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***The adaptive geometrey of savanna trees:***

*a comparative study of the architecture and life history of Acacia karroo Hayne. in savanna, forest, and arid karoo shrubland environments.*

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## Abstract

Various morphological and life history attributes of *Acacia karroo* Hayne. were investigated in five populations from three environments in South Africa: forest (Cape Vidal, Natal), arid shrubland (Prince Albert, karoo) and savanna (Hluhluwe-Umfoloji Game reserve and Itala Game reserve, Natal). I aimed to elucidate on the distinctive characteristics required for trees to survive in savannas. The combination of frequent fires and intense herbivory in savanna environments creates a disturbance regime not encountered by trees in other situations and it was expected that *A.karroo* would display specific adaptations of growth form, life history, and reproductive ecology - adaptations which would reflect the strong selective pressure imposed by fire and herbivory on juvenile savanna trees to grow above flame height and browse limit in order to recruit into the mature canopy.

*A. karroo* in savannas was found to have an unbranched, vertical growth form, and is thus maximising height gain. Reproduction was delayed until the trees were above the reach of flames and herbivores. Savanna *A.karroo* trees had fewer, smaller spines than trees in the other two environments, even though spines are generally considered to be effective in defense against mammalian herbivores. It is therefore suggested that a combination of low 'apparency' to browsers and rapid growth rate is an effective herbivore avoidance strategy in conditions where the need to escape from the fire trap makes a trade-off of growth rate for defensive structures unacceptable. The architecture of mature savanna trees reflects their history of rapid growth in earlier stages and they have smaller canopies, and thus lower reproductive capabilities, than equivalently sized trees in other environments.

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## Introduction

Trees are large, long-lived organisms which persist and maintain themselves in the environment over long periods of time. Two things must therefore be kept in mind when considering their life histories:

- 1: Trees grow through a series of size and developmental stages during which they are under a variety of environmental stresses. Each stage must be physiologically and ecologically competent (Crawley 1997), and developmental constraints imposed at earlier stages of growth will effect the architecture of the mature tree.
- 2: they are potentially able to partition the functions of carbon gain, growth and reproduction in time.

Much of the literature on tree life histories is related to tolerance of stresses such as light and water limitation in the early life history stages (Pascala- in Crawley 1997, and Halle et al 1978). However, trees also exist and flourish in savanna environments where they are exposed to other stresses such as injury from herbivores and from fires. These 'disturbances' are very different from the more long-term 'stresses' of light and water, and it would be expected that trees in savanna habitats would have evolved specialised life histories. The research which has been done into savanna trees certainly suggests that they are influenced by the need to resist/escape from herbivory and fires (Gignoux et al 1997, Bond 1997, Pellew 1983).

Thus it would be very valuable to compare tree life histories in environments where different combinations of environmental factors are operating, but the suites of species found in forests, savannas, and arid areas are generally too different to make this practicable. However, the species *Acacia karroo Hayne*. is an exception. Its distribution ranges from coastal dune forests of Natal, through mesic savannas, to arid karoo environments. It displays a variety of ecological 'types' across these environments (Swartz 1982) but as genetic exchange does seem to occur (Brain 1991) it is still regarded as a single species. It can therefore be assumed that any differences in its biology and ecology will be related to the environmental factors which are dominant in the different environments.

This study therefore aims to

1: Identify characteristics of architecture, life history, and reproductive ecology which allow a tree to survive in environments where it is exposed to injury from fire and herbivores.

2: Assess the trade-offs which are involved in these life history strategies. Survival in these environments requires trade-offs in resource allocation, architecture, photosynthetic ability and thus ultimately reproductive success.

### ***Theoretical background***

#### **The savanna environment**

As Gignoux et al (1997) and Trollope (1984) point out, there is extraordinarily little work on the population biology of savanna trees, compared with the information on tropical forests (Hubbel & Foster 1986), and little attention has been given to what unique attributes are required for a tree to survive in savannas. Savanna biomes are characterised by a tree-grass mix, and juvenile trees are in competition with grass - a very different life form, with very different ecological characteristics (Knoop & Walker 1985, Smythe 1997). Grass does not only have a competitive effect on trees. The continuous grass layer quickly builds up a highly flammable understory and causes very frequent fires which also influence community dynamics (Menaut et al 1990).

Herbivory is something experienced by plants in most environments. However the distinctive large vertebrate herbivores in savannas have been shown to be driving forces in the system, moulding community structure and population biology (Pellew 1983, Dublin et al 1990). The type of herbivory in savannas is also different. As well as normal leaf browsers, savanna plants are exposed to more destructive feeders like rhinos, elephants and giraffes (Emsley 1994, Pellew 1983). Thus the selective regime imposed by a combination of frequent fires and intense mammalian herbivory is unlike anything trees are exposed to in other environments and must have consequences for the life histories of savanna trees.

#### **Fire as a selective force**

Disturbance frequency is a very important factor for a tree, which must build and protect a permanent structure which will persist through many disturbance events (Westoby 1997). Fire in savanna is one of the most frequent disturbances

experienced by trees (every 1-3 years in mesic savannas), and often destroys the entire above-ground component of a small tree (Bond 1997). However savanna fires, being fuelled by grasses, are generally surface fires with a maximum flame height of 2.5-3m (Trollope 1984). A tree therefore needs to grow through this 'grass layer' and get its terminal buds above flame height in order to become part of the mature canopy (Bond and van Wilgen 1996). Gignoux et al (1997) identify two strategies that a seedling might display to achieve this end. It could slowly grow a fire-resistant trunk, protecting its buds, incrementally adding height between fires (stay and resist strategy); or it could resprout from base after a fire, and grow tall rapidly in order to be above flame height before the next fire (escape strategy). *A. karroo* in savannas is showing an 'escape' strategy: its entire above ground parts are killed by fire and it resprouts basally and has a very rapid growth rate (Bond & Maze- unpublished)

The constraints of this strategy in terms of resource allocation and architecture must be very great. Unless a tree can get above flame height before the next fire it will have to start all over again, so it is expected that all resources will be channelled into height gain, creating very different trees from those in forest and arid environments, where seedlings and juveniles are shaped by the need to compete for light, by water stress, and by defence against herbivores.

#### Herbivory as a selective force

Traditionally trees allocating resources to herbivore defences are considered to be trading off growth rate against defence (Herms & Mattson 1992). This must create a conflict for savanna trees, where height gain is such a priority, and herbivory so intense. Is *A. karroo* allocating resources to herbivore defences, and if so, what effect does this have on its ability to escape the fire trap?

Insect herbivory is not discussed in this project- I was unable to assess the relative differences in insect herbivory between different environments, which, by default, I consider to be similar in all environments. Elephant herbivory too is not included, because its effects are distinctive, and it acts on mature trees rather than juveniles.

The browse limit for most mammalian herbivores is about 2.5-3m (Pellew 1983). Thus herbivory, as well as fire, is a stress which is imposed on earlier stages of tree growth. Tannins, spine length and spine density have all been cited as important in

detering mammalian herbivores (Cooper and Owen-Smith 1986, Rohner & Ward 1997).

When considering mammalian herbivory it is important to distinguish between the costs of having leaves removed and the costs of having growing points and structure damaged (Gowda 1997). Trees need to defend themselves against both injuries, but browsing of shoot tips is likely to be much more damaging because it directly retards growth and affects structure. Tannins only protect leaves, but spines, if the tree is highly branched, should be effective in protecting new shoots and preventing structural damage (Milton 1991).

As mentioned above, the type and intensity of herbivory in savannas is different from that in other environments. It is possible that *A. karroo* is displaying different defence strategies in each environment.

## Methods

### Study sites

Five populations of *A. karroo* were sampled, three from a savanna environment, and one each from a forest and an arid karoo environment. Table 1 summarises the relevant details of each sample site.

Table 1: Details of the five sites where *A. karroo* populations were sampled

|                                | forest  | arid karoo                     | shrubland: karoo  | lowland savanna: Hluhluwe-Umfolozi reserve   | upland savanna  |
|--------------------------------|---|--------------------------------|---|--|---|
|                                | Cape Vidal  | Prince Albert                  | Magangene   | Masundwini                                   | Itala Game reserve  |
| Co-ordinates                   | 32° E<br>28° S                                    | 21° 46' 55" E<br>33° 13' 53" S | 32° 07' E<br>28° 04' S                                  | 31° 55' E<br>28° 13' S                       | 31° E<br>27° S  |
| Sampling dates                 | June 1998   | September 1998                 | June 1998   | June 1998                                    | June 1998   |
| Altitude                       | 0m  | 400-600m                       | 200m  | 380m   | 850m  |
| Max temperature <sup>(b)</sup> | 28°C  | 32°C                           | 28°C  | 28°C   | 26°C  |
| Min. temp. <sup>(b)</sup>      | 10°C  | 5°C                            | 10°C  | 10°C   | 6°C   |
| avg. T <sup>(b)</sup>          | 21°C  | 18°C                           | 21°C  | 21°C   | 20°C  |
| Average rainfall               | >1200mm <sup>(b)</sup>                            | <100mm <sup>(b)</sup>          | 985mm <sup>(a)</sup>                                    | 750mm <sup>(a)</sup>                         | 900mm   |
| Fire history                   | no fire   | no fire                        | 1 in 2 years  | 1 in 3 years                                 | 1 in 2 years  |
| Browsers                       | Bushbuck (500)<br>Kudu (1500)<br>Black rhino (12) | Goats<br>Kudu                  | Impala <sup>(a)</sup><br>Kudu<br>Giraffe<br>Black rhino | Impala <sup>(a)</sup><br>Kudu<br>Black rhino | Impala (1800)<br>Kudu (550)<br>Eland (130)<br>Giraffe (180)<br>Black rhino (51) |

References: a- Brookes and Macdonald (1983)

b- Schultze (1997)

### Growth form

At each site 5-10 trees were sampled from each of four size classes: 0-1m 1-3m, 3-6m and >6m. These size classes were chosen with the savanna situation in mind. Trees are faced with different ecological conditions in each of these height classes and it was expected that they would show different resource allocation patterns and growth forms. There were no individuals greater than 5m in the lowland savanna-2 population so there is no data for the largest height class at this site.

### Whole plant measurements

The general shape of each tree was recorded by measuring:

- number, size and angle of basal stems
- height of first branching
- canopy area at widest point

These measures are demonstrated graphically in figure 1.

To this was added an estimate of total leaf area: a unit branch was taken and the number of these units contained in the tree was estimated. The leaves from this branch were dried and weighed so that a leaf area estimate value in g dry weight could be obtained for each tree. Data gathering was done in winter when leaf area was not at its maximum, and *A. karroo* is winter-deciduous in arid areas (Milton 1987) so while this measure is useful for comparing trees within populations it is less valuable between populations.

