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A simulated history of *Aloe dichotoma* recruitment and its link to rainfall: Insights from an isolated population near Kenhardt

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Abstract

Aloe dichotoma populations differ in their rates of recruitment and mortality across the species distribution in South Western Africa. Little is known about how recruitment and mortality rates are affected by local climate and ecological factors. Using repeat photography and a statistical recruitment model, the recruitment history of an emerging population of over 200 *A. dichotoma* individuals near Kenhardt was simulated. Historical rainfall data was used in order to assess the possible link between rainfall and recruitment.

Recruitment patterns were found to be a combination of episodic events of varying length and magnitude superimposed over a background of low-rate continuous recruitment. The largest, most extended episodic recruitment period peaked in the mid-1970s and led to the establishment of most of the individuals in the Kenhardt population. These trees were generally between 150 and 250 cm in height (2013). Newly discovered juveniles below 100 cm in height were predominantly the result of relatively small and brief episodic recruitment events that occurred in the mid and late 2000s. Between episodic recruitment events, evidence for low-rate continuous recruitment is present, particularly in more recent years.

Episodic periods of high-rate recruitment were found to be linked to high rainfall. The largest, most extended recruitment period coincided with the exceptionally high rainfall of the 1970s. The more recent episodic recruitment events also coincided with high rainfall spikes during the 2000s. While correlations between rainfall variables and recruitment were significant, many other factors may affect the strength of this relationship.

The study improves our understanding of the factors influencing recruitment in *A. dichotoma* and provides a framework for future investigations of recruitment history in other *A. dichotoma* populations.

Introduction

Aloe dichotoma, otherwise known as the quiver tree or kokerboom, is an arborescent, desert succulent which occupies a wide geographical range across semi-arid and arid South Western Africa, including both summer and winter rainfall zones. This arid-adapted, succulent species is considered an icon of the succulent karoo and desert biomes. Its distribution ranges from Nieuwoudville in the Northern Cape of South Africa to the Brandberg Mountains in Namibia, occurring near to the west coast and as far inland as Prieska in the East.

Recruitment and survival of these relatively long-lived (<200 years (Vogel 1974)) desert succulents is potentially precarious in some populations due to the impact of the harsh environmental conditions experienced across their range. Due to their vulnerability in the juvenile stage, slow growth and maturation, and often small population sizes, slight changes in the levels of mortality and recruitment could have significant effects on the long-term sustainability of certain populations.

While *A. dichotoma's* distribution and population demography have been well studied (Midgley 1997, Kaleme 2003 unpublished MSc thesis, Foden et al 2007, Hoffman et al 2010, Jack 2011 unpublished MSc thesis), little work has been done toward understanding the key life-history traits of this species. The patterns in which the recruitment of new individuals occurs as well as the environmental conditions required for this recruitment is unknown for this species. Recruitment and mortality was found to vary greatly in different populations across the species distribution (Midgley 1997, Foden et al 2007, Jack 2011 unpublished MSc thesis). This is likely to be predominantly due to the high spatio-temporal variation in climate across this range, especially as it includes both summer and winter rainfall zones (Jack 2011 unpublished MSc thesis). Understanding the interactions between particular populations and their local climate as well as other ecological factors will elucidate the reasons for such variable mortality and recruitment across the species distribution.

Recruitment through the establishment of new juveniles is thought to be predominantly event-driven and episodic in arid environments as climatic conditions suitable for germination and subsequent juvenile survival are relatively rare (Jordan and Nobel 1979, Midgley et al 1997). For example, the recruitment of the large, arborescent desert succulent, *Carnegiea gigantea* (saguaros) is ultimately limited by moisture in the Sonoran Desert and recruitment was found to be particularly dependent on the occurrence of high summer rainfall (Drezner 2004). Importantly, sufficient precipitation during years following germination is critical for juvenile survival (Brum 1973). Similarly, the establishment of *Agave deserti* juveniles, a common desert succulent, requires unusually wet years. Water stress during the juvenile stage was found to be the most important factor affecting establishment (Jordan and Nobel 1979). These long-lived desert succulents are shallow rooted and rely on rainfall as their primary water source. They often grow in cohorts during periods with especially favourable conditions (Jordan and Nobel 1982; Turner 1990).

Although there is limited information on the reproductive ecology of South Africa's arborescent succulents (Cousins and Witkowski 2013), comparable growth form and habitat allow for the reasonable assumption of similar moisture limitations when addressing *A. dichotoma* recruitment in the arid and semi-arid systems of South Western Africa. Detailed investigations into *A. dichotoma* populations are required to determine whether recruitment is episodic, continuous or a combination of both and how environmental factors such as rainfall may influence this recruitment.

