**Acacia** species turnover in space and time in an African savanna

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**Abstract**

**Aim** Patterns of species turnover along environmental gradients are better studied than their causes. Competitive interactions, or physiological tolerance are most often cited as determinants of turnover. Here we investigate differential tree species response to disturbance by fire and mammal browsing as causes of changing dominance of species within and among sites along an altitudinal gradient.

**Methods** We documented the distribution of two *Acacia* species using maps and sample transects. We explored possible causes of species turnover by studying differences between the species in tolerance to grass competition using pot experiments, to browsers by observing patterns of shoot damage, and to fire by comparing the size structure of populations burnt at different frequencies and intensities.

**Results** *Acacia karroo* woodlands were rare and occur at higher elevations than the much more common *A. nilotica* woodlands. Woodland composition seems set to change in future since the pattern of dominance was reversed in juvenile stages. *A. karroo* juveniles were very widespread and far more abundant than *A. nilotica* juveniles. *A. karroo* juveniles were most abundant in tall fire-prone grasslands and were rare on grazing lawns whereas *A. nilotica* showed the reverse pattern. In the pot experiments, growth of both species was suppressed by grasses but there were no significant differences in response between the two species. Juveniles of *A. karroo* were more heavily browsed than those of *A. nilotica*. However juveniles of *A. nilotica* were less tolerant of frequent intense burns than juvenile *A. karroo*.

**Main conclusions** 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. Differential responses to browsing and fire may also explain temporal turnover from *A. nilotica* in the past to *A. karroo* in the present. Changes in the area burnt annually, and in faunal composition, suggest a landscape-scale shift from grazing-dominated short-grass landscapes in the 1960s, favouring *A. nilotica*, to fire-dominated tall grasslands in the 1990s favouring *A. karroo*. We suggest that species turnover due to differential responses along disturbance gradients may be much more widespread than the current paucity of studies suggests.

**Keywords** Savanna, *Acacia*, fire, herbivory, gradients, disturbance ecology.

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**INTRODUCTION**

Changes in species abundance along environmental gradients are commonly observed in many landscapes (Whittaker, 1975). Several hypotheses have been suggested to account for this species turnover. Physiological specialization to different gradient positions is one of the first that comes to mind, yet there seem to be surprisingly few examples where physiological capacity explains local distribution (Woodward, 1992). Interspecific competition has been widely invoked to explain the mismatch between observed pattern
(the realized niche) and physiological potential (the potential
niche). Some of the earliest field experiments in ecology
showed that removal of competitors allowed species to grow
outside their usual range (Tansley, 1917; Connell, 1961).
These, and other studies, led to the wide acceptance of
competition as a major force structuring the distribution and
abundance of species along environmental gradients (e.g.

Views on forces shaping communities have changed
fundamentally over the past two decades. The importance
of competition has been widely challenged as the main
process structuring communities or patterns of species
distribution and abundance (Crawley, 1997). Episodic
disturbance such as drought, floods, fire and hurricanes,
may occur so frequently that species assemblages never reach
competitive equilibrium (Huston, 1979; Pickett & White,
1985). Other ecological processes, such as herbivory or
predation, may modify or override competitive hierarchies
(Louda, 1982, 1989). The most extreme, or null view, is that
all ecological interactions may be too weak to structure
species assemblages. If this were the case, then patterns of
local diversity and composition may reflect little more than
the random sampling of species from the regional species
pool (Hubbell & Foster, 1986; Oksanen, 1996).

The existence of repeated patterns of tree species turnover
along environmental gradients poses a challenge to the null
view of species assemblages. If ecological interactions are
weak, and there is little physiological specialization, then
species should occur as a random mix across landscape
gradients. The converse, of repeated patterns of species
turnover, has been used as evidence against Hubbell &
Foster’s (1986) non-equilibrial model for tropical forest
assemblages (Terborgh et al., 1996). However the existence
of compositional gradients does not necessarily imply that
interspecific competition is the underlying mechanism.
Species may be responding differently to landscape variation
in disturbance frequency or intensity (Bond & van Wilgen,
1996), or to changing predator or herbivore pressure (Louda,
1982). Where this is the case, species distribution should
change with changing patterns of disturbance, or abundance
of herbivores rather than, say, with a changing mix of
competitors. For example, Grimm (1984) argued that tree
species turnover from prairies to tall deciduous forests was
determined by relative tolerance to burning along a gradient
of decreasing fire frequency, and not by a competitive
hierarchy measured by relative tolerance to shading. Chan-
ding fire regimes, rather than physiological growth require-
ments or competitive abilities, also account for the northern
limits of several fire-sensitive conifers in the boreal forests of

