

Shifts in community structure over spatial and temporal gradients: the *Acacia nilotica*-*Acacia karoo* community in the Hluhluwe-Umfolozi Game Reserve

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Abstract

The mechanisms behind shifts in community structure over spatial gradients have seldom been reported. The dynamics of the *A. nilotica*-*A. karoo* community in the Hluhluwe-Umfolozi Game Reserve were investigated to determine the cause of spatial patterning and an apparent shift in community dominance. *A. karoo* juveniles dominate at higher altitudes whereas large expanses of the lower regions consist of mature *A. nilotica* woodlands. Distribution patterns of both species were documented from transect data, in relation to environmental gradients (rainfall), competition (with the herbaceous layer) and disturbance (fire frequency and herbivory). The factors controlling the recruitment and progression from the juvenile to adult stage were investigated and were found to differ for each species. *A. nilotica* is controlled primarily by fire at both stages of life history. *A. karoo* is controlled by both fire and herbivory; herbivory is the primary limitation at the recruitment stage and fire is the primary limitation of the progression from juvenile to adult. Disturbance gradients, from high fire frequency and low herbivore density at high altitudes, to lower fire frequency and higher herbivore density at low altitudes, are responsible for the shift in community structure along the spatial gradient. The disparity between juveniles and adults suggests a temporal shift in dominance from *A. nilotica* to *A. karoo*, and this is due to a change in the disturbance regime of the reserve over the last three decades. It is suggested that the acacia communities of the Hluhluwe-Umfolozi Game Reserve undergo cycles of dominance, depending on the prevailing conditions in the reserve, and the importance of understanding these cycles with regard to management implications is discussed.

Sally He, Keni Ann

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Introduction

A central focus of plant ecology has been the investigation of mechanisms controlling the structure and dynamics of plant communities. Within the field of community ecology, efforts have been concentrated on the determinants of the spatial distribution of species or successional processes involved in compositional changes within communities. However, there have been relatively few attempts to relate spatial patterns to structural processes.

In explaining spatial patterns, emphasis has usually been placed on environmental variables as important determinants of community boundaries and composition. Richards *et al.* (1995, 1997) have demonstrated the importance of soil nutrient content in determining community boundaries and composition in nutrient-poor fynbos. Cole (1982) has provided evidence from three continents that soil moisture availability determines savanna structure while soil nutrient conditions determine community composition.

Competition is a mechanism very often invoked to explain community structure in a variety of systems. For example, competition has been shown to determine the spatial distribution of shrubs and cacti in the Sonoran desert (Yeaton *et al.* 1977), and coexistence in fynbos species (Cowling and Gxaba 1990). A general assumption in theories involving competition is that species best suited to a particular environment eliminate less competitive species and the subsequent outcome is that species are found where they are physiologically best suited to the physical environment. However, this theory does not always hold when tested empirically (e.g. Keddy 1989; Bertness 1991).

Competition is considered to be relatively unimportant in systems in which disturbance constantly disrupts competitive interactions (Hudson 1979). In these situations, it is often the disturbance itself which is the important determinant of community structure. For example, large-scale disturbance such as windthrow in conifer forests (e.g. Ogden and Stewart 1995) and fire in fynbos (e.g. Cowling 1987) have been shown to be important in shaping

community structure by creating recruitment opportunities or initialising successional sequences. Bergeron and Brisson (1990) and Bergeron (1991) explained species distribution in the boreal forests of Quebec by invoking differences in the fire regime in different regions of the landscape. Fire-tolerant pines and hardwood species are adapted to growing in the regions which experience intense fires, whereas spruce-boreal forests develop in the more mesic habitats where fires are less frequent and intense.

Within savanna systems, disturbance in the form of herbivory and fire is a natural occurrence and is considered to be important in shaping communities. In a general sense, savannas consist of a continuous grass component and a largely discontinuous tree component and are characterised by being unstable systems (Walker and Noy-Meir 1982). Periodic changes in community structure take place, in particular changes in the density or spatial extent of the woody component. Landscape-level changes have been reported, for example, a shift from grassland to thicket vegetation (e.g. Archer *et al.* 1988) or a decrease in the woody component (Pellew 1983; Dublin *et al.* 1990), but the emphasis in these studies has been placed on temporal rather than spatial dynamics.

- **Community structure of savannas**

In savanna systems, community structure is largely determined by tree-grass interactions. The rapid growth of grasses affords them a competitive advantage over woody species, although the degree to which tree-grass competition is able to control the density of communities is still uncertain (Menaut *et al.* 1990). An aspect of tree-grass interactions which may often be considered more important than competition is the indirect effect of the grass layer on the woody component by means of providing fuel for fires. Bunch grasses form highly flammable fuels and are responsible for producing what Bond and van Wilgen (1996) termed the Gulliver effect on the woody component. They define Gullivers as “plants, typically multi-stemmed shrubs,

which dominate communities as adults but struggle to emerge from the herbaceous layer as juveniles". Grasses have the combined effect of suppressing woody recruitment through competitive interactions at the seedling stage and fuelling fires which kill or stunt survivors so that they are unable to grow above the grass layer and escape the fires (Bond and van Wilgen 1996). These stunted plants may persist in the grass layer for decades (Menaut *et al.* 1990) until they die through progressive weakening as a result of repeated fires, or until a break in the fire regime affords the Gullivers a chance to escape the danger zone and become adults. In this way, the suppression of fires by heavy grazing or management policies leads to the rapid development of woodland vegetation.

In theory it appears that disturbance may be more important than competition in determining savanna community structure. However, savanna ecologists acknowledge the complexity of savanna systems and stress the importance of considering the combination of environmental factors, competition and various disturbances in studies of savanna dynamics (Norton Griffiths 1979; McNaughton 1983; Trollope 1984). Menaut *et al.* (1990) modelled the effects of fire and competition with grass and neighbours and concluded that disturbance is a key determinant in savanna structure and dynamics. They found competition to be relatively unimportant, but this may be due to the fact that they only took above-ground competition into consideration. Pellew (1983) and Dublin *et al.* (1990) investigated the mechanisms responsible for the decline in the woody component of the Serengeti woodlands, East Africa, and provide evidence that landscape-level cycles of woodiness are determined by the interactions of several disturbance factors rather than a single disturbance factor. By means of a model, Dublin *et al.* (1990) showed that elephant browsing and fire had a greater combined effect on woodland loss than when considered in isolation. Pellew (1983) showed that browsing by elephants caused a decline in mature *Acacia tortilis* woodlands and that tree regeneration in these woodlands was suppressed by giraffe browsing and periodic burning, leading to an overall decline in the extent of *A. tortilis* woodlands.

- **Community structure in the Hluhluwe-Umfolozi Game Reserve**

A large proportion of the woody component of the Hluhluwe-Umfolozi Game Reserve consists of acacia woodland communities in which the most dominant species are *Acacia nilotica* (L.) Willd. ex Del. and *Acacia karoo* Hayne. For the purposes of this study, I regard the association between *A. nilotica* and *A. karoo* as a single community. The distribution of this community is illustrated in Figure 1.

Within the *A. nilotica*-*A. karoo* community, two patterns are evident. Firstly, the relative abundance of each species changes along a spatial gradient. Much of the reserve, particularly further south in the Corridor area (not shown on the map) is dominated by *A. nilotica* woodlands, with only a few scattered mature *A. karoo* woodlands in the extreme north-east. Secondly, there appears to be a trend towards increasing woodiness of the vegetation, as a large proportion of the *A. karoo* component is juveniles. This is evident from the vegetation map (Figure 1) which shows the large extent of the *A. karoo* thickets, i.e. Gullivers. Although *A. nilotica* Gullivers are present to a greater or lesser extent in these acacia thickets, they consist mostly of dense stands of *A. karoo* and *Dichrostachys cinerea* Gullivers within a tall grass sward of tufted perennial grasses (Whateley and Porter 1983). These areas are the most frequently burnt in the reserve and the thicket communities are heavily utilised by browsers as well as grazers for several months following a burn (Whateley and Porter 1983). The differences in relative abundance between the adult and juvenile stages of each species, with the majority of adults being *A. nilotica* and the majority of juveniles being *A. karoo*, suggests a change in species dominance is occurring.

The broad aims of this study were to document the distribution of *A. nilotica* and *A. karoo* in the reserve and to identify the mechanisms responsible for the observed spatial patterns. I considered three possible determinants of community structure in savannas, namely, environmental variability,

competition and disturbance, to see whether the two species showed any differential response to these factors. A differential response suggests that each species will vary in its recruitment, persistence as Gullivers or establishment as adults, depending on the prevailing conditions in the reserve at any one time.

The response to soil moisture availability was tested by documenting the patterns along an altitude gradient. The higher lying areas of the reserve receive a higher rainfall and consequently have a denser grass sward, resulting in shading by the grass and more intense competition between the grass and woody components. The areas of tall, dense grass are suitable for frequent fires and are not utilised by browsers as much as the more arid regions. The spatial distribution of *A. karoo* and *A. nilotica* Gullivers along environmental, competition and disturbance gradients was investigated to determine the driving forces influencing each species. Further observations were made and glasshouse experiments were performed to determine the relative effects of these factors on species distribution. By determining the main factors controlling the distribution of each species and considering these factors together with past conditions in the reserve, I aimed to explain the changing structure and composition of the acacia communities in the Hluhluwe-Umfolozi Game Reserve, over both spatial and temporal gradients.

Study area

The Hluhluwe-Corridor-Umfolozi Game Reserve Complex (28°00'-28°26' S; 31°43'-32°09' E) is situated in KwaZulu-Natal, South Africa (Figure 2). The whole complex (herein referred to as the Hluhluwe-Umfolozi Game Reserve) comprises Hluhluwe Game Reserve (225 km²) in the north which is linked with Umfolozi Game Reserve (447 km²) in the south by the region referred to as the Corridor (227 km²). Both Hluhluwe and Umfolozi Game Reserves were designated in 1895 and although the whole complex was only proclaimed a reserve in 1982, the Corridor has been managed for wildlife since the 1950s (Brookes and Macdonald 1983). The area is bounded by a game fence and is surrounded by the KwaZulu people who once inhabited the area (Whateley and Porter 1983).

The topography of the Complex is hilly, particularly in Hluhluwe Game Reserve (see Plate 1), and altitudes vary from 750 m above sea level in the north to 60 m above sea level in the south. Consequently, Hluhluwe Game Reserve receives a higher annual rainfall (985 mm, n = 50) than Umfolozi Game Reserve (703 mm, n = 21; Brookes and Macdonald 1983). Rain falls mainly between October and March and the period June-August is generally dry (Brookes and Macdonald 1983). Temperatures are warm to hot with frosts occurring very occasionally in some river valleys (Whateley and Porter 1983).

Most of Hluhluwe-Umfolozi Reserve is underlain by shales and sandstones with frequent dolerite intrusions. Acacia woodlands or thickets, particularly *A. karoo* and *A. nilotica*, dominate more than half the reserve (see Figure 1) and are associated with a grass cover of tufted perennials such as *Themeda triandra* and *Cymbopogon* species (Brookes and Macdonald 1983). A large variety of animal species are found in the area, including large herbivores (Whateley and Porter 1983).

Most of this study was conducted in the southern end of Hluhluwe Game Reserve and the Corridor (see Figure 1).

