Hons 1999

The feedback effects of canopy architecture; Why are African Acacias flat-topped?

RESEARCHER: Phil M^{c}Lean
SUPERVISOR: Jeremy Midgley

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

University of Cape Town

BOLUS LIBRARY
C24 0007 6186

CONTENTS:

Check tattle on return.

DATE DUE

CANCELLED
14 FEB 2000

26 APR 2000
CANCELLED

CANCELLED
31 MAY 2000

~~2 OCT 2003~~

ABSTACT:

Only the African acacias have a so-called flat topped crown. This study identifies this architecture using the simple measures of height, diameter and spread. In this way the flat-topped species are identified and differentiated from the other acacia species (*A. nilotica* & *A. tortilis*). It has been suggested that this shape is an anti-herbivore mechanism. We demonstrate how these trees spend a lot of energy in defence, which indicates that the canopy shape is a poor anti-herbivore device. Measurements of the height of grass outside the canopies indicate that these species inhabit areas of long grass. At the same time, our data show that at least one of these species (*A. nilotica*) is extremely fire sensitive (60% mortality). The effect which saves these trees from fire is shorter grass beneath their crowns providing a low-fuel fire buffer for the trunk. However, none of the conventional effects of canopy are able to cause this effect (shade, nutrients). We propose that the shade and nutrient-rich undercanopy grass (as well as the pods of these animal-dispersed trees) encourages large grazing mammals to spend time under these trees. These animals then, are responsible for lowering the height of the grass cover by grazing and trampling, and hence save the trees from fire. We suggest an animal – flat-topped tree mutualism where food and shade are exchanged for seed dispersal and fire protection.

INTRODUCTION:

Savannas are the regions of the world characterised by tree and grass mixtures which are both geographically extensive and socio-economically important. Tropical savannas cover about 1600M hectares of land, which is about one eighth of the global land surface area which includes over half of Africa and Australia (as well as 45% of South America and over 10% of India). More importantly than this, they contain a large and growing proportion of the world's population and the majority of its rangelands and livestock (Scholes & Archer 1997). Consequently, the manner in which they function is of global relevance. These lands are characterised by tall grasses (bunch grasses), short lawn or turf grasses, shrubs and trees (where the trees can be isolated features or dense woodlands). It has been noted in various papers that the trees affect the nature of the grasses in their immediate vicinity (Belsky *et al* 1993, Scholes & Archer 1997, Weltzin & Coughenour 1990, Coe & Coe 1987). These authors all noted that the effect of canopies was to alter the habitat below the tree which in turn influenced the below-canopy species composition and sometimes also the height of these plants. This alteration was attributed to a variety of factors which are reviewed later, but seemed not to be the result of microhabitat (Roos & Allsopp 1997). Whately and Wills (1996) noted the uneven distribution of grass species underneath the canopies of *Acacia nilotica* trees. They noted the significant difference between the short lawns under the canopy (*Panicum maximum* and *Dactyloctenium australe*) and tall bunch grasses between canopies (*Cymbopogon excavantus* and *Themeda triandra*). Trees are able to alter their undercanopy environment and in so doing are able to alter the function and therefore the output of the system. Species in the genus Acacia have a variety of growth forms and it seems feasible that these different forms may have the ability to

1600 Mha

differentially affect their understory by virtue of their canopy architecture. This begs the question: What are the benefits to the tree of this kind of effect? What are the features of canopies shapes that are able to influence the undercanopy environment, do different canopy shapes have different affects and moreover, why?

Perhaps the most obvious potential cause of this undercanopy difference is the shade caused by the trees, particularly when one considers the flat-topped African acacias. In 1993 Belskey *et al* showed a reduction in solar irradiance under canopies from 45% under acacias to a 63% reduction under baobabs. As a consequence, the soil temperatures at 5 and 10 centimetres depths were significantly lower under the canopies. They also found that the range of temperatures under the canopy to be between 24.1 and 25 °C whereas those of between-canopy environments ranged between 26.7 to nearly 30 °C.

All savannas are water limited for at least some portion of the year, so a reduction in the below-canopy evapotranspiration rates could be seen as an advantage for the plants growing there. However the canopy of a tree is able to intercept rainfall. Reportedly between 5 and greater than 50% of gross annual rainfall is intercepted by trees (Scholes *et al* 1997). This water is then unevenly distributed below the canopy by stem-flow and edge-drip where the fine feeder roots of large woody plants are at an advantage as they can tolerate local dry spots. It is thus very surprising then, that Belskey *et al* (1993) found no statistical difference in soil moisture between and under canopies from 5 to 30 centimetres depth. At the same time they showed how the above-ground net primary production was 52% higher under acacias than in the open veld in their mesic sites. This figure rose to 95% at the xeric sites.

Increased soil fertility under canopies is another consideration. Roos and Alsopp (1997) removed soil from under canopies and open grassland sites and cultured *Panicum maximum* grass in them in a glasshouse. They found that the grass grew much larger in the under-canopy soils than in those from the open veld. Since there was no microclimate variation in the glasshouse, it can be assumed that the increase in growth was caused by an increase in soil fertility. It is tempting to attribute this to the N-fixing abilities of leguminous acacias. However, Belsky *et al* (1993) noted higher nitrogen levels in the soils from under acacias *and* a similar elevation under baobabs. This would indicate the lack of N-fixation underneath at least this acacia (*Acacia tortilis*). These results show a zone effect. In other words, the higher nutrient-level soils are a result of their being collected from under trees, not from under a particular species. Most of their results showed significant differences between under canopy and open grassland sites for both trees, little of which was attributable to species differences.

The overall effect of the above influences of canopy, is to promote the growth of the more productive, palatable and shorter lawn grasses beneath the tree. For what 'purpose' would a tree attempt to alter its canopy shape such that it has a greater or lesser effect on the undercanopy environment, and how does this benefit the tree? What are the costs involved in certain canopy shapes? This study attempts to discern, using simple measurements, the costs and benefits associated with the distinctive crown architecture of Africa's flat-topped acacias. A number of questions are raised in this study:

1. What is the variation within the acacias and do our simple measurements accurately define the differences?

2. What is the cost of being flat-topped? It is important for woody plants to escape the fire in savannas. This is usually done by growing above the flame height of the grasses. Height to diameter ratios could be used to give an indication of the height costs to flat-topped trees. The prediction ~~being~~ is that older (thicker) trees will still be shorter than their non-flat-topped counterparts with the same diameter.
3. Do the acacias really have an impact on their undercanopy grasses and if so, how is this impact accomplished (shade, nutrients)?
4. What are the fire impacts on various acacia species? Does the ability to alter the understory habitat have the potential to alter the fire survival of any particular species? More specifically, does the presence of different grasses of different heights influence the ability of certain trees to survive fire?
5. Are there other noticeable trade-offs in the relative bark thicknesses between the various species?
6. Is flat toppedness an~~d~~ anti-herbivore adaptation? The answer to this question may manifest itself as differences in thorn size and densities relative to the size of the leaf for different species.

METHODS:

Site: Our study site was the 96 453 ha Hluhluwe-Umfolozi Game Reserve located in Kwazulu-Natal, South Africa (28°00′-28°26′ S; 31°43′-32°09′ E. see Figure 1). The park is well stocked with a wide variety of large grazers including white rhino, Burchell's zebra and wildebeest as well as some mixed feeders – elephant and impala. All the aforementioned grazers have been present in the area for well over 100 years (Brooks and McDonald 1983). Using the park's road network we identified 15 sites which were dominated by acacias. In this way we sampled 10 species of acacia with a minimum of 10 individuals per species present per site (some sites had more than one species present). *A. robusta* was not included in our study as this is a riverine species which recruits only very rarely in savannah woodland. Species sampled include: *Acacia burkei; A. caffra; A. davyi; A. gerrardii; A. grandicornuta; A. karroo; A. nigrescens; A. nilotica; A. tortilis* and *A. senegal.* Table 1. shows the number of individuals of particular species that were measured at each site.

Sampling: Each site was marked on a map which can be seen in Figure 1. Before sampling commenced, a compass bearing was taken. Walking at random, trees were selected for measurement. At each tree we measured the height, diameter and canopy spread with a meter rule or a surveyor's rod, whichever was most appropriate. For canopy spread we measured the widest portion of the canopy and then the width of the canopy 180° from the first measurement. Diameter was taken at 30cm from the ground. Canopy spread was determined as the average of the two measurements taken per canopy. A one-to-one line has been fitted to the graph simply to aid interpretation as it separates, in a general sense, the flat-topped architecture from other growth forms. Diagrams have also been added which represent the type of architecture on their side of the line.