We studied the distribution pattern of two Acacia species
in a South African savanna and possible processes determin-
ing the patterns. Savannas are highly dynamic mixtures of
trees and grass. The tree grass mixture is influenced by site
conditions, variation in rainfall, fire and herbivory (Scholes
influential equilibrial model for the coexistence of trees and
grasses in savannas based on niche differentiation in the
rooting zone. However several studies have not found the
assumed differences in use of rooting space by trees and
grasses (Belsky, 1994; Le Roux et al., 1995; Seghier, 1995;
Mordelet et al., 1997; Scholes & Archer, 1997). Non-
equilibrial views of savannas invoke variable rainfall, herbi-
vory and fire as determinants of tree demography interacting
in complex ways at different times and places (Pellet, 1983;
Dublin et al., 1990; Prins & van der Jeugd, 1993; Scholes
& Archer, 1997; Higgins et al., 2000). Disequilibrial perspec-
tives on human use of savannas have also argued that, for
example, livestock numbers are determined more by the
exigencies of climate than by density-dependent competition
for forage (Ellis & Swift, 1988; Behnke & Scoones, 1993).

Changes in tree/grass balance have been widely studied in
savannas but there are few studies of changes in tree
distribution along gradients. Yeaton (1988) analysed tree
species turnover in an African Burkea–Terminalia savanna,
arguing that the pattern is determined by competitive differ-
ences in shade tolerance. However, the most shade-tolerant,
and therefore most competitive species, was also the most
rare. Yeaton explained the discrepancy by noting that this
species was more sensitive to fire because its bark was
preferred by porcupines. Yeaton’s study was in a savanna
woodland. In more open savannas, juveniles are too small and
widely spaced in the grass matrix for interspecific competi-
tion to be a likely explanation for tree species turnover.
We were interested in whether differential response of tree
species to competition with grass, or to injury caused by fire
or herbivory, might underlie changing patterns of distribution
and abundance of Acacia species in space and time.

STUDY AREA AND SPECIES

We conducted the study in Hluhluwe Game Reserve (HGR),
part of the Hluhluwe/Umfolozi Park (HUP) situated in
KwaZulu-Natal, South Africa (28°00′–28°26′ S; 31°43′–
32°09′ E). Hluhluwe Game Reserve (225 km²) is hilly
country and is too steep to generate the catenary sequences
typical of old African landscapes. Altitudes range from 40 to
750 m above sea level with mean annual rainfall varying from
c. 600 to c. 1000 mm p.a. Vegetation ranges from acacia-dominated savannas to treeless grasslands at the
highest elevations and includes broad-leaved thickets and
tall forests (Whateley & Porter, 1983). The thickets and
forests seldom burn and probably represent the climatic
potential for plant growth in the absence of top-down control
by fire or herbivory. Tree dominated communities have been
spreading at the expense of more open vegetation since the
1950s (Downing, 1980; Watson & Macdonald, 1983;
Whateley & Wills, 1996; Skowno et al., 1998). The park
has a diverse array of mammal species including both white
and black rhino. Elephant have been absent from the reserve
for most of its history but have recently been re-introduced,
partly to reduce tree densities. More detailed descriptions
of the park, its biota and history can be obtained from Brookes

We focused our study on the acacia savannas and the
distribution and dynamics of the two dominant Acacia
species in the reserve, *A. karroo* and *A. nilotica*. *Acacia karroo* is the most common acacia in South Africa and also the most variable (Ross, 1979; Brain, 1989). The Hluhluwe form of the species is a slender, sparsely branched tree up to 15-m tall. Saplings in size classes from 1 to 3 m are typically single stemmed and very sparsely branched. Although saplings generally produce no seeds, some populations had a small proportion of seed-bearing plants. Pods are dehiscent and seeds are probably passively dispersed. *Acacia nilotica* is a common acacia throughout Africa (Ross, 1979). The Hluhluwe form is a tree with a densely branching canopy seldom exceeding 5-m tall. Saplings have a much more densely branched canopy than *A. karroo*. Pods are only produced in plants > 2 m. Pods are indehiscent and edible and seeds are mammal dispersed.

**METHODS**

**Distribution patterns**

We analysed the altitudinal distribution of the two acacia species in the reserve using a combination of broad-scale map data and detailed transect studies. For broad-scale patterns we analysed the distribution of communities dominated by the two species using a digitally stored vegetation map (Whateley & Porter, 1983) based on a 1 : 50,000 scale map. We studied the distribution of adults and juveniles of *A. nilotica* and *A. karroo* in greater detail by sampling a series of 30 transects distributed through most of the Corridor and HGR. We selected transect sites on a 1 : 50,000 topo map so as to be accessible from the road network and to cover a wide altitudinal range. Map points were then located in the field and the transects were sited at the nearest location to these points in which *A. nilotica* adults occurred in the vicinity. Closed acacia woodlands were avoided.

