 5.5). The statistical efficiency of this measure was also improved by having three replicates. This gave a total of sixty quadrats measuring species performance in each treatment (Table 5.27).

Quadrats were placed every three metres along random transects through each replicate of each treatment (section 4.1.3). Within each quadrat presence/absence, modal height (cm) and areal cover (as a percentage of the total area of the quadrat covered by that particular species) for each species was recorded.

Reference to the geological maps showed this *A. nilotica* woodland area to be over sedimentary geology (Ecca and Beaufort sediments, King 1970). Though the geology for this area is of sedimentary origin, the soil is strongly influenced by colluvial igneous material (dolerite). This forms the predominant parent material for this soil along with some sandstone and shale. The soil form at this site was Hutton, with the series being mesotrophic Doveton and eutrophic Makatini (MacVicar *et al.* 1984; Barrow 1986). The effective soil parent material influencing grass species in this area is therefore assumed to be of igneous origin.

From the model developed in the previous section, the species present and their reaction to key environmental variables on this *A. nilotica* site were therefore hypothesized as being similar to those found on sites over igneous substrate. The range of environmental variables present at this site are within the range used in the development of the model. Specifically, the site is on a foot slope with neutral aspect, at an altitude of 140m and with the number of fires and clearings ranging between 6 - 8 and 1 - 3, respectively. Time since last clearing ranges between 2 and 13 years, depending on specific treatments.

5.8 Analysis

The same analytical methods were used in this experimental approach as were used in the previous analysis. The product of species cover and modal height were used to calculate a volume abundance measure. This volume abundance data was subjected to DCA and the range of sample scores, in terms of standard

deviations (SD), was determined (Table 5.29). Further analysis by CCA appeared appropriate (ter Braak 1988).

5.9 Results and discussion

5.9.1 Detection of outlier species

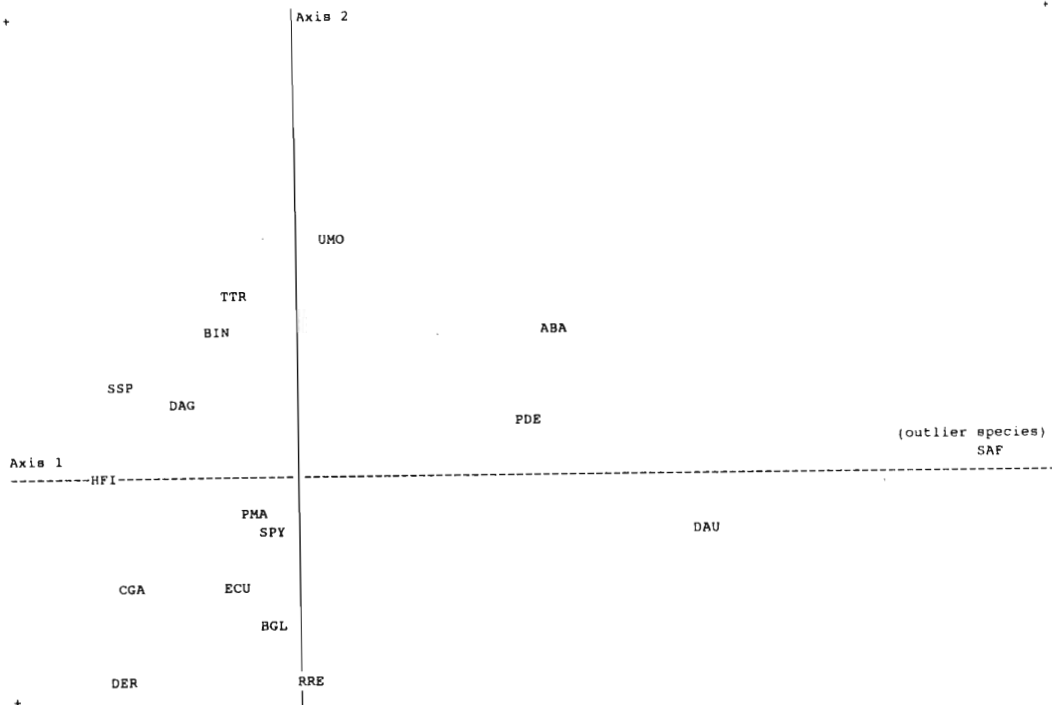


Figure 5.19 Initial species ordinations using DCA on *Acacia nilotica* site, for detection of outlier species.