Five measurements of grass height were taken under the canopy on the north and south sides of the tree (hence the compass bearing). One measurement was taken every 50cm along the surveyor's rod. This was taken at a distance of half the canopy spread for that aspect, away from the trunk. Another five measurements were taken in a between-canopy environment. Unless impossible, these were taken 2m away from the canopy on the eastern side of the tree. We selected the north and south aspects in order to establish whether there were any shade-induced effects on the undercanopy environment. The prediction is that shade-effects will be noticed at the southern aspect more since it is this aspect which will receive the most shade from the canopy. For the results we have used the measure of the average maximum grass height, as not all measures of short (<10cm) grass infer lawn species. Some short grasses were the result of heavily grazed bunch-grass species (a 'bunch lawn'). Therefore, by using the tallest measure across all species we try to prevent this effect from influencing the results (outside or underneath the canopy)?In Figure 6 (A), the average maximum grass height is shown for each region – North under the canopy, South under the canopy and East away from the tree.

For each species we collected or measured five branches. The measurements of interest were: Thorn length, between thorn distance and leaf length. These results will be used to determine a measure of protection against herbivory. As it has been hypothesised that crown shapes (particularly 'flat-topedness') are an anti herbivore response – herbivores being less able to browse the tree beyond the edges (Brown 1960).

Bark thickness to stem diameter was taken for our two flat-topped species (*A. nilotica* & *A. tortilis*) to be compared against that of a known thick-bark fire survivor, *A. davyi*. This would help to establish whether there were any trade-offs in defence against fire.

In order to study fire sensitivity, we identified a recently burned site in an area of the park which has low animal density and long grass. Walking randomly through this site we selected trees and for each, measured its height, diameter and five grass height measurements on the northern side (as this side had been seen to be that with the lowest grass coverage in all our previous sites). The response of the tree to fire was then assessed, by determining whether it was sprouting from the base (SFB), sprouting in the canopy (SIC) or whether it had been killed by the fire (dead and alive before the fire = D + ABF). It was possible to determine if a tree had been alive before the recent fire by observing the diameters of its smallest branches. Had the tree been alive and green at the time of the fire these small branches would still remain, and so would still be seen on the tree (<1cm after the fire). Alternatively, if a tree had been dead at the time of the fire, these small branches would have been consumed in the flames. In this case, the smallest branches would have a large diameter (>1-2cm). We walked at random around this site until we had observed at least 50 *Acacia nilotica* (flat- topped) trees. In the event that a tree was sprouting from its base and in the canopy, the site of more vigorous growth was noted as its response. A summary of the sampling at this site can be seen in Table 2. For the analysis the trees were divided into three size classes, namely:

c. only close

1. < 3m
2. 3.25 – 4.75m
3. > 5m

Analysis: Raw data were input into excel worksheets before being transferred to Statistica. A 2-way analysis of variance was conducted on the data from the burnt site using this program. Percentage survival per size class from the burnt site was ArcSin-transformed so that it would conform to the requirements for ANOVA analysis. The graph for this (Figure 9) was drawn in Excel. 1- and 2-way ANOVAS were run on the grass height data as were LSD post-hoc analyses of the means. These tables and their graphs were produced with the Statistica program.

RESULTS:

ARCHITECTURE:

A plot of the means per species of height and spread shows one way in which our measurements can be used to separate the species in terms of their shape (Figure 2(A)). One can clearly see how *A. tortilis* and *A. nilotica* are grouped together on the flat-topped side of the line. This means that they have a disproportionately large spread for their height. To highlight the point one needs to look at *A. gerrardii* and *A. davyi*. These two trees have roughly the same average height per species as the flat-topped species, but at this height their average spread 1.5 to 2 meters smaller/narrower

Using a plot of diameter against height as the independent variable, one can again see how the two flat-topped species are separated from the others (Figure 2 (B)). Here trees below the one-to-one line have a disproportionately thick trunk for their height (or are short for their stem thickness). In this plot *A. senegal* sits on the line but

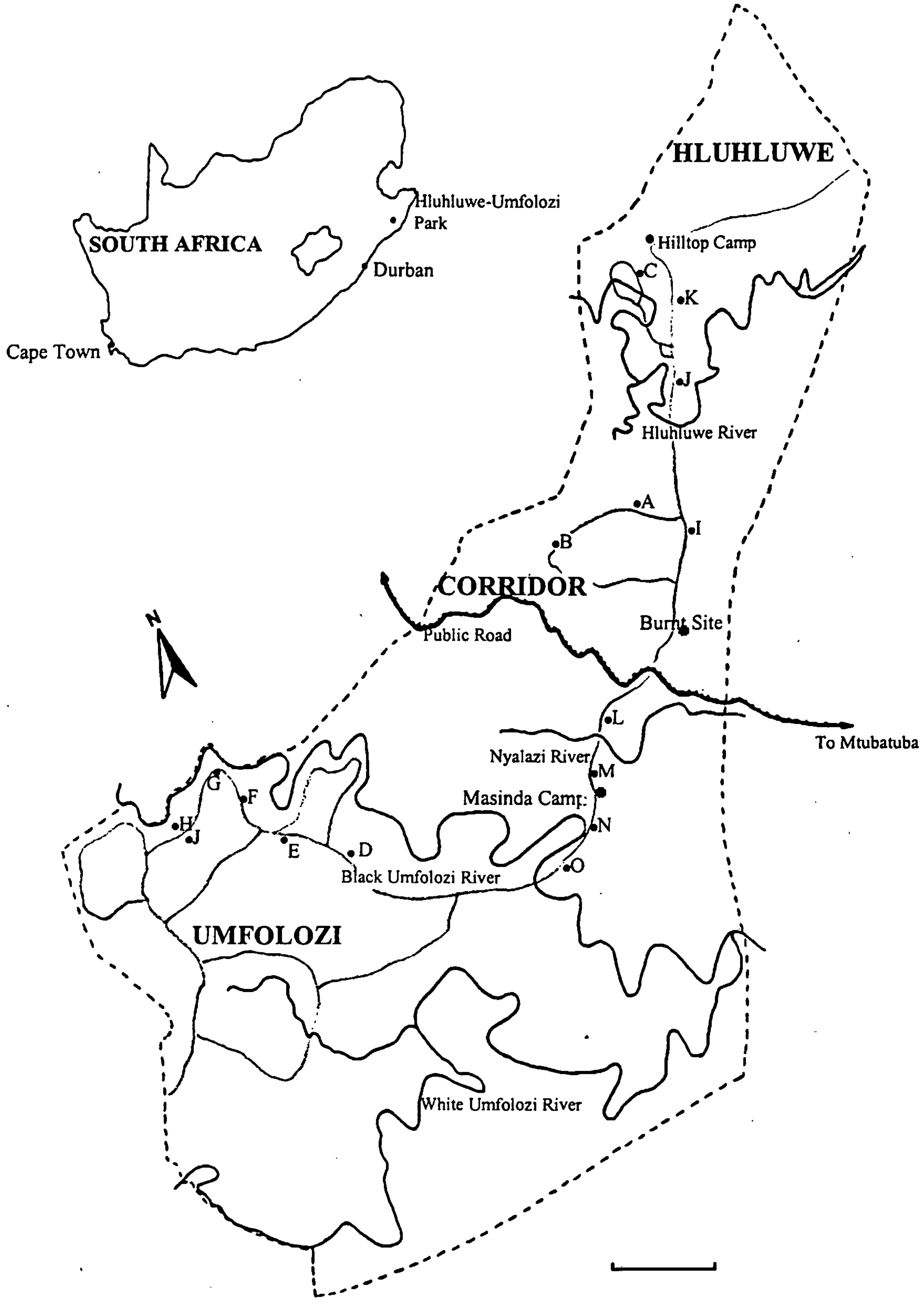

Figure 1: Map of Hluhluwe-Umfolozi Park with study sites

TABLE 1:Number of species observed at each stand

Stand	Species	Number
A	Nilotica	10
B	Gerardii	10
	Nilotica	10
C	Davyii	10
D	Grandi	10
E	Nigres	10
	Tortillis	10
F	Nigres	10
G	Tortillis	10
H	Tortillis	10
	Nilotica	9
	Senegal	10
I	Burkii	1
	Caffra	3
	Nilotica	11
	Gerardii	4
J	Burkii	10
K	Karoo	10
	Caffra	5
	Nilotica	3
L	Nilotica	10
	Caffra	10
M	Nilotica	10
	Tortillis	10
N	Burkii	10
	Tortillis	10
O	Grandi	10
	Nilotica	10
Total:	10	138