Each transect was 40 m in length and 10 m wide. At each site, we examined soil by auguring to a depth of 0.6–1.2 m. We estimated grass biomass using a disc pasture metre (Bransby & Tainton, 1977). The height above the ground at which the disc rests is proportional to grass biomass. We estimated biomass from disc height using an equation derived from comparable grass swards in South Africa (Trollope & Potgieter, 1986):

\[ y = -3019 + 2260x^{0.5} \]

where \( y \) = estimated biomass in kg ha\(^{-1} \) and \( x \) = mean disc height in cm.

Twenty disc readings were taken along the length of the transect and the mean value was calculated. We estimated foliage protective cover of the herbaceous layer by counting hits on live foliage at 100 points along the transect. We noted the dominant grass species and classified the grass cover as ‘grazing lawn’ (*sensu* McNaughton, 1984) or ‘bunch grassland’. Grazing lawns are usually short (< 10 cm), with a low grass biomass and often with patches of bare ground. They are identified qualitatively by the presence of stoloniferous grasses (e.g. *Digitaria longiflora*, *Panicum coloratum*). They indicate areas of prolonged heavy grazing and burn at very low intensities or not at all. Bunch grasslands are dominated by *Themeda triandra*. Although sometimes heavily grazed, these grasslands are generally tall (> 0.6 m) and carry fires.

We divided *A. nilotica* and *A. karroo* individuals into height classes reflecting life history stage rather than age. ‘Seedlings’ are plants < 0.5 m, usually multistemmed with no main shoot. ‘Saplings’ range from 0.5 to 3 m, have a dominant, pole-like, main shoot with secondary branches at the base. Seedlings and saplings are collectively referred to as ‘juveniles’ as most were non-reproductive. ‘Adults’ are single stemmed plants > 3 m and all produce pods. The number within each class was recorded in each transect. When adults of a species did not occur in a transect, we estimated distance to the nearest adult. Species not in sight (< 0 m) were recorded as not being in the vicinity of the transect.

We located each transect on the digitally stored geographic information system (GIS) in order to study their fire history. Fire records extend back to 1935. The perimeter of fires is recorded on GIS but patches within the burn area may escape burning. Thus the fire record represents a maximum estimate of fire frequency. We investigated species response to fire frequency by plotting the proportion of each species occurring in each transect against the total number of fires from 1955 to 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 as the data frequently formed a triangular scatter of points (see figures below). This is a common pattern in ecological studies and expected from the theory of limiting factors (Thomson et al, 1996). The response variable takes a narrow range of values when the limiting factor exerts a strong effect. However when the factor is weak or absent, the response variable may take large or small values depending on other limiting factors. Regression analysis is inappropriate in these circumstances because variance of the response changes with values of the controlling factor. To overcome this problem, we used a test based on the null hypothesis 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. We tested whether the observed values in the two quadrants greater than the median of the independent variable differed from expected values calculated from the frequency of data points in the two quadrants below the median of the independent variable using Fisher’s exact test (Zar, 1996). For other approaches to this common, but poorly resolved, statistical problem, see Scharf et al. (1998), and Garvey et al. (1998).

**Mechanisms underlying distribution patterns**

**Response to competition with grass**

To test whether early seedling establishment was affected by grass, competition experiments were set up in a
glasshouse. In each of 10 pots, two *A. nilotica* seedlings were grown together with a *T. triandra* grass plant which filled most of the pot. In another 10 pots, two seedlings were grown without grass. The same was carried out for *A. karroo*. 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. Data were log-transformed following Bartlett’s test for homoscedacity. Significant differences between treatments were assessed by means of a nested analysis of variance (ANOVA) (Zar, 1996).

Response to browsing
Browsing is an important factor limiting recruitment into adult size classes in African savannas (Pellew, 1983; Dublin et al., 1990). Stem, rather than leaf, removal is more important in preventing the escape of juveniles to taller size classes. Black rhino, kudu and giraffe are all present in the reserve and are capable of browsing relatively large shoots. Black rhino are important browsers of acacia trees in HGR biting off branches up to 25 mm diameter (Emsley & Adcock, 1994). We examined the relative impact of stem browsing on *A. nilotica* and *A. karroo* at three sites with different browsing intensities. Two of the sites, one of which was a grazing lawn, experienced a high browsing pressure, while the third was only lightly utilized. We estimated the degree to which each species is browsed 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 ANOVA (Zar, 1996) to determine any differences between species and between sites.

