THE INFLUENCE OF RAINFALL SEASONALITY AND CLIMATE CHANGE ON THE DEMOGRAPHY OF *ALOE DICHOTOMA*, A LONG-LIVED SUCCULENT TREE FROM SEMI-ARID SOUTHERN AFRICA

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Plagiarism declaration

I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own.

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ABSTRACT

In the arid and semi-arid western parts of southern Africa, *Aloe dichotoma* Masson, a long-lived succulent tree species, is thought to be responding to anthropogenic climate change. However, differences in response across its distribution are likely to be related to rainfall seasonality. This study investigated change in ten *Aloe dichotoma* populations within winter and summer rainfall zones in South Africa and southern Namibia. Using repeat photography over a timespan of approximately 30 years, demographic patterns, population dynamics (including mortality, recruitment and overall population change) and growth were assessed and modelled with climatic variables. Long-term patterns of recruitment and longevity were also investigated by using individual plant growth data to reconstruct recruitment histories for each population. Finally, the influences of climatic conditions on recruitment were evaluated by superimposing historical rainfall and temperature data. Differences in response between rainfall zones are clearly evident throughout. Generalised linear models revealed lower mortality, higher recruitment and positive population change at winter rainfall sites, while summer rainfall sites showed negative population change. Growth data revealed more rapid growth in height of juveniles than adults, and slower growth in height in the winter rainfall zone, most likely related to differences in tree architecture. It is evident that biotic and anthropogenic factors such as herbivory, nurse plants and theft are likely to moderate observable patterns as opposed to driving them. Recruitment modelling suggested that *A. dichotoma* attains a maximum age of 300 to 350 years, and revealed recent recruitment peaks in the winter rainfall zone and peaks around the turn of the 19th century in the summer rainfall zone. Changes in temperature and rainfall are likely to be the main drivers. Rising temperatures within the last century may have driven increased recruitment and low mortality in the cold-limited winter rainfall zone, while decreasing rainfall within the summer rainfall zone, combined with increasing temperatures, may explain this region's low recruitment and high mortality. The advancement of knowledge of broad spatial and temporal patterns in *A. dichotoma* and the likely causes, coupled with fine-scale future studies, will enable more detailed prediction of the species' response to future global change.

1 Introduction

1.1 Population dynamics of long-lived desert plants

Changes in moisture availability and temperature are usually the most important influence on the survival and reproduction of plants (Lambers et al. 1998; Nobel 2005), especially those species in arid and semi-arid areas with temporally and spatially low and variable rainfall and extreme temperatures (Chesson et al. 2004; Schwinning et al. 2004; Picotte et al. 2007). In response, desert plants have evolved a suite of traits to cope with these climatic constraints. One such trait is the ability in many desert plant species to persist for hundreds of years. This allows for reproductive potential to be spread across many years, mitigating against unfavourable conditions on the one hand, and allowing for recruitment during favourable periods on the other (Miriti 1999; Chesson et al. 2004; Morris et al. 2008). These so-called episodic or pulsed recruitment events are common in arid environments and result in many populations exhibiting cohorts of a similar age (Turner 1990). Low-level continuous recruitment may also occur, supplementing these large recruitment events (Watson et al. 1997; Wiegand et al. 2004).

Climate may therefore be considered a fundamental influence on recruitment in arid environments, with biotic factors having an additional effect (Mandujano et al. 2007). For example, interactions with other organisms influence pollination success and seed set, dispersal, competition, nurse plant availability, the degree of herbivory and the incidence of disease in the population, amongst other important processes (Noy-Meir 1974; Ashman et al. 2004; Ghazoul 2005; Maestre et al. 2005; Burdon et al. 2006). Juveniles are generally more vulnerable to physiological stress and biotic impacts such as herbivory (Boega et al. 2007; Barton & Koricheva 2010) and therefore have a lower survival threshold compared to adults (Jackson et al. 2009). Once beyond this threshold, however, they become increasingly resilient and able to persist despite unfavourable conditions (Miriti 1999; Jack 2011). Because the chances of juveniles surviving are generally low, the persistence of adult plants is critical in order to avoid local population extinctions (Silvertown et al. 1993). Adult mortality has therefore been proposed as a key driver in the dynamics of long-lived desert plants and is often linked to extreme weather events such as droughts and heat waves (Miriti et al. 2001).

Climate change is generally expected to result in a greater frequency of extreme weather events (Morris et al. 2008). This is likely to influence desert plants, which may already exist at the limits of their physiological tolerances (Zinyowera et al. 1998; Foden et al. 2007). Spatial variability in the responses of arid-adapted species to climate stress is common (e.g. Steenbergh & Lowe 1983;

Danzer & Drezner 2010). Knowledge of the ways in which populations in different parts of a species' range respond to climate over long time-frames is therefore important in informing conservation efforts (Danzer & Drezner 2010). Longer-term studies are also critical in understanding the patterns and processes of population dynamics of long-lived species. The episodic nature of both recruitment and mortality in arid environments means that if studies have an insufficient duration, they may fail to capture any change, or conversely, may lead to premature warnings of localized species extinctions as has been the case for the saguaro cactus, *Carnegiea gigantea* Britton & Rose (Cody 2000; Danzer & Drezner 2010).

One method of documenting long-term vegetation change is repeat photography. This method has been used extensively to assess change within arid and semi-arid environments (e.g. Hastings & Turner 1965; Hoffman & Cowling 1990; Parker 1993; Rohde 1997; Turner et al. 2003; Webb et al. 2007; Hoffman & Todd 2010) and is especially useful for studying the dynamics of long-lived species (Bullock & Turner 2010). The improved resolution of modern cameras allows more detailed information to be extracted from the photograph (Kaleme 2003). However, due to a limited field of view, field observations are still important for corroborating information extracted from the photographs (Kaleme 2003).

1.2 DRIVERS OF POPULATION CHANGE IN *ALOE DICHOTOMA*, A SOUTHERN AFRICAN KEYSTONE SPECIES

In the arid and semi-arid western parts of Southern Africa, repeat photography has been used to study *Aloe dichotoma* Masson (the quiver tree), an iconic and charismatic long-lived succulent tree species. *A. dichotoma* occurs in Namibia and South Africa over an area of 200 000 km^2 (Jack 2011) and is able to grow within a variety of climatic regimes and habitat types (Powell 2005; Jack 2011). This species may occur either in dense 'forests' with many thousands of individuals or individually (Powell 2005), and it is often the only tree for great distances (Court 1981). Many organisms rely on *A. dichotoma* for food, shelter or nesting (Midgley et al. 1997). Relative to its abundance, *A. dichotoma* has a disproportionately large impact on other species in the environment and can be considered a keystone species (Power et al. 1996; Midgley et al. 1997). Keystone species have often been advocated as requiring 'priority protection' for ecological and biodiversity reasons (Bond 1994; Paine 1995).

In light of the importance of this species, widespread reports of mortality and low recruitment have raised concern over its future (Jürgens 1997; Kaleme 2003; Foden et al. 2007; Foden & Stuart 2009; Midgley et al. 2009). For example, in the late 1990's Jürgens (1997) described

populations containing only dead individuals and others with adults but little to no recruitment. Foden et al. (2007) found that mortality occurred along a latitudinal cline with high mortality and low recruitment along the northern edge of its distribution while populations in the south were doing comparatively better. Regional warming due to anthropogenic climate change and corresponding constraints on the water balance were suggested as the primary mechanisms. This was cited as the first example of negative impacts of anthropogenic climate change on a sessile desert organism in the southern hemisphere (Foden et al. 2007).

Jack (2011), however, presented a different interpretation. Adult mortality was shown to have occurred several decades ago in most cases, while demographic patterns reflected longer-term climatic influences. Differences in the climatic regimes influencing northern and southern parts of its distribution were key in explaining some of the varied responses of populations to climatic conditions (Kaleme 2003; Jack 2011). *A. dichotoma* occurs across both the winter and summer rainfall zones, where climatic parameters may be very different. The winter rainfall zone in the southwest is characterized by mild ocean-ameliorated conditions and predictable rain showers in the winter, which are associated with cold frontal systems (Cowling et al. 1998; Reason & Jagadheesha 2005). Under these seasonally consistent conditions, regular germination and seedling establishment is possible, which has also helped to shape the floral characteristics of the unique Succulent Karoo biome (Cowling et al. 1998). Most of *A. dichotoma*'s range, however, coincides with the summer rainfall zone (including the Nama Karoo and Namib Desert biomes). It is generally considered a more extreme environment, characterized by continental influences and greater fluctuations in temperature and rainfall. Rainfall is mostly associated with tropical-temperate troughs and associated convective rainstorms (Mason & Jury 1997), which are more spatially and temporally variable.

In addition to the contrasting climatic drivers, longer-term climate changes may have had different effects on the two rainfall zones. Chase & Meadows (2007) suggested that the winter rainfall zone has contracted since the last ice age, while Chase et al. (2009) provided evidence from hyrax middens of more humid conditions until 3 500 years ago, followed by increasing aridity until about 300 years ago, particularly within the current summer rainfall region of the western part of southern Africa. In the more recent past, Neukom et al. (2013) have identified a decrease in precipitation within the summer rainfall zone in the 20th century relative to the 19th century, while no significant differences were detected in the winter rainfall zone. Rainfall variability has, however, increased over this period in the winter rainfall zone (Neukom et al. 2013). These drivers may have influenced *A. dichotoma* populations to differing degrees across its current distribution.

Assessments of population dynamics use changes in the number of individuals (both temporally and spatially) to examine the physical and biological processes that may drive these changes (Watkinson 1997). By evaluating differences in recruitment and mortality at the population scale, mechanisms that may differentially impact this species in the winter or summer rainfall zones may come to light. Indeed, windthrow, a phenomenon in which adult plants are blown over during storm events, was recently identified as an important mechanism explaining mortality in parts of the summer rainfall zone (Jack et al. 2014). Even though population dynamics of *A. dichotoma* have been previously studied (Kaleme 2003; Hoffman et al. 2010), spatial coverage has been poor in some areas. There is consequently a need to investigate population dynamics in different parts of its range to strengthen our interpretations of the main drivers impacting the species.

There is also a lack of finer-scale knowledge regarding biological processes with respect to *A. dichotoma*. This includes aspects of reproductive biology, growth and longevity of adults (Midgley et al. 1997). Carbon dating of an adult provided an age of 100 (±45) years (Vogel, 1974) but a lifespan of up to 350 years has since been suggested (Foden et al. 2007; Foden & Stuart 2009). Kaleme (2003) calculated an estimated lifespan of 250 years from preliminary growth rates of different age classes measured from repeat photographs. Faster growth occurred during the juvenile phase (approx. first 50 years), which slowed during adulthood (possibly as long as 150 years), followed by a senescent stage (approx. 50 years) (Kaleme 2003). In similarly long-lived species, such as *A. dichotoma's* sister species *Aloe pillansii* L. Guthrie, it has been possible to use the demographic profiles and growth rates of the surviving individuals to reconstruct their recruitment history (Hoffman et al. 2010). This has enabled the assessment of recruitment patterns over time, thereby allowing the influence of climate on recruitment to be investigated.

1.3   AIMS AND OBJECTIVES

This study investigated how *A. dichotoma* populations, within the winter and summer rainfall zones of its distribution, have changed over time. Firstly, using repeat photography over a timespan of approximately 30 years, and focused at the population and individual plant level, specific attention was focused on demographic patterns, population dynamics (including mortality, recruitment and overall population change) and growth. This was accomplished by investigating the spatial and temporal patterns in ten *A. dichotoma* populations across South Africa and southern Namibia, including several previously unstudied populations. Secondly, temporal patterns of recruitment and longevity over time frames of decades and centuries were also investigated by using individual plant growth data to reconstruct recruitment histories for each population. Finally, the influences of

climatic conditions on recruitment were evaluated by superimposing historical rainfall and temperature data.

It was anticipated from previous research that many of the observed differences in populations would be related to the influences of winter or summer rainfall zones. Population dynamics were also expected to show similar trends to the populations studied by Kaleme (2003), with lower mortality, higher recruitment and more positive population change in the winter rainfall zone. Population demography data were expected to support these observations with more young trees and fewer dead trees likely to be found in the winter rainfall zone. Growth in desert plants is generally higher in areas with more available moisture (e.g. Steenbergh & Lowe 1983) and it was expected that *A. dichotoma* would follow the same pattern. The recruitment responses were also expected to show peaks during periods of higher rainfall and lower temperatures. The insights provided by this study into the dynamics of *A. dichotoma's* population change across its range will not only contribute to the climate change debate in southern Africa but will also translate into better-informed management of this keystone species in the region.