TABLE 2: Number of species in the burnt site

	Species	Number
	Burkii	23
	Caffra	7
	Gerrardii	51
	Karroo	41
	Nilotica	52
Total:	5	174

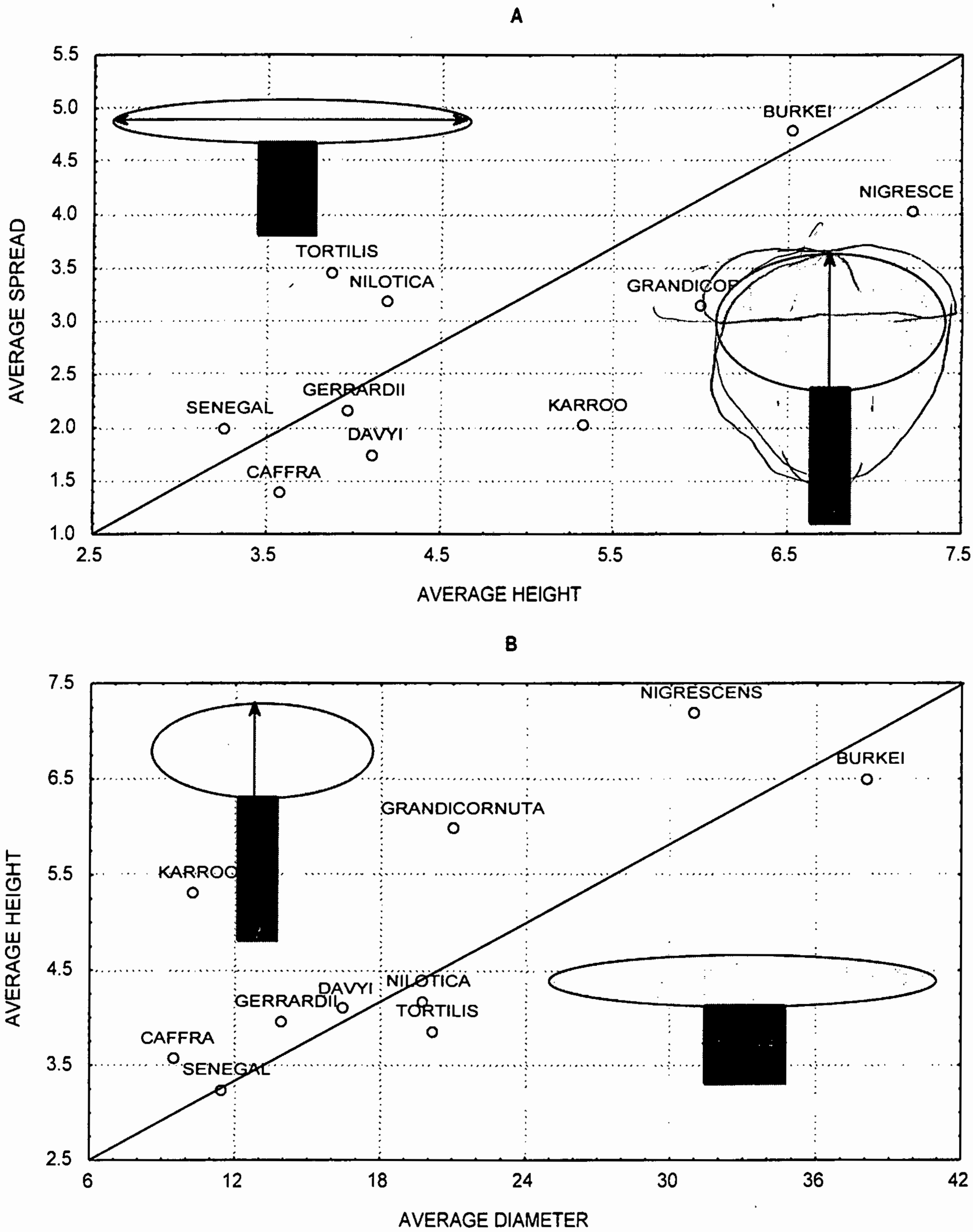

Figure 2: Average heights plotted against average diameters for all species measured (A). Average diameter against average heights for all ~~trees~~ (B). Line represents a 1-1 relationship and diagrams represent the type of shape represented by data points on that side of the line.

A. burkei is again tending towards measurements consistent with flat-toppedness. In order to clarify this allometry, a 3-dimensional graph was constructed using all three above measured variables as axes (Figure 3). This clearly demonstrates that the measurements we took were good enough to separate the flat-topped architecture from other acacia growth forms.

HERBIVORY:

If flat-toppedness is an anti-herbivory response then one may expect such species to have lower allocations to herbivore defence (since their architecture would be doing most of the 'work'). As a measure of this we looked at different aspects of spinescence. Figure 4(A), compares the size of the leaf to the length of the thorn (as a ratio). Plants with a low ratio *(A. grandicornuta)* have a leaf which is equal to, or smaller than the length of the thorn, indicating a well protected leaf. Those species which exhibit a high ratio indicate a small thorn relative to a large leaf. These species' leaves are not well protected from herbivory as the whole leaf protrudes beyond the protective 'basket' of thorns. Here we note the two flat-topped species near the low extreme, indicating a high allocation to herbivore defence.

In the same vein, a ratio of the distance between thorns to their length would give a surrogate measure of anti-herbivory allocation (Figure 4(B)). Those trees which are heavily protected (high allocation) would have large thorns close together, whereas poorly defended species should have small thorns far apart from each other. Note that *A. tortilis* is found near the extreme in favour of heavy protection. The only species to better *A. tortilis* in this respect is *A. grandicornuta,* a species named after its thorny

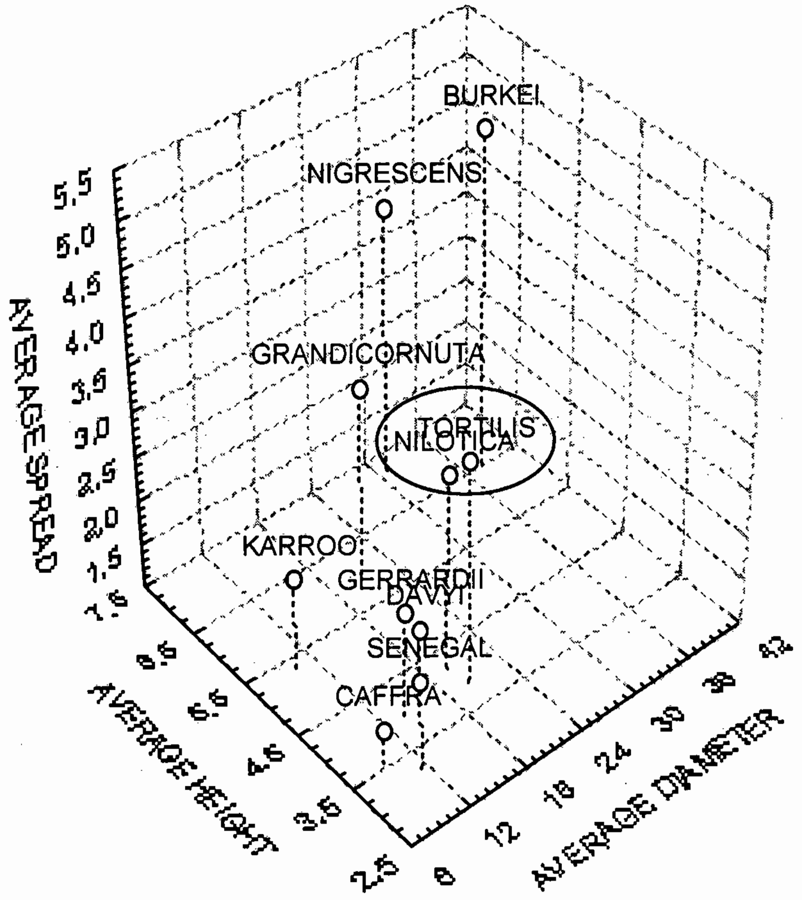

Figure 3: 3-Dimensional plot combining the data from Fig 2. A & B to highlight the difference between the flat-topped species and other architectures.

