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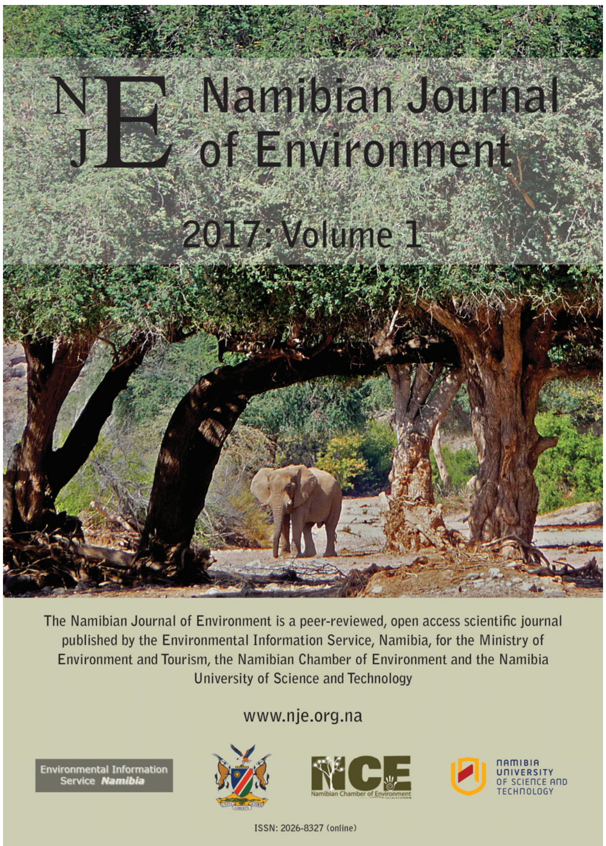

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Growth rates and mortality patterns of *Acacia mellifera* subsp. *detinens* in the semi-arid Highland Savanna, Namibia: Encroachment is not as rapid as previously believed

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ABSTRACT

Perceptions regarding bush thickening in Namibia are rarely tested. It is often thought that bush thickening species such as *Acacia mellifera* subsp. *detinens* grow rapidly and recruit often. We estimated the growth rates and mortality patterns of 31 *A. mellifera* subsp. *detinens* shrubs in the arid Highland Savanna vegetation type in Namibia that were less than one metre tall in 1972, by remeasuring their heights in 2007. Some of these shrubs' heights were also remeasured in 1988. Growth rates were variable but on average individuals grew 3.19 cm in height per year. Growth was slower between 1972 and 1988 (2.67 cm per annum) than between 1988 and 2007 (3.85 cm per annum) for ten individuals remeasured in 1988. Based on these data, individuals of 1.5 m height are likely to be approximately half a century old, individuals of 2 m height 65 years old and individuals of 4 m height well over a century old. Mortality was high over the 35-year period (61.3%). Mortality between 1972 and 1988 was higher (45.2%) than between 1988 and 2007 (29.7%). These results support other studies that suggest that *A. mellifera* subsp. *detinens* is a very slow-growing species in the Highland Savanna, and that mature bush thickets observed today were mostly in existence as mature bush thickets half a century ago. *Acacia mellifera* subsp. *detinens* is a long-lived species, living for well over a century, but is susceptible to drought. Further implications of these findings are discussed.

Keywords: *Acacia mellifera* subsp. *detinens*; bush encroachment; drought; growth rate; Highland Savanna; mortality; Namibia; rainfall; recruitment; saplings; seedlings; vegetation

INTRODUCTION

Much has been written about bush thickening globally, regionally and nationally (O'Connor et al. 2014), yet little empirical evidence is available to support several conflicting theories (Ward 2005, Joubert et al. 2008). For example, some researchers suggest that fire is necessary to stop the transition from a grassy state to a bushy state and that grass competition plays only a secondary role (Joubert et al. 2008, 2012). However, others believe that competition with grass is sufficient to reduce the growth of seedlings and saplings, and even kill them, provided that the perennial grass cover is high and the tufts are healthy (e.g. Ward & Esler 2011). There is also evidence to suggest that the increase in atmospheric carbon dioxide is a primary driver of bush thickening (Bond & Midgley 2012, Buitenwerf et al. 2012).