Methods

Overview

In this study the recruitment patterns of an *A. dichotoma* population near Kenhardt were investigated. The population recruitment history was reconstructed using repeat photography and a statistical recruitment model. Reconstructed recruitment was used to determine if recruitment in this population has been episodic, continuous, or a combination of both. Historical rainfall data from the Kenhardt area was then examined in order to assess the possible link between recruitment and rainfall.

Study site

A relatively young population of *A. dichotoma* situated near Kenhardt (Fig1) in the nama Karoo provided an ideal opportunity to study the recruitment patterns associated with the establishment and growth of a population. This population is special in terms of its potential to provide this information as the date of origin for the population is known. Four original quiver trees were planted at a grave site in 1906, about 8 km out of Kenhardt (Fig1). These four original individuals have remained in the landscape and have led to the recruitment of over 200 new individuals over the last 107 years. Most trees are situated on a gentle, elongated hill where water does not naturally collect. This means that the Kenhardt population is probably limited to using rainfall as its only water source as their extremely shallow roots cannot access groundwater. The site is surrounded by communal land and is subject to some grazing and visitation by people.

Rainfall data was obtained from the South African Weather Service (SAWS) for Kenhardt weather station No. 02512615. Missing data from 1936 -1940 as well as 1959 were replaced by data from Kenhardt station 0251261W (Pol). Temperature data was not available for Kenhardt and therefore an investigation of temperature was not included in the study. The nearest reliable temperature data was from Upington (120km away) and was only available from 1952 onward. This data was inappropriate for a detailed investigation of temperature in Kenhardt.