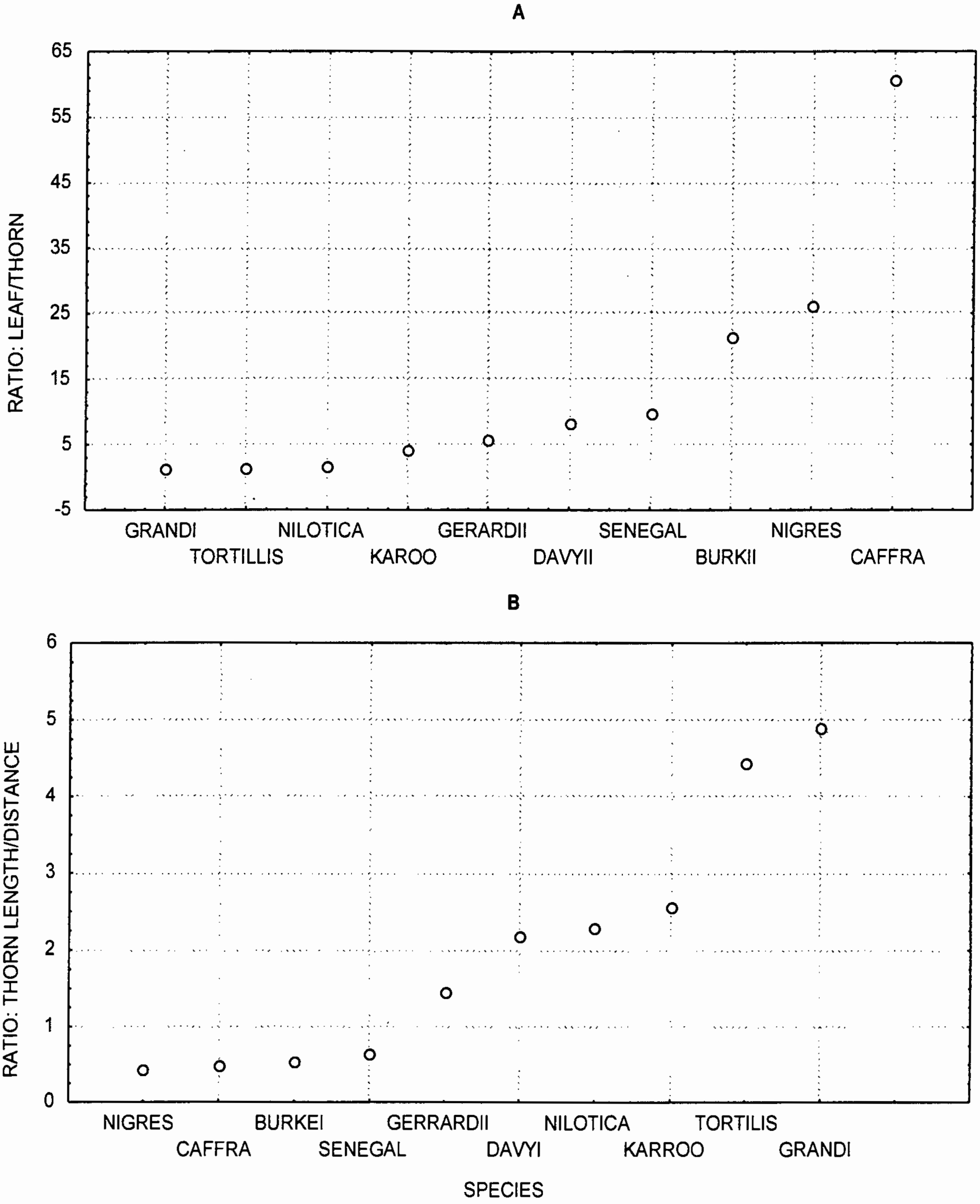

Figure 4: **A** shows, in ascending order, the ratio between leaf size and thorn size for the acacias we measured (a low ratio is indicative of a well protected leaf). **B** is an ascending plot of the ratio between thorn length and the distance between thorns (the higher the ratio the more protected the tree is against herbivore attack).

protection. *A. nilotica,* is also seen to be in the top 40%. The flat topped trees would then appear to be well protected against herbivore attack.

CANOPY EFFECT:

When comparing grass height across species and canopy position (Figure 5(A)), one notes the large difference between the height of grasses beneath *A. nilotica* trees and the grass found in the intercanopy spaces. We used the measure of maximum grass height for our results as not all measures of short (<10cm) grass infer lawn species. Some short grasses were the result of heavily grazed bunch-grass species (a 'bunch lawn'). Therefore by using the tallest measure across all species we try to prevent this effect from influencing the results (outside or underneath the canopy). The measure 'Outside' gives us an indication of what the grass cover would be like in the absence of animals. The average maximum grass height is shown for each region – North under the canopy, South under the canopy and East away from the tree. Note the large difference between the height of grass beneath *A. nilotica* trees and the grass found in their intercanopy spaces. The difference in grass height between the area outside the canopy and that underneath it would give a clearer indication of the effects of different trees on their understory (Figure 5(B)). This was calculated as 'East (outside) maximum', minus the average maximum height for North and South undercanopy positions. The line indicates zero difference between undercanopy and between-canopy grass height. Those species above the line show large positive differences, meaning that the grass is shorter underneath the canopy. In the case of *A. nilotica,* the grass is on average 35cm shorter underneath the canopy than in the open veld. Species below the line have grass which is, on average, longer underneath the canopy of the tree than