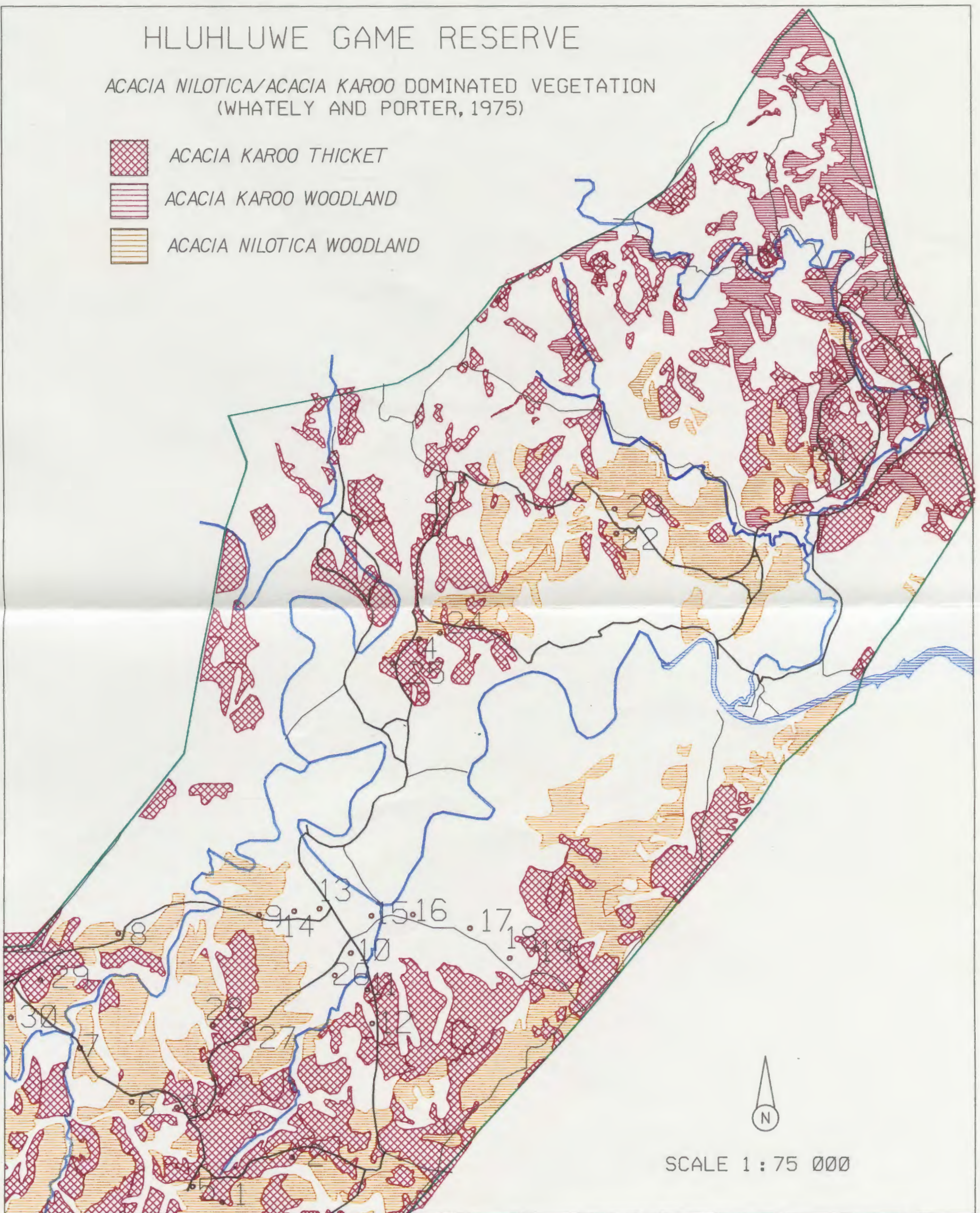


Figure 1. A section of the vegetation map of the Hluhluwe-Umfolozi Game Reserve, showing the distribution of *Acacia nilotica* and *Acacia karoo* woodlands and *A. karoo* thickets in the northern part of the Corridor and Hluhluwe Game Reserve. The location of each transect in this study is illustrated.

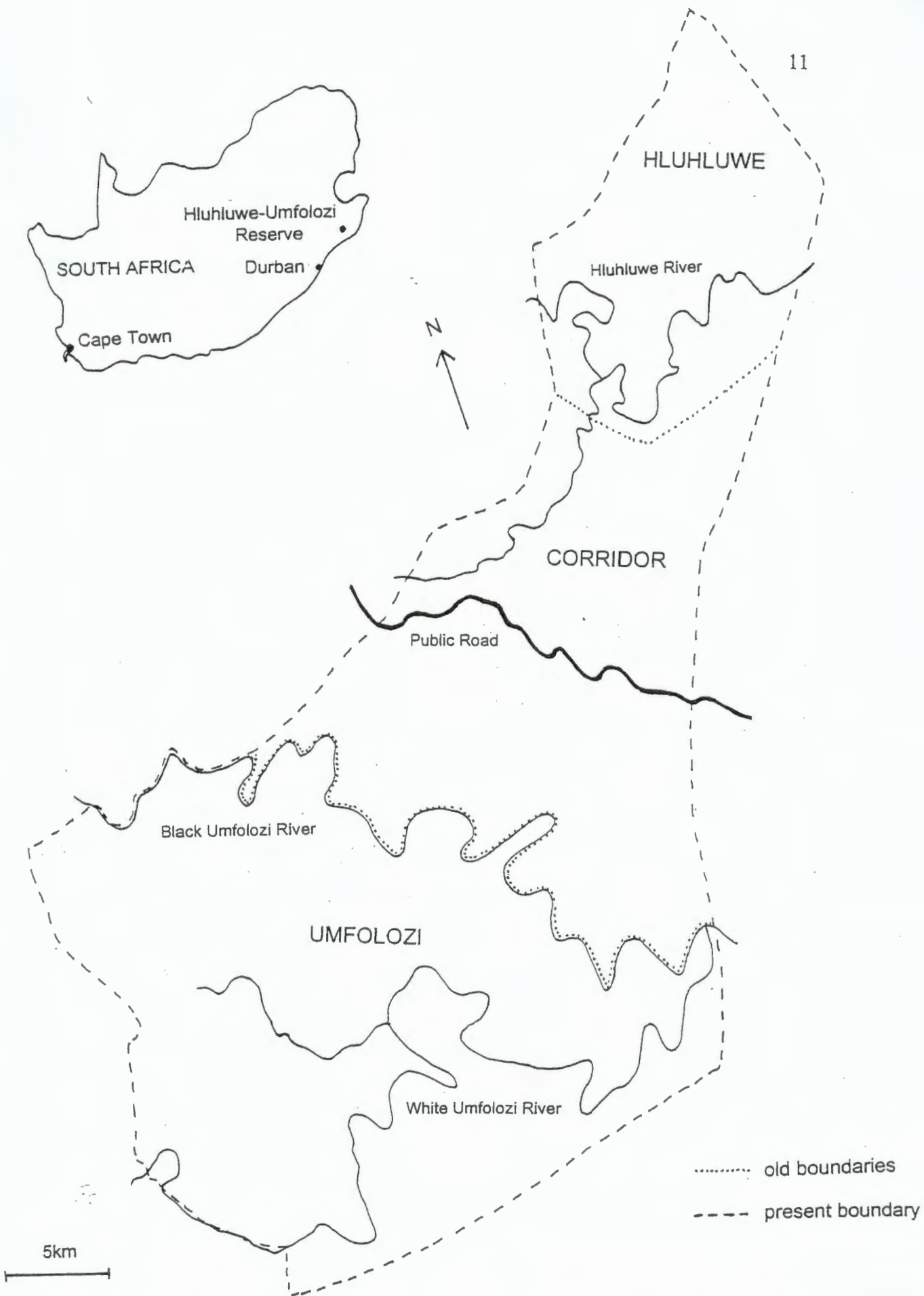


Figure 2. Map of the Hluhluwe-Corridor-Umfolozi Game Reserve Complex in KwaZulu-Natal, South Africa, showing the boundaries of the original Hluhluwe and Umfolozi Game Reserves.



Plate 1. Photograph of Hluhluwe Game Reserve, illustrating the hilly topography of the region, and the extent of the *A. nilotica* woodlands in the lower-lying areas. Invasion of predominantly *A. karoo* Gullivers into the areas of tall, dense grass is shown in the foreground.



Plate 2. An advanced grazing lawn situation in the Corridor region of the Hluhluwe-Umfolozzi Game Reserve, showing the predominance of stoloniferous grass species. Note the absence of *Acacia* Gullivers.

Methods

Distribution patterns

The distribution of adults and juveniles of *A. nilotica* and *A. karoo* in relation to environmental variables was studied by sampling a series of 30 transects distributed through most of the Corridor and Hluhluwe Game Reserve. These transects were sampled at a range of altitudes in order to cover a range of grass biomass, the assumption being that the high altitudes receive more rainfall and therefore have a higher grass biomass, whereas the lower lying areas should be drier and consequently have a lower grass cover. At each site, the soil was examined by auguring and was found to be sandy clays derived from dolerite over most of the transects. The approximate location of each transect was chosen by marking positions near to roads on a map. The site of each transect was then selected as the nearest location to these points in which *A. nilotica* adults occurred in the vicinity. Each transect was run along the contour to minimise within-transect differences in soil moisture.

Each transect was 40m in length and 10m wide. A surrogate measure of grass biomass was determined for each transect with the use of a disc pasture meter (Bransby and Tainton 1977). The height above the ground at which the disc rests is calibrated for grass biomass and although this measure is in cm rather than units of weight, I refer to the degree of grass cover as grass biomass throughout the text. Twenty biomass readings were taken along the length of the transect and the mean value was calculated. This provides a measure of the height of the grass sward. The density of the grass cover was estimated by counting the proportion of steps out of 100 in which my boot landed on bare ground.

A. nilotica and *A. karoo* individuals were divided into age groups defined as: adults (>3m), Gullivers (0.5-3m, regardless of whether they were fruiting or not), and seedlings (<0.5m). Within each transect, the number of adults, Gullivers and seedlings of *A. nilotica* and *A. karoo* were noted. The number of individuals that were fruiting was recorded for each species. For all those

species which did not occur as adults in the transect, the distance to the nearest adult was estimated. Species not in sight, (approx. 100m) were recorded as not being in the vicinity of the transect.

At each transect, note was taken of the dominant grass species and transects were classified as grazing lawns or non-grazing lawns on a basis of the dominant species. The presence of stoloniferous grasses (e.g. *Cynodon dactylon*) indicates heavy grazing pressure, and the degree of bare ground (from the boot cover method) also gives an indication of grazing intensity. Such areas were defined as grazing lawns (sensu McNaughton 1984; see Plate 2). Differences in the abundance of Gullivers of each species on grazing lawns and non-grazing lawns were investigated by log-transforming the data and performing a Student's t-test (Zar 1996). All statistical tests were performed using the computer program STATISTICA.

Fire records for the reserve extend back to 1955 and the fire record of each individual transect was available. Thus it was possible to investigate the relative response of each species to fire frequency by plotting the proportion of each species occurring in each transect against the total number of fires from 1955 to 1996. These data were analysed for trends by performing a Pearson's product-moment correlation (Zar 1996).

Analysis of transect data

The relationships between variables were studied by plotting scatter diagrams. Regression analyses were performed where possible but these tests were problematic since the data frequently showed the patterns illustrated in Figure 11 (page 24). The biological interpretation of this kind of pattern is clear. At low values of the independent variable, the dependent variable can take a wide range of values. At high values, however, the dependent variable is strongly limited. Regression analysis is inappropriate in these circumstances.

To overcome this problem, an unconventional technique of data analysis was developed. A comparable method for data which shows similar trends has previously been developed by Tukey (W. J. Bond, pers. comm.). The null hypothesis is that points are distributed in an equivalent manner at high and low values of the independent variable. Each graph was divided into four quarters along the median line of each axis and the number of data points in each block was counted (see Figure 3). A Fisher exact test (Zar 1996) for small sample sizes was performed, with the expected values calculated using the following formulae:

$$\text{exp}_B = [n_A / n_{(A+C)}] * n_{(B+D)}$$

$$\text{exp}_D = [n_C / n_{(A+C)}] * n_{(B+D)}$$

where: exp_B = expected value of block B,

n_A = number of data points in block A etc.