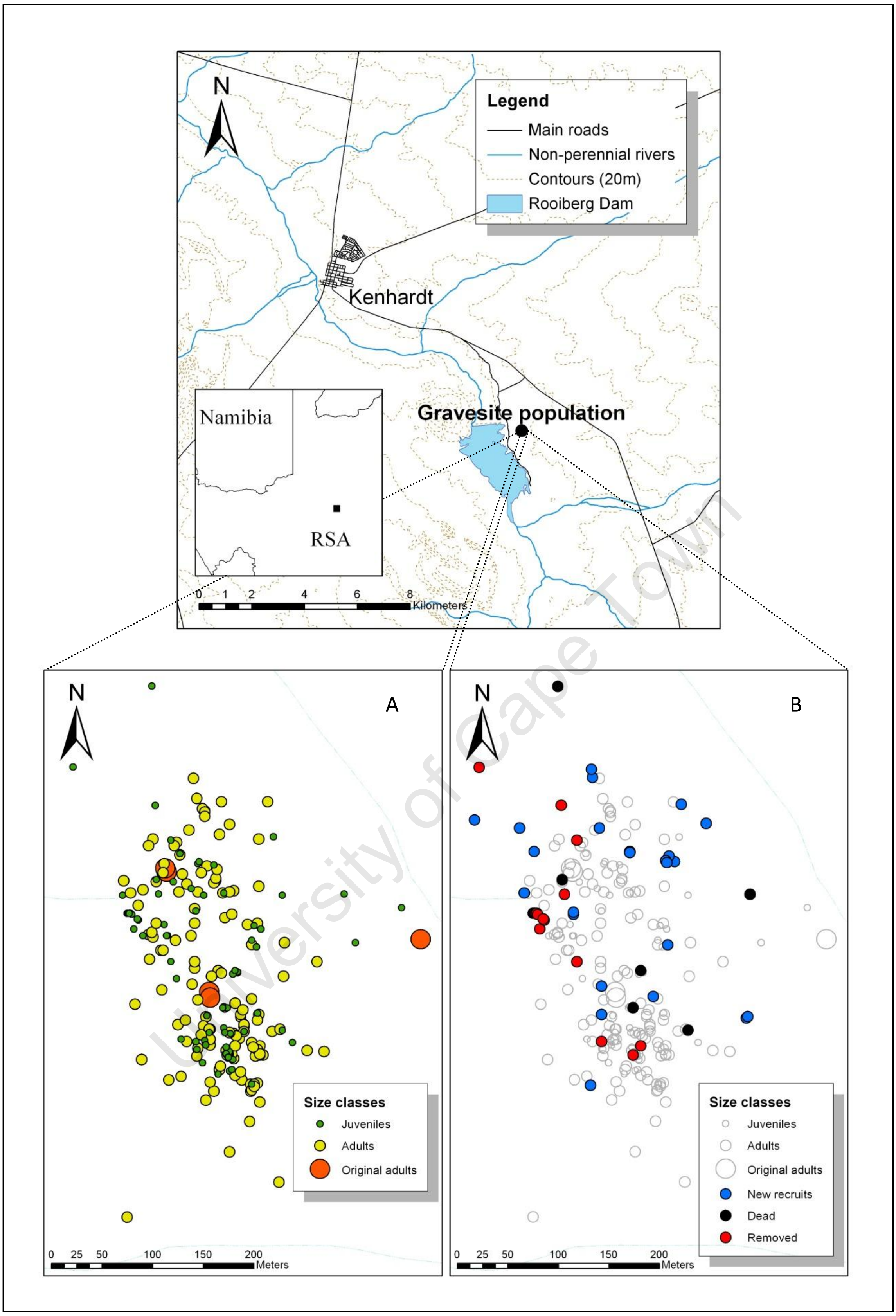

Figure 1: Map of the study area showing the location of the *A. dichotoma* population and the basic population demography. A = population structure in 2008. B = population changes in 2013

Estimating tree age/recruitment year

In order to reconstruct the recruitment history of the Kendardt population, the likely age of each tree must be calculated. In its simplest form, Age = Height/Growth Rate. Tree heights were measured but growth rates were determined using probability density functions.

Generating growth rate probability density functions (PDFs)

A. dichotoma growth rate is not linear and may vary greatly throughout an individual tree's life time. This variation stems from intrinsic, size-specific differences in growth rate, resource availability, microclimate and individual health. It was therefore not possible to simply measure an individual's growth over a single time period and assume this to be its constant growth rate. Instead probability density functions (PDFs) were produced in order to incorporate the variation in possible growth rates.

Growth rate PDFs were produced using the measured growths of all individual trees in the population over 5 years. A Gaussian Kernel function in R was used to fit these growth rate distributions. Two separate PDFs were produced for trees above 300 cm tall and trees below 300 cm tall (PDF>300 & PDF<300 respectively). These two size classes have significantly different growth rates, t (196)= -3.92, $p<0.001$ (Fig5). Two separate PDFs were therefore required to represent the difference in the range of growth rates between these two size classes. PDF>300 peaked in density at 0.017m/yr (1.7cm/yr) and PDF<300 peaked in density at 0.046m/yr (4.6cm/yr) (Fig2). Peaks in 'density', a relative measure of likelihood produced by the model, represent growth rates that were most likely to occur within each size class and were selected for most often by the model.

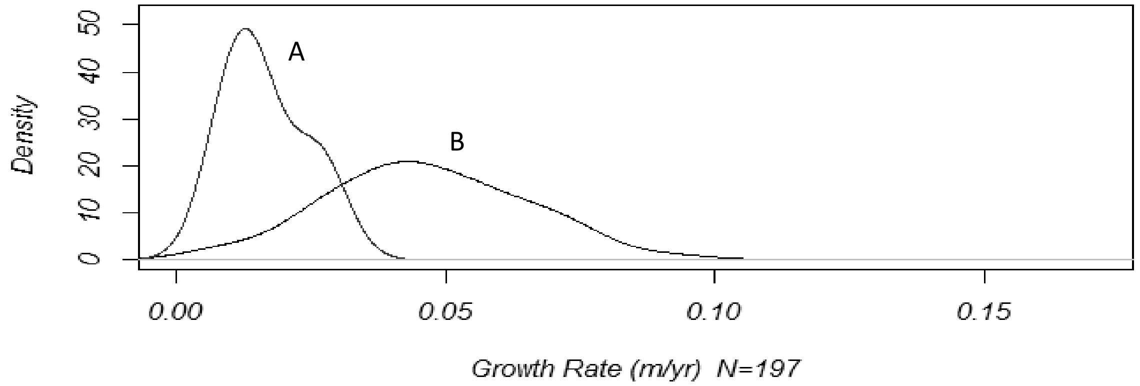

Figure 2: Growth rate probability density functions for trees above (n=7) and below (n=198) 300 cm in height (PDF>300 and PDF<300 respectively). A = PDF>300. B = PDF<300

The recruitment model explained

The natural variation in growth rate was incorporated in our statistical recruitment model through the use of the growth rate PDFs. Possible yearly growths drawn from the PDFs were sequentially subtracted from tree height in order to calculate tree age (Fig3).