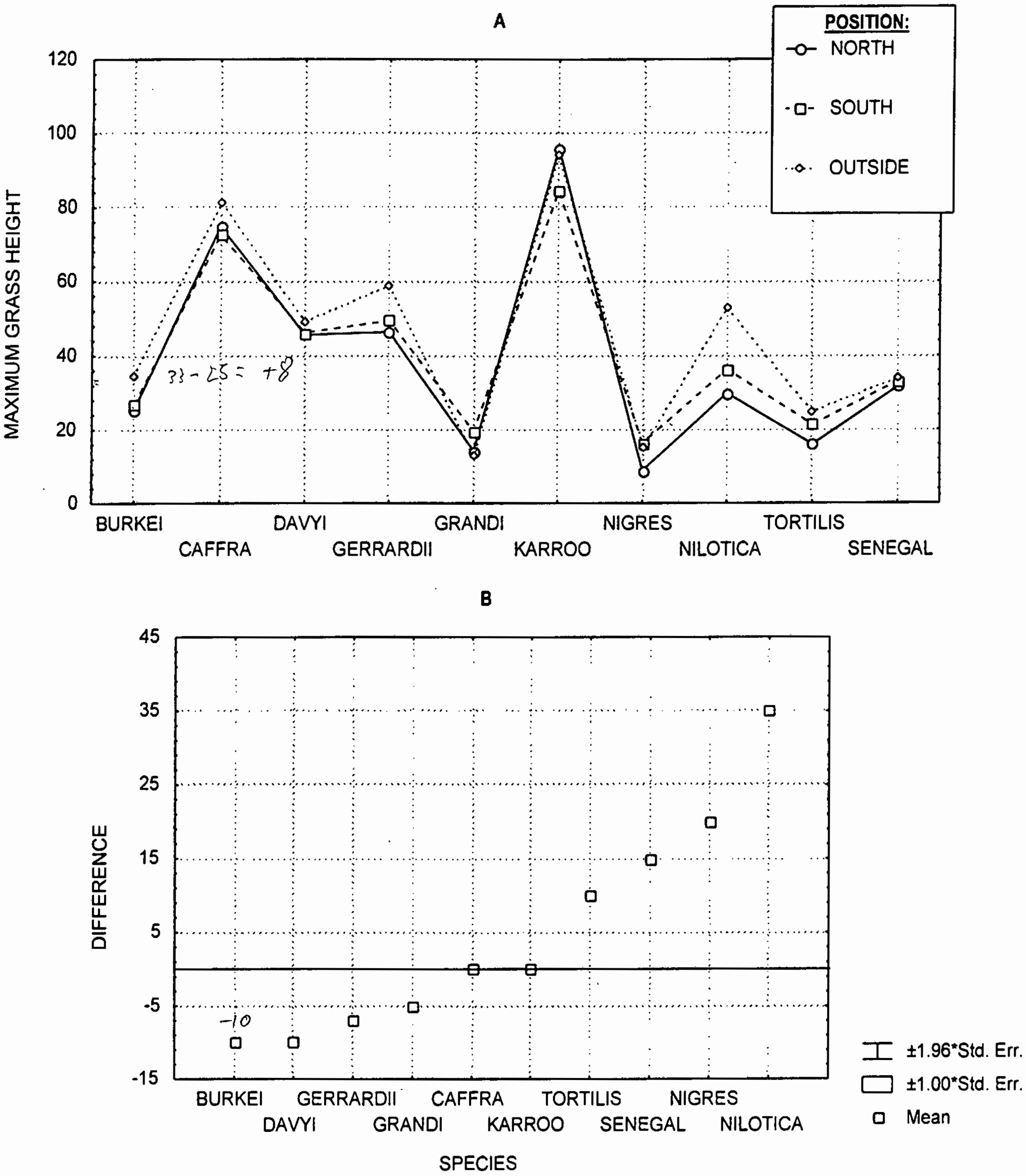

Figure 5: Graph showing the maximum grass heights under the three measured aspects of each canopy for all the species (F{18,678} = 1.39, p<0.127)(**A**). Graph showing the difference between the maximum grass height underneath the canopy of each species, and the maximum height outside their canopies (**B**). The line indicated zero difference. Those points above the line have taller grass outside their canopies than below.

– there is something wrong in (B)!
[illegible] have
positive differences

it is in the open veld. Of interest here is *A. burkei,* which showed up in the allometry to have been somewhat flat-topped, but here seems to have a positive influence on the height of grass below its canopy. This could have been due simply to the height of this species – it is possible that our measurements were less accurate for very tall trees. Alternatively, this species may be too tall to have an effect on the understory. Conversely and very importantly, both the flat-topped species demonstrate a negative influence on undercanopy grass height. — as do most of them!

Overall, there is a tendency for all tree shapes to negatively affect their undercanopy grass heights (see Figure 6(A)). Surprisingly, the values for North and South are also different from each other (Fig 6(A)). This means that the grass on the southern aspect of the canopy is more often longer than that under the northern aspect of the canopy.

HABITAT:

In what kind of landscape and habitat do we find the different species? One can see the differentiation between the species in terms of the kinds of grasslands they are most commonly found in (see Figure 5(A)). It is quite clear from this that *A. nilotica* is found in long grass. The mean grass height outside its canopy is just shorter than that for *A. gerrardii,* which is roughly second behind *A. caffra* and *A. karroo.* Referring to Figure 6(B), one again notes *A. nilotica* as being among the group of long-grass species (*A. caffra, A. karroo* & *A. gerrardii*). Here the flat-topped species even appears to inhabit longer grass than that of the known fire survivor, *A. davyi.* The data from Figure 6(B) supports the notion that flat-topped species are to be found in long grass.

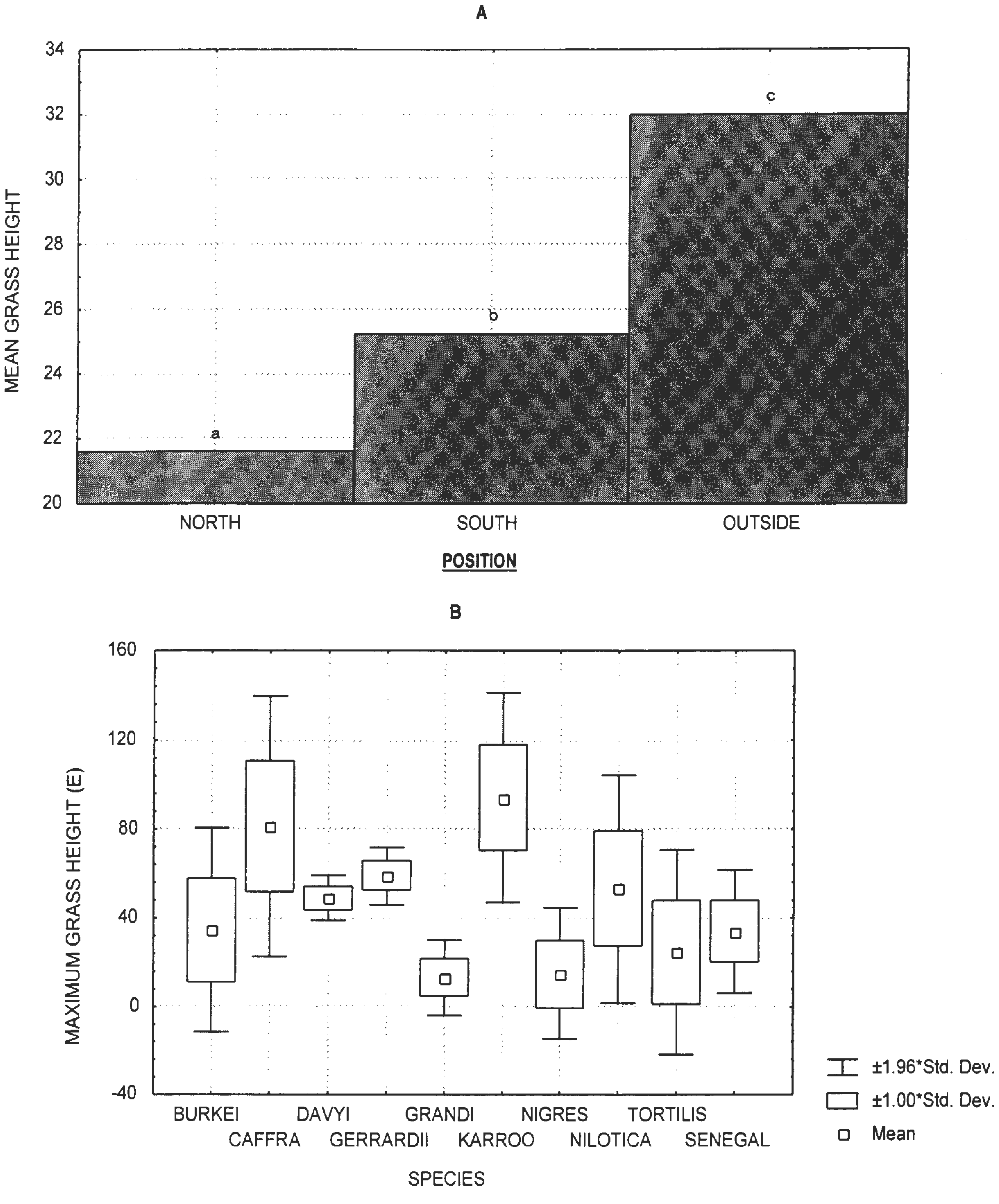

Figure 6: Mean grass height over all species for all three aspects. Small-case letters indicate statistically significantly different means (F{2,699} = 29.70, p<0.000) (**A**). **B** shows the means of the maximum grass height for 'East' - (outside the canopy) for all species.

FIRE:

Bark thickness is used to infer fire survivability. Our flat-topped trees are compared with a known post-fire canopy sprouter, *A. davyi*, in terms of bark thickness (relative to stem diameter). It is clear how neither species of flat-topped tree can compare in bark thickness to *A. davyi* (Figure 7). *A. nilotica* is the closest of the two but will be seen to be a very poor survivor in the following figures.

These next two figures are from the data collected at the burnt site. Figure 8 shows the percentage survival for each of three size classes within each species found. Labelled above each prominent peak is the response to the fire. One can see how only *A. burkei* and *A. nilotica* have plants over 5 meters which were unable to survive the flames. On the other hand, *A. caffra* was able to sprout after the fire with a 100% success rate, even when the parent plant had been shorter than 3 meters (effectively within the grass layer). Looking at fire response without the complication of height classes, we are faced with Figure 9. This figure shows the relative percentage responses of the five species encountered at the burnt site. From this graph one can distinguish the species quite clearly on the basis of their responses. *A. burkei* and *A. gerrardii* are clearly those which are able to sprout from the old canopy after the fire. *A caffra* and *A. karroo* are basal sprouters which experience very little or no fire-related mortality. *A. nilotica* on the other hand, is obviously very fire sensitive with more than 60% of observed individuals having succumbed (a population-threateningly high proportion). Mortality in this species is very high which suggests that it is poorly adapted to fire (confirmation that its relatively thin bark has limited fire-prevention capability). The other species observed, differed in their response but were clearly able to survive the fire, with mortalities low enough not to affect their populations.