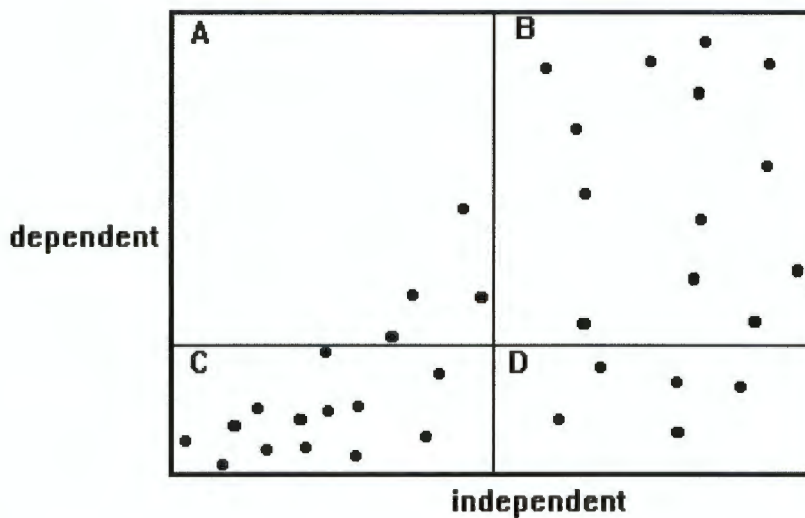


Figure 3. A hypothetical representation of recorded transect data, indicating the steps by which data which did not display linear relationships were analysed. Thin lines represent the median values along each axis. Block labels refer to the formulae above.

Mechanisms underlying distribution patterns

- **Response to competition with grass**

The conditions of grass cover in the reserve at present are not necessarily representative of the conditions at the time of seedling establishment when competition is expected to be the most intense. Therefore, competition experiments were performed in the glasshouse at the University of Cape Town.

In each of ten pots, two *A. nilotica* seedlings were grown together with a *Themeda triandra* grass plant which filled most of the pot. In another ten pots, two seedlings were grown without grass. The same was done for *A. karoo*. The pots were intermingled and periodically reshuffled to ensure that they all experienced the same conditions of light and temperature, and each pot was supplied with the same amount of water and nutrients. A Rorison solution of nutrients was given to the plants once a week. The plants were harvested after 14 weeks and dried in an oven at 70°C for 48 hours. The dry mass of the above and below ground component of each individual was calculated and data were log-transformed following Bartlett's test for homoscedacity. Significant differences in these data between the species and treatments were assessed by means of a nested analysis of variance (Zar 1996).

- **Response to browsing**

The relative impact of browsing on *A. nilotica* and *A. karoo* was examined at three sites with different browsing intensities. Two of the sites, one of which was a grazing lawn, experience a high browsing pressure, while the other site appears not to be utilised much by browsers. The degree to which each species is browsed was measured by counting the number of branches which had been bitten off from each of 25 individuals of both species. Bartlett's test for homoscedacity was performed, followed by a two-way analysis of variance (Zar 1996) to determine any differences between species and between sites.

The relative proportion of bites from each species was graphed against the total number of bites at each site to determine whether selection of species is a function of availability or preference.

- **Response to fire**

The response of each species to differing fire regimes was investigated at two adjacent sites separated by a vehicle track in the Corridor. In the period 1993 and 1997, the site above the track experienced only one cool burn, in 1995, whereas the site below the road experienced three successive intense burns, in 1994, 1995 and 1996. The heights of approximately 60 *A. nilotica* and 100 *A. karoo* were estimated at each site and each individual was classified as having sprouted from the base since the last fire or surviving the fire with its canopy intact. The survivors were distinguished by having a charred base and robust thorns on the stem which would not have developed yet on the resprouters. This is an area of very tall dense grass and it was assumed that the effects of browsing on plant height were negligible. The response of each species to frequent, high intensity burns versus infrequent, low intensity burns was determined by comparing the stem height class distributions of individuals subjected to the different fire regimes. A smaller size class in which most surviving individuals fall indicates a superior ability to survive fire. All resprouters are expected to have been pruned to ground level by the fire and therefore the species with more individuals in the larger size class can be interpreted as having a faster growth rate.

Historical records

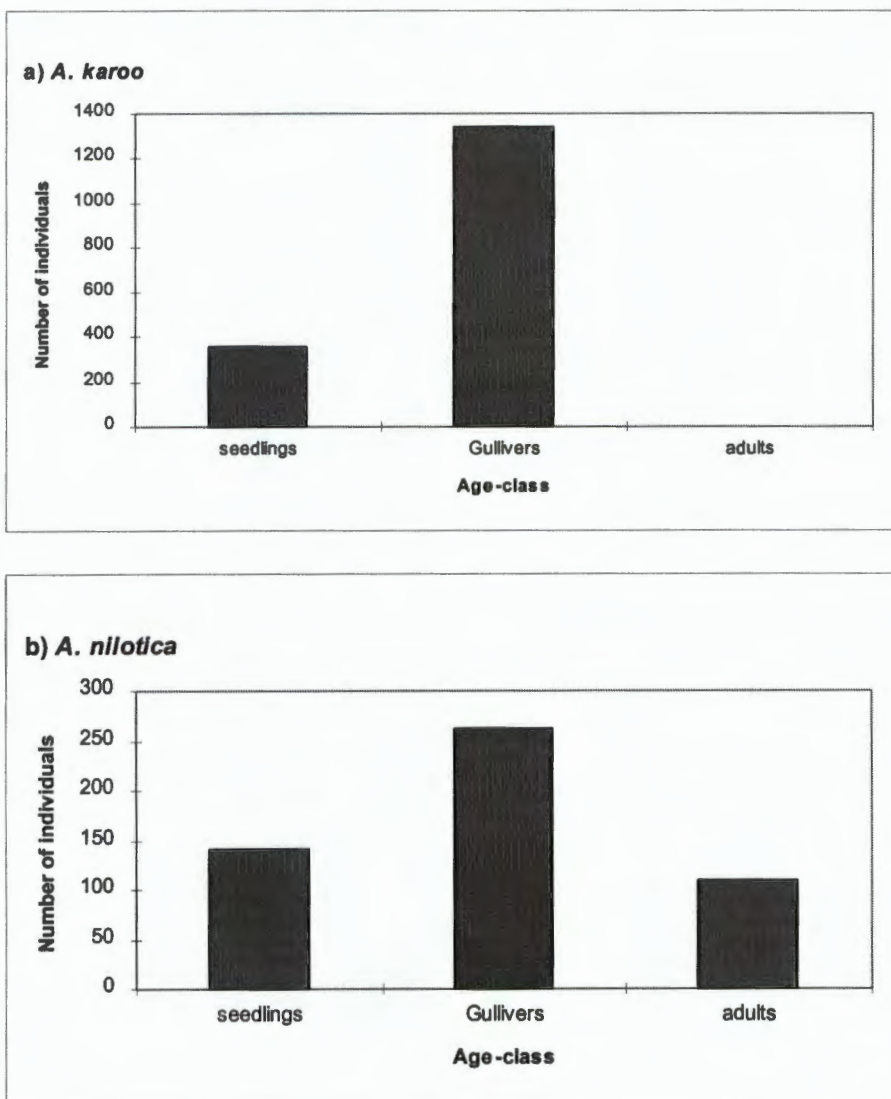
Contemporary patterns have been influenced by historical events or past conditions of the reserve. Historical information was obtained by examining records of rainfall and animal densities supplied by Natal Park Board. Additional information about animal densities was obtained from a few key

references (Brookes and Macdonald 1983; Owen-Smith 1992). Vegetation maps of the reserve by Henkel (1937), one from 1961 (anon.) and Whateley and Porter (1975) were consulted. A series of fixed point photographs from various parts of the reserve provided extra information on rates of growth, changes in grass cover and trends towards bush encroachment.

Results

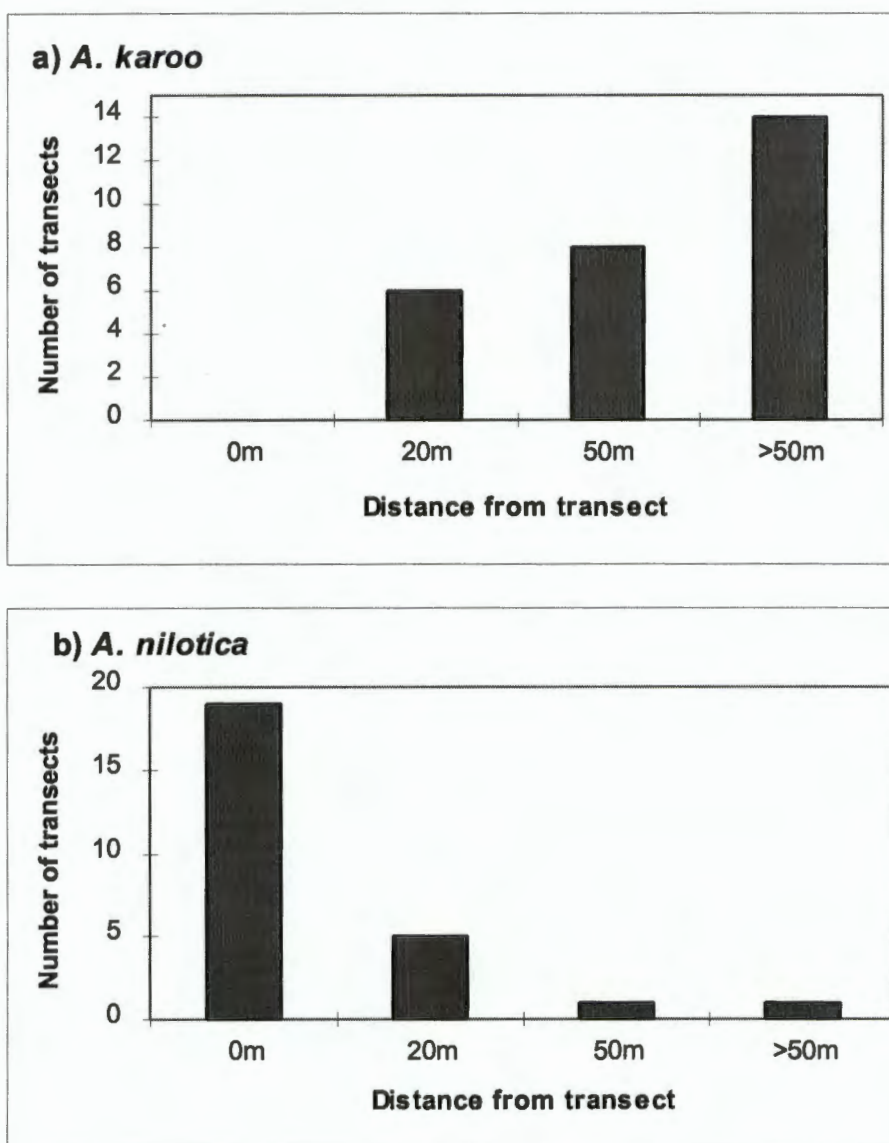
Community structure at present

Despite the fact that there were no *A. karoo* adults recorded in any of the 30 transects, there were over four times as many *A. karoo* juveniles as *A. nilotica* juveniles (Figures 4a-b). The presence of *A. nilotica* adults in the transects indicates that they are more abundant than *A. karoo* adults. Therefore these data suggest that a shift in acacia community composition is occurring in Hluhluwe-Umfoloji Game Reserve.



Figures 4a-b. The age-class distributions of individuals of a) *A. karoo*, and b) *A. nilotica* sampled in a series of 30 transects. Seedlings = plants <0.5 m; Gullivers = plants 0.5-3 m; adults = plants >3m.

From the data presented in Figures 5a-b, it appears that *A. karoo* has a remarkable dispersal ability. Although *A. karoo* juveniles were found in all but two transects, no transects contained *A. karoo* adults. Only half of the transects which had *A. karoo* juveniles present had adults within a radius of 100m. In contrast, *A. nilotica* adults were found within 50m of all but one transect which contained *A. nilotica* juveniles. These results for *A. nilotica* may be slightly biased because transects were chosen on a basis of there being adults in the vicinity, but observations made in the field support these patterns.



Figures 5a-b. The number of transects containing adults of a) *A. karoo*, and b) *A. nilotica* within the transect (0m), within 20 m of the transect, within 50 m of the transect, and not within sight of the transect (>50m). Data are for all transects in which Gullivers were present.