### Shoot structure

This was measured on a randomly chosen branch of standard basal diameter 1.2cm. The length of the longest branch (shoot length) and the total length of all the shoots on the branch unit (total length) were measured. These two values can be expressed as a ratio of total length:shoot length (see figure 1) giving an indication of the degree of branching shown by the tree.

Highly branched trees are maximising photosynthetic area and also restricting access of mammal herbivores. Less branched trees are maximising shoot extension (height) at the expense of these factors. Branch ratios were therefore taken above and below 3m in each environment.

### *Response to injury:*

shoot structure and growth under intensive herbivory was investigated on a grazing lawn at Hluhluwe-Umfolozozi reserve. The trees in this environment had been exposed to intense browsing pressure for an extended period of time. A comparison was made between *A. karroo* and *A. nilotica* (a co-occurring species with a much slower growth rate- Smythe 1997). For trees over a range of sizes the number of growing points (shoot tips) and the number of obviously browsed shoots (bite points) was counted at three heights: below 1m, 1-2m and above 2m.

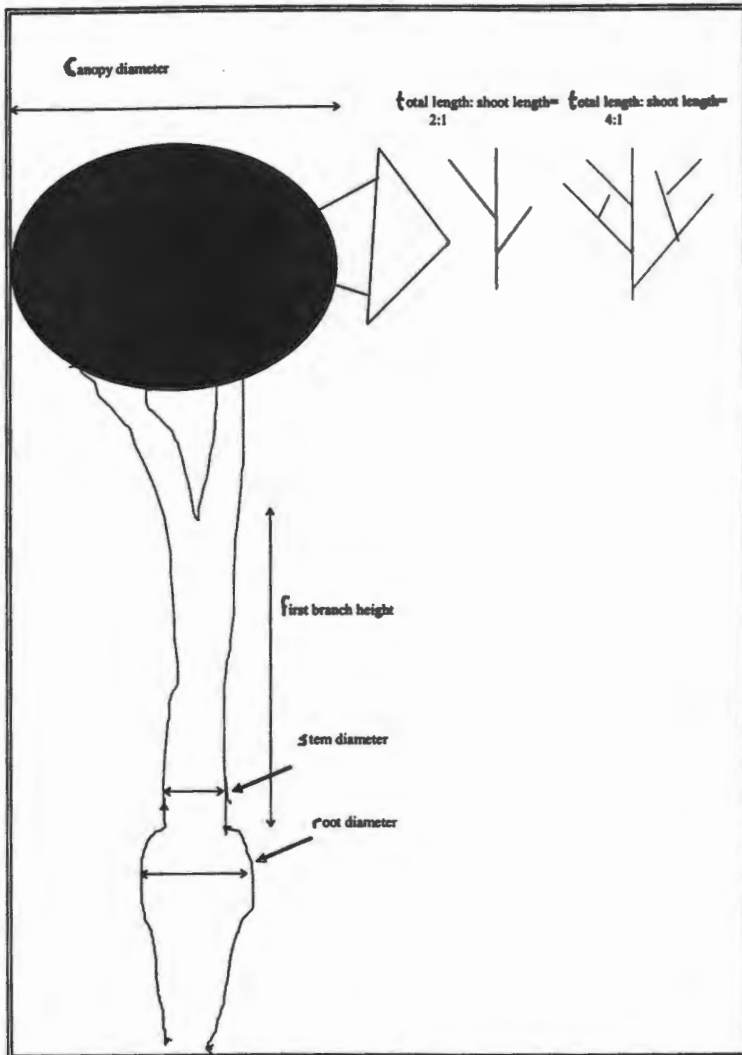


Figure 11: Diagram showing the various growth form measurements taken for each sampled tree. The morphological significance of the branching ratio is also illustrated.

### Root structure

The roots of each sampled tree in size classes 1-3 were excavated to about 40cm, giving a total of more than 100 trees excavated over the study sites. The widths of the stem at ground level, the root base just below the surface, and the main root at 20cm depth were measured. It was also noted how many lateral roots were visible.

### *Response to injury: root reserves*

A sample of root tissue from within the first 10cm was taken from each tree. For younger trees the entire root was taken, in older ones it was only possible to take a sample from the outer few cm of the stele. The outer bark was removed from these samples and they were dried at 70°C, ground and analysed for starch using a phenol-sulphuric acid colorimetric method (Buyse and Merckx 1993). Some loss of starch due to respiration of the roots is likely to have occurred because they were not dried immediately but this is assumed to have been constant for all sample populations.

### **Defences**

#### Defences against herbivory

It is not easy to get a good indication of the way in which plants are defending themselves against herbivory. The relative importance of chemical and structural defences and the difficulty in assessing the damage done by different kinds of herbivory all complicate the problem (Rohner and Ward 1997). Because of the constraints of this project, tannins and leaf defences were not considered. Allocation to herbivore defences was assessed by measuring spines. On each tree a randomly selected branch was measured for:

1. spine density (number of spine pairs per cm). On one shoot total spine number and shoot length were measured. The length of 11 spine pairs was another method used. These two methods gave similar results (t-test, dependent samples,  $t_{(47)} = -1.76$   $p < 0.05$ ).
2. average spine length. This was estimated for one shoot. The size of spines on a single shoot is very variable. I used an estimated average length because I was less interested in the variation on this scale than on larger-scale variation at

different heights and between entire trees. A check on this subjective estimate was performed on the karoo population where exact lengths of every spine on a branch were averaged and compared with the estimates for the same population and size class. There was no significant difference between these two averages (Mann-Whitney-U  $Z_{(5,26)} = 0.86$ ,  $p > 0.05$ )

3. Average maximum leaf length. This was estimated in the same way as spine length because it has been suggested that the utility of spines lies not only in their length but in their length relative to leaf length (Rohner and Ward 1996).

### Defence against fire

Bark thickness can be used (in combination with stem diameter) to assess a tree's 'intrinsic' resistance to fire (Gignoux et al 1997, Gill and Ashton 1968). Fires are hottest in the first 50cm above ground level (Gignoux et al 1997). Therefore bark thickness and stem diameter were measured at 50cm above ground level. Bark thickness was measured to 0.5mm accuracy with callipers. Bark was considered to be all tissues external to wood (sensu Hedge et al 1998).

### ***Population biology***

#### Demographics

The size structure of the different populations was obtained by walking a number of straight line transects through the communities and noting the height of any *A. karroo* trees within 1m on either side of the transect. The upland savanna population (Itala game reserve) was not sampled. At least 50 trees were sampled at each site.

#### Reproduction

Reproductive allocation was measured by estimating the number of pods. *A. karroo* retains its pods on the tree so this was a reliable measure of the reproductive effort of a tree for 1998. Seeds were also collected from each environment and weighed.

#### ***Controlled growth experiment***

Much of the theory involved in this project assumes that the differences seen in the various environments are genetic rather than environmental. This was demonstrated to a certain extent by Swartz (1982), but detailed information on allocation patterns under controlled conditions was not available. Plants from the arid shrubland,

lowland savanna, and forest environments were therefore grown from seed in a controlled greenhouse conditions to test this assumption.

Seeds were scarified for 3m and then germinated in at 25°C in germination chambers. As soon as possible after germination one seed from each population was planted in pots of river sand (30cm diameter x 50cm depth). Soil from the roots of an *A. karoo* tree from Kirstenbosch was added to each seed to aid nodulation. It was assumed that no root competition would occur during the experiment because in a similar experiment with 5 trees in the same sized pots no meeting of root systems was observed after one year.

The seedlings were watered every 3-4 days with 1/2 strength hoagland's solution. After 3 months the seedlings started showing signs of nitrogen deficiency and it was assumed that their nodular system had not developed. Therefore nitrate and ammonium were added to the nutrient solution. Every 1-2 weeks the pots were rotated and moved around to avoid biases based on light availability. From the 8th of July height measurements were taken every few weeks to monitor the growth patterns of the seedlings.

Seedlings were harvested after 129 days (4.5 months) and compared in terms of:

***shape:***

Stem length, root length, root diameter (in relation to stem diameter), length of all spines, and leaf area were measured for each seedling.

***carbon allocation:***

Plants were then divided into root, stem, leaves and spines. These were dried for 24 hours at 80°C and weighed.

***Data analysis:***

Methods for data analysis follow Zar (1996), using STATISTICA (version 5) software. Where the assumptions of equal variance and normality were not met the data was either logged, or equivalent non-parametric tests were run. Tukey's HSD post hoc comparison of means was run after all ANOVAS, and when the non-parametric Kruskal-Wallis test returned significance this was also investigated with Tukey's HSD test.

## Results

### *Growth form*

#### Whole plant measurements

Table 2 presents a summary of the growth form data for each size class in each environment. This is displayed graphically in Figure 2. The differences between environments are especially noticeable in stages 2 and 3.

#### Shoot structure

Branching ratios below 3m differed significantly between the environments (ANOVA  $F(4,93)=29.78$   $p<0.01$ -logged data). Savanna forms showed the least amount of branching (Figure 3) and forest forms the most. Between the three savanna forms, lowland savanna-2 was significantly less branched than upland savanna or lowland savanna-1 (which were not significantly different from each other).

It is interesting to note how branching changed above 3m. In the forest and arid shrubland (karoo) populations trees are slightly less branched while savanna forms branch more. These differences are not significant however. Also, above 3m the differences between environments are not so apparent- while they were significant (Kruskal Wallace  $H(3,N=40)=8.27$   $p<0.05$ ) a Tukey's HSD post hoc test showed that the only differences were between the extremes (forest and lowland savanna 2).

Figure 4 shows this branching pattern over the size classes. Forest trees remain highly branched throughout growth, karoo individuals are highly variable, and savanna size class two and three are the least branched.

#### *Response to injury:*

Table 3 shows the average number of shoot tips (potential browse points) and number of bite points (previously browsed shoots) for *A. karoo* and *A. nilotica* trees under intensive herbivory at Hluhluwe-Umfolozi reserve. Data is shown at three heights and for trees less than a meter tall, 1-2m tall, and greater than 2m.

The average number of shoot tips for each bitten shoot is also indicated.

A value greater than 1 suggests

- 1- that a tree is not eaten often and/or
- 2- that a tree branches in response to herbivory (initiates more than one auxiliary bud- Crawley 1997).

Values less than 1 suggests

- 1- that a tree is highly edible
- 2- that a tree's response to herbivory is not lateral branching.