Examination of the ranked species scores and an initial species ordination by DCA (Fig. 5.19) reveals *Sporobolus africanus* as an 'outlier' species on these sites. It was subsequently dropped from the analysis. The model developed in the previous section reveals that this species is restricted to sites over sedimentary geological and soil substrate. Even though the geology for this area is of

sedimentary origin, the soil is strongly influenced by colluvial igneous material (dolerite). Therefore the effective substrate influencing grass species here is of igneous origin and explains why this species appears as an outlier in this analysis.

5.9.2 Ordination of sites and species

Ordination of the volume abundance data using CCA, shows that the first two axes account for the bulk of the variance in the data (94 %, Table 5.29). It was therefore assumed that these first axes are displaying the biologically relevant information.

Table 5.29: Summary statistics on the length of ordination axes by DCA and CCA; their corresponding eigen values; species-environment correlation; percentage variance accounted for and the fraction of variance explained for respective axes at the *Acacia nilotica* site.

Axis	Length axes (SD)from DCA	Eigenvalue from DCA	Eigenvalue from CCA	Spp-environment correlation for CCA	% Var account-ed for CCA	Fraction variance explained for CCA
1	3.36	0.456	0.414	0.96	59.2	0.592
2	1.86	0.296	0.244	0.90	94.2	0.350
3	1.43	0.123	0.030	0.66	98.5	0.043
4	1.20	0.055	0.011	0.30	100.0	0.015

The species/environment correlation for the first two axes were $r = 0.96$ and 0.90 respectively (Table 5.29 and 5.30) indicating a high correlation between the species abundances and measured environmental variables. Hence, the measured environmental variables account for the main variation in species abundances.

Table 5.30: Correlation matrix of environmental axes with species axes; of environmental variables with species axes; of cumulative percentage variance; of correlation matrix of environmental variables with each other; and of mean, standard deviation and variance inflation factor for all environmental variables used in the analysis of species volume data on *A. nilotica* site. Significant values highlighted in bold.

SPEC AX1	1.0000			
SPEC AX2	-.0577	1.0000		
SPEC AX3	.0106	-.0600	1.0000	
SPEC AX4	.0854	-.2108	.3826	1.0000
ENVI AX1	.9603	.0000	.0000	.0002
ENVI AX2	.0000	.8955	.0000	.0001
ENVI AX3	.0000	.0000	.6608	.0000
ENVI AX4	.0000	.0000	.0000	.2926
WD_COV	.8881	-.0867	-.2429	.0042
NO_FR	-.4665	-.7786	-.0325	-.0220
NO_CL	-.7177	-.0789	.1414	.1820
TSLC	.7580	-.1095	-.3684	-.0660
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4
% Variability and cumulative	59.3	35.0	4.2	1.5
% variability accounted for by axes	59.3	94.3	98.5	100.0
WD_COV	1.0000			
NO_FR	-.3480	1.0000		
NO_CL	-.7530	.3828	1.0000	
TSLC	.9437	-.2329	-.8394	1.0000
	WD_COV	NO_FR	NO_CL	TSLC
Variable name:	Weighted mean	Standard deviation	Variance inflation factor (VIF)	
WD_COV	12.6930	28.1512	13.1845	
NO_FR	6.7685	.9728	1.6613	
NO_CL	2.1718	.6722	4.6969	
TSLC	4.6335	3.8196	19.7560	

Woody cover (WD_COV), time since last clear (TSLC) and number of clearing events (NO_CL) are highly correlated with the first species axis ($r = 0.89, 0.76$, and -0.72 respectively). This shows that the first axis extracted by CCA is primarily one associated with the effects of clearing on herbaceous volume abundance. The number of fire events (NO_FR) is strongly correlated with the second species axis extracted by CCA ($r = -0.78$). The second axis extracted

from the species data is therefore primarily associated with the effects of fire frequency on grass abundance.

The variance inflation factor (VIF), for time since last clearing (TSLC), is nearly 20 (Table 5.30). This indicates almost perfect correlation with other variables, woody cover in this case ($r = 0.94$). Variables with a high VIF (ie. >20) have no unique contribution to the regression equation and therefore do not merit interpretation (ter Braak 1986 and 1988).