Patterns along environmental gradients

• Rainfall

There were significantly less *A. karoo* juveniles in each transect at lower altitudes ($p < 0.05$; Fisher exact test; Figure 6). This suggests a potential relationship with rainfall as we expect the higher altitudes to receive more rainfall than the lower areas.

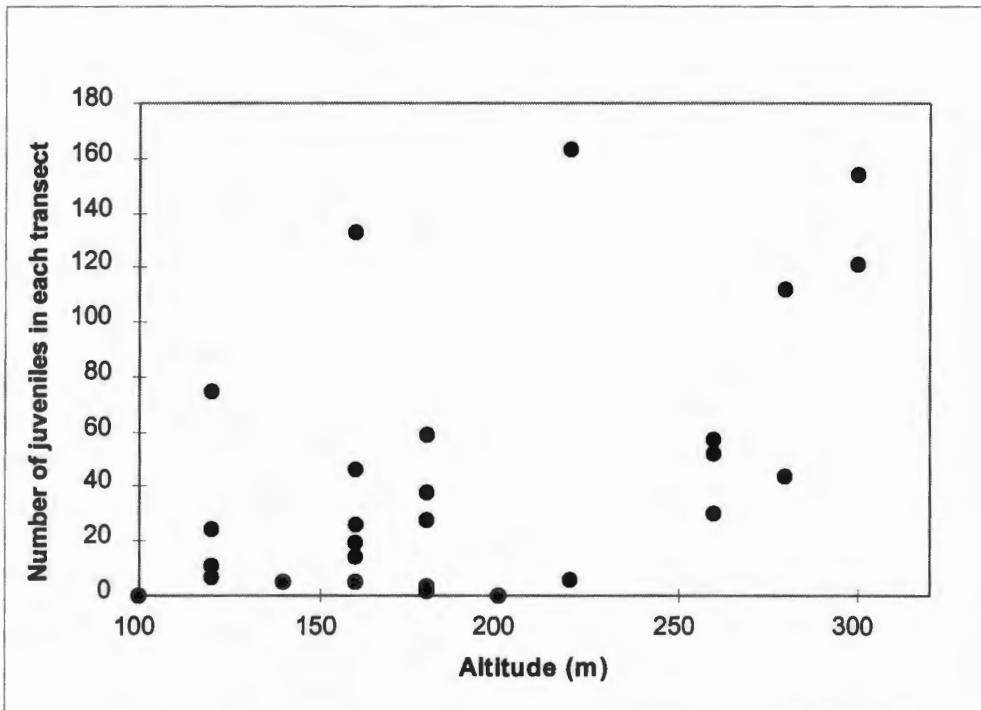


Figure 6. The relationship between the number of *A. karoo* juveniles recorded in each transect and altitude ($p < 0.05$; Fisher exact test).

In contrast, *A. nilotica* shows the opposite trend. Most of the *A. nilotica* woodlands occur in the valley bottoms and lower hills and this is reflected in the relationship between *A. nilotica* adults and altitude ($p < 0.05$; Fisher exact test; Figure 7). *A. nilotica* adults are more common in the low lying, drier regions of the reserve and occur more sparsely in the high rainfall areas. This could be interpreted to mean that *A. karoo* is the more mesic species, requiring high rainfall to grow, whereas *A. nilotica* is a more xeric adapted species. However, no similar trend of decreasing occurrence with increasing altitude was found for the *A. nilotica* juveniles ($p > 0.05$; Fisher exact test;

Figure 8). This implies that the distribution of acacias is not determined by rainfall, and that the apparently limited recruitment of *A. nilotica* is not directly related to soil available moisture.

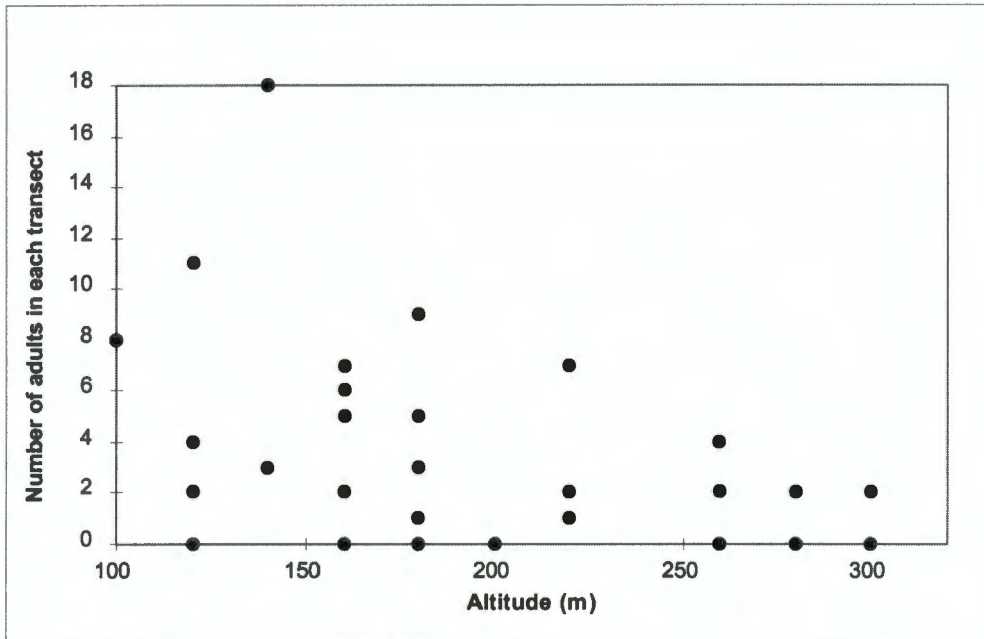


Figure 7. The relationship between the number of *A. nilotica* adults recorded in each transect and altitude ($p < 0.05$; Fisher exact test).

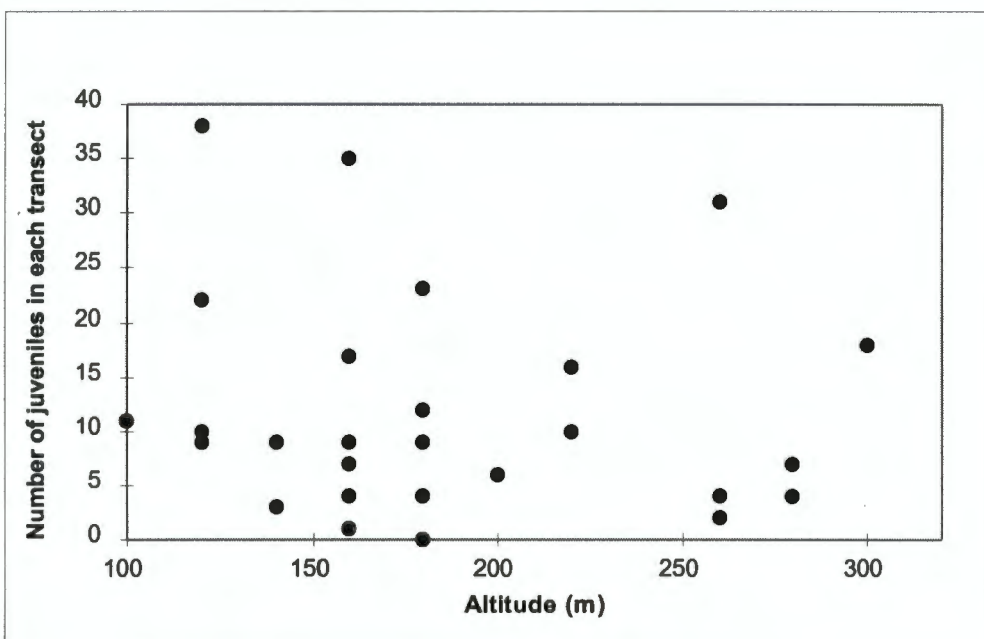


Figure 8. The relationship between the number of *A. nilotica* juveniles recorded in each transect and altitude ($P > 0.05$; Fisher exact test).

- **Grass biomass**

Grass biomass was found to increase with increasing altitude ($r=0.603$; $p<0.05$; Figure 9). This is expected because grass production increases with increasing rainfall (Rutherford 1980). In addition to this, temperatures are lower at the higher altitudes and consequently evapotranspiration is less, resulting in more effective rainfall. There were more *A. nilotica* juveniles in areas of low grass biomass and low numbers of juveniles in the high grass areas ($p<0.05$; Fisher exact test; Figure 10). Again, *A. karoo* shows the opposite trend ($p<0.05$; Fisher exact test), with the transects containing the lowest numbers of juveniles being those with the lowest grass biomass (Figure 11). The surrogate measure of grass biomass is presented as disc pasture meter height above the ground (in cm), and is referred to as grass biomass throughout the text.

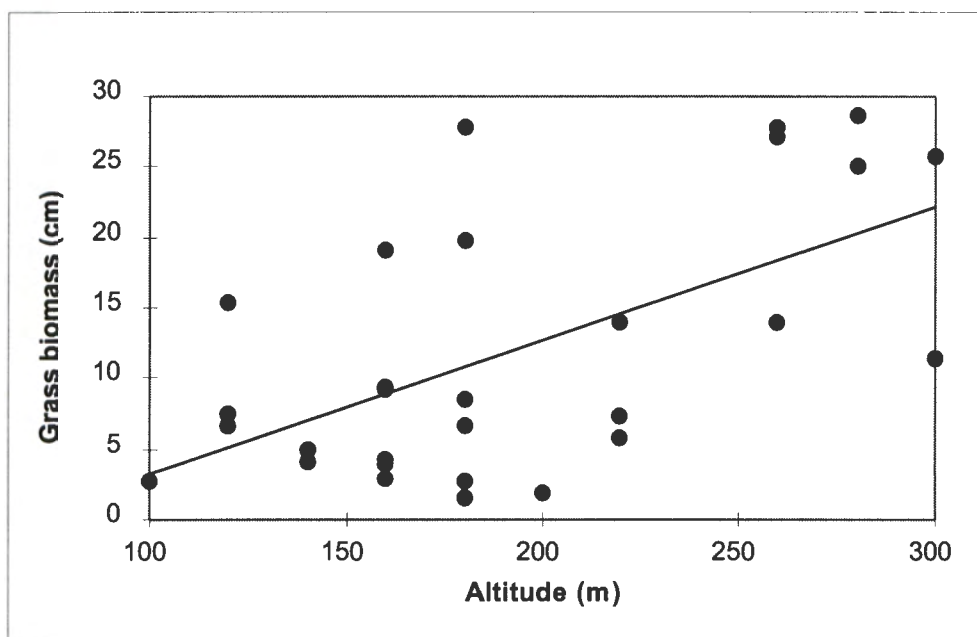


Figure 9. The relationship between the surrogate measure of grass biomass in each transect and altitude ($r=0.603$; $p<0.05$).

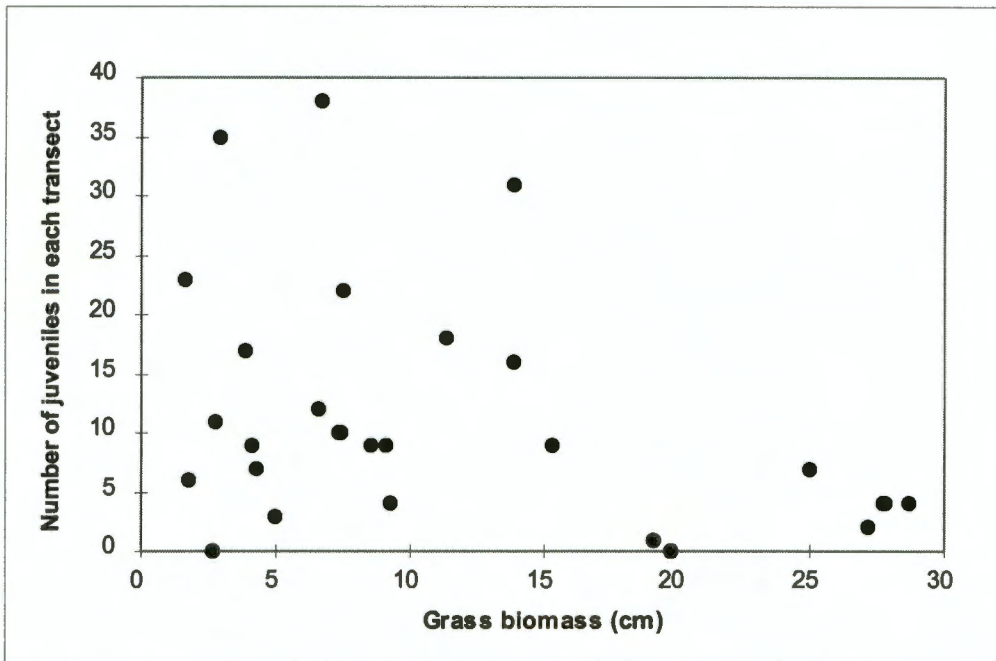


Figure 10. The relationship between the number of *A. nilotica* juveniles and the surrogate measure of grass biomass of each transect ($p < 0.05$; Fisher exact test).