2 METHODS

2.1 STUDY SPECIES

Aloe dichotoma's distribution extends along mountain ranges and rocky terrain on either side of the vast Bushmanland plains in the Northern Cape Province of South Africa into Namibia, as far north as the Brandberg mountains (Carter et al. 2011). This amounts to a latitudinal extent of ten degrees between 32°S and 21°S (Foden et al. 2007; Jack 2011) (Figure 2.1).

This species takes the form of a large single-stemmed tree with a maximum height of approximately 6-7 m (Carter et al. 2011). Its leaves are succulent and arranged in a whorled rosette around the terminal branches. Seedlings have a single rosette of leaves, but as they grow, dichotomous branching events result in the formation of a rounded crown. Adults tolerate more extreme drought conditions due to a smaller surface-area-to-volume ratio (which decreases water loss) and a larger water storage and nutrient acquisition capacity (Jack 2011).

Yellow flowers are produced on inflorescences above the rosettes between June and August (Coates Palgrave 2002), although highly variable flowering times (between March and October) have been recorded across its range (Smith & Steyn 2005). Fruiting follows between September and November (Curtis & Mannheimer 2005). Seeds are wind-dispersed (Foden et al. 2007), but fall predominantly near the parent plant due to only weakly developed seed 'wings' (Kamstra 1971). Anecdotal evidence suggests that seeds remain viable for up to two years in the wild (Powell 2005). Nurse plants are thought to be crucial to successful seedling establishment throughout *A. dichotoma*'s range (Foden et al. 2007).

Threats to individuals include physical damage associated with herbivory and disease, as well as windthrow and theft (Jack et al. 2014). Midgley et al. (2007) suggested that adult mortality was mostly due to baboon (*Papio ursinus* Kerr) and porcupine (*Hystrix africaeaustralis* Peters) damage at sites in the Richtersveld. Although the sap may make leaves unpalatable to livestock, it has been suggested that goats and donkeys may eat them (Midgley et al. 1997). Scale insects and diseases, including the fungal disease referred to as 'Aloe rust', have been observed on the leaves of *A. dichotoma* (Midgley et al. 1997; Foden et al. 2007) but are not thought to result in mortality. The species is prized by collectors (Midgley et al. 1997) and smaller individuals in accessible populations are frequently removed (Powell 2005; van Blerk 2013).

2.2 STUDY SITES

Study site selection was determined by the availability of several historical photographs of *Aloe dichotoma* individuals and populations in the Northern Cape province of South Africa and Karas district of Namibia. This amounted to 12 study sites distributed across half of *A. dichotoma's* latitudinal range, from Gannabos, near Nieuwoudtville, South Africa in the south to Keetmanshoop, Namibia in the north (Figure 2.1). Three of these sites (Kabas, Coboop and Skuitklipkop) occurred in close proximity to each other (<25 km) and were therefore combined to form a single site, henceforth referred to as Onseepkans. Of the ten sites, three occurred within the winter rainfall zone and seven within the summer rainfall zone (Figure 2.1; Table 2.1). No photographs were obtained for populations closer to *A. dichotoma's* northern latitudinal limit.
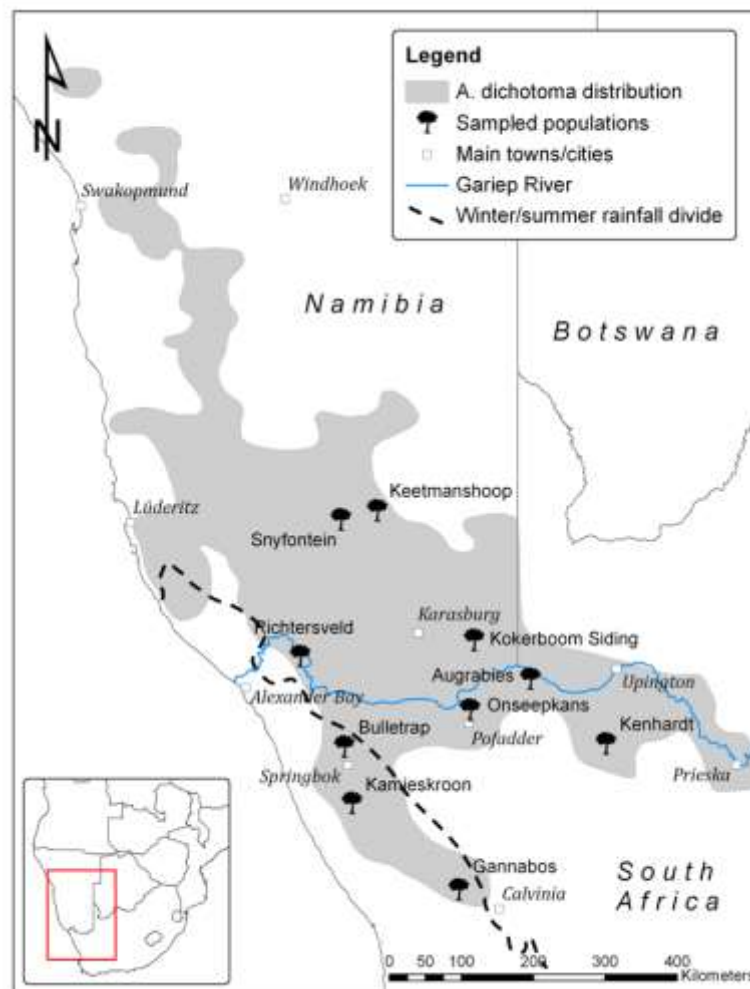

Figure 2.1. Map showing the location of ten study sites across Aloe dichotoma's *distribution, as well as the boundary between the winter and summer rainfall zones (courtesy of Jack 2014).*

Table 2.1. Location and climate information for ten Aloe dichotoma *study sites in South Africa and Namibia. GPS co-ordinates, season of rainfall, annual precipitation, precipitation seasonality (coefficient of variation) and annual mean temperature are provided.*

Site	GPS co-ordinates	Season of rainfall	Annual precipitation (mm)	Precipitation seasonality (%)	Annual mean temperature (°C)
Gannabos	31.229648 °S; 19.266203 °E	Winter	186	59	18.8
Kamieskroon	30.148577 °S; 17.927017 °E	Winter	223	59	15.6
Bulletrap	29.441955 °S; 17.832635 °E	Winter	146	57	17.7
Kenhardt	29.402715 °S; 21.10335 °E	Summer	167	67	19.2
Onseepkans	28.977596 °S; 19.403635 °E	Summer	116	69	20.5
Augrabies	28.589295 °S; 20.156387 °E	Summer	152	75	20.3
Richtersveld	28.308319 °S; 17.281845 °E	Summer	82	37	17.3
Kokerboom	28.106469 °S; 19.454508 °E	Summer	145	84	19.5
Snyfontein	26.593234 °S; 17.787376 °E	Summer	125	104	20.7
Keetmanshoop	26.48038 °S; 18.244265 °E	Summer	153	104	20.6

2.3   DATA COLLECTION

Data were collected during four field trips between September and December 2013. Historical photographs with appropriate numbers of visible *A. dichotoma* individuals, taken between 8 and 47 years ago, were acquired from the historical photograph collection maintained by the Plant Conservation Unit at the University of Cape Town. Populations for which a sufficient numbers of photographs were available were revisited, amounting to a total of 150 repeat photographs of different populations and 359 repeat photographs of individual plants.

At each of the ten sites (except for Kamieskroon, where the population was considered too small), size class and density information were captured from linear transects of varying lengths. These were usually between 300–500 m long by 60–100 m wide, running through the densest part of the population. GPS points taken at the start and end of each transect were used to measure the length and determine the area surveyed. The number of individuals in six age classes was recorded, based on an adaptation of the classifications of Hoffman et al. (2010): seedling (below 1 m in height), juvenile (single stemmed, no dichotomous branching events), sub-adult (only a few dichotomous branches), mature adult (many dichotomous branches), senescent adult, and dead (skeletons). The counts from each transect were converted to density of individuals per hectare.

Repeat photographs were set up by relocating the exact sites at which original photographs were taken using visual cues such as individual trees, rocks or GPS data where available. A tripod-mounted Canon 5D MKII camera was used to retake the historical images. To measure the change in height over time, a calibrated ranging rod was positioned beside individuals considered close enough

to warrant measurement. Additional repeats were taken, with the same field of view as the original photograph and zoomed in on the individual tree if required. Various allometric measurements, such as basal circumference, number of dichotomous branching events and number of terminal branches, were recorded for each individual, along with information about tree health.

2.4 DATA ANALYSIS

2.4.1 CLIMATIC DATA

Data selection

Climate data were obtained in the form of biologically-meaningful climate variables (BioClim) derived from the WorldClim dataset (Hijmans et al. 2005). These data are based on monthly temperature and precipitation averages for the period 1950–2000 which have been interpolated at a resolution of approximately 1 km across terrestrial areas on Earth (Hijmans et al. 2005). The data can therefore be used to discern spatial differences in climate.

From a total of 19 BioClim variables available, a subset containing the 13 most appropriate for this study was selected based on the analysis undertaken by Jack (2011) (Table 2.2). Potential Evapotranspiration (PET) and an Aridity Index (AI) were also derived from WorldClim data according to the following equations:

$$Potential\ Evapotranspiration\ (PET) = 0.0023 \times RA \times (T_{mean} + 17.8) \times TD \times 0.5$$

$RA = mean\ monthly\ extra\text{-}terrestrial\ radiation\ at\ the\ top\ of\ the\ atmosphere$
$T_{mean} = mean\ monthly\ temperature$
$TD = mean\ monthly\ temperature\ range.$

$$Aridity\ Index\ (AI) = \frac{Mean\ Annual\ Precipitation\ (MAP)}{Mean\ Annual\ Potential\ Evapotranspiration\ (MAE)}$$

Therefore, the lower the Aridity Index, the more arid the conditions experienced at the site.

Table 2.2. Subset of 15 climatic variables used to determine differences in climate for the sites. This dataset consists of 13 BioClim variables and two other climatic variables (Potential Evapotranspiration and Aridity Index) derived from the WorldClim dataset (Hijmans et al. 2005).

Temperature variables (n=7)	
BIO1	Annual mean temperature
BIO4	Temperature seasonality (standard deviation*100)
BIO7	Temperature annual range (BIO5-BIO6)
BIO8	Mean temperature of wettest quarter
BIO9	Mean temperature of driest quarter
BIO10	Mean temperature of warmest quarter
BIO11	Mean temperature of coldest quarter

Precipitation variables (n=8)	
BIO12	Annual precipitation
BIO15	Precipitation seasonality (coefficient of variation)
BIO16	Precipitation of wettest quarter
BIO17	Precipitation of driest quarter
BIO18	Precipitation of warmest quarter
BIO19	Precipitation of coldest quarter
PET	Potential evapotranspiration
AI	Aridity Index

In addition to averaged climate information, historical climate trends in the form of monthly rainfall (mm) and average maximum and minimum temperatures (°C) were obtained from the South African Weather Service and Namibian Meteorological Service for the longest time periods available. Climate stations were selected as close to the studied populations of *A. dichotoma* as possible.

Classification of sites based on season of precipitation

Two BioClim variables, mean temperature of wettest quarter and mean temperature of driest quarter (BIO8 and BIO9), were used to separate sites into those receiving precipitation predominantly in winter or summer months. If the mean temperature of BIO8 was lower than that of BIO9 (i.e. the difference was negative), the site was classified as receiving precipitation mostly in winter and vice versa. Nine of the sites had large differences and were therefore easily classified as receiving either winter or summer precipitation. The Richtersveld site, however, was only weakly positive, suggesting that it receives slightly more precipitation during the warmer summer months. The precipitation seasonality variable, BIO15, which was the lowest for Richtersveld at only 37% (ranging between 57% and 104% for the other sites) confirmed that precipitation is not strongly seasonal at this site. The Richtersveld National Park exists at the boundary of the winter and summer rainfall regions (Odendaal & Suich 2007) (Figure 2.1). This site was therefore classified as receiving

summer rainfall for the purposes of graphical representations but was removed from analyses that compared winter and summer precipitation because of its intermediate status.

Principal Component Analysis

Due to the large number of climate variables (Table 2.2) and likelihood that many would be co-correlated, a Principal Component Analysis (PCA) was undertaken to reduce the number of variables, whilst retaining as much of the original variation as possible (Jolliffe 2002) and minimising assumptions of the ways in which these variables influence *A. dichotoma* prior to analysis. This was accomplished by transforming the dataset to new sets of ordered variables in which only the first few contained most of the variation present in the original dataset (Jolliffe 2002).

The 15 variables were divided into two groups: those related to either temperature (n=7) or precipitation (n=8), and analysed separately. This is due to the difficulties in interpreting PCA's based on contrasting groups of variables (Quinn & Keough 2002), and constraints on the number of variables able to be tested using the 'prcomp' function based on the limited number of sites (version 3.0.2, R Core Team, Vienna, AT).