Response to fire
Fire kills the shoots of juvenile acacias, a process called ‘topkill’ (Trollope, 1984). Topkill, like heavy browsing, also prevents growth of juveniles into adults. Burnt plants very seldom die but usually resprout. The extent of topkill is a function of plant height and fire intensity (Trollope, 1984). Plants taller than 2–3 m escape topkill. Most fires in HUP cause juvenile plants to coppice from the base but sprouting can occur higher up the stem after less intense burns. Successive intense burns cause progressive weakening of the plant and reduced regrowth after fire (Trollope, 1984). We investigated the response of each species to differing fire regimes in a fire management experiment at two adjacent sites (each > 5 ha in extent) in tall dense *Themeda* grassland in the Corridor. The sites occur on the same hill slope, with the same slope angle and aspect and the same blocky, black, clay soils derived from dolerite. Between 1993 and 1997, the low frequency site was burnt once with a low intensity burn in 1995. The adjacent high frequency site was burnt with three successive intense burns in 1994, 1995 and 1996. We compared regrowth height of the two species in the two burn treatments. The heights of approximately 60 *A. nilotica* and 100 *A. karroo* randomly sampled juveniles were recorded at each site. We classified each individual as a ‘resprouter’ if it had sprouted from the base since the last fire or ‘survivor’ if it had survived the fire with its canopy intact. The survivors could be distinguished by the presence of a charred stem base and charred thorns from the previous burn. Species differences in fire response were measured by comparing size class distributions in the two treatments. A relative shift to smaller size classes would indicate progressive weakening of regrowth response with successive intense annual burns.

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 kept at the Hluhluwe research centre. Additional information on animal densities was obtained from Brookes & Macdonald (1983). Vegetation maps of the reserve by Henkel (1937), one from 1961 (Anonymous) and Whateley & Porter (1983) were consulted. A series of fixed photo points from various parts of the reserve starting in the 1960s provided additional information on rates of growth, changes in grass cover and trends towards bush thickening.

RESULTS

Distribution patterns

Figure 1 shows the altitudinal variation in the distribution of the two species derived from Whateley & Porter’s (1983) vegetation map. *Acacia nilotica* woodlands cover a much larger area than *A. karroo* woodlands and peak at lower altitudes.
elevations (mode 200 m vs. *A. karroo* at 280 m). Whateley & Porter (1983) also mapped grassland with ‘invading’ trees or thickets of small *A. karroo*, our sapling size class. These map units are much more extensive than *A. karroo* woodlands and peak at the same mode as *A. nilotica* (Fig. 1).

A total of 111 *A. nilotica* adults (median 62.5 ha\(^{-1}\)) was recorded in the transects but not a single adult of *A. karroo*. The relative dominance of the two species was reversed in the juveniles (plants < 3 m). Here *A. karroo* exceeded *A. nilotica* more than threefold (*A. karroo* median density 725 ha\(^{-1}\); *A. nilotica* median density 225 ha\(^{-1}\)) and occurred in 28 of the 30 transects. The mismatch between adult and juvenile abundance indicates that acacia composition is changing over very large areas of Hluhluwe suggesting future landscape-level changes in woodland composition. From the data presented in Table 1, it appears that *A. karroo* has a remarkable dispersal ability, despite its dehiscent pods and apparently passively dispersed seeds. Although *A. karroo* juveniles were found in all but two transects, no transects contained *A. karroo* adults. Only half of the transects which had *A. karroo* juveniles present had adults within a radius of 100 m. However in some transects, a small number of sapling-sized plants produced seeds and may contribute to seedling populations. *Acacia nilotica* adults were found within 50 m of all but one transect containing *A. nilotica* juveniles.

**Landscape patterns**

There were significantly fewer *A. karroo* juveniles in each transect at lower altitudes (Fig. 2). *Acacia nilotica* adults showed the opposite trend. Most *A. nilotica* woodlands occur in the valley bottoms and lower hills and this is reflected in the transect data showing a negative relationship between *A. nilotica* adults and altitude (Fig. 3a). However, no similar trend of decreasing abundance with increasing altitude was found for *A. nilotica* juveniles (Fig. 3b). This implies that the distribution of adults of this species is not limited by failure of seedling recruitment.

Altitudinal gradients are associated with a complex of environmental factors. At Hluhluwe, grass biomass was positively correlated with increasing altitude (\(r = 0.591, P < 0.01\)). The frequency of fires (number recorded between 1955 and 1996) was also positively correlated with altitude (\(r = 0.792, P < 0.001\)) and with the grass biomass we recorded in 1997 (Fig. 4; \(r = 0.744, P < 0.001\)). The grass biomass we recorded in 1997 may therefore be representative of historical patterns of grass fuel.