Recruitment is continuous in some species such as *Prosopis glandulosa* in semi-arid grasslands in Texas, USA (Brown & Archer 1999). However, Watson et al. (1997) have demonstrated both episodic peaks in, and continuous recruitment of, two shrub species in arid rangelands in western Australia. In other species such as *Acacia* (*sensu lato*) *mellifera* subsp. *detinens* in semi-arid southern African savannas recruitment occurs episodically and infrequently, during periods of protracted above average annual rainfall (Joubert et al. 2008, 2013). Seymour (2008) showed episodic recruitment from seed, but a continuously recruiting sapling bank, for *A. erioloba* in an arid South African savanna. These observed responses in arid rangelands clearly show that the process of thickening does not follow a uniform pattern among all species and in all environments.

Little has been written on the growth rates of individuals of encroaching species. This is despite its importance in understanding encroachment rates and patterns and in improving predictions of sustainability for wood industries such as charcoal production and biomass energy plants. This short paper presents growth data of *A. mellifera* subsp. *detinens* from height measurements taken in 1972, and repeated in 1988 and 2007, in the Highland Savanna. It also reports on the mortality rates of the measured individuals over the same period.

METHODS

Study Site

The Highland Savanna vegetation type (Giess 1998) has a mean annual rainfall of approximately 360 mm (CV=40%) in Windhoek. It is characterised by woody species including *A. hereroensis*, *A. hebeclada* subsp. *hebeclada*, *A. mellifera* subsp. *detinens*, *A. reficiens*, *Euclea undulata*, *Dombeya rotundifolia*, *Tarchonanthus camphoratus*, *Searsia marlothii*, *Albizia anthelmintica* and *Ozoroa crassinervia*. Valuable climax grasses include *Brachiaria nigropedata*, *Anthephora pubescens*, *Heteropogon contortus* and *Digitaria eriantha*, but *Eragrostis nindensis* (considered a subclimax grass) is usually the most abundant (Joubert 1997). On many farms, the climax grasses are largely absent, being replaced by *Michrochloa caffra* and various annual pioneer species including *Aristida adscensionis*.

This study was undertaken on the farm Sonnleiten which is located about 20 km east of Windhoek in the Highland Savanna vegetation type. The farm has been in existence for over a century, and over this period has been used primarily for cattle production. In the 1970s, Mr. Argo Rust, the farm owner, adopted the high intensity, short duration method of grazing, as prescribed by the principles of Holistic Resource Management (Savory 1991). Wildlife species include kudu (*Tragelaphus strepsiceros*), oryx (*Oryx gazella*) and springbok (*Antidorcas marsupialis*). Currently, the farm is largely encroached with *A. mellifera* thickets and very little perennial grass cover occurs.

Sonnleiten is approximately 5,000 ha in extent, which is a typical size for a commercial farm in the Highland Savanna. The farm is characterised by steep mountainous slopes that are covered by lithic leptosols, typically <30 cm in depth, with a high proportion of schist and quartz gravel, as well as deeper eutric leptosol pediments below these slopes (Mendelsohn et al. 2002).

Data Collection

Rainfall data were obtained from Neudamm Agricultural Office, approximately 5 km from the study site on Sonnleiten Farm.

In 1972, four permanent circular plots with a radius of 5 m (78.54 m^2) each were established on Sonnleiten by Argo Rust. Within each plot, all woody, perennial plants were mapped and their heights measured. In 1988, one of the plots, which contained 10 surviving individuals of *A. mellifera* subsp. *detinens*, was remeasured. By November 2007, a total of 31 individuals remained alive in the four plots and these were remeasured. Although height is not as good an indicator of biomass growth as are other parameters (Hasen-Yusuf et al. 2013), the continued use of height was necessary for comparisons with 1972. Mean annual growth rates were determined from the height data. Mortality was also recorded. It was possible to determine the growth rates and mortality patterns for two periods for ten of these trees (Period 1: 1972-1988 [16 years]; Period 2: 1988-2007 [19 years]). The difference in growth rates during these two periods was tested for significance using the using a Wilcoxon Matched Pairs Test (Statsoft 2004) to account for non-normally distributed data. The mean sizes of the ten trees that were measured in all three years (1972, 1988, 2007) were fitted to a linear model (Statsoft 2004) in order to get an approximate establishment time for the individuals, and a prediction for future size of individuals in 25 years.