The variables within each group were scaled using the 'scale' function in R so as to ensure that no single variable was assigned a disproportionate weighting, while the 'prcomp' function in R was used to extract the components according to the principal axis method (version 3.0.2, R Core Team, Vienna, AT), followed by an application of the Kaiser criteria and scree tests to determine the most important components (Kaiser 1960; Jolliffe 2002).

Once these four principal components were selected for inclusion in the modelling exercise, an indication of which of the original climate variables was most strongly correlated with the new components was required for interpretation, as well as the directionality of this relationship (either positive or negative). This was achieved by analysing the loadings of the BioClim variables on the components using the biplots (Figure 3.1 a & b) and the loadings values (Table 3.1). Both magnitude and directionality of the loadings were therefore important. These four derived components were then used in place of the original 15 variables when performing Generalised Linear Models (GLMs) on population dynamics and growth data.

2.4.2 POPULATION DYNAMICS

Photograph analysis

Repeat photographs which contained more than seven individuals were chosen from the 150 repeats to assess population dynamics at each site. Of these, photographs from approximately the

same time-frame (mostly taken 26 years ago, but ranging between 16 and 43 years ago) were selected, leaving a total of 70 photographs. Original and repeat photographs were matched using Adobe Photoshop CS5 (version CS5, Adobe Systems Incorporated, San Jose, CA, US). Photographs were overlaid in Photoshop and two fixed points (such as rocks) were selected, based on their visibility in both original and repeat photographs and location in the same plane as the individual to be measured. The distance between these points was measured using the ruler tool. In most cases, the repeat photograph was downsized as follows:

$$Downsized\ repeat\ photograph\ width = \frac{distance\ in\ original}{distance\ in\ repeat} \times width\ of\ repeat\ photograph$$

The repeat image was then dragged onto the original image and the free transform tool used to ensure that both photographs were tilted to the same angle. Once adequately matched, individuals that had died, recruited or persisted between the two photographs were identified and counted (Figure 2.2).

Figure 2.2. Example of matched photograph pair showing changes in Aloe dichotoma *population at Keetmanshoop between 1997 (top) and 2013. White markers show living individuals, while red markers show dead individuals. It is evident that three trees died in the interim, while none recruited. Original photograph courtesy of Norbert Jürgens.*

Statistical analysis

Based on the count data of individuals, the following equations from Hoffman et al. (2010) were applied to determine annual average mortality, recruitment and population change:

$$Mortality = (\frac{N_t - N_n}{N_0})^{\frac{1}{y}} - 1$$

$$Recruitment = (\frac{N_n + N_0}{N_0})^{\frac{1}{y}} - 1$$

$$Population\ change = (\frac{N_t}{N_0})^{\frac{1}{y}} - 1$$

N_0 = number of individuals in original photograph
N_t = number of individuals in repeat photograph
N_n = number of new individuals in repeat photograph
y = number of years between photographs

The data were explored according to methods recommended by Zuur et al. (2010), whereafter statistical analyses were undertaken using R (version 3.0.2, R Core Team, Vienna, AT). The relationships between the three measures of population dynamics and various factors (sites, rainfall zones, and the climate and precipitation variables from the PCA) were assessed using GLMs. Pairwise least-squares means analyses with a Bonferroni correction were also undertaken for comparisons between sites. Due to the fact that there was no variability in climate within sites, site could not be added as a random effect and the data were therefore assessed for broad relationships across all sites. Mortality data were transformed to fulfill the prerequisites of the Gaussian distribution family (identity link). This was done by obtaining an absolute value, scaling this to remove zero values (by adding 0.01 to each value), and log transforming the data. Although in some cases log transformations are not recommended for count data (O'Hara & Kotze 2010), in this study an annual rate of count data were used and it was not possible to apply the Poisson distribution, which requires whole numbers. The negative binomial distribution was another alternative but analysis of the residuals revealed that it was a poor fit. Recruitment data were scaled so that a Gamma distribution (identity link) could be applied and population change was analysed untransformed, with a Gaussian distribution (identity link).

2.4.3 GROWTH (CHANGE IN HEIGHT)

Photo analysis

Repeat photographs which contained trees close enough to measure change in height were chosen from the 359 trees photographed, leaving a total of 298 individuals. All photographs were used regardless of the time-frame captured to ensure that sample sizes were sufficiently large for statistical analyses. Most were taken 26 years ago but this differed for a few sites. Most notably, growth at Bulletrap could only be captured over the last 8 years, and at the Richtersveld site, over the last 9 to 26 years.

In determining growth of individual trees, the original and repeat photographs were matched using the same approach as for population dynamics. The most appropriate of the three repeat images with the ranging rod was selected based on the following protocol. Where individuals were sufficiently close to the foreground such that the measurements on the ranging rod were legible, the full extent of the image was used, but if required a zoomed repeat image was used. In cases where zoomed images were used and downsizing (as per population dynamics) would have ~~had~~ made the ranging rod illegible, the original image was upsized by interchanging the numerator and denominator in the previous equation such that:

$$Upsized\ original\ photograph\ width = \frac{distance\ in\ repeat}{distance\ in\ original} \times width\ of\ original\ photograph$$

The procedures deviated slightly after the tilt of the two photographs was matched, at which point it was ensured that the position of the individual tree was closely matched. This was done based on the most static features such as trunk-scars and rocks near the base of the tree. The final step involved measuring the height of the tree in the original and repeat. This was done using the line tool to trace the edge of the ranging rod. This shape was then duplicated and tilted by 90° so as to lie perpendicular to the ranging rod, and used to measure the highest rosette to an accuracy of 0.5 cm. By changing the opacity of the repeat photograph, the same could be done for the original tree. Where possible, the same rosette was utilised. This yielded the original and repeat heights of the tree. The annual average change in height was selected as a simple measure to approximate growth. It was obtained using the following equation, where the denominator (calculated in Excel) reflects the years between photographs:

$$Change\ in\ height\ (cm/year) = \frac{height\ in\ repeat - height\ in\ original}{(date\ of\ repeat - date\ of\ original)/365}$$

Age class classification

An agglomerative hierarchical cluster analysis was performed on the change in height data in R (version 3.0.2, R Core Team, Vienna, AT) using the 'pvclust' package (version 1.2-2, Suzuki & Shimodaira 2011). The aim was to determine the number of age classes into which the change in height data might naturally cluster. A Euclidean distance measure and the Ward clustering method (Ward 1963) were selected because change in height was a continuous variable, and a more sensitive clustering method was preferred (Everitt et al. 2011).

It was decided to perform the cluster analysis on a single site so as to ensure that potential differences in growth between sites did not obscure patterns of growth within age classes. This was also necessary due to statistical considerations: Bulletrap was used to perform the cluster analysis as it was the only site at which sample sizes of both juveniles and adults were sufficiently large for an accurate analysis. Many juveniles at Bulletrap had suffered high levels of herbivory, identified by the fact that they showed no dichotomous branching events but had resprouted multiple rosettes. These were excluded in addition to two juvenile outliers, which had experienced severe stem damage and showed extremely low change in height values as a result. This was done to remove the influence of herbivory as far as possible for the cluster analysis, but these individuals were not excluded from further assessments of growth.

It was also necessary to distinguish age class membership so as to build it into the recruitment model and identify the point at which juvenile (as opposed to adult) change in height should be applied. Based on an analysis of scatterplots for the Bulletrap data showing change in height as a function of various allometric characteristics (including height, basal circumference and number of terminal branches) for trees identified as adults and juveniles using the cluster analysis, height was selected as the most important discriminator of class membership. Juveniles were defined as those individuals with a height of 0–3 m and adults as greater than 3 m (Figure 3.4). This rule was then applied to individuals at all other sites, with trees classified as either adult or juvenile based on their height. The classification was checked for each tree against age classes assigned during the fieldwork (based on the number of dichotomous branching events).

Statistical analysis

Change in height data were explored according to the methods of Zuur et al. (2010). Relationships between adult or juvenile change in height between sites, rainfall zones, and climate variables from the PCA were assessed using GLMs in R (version 3.0.2, R Core Team, Vienna, AT). Pairwise least-

squares means analyses with a Bonferroni correction were also used to compare adult and juvenile change in height between sites. Adult change in height was assessed using the Gamma distribution (identity link). Juvenile change in height was assessed using the same distribution (log link).

Recruitment modelling

Damaged juveniles (individuals with no dichotomous branching events but more than one rosette) were removed from recruitment modeling. This is because it was observed that these multi-stemmed individuals generally showed slower change in height values and rarely matured into reproductive adults, suggesting that they do not contribute significantly to the population.

Bulletrap was the only site at which sufficient numbers of juveniles were obtained for the recruitment model. Because the majority of sites which did have juveniles fell within this range, a 'universal' juvenile population was created using values from all of the sites. One of the assumptions of the recruitment model was therefore that juvenile growth did not differ significantly between sites. Sufficient data were available for adults at all sites (except Kamieskroon, which could not be modelled due to sample size limitations) allowing the use of adult data from the site itself. According to the methodology outlined by Durbach (2013 unpubl.), Probability Density Functions (PDFs) were fitted to change in height data using a Gaussian Kernal function in R (version 3.0.2, R Core Team, Vienna, AT). This incorporated variability in growth due to differences in factors impacting the growth of an individual over time, for example water availability, herbivory and damage and resulted in separate adult and juvenile PDFs being derived for each site. Equations describing an individual's growth over its lifetime were derived by randomly selecting change in height values from the PDFs on an annual basis. Those change in height values with the highest probability of occurrence in the population were selected most often. Both the adult and juvenile rates of change were applied, with a shift between them at 3 m. This was repeated 10 000 times.

Recruitment events at each site were estimated by incorporating height data of trees at that site and applying the growth equation to subtract an annual change in height from each tree until it reached a height of zero. A histogram of potential recruitment dates was bootstrapped to obtain an average recruitment distribution for each population. Where available, annual rainfall and maximum temperature data for the longest possible time-frames were superimposed onto recruitment distributions.

3 RESULTS

3.1 CLIMATIC DATA

Principal Component Analysis

The Principal Component Analysis resulted in the selection of four new components which best described the variation of the 15 BioClim-derived variables. For the temperature variables, the first two components had Eigenvalues greater than 1 (Temp. 1=5.3, Temp. 2=1.1) and the scree test confirmed that these components were meaningful (Figure 3.1a). Together, they accounted for approximately 91% of the total variance (Temp. 1=76%, Temp. 2=15%). For the precipitation variables, the first two components had Eigenvalues greater than 1 (Precip. 1=4.6, Precip. 2=2.8) and the scree test confirmed that these components were meaningful (Figure 3.1b).Together, they accounted for approximately 92% of the total variance (Precip. 1=57%, Precip. 2=35%).