Table 3: The average number of shoot tips (potential browse points) and number of bite points (previously browsed shoots) for *A. karroo* and *A. nilotica* trees under intensive herbivory at Hluhluwe-Umfolozi reserve. Data is shown at three heights and for trees less than a meter tall, 1-2m tall, and greater than 2m.

|          | no. of shoot tips<br>(median of 10 values) |      |        |      |           |      | no. of bite points<br>(median of 10 values) |      |        |      |           |      | average number of shoot<br>tips for each bite point |      |        |      |           |      |
|----------|--|------|--------|------|-----------|------|---|------|--------|------|-----------|------|---|------|--------|------|-----------|------|
|          | <1m trees                                  |      | <1m>2m |      | >2m trees |      | <1m trees                                   |      | <1m>2m |      | >2m trees |      | <1m trees   |      | <1m>2m |      | >2m trees |      |
|          | A.k.                                       | A.n. | A.k.   | A.n. | A.k.      | A.n. | A.k.  | A.n. | A.k.   | A.n. | A.k.      | A.n. | A.k.  | A.n. | A.k.   | A.n. | A.k.      | A.n. |
| below 1m | 3  | 21.5 | 1      | 14   | 0         | 5    | 1.5   | 3.5  | 3      | 9    | 3.5       | 12   | 1.3   | 7.3  | 0.5    | 3.5  | 0.3       | 0.9  |
| 1-2m     |  |      | 5      | 35   | 6.5       | 30   |   |      | 7      | 11.5 | 7         | 14   |   |      | 1.0    | 3.1  | 1.9       | 3    |
| above 2m |  |      |        |      | 8         | 16   |   |      |        |      | 2         | 0    |   |      |        |      | 1.9       | ~    |

### Root structure

In Figure 5 differences in root and stem volumes (indicated by area differences above and below soil surface) are shown across environments for each size class (significant differences indicated- Mann-Whitney U). Where a tree was multi-stemmed each stem area was calculated separately and then summed. In the first two size classes it is clear that the savanna forms have much larger root bases than their above ground volume would predict.

### *Response to injury: root reserves*

Analysis of the starch content in the roots did not give very interpretable results. Figure 6 shows average starch concentrations for each environment. The three savanna populations have markedly different concentrations and the variance is very high. Statistical tests showed the corridor population to be significantly different from all other populations and the karoo to be different from savanna forms, but not the forest form. (ANOVA  $F_{(3,70)} = 33.69$   $p < 0.01$ )

## ***Defences***

### **Defence against herbivory**

Spinescence was analysed for differences above and below 3m within each environment and for differences between different environments at these heights. The data is summarised in Figures 7-9.

#### ***Spine length (Figure 7)***

Spines are longest in arid shrublands and smallest in savanna environments. The forest, karoo and savanna environments are all significantly different from each other, and the three savanna populations are similar to each other (ANOVA logged data,  $F_{(4, 112)} = 17.49$   $p < 0.01$ ). Above three meters these differences between environments are not so apparent - only the upland savanna form is significantly different from the rest (Kruskal Wallace  $H(3) = 8.096$ ,  $n = 35$   $p < 0.05$ )

spine length seems to decrease above 3m within each environment but this was only significantly different in the arid shrubland and upland savanna forms (T-test, independent samples, arid shrubland  $t_{(37)} = 2.27$  upland savanna.  $T_{(28)} = 4.11$   $p < 0.01$ ).

#### ***Spine density (Figure 8)***

The length of spines is inversely related to spine density ( $r = -0.35$ ,  $p < 0.01$ ) However the differences between environments in spine density were not so apparent. Only upland savanna and arid karoo shrubland were significantly different from each other below 3m (Kruskal-Wallace  $H(4) = 14.24$   $n = 114$ ,  $p < 0.01$ ). Above 3m there were no significant differences.

Within each environment spine density decreased above 3m in the same way that spine length decreased. This was significant for all environments except lowland savanna 1 (Mann-Whitney-U  $p < 0.05$ ): Vidal  $U(21,7) = 36.5$ ; karoo  $U(26,13) = 92$   $z = 2.29$ ; Itala  $U(22,7) = 29$   $z = 2.45$ ).

#### ***Spine length and leaf length (Figure 9)***

leaves are at least 2x as long as the spines in all environments except the arid shrublands. This is particularly noticeable in the savanna forms.

### *Over size classes*

From Figures 7 and 9 it is clear that there is a lot of variation in spine length within each environment. Much of this variation can be explained when the data is separated into size classes (Figure 10). In savanna environments spine length remains constant at a base level (the minimum size shown in other environments) throughout size classes.

### Defence against fire

The expected logarithmic relationship between bark thickness and stem circumference (Gill & Ashton 1968) was found in each environment. (Figure 11:  $r$  ranged from 0.93-0.97). Bark thickness at 60cm circumference was calculated from the equation for the regression line for each environment (Table 4). Stem circumference for 3m trees was also calculated (correlation of height and stem circumference  $0.95 < r < 0.97$ ) and this allowed for a calculation of the bark thickness of 3m trees in each environment.

Table 4: Fire resistance characteristics for each environment (calculated from regression slopes)

| environment    | bark thickness (mm)<br>for 60cm girth | stem circumference (cm)<br>for 3m trees | bark thickness (mm) for<br>3m trees |
|----------------|---------------------------------------|---|-------------------------------------|
| forest         | 3.0                                   | 11.5                                    | 1.5                                 |
| arid shrubland | 6.9                                   | 16.7                                    | 4.5                                 |
| L. savanna-1   | 8.9                                   | 12.4                                    | 5.2                                 |
| L. savanna-2   | 7.8                                   | 12.6                                    | 4.6                                 |
| U. savanna     | 12.7                                  | 18.4                                    | 7.7                                 |

### *Population biology*

#### Demographics

Size distribution was markedly different in each environment (Figure 12). Arid shrublands show a fairly normal height distribution whereas savannas are skewed towards the smaller sizes and forests towards the larger trees.

#### Reproduction

Figure 13 shows the allocation to reproduction (pod number) in relation to height for each environment. Individuals in the arid karoo start reproducing at a much smaller size than other populations. Neither forest nor savanna trees produced pods at less than 3m height.

## Controlled growth experiment

### Shape

Table 5 summarises the data for each environment (see also plate I). Kruskal-Wallis tests were performed for each variable and significant differences ( $p < 0.05$ ) are indicated. Arid shrubland seedlings show extensive growth below ground and they have smaller leaves than other environments. That savanna forms have smaller spines is already evident at the seedling stage, and their roots are thicker in comparison with their stems than forest and karoo shrubland seedlings. Seed weight is also different in each environment, forest forms have the largest seeds and savanna trees the smallest.

Table 5: Data on the structure of seedlings from each environment grown from seed under greenhouse conditions. Significant differences (Kruskal-Wallis  $p < 0.05$ ) are indicated (<sup>abc</sup>).

|                                    | forest             |       |    | arid shrubland     |       |    | lowland savanna    |       |    |
|------------------------------------|--------------------|-------|----|--------------------|-------|----|--------------------|-------|----|
|                                    | mean               | sd    | n  | mean               | sd    | n  | mean               | sd    | n  |
| length of stem (cm)                | <sup>a</sup> 11.9  | 3.8   | 10 | <sup>b</sup> 5.8   | 1.6   | 10 | <sup>b</sup> 5.9   | 2.3   | 10 |
| length of root (cm)                | <sup>a</sup> 32.2  | 7.4   | 10 | <sup>a</sup> 29.5  | 11.2  | 10 | <sup>b</sup> 19.4  | 6.3   | 10 |
| root length: stem length           | 2.9                | 1.1   | 10 | 5.5                | 2.5   | 10 | 4.1                | 2.9   | 10 |
| avg. spine length (mm)             | <sup>ab</sup> 6.2  | 1.4   | 10 | <sup>a</sup> 7.4   | 1.2   | 10 | <sup>b</sup> 4.7   | 1.9   | 10 |
| root diameter: stem diameter       | <sup>a</sup> 1.0   | 0.1   | 10 | <sup>a</sup> 0.9   | 0.2   | 9  | <sup>b</sup> 1.6   | 0.4   | 9  |
| area of leaflet (cm <sup>2</sup> ) | 1.9                | 0.7   | 10 | 1.4                | 0.6   | 10 | 1.9                | 0.6   | 10 |
| weight of seed (g)                 | <sup>a</sup> 0.089 | 0.019 | 20 | <sup>b</sup> 0.034 | 0.006 | 20 | <sup>c</sup> 0.023 | 0.008 | 20 |

### Carbon allocation

Figure 14 shows percentage biomass allocation to roots, stems, leaves, and spines. There are no obvious differences in carbon allocation between environments, despite the obvious morphological differences in Table 4.

Table 2: Data on the growth form of *A. karroo* in different environments over 4 size classes. Stem angle and diameter are summarised as value for largest stem, and combined average of all other stems. Average stem number is rounded off to the nearest integer, n ranges from 5-10 for each size class.