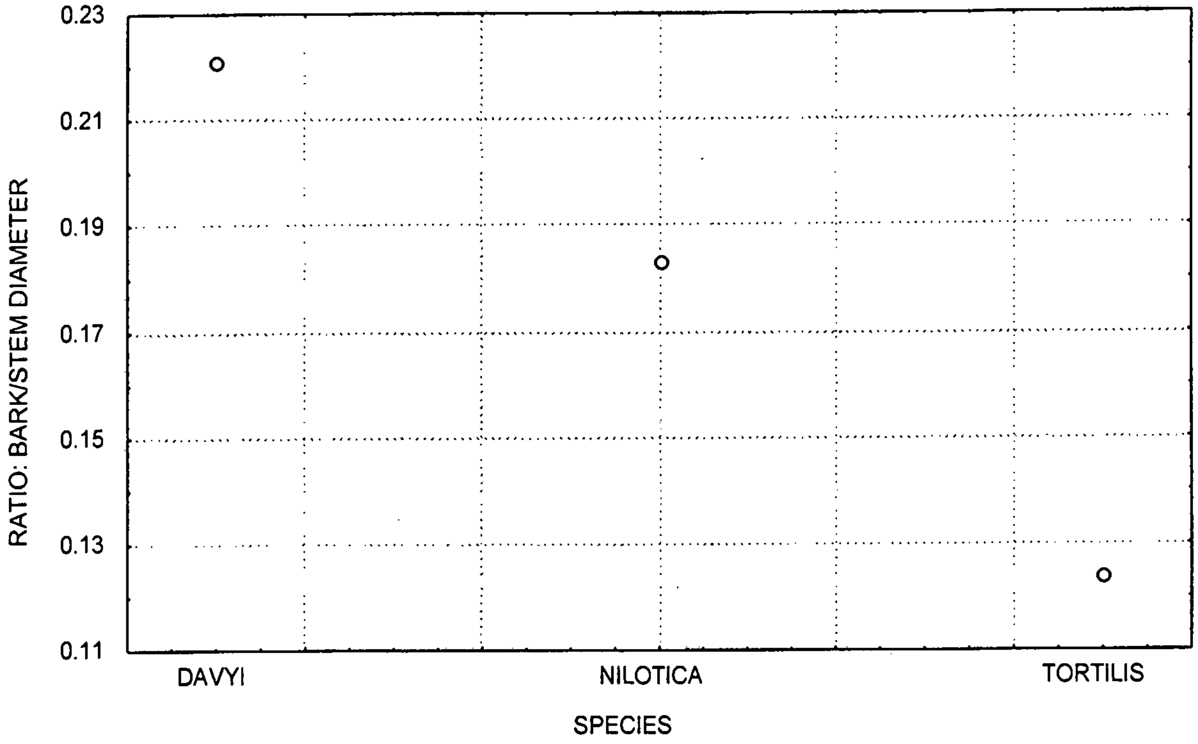

Figure 7: Ratio of bark thickness to stem diameter for known fire-surviving canopy sprouter *A. davyi* compared to that of our two flat-topped species.

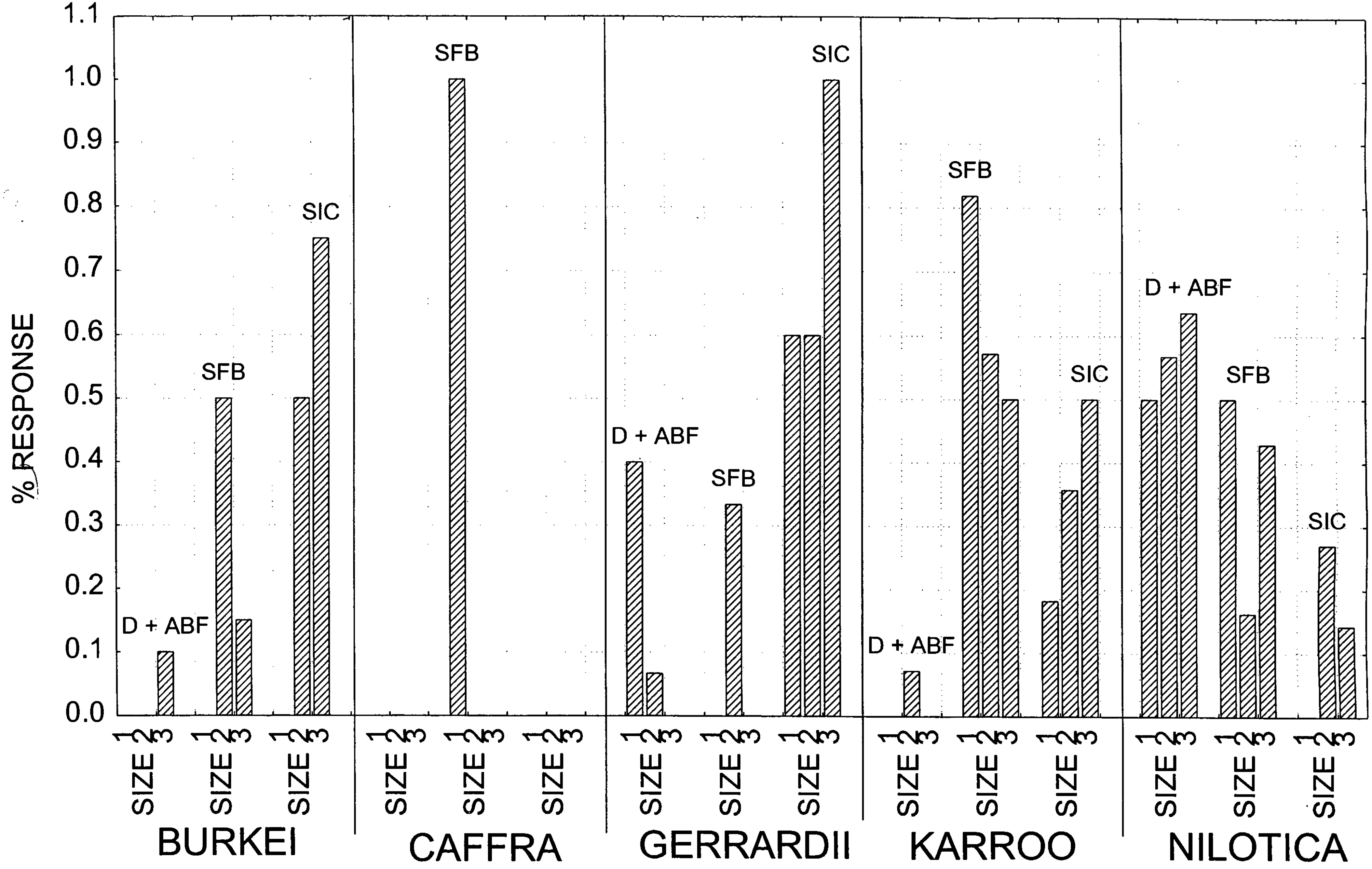

Figure 8: The response to fire by the five species at the site in terms of percentage response per size class per species (Size class **1** = < 3m; **2** = 3.25-4.75m; **3** = >5m). The graph is labelled with the abbreviations for the response categories (see Methods).

