

SLOWLY DOES IT: *ACACIA ERIOLOBA* GROWING LARGE IN SOUTHERN KALAHARI SAVANNAS

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Abstract

I studied demography of camelthorn, *Acacia erioloba* (Meyer) in the Kalahari savannah near Kimberley, and carried out experiments to ascertain the influence of supplementary water and protection from herbivores, and competition with grass, on *A. erioloba* sapling growth. I also investigated the influence of fire on *A. erioloba* demography. The role of fire in semi-arid savannas is not deemed as important as in mesic savannas because fires are more rare in semi-arid environments. But, although infrequent, fires may have important consequences for woody species' abundance, density and population size structure, especially in light of relatively slow growth rates and relative fire intolerance in semi-arid systems. Experiments on sapling growth rates showed that a combination of slow growth rates and competition from grass for light and possibly water are influential in suppressing progress by saplings to larger size classes. The relationship between *Acacia* growth and belowground stem size was positively linear, implying that larger plants have faster growth rates. Furthermore, the coefficient of the relationship between growth and belowground stem size was greater for *Acacia* from which surrounding grass had been removed than for those from which grass had not been removed, although this difference was not statistically significant. These differences may be biologically significant, however, with removal of grass allowing some advantage to trees growing in areas where escape from fire and herbivory is all-important. Fire had the greatest effect on the largest size class of *A. erioloba*, where trees either died or only suffered minor damage. High mortality rates suggest that although able to resprout, *A. erioloba* is fire-sensitive and, in combination with being slow growing, may explain its restriction on Kalahari sands to areas where rainfall is less than 900mm.year⁻¹.

1. Introduction

Large trees are important for the maintenance of certain biodiversity patterns and processes in the southern Kalahari, providing nest sites for birds, particularly larger raptors and sociable weavers (*Philetairus socius*), and a microhabitat for a number of fruited plant species (Dean *et al.*, 1999). In addition, *A. erioloba* wood is in great demand as a source of firewood in South Africa's major cities, and rates of harvesting in some areas are considered unsustainable, given the slow growth rate of these trees (Anderson & Anderson, 2001; Powell, 2001; Milton *et al.*, 2002; Raliselo, 2002). It is therefore informative to examine some of the processes facilitating or hindering establishment of the large tree component (i.e. *Acacia erioloba*) in the southern Kalahari.

Within the drier parts of the range of *A. erioloba*, groups of trees of roughly the same size, assumed to be cohorts, are often seen. This cohorted nature of acacias in arid areas is widely interpreted as evidence of the importance of abiotic factors (particularly quantity and pattern of rainfall) to intermittent successful recruitment (Ernst *et al.*, 1990; Barnes *et al.*, 1997; Midgley & Bond, 2001).

Alternatively, what appear to be cohorts may not be even-aged individuals at all. For example, previous clearing, cattle grazing (with concomitant release from grass competition), or release from browsing can allow seedlings of different age classes to escape simultaneously, giving the appearance of cohorted recruitment (Hoffman *et al.*, 1994; Milton & Dean, 1995; Timberlake *et al.*, 1999).

Within fire-prone savannas, species comprising the woody element display a variety of adaptations for dealing with the adversity associated with regular fires, from strategies of investment in below-ground growth to enable resprouting (Bond & Midgley, 2003), to elevated germination rates in response to fire (Sabiiti & Wein, 1987; Mucunguzi, 1995). Most, perhaps all, African *Acacias* demonstrate at least some ability to resist fire and resprout, although mortality has been observed in a variety of species (see Midgley & Bond, 2001 and references therein). The geographic restriction of *Acacia erioloba* to arid areas suggests that adaptations to fire have not been as important in this species as for other acacias. This species is clearly an arid to semi-arid system *Acacia*, with rainfall over its range varying from less than 40mm.year⁻¹ to 900mm.year⁻¹ (Barnes *et al.*, 1997).