The majority of the climatic variables were strongly correlated with either component 1 or component 2, although there were a few cases where BioClim variables were strongly correlated with both components. The main finding of the PCA was that the principal components were most strongly associated with variation around the seasonality of the climatic regime (Temp. 1 and Precip. 1.), followed by variation around the amount of precipitation and range of temperatures experienced at a site (Temp 2. and Precip. 2).
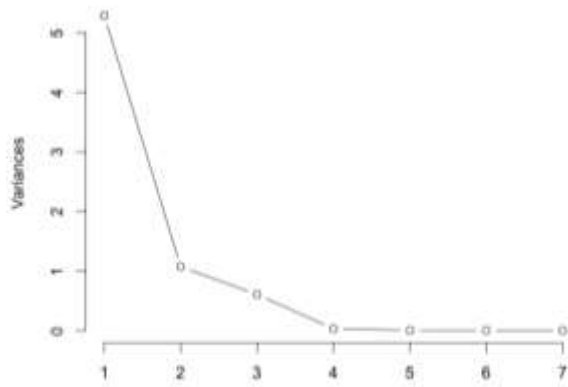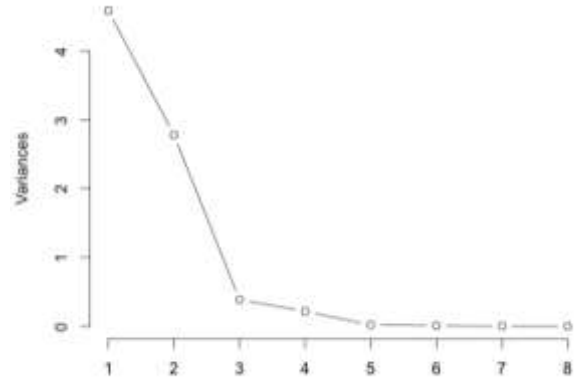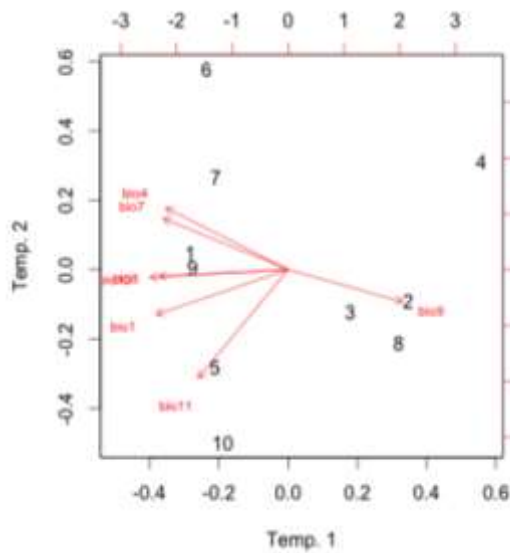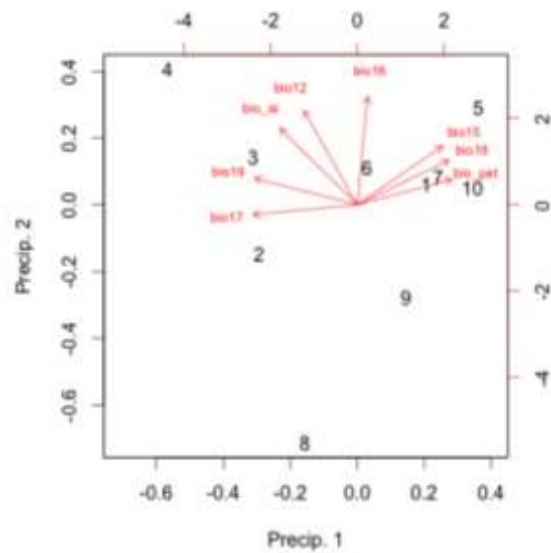
Figure 3.1. Outputs from Principal Component Analysis for temperature (n=7) and precipitation (n=8) variables at each of the 10 study sites. Figures a) and b) show scree plots depicting the amount of variance explained by each component, while biplots c) and d) show the relationship between the climatic variables and the first two components, with sites 1 to 10 ordinated on the plot (1=Augrabies, 2=Bulletrap, 3=Gannabos, 4=Kamieskroon, 5=Keetmanshoop, 6=Kenhardt, 7=Kokerboom Siding, 8=Richtersveld, 9=Onseepkans, 10=Snyfontein). The left and bottom axes represent the loadings of the BioClim variables on the principal components and the right and top axes represent the principal component score (i.e. the output value of the PCA utilised in the GLMs). BioClim variables (arrows) with the most positive or negative loading values are those that were most strongly correlated with the new principal components.

Table 3.1. Loadings of BioClim variables on the first two principal components chosen for temperature (Temp. 1 and Temp. 2) and precipitation (Precip. 1 and Precip. 2). The absolute value of each loading value indicates the strength of the correlation between that variable and each principal component. The sign of the loading value represents the directionality of the relationship between variables and the component.

| BioClim variables		Loadings on component 1	Loadings on component 2
Temperature		Temp1.	Temp2.
BIO1	Annual mean temperature	-0.407	-0.308
BIO4	Temperature seasonality (standard deviation*100)	-0.378	0.423
BIO7	Temperature annual range (BIO5-BIO6)	-0.385	0.349
BIO8	Mean temperature of wettest quarter	-0.400	-0.046
BIO9	Mean temperature of driest quarter	0.353	-0.222
BIO10	Mean temperature of warmest quarter	-0.427	-0.054
BIO11	Mean temperature of coldest quarter	-0.277	-0.742
Precipitation		Precip 1.	Precip 2.
BIO12	Annual precipitation	-0.228	0.516
BIO15	Precipitation seasonality (coefficient of variation)	0.363	0.323
BIO16	Precipitation of wettest quarter	0.044	0.592
BIO17	Precipitation of driest quarter	-0.444	-0.054
BIO18	Precipitation of warmest quarter	0.391	0.245
BIO19	Precipitation of coldest quarter	-0.439	0.145
BIO_AI	Aridity Index	-0.329	0.419
BIO_PET	Potential evapotranspiration	0.404	0.139

3.2 POPULATION DEMOGRAPHY

Demographic profiles from nine of the ten sites investigated (Kamieskroon was excluded because there were too few individuals in the population) revealed considerable differences in population structure between those occurring in the summer versus winter rainfall zones (Figure 3.2). Several sites in the summer rainfall zone revealed zero to little recruitment, with seedling and juvenile age classes completely absent at Richtersveld and Kokerboom, and present, but at a very low density at Kenhardt and Augrabies. There was also a very high proportion of dead individuals at Kenhardt and Augrabies, and a high proportion of dead individuals at Onseepkans and Snyfontein.

Gannabos and Bulletrap (both in the winter rainfall zone) showed evidence of recent recruitment, with a much higher density of seedlings, juveniles and sub-adults, but also a lower density of dead individuals than was apparent at sites in the summer rainfall region (Figure 3.2).

a) Gannabos
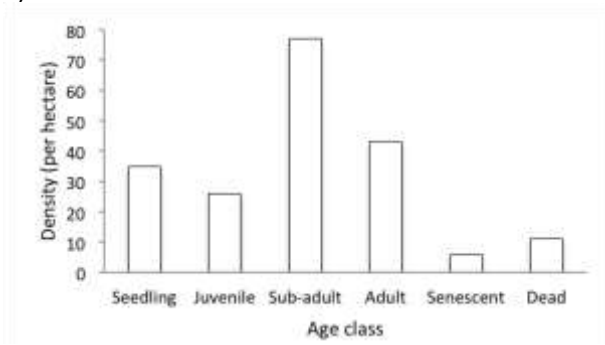
b) Bulletrap
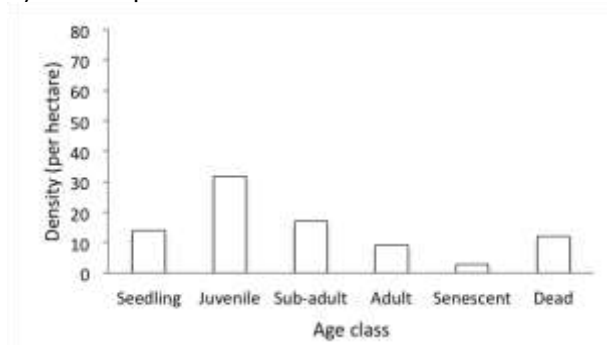
c) Kenhardt
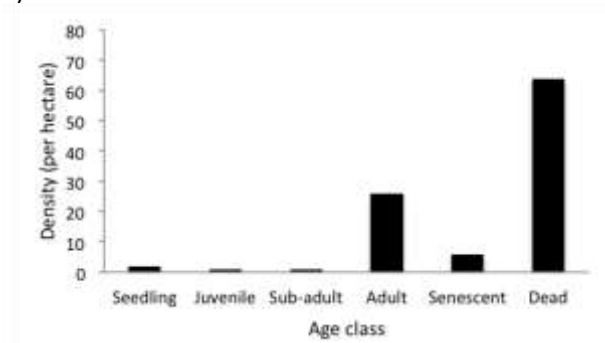
d) Onseepkans
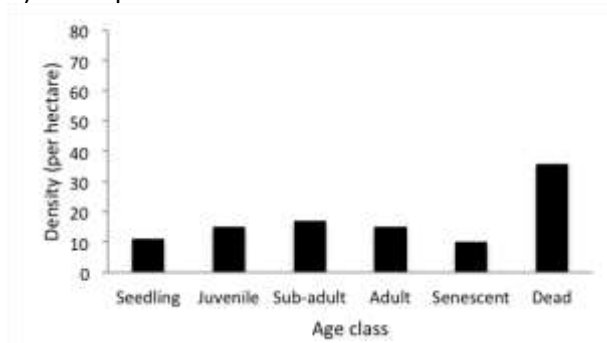
e) Augrabies
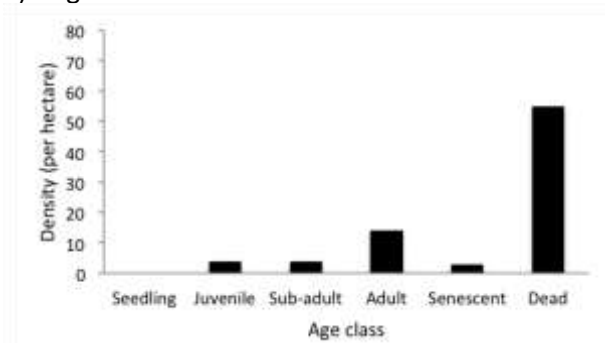
f) Richtersveld
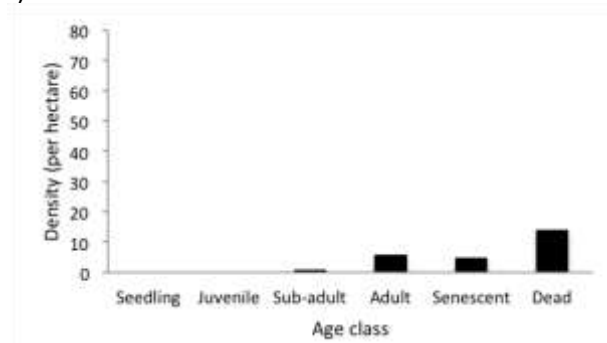
g) Kokerboom
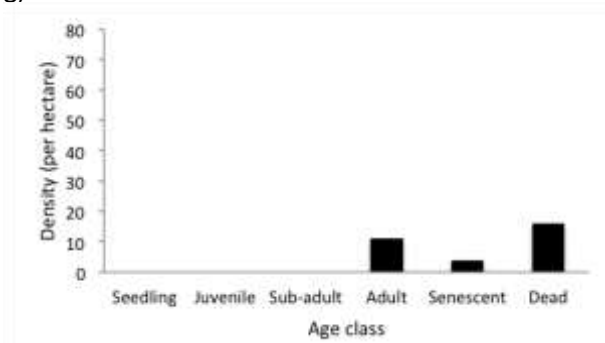
h) Snyfontein
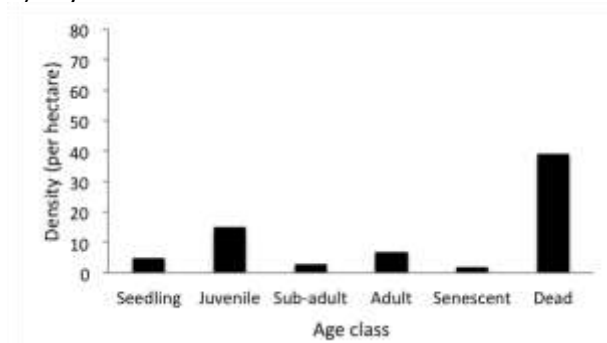
i) Keetmanshoop
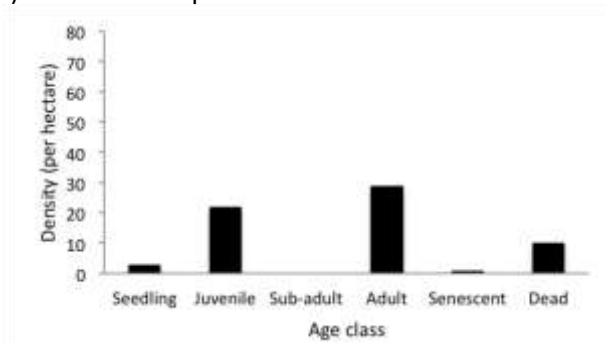
Figure 3.2 a) – i). Demographic profiles of nine Aloe dichotoma *populations within South Africa and Namibia, based on data obtained from transects. Sites are arranged latitudinally from south to north. Winter rainfall sites are indicated by white bars, while black bars show summer rainfall sites. The density, i.e. number of individuals per hectare, of each of six age classes, namely: seedlings, juveniles, sub-adults, adults, senescent adults and dead individuals is shown.*

3.3 POPULATION DYNAMICS

The photographic analysis of the changes in population structure over the last 30 years revealed significant differences in annual mortality, recruitment and population change between sites (Figure 3.3). Mean values for each site are provided (Table 3.2).

Pairwise least-squares means analyses confirmed these patterns. In terms of mean annual mortality, Gannabos had the lowest value (0.003), which was lower than that at Kenhardt, Onseepkans, Augrabies, and Snyfontein ($p=0.005$, $p=0.004$, $p<0.0001$ and $p<0.0001$ respectively; Appendix, Table A.1). Similarly, Keetmanshoop also showed a lower annual mortality than that of the aforementioned four sites ($p=0.033$, $p=0.007$, $p=0.000$, $p<0.0001$ respectively). Snyfontein had the highest mean annual mortality (0.041), which was higher than that at Gannabos, Bulletrap, Onseepkans, Richtersveld and Kokerboom ($p<0.0001$, $p=0.002$, $p=0.000$, $p<0.0001$, $p=0.002$).