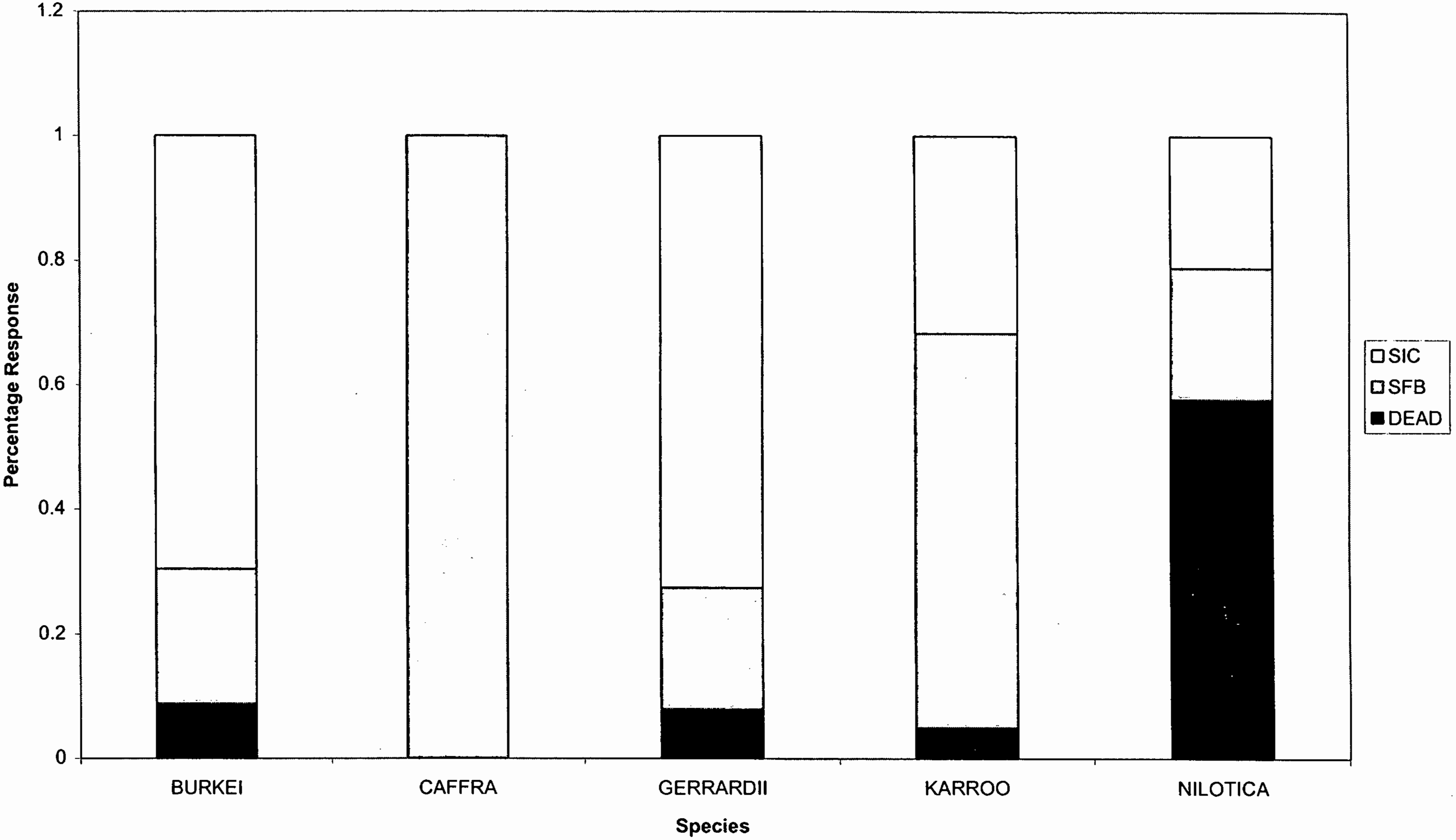

Figure 9: Percentage response to fire per species. Here each species is divided according to its response to the fire. (see Methods for the abbreviations of the response categories).

DISCUSSION:

Our results tell a very interesting story. Flat-toppedness as an architecture was nicely defined by our simple measurements and was shown to be different from other canopy shapes (Figs. 2(A),(B) & Fig 3). It is interesting to note that both *A. burkei* and *A. senegal* are also above the line indicating a measure of flat-toppedness. This may be due to the simplicity of our measure of allometry, especially when one considers that there are not only two possible growth forms of *Acacia*. In fact it is most likely that the cluster of *A. senegal, A. caffra, A. gerrardii* and *A. davyi* represent another type of as yet undefined architecture.

Herbivory and cost:

Not only do these diagrams separate the acacia species in terms of shape, but they also indicate a cost of this shape to the tree. These trees are disproportionately short for their diameter which indicates that they have a longer exposure to the 'danger zone' between fire and browsing animals. Furthermore, these flat-topped trees were found predominantly in areas of long grass (see Figure 6(B)). To survive in this environment, woody plants need to be able to survive in spite of fire and/or herbivory.

It would seem, though, that this crown shape is not necessarily an anti-herbivore mechanism. The leaves of both flat-topped species were very well protected by thorns. It may be argued that the length of the thorns is not all important, especially when it comes to browsers like the giraffe which uses its tongue to strip green vegetation from stems between long thorns. In this case, small backward-pointing hooks provide a greater defence. However, the thorns of *A. nilotica* are conspicuously backward facing and *A. tortilis* has a dual thorn strategy which includes hooks (common name, 'Haak-en-Steek' meaning hook and spike). If this canopy type is anti-herbivore, then why do these two flat-topped trees invest so heavily in thorny protection? Using information from a field-guide, one can see how the leaves of these trees are quite small in comparison with other leaves in the genus (Steyn 1994). Cooper and Owen-Smith (1986) found that this combination (spinescence and small leaves) was able to effectively deter kudus from extensive browsing This is a further indication that their shape is minimally effective against predation since they still have to invest in extra anti-predator defences. Gondwa (1997) concluded that *A. tortilis* has an inducible response of increased spinescence to herbivory. It seems wasteful that a tree should expend reserves on inducible anti-herbivore responses if the canopy shape was able to deter these predators. If this shape is able to reduce herbivory, it seems to be only weakly successful. A long-term study of herbivory on these trees would be needed to confirm our data, but as a surrogate measure of expenditure, our method strongly suggests that there is some other driving mechanism behind this unique shape.

Fire and cost:

In order to survive fires trees can do three things: They can concentrate on upward growth so as to escape vertically from the dangers of the flames (eg. *A. burkei* & *A. gerrardii*); They can invest in corky bark and re-sprout in the canopy after the fire has swept by (eg. *A. davyi*); or, they can be completely destroyed by the fire, only to sprout from lignotubers (eg. *A. karroo* & *A. caffra*). These strategies can be seen by the responses of the abovementioned trees to fire at the burnt site (see Figs. 8 & 9). *A. burkei* and *A. gerrardii* were clearly tall enough to have escaped the heat of the flames since most of the trees observed are sprouting in their canopies (70 and 75% respectively). The original trees of *A. karroo* and *A. caffra* were mostly destroyed in the fire. However, they were clearly unaffected by this as most (if not all) were sprouting from the base. It was typical to see numerous new basal shoots coming up near the old stem. It is also very evident that the flat-topped *A. nilotica* is incapable of dealing with fire, having experienced a significantly high mortality (60%). *A. tortilis* was not evident in the burnt site but has very thin bark relative to stem diameter (see Fig. 7), and so would presumably suffer the same fate as its other flat-topped cousin. It should strike the reader as strange how the flat-topped trees are so obviously unable to cope with fire, but that they tend to grow in areas of long grass. This counterintuitive notion suggests that there is some other mechanism at work selecting for this canopy shape.

The height-diameter and height-spread diagrams in figures 2(A), (B) & 3, combined with the knowledge that these trees succumb to fire and that they live in long grass, enables us to deduce a cost to the tree. These trees are not growing as tall as their counterparts in the long grass environment and so are unable to rapidly escape the fire vertically. Why then are they still found in this habitat since natural selection should have acted against them long ago?

It is fairly clear that this canopy shape is not a random event, but that it must be being selected for, and selected for rather strongly to offset the negative effects of cost.