To date, studies after uncontrolled natural fires on the influence of fire on *A. erioloba* demography have been opportunistic. Their findings have been diverse. This may partly be because fires are almost

impossible to replicate, since season, fuel load, frequency of burning, as well as weather conditions and type of fire all influence the intensity of the fire and its ultimate influence on vegetation (Bond & van Wilgen, 1996). Even so, the variation in response to fire of different *A. erioloba* populations has been sizeable. For example, Barnes (1999; 2001) found almost no mortality, even amongst “seedlings”, when large areas of her study site at Savuti burnt. At the other extreme, a fire in the Kalahari Gemsbok Park (now Kgalagadi Transfrontier Park) killed nearly one third of all trees at all sites, with large trees suffering the highest mortalities (approximately 75% mortality rate) (Van der Walt & Le Riche, 1984). Similarly, in a study carried out in Botswana, Skarpe (1980) found about 30% mortality, although in her study, mortality was greatest amongst smaller individuals. Two fires within my study sites (Vaalbos and Susanna, which had fires 6 and 18 months prior to the study, respectively), enabled collection of data regarding mortality rates amongst different size classes.

This study therefore set out to address the following:

1. Does the size class distribution of *Acacia* species at two sites near Kimberley, Benfontein and Susanna, suggest cohorted or continuous recruitment, or cohorted release?
2. How does provision of supplemental water influence growth rates in *A. erioloba* saplings?
3. How does exposure to herbivores (both grazers and browsers) influence relative growth rates of *A. erioloba* saplings?
4. Does competition from grass influence *A. erioloba* sapling growth?
5. How does mortality and resprouting response after fire differ among *A. erioloba* height size classes?

2. Methods

2.1 Acacia demography

I surveyed *Acacia* demography in randomly sited plots within the sandveld of two farms, Benfontein (35 plots) and Susanna (18 plots), in the Kimberley area. Plots were 25m x 25m. I thoroughly searched each plot for *A. erioloba* of all sizes. For each individual found, I recorded height, maximum canopy width (d_1) and canopy width at 90° to d_1 (d_2), number of stems, diameter of thickest stem above ground (d_a), and for small (<1.5m) individuals, I measured stem diameter 3cm below ground (d_b).

2.2 Exclusion plots

I set up five plots of 300m x 300m on both Benfontein and Susanna. Within each plot, I first searched for 12 saplings, allocating each to a treatment. Each plot had three replicates of each of the following treatments: herbivores excluded (A); herbivores excluded and supplemental water given (B); herbivores not excluded and supplemental water given (C); and no supplemental water, no exclusion of herbivores (i.e. controls) (D) (Table 1). I endeavoured to ensure equal representation of different size classes within each treatment, because larger (assumed older) individuals may potentially grow faster than smaller individuals. Therefore, there were 30 saplings in each treatment distributed across 10 sites at two different farms. Exclusion plots were built around individual saplings, and were made of wire mesh (2.5cm holes), supported by iron rods (1.2cm diameter, 1.4 m height), which effectively excluded any herbivores larger than a small rodent. The same amount of supplemental water (5l over an area of 1m²) was given to the “water treatments”, once every two weeks for the summer growth period (i.e. the five months from November 2003 to March 2004), the time over which the experiment was run.

Table 1. Treatments used for saplings at each plot

	Exclosure	Water	
A	Herbivores excluded	No water	
B	Herbivores excluded	Water	3 x each treatment (A, B, C & D) at 10 sites on two farms
C	No exclosure	Water	
D	No exclosure	No water	

After 5 months, I measured height of the tallest growing stem, the extent of the canopy (d_1 , the longest axis, and d_2 , at right angles to it), number of stems, and diameter of the thickest live stem.

2.3 Grass-removal experiment

In September 2004, using the same individuals from the Benfontein plots as used for the exclusion experiment, I removed exclusion plots and cleared entire grass plants in a 1m^2 area around half of the saplings, leaving the other saplings as controls. After 6½ months, and a summer season of not exceptionally high, but consistent rainfall (257 mm), I measured the length of all new growth on the saplings.

2.4 Influence of fire on *A. erioloba* demography

Data were gathered after fires on two sites in March/April 2003. Both sites had burnt in the summer, near the beginning of the wet growing season. The first site, Vaalbos, had burnt 6 months prior to data collection, in October 2002. The second site, Susanna, had burnt in November 2001.

I do not have details of the circumstances of the fire on Susanna. The fire on Vaalbos was a headfire, having started on the neighbouring property on a hot ($36\text{ }^\circ\text{C}$) and windy ($70\text{ km}\cdot\text{hr}^{-1}$) day (Deon Joubert, *pers. comm.*). Owing to low herbivore densities on Vaalbos National Park, fuel loads were very high (C. Seymour, *unpubl. data*).