RESULTS AND DISCUSSION

The data show a very slow increase in height of *A. mellifera* subsp. *detinens* shrubs over 35 years (Table 1). The maximum growth rate of just over 7 cm / annum was for an individual growing in an area of minimal competition, on a pediment soil that was much deeper than in the other areas. The next highest growth rate was 4.6 cm / annum. The mean annual growth rate for the ten individuals remeasured in 1988 was significantly lower in the first period (1972-1988) than in the second period of measured growth (1988-2007) (Table 1). The absolute growth rate of larger and older individuals would tend to be greater than smaller and younger individuals. None of the individuals was judged to be senescent.

Figure 1 shows the change in height of the ten individuals measured at all three time-steps (1972, 1988, 2007). Extrapolation of the regression equation suggests that for saplings that were measured in 1972

Table 1: *Annual growth rates of* Acacia mellifera *subsp.* detinens *shrubs between 1972 and 2007.*
Size range 1972 = 20-100 cm; 2007 = 106-288 cm

Period	N	Mean (cm)	Min (cm)	Max (cm)
1972-2007 (35 years)	16	3.19 (± 1.50)	0.95	7.09
1972-2007 (35 years)	10	3.12 (± 0.94)	1.43	4.6
1972-1988 (16 years)	10	2.34 (± 1.38)	-0.63	3.75
1988-2007 (19 years)	10	3.78 (± 1.05)	2.63	6.37

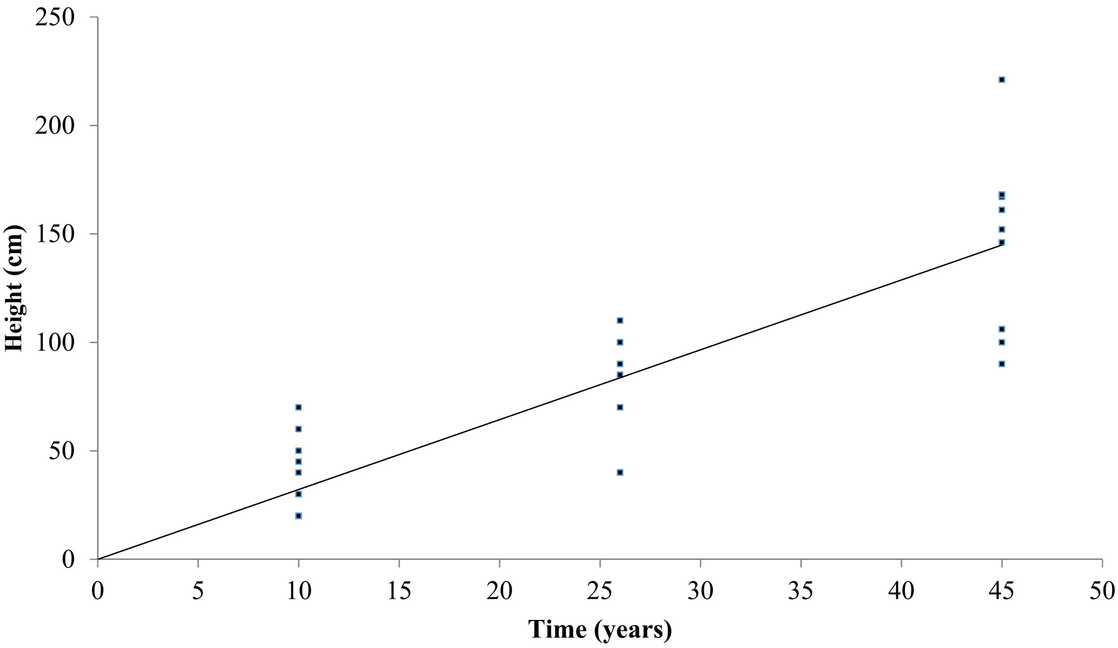

Figure 1: *Regression line fitting the heights of ten* Acacia mellifera *subsp.* detinens *shrubs between 1972, 1988 and 2007. The equation is Stem height (cm) = 3.219 x years. The adjusted R^2 value is 0.712. Some individuals have the same values which is why fewer than ten data points are illustrated at each time step.*