Shade and Nutrients:

The trick of these trees is shade. This is hardly a surprising find since this concept was visited by Belsky *et al* (1993) and Weltzin & Coughenour (1990). However, these authors failed to find the indirect connection between shade and shorter grass, as I will discuss later. Shade underneath a canopy by itself does not seem to alter the grass height. One can see how in, Figure 6(A), the grass is shorter under the canopies of trees but longer under the southern aspect. If shade alone was causing grass to be shorter under the canopy, then it should follow that the grass on the southern side would be shorter than that facing the full sun at the north. It may in fact be that the shade provided to the southern aspect lowers evapotranspirational rates in the understory, which in turn elevates water use efficiency enabling the plants growing here to grow taller. This sentiment is mirrored by Belsky *et al* (1993), Scholes & Archer (1997) and Weltzin & Coughenour (1990), who all mention how shade lowers soil and plant leaf temperatures, thus making more water available to the understory plants. Interestingly though, Belsky *et al* (1993) found that soil moisture did not differ significantly between undercanopy positions and the open grassland when looked at over the long-term. This kind of microenvironment would perhaps be too shady for the bunch-grass species (*Themeda triandra, Hyparrhenia filipendula*), but may favour the shade tolerant species, *Panicum maximum*. *Panicum maximum* is able to grow fairly tall if unchecked by grazers. Still, there is clearly a big difference in grass height underneath the canopies of some trees when compared to open veld adjacent to them. Most prominent among these trees are our flat-topped species (most notably *A. nilotica* – see Figure 5(B)). So this canopy architecture has the effect of lowering the grass height underneath the canopies of the trees.

One could argue that it is a nutrient effect. This line of reasoning has also been considered by many authors (Belsky *et al* 1993, Roos & Allsopp 1997, Scholes & Archer 1997), who note the ability of these trees to enhance their understory nutrient status. This they see as being accomplished by litter fall and the increased cycling of nutrients associated with understory animal visitation. The raised nutrient status of the soil will then enable certain species to outcompete their neighbours resulting in a compositional change (if nothing else). Here it should be noted that Belsky *et al* (1993) found similar effects under both their study trees and concluded that the potential N-fixing capabilities of the Leguminous *A. tortilis* were either negligible or non-existent. This suggests that the effect then has something to do with the canopy alone, and is therefore not related to other species-specific factors.

Strangely enough, the height and composition of grasses beneath canopies was not uniform within species and distinct between species. In other words, sometimes the canopy did not seem to have the predicted effect. In the field it was not uncommon to see a flat topped tree with long grass underneath it. If the lowering of grass height was purely a canopy effect, one should never find a flat-topped tree with long grass under the canopy, as every canopy should produce similar effects. If the observed effect is not a species effect, then a secondary effect of canopy shape on understory is implied. What then is this second effect if shade and/or nutrients alone fail to explain the observed canopy effects?

Mutualism:

We propose that the grass height effect is the product of animals. By providing shade, the tree essentially incorporates Africa's large grazing herbivores into a mutualistic relationship. By resting and occasionally grazing beneath the canopies of flat-topped trees, the animals lower the height of the undercanopy grasses. Weltzin & Coughenour (1990) saw the savanna tree understory as 'an accessible and important microhabitat for grazers'. With this they almost reached the same conclusion as this study, especially when they noted the effects of shade produced by the trees. They mention how shade is sought by these herbivores which trample on the understory vegetation and raise the local nutrient pool with their urine and faeces. In this manner they act as an important understory disturbance, the effect of which is to lower the average grass height here. In their paper, they presume that the ability to tolerate herbivory and trampling is one of the less important characteristics of understory grasses. We believe that this is probably their single biggest advantage. These are the characteristics which allow lawn and/or shorter grasses to dominate beneath the canopy. This being the case, what are the benefits to the tree, since there are certainly costs to the tree associated with this canopy shape?

Why?:

We further propose that the effect of animals shortening the grass enables these trees to survive fires. When a fire next sweeps the landscape, it burns vigorously in the long grass but, because there is much less fuel in the shorter grass beneath the canopies, the fire is unable to burn vigorously here. In this way, the tree is spared the damaging effects of close encounters with fire. The cambium in the trunk survives the heat of the flames and the tree survives. Adding strength to this argument is the fact that the two flat-topped species we sampled are both animal-dispersed having relatively thick indehiscent pods which are high in nutrients (Coe & Coe 1987). These pods may then be another attractant to animals which would spend more time under the acacia's canopy foraging for the nutritious pods. This off-the-ground foraging by the animals may be very important to the tree by further shortening the undercanopy grass and by removing thicket and forest seedlings (accidentally consumed along with the pods, or trampled on). So these trees are able to protect themselves from the negative effects of their shade in terms of successional pressure from these shade-tolerant species. The seeds of these trees rely on the animals for their dispersal as they are heavy and not readily wind dispersed, as is the case with most of the dehiscent species of acacia (Coe & Coe 1987), further evidence of the animal-plant mutualism.

The flat topped species are also both only weakly deciduous, meaning that they provide a measure of shade even in the dry winter months. This may be their most important trait, as the stoloniferous lawn species cannot invade bunch grass areas unless individual bunch grasses are dead and their mass of root material destroyed (Bond *pers comm.*). So at the time of year when these bunch grasses are most stressed due to drought, they are less likely to be able to stand the pressures of herbivores trampling and perhaps also eating them (the hoofed herbivores concentrate a large weight through their hooves which may be able to destroy the root masses of bunch grasses). This animal-tree mutualism explains many of the problems with understory differences in grass height away. The tree is shaped as it is in order to maximise the shade area beneath itself and thus encourage animals to dwell there. Animals though, do not choose which species of tree they will rest under (although the flat-topped acacias try their best to be the shade-plant of choice). This goes a long way to explaining why one sometimes finds flat-topped trees with long grass under their canopies, and short grass under the canopies of trees that are not flat-topped. Why else would one find these differences between trees of the same species close to each other when surely all other aspects concerning canopy and possible soil differences would be nil? Animals will rest under any tree which provides them with shade and will perhaps choose another crown shape in the absence of flat-tops. Therefore, while the flat-topped acacias try to make their understory more attractive to large animals it is still possible under this hypothesis to find shorter grass under the canopy of any tree which is not flat topped, so long as it provided enough shade.

CONCLUSION:

Flat-topped trees are sensitive to herbivory and spend much energy attempting to deter predation. Their canopy shape is not an effective anti-herbivore defence. These trees are very sensitive to fire and yet live in areas of long grass. We conclude then, that their canopy shape is an anti fire mechanism. This is a secondary affect as the existence of a canopy and its shape are unable to alter grass height beneath the tree. Having said that, species composition of the understory is markedly affected. The shade and grazing opportunity provided by the canopy encourages large mammalian herbivores to spend time under these trees. These animals keep the grass markedly shorter under the tree through grazing and trampling. This short grass protects the tree from fire as it presents a buffering, low-fuel zone around its base. Fires burn up to the short grass but are unable to create enough heat near the base of the tree to damage its sensitive cambium. These trees are also animal dispersed, and their nutritious pods provide further incentive for animals to visit the undercanopy environment. In this way the tree employs animals into a mutualistic relationship – shade and high-nutrient food, for seed dispersal and fire protection.

ACKNOWLEDGEMENTS:

I thank my supervisor, Jeremy Midgely for his help and guidance. Thanks also to Dave Balfour and the staff at Hluhluwe-Umfolozi Park. Special thanks to Gonzalo Aguilar, for the much appreciated computer advice at all hours of the night. I also thank the UCT Botany Department for the funding and facilities provided.

REFERENCES:

Belsky, A., Mwonga, S., Amundson, R., Duxbury, J., Ali, A. 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. *Journal of Applied Ecology.* 30: 143 – 155.

Brooks, P. & MacDonald, I. 1983. The Hluhluwe-Umfolozi Reserve: an ecological case history. In: Management of large animals in African conservation areas. (ed) N. Owen-Smith. Pp 51 – 78, Haum Educational Publishers, Pretoria, South Africa.

Brown, W. 1960. Ants, Acacias and browsing animals. *Ecology* 41: 587 – 592.

Coe, M. & Coe, C. 1987. Large herbivores, acacia trees and bruchid beetles. *South African Journal of Science.* 83: 624 – 635.

Cooper, S., Owen-Smith, N. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia.* 68: 446 – 455.

Gondwa, J. 1997. Physical and chemical responses of juvenile *Acacia tortilis* trees to browsing. Experimental evidence. *Functional Ecology.* 11: 106 – 111.

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

Scholes, R. & Archer, S. 1997. Tree-Grass interactions in savannas. *Annu. Rev. Ecol. Syst.* 28: 517 – 544.

Steyn, M. 1994. S.A. Acacias: Identification Guide. Conservation Press. Johannesburg, South Africa.

Whately, A. & Wills, A. 1996. Colonisation of a sub-tropical woodland by forest trees in South Africa. *Lammergeyer.* 44: 19 – 30.

Weltzin, J. & Cougenour, M. 1990. Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. *Journal of Vegetation Science.* 1: 325 – 334.