There were fewer differences in recruitment between sites, which was generally very low throughout all sites. Gannabos, Kamieskroon and Bulletrap had higher mean annual recruitment than Kenhardt, Richtersveld and Kokerboom, but these differences were not significant (Appendix, Table A.2). Onseepkans, however, had a higher mean annual recruitment rate (0.009) than Kenhardt, Richtersveld and Kokerboom ($p=0.038$, $p=0.004$ and $p=0.007$ respectively).

Population change captured the combination of mortality and recruitment patterns at each site and provided an indication of the trajectory of the populations within the last 43 years (Appendix, Table A.3). Gannabos had the highest positive mean annual population change (0.013), which was higher than Kenhardt, Augrabies and Snyfontein ($p=0.005$, $p=0.005$, $p=0.000$). Bulletrap, which had the second highest mean (0.009), showed the same pattern ($p=0.048$, $p=0.049$, $p=0.013$ respectively). While Augrabies and Kenhardt had the lowest mean annual population change (-0.025), there were no significant differences between these and other sites. Snyfontein had the next lowest mean (-0.024), which was lower than that of Onseepkans and Keetmanshoop ($p=0.045$ and $p=0.011$).

a)

b)

c)
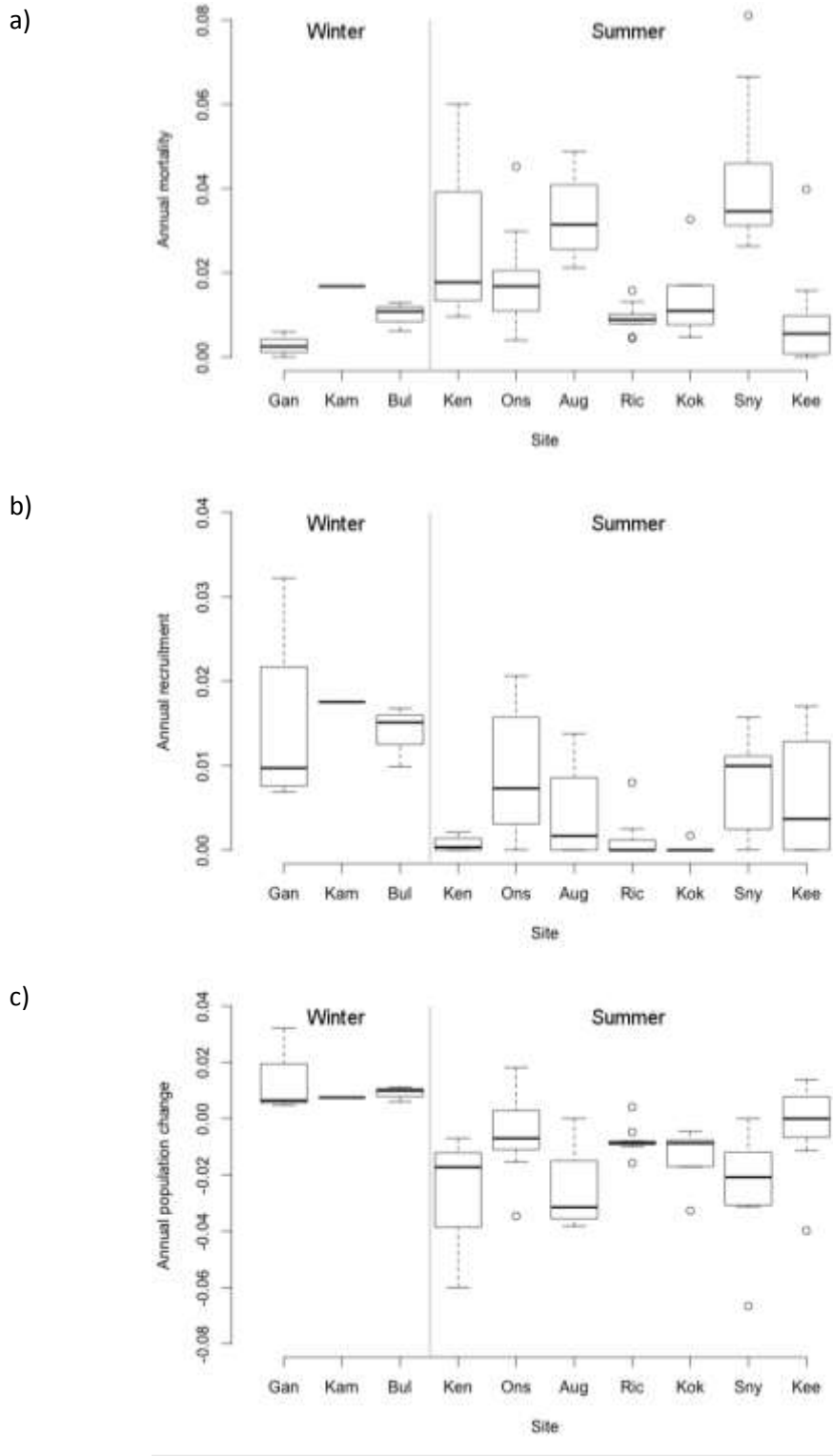
Figure 3.3. Box and whisker plots showing annual changes in population dynamics for ten Aloe dichotoma *populations within South Africa and Namibia, arranged latitudinally from south to north, as derived from analysis of repeat photographs (n=70). The line represents the median and the box the interquartile range of the data, while the whiskers extend to a maximum of 1.5 times the interquartile range, and any other values have been classified as outliers (circles). Figure 3.3 a) shows annual mortality (absolute value of mortality index utilised), b) annual recruitment and c) annual population change for each site.*

Table 3.2. Results of the pairwise least-squares means analysis from GLMs to determine the mean annual change for mortality, recruitment and population change (dependent variables) at each site (fixed effect) for repeat photographs of Aloe dichotoma *(n=70). The back transformed mean annual change for mortality and recruitment are provided (population change was modelled in its original format and therefore does not require back transformation). Untransformed parameter estimates and Standard Error have also been provided. Pairwise significance test results of differences in means between sites can be found in the Appendix (Tables A.1, A.2 & A.3).*

Site	Mean annual change	Estimate	Standard Error
Mortality (n=70)			
Gannabos	0.003	-1.899	0.074
Kamieskroon	0.017	-1.571	0.149
Bulletrap	0.010	-1.703	0.086
Kenhardt	0.022	-1.494	0.074
Onseepkans	0.017	-1.572	0.036
Augrabies	0.032	-1.375	0.074
Richtersveld	0.009	-1.722	0.045
Kokerboom	0.013	-1.640	0.067
Snyfontein	0.041	-1.296	0.050
Keetmanshoop	0.006	-1.784	0.043
Recruitment (n=70)			
Gannabos	0.015	0.025	0.004
Kamieskroon	0.018	0.028	0.009
Bulletrap	0.014	0.024	0.005
Kenhardt	0.001	0.011	0.002
Onseepkans	0.009	0.019	0.002
Augrabies	0.004	0.014	0.002
Richtersveld	0.001	0.011	0.001
Kokerboom	0.0003	0.010	0.002
Snyfontein	0.008	0.018	0.002
Keetmanshoop	0.006	0.016	0.002
Population change (n=70)			
Gannabos	0.013	0.013	0.007
Kamieskroon	0.007	0.007	0.014
Bulletrap	0.009	0.009	0.008
Kenhardt	-0.025	-0.025	0.007
Onseepkans	-0.006	-0.006	0.003
Augrabies	-0.025	-0.025	0.007
Richtersveld	-0.008	-0.008	0.004
Kokerboom	-0.014	-0.014	0.006
Snyfontein	-0.024	-0.024	0.005
Keetmanshoop	-0.002	-0.002	0.004

Analyses revealed differences in demographic profiles and possibly population dynamics between sites in winter and summer rainfall zones. All of the winter rainfall sites experienced population increases (albeit small increases in some cases), while all of the summer rainfall populations had declined. This was explicitly tested using a GLM (excluding Richtersveld because of its weak seasonal effect) that revealed significantly lower mortality, higher recruitment and higher positive population change at winter rainfall sites (Table 3.3).

Table 3.3. Results of GLMs assessing the relationship between rainfall zone (fixed effect) and annual mortality, recruitment, and population change (dependent variables) for Aloe dichotoma as derived from analysis of repeat photographs (n=59). Summer was used as the intercept in all cases (indicated in italics). Back transformed mean annual changes are provided, along with parameter estimates, Standard Error and P values from the models.

Rainfall zone	Mean annual change	Estimate	Standard Error	P
Mortality (n=59)				
Summer	0.018	*-1.558*	*0.031*	*< 0.0001**
Winter	0.006	-0.226	0.084	0.010*
Recruitment (n=59)				
Summer	0.006	*0.016*	*0.001*	*< 0.0001**
Winter	0.015	0.009	0.004	0.017*
Population change (n=59)				
Summer	-0.012	*-0.012*	*0.002*	*< 0.0001**
Winter	0.011	0.023	0.006	0.001*

* Significantly different from intercept mean (at significance level of 0.05)

The relationship between population dynamics and the prevailing climate was further explored using GLMs with either temperature or precipitation components as fixed effects (Table 3.4). Mean annual mortality had a negative relationship with Temp. 1 and a positive relationship with Precip. 1. Thus mortality increased as annual mean temperature, annual temperature range, and mean temperature of the wettest and warmest quarters increased, and mean temperature of the driest quarter increased. A similar pattern was found for precipitation, where mortality increased as precipitation seasonality (analogous to the co-efficient of variation or precipitation variability), precipitation of warmest quarter and potential evapotranspiration increased and precipitation of driest quarter and coldest quarter decreased. Recruitment only showed a significant relationship with Precip 2., suggesting a positive relationship between recruitment and the amount of precipitation (Table 3.4). Population change, however, exhibited the opposite response to mortality, sharing a positive relationship with Temp. 1 and a negative relationship with Precip. 1.

Table 3.4. Results of GLMs assessing the relationship between climate variables (PCA outputs) describing temperature (Temp. 1 and Temp 2.) and precipitation (Precip 1. and Precip. 2) (fixed effects) and annual mortality, recruitment, and population change (dependent variables) for Aloe dichotoma*. Back transformed mean values for each category are provided, along with parameter estimates, Standard Error and P values from the models. Intercepts are indicated in italics.*

Temp. variables	Mean annual change	Estimate	Standard Error	P	Precip. variables	Mean annual change	Estimate	Standard Error	P
Mortality (n=70)									
(Intercept)	0.013	*-1.644*	*0.029*	*<0.0001**	(Intercept)	0.012	*-1.654*	*0.032*	*<0.0001**
Temp. 1	0.011	-0.043	0.014	0.004*	Precip. 1	0.015	0.053	0.020	0.010*
Temp. 2	0.012	-0.020	0.029	0.507	Precip. 2	0.012	-0.006	0.015	0.676
Recruitment (n=70)									
(Intercept)	0.006	*0.016*	*0.001*	*<0.0001**	(Intercept)	0.008	*0.018*	*0.001*	*<0.0001**
Temp. 1	0.006	0.000	0.000	0.775	Precip. 1	0.006	-0.001	0.001	0.109
Temp. 2	0.005	-0.001	0.001	0.161	Precip. 2	0.009	0.001	0.000	0.035*
Population change (n=70)									
(Intercept)	-0.007	*-0.007*	*0.002*	*0.002**	(Intercept)	-0.005	*-0.005*	*0.002*	*0.045**
Temp. 1	-0.005	0.003	0.001	0.023*	Precip. 1	-0.009	-0.005	0.002	0.004*
Temp. 2	-0.007	0.000	0.002	0.984	Precip. 2	-0.004	0.001	0.001	0.51

* Significantly different from intercept mean (at significance level of 0.05)