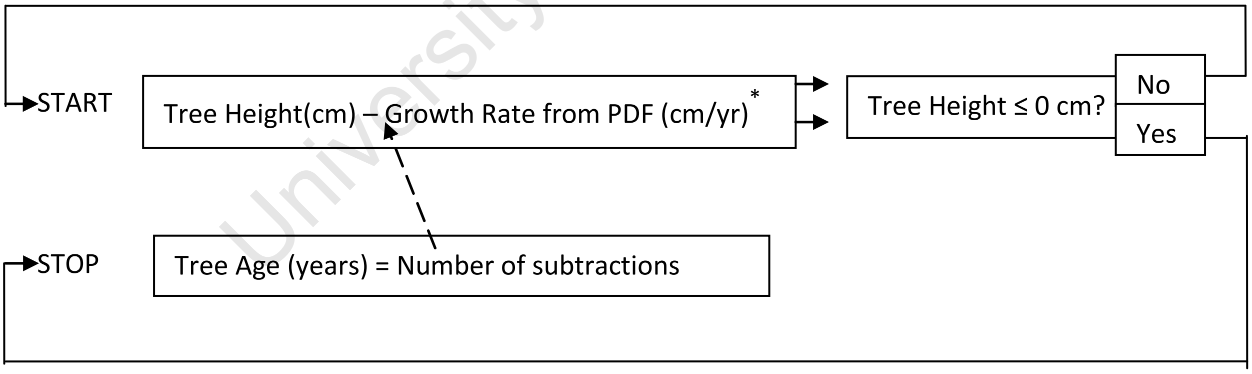

Figure 3: Model used to calculate tree age (years) using tree heights (cm) and growth rates (cm/yr) drawn from growth rate probability density functions

[*] For trees above 300 cm in height, growth rates were drawn from PDF > 300 and subtracted until tree height fell below 300 cm. Once below 300 cm in height growth rates were drawn from PDF < 300 (see “Generating growth rate probability density functions (PDFs)”)

For each *A. dichotoma* tree, a distribution of possible tree ages was produced by the model through 10 000 bootstrap replications. The distribution of possible ages for each tree was combined to produce a recruitment year PDF for the whole population (Fig6). This is an empirical distribution of possible recruitment dates for the population. ‘Density’ values for this output represent the combined relative likelihood of recruitment in each year that has occurred in the population since its origin.

Growth rate measurements in the field:

In order to create the PDFs for growth rate, the change in height of each tree in the population over 5 years was measured. For this study, an original database of 240 Kenhardt *A. dichotoma* photographs from 2008 was used. Using the 2008 photographs as references, a second photograph of each tree was taken in 2013. To ensure a close match between 2008 and 2013 photos, careful attention was paid toward camera angle, camera height and distance from tree. GPS co-ordinates and marked rocks were used to relocate individual trees in the 2008 photos. Photographs were taken using a Canon 400D and camera-settings were kept constant. In both original and repeat photographs a ranging rod was placed next to the tree, upright and in line with the centre of the stem, relative to the position of the photographer.

The original and repeat photographs for each tree were analysed in order to determine growth rate over the last 5 years. Two measuring techniques were used including reading tree heights off the ranging rod for trees below 300 cm tall and matching photographs of trees above 300 cm tall. Photos of trees >300 cm were carefully matched as their height introduced possible error of parallax with regard to reading heights straight off the ranging rod.

Results

Description of the Kenhardt population:

The majority of Quiver Trees photographed in both 2008 and 2013 were between 150-250 cm tall in 2013 (Fig4). There were very few large adults or juveniles present in our repeat photography data. A group of 18 juveniles (all < 100cm tall) that were photographed in 2008 were found to be missing upon returning to the site in 2013. It is likely that these 18 juveniles were illegally removed due to the absence of their decaying remains in the landscape. Evidence of excavation was also present at the exact locations recorded for these juveniles in 2008. Twenty five new juveniles were discovered in the 2013 study and were all under 100 cm in height. The majority of the newly discovered juveniles were between 10-40 cm in height, but individuals up to 88 cm were also recorded (Fig4). The taller of these juveniles may have germinated before the study in 2008 but due to their small size were not identified.

Figure 4: Frequency distribution of *A. dichotoma* heights in the Kenhardt population in 2013. Data includes all trees that were photographed in both 2008 and 2013 (dark bars) and the newly discovered juveniles (light bars)

While no clear relationship between growth rate and tree height existed in the data, the 7 largest individuals in the population appeared to have consistently low growth rates (<3cm/yr) (Fig5). The growth rate of individuals > 300 cm is significantly lower than the growth rate of individuals < 300 cm.