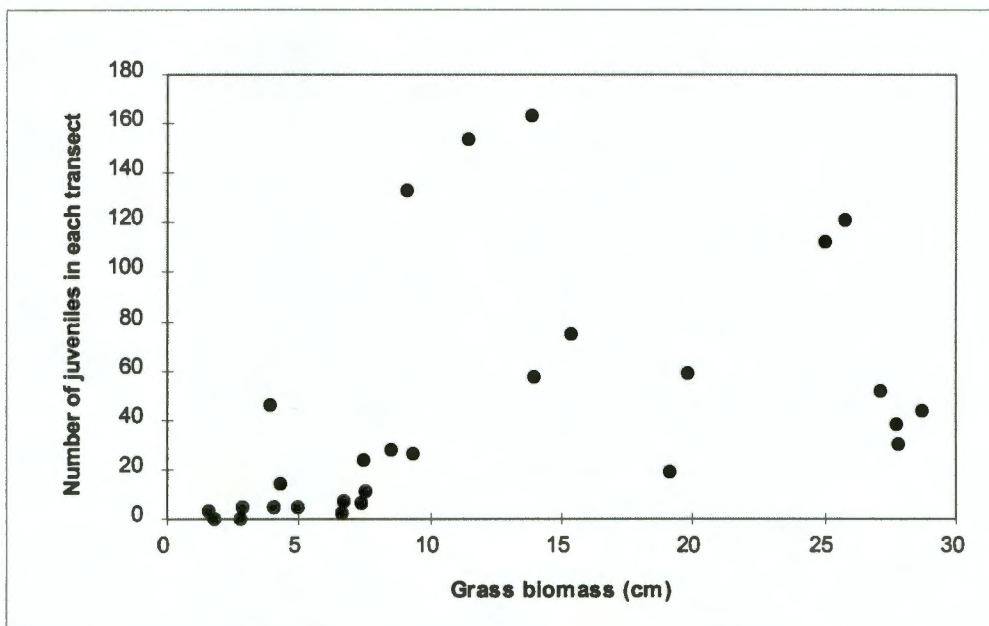


Figure 11. The relationship between the number of *A. karoo* juveniles and the surrogate measure of grass biomass of each transect ($p < 0.05$; Fisher exact test).

- **Browsing**

The *A. karoo* juveniles showed a distinct clumping at the low end of the grass biomass scale (Figure 11). From my initial observations, *A. karoo* Gullivers appeared to be present in abundance through most of the study area, suggesting that grass cover does not influence the distribution of *A. karoo*. The transects which show the clumping in Figure 11 correspond to those which were identified as occurring on grazing lawns. Grazing lawns were distinguished by a compositional change in grass species, in particular the presence of stoloniferous grasses which indicate a longer history of intense grazing (McNaughton 1984).

I classified each species as occurring on a grazing lawn or non-grazing lawn, and the results showed a marked decline in the numbers of *A. karoo* juveniles on the grazing lawns (mean=27.4 for grazing lawn and mean=73.7 for non-grazing lawn; $t=3.34$; $df=25$; $p<0.05$). In contrast, there was no significant difference between the number of *A. nilotica* juveniles on the grazing lawns compared to the non-grazing lawns (mean=12.4 and mean=14.4 respectively; $t=1.50$; $df=25$; $p>0.05$).

These results are represented by Figures 12a-b. Under non-grazing lawn conditions, *A. karoo* is distinctly more abundant than *A. nilotica* (see Figure 12a). To a certain extent this pattern is reversed on the grazing lawns as the proportion of *A. nilotica* is generally higher under these conditions (see Figure 12b). These data suggest that *A. karoo* is not well suited to the conditions on the grazing lawns.

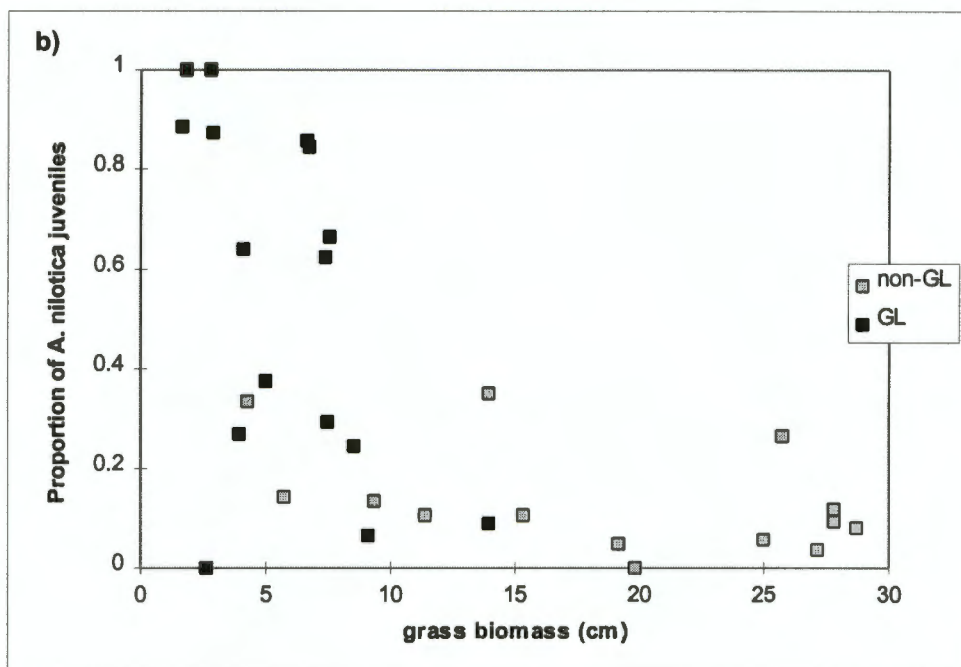
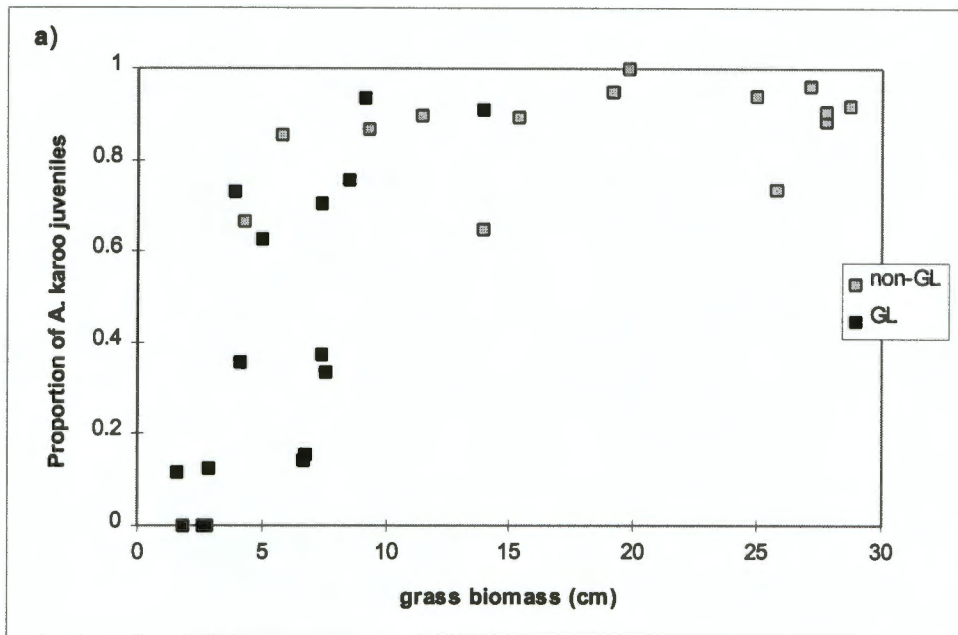


Figure 12a-b. The relationship between a) the proportion of *A. karoo* Gullivers, and b) the proportion of *A. nilotica* Gullivers (out of the total number of *A. karoo* and *A. nilotica* Gullivers) in each transect, and the surrogate measure of grass biomass, in a grazing lawn situation (GL) and a non-grazing lawn situation (non-GL). Both graphs are presented for ease of comparison.

- **Fire**

Fire frequency, as recorded from fire maps, is related to the amount of grass biomass ($r=0.659$; $p<0.05$; Figure 13). The grass biomass I recorded in 1997 therefore appears to be representative of the historical patterns of grass fuel.

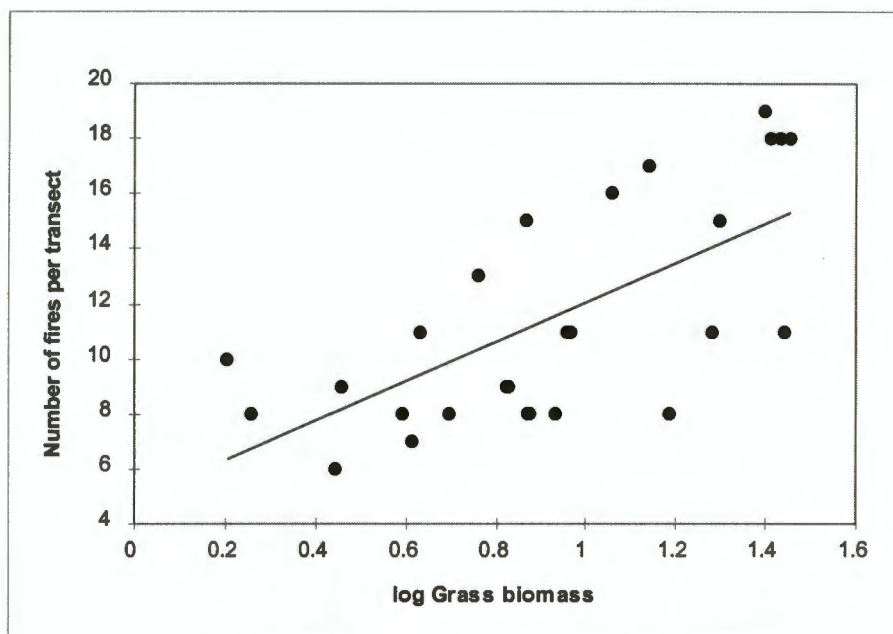


Figure 13. The relationship between the number of fires experienced by each transect from 1955-1996 and the log of the surrogate measure of grass biomass (in cm) for each transect ($r=0.659$; $p<0.05$).

The trend in increasing fire frequency in the reserve over the last few decades is illustrated in Figure 14. The relationship between the proportion of *A. nilotica* juveniles in each transect and the number of fires experienced by each transect from 1955-1996 was significant ($r=0.566$; $p<0.05$), indicating that *A. nilotica* and *A. karoo* respond differently to an increase in fire frequency (Figure 15). Transects with the lowest proportions of *A. nilotica* are those which experienced the highest fire frequencies, suggesting that *A. nilotica* is sensitive to a high fire frequency. This is reflected in the negative relationship between the number of *A. nilotica* adults and the number of fires from 1960-1980 which is considered to be the period in which these individuals established themselves as adults ($p<0.05$; Fisher exact test; Figure 16).