Woody cover and the number of clearing events are strongly negatively correlated ($r = -0.75$) indicating that with increasing frequency of clearing, woody cover is concomitantly reduced. Woody cover and time since last clear on the other hand are strongly positively correlated ($r = 0.94$) indicating that with increasing time after clearing there is an increase in woody cover. This is also predicted by the current secondary successional model for Hluhluwe (Wills and Whately 1983; King 1987).

The first axis in the CCA ordination diagram accounts for 59% of the variance in the data set and is primarily a woody cover gradient. The second axis accounting for 35% of the variance and is a fire event gradient.

Figures 5.18 and 5.20 show that sites that have been uncleared since 1962 (ie. the control) dominate the one end of the first ordination axis. Vegetation on these sites consists of sub-continuous to continuous microphyllous (eg. *Acacia nilotica* and *Dichrostachys cinerea*) and broadleaf (eg. *Diospyros simii* and *Berchemia zeyheri*) woodland. Sites that are assumed to have had similar herbaceous composition as the control sites (uncleared since 1962) but were then cleared in 1985 and some again in 1988, are now grassland. These sites dominate the other end of the first ordination axis. Intermediate along this axis are sites which have only been recently cleared (1988).

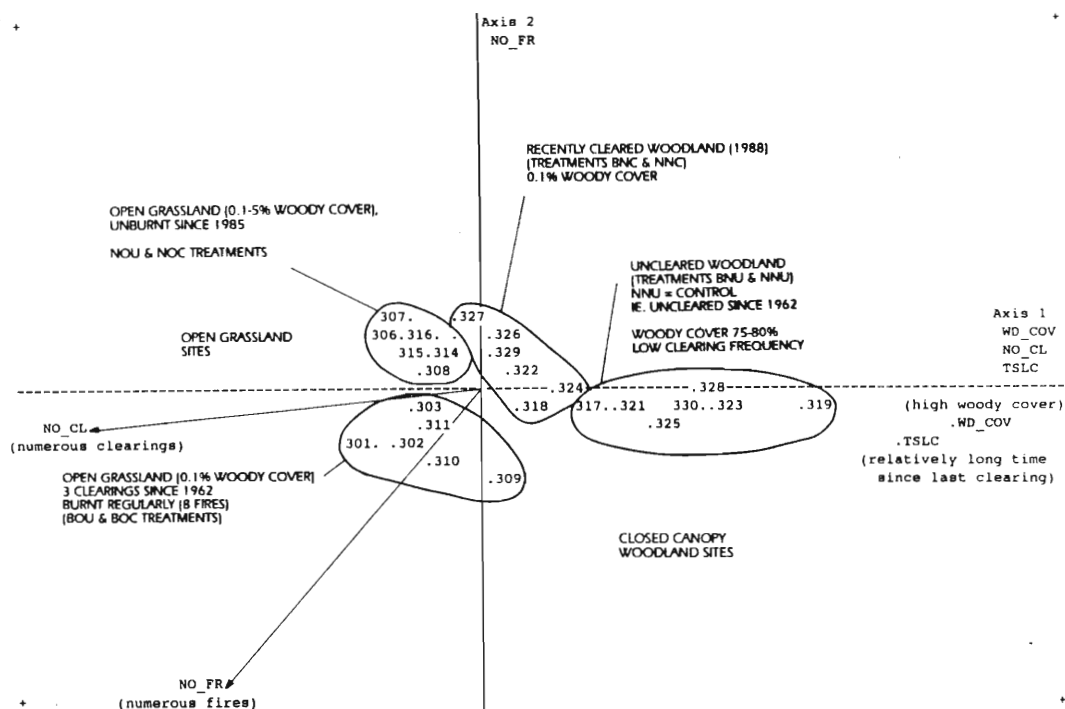


Figure 5.20 CCA Joint plot of sites and environmental variables for *Acacia nilotica* site.

Site numbers correspond with those in Fig. 5.18. Variable acronyms and explanation as per Table 5.28. Variables significantly correlated with axes, listed under respective axes.

Open grassland sites which have been burnt twice since clearing in 1988 are at one end of the number of fire events gradient (second axis), whilst open grassland sites unburnt since clearing in 1988 are at the other end of the fire gradient.