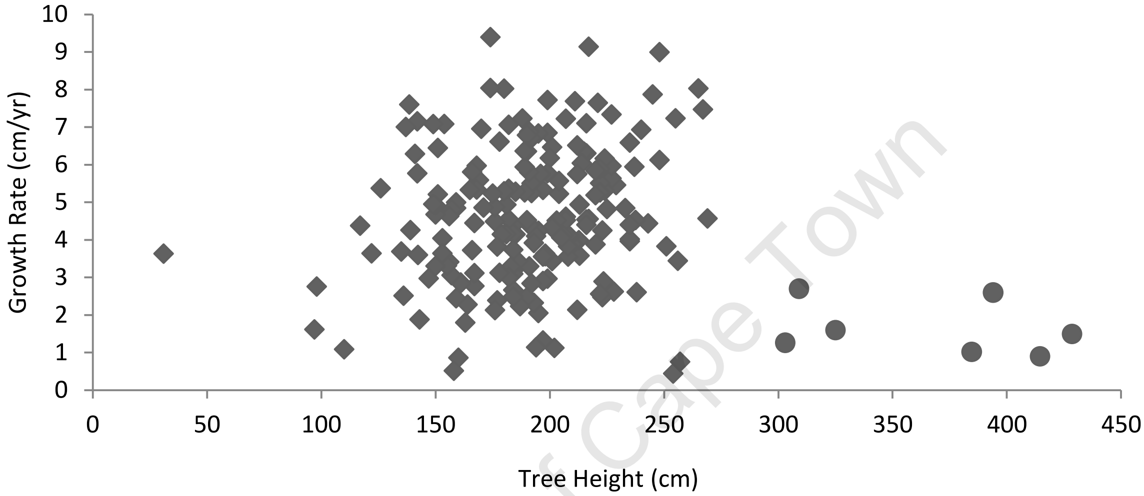

Figure 5: Tree height (cm) related to growth rate (cm/yr). Growth rate obtained from analysis of 198 repeat photographs (2008 &2013). Circles = trees larger than 300 cm. Diamonds = trees smaller than 300 cm.

Recruitment and rainfall:

Recruitment appears to have varied greatly in magnitude over time (Fig6). A very low probability of recruitment was present before the 1950s. The first and largest recruitment peak began to rise around the 1950s and reached a maximum density (i.e. the relative probability of recruitment) in the mid 1970s, before tailing off. The second, smaller recruitment peak included two, brief recruitment spikes in the mid and late 2000s. Between these high recruitment events seen in the 1970s and 2000s, a relatively low rate of recruitment was present.

Total annual rainfall has been highly variable between 1909 and 2012 and has fluctuated around a median of 127.45 mm/yr (Fig6). From the 1940s up until the late 1950s, numerous above average rainfall years occurred. These above average years were consistently separated by below average rainfall years. In contrast exceptionally high rainfall occurred during the 1970s. During this time relatively few years with below average rainfall occurred. Since the 1970s, punctuated, above average rainfall events have occurred, some continuing over more than a single year. Since the mid 2000s, two large rainfall events have been separated by a single year of below average rainfall. The largest rainfall spikes occurred in 1976 with 484.8 mm, 2006 with 349.5 mm, 1978 with 324.8 mm, 1974 with 321.4 mm and 1950 with 304.8 mm.

Overlaying recruitment probability and rainfall indicated that most recruitment occurred roughly during the largest rainfall peak and that more recent recruitment peaks matched rainfall spikes closely (Fig6). A correlation between annual rainfall (oct-sep) and yearly recruitment probability suggested that some of the variation in recruitment is significantly related to rainfall (r= 0.2124, t<0.05).