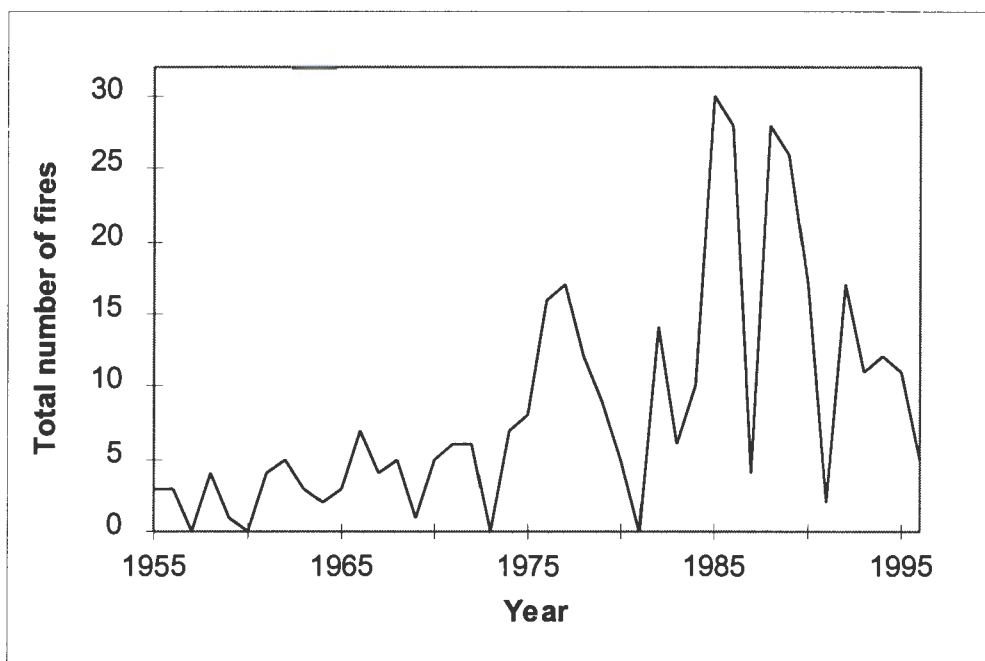


Figure 14. The trend in the total number of fires at 30 sites in the Hluhluwe-Umfolozi Game Reserve from 1955 to 1996. "Total number of fires" refers to the number of transects included in a burnt area for any given year.

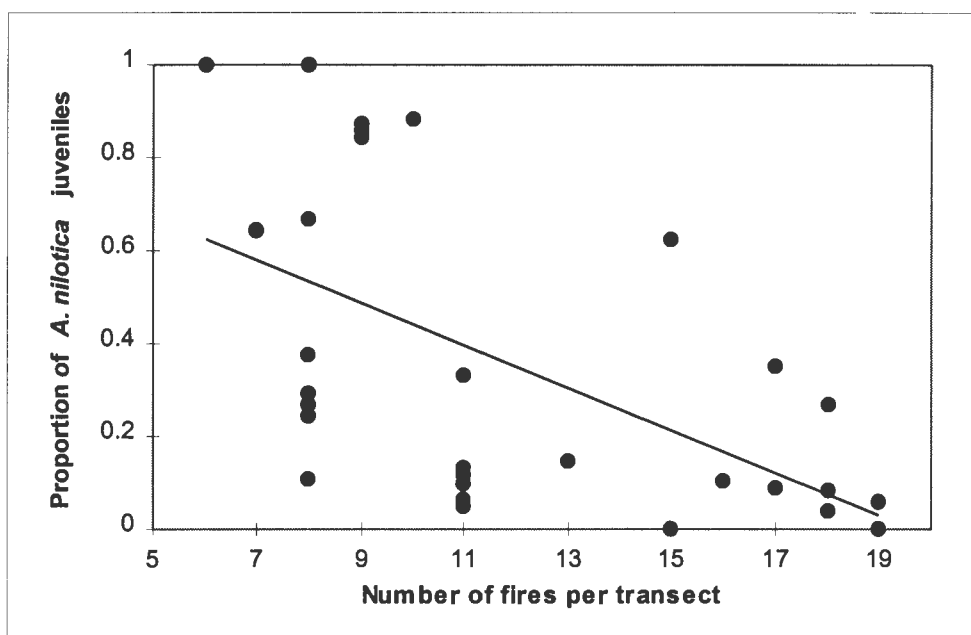


Figure 15. The relationship between the proportion of *A. nilotica* juveniles in each transect and the number of fires experienced by each transect during the period 1955-1996 ($r=0.5662$; $p<0.05$). The inverse relationship for *A. karoo* is not presented.

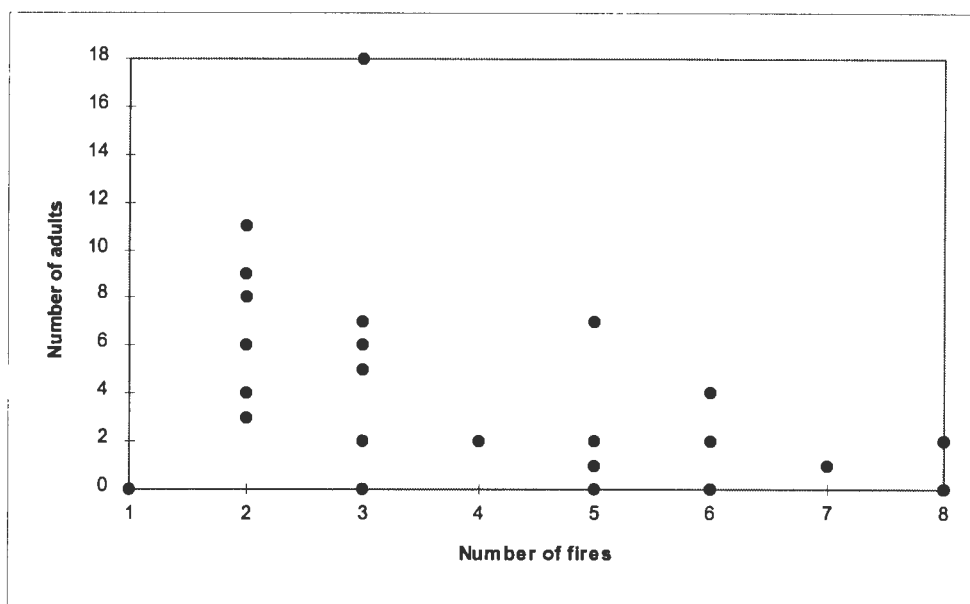


Figure 16. The relationship between the number of *A. nilotica* adults present in each transect and the number of fires experienced by each transect during the period 1960-1980 ($p < 0.05$; Fisher exact test).

Mechanisms underlying distribution patterns

- **Competition with grass**

Both species showed a significant interaction with grass in terms of total biomass ($F_{(1,62)} = 25.832$; $p < 0.05$). Figure 17 shows that total biomass decreased in the individuals of both species when grown with grass, implying that both species compete with grass. However, the lack of any significant interaction between each species and their response to growing with grass ($F_{(1,62)} = 3.631$; $p > 0.05$) suggests that the two species do not respond differentially to competition with grass. This is illustrated by the similar slopes of the dotted lines joining the mean total biomass of each species in Figure 17.

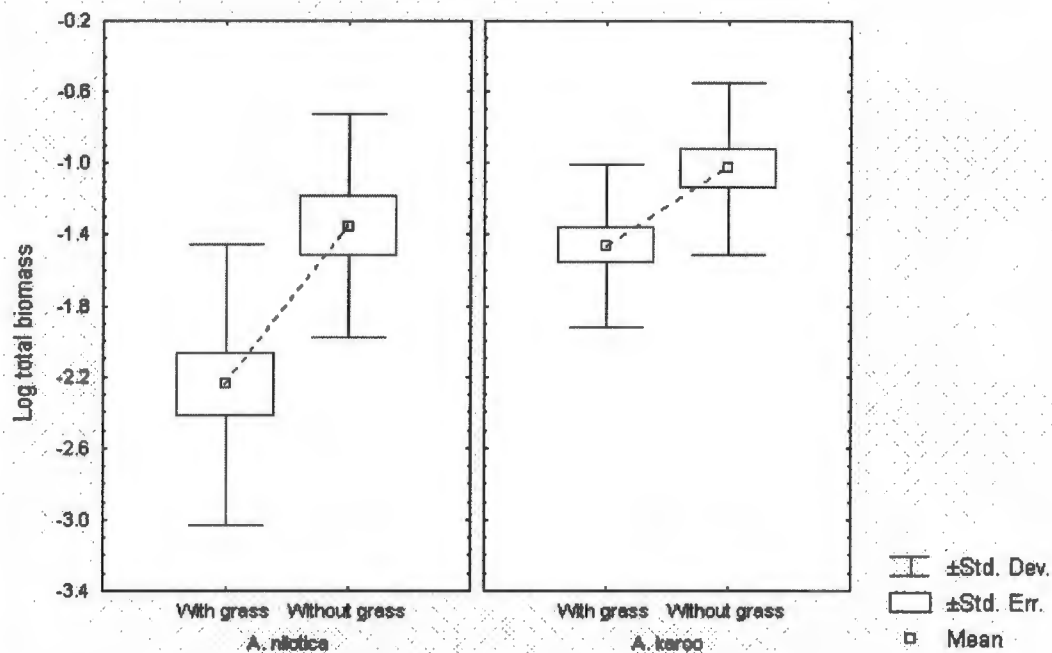


Figure 10. The log of the mean total biomass of *A. nilotica* and *A. karoo* individuals grown with *Themeda triandra* grass and without grass. No species differences are evident ($F_{(1,62)}=3.631$; $p>0.05$) but both species show a significant decline when grown with grass ($F_{(1,62)}=25.832$; $p<0.05$). The dotted line joins the means of each species grown with grass and without grass.

Although no interaction between species and grass cover was evident when total biomass was considered, there is a significant interaction when above ground biomass was considered alone ($F_{(1,62)}=4.650$; $p<0.05$). The mean values of above ground biomass are presented in Table 1, with the values of below ground biomass, for which no interaction exists ($F_{(1,62)}=3.420$; $p>0.05$). The shoot: root ratios of each species and each treatment is also presented in Table 1 and these data show that *A. karoo* has a lower shoot: root ratio and significantly more root biomass than *A. nilotica* ($F_{(1,62)}=18.377$; $p<0.05$). Of the *A. karoo* plants grown with grass, 100% ($n=20$) had nitrogen-fixing nodules on their roots, whereas only 36.8% ($n=19$) individuals of *A. nilotica* had root nodules. Root nodules were not present on any of the plants grown without grass.

Table 1. The mean values of above ground biomass, below ground biomass and the shoot: root ratio for *A. nilotica* and *A. karoo* individuals grown with *Themeda triandra* grass and without.

SPECIES	ABOVE GROUND BIOMASS (g)		BELOW GROUND BIOMASS (g)		SHOOT:ROOT RATIO	
	With	Without	With	Without	With	Without
<i>A. nilotica</i>	0.0876	0.2216	0.0465	0.0834	2.234	2.657
<i>A. karoo</i>	0.1594	0.2822	0.0957	0.1180	1.631	2.485

• Response to browsing

Transect data suggest a differential response of each species to increased herbivore pressure. The assessment of browsing pressure on each species (see Table 2) provides strong evidence that *A. karoo* is the favoured species and that *A. nilotica* is relatively unpalatable, having significantly fewer bites than *A. karoo* ($F_{(2,144)}=101.65$; $p<0.001$). Differences in browsing pressure exist between the sites ($F_{(2,144)}=35.92$; $p<0.001$), indicating that browsing pressure is greatly increased on grazing lawns. The two-way ANOVA based on a combination of both site and species shows that both species are browsed more on grazing lawns than on non-grazing lawns ($F_{(2,144)}=7.10$; $p<0.01$). Figure 18 provides evidence that as browsing pressure increases, a greater proportion of *A. nilotica* is eaten, presumably as the availability of *A. karoo* declines.

Table 2. The average number of branches bitten off 25 individuals of each species, at 3 sites presented in order of herbivore pressure.