In most cases, the skeleton of this hardwood tree remains after fire, allowing height before burning to be estimated. At Vaalbos, five sites were chosen and a tree was randomly selected as a starting point. At least 30 trees were surveyed within the immediate vicinity of each randomly chosen tree. At Susanna, three sites were chosen and about 20 trees were sampled at each of the three sites. No data were collected for trees below 1m in height. At both sites, I measured tree height with a telescopic pole, but in cases where the trees had been felled by the fire, a tape measure was used to obtain a best estimate of height before burning. Resprouting on trees and part of tree resprouting were also noted.

2.5 Statistical methods

For the exclusion plot experiment, I used changes in height as a measure of growth. This method is susceptible to mis-measurement (e.g. soil level shifts relative to the top of the plant). I therefore excluded outliers by removing all observations outside the range of ± 1.5 standard deviations around each group mean, this resulted in removal of 2 data points from group A, 3 from group B, 1 from group C and 4 from group D. I applied an ANOVA to the exclusion plot data to ascertain any significant differences between groups.

Since the two fires were separate events, all analyses for the two sites were carried out separately.

3. Results

When considered in terms of height, more than 80% of *A. erioloba* at both sites were saplings, suggesting cohorted recruitment. Assessment of below ground stem diameter revealed a wide range of sizes, however, indicative of continuous recruitment, with few opportunities for escape.

There were no significant differences in height increases between plants that received supplemental watering and those that did not. There was also no significant difference between plants protected from herbivory and those not protected. There was, however, an interaction between supplemental water and protection from herbivores. Plants that had been watered but not protected did significantly better than those that had been watered and protected (Figure1).

Growth was significantly linearly related to belowground stem size for *A. erioloba* for both plots with and without grass. Although the slope of the relationship between growth and stem size was greater for plants from which grass had been removed, comparison of residuals showed that these differences were not statistically significant.

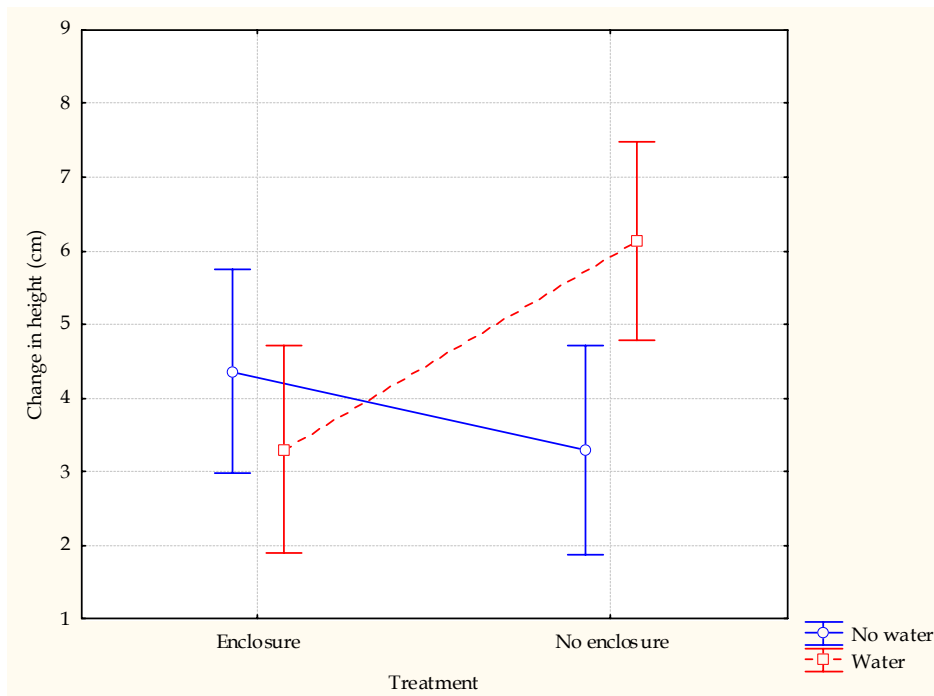


Figure 1 Least Square Means plot showing interaction between water and enclosure effects. Vertical bars denote 0.95 confidence intervals; $F(1.006) = 7.7356$; $p < 0.01$.