| size class | environment    | height (m) | stem no. | angle of largest stem | avg. angle of rest of stems | diameter of largest stem (cm) | avg. diameter rest of stems (cm) | height of first branch (cm) | canopy area (m <sup>2</sup> ) | leaf area estimate (g dry wt) |
|------------|----------------|------------|----------|-----------------------|-----------------------------|-------------------------------|----------------------------------|-----------------------------|-------------------------------|-------------------------------|
| 1          | Forest         | 0.75       | 2        | 75                    | 29                          | 1.2                           | 0.7                              | 20                          | 0.4                           | 24                            |
| 1          | Arid shrubland | 0.60       | 4        | 86                    | 70                          | 0.9                           | 0.5                              | 4                           | 0.5                           | 11                            |
| 1          | L. savanna 1   | 0.99       | 2        | 83                    | 45                          | 1.5                           | 0.6                              | 27                          | 0.3                           | ~                             |
| 1          | L. savanna 2   | 0.51       | 2        | 66                    | 35                          | 1.1                           | 0.5                              | 9                           | 0.1                           | 7                             |
| 1          | U. savanna     | 0.63       | 5        | 32                    | 45                          | 1.8                           | 0.9                              | 22                          | 0.5                           | 8                             |
| 2          | Forest         | 2.26       | 3        | 84                    | 37                          | 3.8                           | 2.2                              | 53                          | 5.1                           | 245                           |
| 2          | Arid shrubland | 2.39       | 9        | 74                    | 63                          | 6.0                           | 3.0                              | 0                           | 13.3                          | 471                           |
| 2          | L. savanna 1   | 2.31       | 1        | ~                     | ~                           | 4.5                           | 2.4                              | 116                         | 1.5                           | ~                             |
| 2          | L. savanna 2   | 2.10       | 1        | 90                    | 90                          | 3.7                           | 0.7                              | 139                         | 1.0                           | 22                            |
| 2          | U. savanna     | 2.02       | 1        | 89                    | 85                          | 6.2                           | 1.9                              | 74                          | 3.1                           | 35                            |
| 3          | Forest         | 4.49       | 2        | 84                    | 73                          | 8.8                           | 4.0                              | 61                          | 29.8                          | 882                           |
| 3          | Arid shrubland | 4.04       | 5        | 84                    | 54                          | 17.9                          | 6.8                              | 66                          | 32.4                          | 1179                          |
| 3          | L. savanna 1   | 4.06       | 1        | 90                    | 30                          | 7.9                           | 2.3                              | 114                         | 6.7                           | 206                           |
| 3          | L. savanna 2   | 4.17       | 2        | 90                    | 90                          | 6.3                           | 4.9                              | 118                         | 2.1                           | 73                            |
| 3          | U. savanna     | 3.63       | 1        | 90                    | ~                           | 12.8                          | ~                                | 60                          | 7.2                           | 91                            |
| 4          | Forest         | 10.50      | 2        | 86                    | 77                          | 38.4                          | 29.1                             | 198                         | 153.7                         | 7188                          |
| 4          | Arid shrubland | 6.80       | 3        | 65                    | 65                          | 29.6                          | 24.4                             | 30                          | 81.5                          | 93                            |
| 4          | L. savanna 1   | 8.65       | 1        | 90                    | ~                           | 17.8                          | ~                                | 330                         | 21.0                          | 607                           |
| 4          | L. savanna 2   | ~          | ~        | ~                     | ~                           | ~                             | ~                                | ~                           | ~                             | ~                             |
| 4          | U. savanna     | 7.83       | 1        | 90                    | 85                          | 29.3                          | 12.0                             | 93.7                        | 48.9                          | 6320                          |



Plate I: *Acacia karroo*: 4.5 month old seedlings grown under identical greenhouse conditions. Left- savanna form (Hluhluwe-Umfolozi Reserve), Middle- arid shrubland form (karoo), Right- forest form (St Lucia)

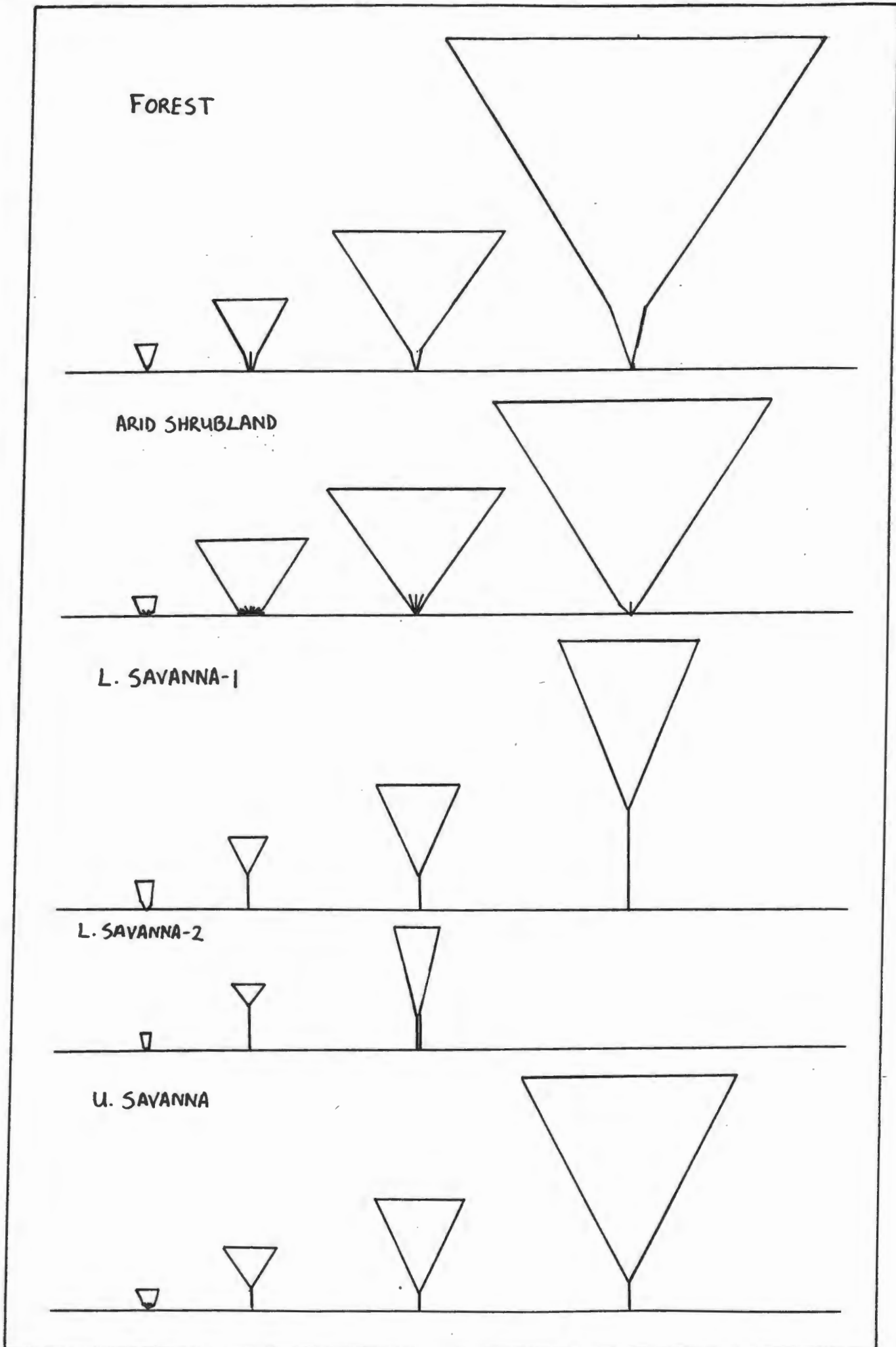


Figure 2: Basic architecture of *Acacia karoo* in forest, arid karoo shrubland and savanna environments. Figures drawn from data in table 2.

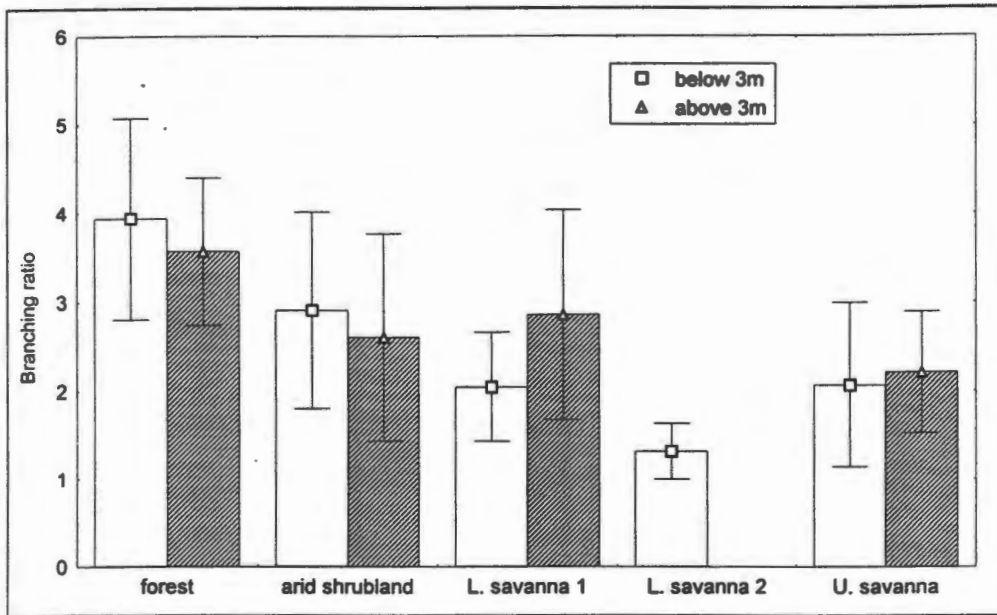


Figure 3: Branching ratios (total branch length: length of longest shoot) above and below 3m for each environment: mean and std deviation,  $n=\pm 30$ . Below 3m savanna forms are significantly less branched, above 3m these differences are not significant.

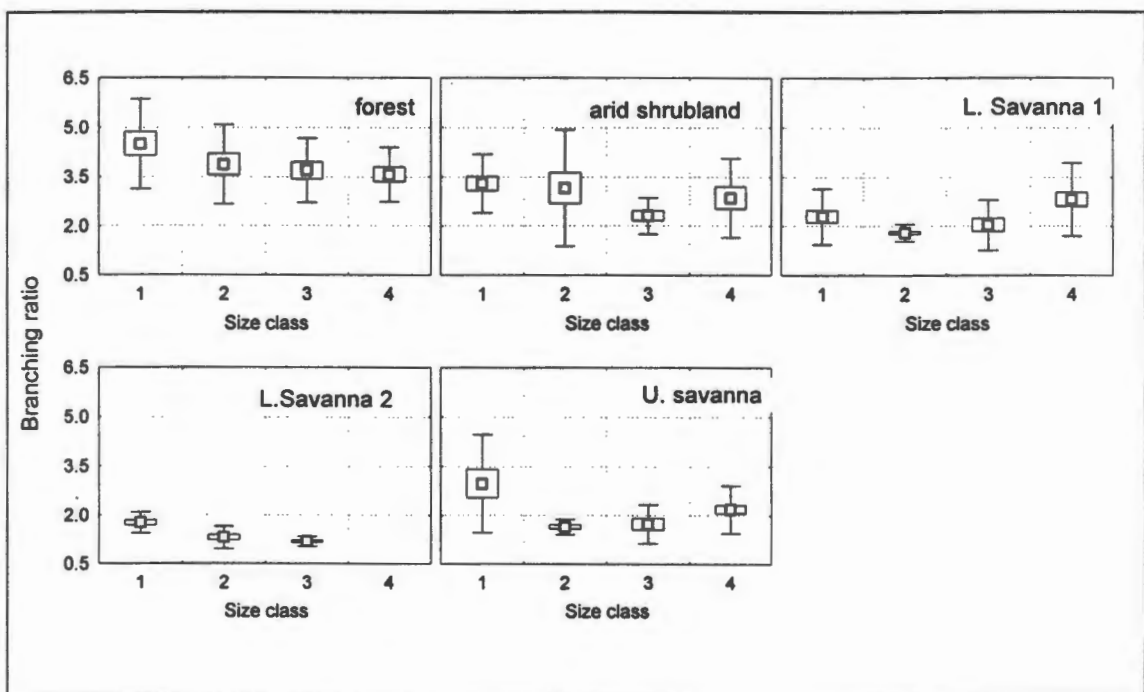


Figure 4: Branching ratios (total branch length: length of longest shoot) across size classes for each environment (mean and std. deviation).