The distribution of grassland types was also related to the altitudinal gradient. Grazing lawns, identified by the presence of stoloniferous grasses, were more common at lower elevations (median 160 m, maximum 220 m, minimum 100 m) but were absent at higher elevations. Bunch grasslands occurred across the entire altitudinal range in Hluhluwe but dominated the landscape at higher elevations (median 240 m, maximum 300 m, minimum 120 m). *Acacia*

### Table 1

Proximity of juveniles to adults reported as number of transects within 0, < 20, < 50 or > 50 m from the nearest adult. Where no adults were visible from the transect, distances are reported as > 50 m.

<table>
<thead>
<tr>
<th>Species</th>
<th>0 m</th>
<th>20 m</th>
<th>50 m</th>
<th>&gt; 50 m</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. karroo</em></td>
<td>0</td>
<td>6</td>
<td>8</td>
<td>14</td>
</tr>
<tr>
<td><em>A. nilotica</em></td>
<td>19</td>
<td>5</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>

**Figure 2** The relationship between density of *A. karroo* juveniles and altitude (\(P < 0.05\); Fisher exact test, see text). Points are stems ha\(^{-1}\) at each of 30 transects.

**Figure 3** The relationship between the density of *A. nilotica* and altitude. (a) adults (\(P < 0.05\); Fisher exact test) (b) juveniles (n.s., Fisher exact test).

distribution differed markedly between the two grassland types (Table 2). Acacia karroo saplings were 10 times more abundant in transects in bunch grasslands than in grazing lawns although ‘seedling’ numbers were similar. Acacia nilotica saplings and ‘seedlings’ were slightly, but not significantly, more abundant in grazing lawns. The proportional contribution of each species changed markedly with grassland type with A. karroo dominating in bunch grasslands and A. nilotica in grazing lawns.

Mechanisms underlying distribution patterns

Competition with grass

In the pot experiments, both species showed a significant decrease in biomass when grown with grass ($F_{1,62} = 25.832; P < 0.05$). Acacia nilotica growth was relatively more negatively affected (Fig. 5) but the difference was not significant over the experimental period (ANOVA interaction term $F_{1,62} = 3.631; P > 0.05$). Patterns of biomass partitioning above and below ground are shown in Table 3. There was a significant interaction between species and treatment for shoot biomass ($F_{1,62} = 4.650; P < 0.05$) but not for root biomass ($F_{1,62} = 3.420; P > 0.05$). Acacia karroo had a lower shoot–root ratio and significantly more root biomass than A. nilotica ($F_{1,62} = 18.377; P < 0.05$). Of the A. karroo 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.

Response to browsing

Black rhino was the main browser as assessed by patterns of shoot damage. Direct assessment of browsing pressure on each species (Table 4) provided strong evidence that A. karroo is the favoured species and that A. nilotica

<table>
<thead>
<tr>
<th>Table 2</th>
<th>Density of acacias on transects through grazing lawns vs. bunch grassland. Lawns are heavily grazed but seldom burn. Bunch grasslands are lightly grazed and frequently burn. Values are medians of plants ha$^{-1}$ (lower and upper quartiles in parentheses). No adult A. karroo were recorded in transects. Statistical test is Mann–Whitney (n.s. = $P &gt; 0.05$).</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species, size class</td>
<td>Bunch grassland ($n = 16$)</td>
</tr>
<tr>
<td>Bunch grassland</td>
<td>Grazing lawn</td>
</tr>
<tr>
<td>Saplings</td>
<td></td>
</tr>
<tr>
<td>A. karroo</td>
<td>1312.5 (725–1700)</td>
</tr>
<tr>
<td>A. nilotica</td>
<td>87.5 (50–375)</td>
</tr>
<tr>
<td>Seedlings</td>
<td></td>
</tr>
<tr>
<td>A. karroo</td>
<td>125.0 (25–550)</td>
</tr>
<tr>
<td>A. nilotica</td>
<td>62.5 (0–150)</td>
</tr>
<tr>
<td>Total juveniles</td>
<td></td>
</tr>
<tr>
<td>A. karroo</td>
<td>1387.5 (750–2275)</td>
</tr>
<tr>
<td>A. nilotica</td>
<td>125.0 (100–575)</td>
</tr>
<tr>
<td>Adults</td>
<td></td>
</tr>
<tr>
<td>A. nilotica</td>
<td>50.0 (0–100)</td>
</tr>
</tbody>
</table>

$\text{Figure 4}$ The relationship between grass biomass and number of fires recorded in transect areas between 1955 and 1996. Biomass was estimated using a disc pasture meter. The regression equation is, number of fires = $7.2838 + 0.00108 \times$Grass biomass $\tau = 0.744, P < 0.001$.