3.4 GROWTH (CHANGE IN HEIGHT)

Age class classification

The cluster analysis at Bulletrap revealed two natural groupings for change in height – 'adults' and 'juveniles' – which generally separated well at a height of 3 m. This was tested by classifying all individuals as adult or juvenile according to on-site classifications taking into account the growth form and number of dichotomous branches, and plotting it against actual height (Figure 3.4). For the majority of sites, juveniles were less than 3 m in height, and adults greater than 3 m. However, there was some overlap at Gannabos. For the purposes of the analysis of growth, these trees remained as originally classified, but were removed from the recruitment model, where a height of 3 m was used to differentiate the application of adult or juvenile rates of change in height.
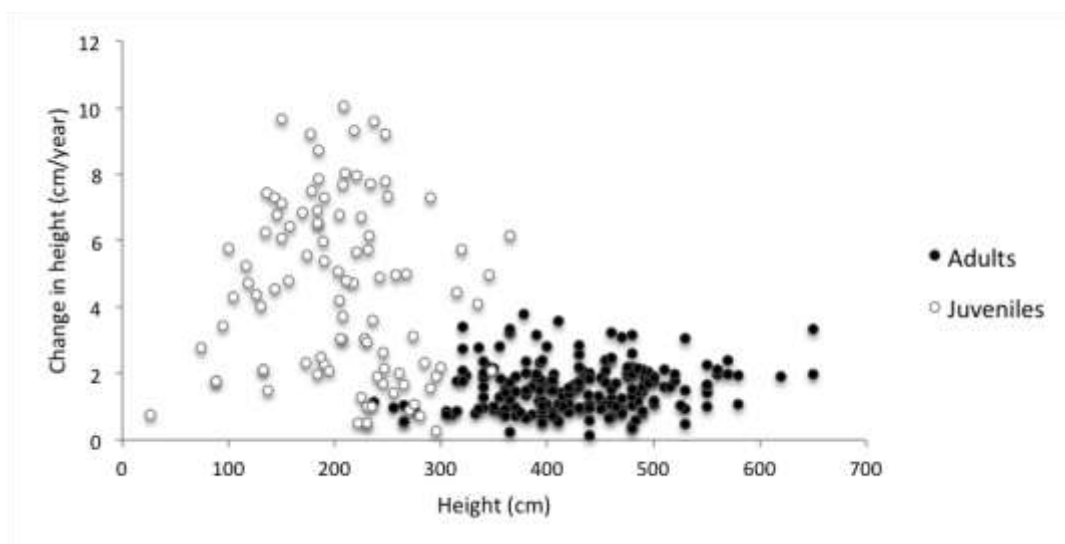
Figure 3.4. Scatterplot showing the relationship between height and the change in height (cm/year) for all Aloe dichotoma *individuals across ten populations. A cluster analysis based on Bulletrap and tested across all other sites suggested that in most cases, a height of 3 m could be used as a threshold between adult and juvenile rates of change in height.*

An assessment of the architecture of trees classified as adults revealed that Richtersveld had the lowest mean number of live terminal branches (51.79 ± 5.82), while Gannabos had the highest (129.21 ± 17.04). This was the only significant difference between sites (p=0.0008). There was no significant difference between the number of live terminal branches in the winter rainfall zone (100.34 ± 10.06) and the summer rainfall zone, excluding Richtersveld (86.75 ± 5.27) (p=0.179).

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Patterns of growth

The change in height in a single rosette was used to provide a simple indication of tree growth and thus identify broad spatial differences in growth rates between populations. However, it should be noted that image resolution, photo-angle, rosette shape, hidden growth points, and photo-matching procedures all introduce small amounts of error in estimations of individual tree growth. A more detailed analysis would require consideration of the number of dichotomous branching events and terminal branches and how growth is divided between these features (Appendix, Figure B.1 & Figure B.2). Pairwise least-squares means analyses revealed an apparent difference between the annual change in height in adult trees at Richtersveld compared to many other sites (Figure 3.5; Table 3.5). The mean change in height at Richtersveld was 2.57 cm/year for adults, which was significantly higher than that at Gannabos (1.29 cm/year), Kamieskroon (1.56 cm/year), Keetmanshoop (1.62 cm/year) and Kokerboom (1.64 cm/year) ($p<0.0001$, $p=0.092$, $p=0.001$, $p<0.0001$).

Juvenile growth was more difficult to characterize due to the small number of juveniles captured in photographs at most sites except Gannabos and Bulletrap (n=27 and n=53). The mean annual change in height for juveniles was generally higher than that of adults. Mean juvenile change in height was highest at Keetmanshoop (7.8 cm/year), significantly higher than at Gannabos (1.61 cm/year) and Onseepkans (3.11 cm/year) ($p=0.001$ and $p=0.049$ respectively) (Appendix, Table B.1 & B.2.). The mean change in height was lowest at Gannabos (1.61 cm/year), significantly lower than that at Bulletrap (5.91 cm/year), Onseepkans (3.11 cm/year) and Keetmanshoop (7.80 cm/year) ($p<0.0001$, $p=0.020$ and $p=0.001$ respectively). Bulletrap showed a large range in juvenile change in height values.

a)

b)
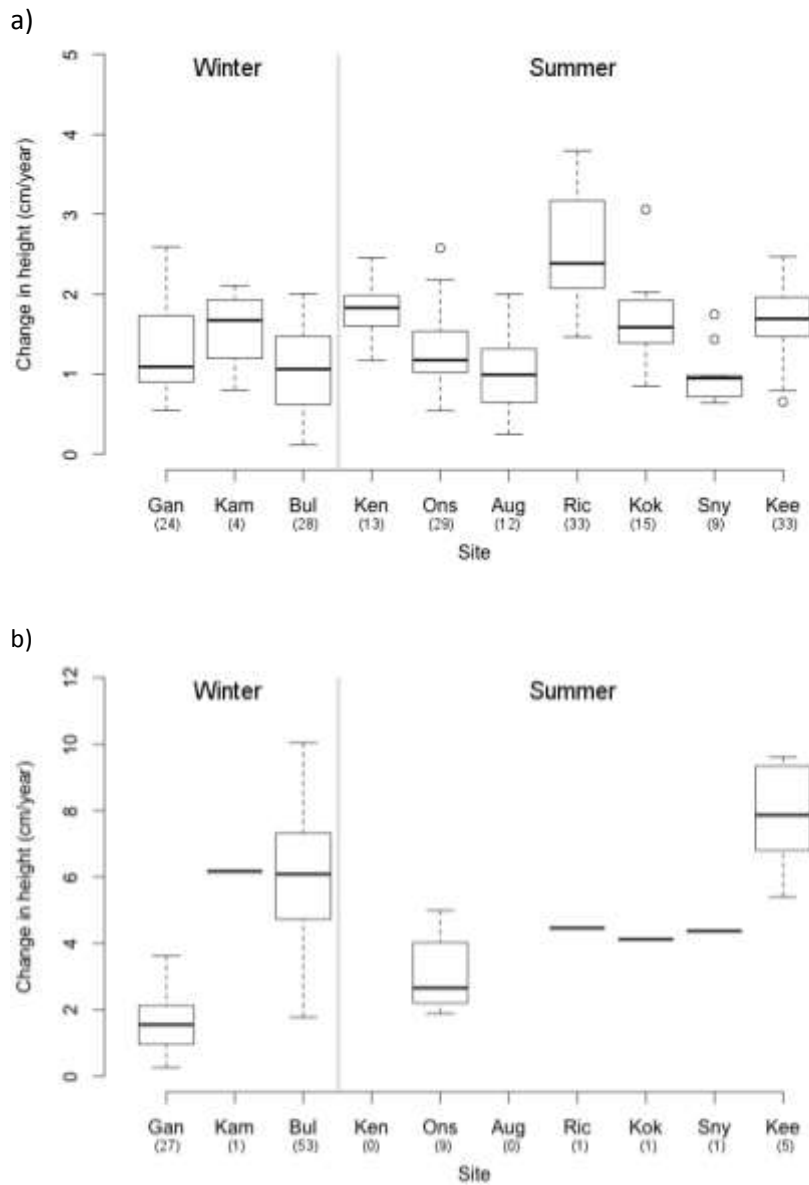
Figure 3.5. Boxplots showing change in height (cm/year) for Aloe dichotoma *individuals at ten sites, arranged latitudinally from south to north, in winter and summer rainfall regions within South Africa and Namibia. The line represents the median and the box the interquartile range of the data, while the whiskers extend to a maximum of 1.5 times the interquartile range, and any other values have been classified as outliers (circles). Figure 3.5 a) shows measurements for adult trees (n=200), while b) shows measurements for juvenile trees (n=98). The number of individuals measured at each site is indicated in brackets.*

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Table 3.5. Results of pairwise least-squares means analysis on the results of GLMs to determine the mean change in height for adult and juvenile Aloe dichotoma *(dependent variable) at each site (fixed effect). Because the data were not transformed prior to analysis, the mean could be calculated directly from the parameter estimate. Standard Errors have also been provided. Pairwise significance test results of differences in means between sites are in the Appendix (Tables B.1 & B.2).*

Site	Mean change in height (cm/year)	Estimate	Standard Error
Adults (n=200)			
Gannabos (24)	1.29	1.29	0.10
Kamieskroon (4)	1.56	0.27	0.32
Bulletrap (28)	1.12	-0.17	0.13
Kenhardt (13)	1.81	0.52	0.22
Onseepkans (29)	1.31	0.02	0.14
Augrabies (12)	1.03	-0.26	0.15
Richtersveld (33)	2.57	0.35	0.19
Kokerboom (15)	1.64	-0.30	0.16
Snyfontein (9)	0.99	0.33	0.15
Keetmanshoop (33)	1.62	1.29	0.10
Juveniles (n=98)			
Gannabos (27)	1.61	1.61	0.13
Kamieskroon (1)	6.17	4.56	2.54
Bulletrap (53)	5.91	4.30	0.33
Kenhardt (0)	-	-	-
Onseepkans (9)	3.11	1.51	0.43
Augrabies (0)	-	-	-
Richtersveld (1)	4.46	2.85	1.83
Kokerboom (1)	4.12	2.51	1.69
Snyfontein (1)	4.37	2.76	1.80
Keetmanshoop (5)	7.80	6.19	1.43

Differences in annual change in height between winter and summer rainfall zones were explicitly tested (once again excluding the Richtersveld due to the low degree of seasonality of its climate), which showed that adult trees in the winter rainfall zone had a lower mean change in height (1.22 cm/year) than those in the summer rainfall zone (1.45 cm/year) (p=0.009, Table 3.6). No relationship was detected for juveniles.

Table 3.6. Results of GLMs assessing the relationship between rainfall zone (fixed effect) and annual adult and juvenile change in height (dependent variables) for Aloe dichotoma *at nine sites (excluding Richtersveld). Summer was used as the intercept in all cases (indicated in italics). Mean annual change in height values are provided, along with parameter estimates, Standard Error and P values from the models.*

Rainfall zone	Mean change in height (cm/year)	Estimate	Standard Error	P
Adults (n=167)				
Summer	*1.45*	*1.448*	*0.054*	*< 0.0001**
Winter	1.22	-0.225	0.085	0.009*
Juveniles (n=97)				
Summer	*4.72*	*4.721*	*0.692*	*< 0.0001**
Winter	4.48	-0.241	0.751	0.749

* Significantly different from intercept mean (at significance level of 0.05)

The mean annual change in height of adults and juveniles had a positive relationship with Temp. 1 and a positive relationship with Precip. 1 and Precip. 2 (Table 3.7). This indicated that change in height increased as annual mean temperature, annual temperature range, and mean temperature of the wettest and warmest quarters decreased, and mean temperature of the driest quarter decreased. The opposite was found for precipitation, where change in height increased as precipitation seasonality (analogous to the co-efficient of variation or precipitation variability), precipitation of warmest quarter and potential evapotranspiration increased and precipitation of driest quarter and coldest quarter decreased. Surprisingly, change in height also increased as the sites became more arid, i.e. as annual precipitation, precipitation of the wettest quarter and the aridity index value decreased.

Table 3.7. Results of GLMs assessing the relationship between climate variables (PCA outputs) describing temperature (Temp. 1 and Temp 2.) and precipitation (Precip 1. and Precip. 2) (fixed effects) and annual adult and juvenile change in height values for Aloe dichotoma *(dependent variables). Mean values for each category are provided (and have been back transformed where necessary), along with parameter estimates, Standard Error and P values from the models. Intercepts are indicated in italics.*

Temp. variables	Mean annual change	Estimate	Standard Error	P	Precip. variables	Mean annual change	Estimate	Standard Error	P
Adults (n=200)									
(Intercept)	1.578	*1.578*	*0.050*	*< 0.0001**	(Intercept)	1.501	*1.501*	*0.045*	*< 0.0001**
Temp. 1	1.664	0.086	0.025	0.001*	Precip. 1	1.560	0.058	0.026	0.024*
Temp. 2	1.619	0.041	0.058	0.479	Precip.2	1.378	-0.123	0.028	< 0.0001*
Juveniles (n=98)									
(Intercept)	3.718	*1.313*	*0.106*	*< 0.0001**	(Intercept)	5.013	*1.612*	*0.090*	*< 0.0001**
Temp. 1	4.041	0.083	0.037	0.028*	Precip. 1	5.930	0.168	0.046	< 0.0001*
Temp. 2	3.076	-0.190	0.200	0.346	Precip.2	4.149	-0.189	0.066	0.005*

* Significantly different from intercept mean (at significance level of 0.05)

Recruitment modelling

Recruitment modelling based on annual change in height values revealed that living individuals could have recruited as far back as the 1700s (Figure 3.6). Modelled recruitment density and dates of peak recruitment provided an idea of whether recruitment was predominantly trickle or episodic and pulsed in nature. Where available, historical rainfall and maximum temperature was overlain on the recruitment graphs to assist in determining if recruitment events were tied to climate.