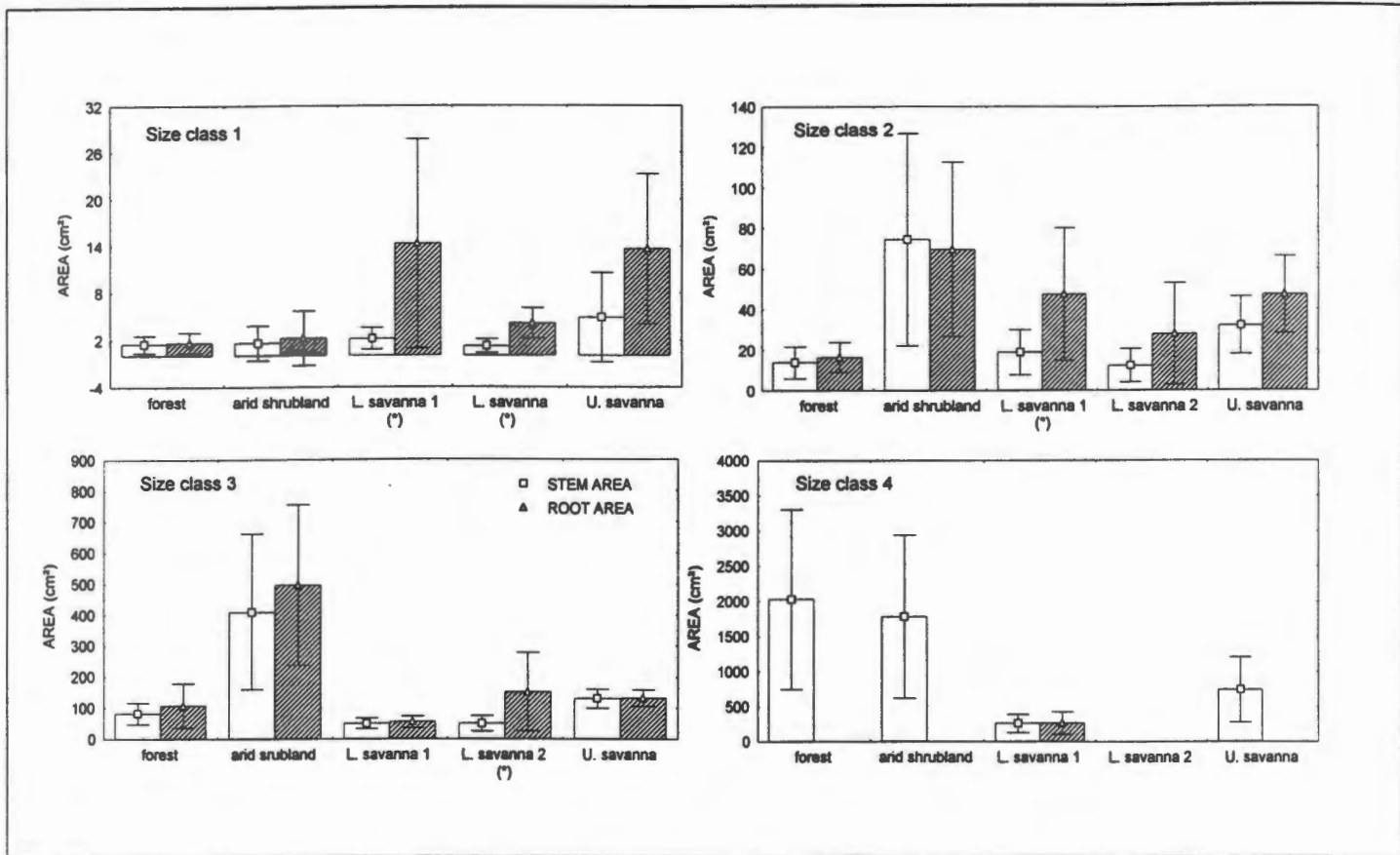


Figure 5: Comparisons of stem area (at 0m) and root area (just below the surface) across environments and over different size classes (A-D). Mean and std deviation,  $n = \pm 7$ . Significant differences within environments indicated (\*)  $p < 0.05$ . Savanna forms have swollen roots in relation to their above ground stems in the smaller size classes.

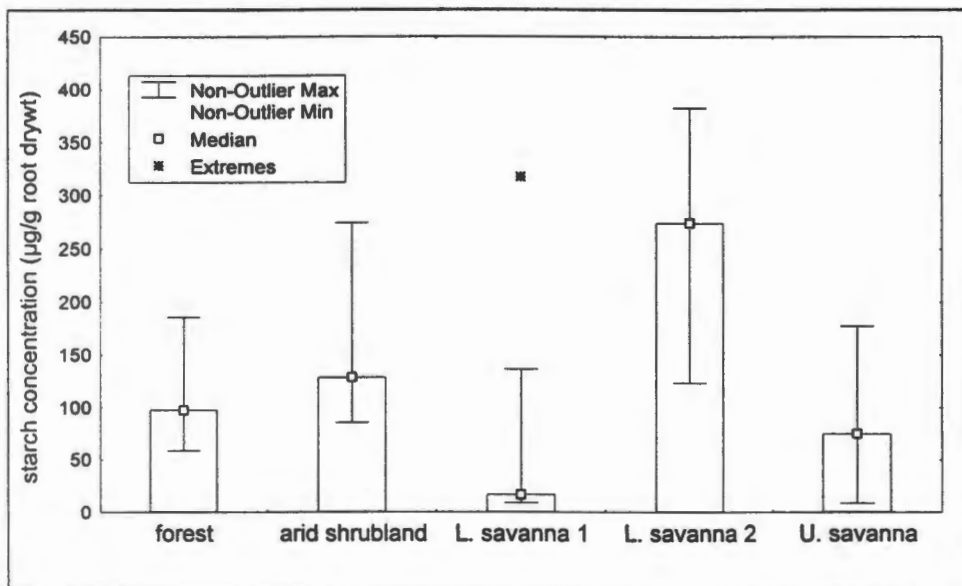


Figure 6: Root starch concentrations of *A. karroo* trees in the each environment. Median and extremes:  $n = \pm 25$

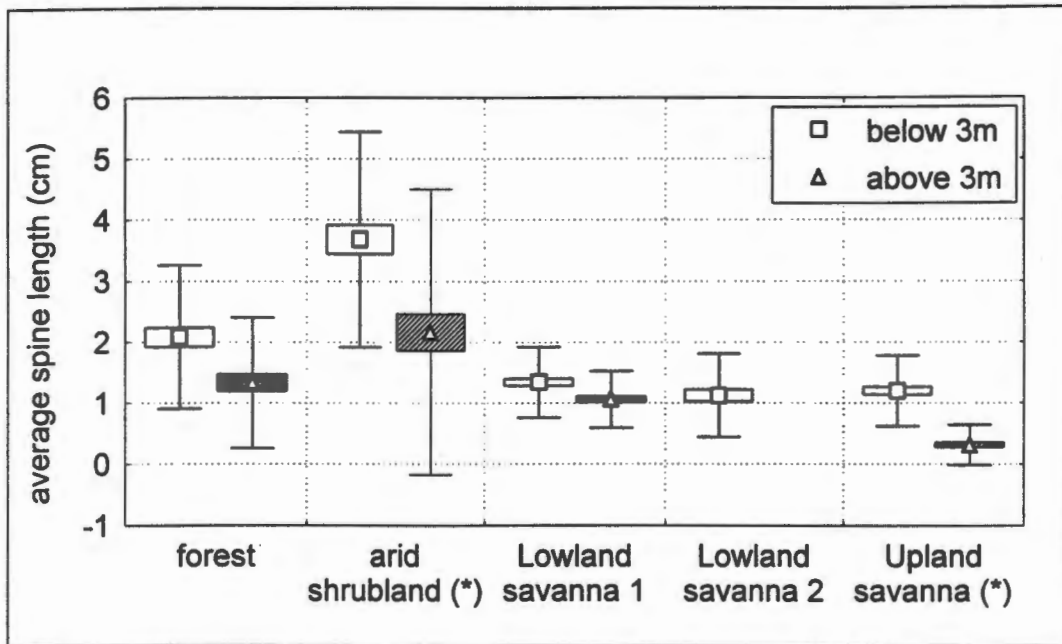


Figure 7: Spine lengths above and below 3m for each environment. Trees in the arid karoo have large thorns and savanna trees have the smallest. These differences are less apparent above 3m. Mean, std error (box) and std. deviation (whisker). Significant differences within environments indicated (\*)  $P < 0.05$ .

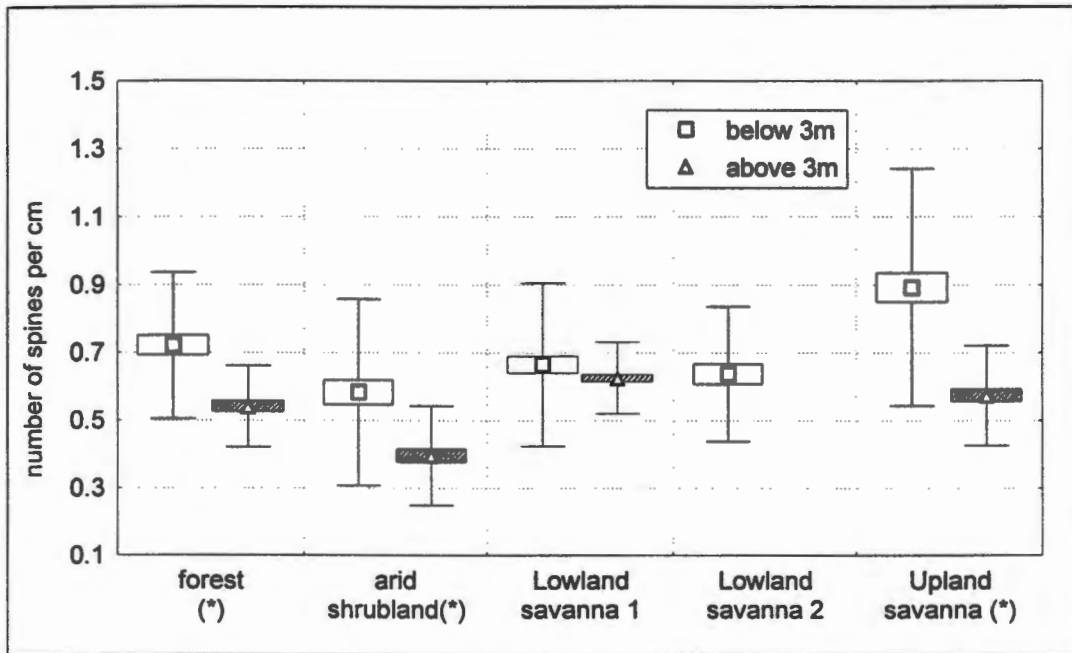


Figure 8: Spine density in each environment above and below 3m. Mean, std error (box) and std deviation (whisker). Significant differences within environments indicated (\*)  $p < 0.05$ .