$\text{Figure 5}$ The effect of competition with grass on the growth of A. nilotica and A. karroo seedlings. The box-whisker plots show mean, standard deviation (SD) and range of whole plant dry mass (log transformed) grown with or without T. triandra for 14 weeks. Dotted lines join the means of each species grown with and without grass. There was no statistically significant difference between species at harvest ($F_{1,62} = 3.631; P > 0.05$) but both species grew significantly less with grass ($F_{1,62} = 25.832; P < 0.05$).
is relatively unpalatable, having significantly fewer bites than A. karroo (F2,144 = 101.65; P < 0.001). The number of bites differed significantly among sites (F2,144 = 35.92; P < 0.001), with the highest number 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 tall grass swards (F2,144 = 7.10; P < 0.01). Table 4 shows that as browsing pressure increased, a greater proportion of A. nilotica was eaten, presumably as the availability of A. karroo shoots declined. Black rhino was the main browser biting off shoots up to 25 mm diameter.

Response to fire

The size class distributions of individuals in the two adjacent sites with different burning histories are shown in Fig. 6. Those species which survived 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. karroo, indicating that A. nilotica is better able to resist top-kill (Fig. 6a & c).

Frequent burning caused progressive weakening of juveniles top-killed by fire indicated by reduced height of resprouts. The frequency distribution of resprouting height classes shows that the two species responded differently to repeated burning (Fig. 6b & d). Acacia nilotica was intolerant of frequent burning with most (65.6%) juveniles reverting to ‘seedling’ sized resprouts (relative to 7.8% in the low burn control). In contrast, A. karroo were resprouting vigorously in the frequently burnt site and only 23.4% had reverted to ‘seedling’ sized plants (relative to 4.8% in the low burn control).

DISCUSSION

Although both A. nilotica and A. karroo occur throughout the study area, the relative abundance of the two species changed along a spatial gradient. Acacia nilotica woodlands are most prominent in the low-lying regions of Hluhluwe whereas A. karroo woodlands are more restricted and occur at higher elevations. Similar patterns of species turnover along complex altitudinal gradients are common in many ecosystems (Whittaker, 1975). The peculiar feature of this community, however, is in the juvenile stages. Acacia karroo juveniles were far more abundant and widespread than their adults and outnumbered A. nilotica juveniles by four to one – despite the overwhelming dominance of A. nilotica adults. Clearly the system is not in any kind of equilibrium. The remarkable difference between adult and juvenile abundance, at a landscape scale, points to past changes in recruitment environments and future change in woodland dominance. Is there a set of common factors explaining both spatial and temporal species turnover?

The mismatch between adult and juvenile distribution of the two species suggests that physiological constraints on seedling recruitment are not a significant factor limiting distribution. Acacia nilotica trees dominate where the recruits are now greatly out-numbered by A. karroo, and A. karroo recruits occur far beyond the narrow limits of their adults. Physiological constraints may ultimately limit A. karroo at low elevations in the drier Umfolozi section of HUP since O’Connor (1995) found that A. karroo did not establish in years with < 500 mm rainfall in the eastern Cape region of South Africa. However we found A. karroo juveniles across the entire altitudinal range in HGR.

Competition with grass

Competition is considered a major structuring force in many systems. In savannas, competition occurs between grass and tree seedlings – the grass layer shades the establishing woody seedlings and both grasses and tree seedlings compete for water and nutrients (Knoop & Walker, 1985; Skarpe, 1992; Scholes & Archer, 1997). Smith & Goodman (1986) found that A. nilotica was unable to establish under tree canopy shade, whereas O’Connor (1995) found that seedling establishment and survival of A. karroo in the eastern Cape was enhanced by experimental shading with shade cloth. In the pot experiments, which included both above- and below-ground effects of grass competition, the herbaceous layer had a negative effect on both species. The effect was slight, but not significantly, more negative for A. nilotica.

Competitive effects are weak in these experiments and suggest that seedlings establish too frequently for grass competition to account for landscape pattern of the acacias. This is confirmed by A. nilotica sapling and seedling densities which were more than double those of adults.
Juvenile escape opportunities, rather than lack of seedlings, limits the extent of *A. nilotica* woodlands.

**Browsing**

In order for browsing damage to account for species turnover at Hluhluwe, gradients in browsing intensity should exist across gradients in the landscape and the two species must differ in their response to browsing. A gradient of browsing and grazing intensity appears to exist in the reserve, decreasing with increasing altitude. Animals congregate in the less hilly, shorter grass areas whereas the tall grasslands in the Hluhluwe hills are less utilized (Whateley & Porter, 1983). The distribution of grazing lawns matches this gradient as they are restricted to lower elevations. Grazing lawns support concentrations of white rhino, impala, wildebeest, warthog and zebra (Owen-Smith, 1988). They are also preferred browse sites for black rhino, a key browsing megaherbivore and the main agent causing acacia browse damage. Black rhinos avoid tall grass areas in Hluhluwe (Emsley *et al.*, 1994) so that juvenile acacias are only lightly browsed at higher rainfall sites.