Winter rainfall sites displayed a unique recruitment profile, with a relatively more recent recruitment peak around 1960 at Gannabos and around 1975 at Bulletrap. Summer rainfall sites displayed varied recruitment curves, which could be classified as one of three types: bi-modal, strongly unimodal and weakly unimodal. Onseepkans and Snyfontein both showed similar recruitment curves with two peaks: one in the mid- to late 1800s and a second smaller peak in the mid- to late 1900s. Kenhardt, Richtersveld, Kokerboom and Keetmanshoop had a single pronounced recruitment peak around 1900, or in the case of Kokerboom, around 1830. In all cases, recruitment in the summer rainfall zone was spread across a longer time-frame than the more recent recruitment events at the winter rainfall sites. Finally, Augrabies showed a slightly different recruitment curve with a small peak of low amplitude around the mid-1800s.
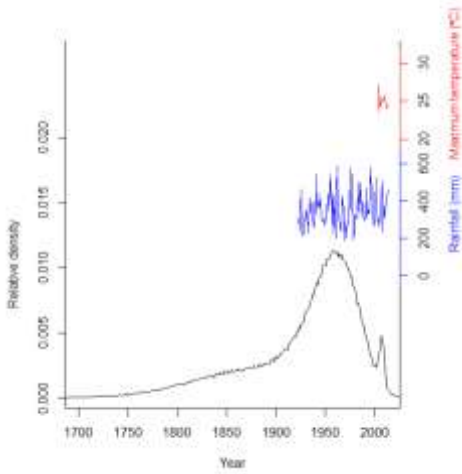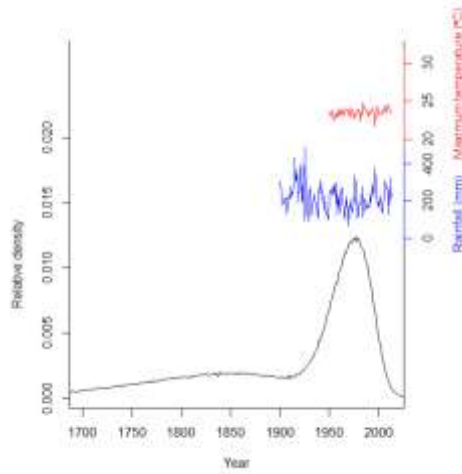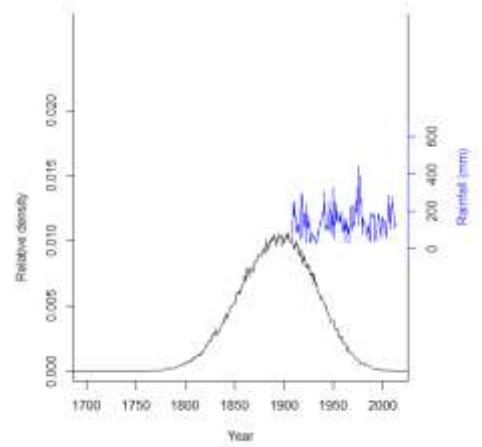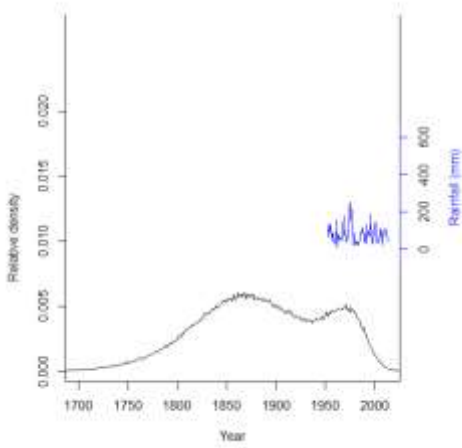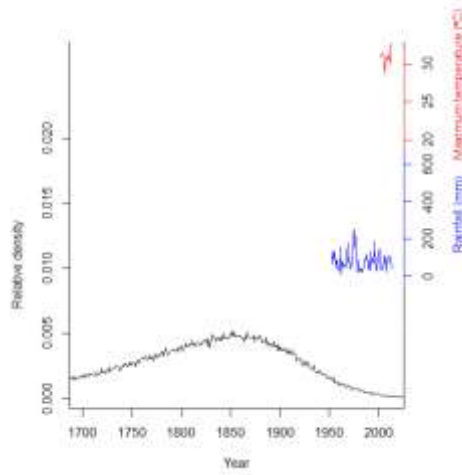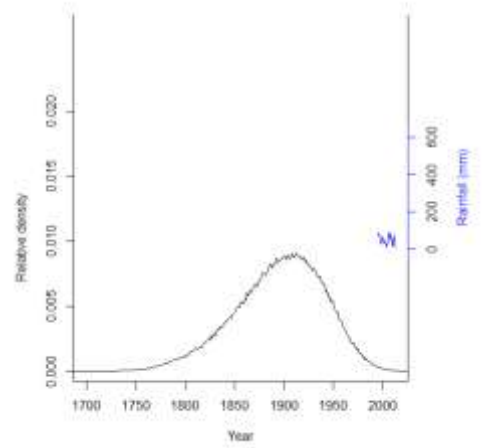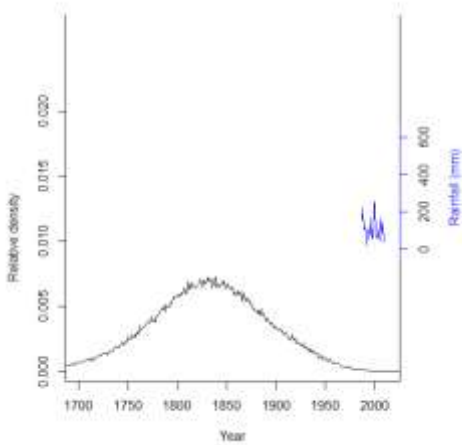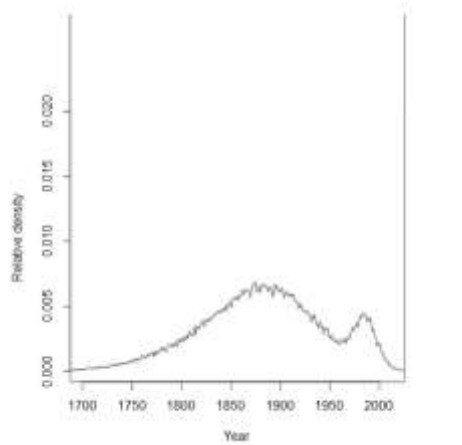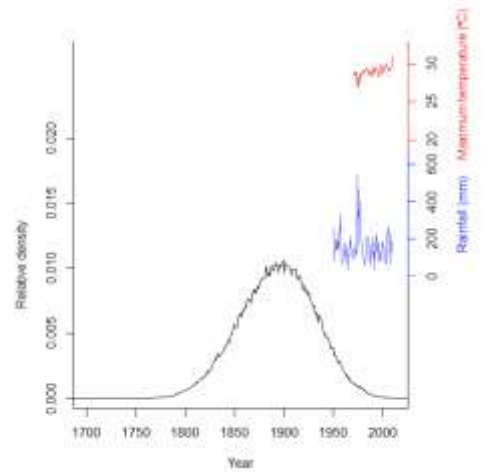
Figure 3.6. Recruitment curves for Aloe dichotoma *at nine sites within South Africa and Namibia, arranged latitudinally from south to north. Gannabos and Bulletrap represent winter rainfall sites, while the rest can be considered summer rainfall sites (although Richtersveld has a low seasonality). Recruitment data were obtained by combining annual change in height for adults (> 3m) at the specific site and juveniles (≤3m) from a 'universal' juvenile population to form a growth curve for the possible lifespan of a tree at each site. Potential rates of change in height from the curve were applied to each tree in each population for which height data were available in 2013 and used to determine the age of each tree and thus the date of recruitment (10 000 replications). The approximate relative density of recruitment is plotted for the period 1700 –2013, with maximum temperature and total rainfall plotted where available.*

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4 DISCUSSION

In the absence of detailed field surveys carried out over long time periods, historical photographs provide an important window on past demographic patterns. Re-taking these photographs allows one to explore how aspects of population dynamics, such as recruitment, growth and mortality, have changed through time. Such an analysis was performed on photographs of *Aloe dichotoma* populations spanning approximately the last thirty years. This analysis revealed differences in the current states, as well as differing trajectories of change for populations in the winter and summer rainfall zones.

4.1 POPULATION DEMOGRAPHY AND DYNAMICS

Age class structure can assist with identifying regeneration trends through time (Pierson & Turner 1998). In this study, demographic profiles of sites differ between rainfall zones, with winter rainfall sites showing denser populations with many juveniles and fewer dead trees, compared to summer rainfall sites with sparse populations, absent or few juveniles and many dead trees. This supports the trends in population dynamics from the analysis of repeat photography that follows. It also confirms that cohorts of the same age class are present at many of the sites, as would be expected if recruitment was linked to episodic events (Turner 1990).

Patterns and rates of mortality in *A. dichotoma* have been previously investigated, with a large range in mortality rates reported (Kaleme 2003; Foden et al. 2007; Hoffman et al. 2010; Jack 2011). This study found a mortality range of between 0.3% and 4.1% per annum, which was similar to the range of 0.8% and 3.8% per annum reported by Hoffman et al. (2010). Mortality at winter rainfall sites was three times lower than at summer rainfall sites, which is suggestive of a strong influence of rainfall seasonality on mortality. This was confirmed by the relationship found between climate and mortality, which suggested that mortality increased as sites became more controlled by a summer rainfall climate. If mortality was due to stress caused by water deficits (Foden et al. 2007), an effective increase in the amount and consistency in supply of water to plants in areas with winter rainfall could be responsible (Cowling et al. 1998). Similarly, the unexpectedly low mortality rates at Keetmanshoop could be a result of decreased juvenile mortality due to watering by the landowner. In addition, lower temperatures during the winter rainy season slow evaporation rates, thereby allowing individuals to store a greater proportion of the rain that

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does fall. Similar differences in precipitation seasonality influence the range of the functionally similar *Carnegiea gigantea* (saguaro cactus) in the Sonoran Desert (Drezner 2003). This provides further confirmation for the influence of climatic zone differences in helping to maintain spatial patterns of higher mortality within the summer versus winter rainfall zone, as proposed by Kaleme (2003) and Jack (2011).

Juveniles generally cannot tolerate as large a range of environmental variability as adults (Jackson et al. 2009), and a greater sensitivity of juvenile *A. dichotoma* has been suggested based on responses to climate and solar radiation across its range (Jack 2011). The low number of juveniles found in this study, and recruitment values of between 0.03% and 1.8% per annum are therefore unsurprising. Clear differences in recruitment were found between some sites and between rainfall zones, with more than twice as much recruitment occurring at winter rainfall sites. This may be linked to rainfall, but *A. dichotoma* is also likely to be strongly influenced by high temperatures, as has been found for other desert plant species. For example, very small seedlings of *C. gigantea* provided with additional water on a weekly basis during the recruitment season surprisingly did not show enhanced survival (Turner et al. 1966), whilst a third of shaded and watered seedlings survived. Young plants have a limited water storage capacity (Drezner 2004), and if temperatures are high enough, they may become desiccated between rainfall events. The CAM photosynthetic pathway in *C. gigantea* (and *A. dichotoma)* may also compound water stress at high temperatures. Under such conditions CAM becomes less effective, enabling faster transpiration rates and therefore greater water loss (Despain 1970, 1974). It is proposed that higher recruitment in the winter rainfall zone is likely a result of moderate rainfall in combination with less extreme maximum summer temperatures, thus resulting in generally lower aridity at these sites compared to summer rainfall sites.

Biotic and other factors could have influenced the lack of a significant relationship between recruitment and climate. For example, awareness of the importance of nurse plants for facilitating recruitment in extreme environments is growing (Holmgren et al. 1997). The aforementioned study of seedling survival by Turner et al. (1966) showed the importance of shade (and by extrapolation, nurse plants). Young juvenile *A. dichotoma* were observed to be growing from underneath nurse plants at almost all of the sites at which they were found, highlighting the importance of nurse plants across the range of this species. Various species are utilised as nurse plants as *A. dichotoma's* distribution encompasses three biomes and many different vegetation types (Jack 2011). Therefore, the architectural

structure of a nurse plant is arguably more important than the particular species, as this determines the degree of shading (Parker 1989; Drezner 2006a). Recruitment success, and ultimately population density, is therefore linked to a certain degree, to the amount of cover that nurse plants provide (Drezner 2006b). Nurse plants may also allow the nursed species to recruit and establish in climatically marginal areas where they might otherwise be unable to do so, thereby extending or maintaining the range of the nursed species (Drezner & Garrity 2003). The influence of herbivory, which is discussed in detail in relation to growth, could also be impacting recruitment values.