Table 2. Summary data for Vaalbos and Susanna

Site	n	Dead	Resprout	Survival %
Vaalbos	166	23	139	86%
Susanna	60	16	42	73%

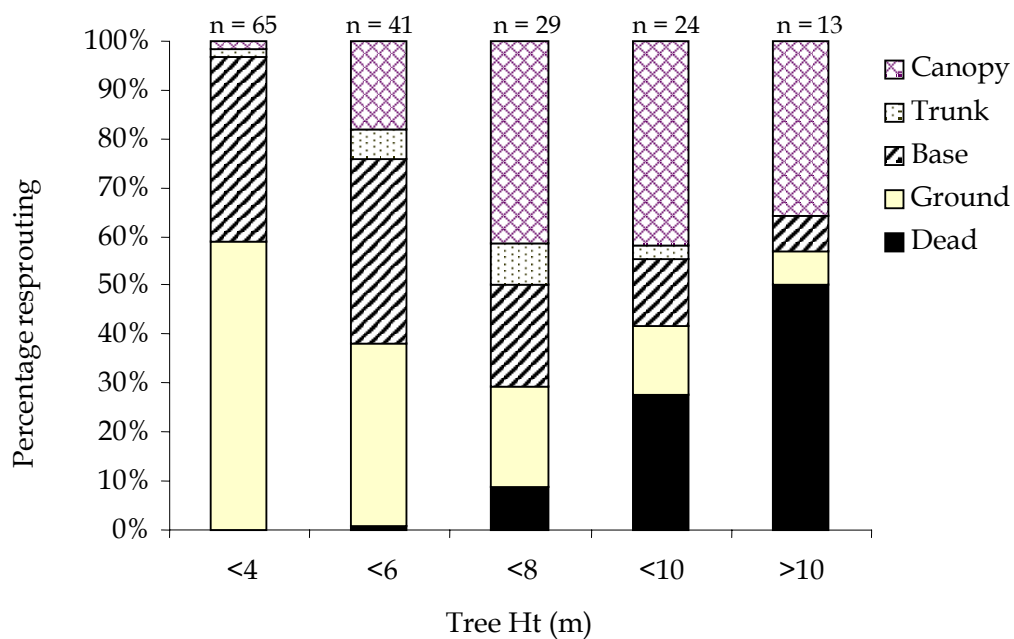


Figure 2. Resprouting response or mortality according to size class at Vaalbos.

Table 2 contains a summary of the survey of burnt areas at Vaalbos and Susanna. A number of trends were evident from resprouting and mortality data according to size class. Firstly, the percentage of individuals sprouting at ground level or from the base of the tree was far higher for smaller than larger individuals; secondly, the percentage of individuals sprouting from the trunk or canopy increased with increasing tree size; lastly, mortality rates were far higher in the largest size classes than in other size classes (see Figure 2 for resprouting and mortality response at Vaalbos). In other words, resultant proportional representation of tree size classes after fire sees total number of trees decline (average survival over both sites was 81.7%), and amongst surviving trees, proportion representation of large trees declined at both sites.

4. Discussion

Below ground stem sizes in this study revealed few true seedlings. Furthermore, although in terms of height, saplings appeared to be the same size, the array of sizes in belowground diameter suggests that these seedlings are of differing ages, and that seedlings “dribble” into the system. The predominance of short plants here implies that once established, many plants have yet to escape to higher size classes, so in the Kimberley area, escape or reversals can present a major obstacle to reaching maturity.

But what is preventing escape? Results of the exclusion plot experiments and removal of grass suggested that neither water availability nor competition from grasses exclusively govern growth rates, although these factors produced significant differences in concert. Many studies point to detrimental effects of herbivory on woody plant growth and survival rates (Belsky, 1984; Weltzin *et al.*, 1997; Barnes, 1999; Augustine & McNaughton, 2004). Browsing was noted on two thirds of the unprotected plants, but because exclusion of herbivores also excluded grazers, the negative effects of competition with grass obscured any positive effects of protection from browsing.

Inability to escape is exacerbated by slow growth rates for *A. erioloba* saplings, keeping them within heights at which negative effects from herbivory, fire and competition with grasses for light (and perhaps water) are influential. The group that fared best in the exclusion plot experiment only achieved mean height increases of 60mm during one growing season (95% confidence intervals: 40 and 80 mm). Barnes (1999) found similar growth rates in her study, where average increase in seedling height was only 48mm per growing season, although browsing seems to have been more intense at her sites. At a drier site, Kgalagadi Transfrontier Park (mean annual rainfall = 233mm.year⁻¹), van Rooyen *et al.* (1994) found average growth rates of 65 mm a year between 1978 and 1994.