Site	Average number of branches bitten off each individual	
	<i>A. karoo</i>	<i>A. nilotica</i>
Sivivaneni	4.72	0.56
Viewpoint	14.68	3.12
Grazing Lawn	16.6	6.12

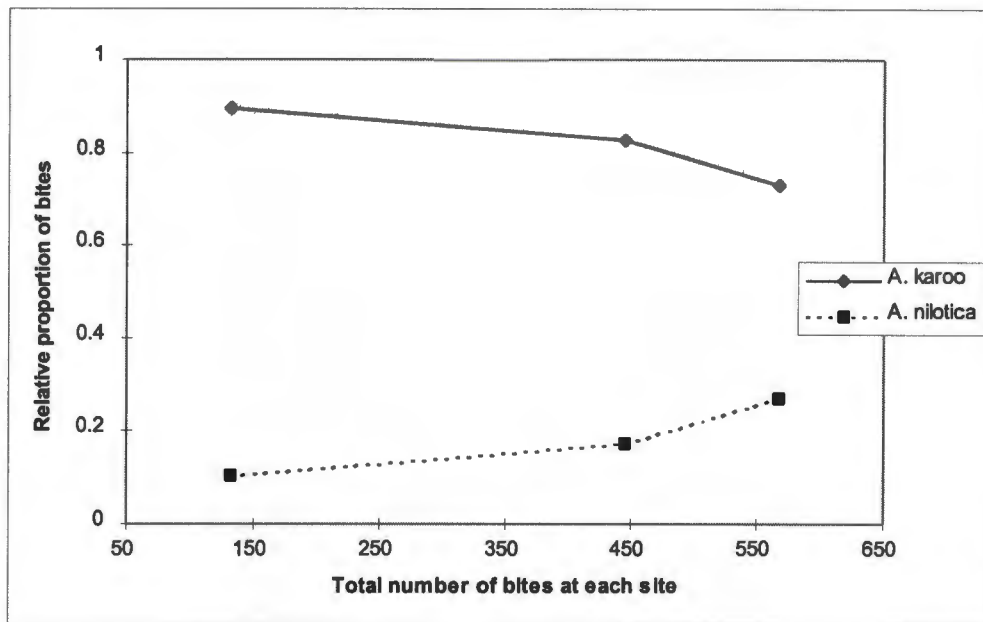


Figure 18. A representation of the relative increase in the proportion of branches bitten off *A. nilotica* compared to *A. karoo*, as browsing pressure increases. Increased browsing pressure is inferred from the increase in total number of bites from both species.

- **Response to fire**

The size class distributions of individuals in the two adjacent sites with different burning histories are shown in Figures 19a-d. Those species which survive topkill are referred to as survivors, whereas those species which were burnt to the base and then resprouted are referred to as resprouters. The majority of survivors fall into a smaller size class for *A. nilotica* than *A. karoo*, indicating that *A. nilotica* is able to survive at a smaller size (Figures 19a & c). We expect fires to reduce the height of each species to a similar level, depending on the intensity of the fire. A more intense fire will cause a reduction in height to a lower level than a less intense fire (compare Figures 19a & c and 19b & d), although these data are slightly biased because the individuals from the intense fire site have been growing for a year less than the others. The data imply that *A. nilotica* grows slowly as the majority of individuals are small. In contrast, *A. karoo* survivors show a normal distribution along the range of size classes, and this suggests that the species regrows rapidly following fire (Figure 19a). This is supported by the results for

resprouters which are likely to have all been reduced to ground level. Again, *A. karoo* shows a greater number of larger individuals compared to the slow-growing *A. nilotica*, which has very few individuals over 1.5 m (Figure 19d). In the case of *A. nilotica*, it is likely that more energy is invested into survival features (e.g. corky bark) than *A. karoo* which invests more energy into rapid growth than survival.

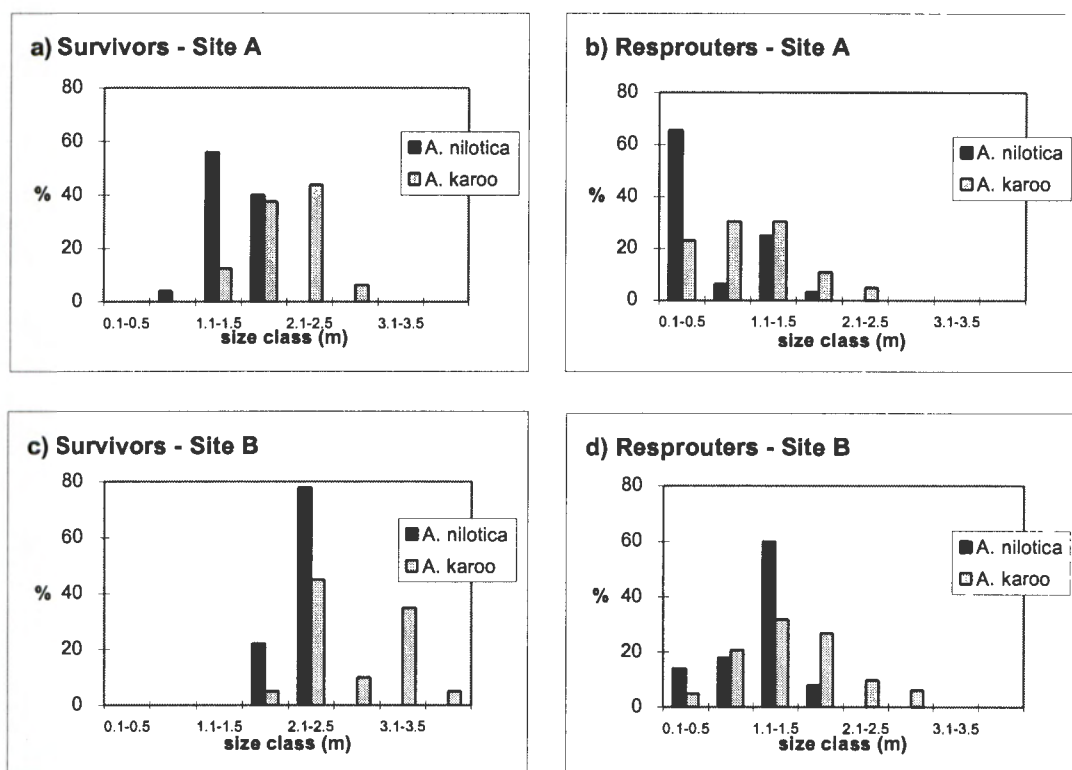


Figure 19a-d. The size-class distributions of *A. nilotica* and *A. karoo* juveniles at two adjacent sites with different fire histories. Site A experienced three intense burns in 3 years; Site B experienced one less intense burn in 3 years. Individuals were classified as Survivors or Resprouters (see text).

Discussion

In this study, I discuss the dynamics of two dominant species in the *Acacia* woodland community of the Hluhluwe-Umfolozi Game Reserve, namely, *A. nilotica* and *A. karoo*. Two points of interest arise from initial observations of this community. Firstly, although both *A. nilotica* and *A. karoo* occur throughout the study area, the relative abundance of the two species changes along a spatial gradient. Most of the low-lying regions of the reserve consists of mature *A. nilotica* woodlands which decrease in extent with an increase in altitude, whereas *A. karoo* increases in abundance with increasing altitude. Secondly, *A. karoo* juveniles have a much wider distribution than *A. karoo* adults and are four times as abundant as *A. nilotica* juveniles, suggesting a possible change in species dominance. In order to interpret these spatial and temporal patterns, I investigated the factors responsible for determining community structure.

Determinants of community structure

- **Rainfall**

It is generally accepted that soil moisture availability determines the abundance of woody species in savannas (Walter 1971; Knoop and Walker 1985; Skarpe 1992) and Smith and Goodman (1986) report a physiognomic gradient of increasing tree density with increasing altitude. However, in the Hluhluwe-Umfolozi Game Reserve, the *A. nilotica* woodlands are largely restricted to the drier Corridor and the lower hills of Hluhluwe. As both species are capable of establishing and persisting as Gullivers throughout the study area, it is unlikely that the difference in the distribution of these species is related to rainfall. O'Connor (1995) found that *A. karoo* was unable to establish in years in which rainfall was less than 500 mm, and this may be a partial explanation for the decline in abundance of *A. karoo* in the lower rainfall areas.

- **Competition with grass**

Competition is considered a major structuring force in many systems, especially in savannas where the grass layer shades the establishing woody seedlings and both components compete for water and nutrients (Knoop and Walker 1985; Skarpe 1992). Smith and Goodman (1986) found that *A. nilotica* was unable to establish under shady conditions, whereas O'Connor (1995) found that seedling establishment and survival of *A. karoo* was actually enhanced by the grass layer. In this study, I found the herbaceous layer to have a negative effect on both species. However, neither species is influenced more than the other, indicating that competition with the grass layer is not responsible for the spatial patterns in the *A. nilotica*-*A. karoo* community. I propose that competition between both species and grass is not an important determinant of community structure because the acacias develop nitrogen-fixing nodules which aid in nutrient acquisition, so that competition with grass for resources is limited. *A. karoo* shows a greater ability to produce these nodules and this may explain why this species is apparently better able to establish in areas of high grass cover.

- **Disturbance**

Disturbance has been identified as a major determinant of community structure in several systems (e.g. Ogden and Stewart 1995; Cowling 1987) and many studies have demonstrated the importance of disturbance in savannas (Norton-Griffiths 1979; Pellew 1983; McNaughton 1984; Dublin *et al.* 1990). In particular, Pellew (1983) and Dublin *et al.* (1990) have shown how the interaction between browsing and fire determines the structure of the *Acacia* woodlands in the Serengeti. Pellew (1983) states that heavy browsing by elephants reduces the density of adult *A. tortilis* trees while the combination of browsing of juveniles by giraffe and fire limit the regeneration of the *A. tortilis* woodlands.

In order for disturbance to be implicated as the major structuring force of the *A. nilotica*-*A. karoo* community in the Hluhluwe-Umfolozi Game Reserve, differences must exist between the two species in the degree to which disturbance influences their survival. In addition to this, disturbance gradients must exist in order to explain the observed spatial shift in community dominance.

Browsing

There is strong evidence that *A. karoo* is utilised more by browsers than *A. nilotica*, and this suggests that conditions of high browsing pressure have a greater influence on *A. karoo* than *A. nilotica*. Evidence from the grazing lawn situations, where browsing pressure is high, suggests that disturbance in the form of browsing can significantly limit the recruitment and survival of *A. karoo*. Although acacia seedlings are able to resprout following pruning, Seif El Din and Obied (1971) found that browsing was responsible for seedling mortality of *A. senegal* seedlings in the Sudan, and it is likely that browsing influences the distribution of the more palatable woody species.

Gradients of browsing pressure exist in the reserve, decreasing in intensity with an increase in altitude. Animals congregate in the less hilly, shorter grass areas of the Corridor, although the thickets of *A. karoo* Gullivers in Hluhluwe are frequently utilised by browsers (Whateley and Porter 1983). In the latter situation, it is likely that browsing does not effectively limit the recruitment of *A. karoo* but constant pruning of the Gullivers retains them within the grass layer so that the combination of browsing and fire prevents them from establishing as adults.

Fire

In addition to the gradient of browsing pressure, a gradient of fire frequency and intensity exists in the reserve. The low-lying areas, in which grass density and height is lower, experience fewer fires than the areas of dense, tall grass swards in Hluhluwe, and these fires are generally less intense. Spatial patterning as a result of differences in fire intensity has been documented in the boreal forests of Quebec (Brisson and Bergeron 1990; Bergeron 1991).

In savannas, fire limits both recruitment and the progression of individuals from the Gulliver stage to adults (Trollope 1984). Savanna trees have a large capacity to resprout following fires and are only killed after they have become progressively weakened by frequent, or particularly intense, fires (Trollope 1984; Bond and van Wilgen 1996). Some species are more tolerant of fires than others and therefore different species respond differently to the same fire regime.