Even though some of the treatments were supposed to have burnt in terms of the experimental design ie. **BNC** and **BNU** (Burnt split, Newly cleared area, Cleared and Uncleared 1988), imposed experimental fires carried poorly through these treatments (sites 317, 318, 319, 324, 325 and 326). This was due to sparse fuel loads under the woodland canopy on uncleared sites (**BNU**, sites 317, 319 and 325). On the sites only cleared in 1988 (**BNC**, sites 318, 324 and 326), fires burnt poorly because of insufficient fuel. This was because of only one seasons

growth between clearing (1988) and the imposition of fire (1989) in which a reasonable fuel load could develop to carry a fire.

Due to this limited effect of fire in the treatments **BNU** and **BNC**, they were closely associated with treatments **NNU** and **NNC** (Non-burnt split, Newly cleared area, Uncleared and Cleared 1988) in terms of physical disturbance (sites 321, 322, 323, 327, 328 and 329). This relationship is visible in the clustering of sites on the ordination diagram where treatments **BNU** and **NNU** are together and **BNC** and **NNC** treatments are similarly grouped together (Fig. 5.20).

Site 318 (treatment **BNC**) may initially appear as an anomalous site in Figure 5.20 as it appears to be more strongly associated with the sites that have been burnt more frequently. As indicated above, the **BNU** and **BNC** treatments which should have burnt in terms of the experimental design (burnt split Fig. 5.18) burnt poorly. However, site 318 was one of the few sites of the **BNC** treatment that burnt well. This was because it had one of its edges 'open' to the area cleared in 1985 and which is now predominantly grassland (Fig. 5.18). Imposed experimental fire from the burnt split in the grassland area was able to carry over into the adjacent 'woodland grassland' of site 318. Fire was therefore able to affect grass volume abundance on this site whereas its influence was not felt in the other treatments that should have burnt as part of the experimental design.

Sites 309 and 310 may also appear to be slightly aberrant in the overall ordination diagram but this is probably due to the effects of white rhino preferentially grazing these blocks (pers. obs.). The effect of this was to reduce the modal height and hence species volume abundances on these sites. This produced effects similar to those exhibited in the sites which had a higher woody cover, ie. with increasing woody cover species volume abundance was reduced. The grazing effects of ungulates (particularly the likes of White Rhino) are essentially an uncontrollable factor and had initially been assumed to be uniform over all treatments in the design of the experiment.

5.10 Model testing and species response to burning and clearing

As the dominant soil forming material is assumed to be of igneous origin at this *A. nilotica* site, the model developed in section 5.5 (Fig. 5.17) indicates that the following species are potentially present here:

Bothriochloa bladhii, *B. insculpta*, *Chloris gayana*, *Cymbopogon excavatus*, *Cymbopogon sp.*, *Dactyloctenium australe*, *Digitaria eriantha*, *D. argyrograpta*, *Diheteropogon amplexans*, *Eragrostis curvula*, *Heteropogon contortus*, *Hyparrhenia filipendula*, *H. hirta*, *H. rufa*, *Panicum coloratum*, *P. deustum*, *P. maximum*, *Sporobolus pyramidalis*, *Setaria sphacelata*, *Trachypogon spicatus*, *Themeda triandra* and *Urochloa mosambicensis*.

The model indicates that the major variable affecting species distributions on sites over igneous material is percentage woody cover. Species potentially present on sites with low woody cover (0.1 - 40%) are:

Bothriochloa bladhii, *B. insculpta*, *Chloris gayana*, *Cymbopogon excavatus*, *Digitaria eriantha*, *D. argyrograpta*, *Diheteropogon amplexans*, *Eragrostis curvula*, *Heteropogon contortus*, *Hyparrhenia filipendula*, *H. hirta*, *H. rufa*, *Panicum coloratum*, *P. deustum*, *P. maximum*, *Sporobolus pyramidalis*, *Setaria sphacelata*, *Trachypogon spicatus*, *Themeda triandra* and *Urochloa mosambicensis*.

Whilst species potentially present on sites with high woody cover are:

Dactyloctenium australe, *Panicum deustum*, *P. maximum* and *Urochloa mosambicensis*.

Actual species response to the environment on this *A. nilotica* site is shown in Fig. 5.21. Perpendicular projection of species in the ordination onto the environmental axes of the biplot determines the approximate response of those species along the gradient (ter Braak 1988). Reference to a biplot of sites and environmental variables (Fig. 5.20) and then cross referencing sites with the

original environmental data, gave the range of environmental variables experienced along the species ordination axes.