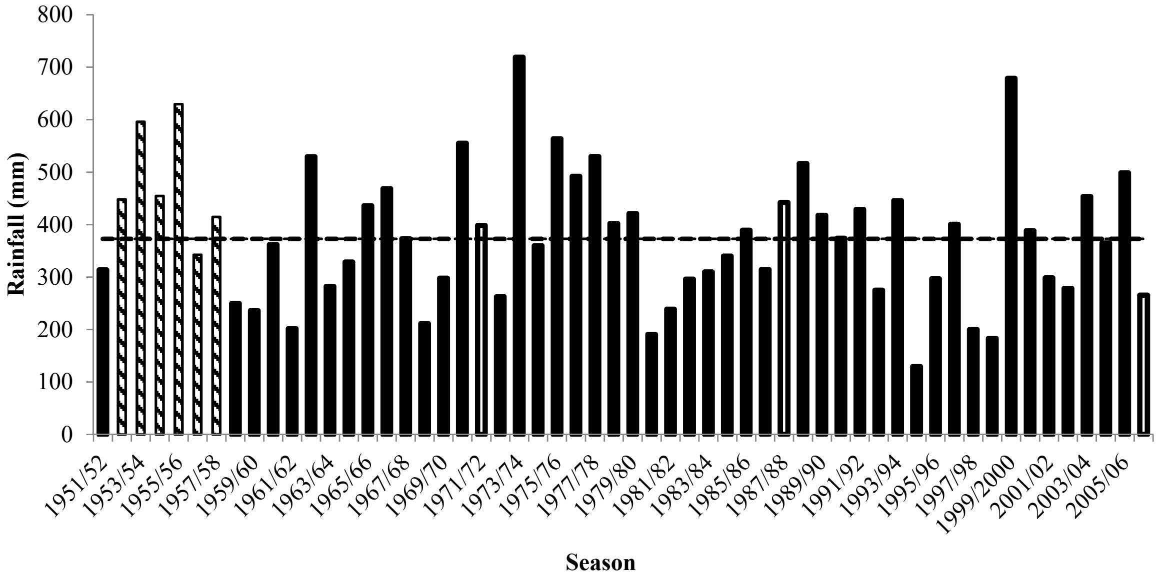

Figure 2: *Rainfall data from Neudamm Agricultural College from 1951-1952 to 2006-2007. The patterned bars denote the rainfall during the likely time of establishment of the cohort of plants measured. Open bars denote the rainfall at the time the plants were first measured (1972), measured again (1988) and for the last time (2007).*

germination occurred ten years previously (i.e. in 1962), assuming a linear pattern in height growth. However, germination of the 31 individuals measured is much more likely to have occurred between 1952 and 1958, when there were two (1952-1953 and 1953-1954) and three (1955-1956; 1956-1957 and 1957-1958) successive seasons of above average rainfall (Figure 2).

Recruitment is dependent upon rare, protracted above average rainfall periods (Joubert et al. 2008, 2013), as was experienced in the 1950s (Figure 2). If this is the case, then the saplings measured in 1972 would have been between 14 and 19 years old. Saplings that germinated in 2001 on Krumhuk farm nearby were typically less than 10 cm high after six years of growth, with mean stem diameters of around 5 mm