These apparently slow growth rates may be because most early growth is concentrated belowground: a seedling only 25 cm high can have roots longer than 320 cm (Leistner, 1967), and even a tiny seedling (5cm high and estimated to be two months old) can have a tap root of nearly 110 cm (C. Seymour & O. Huyser, *unpublished data*). Larger individuals have been recorded to have roots to depths of 60m (Canadell *et al.*, 1996).

If well-established saplings are deep-rooted, then provision of supplementary water should not be expected to significantly influence growth. Indeed, the group that received supplementary water and protection from herbivores fared worst of all, likely because the grasses monopolized supplementary water (see e.g. Knoop & Walker, 1985; Weltzin & McPherson, 1997; Schenk & Jackson, 2002; van Langevelde *et al.*, 2003) responding with far greater growth rates than the *Acacias*, and outcompeting them for light. Removal of grass by grazing likely reduces competition for water, but more importantly for shade intolerant, deep-rooted species like *A. erioloba*, it reduces competition for light.

Warner and Chesson (1985) coined the term “storage effect” to describe the phenomenon whereby successful recruitment to adult size classes is episodic and a species’ continued existence relies on the continued survival of its adult population. Recruitment events are effectively stored in the adult population until favourable recruitment conditions arise. This could account for the exceptional longevity, estimated to be up to 300 years (Barnes *et al.*, 1997), of *A. erioloba* compared to other *Acacias*. More important, however, is that the adult population is critical to continued existence of the species, and unchecked harvesting of adults is of conservation concern, for both the species and the biota and ecosystem processes so reliant upon it. Saplings are not reproductive, hence the population is dependent upon proportionally few long-lived individuals for the majority of the reproductive effort. The seedling bank does suggest, however, that once escape is achieved, there will be incremental recruitment into larger size classes.

Of interest for future work would be how anthropogenic increases in atmospheric CO₂ will affect growth rates of *A. erioloba* seedlings, since increased CO₂ is expected to favour woody plants (Bond & Midgley, 2000; Bond *et al.*, 2002), and increase their water use efficiency (Polley, 1997). Climate change itself as a consequence of global warming is expected to see more extreme events (both droughts and floods) as well as fires, so modeling exercises may be able to shed light on anticipated change. Furthermore, recent work carried out in Amazonia (Laurance *et al.*, 2004) found that representation of faster-growing tree genera had increased within long-term monitored plots, likely as a result of elevated CO₂. It would be

interesting to know if such changes would be likely between, say, *A. erioloba* and bush encroaching species like *A. mellifera*, which although are both “*Acacia*” at present, are polyphyletic (see Orchard & Maslin, 2003; Luckow *et al.*, 2005 for a brief overview of the naming debate).

High mortality rates in *A. erioloba* during fire lead to a number of predictions. Firstly, high mortality rates for large *A. erioloba* suggest that above a certain threshold of fire frequency, populations are unable to persist. These mortality rates are no doubt influenced by fuel load, amount of plant biomass beneath the tree canopy and the existence of nesting and other materials within the tree canopy.

Secondly, the storage effect (Warner & Chesson, 1985), in which there is selection for longevity to compensate for rare recruitment events, should be counterbalanced by high mortality rates of larger (arguably, older) individuals, so there may be differences in longevity between populations as one moves across the aridity gradient. In other words, in areas with higher rainfall, recruitment is likely to be more frequent, and fires are also more frequent. There has likely been more pressure on populations in arid areas to evolve longevity than on populations in more mesic areas, where mortality to fire and recruitment are both more common. In addition, fire frequency in different parts of the geographic distribution of *A. erioloba* may have selected for genetic variation between populations. This would certainly concur with the finding that height growth in this species was strongly negatively correlated with latitude of the origin of seeds (Barnes *et al.*, 1997). Lower latitude sites in which *A. erioloba* occurs tend to be wetter, and by implication, have more frequent fires, so there would have been evolutionary pressure for seedlings to grow taller faster in areas with higher fire frequency.

Thirdly, tree architecture is likely to change with fire frequency, so there may be a difference in tree shapes with age across the aridity gradient. Archibald and Bond (2003) found fire to exert considerable selective pressure on tree architecture in South African savannas. I would therefore predict that lower hanging branches on large individuals would only be seen in the more arid extent of the range of *A. erioloba*.

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