As predicted by the model woody cover is the most important variable accounting for variation in species volume abundance on this *A. nilotica* site. Under conditions of high woody cover (eg. in closed canopy woodland with woody cover 75 - 80%) the predominant species are *Dactyloctenium australe* and *Panicum deustum*. At the other extreme, in open grasslands with woody cover 0.1 - 5%, *Chloris gayana*, *Digitaria eriantha*, *Hyparrhenia filipendula*, *Setaria sphacelata* and *Themeda triandra* dominate. Intermediate along this woody cover gradient are species such as *Bothriochloa bladhii*, *B. insculpta*, *Panicum maximum*, *Digitaria argyrograpta* and *Sporobolus pyramidalis*.

At low woody cover on this site, the following species, *Bothriochloa insculpta*, *Eragrostis curvula*, *Hyparrhenia filipendula*, *Sporobolus pyramidalis* and *Themeda triandra*, are also some of those predicted by the model as being present at higher clearing frequencies. Other species appearing to favour relatively more frequent clearings on this site were *Digitaria eriantha* and *Setaria sphacelata*. This response to clearing frequency is probably due more to changes in woody cover, experienced by the herbaceous species, than as a direct response of grasses to the physical disturbance of clearing.

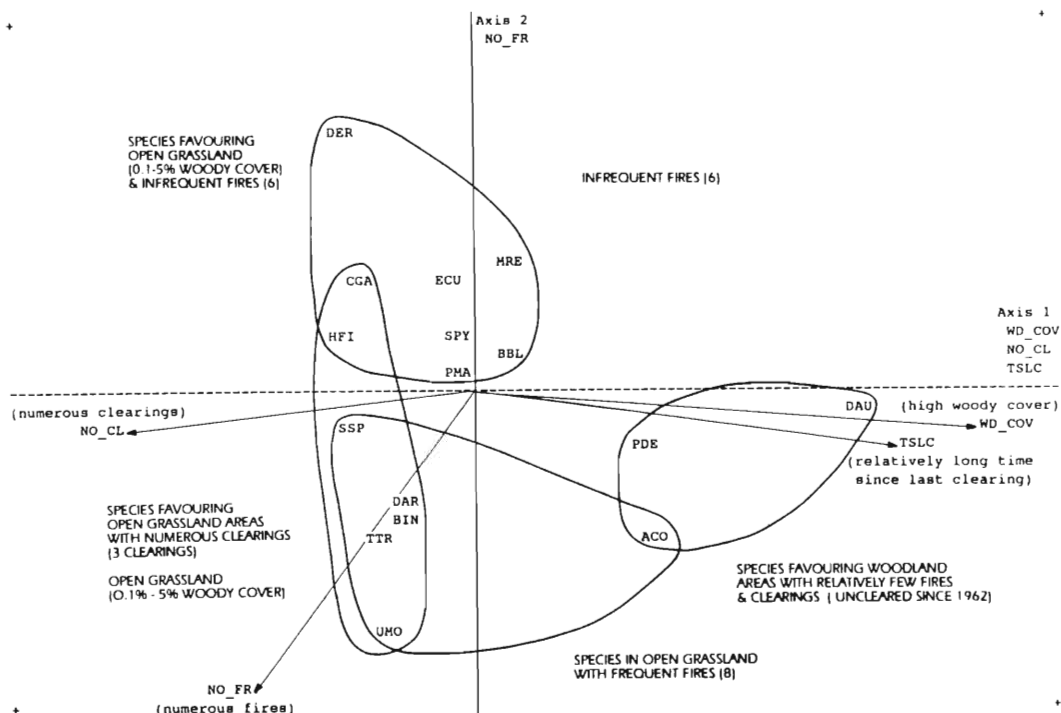


Figure 5.21 CCA Biplot of species and environmental variables for *Acacia nilotica* site.

Variable acronyms and explanation as per Table 5.28. Variables significantly correlated with axes listed under respective axes.

Chloris gayana, *Eragrostis curvula* and *Sporobolus pyramidalis* were predicted to favour less frequent fire, whilst *Urochloa mosambicensis* should favour a combination of high fire and clearing and *Bothriochloa bladhii* lower clearing.

Figure 5.21 shows that these results are in agreement with those proposed in the model for the response of species to changes in woody cover, fire and clearing regime over this substrate.