Our observations of shoot damage on saplings provide strong evidence that *A. karroo* is utilized more by browsers than *A. nilotica* (Table 4). This is consistent with studies of these species elsewhere in South Africa (Owen-Smith & Cooper, 1987). The impact of browsing is also greater as *A. karroo* juveniles are sparsely branched so that loss of a shoot has much greater impact on growth than in *A. nilotica* which is densely branched. These species differences in response to browsing appear to be responsible for the 10-fold difference in sapling density of *A. karroo* on and off grazing lawns and suggest that disturbance in the form of browsing can significantly limit recruitment and survival of *A. karroo*. Heavy browsing has been implicated in preventing the escape of acacia juveniles into taller size classes elsewhere in Africa (Pellew, 1983; Dublin *et al.*, 1990) and in preventing early seedling recruitment (Prins & van der Jeugd, 1993).

**Fire**

In addition to the gradient of browsing pressure, a gradient of fire frequency and intensity exists in the reserve (Balfour & Howison, in press). Fire is limited by the availability of dry season grass fuel. The low-lying areas, with less grass fuel, experience fewer, less intense, fires than the tall grass swards of Hluhluwe. Closely cropped grazing lawns do not burn. In savannas, fire limits both recruitment and the progression of individuals from the sapling stage to adults (Trollope, 1984; Higgins *et al.*, 2000). Savanna trees have a large capacity to resprout following fires but are progressively weakened by frequent, or particularly intense fires (Trollope, 1984; Bond & van Wilgen, 1996). Some species are more tolerant of fires than others and, therefore, respond differently to the same fire regime.

Figure 6 The effects of different fire histories on stem height class distributions of *A. nilotica* (open bars) and *A. karroo* (hatched). The high frequency burn site experienced three intense burns in 3 years; the adjacent low frequency site experienced one low intensity burn over the same period. Individuals were classified as survivors if stems survived the previous fire or resprouters if stems were killed to ground level in the previous fire.
In our study, *A. karroo* regrew more quickly following a fire than *A. nilotica*. It also retained its capacity to resprout after frequent, intense fires, whereas *A. nilotica* was progressively weakened by successive intense fires. Unlike *A. karroo*, few plants were able to sprout shoots taller than 0.5 m after three successive annual burns (Fig. 6). Densities of *A. nilotica* were about three times lower in the high frequency site (Fig. 6) whereas *A. karroo* densities were comparable at high- and low-fire frequencies. These results indicate that *A. nilotica* is less tolerant of fire than *A. karroo* and that frequent, intense burns are capable of reducing the density of *A. nilotica* saplings. Differences in fire response may be related to differences in allocation patterns. *Acacia karroo* allocated proportionally more biomass to roots than *A. nilotica* and that frequent, intense burns are capable of reducing the density of *A. nilotica* saplings. Differences in fire response may be related to differences in allocation patterns. *Acacia karroo* allocated proportionally more biomass to roots than *A. nilotica* in the glasshouse-grown plants. The two species also differ in root starch reserves in the sapling class with *A. karroo* having up to 60% starch concentration compared with 30% in *A. nilotica* (W.J. Bond and K. Maze, unpublished data).

The relative effect of fire on each species matched the spatial patterns in the reserve. *Acacia karroo* juveniles were common at sites with high grass fuel loads and high fire frequencies. The current fire regimes applied by the park staff are aimed, in part, at preventing the progression of *A. karroo* juveniles to adults and *A. karroo* woodlands are still rare in the reserve.

**Shifts in community structure along spatial gradients**

The response of the two acacia species to fire and browsing is illustrated diagrammatically in Fig. 7. Juvenile *A. karroo* is more abundant than juvenile *A. nilotica* in tall, dense grass swards where fires burn fiercely but browsing is light. Juvenile *A. nilotica* is more abundant than juvenile *A. karroo* in short grasslands subject to intense browsing but declined in relative abundance in tall grass areas that burn frequently. The scarcity of *A. karroo* woodlands is not because of scarcity of juvenile recruitment but is the result of escape opportunities for them to grow into adults. Frequent intense fires have largely prevented the emergence of juveniles to heights where they could escape fire and become adults.