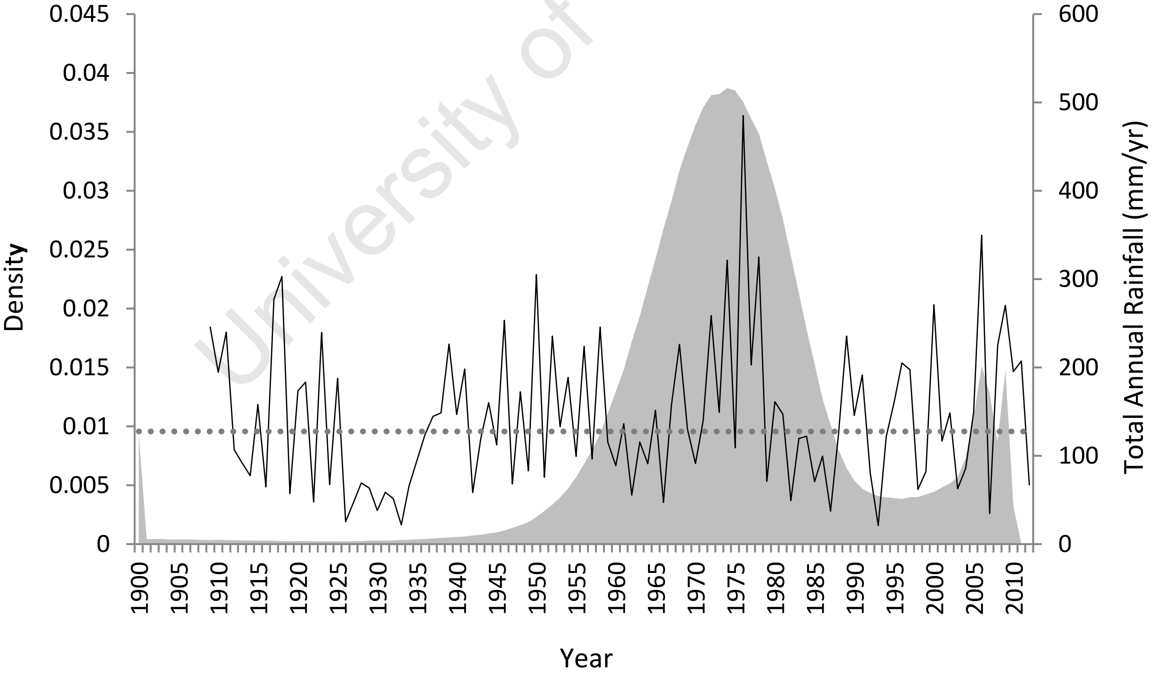

Figure 6: Recruitment probability density function (shaded grey area) from 1900 to 2012 for the Kenhardt *A. dichotoma* population and total annual rainfall (Oct-Sep) from 1909 to 2012 (black line). Rainfall data before 1909 was not available. The median rainfall of 127.45mm/yr is included (dotted line). Data for recruitment probability function includes all 198 re-photographed trees and 25 newly discovered juveniles.

Standardised precipitation index (SPI) values vary greatly since 1910 indicating the occurrence of unpredictable, variable periods of drought and high rainfall throughout the population's history (Fig7). SPI is a measure of the relative likelihood of a rainfall event occurring, taking into account the surrounding rainfall years. This allows for an objective interpretation of which periods were wet and which were dry relative to the history of rainfall in the Kenhardt area. The first half of the rainfall record from Kenhardt has been dryer than the second, with an extended period showing extremely low SPI values. High rainfall periods during the first half of the rainfall record show only moderately high SPI values. While periods with low SPI values were frequent during the second half of the rainfall record, extended periods with extremely high SPI values indicate a wetter recent history in the Kenhardt area. A correlation between average SPI (oct-sep) is significantly related to the probability of recruitment (r = 0.28, t= <0.01).

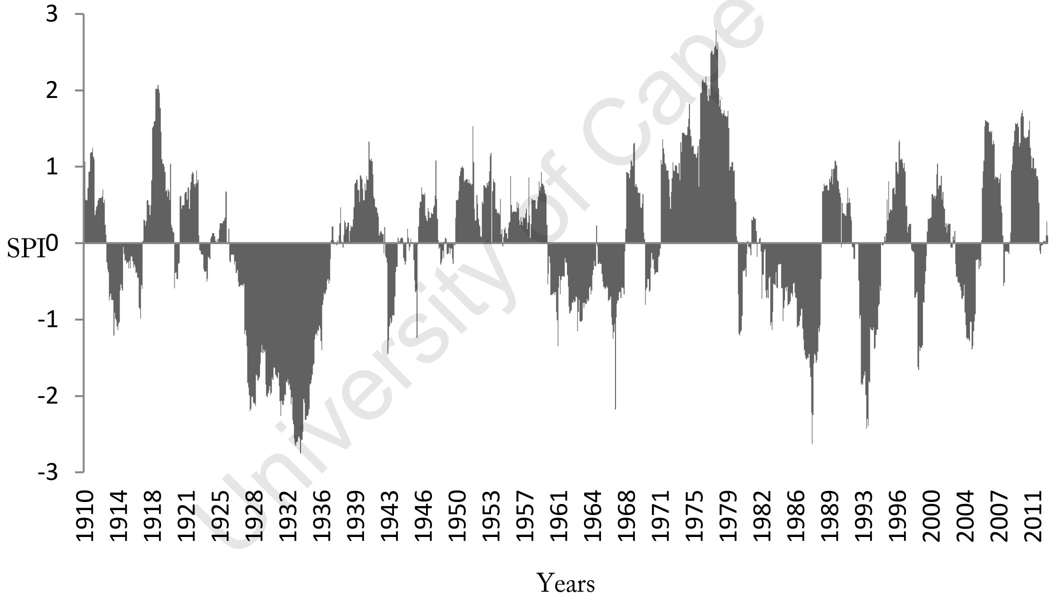

Figure 7: Standardised precipitation index (SPI) of Kenhardt rainfall from 1910 – 2012 using a 24 month time scale.