The model indicates potentially more species in the open grassland than encountered on this site. This is because the model considers open grassland as

being from 0.1 to 40% wood cover ie. covering a broader range of woody cover than that experienced by the grasslands on this site (0.1 - 5%). The model was also constructed from a larger sample, taken over a wider spatial range, therefore increasing the likelihood of observing more species.

The other major axis identified in this analysis which was accounting for variability in the species data was the number of fire events. With relatively frequent fires (8 burns since 1955) species such as *Urochloa mosambicensis*, *Themeda triandra*, *Bothriochloa insculpta* and *Digitaria argyrograpt* predominate. Decreasing the frequency of fires (6 burns since 1955) favours species such as *Bothriochloa bladhii*, *Sporobolus pyramidalis*, *Eragrostis curvula*, *Chloris gayana* and *Melinis repens*.

As the number of fire and clearing events increases, woody cover would be expected to decrease. There is only a weak correlation between number of fire events and woody cover ($r = -0.35$) although the correlation between number of clearing events and woody cover is strongly negative ($r = -0.75$, Table 5.30). Not unexpectedly this indicates that clearing has a more pronounced effect on reducing woody cover than does fire.

Of interest is the dispersion of species along this woody cover gradient. Examination of Figure 5.21 reveals only three species adapted to high woody cover conditions (75 - 80%) whilst thirteen species are adapted to the more open grassland conditions (0.1 - 5% woody cover). There is therefore greater grass species diversity in the open grasslands compared to under the woodland canopy. Along with this assertion, the model predicted a lower fraction of the total number of species over igneous geology would be found at higher woody cover. This is probably due to the greater stress (shading, moisture deficit) and competition (for nutrients, space, light and moisture) in this woody habitat.

Species optima along this gradient are closer to each other in the open areas than those in woodland areas. This indicates greater niche separation of herbaceous species in the woodlands compared to the grassland.

The relationship between grass species and the number of fire events axis reveals that those species which favour more numerous fires (8 burns since 1955) are also those found in open grasslands eg. *Themeda triandra* and *Urochloa mosambicensis*. Those species enjoying fewer fires (6 burns since 1955) on the other hand, are also those found in the more closed woodland areas eg. *Panicum deustum* and *Dactyloctenium australe*. These results are not surprising and are similar to those obtained in the broader survey of species response to environment. A greater fire frequency is possible in grassland areas where fuel loads and climatic conditions are more conducive to regular fires.

For the model to be tested and improved in terms of its predictive ability, more sites with detailed histories, different geological substrates and clearing regimes would need to be examined and compared to the results predicted by the model.

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSIONS

This discussion serves to answer the final objective of this study. Namely: what the likely consequences are of disturbance by fire and bush clearing on herbaceous vegetation in HGR.

Evidence from the literature review (eg. West 1971; Vesey Fitzgerald 1973; Phillips 1974; Werger 1978; Hall 1984a; Kruger 1984) and previous work performed in HGR (eg. Ward 1961; Wills and Whately 1983; King 1987) indicates that this area is climatically a potential forest climax. It is only through the modifying influences of fire, man and herbivores which has prevented this from happening completely in this reserve. The extent to which these influences are part of the 'natural ecosystem' of the area, and to which period in history one draws the line for 'natural' factors operating on this ecosystem, is both contentious and debatable.

In the absence of fire, significant large herbivore impact eg. elephant damage, the regular removal of bush in control exercises, or the large scale utilization of wood by man, the vegetation equilibrium in this reserve appears to shift in favour of woody species (Watson and MacDonald 1983; Wills and Whately 1983; King 1987). King (op cit.) notes that in the absence of regressive influences, bush encroachment is ecologically inevitable in HGR.

Results from this work strongly support Coles (1982) contention that within climatic limits, the main control on the distribution of plant communities is through edaphic factors - in this case geological and soil parent material. Hypothesized soil depth (and soil moisture) relations with topographic position

(Walker 1982; Stuart-Hill 1985) are shown to be important (this study and King 1987) in the distribution of plant communities.

As noted by Walker (1982) fire and herbivores are two of the most important forms of disturbance which modify the inherent structure imposed on savannas by climate and soil type. Unfortunately, due to logistical limitations, herbivory could not be examined in any great depth in this work, however, the effects of fire received attention.