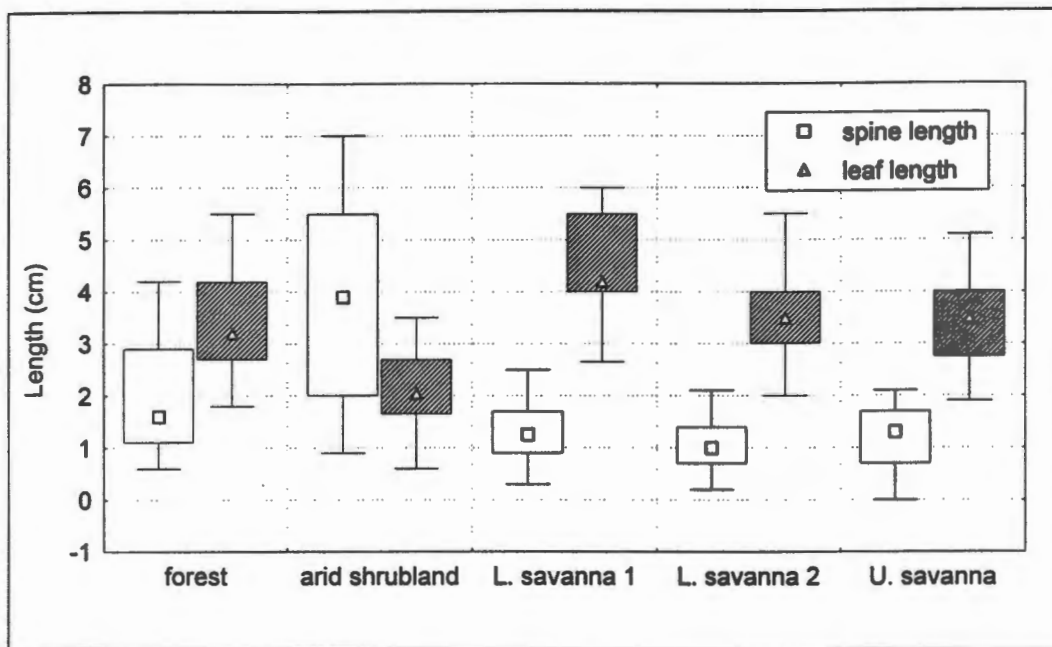


Figure 9: Average spine lengths in relation to average max. leaf lengths in each environment. Median  $\pm$ 75%. *A. Karroo* in arid shrublands is deciduous which could explain the difference in leaf length.

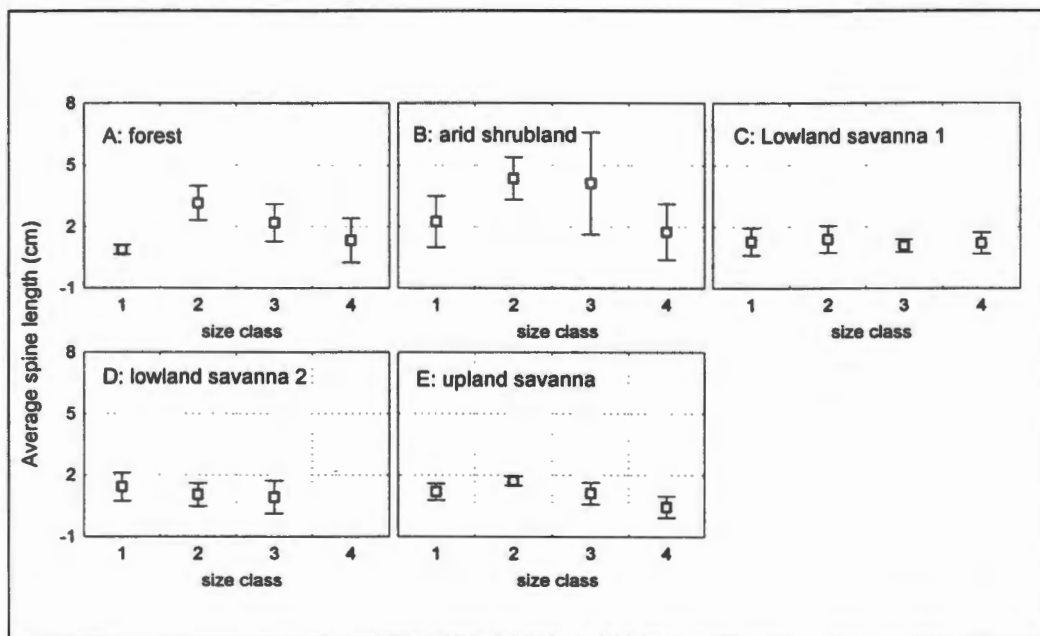


Figure 10: Variation in average spine length over size classes. Mean and std dev. All values (below and above 3m) included. Trees in savanna environments show the least amount of variation of spine length with size.

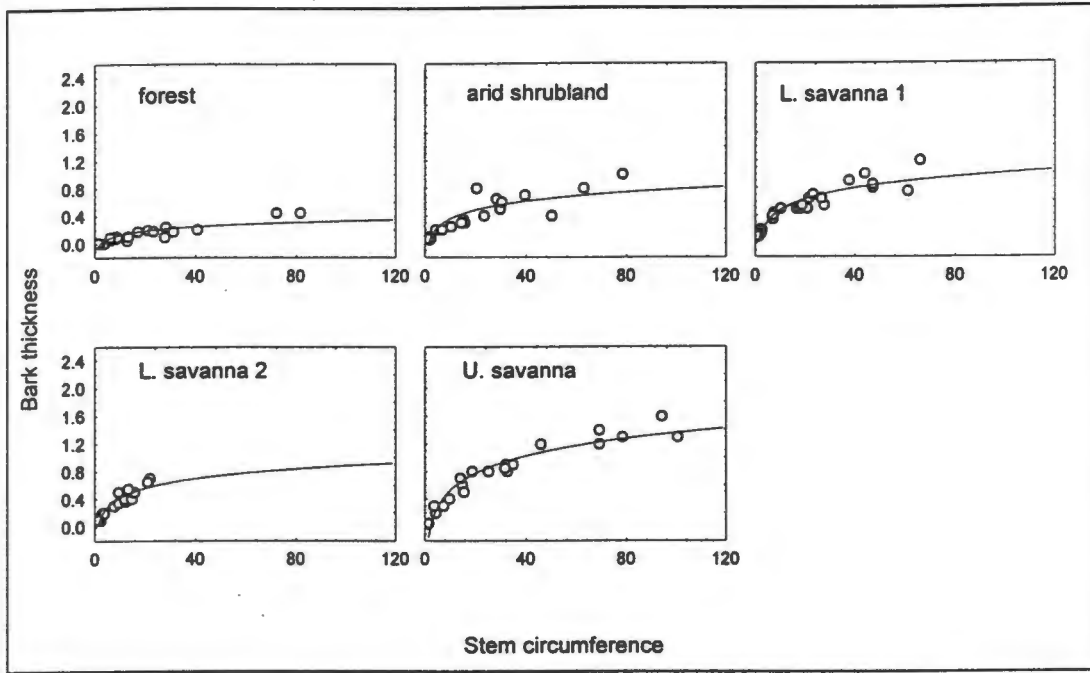


Figure 11: Logarithmic relationship between bark thickness and stem diameter in *A. karroo* in each environment. ( $r$  ranges from 0.93-0.97)

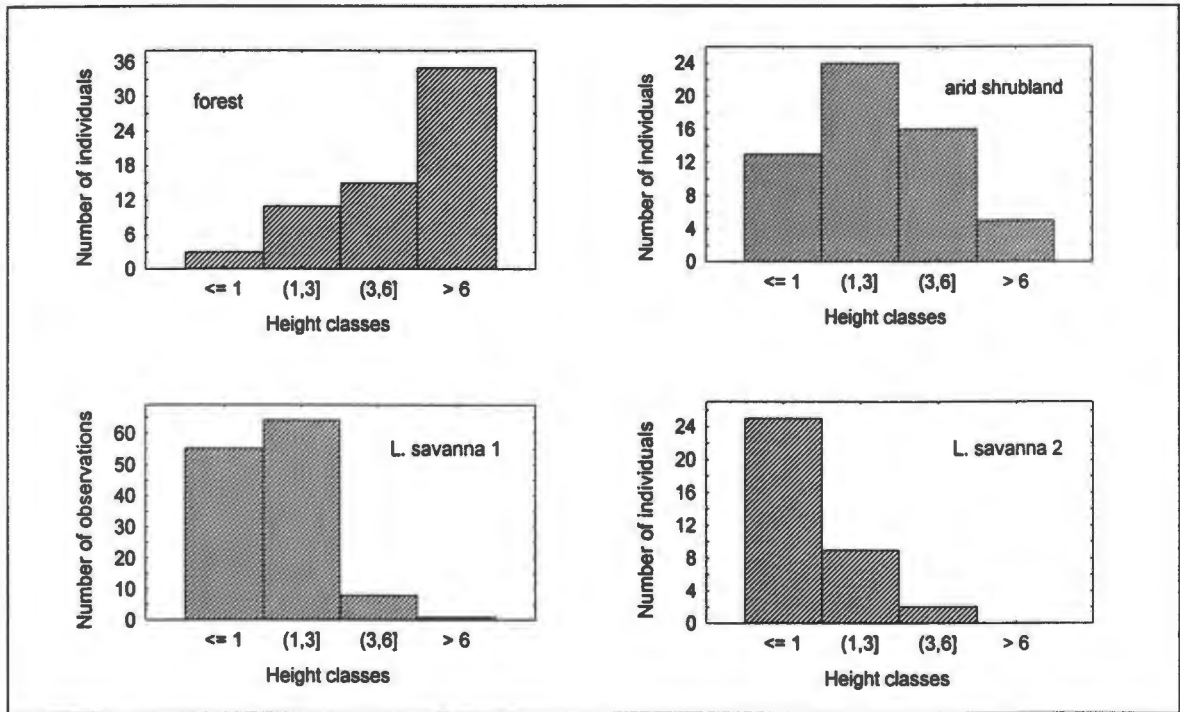


Figure 12: Size structure of the *A. karroo* populations at each sample site (upland savanna not sampled). Savanna populations are skewed towards the smaller size classes.