(Joubert et al. 2013). However, seedlings at Neudamm College, germinating in 2007, grew faster (Joubert 2014), suggesting large variability in early growth rates, dependent upon rainfall. The growth rates after recruitment are likely to be slower in absolute terms, but variable, and highly dependent upon soil moisture. It is likely that the individuals measured at Sonnleiten were between 49 and 54 years old in 2007. Shrubs between 1 m and 2 m are typically believed by rangeland managers to be around 10 years old. This misconception could be due to: i) the observation of trees with faster growth rates in micro-environments where water accumulates and ii) the rapid growth rate of resprouts from the stumps of trees either cut or burnt or suckering from lateral roots after extreme disturbance, for example in borrow pits. Forecasting with the regression model shown in Figure 1 suggests that the individuals would only reach a height of approximately 2 m at approximately 65 years. Growth rates measured at Sonnleiten, however, are from individuals growing in shallow soils under more arid conditions than many areas where encroachment is a more serious problem. For example, heavily encroached areas in Thornbush Savanna typically have >400 mm annual rainfall and are characterised by having deeper soils with a higher clay content than are found at the study site at Sonnleiten. Thus, growth rates in these areas of higher rainfall and finer and deeper soils are more likely to be closer to the maximum (7.09 cm per annum) measured for a single individual growing on deeper soils at Sonnleiten.

The mortality rates observed in this study (Table 2) were surprisingly high. It is not known how much of the mortality was due to self-thinning, but drought stress and fungal dieback are likely to have contributed greatly. Mortality in the first period was much higher than in the second period. Unpublished data (Joubert) and farmer knowledge suggest that sapling mortality can be very high, particularly in dry years. There were five consecutive below average rainfall years (1980-1981 to 1984-1985) in the first period, as opposed to three periods of two consecutive years of below average rainfall (1994-1995 to 1995-1996; 1998-1989 to 1999-2000 and 2001-2002 to 2002-2003). These protracted periods of below average rainfall are likely to have been the major cause of mortality.

The slow growth rates shown here, the high mortality rates, and the rareness of recruitment events, as shown in other studies (Joubert et al. 2008) support the authors' view that woody plant encroachment is generally a much slower process than previously supposed. Joubert (2014), using aerial photos, showed that a 25-50% increase in cover occurred in the 50-year span between 1958 and 2007 on Sonnleiten Farm. However, the mean increase on

Table 2: *Mortality patterns of 31* Acacia mellifera *subsp.* detinens *shrubs on Sonnleiten Farm.*

Time period	**Number of individuals or %**
Population in 1972	**31**
Survivors from 1972 in 2007	**12**
Died by 1988	**14**
Died between 1988 and 2007	**5**
Mortality overall	**61.3%**
Mortality 1972 to 1988	**45.2%**
Mortality 1988 to 2007	**29.4%**

three farms studied was 14-26% and some mature thickets decreased by 17-35% during this time.

In another study using matched photography spanning 130 years, Rohde and Hoffman (2011) found an overall increase in woody cover of 1.5% (range -5% to 15%) for shrubs <1.5 m and 22% (range -5% to 48%) for trees >1.5 m in what they termed "tree and shrub savannas" which broadly corresponds with the Highland Savanna in this study. This would be viewed as surprisingly modest by most rangeland managers and scientists in Namibia today. The current perception that existing thickets of large trees were initiated during a drought period coinciding with a foot-and-mouth outbreak in the late 1950s is disproven by these observed slow growth rates of species. Based on this study, thickets with 4 m trees are likely to have established more than a century ago.

Growth rates in deeper soils, with higher clay and nutrient contents, and in higher rainfall areas are likely to be significantly higher, as is reflected by the higher growth rate of the individual growing in deeper soils in this study (more than double the mean). Joubert et al. (2013) show that seedling and sapling growth, in the first six years, is much slower than the growth of the mature shrubs in this study.

CONCLUSION

Acacia mellifera subsp. *detinens* is a slow-growing species, contrary to current popular perceptions of the species being an "aggressive invader". Combining this with the fact that recruitment is highly episodic (Joubert et al. 2008, 2013), it appears that preventative management of bush thickening by this species is easier than was previously supposed. Currently observed thickets of mature *A. mellifera* subsp. *detinens* trees are likely to be much older than previously thought. The perception that bush thickening is the single most important factor explaining the perceived decline in rangeland productivity since the late 1950s (De Klerk 2004) is challenged by this study, and other recent studies (e.g. Rohde & Hoffman 2011, Joubert 2014).

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