Increasing numbers of fires shifts the composition of the herbaceous community away from shorter, low biomass producing, shade tolerant species such as *Dactyloctenium australe* and the more unpalatable species eg. *Eragrostis curvula* and *Sporobolus pyramidalis*, through to taller more open grassland species eg. *Themeda triandra* and *Setaria sphacelata* on the *A. nilotica* site. This is only achieved however if there is an accompanying decrease in woody cover with increased fire frequency.

The effect of regular burning appears to be, in limiting the growth of shrubs; reducing areal cover, and hence shading effects (MacDonald 1980, 1981); and stimulation of those herbaceous species, eg. *Themeda triandra*, which favour a regular fire regime (Davidson 1953; van Wyk 1972; Harrington and Ross 1974; Robinson *et al.* 1979; Edroma 1984). In perennial grasses fire removes moribund material thereby allowing more light to reach the younger, photosynthetically more efficient tillers at the base of the plant. The number of these tillers also increases due to the removal of apical dominance. Higher daytime temperatures and increased net radiant flux density of burnt areas have been recorded in southern African grasslands (Savage 1980). This serves to produce conditions more favourable for photosynthesis than on unburnt areas. The cooler temperatures at night on these burnt areas also result in lower respiration rates (Savage *op. cit.*).

Protection from fire generally leads to a marked reduction in biomass and yield, particularly in those areas which are able to support a closed canopy woodland or forest which shades out the grass (Brookman-Amissah *et al.* 1980; San Jose and Farinas 1983).

Current theory suggests that fire is only one of a number of interacting factors affecting savanna structure and dynamics (Huntley and Walker 1982; Bourliere 1983; Tothill and Mott 1985).

Results of this study indicate that as woody cover increases there is a change in the herbaceous vegetation composition. Associated with this composition change is a reduction in species modal heights and cover. This appears to be part of the inherent morphological limitations of the different species as they occur along the woody cover gradient. Kennard and Walker (1973) have also observed that a characteristic feature of tropical and sub-tropical savannas is the difference in grass growth between open and tree covered areas. Removal of woody cover, by bush clearing and increased fire frequency, allowed the herbaceous community to revert to tall, fire-climax species, as well as increase the grass species diversity.

Work by Jackson (1974) and Barnes (1982) has shown that there is an exponential increase in grass production with decreasing tree and shrub densities. Dye and Spear (1982) also showed increasing grass yields as a result of bush clearing. The larger volume abundances of species, in areas studied that had been bush cleared compared to those that had not, validated these previous authors findings.

What the exact causes of this change in herbaceous composition are (be it shade intolerance, soil moisture or nutrient changes etc.) is beyond the scope of this project and require further elucidation. It is probably no single factor but rather a combination of events, opportunities and conditions which facilitates the change

in herbaceous species composition to those species better adapted to the new environment.

From work performed by Kennard and Walker (1973), in a savanna area in Zimbabwe, the observed absence of *Panicum maximum* from the open sites is due not so much to the competition with other grasses, but rather because exposure to full sunlight markedly reduces the survival of *P. maximum* seedlings. The litter layer associated with the tree canopy, on the other hand, was found to reduce germination of the more open grassland species eg. *Heteropogon contortus* and *Hyparrhenia filipendula*. This suggests that the close association between *P. maximum* and closed tree canopies, is determined during the seedling stage of grass growth.

Bosch and van Wyk (1970), on the other hand, claim that in the northern Transvaal the *Panicum*-tree association is largely due to soil enrichment by the trees. These latter authors and Olsvig-Whittaker and Morris (1982) found that sites under tree canopies were associated with a higher rate of water infiltration, higher soil water-holding capacity as well as higher soil nutritional and organic carbon status, as compared to open grassland areas. There is also a reduction in irradiance (measured with a tube solarimeter, pers. obs.) and lowered mean surface temperatures, under the woody canopy (Kennard and Walker 1973).

Work conducted by Deshmukh (1986) on grasslands in Kenya revealed that the continued dominance of *Themeda triandra* in the communities studied was related to the frequency of fire. Similar conclusions were reached by Downing (1974) in work in Umfolozi Game Reserve, Zululand, where it appears that periodic burning of *T. triandra* is essential to maintain its vigour. Since *T. triandra* is both productive and palatable (Mentis and Tainton 1984), occasional burning should improve grazing resources. Other workers have corroborated the results found here ie. that frequent fires can lead to an increase in the numbers of more palatable grasses such as *T. triandra* and *Heteropogon contortus* (Norton-Griffiths

1979) as well as increasing the acceptability and availability of certain grass species (Tainton and Mentis 1984).