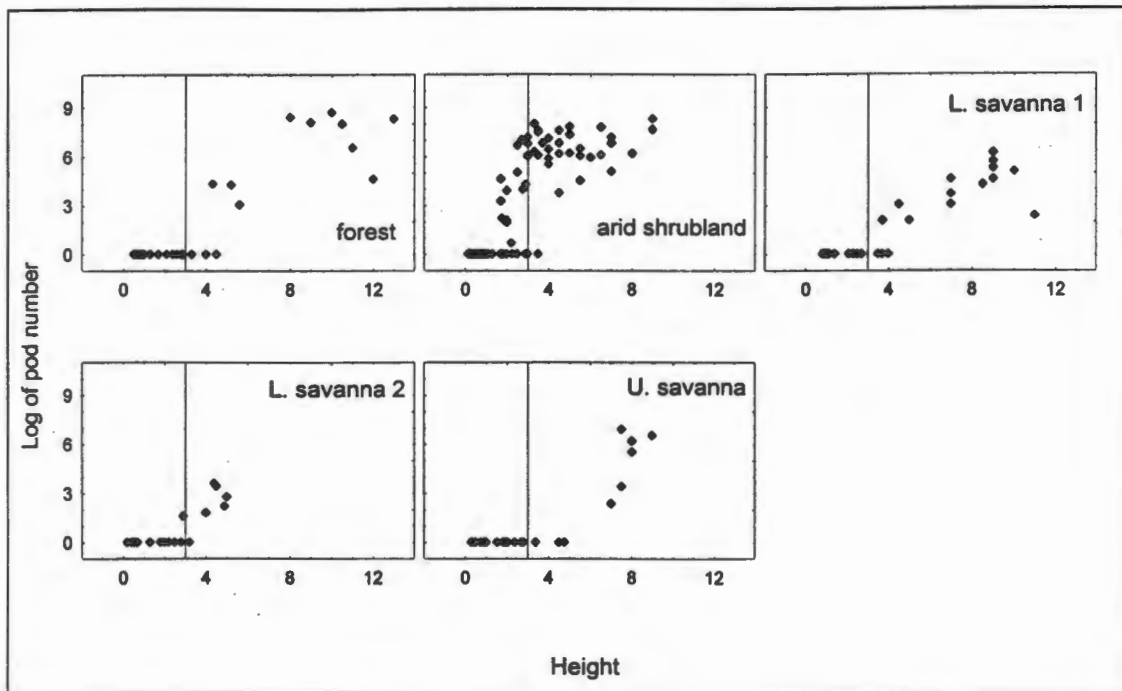


Figure 13: Reproductive effort of *A. karroo* trees in different environments in relation to tree height. Trees in savannas do not start reproducing below 3m (indicated)

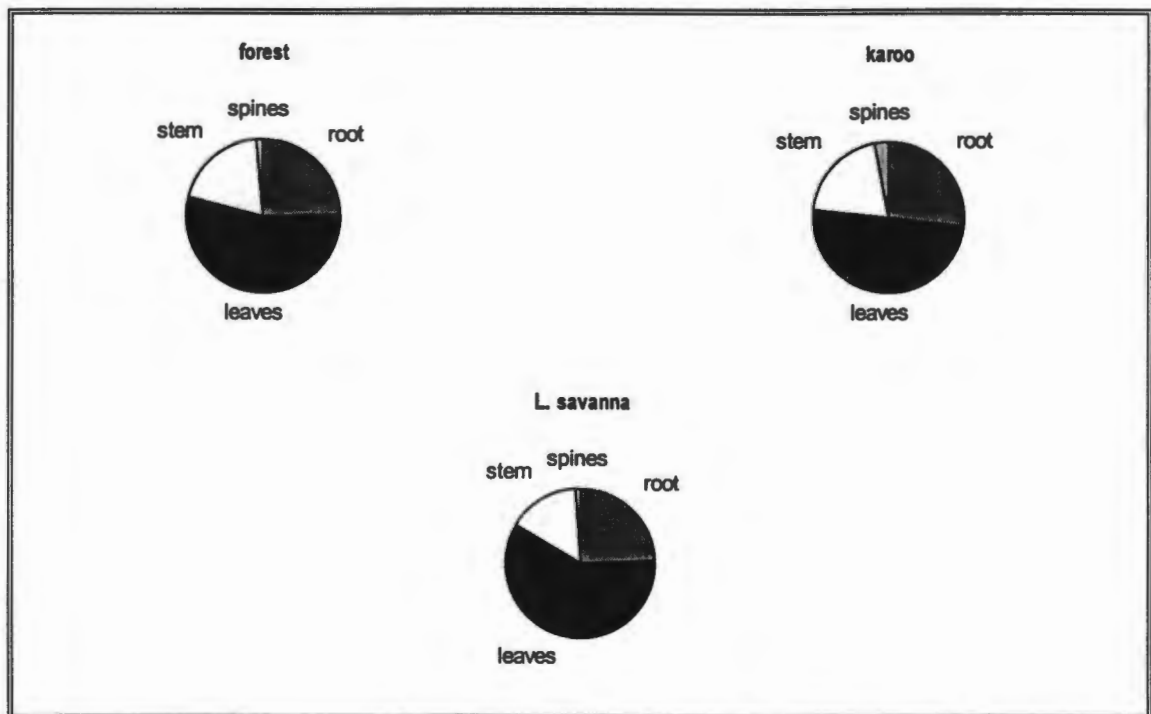


Figure 14: Percentage biomass allocation to roots, stems, spines and leaves in terms of dry weight for *A. karroo* seedlings from forest, karoo and savanna environments.

## Discussion

### *Savanna trees and fire*

#### Growth form

The morphological data in this project supports the theory behind tree growth in environments with fire. Compared with trees in non fire environments, small savanna *A. karroo* trees are maximising height gain. The diagrams in Figure 2 show clearly how different the 1-3 meter trees in savanna environments are from trees in both open (arid shrubland) and light limited (forest) environments. They have single vertical stems, and the height at which they first branch is double that of forest trees (Table 1). Until savanna *A. karroo* trees are above three meters they are less branched (Figure 3&4), and have fewer herbivore defences (Figure 10) than similar sized trees in forest or arid shrubland environments.

For forest trees in light limited environments, height gain is also a priority (Halle et al 1978), and it would be expected that they too would be allocating a great deal of resources to vertical growth. However, compared with savanna trees they have highly branched spreading growth forms (Figure 2&3) and well developed herbivore defences (Figures 7-10). The pressure on savanna trees to grow tall must therefore be very great. Growth rates of 1m a year for in *A. karroo* juveniles have been recorded in savanna environments (pers. obs, & Maze, unpublished data).

#### Defence against fire

##### *Bark thickness*

Growing high enough to have leaves escaping the fire is of no use unless the stem tissue is also protected from the fire. This depends on both bark thickness, and stem diameter (Gignoux et al 1997). Bark thickness values for mature savanna *A. karroo* (60cm girth) are slightly less than those reported for eucalypts in Australia (9-18cm at 60cm girth- Gill and Ashton 1986) but well within the range for other savanna tree species (Gignoux et al 1997). It is the 3m tall savanna trees for whom bark thickness is expected to be most important, because they have a chance of avoiding topkill (Trollope 1984) and regrowing after fire from surviving above ground structures. Thus their stem diameter and bark thickness must be at some minimal level of fire resistance (table 4).

Gill (1981) notes that thick bark, while a necessary defence against fire, is beneficial to plants for other reasons in non-fire environments. Thick bark is a protection against pathogen attack (Shain 1995) and is generally associated with highly

disturbed environments (Hedge et al 1998). Thus it is not an attribute which can be said to be specific to trees in fire systems and *A. karroo* trees in arid shrublands also have thick bark compared with that of forest trees.

### Response to injury

The swollen root bases in savanna *A. karroo* trees are an indication of a past history of resprouting after above ground structures are destroyed by fire (Figure 5). The seedlings in the greenhouse already have thicker roots than other environments (Table 5) and these swollen structures might also be serving as storage areas of starch reserves for rapid growth between fires (Bowden & Pate 1993). However the comparative data on starch concentrations did not make this clear (Figure 6).

### Population biology

These large root bases in size class 1& 2 trees indicates that in savannas many of the smaller *A. karroo* trees are quite old: that their above ground structures are destroyed every time there is a fire and that they resprout each time from this root base. Thus it is expected that the population would consist largely of these 'gullivers' (similarly sized but not necessarily similarly aged trees growing within the grass layer - Bond and van Wilgen 1996). The size distribution of the population reflects this (Figure 12): there are very few trees above 3m in savanna environments. A normal population structure for trees is shown by arid shrubland acacias. In light limited environments, where seedling establishment is rare, a top-heavy size distribution is expected like that of the *A. karroo* forest population (Figure 12) (Lusk and Ogden 1992). The demography of savanna populations is therefore distinctive.

### Reproduction

This fire-structured life-history strategy also results in specific reproductive characteristics. Trees generally only allocate resources to reproduction when their needs for growth and survival have been met (Crawley 1997) and modelling can predict that a tree will maximise its fitness in environments with frequent fires if it delays reproduction until it is above the fire layer (Bond unpublished work). Figure 13 shows clearly that savanna trees only start reproducing above 3m. In forest environments trees also reproduce only when they reach canopy height and are no longer under stress for light. This is in startling contrast to arid shrubland environments, where there is no clear height at which such an allocation shift would be adaptive.

Measurements of seed size (Table 5) also reflect different stresses in each environment. Large seeds are thought to be beneficial in environments where seedlings establish in the shade, and in environments prone to drought (Jurado & Westoby 1992). Both forest (light limited) and arid shrubland (drought prone) *A. karroo* trees have larger seeds than trees in savannas where these two factors are not as important for seedling survival.

### Consequences of a fire-adapted life history

The rapid growth shown by *A. karroo* to escape fire in savannas has its price: the three factors traditionally considered important in tree design are light interception, reproductive success and mechanical stability (Nicklas 1988). Growth forms which maximise these factors are spreading and highly branched, like those of arid shrubland and forest environments (Figure 2). Below 3m savanna trees are maximising shoot extension at the expense of branching, delay reproduction, and have single thin vertical stems (Figure 2). It is obvious that frequent grass fires impose an incredibly harsh selective regime on tree-like growth forms which necessitate drastic trade-offs in tree architecture and growth.