**Temporal shifts in community structure along temporal gradients**

Where competition underlies species turnover along gradients, changes in the mix of competitors should result in changes in position on environmental gradients. Where competition is not important in shaping local distribution patterns, changes in disturbance or herbivory may lead to distribution changes. The disparity between adult and juvenile abundance patterns in HGR suggest that current conditions are different from those when the adults established. Have there been changes in the disturbance regime over time that match changes in space? Hluhluwe has seen large changes in both fire frequency and animal densities since the 1950s. Several lines of evidence suggest a relative shift from a grazing dominated landscape in the 1960s and early 1970s to a fire-dominated one today. Balfour & Howison (in press) have recently analysed fire records for the last 40 years in HUP. Fire is limited by the availability of grass fuels so that the size of the area burnt annually fluctuates with the regional rainfall cycle of wet- and dry-periods (Tyson, 1986). Larger areas burn in wet cycles. Wet period burnt areas increased from a mean of 129 km² per year in the earliest period (1957–64) to 345 km² in the second (1975–78) to 524 km² in the third (1984–91). This is consistent with a change from short-grass systems in the 1960s to tall grass systems in the late 1990s. However interpretation is complicated by changes from a fire suppression policy in the early period to prescribed burning in the last (Balfour & Howison, in press).

There have also been marked changes in animal numbers. Low densities (and tall grass cover) have been estimated for the 1920s through to 1950 after which there was very rapid increase of short grass specialists matched by a decline of some species preferring tall grass (Deane, 1962; Mentis, 1970). The earliest reliable ‘modern’ census dates from 1973 and 1975. Several species have shown marked population changes since then. Warthog and impala both prefer short grass habitats. Warthog have declined from 1000 to 2000 animals in the early 1970s to 100–400 animals in the 1990s. Impala have declined from 6600 in 1973 to 2100 in 1996. Black rhino have also declined at Hluhluwe. Rhino numbered around 200 in the 1970s but collapsed to less than half that number in the 1980s and 1990s. The decline has been explicitly linked to vegetation change (Emsley & Adcock, 1994). Rhinos are known to prefer short grass areas for browsing (Emsley & Adcock, 1994). In contrast, buffalo, which graze in tall grasslands in this area, have increased from 1000 in the 1970s to double that number in the 1990s.

The pattern of increase in tall grass grazers and decrease in short-grass grazers supports the idea of landscape scale changes in grass cover at Hluhluwe since the 1960s. Further

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**Figure 7** A diagrammatic representation of the response of *A. nilotica* and *A. karroo* saplings to gradients of browsing intensity and fire.
support comes from long-term photo-monitoring sites some of which show dramatic changes from short grass in the late 1960s to tall grass swards from the 1980s. We suggest that the temporal switch from *A. nilotica* dominated woodlands, to *A. karroo* dominated juveniles has been caused by landscape-scale changes in the grass sward and in the relative importance of fire and herbivory. *Acacia nilotica* is tolerant of high herbivore pressure and would have been favoured during the 1960s period of short-grass, high animal densities and low fire frequencies. Aerial photography and ground-based photo sites indicate that the cohort of *A. nilotica* which produced current *A. nilotica* woodlands probably dates from that period (Skowno et al., 1998). Circumstances changed to favour *A. karroo* from the 1970s as tall grass areas expanded, herbivore numbers declined and fires increased.

Changes in system state from woodlands to grasslands have been reported for *acacia*-dominated landscapes elsewhere in Africa (Laws, 1970; Caughey, 1976; Norton-Griffiths, 1979; Dublin et al., 1990; Sinclair, 1995; Cumming et al., 1997). Elephants were major agents of woodland destruction in these examples but Hluhluwe has had no elephants until recently. Owen-Smith (1988, 1989) has argued that all mega-herbivores (animals > 1000 kg) can shape vegetation over landscape scales. Prins & van der Jeugd (1993) have shown that smaller mammals can also prevent tree escape and that cohorts of trees in East Africa owe their origin to anthrax outbreaks in impala. Fire is an equally influential generalist ‘herbivore’ over large parts of the globe (Bond & van Wilgen, 1996). African landscapes are one of the few remaining areas on earth where we can observe the interplay between the remnants of the Pleistocene megafauna and fire, two major agents of disturbance on plant distribution.

**CONCLUSIONS**

Turnover of two acacia species along an altitudinal gradient appears to be controlled by their different response to gradients of fire and browsing intensity. Establishing the processes that underlie species patterns over landscape gradients is important for predicting vegetation change. We suggest that the current disequilibrium between adult and juvenile acacia abundance has been caused by changes in disturbance processes in this savanna. Examples of processes other than competition or physiological specialization are still rare in the analysis of plant species distributions along gradients. How often are tree species confined to habitats which offer refuge from large herbivores, rather than because they offer suitable growing conditions? Has the extinction of many large browsing species in many African (and other) ecosystems, or changes in fire regime, altered the distribution of tree species? Direct and indirect manipulations of fire regimes and browsing mammals are common in many ecosystems. We suggest that the effects of such manipulations on tree species distribution may be much more widespread than the current paucity of studies suggests.

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**REFERENCES**


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