The removal of moribund material, and the general stimulus given to the plant as a result of fire, keeps the grass layer in a productive and palatable growth phase. In grasslands and savannas, plant diversity is also maximized with light or moderate defoliation, whilst reduced with extreme defoliation (Walker 1974; Mentis and Collinson 1979; Robinson *et al.* 1979). Maintaining a high biotic diversity is within the reserves management objectives.

King (1987) in a thorough review of the effects and history of fire in HGR, feels that almost from proclamation, the fire regime has been drastically altered. Fire frequency, which historically appears to have been at least biennial and probably annual, has been markedly reduced. Even in recent years when management burning has been increased, the frequency of fires is still probably far from its historical level. The season of burn has also been shifted from the historical winter, prior to the spring rains, to somewhere after the onset of these rains (King *op cit.*). These factors are probably all to the detriment of the important fire-climax grass species indigenous to the area.

What this study has shown is that within the constraints of certain abiotic variables (eg. geology and soil type) the herbaceous community will react in a reasonably predictable manner, given particular management inputs eg. burning and bush control.

With increasing fire frequency and bush control, the community appears to shift from closed woodland, shade tolerant grasses, through to more high producing, palatable grasses associated with open, fire climax grasslands. With regular fires this community appears in the short term to be able to 'hold its own,' if not increase in vigour in the dynamic equilibrium of these systems. As noted by Frost and Robertson (1985), however, fire probably cannot prevent woodland

regeneration after clearing in areas where conditions are particularly favourable for woody plant growth. Werger (1978) has stated that in areas of southern Africa receiving more than 500mm rain per year, with no more than three months of the year receiving no rain, this is sufficient to sustain closed-canopy woodland or forest vegetation types. This is on the assumption that no other environmental factors are limiting.

With regular (biennial or annual) fires, and possible follow-up treatments in bush cleared areas, the vegetation should be able to be maintained as productive and diverse grasslands. In the absence of this management, the grass communities will shift towards more shade tolerant, unproductive grasses associated with high woody cover. In the short term, bush clearing activities would appear to be most effective over sites on igneous substrate, at higher altitudes, where successional rates are slowest. This is in comparison to sites at lower altitudes over sedimentary geology.

Yodzis (1978) claims that competitive dominants are selectively reduced by disturbance. The very attributes that contribute to a species competitive dominance (such as tall, leafy shoots; Grime 1979) are those characteristics which also make them susceptible to disturbances in the form of herbivory and fire. Grass species which have these characteristics, eg. *T. triandra*, although affected by these disturbances, are also adapted to them. These grasses have evolved under a fire and grazing regime which allows them to be able to still compete successfully in those systems in which they are present. In habitats of higher 'stress' however, for example in areas of high woody cover associated with bush encroachment, these competitive plants are not able to perform as well as those species adapted to these conditions eg. *D. australe* and *P. maximum*.

Despite the lack of long-term records, there appears to be ample evidence that the savannas have been and are still subjected to marked changes (eg. Walker and Noy-Meir 1982; Watson and MacDonald 1983; Wills and Whately 1983; King

1985). They lie in an intermediate and variable climatic belt and hence climatic shifts are felt immediately. These shifts are reflected in constant changes of the amounts of grass and woody vegetation. They are subject to major perturbations such as fire, drought and floods, as well as the more recent effects of Iron Age Man (Feely 1980), overgrazing by cattle and goats, excessive over-hunting and the removal of vegetation for firewood and cultivation (Hall 1984). They still manage, however, to exist and even to re-establish after virtual elimination indicating a degree of resilience (Walker and Noy-Meir 1982). As a result of the 'derived' nature of many southern African grasslands and savannas, there appears always to be an inherent tendency for invasion by woody species into these areas and consequent changes in community structure, including the herbaceous layer.

The total response of a plant is a complex function varying with different environmental, sociological and competitive relationships, (Mueller-Dombois and Ellenberg 1974). Many of the apparent anomalies in savanna structure today are due to these relationships as well as the effect of stochastic, episodic events (ie. major droughts, rinderpest and man) which may have a sudden and marked effect on the composition and structure of the savanna. This makes their study both challenging and fascinating.

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