Discussion

The results of this study have not only documented the age class structure of the relatively young, emerging population of *Aloe dichotoma* near Kenhardt, but have also reconstructed the recruitment history of the remaining trees. These new findings have shed light on how populations may establish from parent plants, and how local climate and other ecological factors potentially affect this establishment.

Population demography: Recruitment and mortality

The Kenhardt *A. dichotoma* gravesite population appeared to be relatively healthy with high levels recent recruitment and low levels of mortality when revisited in 2013 (Fig1). However, the population size did not change much between 2008 and 2013 however due to the illegal removal juveniles. Of the dead trees found, most were juveniles and were identified by small fragments of their decaying remains. Juvenile mortality is likely to be underestimated in most studies as the remains decay relatively quickly compared to the remains of larger individuals. Furthermore, the juvenile stage in plants is often very sensitive and the probability of mortality decreases with increasing size (Steenbergh and Lowe 1969).

Recruitment patterns

Recruitment patterns appear to have been a combination of both episodic events superimposed over and trickle of continuous recruitment (Fig6). High rates of recruitment occurred episodically over extended, varying periods of time. Between these large magnitude recruitment events, a trickle of low-rate continuous recruitment occurred, particularly in more recent years. Close to the end of the century, many trees from the initial large, episodic recruitment event would have reached the reproductive adult stage. A larger seed rain from a greater number of contributing adults would increase the chances of seed landing in a wider range of micro-sites. This could in turn increase the probability that some of these seeds germinate under slightly less favourable conditions and survive, thereby contributing to a previously absent background trickle.

Due to major recruitment events taking place over extended periods of years and the occurrence of a continuous trickle of background recruitment, narrow size class cohorts were not formed in this population. Differences in the individual growth rates would have also contributed as different size trees of the same age were likely to exist in some cases.

Rainfall and recruitment

While total annual rainfall and SPI were significantly correlated with the probability of recruitment, only a limited amount of the variation in recruitment could be explained by these variables. Periods of high rainfall during the first half of the century were not accompanied by high rates of recruitment, while high recruitment rates do coincide with the wet periods in the later half of the century (Fig6). This is probably due to a number other factors which may influence the strength of the relationship between rainfall and recruitment. These factors are discussed further here.

Due to their slow growth, it would have taken the four original trees between 30 and 40 years to reach reproductive maturity. High rainfall before the mid 1920s is unlikely to have lead to any recruitment as no seeds would have been produced during this time. Flower number and seed production in aloes is correlated with plant height (Symes 2012, Cousins and Witkowski 2013) meaning that the ability of the initial four individuals to give rise to new recruits would have increased over time. Relatively lower flower and seed production by the original trees may contribute to the general lack of high recruitment rates during high rainfall events between the mid 1930s and late 1950s. Some recruitment may have taken place however as the probability of recruitment begins to rise during the late 1940s (Fig6). The build-up of a seed bank over time would be unlikely to contribute here as aloe seeds are unlikely to survive beyond a single flowering season (Symes 2012).

The continuity of high rainfall events appears to play an important role in securing the establishment of newly recruited juveniles. Numerous high rainfall years occurred from the 1940s until the end of the 1950s however these events were brief and were consistently separated by low rainfall years. This discontinuity of high rainfall appears to have been unfavourable for the survival of individuals past the early juvenile stage. The juvenile stage in plants is often very sensitive and the probability of mortality decreases with increasing size (Steenbergh and Lowe 1969). Juvenile mortality in *A. dichotoma* may be due to vulnerability to a number of factors including water stress and herbivory (Midgley et al 1997). Importantly, post-germination environmental conditions are a crucial factor influencing the survival and establishment of new juveniles after their germination (Bullock et al 2005) as the influence of climatic conditions may be most strongly linked to the early stages of recruitment (Matthes and Larson 2006). Due to the sensitivity of the juvenile age class, a single above average rainfall year may not be sufficient to secure the establishment of a newly germinated juvenile, and extended periods of high rainfall may be required (Turner 1990). Therefore the potential for the establishment of new juveniles during the 1940s and 1950s is likely to have been affected by the discontinuity of rainfall during this time.

Environmental conditions during seed production could also play an important role in determining the magnitude of a recruitment event. For example, drought could lead to low numbers of pollinators (Mueller et al 2005) which in turn would lead to low seed set and a low potential for a high magnitude recruitment event in the population. Similarly, inflorescences could be removed by antelope or baboons, or seed capsules could be attacked by pathogens, thereby limiting the amount of viable seed produced.