### ***Savanna trees and herbivory***

As shown above, the life history and architecture of savanna trees can be explained in terms of the fire regime, but this is not sufficient. Pellew (1983), and Trollope (1984) both stress the importance of mammalian herbivory in retarding growth of savanna trees and preventing recruitment.

To a savanna tree, for whom height is a priority, damage to growing points and shoot tips is likely to be much more harmful than herbivory of leaves because it would directly inhibit growth and affect the chances of recruiting into the mature canopy. Thus it is the herbivores which bite off shoots, not the browsers which are going to be imposing the strongest pressure on trees and I will concentrate on this in comparing herbivore defence strategies between environments.

### Spines as mammalian herbivore defences:

It is not easy to isolate the function and utility of spines. Gowda (1996) showed how spines decrease the amount of shoot/stem herbivory but increase the amount of leaf herbivory. At most sites in this study (except the arid shrubland where *A. karroo* trees are deciduous in winter), leaves are at least 2x as long as spines and it is therefore simplistic to regard spines as defending leaves. It is likely, as Milton (1991)

suggests, that spines are useful in preventing access to plants and protecting structure.

It is important to emphasise that the effectiveness of spines depends not only on their size and density. A highly branched growth form in combination with large spines can create an effective barrier, but long spines alone would not be as efficient (Figure 15). The normal response of trees to herbivory is to initiate more apical meristems and become highly branched (Crawley 1997). Thus branching pattern and spinescence together determine how well defended a tree is to herbivory.



Figure 15: diagrammatic illustration of the effectiveness of spines combined with branching as compared with spines alone in deterring browsers.

### Spinescence in *A. karroo*

Therefore an *A. karroo* tree which is effectively defended against herbivores would be expected to have long, dense spines and a highly branched growth form. This is evident in *A. karroo* in both the arid shrubland and the forest (Figures 3,7)-environments which, except for the presence of mammalian herbivores, are very different.

In comparison, *A. karroo* in savannas has much smaller spines and long unbranched shoots, especially in the smaller stages below 3m (Figures 3&4). Figure 10 shows that maximum spine length in savanna trees is the same as the minimum base level in size class 4 trees in other environments. Is it possible that *A. karroo* is trading off defence against herbivores for the sake of rapid growth to escape fire? This would imply that injury due to fire is much more damaging than browsing. The information available does not support this idea. Pellew 1983 shows how herbivory of *Acacia tortilis* effectively slows growth rate, keeps the trees below 3m, and prevents recruitment into the mature canopy. Trollope (1984) too, cites experiments which show how influential mammalian herbivory is in retarding growth of savanna trees, and preventing re-establishment of trees after fire. Therefore the growth of *A. karroo* deserves more attention with regard to herbivory.

## Avoiding herbivory vs defence against herbivory

In general organisms can prevent predation by

- 1 defending themselves (becoming inedible or preventing predators from gaining access to them)
- 2 avoiding the predators (camouflage or active escape)

Understandably avoiding predation is not often a strategy considered for plants. However, plants can be said to be more or less 'apparent' to herbivores depending firstly on how much of the landscape they occupy, and secondly on how long they occupy a space (Feeny 1979 in Grubb 1992) and this should affect their chances of being eaten by a herbivore at any one time. Considering that the browsing limit for most herbivores is less than about 2.5m, avoiding the browser is a possibility for trees if they can escape predation for long enough to grow above browse height. This browse limit could be considered as a 'herbivore trap' for juvenile trees in the same way as the grass fuel layer is considered a 'fire trap' in that it prevents recruitment of mature trees into the canopy (Pellew 1983). Not being noticeable to potential browsers and having a fast growth rate are two attributes, which combined, may allow a tree to survive and establish even in conditions with high herbivory.

### *A. karroo* : defence or escape?

In savannas *A. karroo* is maximising height gain and shoot elongation, this much is clear from Figures 2-4). This architecture can be explained by the need for rapid growth to 'escape' the fire trap. A strategy for avoiding herbivores would be complementary under these conditions because traditional methods of herbivory defence involve diversion of resources to spines, lateral branching, and therefore reduced vertical growth.

The lower a shoot is to the ground the more likely it is to be seen and bitten. To show that *A. karroo* is effectively avoiding herbivores one would need to show that there was a high enough chance that its growing shoots would remain unbitten before it grew above browse height.

Consider browsing of rhino for example: black rhinos bite off entire shoots of up to 1cm diameter causing severe damage to trees, but rhino browsing is concentrated below 1m (Emsley 1994). *A. karroo* can grow at least 1m in a year (Maze, unpublished, pers. obs.). What characteristics would a tree have to have to minimise the chances of getting eaten during this year?

Table 3 shows that for the same sized tree at the same height, *A. karroo* has much fewer shoot tips (potential browse points) than the slower growing, well defended *Acacia nilotica*. Two meter tall *Acacia karroo* trees have no shoot tips below 1m and thus could be said to have 'escaped' from black rhino herbivory. One can also look at the browse history of the trees by counting the number of bitten shoots (bite points) at different heights. 2m tall *A. karroo* trees were bitten on average only 3.5 times before growing above 1m whereas *Acacia niloticas* were bitten 12 times. Considering that *Acacia nilotica* is generally considered less edible and better defended against herbivory than *A. karroo* (Owen Smith and Cooper 1987), this is a telling evidence for the argument that the vertical unbranched growth form of *A. karroo* makes them less apparent to herbivores both in terms of shoot tips available and time spent at a size available to herbivores.

As mentioned earlier, the general response to herbivory is lateral branching (Crawley 1997) presumably to improve the defensive structure (Milton 1991). However, the ratio of growing shoot tips, to past bite points in *A. karroo* shows that herbivory does not initiate more lateral branches in savanna *A. karroo* trees (Table 3). A browsed *A. karroo* shoot will initiate only one meristem and continue vertical growth.

This data is supported by a study done by Emsly (1994) also at Hluhluwe reserve. He found *A. karroo* to be less 'preferred' than other acacia species, which means that, considering its abundance in the environment, it was browsed less than other acacias. This is surprising as *A. karroo* is highly edible (Owen Smith and Cooper 1987). This information could mean that is less 'apparent' than other species due to its vertical growth habit.

This is all very well for black rhinos, which browse below 1m, but what of giraffes? The maximum browse height of an adult bull giraffe is 5.75m (Pellew 1983). An edible *A. karroo* is unlikely to avoid being browsed for the time for the time it takes to reach that height, nor could it maintain rapid growth for so long. One explanation for this could be that this growth form of *A. karroo* is only found in high lying regions of northern Natal (Swartz 1982), and it is unclear whether giraffe originally occurred there (Brookes and Macdonald 1989). Perhaps this growth form of *A. karroo* is something which only could have arisen in an environment without giraffe. On the other hand, Pellew (1983) also states that more than 70% of giraffe browsing occurs below 3m, when *A. karroo* is expected to be growing tall with few lateral shoots due to fire.

## Fire and herbivory

It is unlikely that the rapid-growth-herbivore-avoidance strategy postulated here for *A. karroo* is as effective as other herbivore defences. In forest and arid karoo environments, which also are exposed to high herbivory, *A. karroo* trees display more common herbivore defences and have a highly branched, spinescent structure (Figures 2-4, 7-10). Other acacia species in savanna environments also have many spines and are highly branched (Gowda 1996). However, when rapid growth is a priority for another reason, as seems to be the case for *A. karroo* in fire environments, perhaps it is more beneficial to trade off a less effective strategy for dealing with herbivores against the loss of height which would accompany spines and branching.

### ***The architecture of mature savanna trees***

The differences between environments in spines and branching pattern disappear above three meters (figs 4,7,8,10). This lends evidence to support our assumption that spines are attributes functioning in defence against vertebrate herbivory and that trees above 3m trees in all environments are allocating minimal resources to defense against browsers.

As mentioned earlier, because they are long lived, trees have the potential to separate functions in time. For savanna trees, the increased branching pattern and initiation of reproduction above 3m indicates that the emphasis has shifted from growth and survival to maximising photosynthesis and reproduction. However, the restrictions entailed by rapid growth during early life history stages have consequences for the mature trees.

Table 6 shows canopy area, leaf area and reproductive effort for 6m trees from each environment. Savanna trees have markedly smaller canopy and leaf areas. One can also see in Figure 14 that stem area in mature savanna trees is less than that of trees in other environments. Thus a history of strong environmental pressures for rapid vertical growth have resulted in a characteristically thin unbranched stem in the mature tree. This is likely to be less mechanically stable (McMahon 1975) than forest or karoo tree architectures and therefore unable to support a full canopy. A smaller canopy and leaf area will limit the photosynthetic and reproductive potential of mature savanna trees.

Table 6: Canopy area, leaf area and reproductive effort for 6m trees in each environment. (Height is logarithmically related to canopy area and leaf area, values were calculated from the regression line equation. Reproduction at 6m calculated as an average of reproduction for all sampled trees >4m <8m)

| environment    | canopy area<br>at 6m<br>(m <sup>2</sup> ) | leaf area<br>at 6m<br>(g dry weight) | reproduction<br>at 6m<br>(pod number) |
|----------------|---|--------------------------------------|---------------------------------------|
| forest         | 41.3                                      | 1736                                 | 1166                                  |
| arid shrubland | 63.2                                      | 2256                                 | 1185                                  |
| L. savanna 1   | 9.3                                       | 333                                  | 37                                    |
| L. savanna 2   | 5.4                                       | 63                                   | 19                                    |
| U. savanna     | 25.9                                      | 111                                  | 394                                   |

Thus mature savanna trees have traded off reduced light interception, reproductive success and probably mechanical stability in order to get where they are. The resulting tree architecture is unlike that found in any other environment.

#### **Conclusions : The adaptive geometry of savanna trees**

That the differences apparent in *A. karroo* architecture in each environment are due to genetic differences is clear from the controlled greenhouse experiment (Table 5). Thus the specific attributes of savanna trees can truly be said to be adaptations to the conditions experienced by these trees. I have discussed these attributes in terms of two factors which seem to play a dominant role in community dynamics in savannas - fire and browsing - and shown that trees growing under these conditions differ remarkably from trees in other environments where the adaptive geometry of tree growth is better understood.

The most obvious characteristics, and those focused on in this study are those of architecture- even the 4 month old seedlings had marked differences in structure (Table 5), which were not mirrored in their carbon allocation patterns (Figure 14). The characteristics of shape and growth form evident in small savanna *A. karroo* trees can be explained in terms of the need to grow fast and escape from the area below 3m where they are vulnerable to fire and herbivores, however, these characteristics have far reaching effects on the design and reproductive ability of the mature trees.

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