A. karoo recovers more quickly following a fire than *A. nilotica* does. It grows rapidly and therefore reaches 'escape height', the height at which it escapes the flames in the grass layer, sooner after fire than *A. nilotica* does. It appears to retain its capacity to resprout even after frequent, intense fires, whereas *A. nilotica* appears to be progressively weakened by successive intense fires. Results from the glasshouse competition experiments suggest that *A. karoo*, which has a higher root biomass, has a large investment of resources below ground and this provides energy for repeated resprouting and rapid growth. In the two adjacent stands with different fire histories that I studied, the density of *A. nilotica* in the stand which had experienced three successive intense burns was about three times less dense than the stand which had burnt once in three years. *A. karoo* did not show the same reduction in density and this indicates that *A. nilotica* is less tolerant than *A. karoo* to fire, and that frequent, intense fires are capable of reducing the density of *A. nilotica* Gullivers.

The relative effect of fire on each species matches the spatial patterns in the reserve. *A. nilotica* is more abundant in the Corridor, where fires are less frequent and probably less intense due to the lower grass biomass, than it is at the higher altitudes where fires are generally more frequent and intense. *A. karoo* is able to withstand these frequent fires and no reduction in Gulliver density is evident at higher altitudes, although the progression from Gulliver to adult appears to be limited as *A. karoo* adults are very rare in the reserve.

Shifts in community structure along spatial gradients

I have established that *A. nilotica* and *A. karoo* respond differently to different disturbances, and that the intensity of these disturbances changes along a spatial gradient. The relative impact of browsing and fire on the spatial distribution of *A. nilotica* and *A. karoo* Gullivers is illustrated in Figure 20. These disturbances influence the spatial distribution of Gullivers both in the establishment of seedlings and the persistence of established Gullivers. The spatial gradient is from areas of low grass biomass (at low altitudes), to areas of high grass biomass (at high altitudes). Grazing lawns are included at the bottom end of the scale because they represent the extremes of high browsing pressure and low fire frequency. See the figure heading for an explanation of the widths of each lozenge-shaped block.

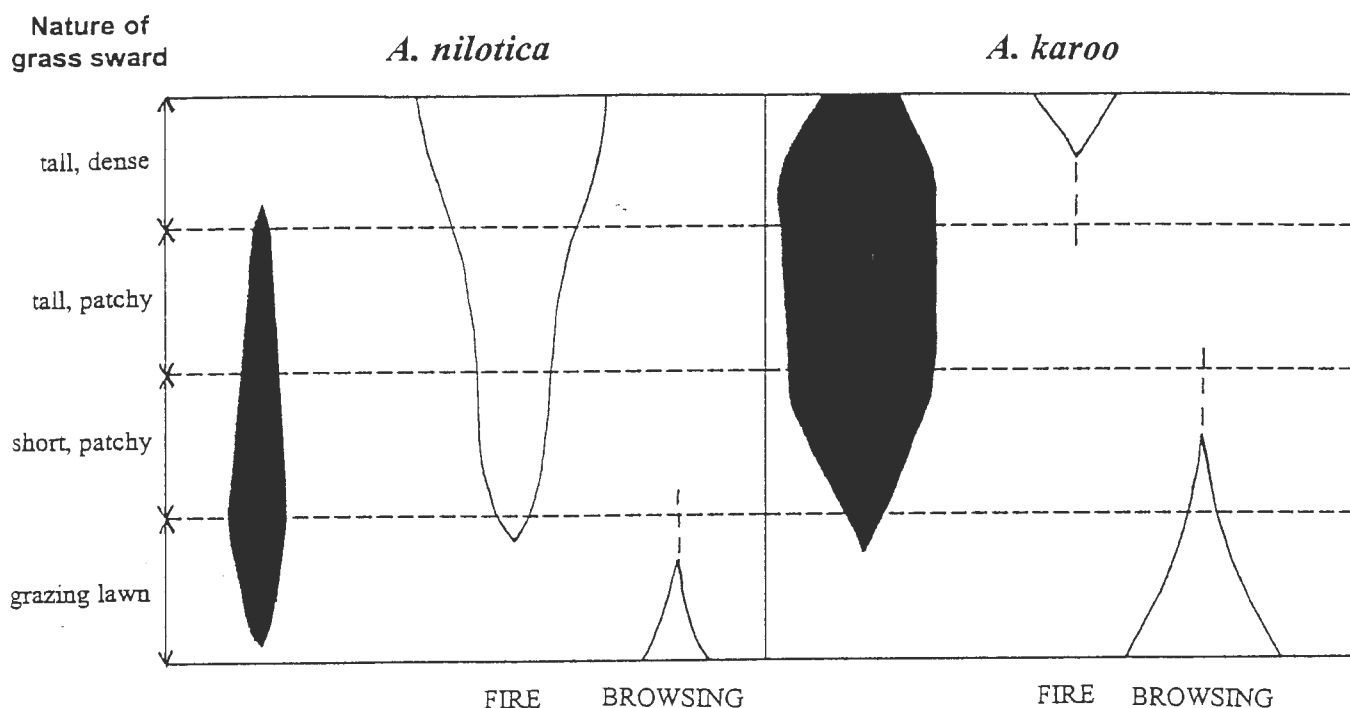


Figure 20. A diagrammatic representation of the distribution of Gullivers within the *A. nilotica*-*A. karoo* community (shaded blocks), together with the relative influences of the two major determinants of community structure, fire and browsing (unshaded blocks). Both the distribution and relative abundance of the disturbances varies along a spatial gradient of increasing grass biomass. The width of the shaded blocks represents the relative abundance of Gullivers of each species, and the width of the unshaded blocks represent the relative influence of each disturbance at each point along the spatial gradient.

A. karoo is more abundant than *A. nilotica* at the Gulliver stage, particularly in areas with a tall, dense grass sward where fires have a large impact and browsing is limited. Records show that animal densities are not particularly high at present, and therefore the distribution of *A. karoo* Gullivers is only limited at the extreme end of the scale. *A. nilotica* is not limited under conditions of low grass biomass but shows a decline in abundance as grass biomass (i.e. fuel load) increases. The distributions of the adults are not illustrated as the same disturbances influence the progression from Gulliver to adult. However, in the long grass areas the effect of browsing is greater on *A. karoo* Gulliver escape than on Gulliver establishment because the seedlings are protected in the grass layer. Therefore, a large degree of overlap between the spatial influence of fire and browsing occurs and this accounts for the restricted distribution of *A. karoo* adults in the reserve.

Shifts in community structure along temporal gradients

If the spatial distribution of *A. nilotica* and *A. karoo* can be explained by differences in disturbance intensity along spatial gradients in the reserve, then changes in the disturbance regime over time should reflect temporal changes in the distribution of acacias. The disparity between the spatial distribution and abundance of *A. karoo* Gullivers and adults suggests that current conditions are different to what they were previously when the adults established.

The distribution of *A. karoo* is determined by the interaction between fire and browsing. High browsing pressure limits the establishment of *A. karoo* Gullivers whereas high fire frequency, singularly or in combination with browsing, limits the progression from Gulliver to adult. In the past, conditions of low fire frequency and high animal densities prevented both the establishment of *A. karoo* Gullivers and the escape of Gullivers from the grass layer, and this interaction between fire and browsing is responsible for the lack of *A. karoo* adults in the reserve today. *A. nilotica*, which is relatively unaffected by browsing and is tolerant of infrequent fires, established periodically as mature woodlands. Within the last two decades, fire frequency has increased to the extent that *A. nilotica* Gullivers are not only unable to establish as adults, but are most probably being reduced in density. Over this period animal densities have declined and *A. karoo* has been released from the influence of browsing pressure on seedling establishment. Individuals of this species are not killed by frequent fires, and the observation that some Gullivers fruit before they become adults suggests that the extent of the *A. karoo* thickets is increasing as new seedlings establish. Thus *A. karoo* is contributing to the increase in the woody component of the Hluhluwe-Umfolozi Game Reserve which has been of concern in the reserve for decades (Vincent 1970; Downing 1980; Brookes and Macdonald 1983).

These cycles in species dominance as a result of disturbances rather than succession have been reported for other savanna systems. Pellew (1983) documents a series of perturbations, such as changes in herbivore density

and rainfall, which lead to a change in the *A. tortilis* woodlands of the Serengeti over 2 decades. In the Hluhluwe-Umfolozi Game Reserve, historic events and conditions of the region are responsible for the cycles of abundance within the *A. nilotica*-*A. karoo* community and these are documented in Appendix 1.

Management Implications

It is clear that the structure of the *A. nilotica*-*A. karoo* community is controlled by the interaction between fire and browsing. Management practices which have dealt with these two disturbances in the past, have largely been responsible for changes in the structure of this community. Bush encroachment, caused primarily by *A. karoo*, is a serious problem in the reserve at present, and understanding the factors controlling the establishment and persistence of *A. karoo* is essential in overcoming this problem.

With regard to the *Acacia* woodland communities, the primary concern of reserve managers is to halt the spread of woody species and reduce the extent of existing thickets. However, the current use of intensive management is having serious implications on the persistence of *A. nilotica*. Based on evidence presented in this study, I propose that a combination of fire and intensive herbivore pressure will be more effective in reducing *A. karoo* Gulliver density. This combination will allow a less intense fire regime which will ensure *A. nilotica* remains in the system, although it appears that over a large proportion of its range, a change in dominance to *A. karoo* has been initiated. This study illustrates the importance of interactions in savanna systems and highlights the need for an understanding of community dynamics for reserve management to be effective.

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Appendix 1.

Since the reserve was proclaimed in 1895, there has been a large increase in the extent of the woody component. Within the *Acacia* woodland community, I believe there have been cycles of abundance of *A. nilotica* and *A. karoo*, due either to management decisions or natural events. Perturbations to the system which favour one, both, or neither species, result in pulses of recruitment or reductions in the populations of each species. Here, I document some of the major events which I consider to have influenced the structure and composition of the *A. nilotica*-*A. karoo* community.

Pre-1900s: Before the reserve was proclaimed, the area was inhabited by humans who maintained the vegetation as an open grassland by frequent burning for agriculture and by intensive herbivore pressure from their livestock. Feeley (1980) states that these early inhabitants constantly moved around, affecting the vegetation as they did. As an area was abandoned, another group would re-occupy the area shortly afterwards and very few areas were probably never used (Feeley 1980). The domestic practices of the people living in this area kept the vegetation as an open savanna and restricted the spread of Gullivers so that the acacia communities were of limited extent.

1895-1955: During this period, fire was largely excluded from the reserve (Vincent 1970). The *A. nilotica*-*A. karoo* parklands evident in the 1961 vegetation map suggest that both species took advantage of these conditions, but both are relatively short-lived and these trees have already died. The dominant species was *A. nilotica* as *A. karoo* Gulliver density was still low due to high herbivore pressure by game and by livestock which remained in the Corridor until the 1950s (Vincent 1970).

Mid-1960s: This period was characterised by high densities of game and very low rainfall and a combination of these two factors resulted in very low grass cover which is evident from fixed-point photographs from 1965. During this period of low grass cover, fires were infrequent through most of the park.

The low grass biomass and long fire intervals benefitted *A. nilotica* and I propose that at this time some of the older cohorts of *A. nilotica* in the reserve today became established as adults. There is evidence for the development of *A. nilotica* woodlands at this time from fixed-point photographs. Forage would have been scarce during this dry period and both browsing of seedlings and pruning of Gullivers controlled the establishment of *A. karoo*. A few *A. karoo* Gullivers would have escaped the intense browsing pressure during this time and would have been able to take advantage of the break in the fire regime and I believe that this accounts for the isolated *A. karoo* adults seen in the park today.

Early 1980s: It was believed at this time that animal densities were too high for the reserve and large numbers of game were culled between 1981 and 1983. The subsequent decline in browsing pressure was probably responsible in part for the explosion of *A. karoo* Gullivers we see in the reserve today, but there has been no corresponding break in the fire regime and the Gullivers have been unable to escape the grass layer.

1990s: The conditions in the reserve at present favour the establishment of *A. karoo* but limit the escape of both species. Fire frequency is so high that I believe the density of *A. nilotica* Gullivers is being reduced. Many individuals in the *A. nilotica* woodlands are beginning to senesce and it appears that in the future, *A. karoo* woodlands will dominate the reserve.