Other factors influencing recruitment

The role of nurse plants in facilitating the establishment of *A. dichotoma* is presently unexplored, however much is known about this phenomenon from other arid ecosystems (Nobel 1980, Drezner 2004). Nurse plants may provide a host of benefits for newly developing juveniles, such as extra moisture, shade from harsh sunlight, cooler temperatures and protection from herbivory (Smith and Correia 1992, Rojas-AreHchiga 2000). These factors are important as young juveniles have limited water storage capacity and small sizes which make them vulnerable to herbivores. Juveniles in the Kenhardt population were almost exclusively emerging from small shrubby bushes in the landscape. Nurse plant density at the study site may vary greatly over time and may influence the relationship between recruitment and rainfall. Nurse plants may become sparse or less leafy during extended low rainfall periods or periods of high grazing pressure and therefore have a lower capacity to intercept and protect *A. dichotoma* seeds dropped from their parent plants.

Temperature is also likely to influence the relationship between recruitment and rainfall. While very low temperatures could inhibit plants growth, high temperatures increase evaporative demand which could lead to plant stress or death during dry periods. Furthermore, it is known that germination is inhibited at extreme temperatures (Bairu 2009). While temperature data was not available for the Kenhardt region, data from Upington (120 km north of Kenhardt) suggested that temperatures generally fell with the acceptable bounds for germination without inhibition (see Appendix, Figure 1).

These factors are likely to have affected the patterns of recruitment and the relationship between recruitment and rainfall. Further work is required to determine the relative importance of each.

Model improvements

Our model outputs could be improved incorporating more growth rate measurements from juvenile individuals, as well as mature adults. Due to the illegal removal of almost all juveniles photographed in 2008, the modelled growth rate does not include this age class, for which growth rates might well differ considerably from other age classes. Beside the loss of growth rate data, the illegally removed juveniles also lead to missing recruitment peaks in the recruitment year probability density function. Their recruitment may have coincided with high rainfall events between the 1970s recruitment and the 2000s recruitment events. Similarly, a greater number of growth measurements for large mature adults would increase confidence in the PDF for individuals greater than 300 cm tall.

Lastly the recruitment model could benefit from a more in-depth exploration of how other tree metrics link to tree age. It is possible that younger trees increase in height faster that older ones, thereby eroding differences in recruitment date as time passes. At present, the model relies totally on height to distinguish differences in age between individuals. Including other features of the trees that change with age could help improve model accuracy.

Conclusions

The recruitment model provides an effective way to reconstruct the history of population recruitment based on tree heights and growth measurements. The pattern of both episodic and continuous recruitment in the Kenhardt population should be compared with other populations across the species distribution in order to assess the variability in recruitment patterns of different populations and how environmental factors may influence these patterns. This study provides a framework for the investigations of recruitment history in other emerging quiver tree populations in the future. This framework is somewhat flexible as it can be customised for any population by measuring growth rates in that population. Studies such as this one, if carried out on further populations, could help us to better understand the life history of *Aloe dichotoma* as a species as well as other arid adapted desert succulents.

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Appendix

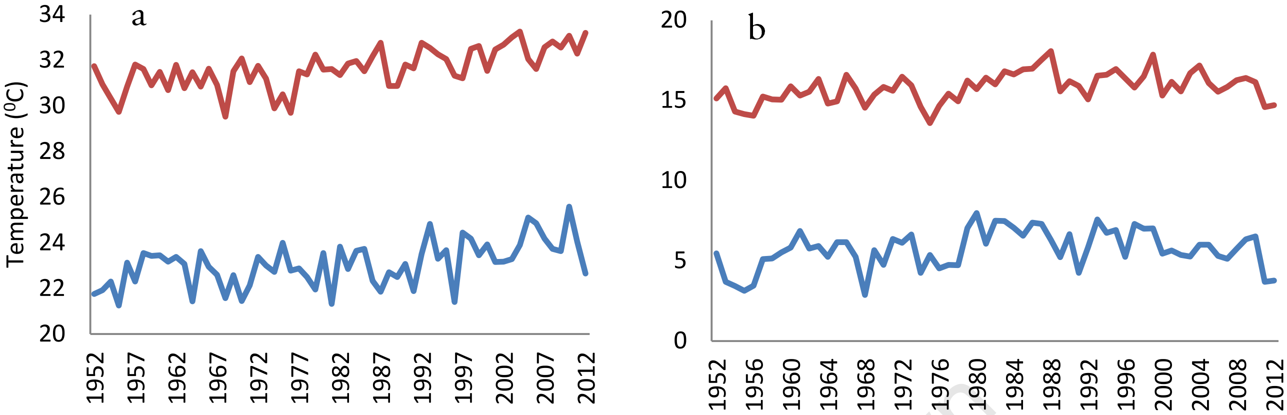

Figure 1: Summer (a) and winter (b) maximum (red line) and minimum (blue line) temperatures (^{0}Celsius) from Upington weather station 03174741.

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