Human impact in the form of theft is likely to be influencing recruitment values at sites close to urban centres. At Keetmanshoop, for example, this was confirmed by the landowner. Juveniles or individuals of intermediate size are more often stolen, which could explain some of the low recruitment values and the lack of an intermediate size class at this site. This is also likely to influence populations at Kamieskroon, Bulletrap, and Kenhardt due to their proximity to well-travelled roads (e.g. van Blerk 2013).

The generally low recruitment observed at sites in this study should, however, be interpreted with caution due to high spatial variability. For example, almost no recruitment was noted at the sampled Kenhardt site within the last 50 years, even though it is the third least arid site of all according to the aridity index. In contrast, a nearby population (approx. 11 km to the east) that started with four planted individuals in 1906 has since grown to well over 200 individuals (van Blerk 2013). This highlights the considerable spatial and temporal population fluctuations that characterize desert succulents (Vandermeer 1980; Steenbergh & Lowe 1983), and the possible importance of smaller-scale differences in abiotic and biotic factors.

In the ten populations included in this study, the greatest change over the last 30 years was in terms of mortality rather than recruitment. Overall population change ranged from growth of 1.3% to a decline of 2.5% per annum. This was the same order of magnitude as growth of 0.9% to a decline of 4.73% per annum recorded by Foden et al. (2007) over the 20th century, and suggests that rates of population change of the species have not changed appreciably within the last thirty years. All winter rainfall sites indicated population growth, with a mean of 1% per annum, while all summer rainfall sites exhibited a decline in population growth, with a mean of -1% per annum. Further support for different trajectories of population change was provided by the relationship between population dynamics and climate. This affirmed the findings of Kaleme (2003) and Hoffman et al. (2010), providing

strong support for the influence of different precipitation regimes on population dynamics in *A. dichotoma*.

Population dynamics in the area along the Gariep River merit further discussion. At Augrabies, mortality was high and consistent with mortality in nearby, previously studied populations (Foden et al. 2007; Midgley et al. 2009; Jack 2011) and coupled with low recruitment. This points to the fact that the climate in this area is particularly harsh, and confirms a linkage between climate and mortality of adults and juveniles (e.g. Foden et al. 2007; Jack 2011). Along with many other sites in the summer rainfall zone, Augrabies showed that mortality rates were likely to be too high for the population to be sustained with rare episodic recruitment events, a pattern detected by Foden et al. (2007) and Midgley et al. (2009) for many sites. Wiegand et al. (2004) suggest that low-level continuous recruitment is important in sustaining populations with infrequent episodic recruitment events. Patterns of recruitment over time may enable us to predict whether declining populations in the summer rainfall zone, such as Augrabies, are likely to be maintained over the long-term, and are investigated in the following sections.

4.2   GROWTH (CHANGE IN HEIGHT) OF ADULTS AND JUVENILES

The change in height of adults and juveniles was measured as a simple way of approximating growth, with the aim of deriving a model describing recruitment in *A. dichotoma* across a large geographical area – something that had not previously been attempted. From the model one could then determine if recruitment patterns were different between populations or across the winter-summer rainfall divide. Growth patterns also afforded insight into many other processes affecting *A. dichotoma* populations. Like its sister species *Aloe pillansii*, growth in *A. dichotoma* varies by age and is somewhat correlated with height (Duncan et al. 2005). Change in height of *A. dichotoma* juveniles was between 1.2 and 5 times faster than adults, compared to 2.5 times faster in *A. pillansii* (Duncan et al. 2005). Preliminary observations of growth in *A. dichotoma* revealed that change in height was more rapid when the tree had fewer rosettes (Saillard 2010 unpubl.). Initially, a linear relationship was found between the height and circumference of unbranched juveniles, followed by a negative exponential relationship between these two measures in adults. This was as a result of adults repeatedly branching dichotomously, thereby spreading their growth across an ever-increasing number of branches. This demonstrates the complexities associated with

describing growth rates of a branched plant, and supports the use of the simpler 'change in height' as an indicator of growth in this study.

Moisture availability is a limiting factor in arid areas and is therefore of critical importance to growth (Nobel 2005; Lambers et al. 2008). A positive relationship between rainfall and growth rate has been documented for many desert succulent species (Parker 1988; Schwinning & Sala 2004). Contrary to what was expected, rainfall amount and growth were not well correlated for the populations investigated in this study. A comparison of adult growth between sites revealed that annual change in height at Richtersveld was up to 2.5 times higher than at other sites. In addition, this site was the most arid according to the aridity index, with an annual rainfall of only 82 mm. Interestingly, trees at Richtersveld had fewer terminal branches (mean of 51) compared to individuals at the other sampled sites. However, because of the large range in adult ages, the only significant difference was at Gannabos (mean of 129). Having fewer terminal branches (and therefore rosettes) could be an adaptation to harsh, hyper-arid conditions whereby the tree limits leafy material and, consequently, water loss. Indeed, a similar mechanism to curtail water loss influences the architecture of *C. gigantea*. Moisture-stressed individuals produce fewer branches to decrease stem surface area and associated cuticular and transpirational water losses (Yeaton et al. 1980). Architectural differences as adaptations to aridity are also likely to account for the significantly faster change in height of adult trees in the summer rainfall zone, where all sites except Kenhardt were more arid than those in the winter rainfall area.

The architecture of adult trees could potentially have other far-reaching influences on, for example, reproductive output. *C. gigantea* also produces flowers and fruit on terminal branches (Johnson 1924), and reproductive output increases proportionally as branching increases (Steenbergh & Lowe 1977; Turner et al. 1995). While it is seldom observed that all rosettes on *A. dichotoma* produce flowers, having fewer rosettes could limit the potential number of flowers and seeds produced under optimal conditions. While this is unlikely to be the main factor driving recruitment differences between different populations of *A. dichotoma*, it could contribute to the high recruitment at winter rainfall sites and the relatively low recruitment at many summer rainfall sites.

Juveniles represent a more simplified form to study differences in growth within and between rainfall zones, as there are no confounding architectural differences such as branching patterns. Despite this simplification, no significant differences in growth were detected between rainfall zones, which was likely an artifact of the dearth in data points at

all sites except Gannabos and Bulletrap. Some significant differences were found between sites. The juveniles at Gannabos had the lowest mean annual change in height of only 1.61 cm/year, which was distinct from all other sites, including the other winter rainfall sites (approximately 6 cm/year). The reasons for slower growth at Gannabos were unclear, as the available climate variables at this site did not differ substantially from either of the other two winter rainfall sites. However, a strong north aspect preference at Gannabos may be indicative of strong selection for warmer slopes and may point to temperature as the factor limiting growth, as has been recorded in *C. gigantea* (Steenbergh & Lowe 1976; Turner et al. 1995; Drezner 2004). Keetmanshoop, on the other hand, showed the fastest rate of change in height (mean of 7.8 cm/year). However, this should be considered an anomaly since many of the struggling juveniles are watered by the landowner. Notwithstanding human influence, this suggested a positive relationship between precipitation and growth, in line with the growth patterns of similar desert succulents (Parker 1988; Schwinning & Sala 2004).

This study showed that rates of growth, especially in juveniles, were highly variable. This was in line with other studies on *A. dichotoma*, as well as other desert succulents (Escoto-Rodríguez & Bullock 2002; Drezner 2005). For example, Duncan et al. (2006) found that juveniles of *A. pillansii* exhibited more variable growth rates than adults (Duncan et al. 2006) and Powell (2005) and Saillard (2010 unpubl.) found that physical damage and climate played an important role in limiting growth in *A. dichotoma*. Besides microclimatic differences associated with different micro-niches, variability in change in height within a single site is likely to be partially the result of biotic factors, such as physical damage. Bulletrap was the site with the most variable juvenile change in heights and also the site most heavily impacted by herbivory (most likely donkeys). The majority of individuals showed bark removal and some degree of stem damage. Where rosettes had been removed, the occasional resprouting of multiple rosettes caused these individuals to have lower annual change in height, as well as a reduced chance of long-term survival, as these branches are thinner and weaker and more likely to break in the future. Apart from simply damaging the plant, herbivory also appeared to result in juvenile mortality in many instances, and occurred across different land uses: on private farms, and in unprotected and protected wilderness areas. Conversely, anecdotal evidence suggested that herbivory was unlikely to be a significant cause of mortality in adult *A. dichotoma*, due to their larger size and therefore greater resilience in the face of damage. However, Foden et al. (2007) found that stem damage correlated with adult mortality at the landscape level, suggesting that its importance was contingent upon the aridity of the site and the likelihood of herbivores to

seek alternative water and food sources (Foden et al. 2007; Midgley et al. 2009). As in a previous study investigating the causes of mortality in *A. pillansii* by Duncan et al. (2006) it was difficult to disentangle the influences of abiotic and biotic factors on growth and mortality in *A. dichotoma*. The results show that both are likely to be influencing the growth patterns in adult and juvenile *A. dichotoma* to varying degrees across its range.

4.3 RECRUITMENT MODELLING

Annual change in height and the heights of living individuals were used to model the relative density of recruitment events over time. This enabled estimation of the longevity of the species. Recruitment events stretched back as far as 1700 at most sites, supporting assertions that this species may live much longer than the 100 years suggested by Vogel (1974), and to a maximum age of 300 to 350 years (Foden et al. 2007; Foden & Stuart 2009). The longer an organism's lifespan, the greater the number of years available for reproduction, and the greater its ability to buffer itself against unsuitable conditions (Chesson et al. 2004).

Overlaying climate trends onto the recruitment curves illustrated just how poor the temporal depth and spatial coverage of the data is. This made it very difficult to confidently link recruitment peaks with highly variable rainfall. The recruitment curves show some evidence of a relationship between rainfall and recruitment. While some sites showed evidence of recruitment peaks after periods of high rainfall at that site (Bulletrap and Onseepkans), there were also sites at which no recruitment peaks were observed after high rainfall (Kenhardt, Augrabies and Keetmanshoop).

Winter rainfall sites displayed a unique recruitment profile with relatively more recent recruitment peaks around 1960 and 1975 at Gannabos and Bulletrap respectively, and lower-level recruitment prior to that. At Bulletrap, where rainfall records were available from the late 1800s, it appeared that the increase in recruitment around 1920 could be associated with a number of years of high rainfall around this time. This is supported by decadal-scale evidence for wetter conditions in the winter rainfall zone around 1920 and 1950 (Neukom et al. 2013). This would suggest that episodic recruitment events in response to rainfall were important in shaping the populations at Bulletrap and Gannabos. The demographic profiles for these populations confirm an abundance of juveniles at each of these sites. However, while rainfall is clearly important, other biotic and abiotic factors need also to align for these recruitment pulses to have a lasting success (Drezner 2006a).

The summer rainfall sites showed more varied recruitment patterns, described as either bimodal, unimodal with low variance, or unimodal with high variance. Rainfall records were only available for very limited timescales, and general trends were therefore inferred from Neukom et al. (2013). In the summer rainfall zone, the wettest period of the last 200 years was between 1870 and 1900, followed by dry periods around 1930, 1945 and from the 1970s onwards. Onseepkans and Snyfontein both showed similar bimodal recruitment curves. One peak occurred in the mid to late 1800s and the second smaller peak in the mid to late 1900s. Kenhardt, Richtersveld, and Keetmanshoop had a single pronounced recruitment peak around 1900, or in the case of Kokerboom, around 1830. It seemed that recruitment peaked around the time of the wettest period of the last 200 years, and began to decline around the time of the two following dry periods of 1930 and 1945. In all cases, the recruitment window was wider for summer rainfall sites compared to the more concentrated recruitment events in the winter rainfall area. Finally, Augrabies showed a slightly different recruitment curve with a small peak in the mid 1800s, which suggests a low rate of continuous recruitment before this point. This recruitment pattern could be related to the current high rate of mortality observed at this site and in the Gariep River valley generally (Foden et al. 2007; Midgley et al. 2009; Jack 2011). In other words, trees which recruited in the early- to mid-1800s may now be reaching their age limit and dying.

While a very limited temperature record was available at only four sites, higher maximum temperatures seemed to have no observable impact on recruitment at each site. Notwithstanding the absence of a clear relationship, maximum temperatures at winter rainfall sites (Gannabos and Bulletrap) were around 5 °C lower than those at summer rainfall sites (Augrabies, Keetmanshoop), which was likely to lead to higher recruitment in the winter rainfall zone. Drezner (2004) suggested that desert succulents are controlled by climatic extremes as opposed to averages, and an analysis of recruitment patterns at shorter timescales and at micro-scale (at which juveniles are likely to respond) may clarify the linkages between climate and temporal recruitment patterns.

The recruitment curves suggest that episodic recruitment is occurring in most populations, with little continuous recruitment evident. Wiegand et al. (2004) found that low levels of continuous recruitment act as an 'ecological buffer' because they ensure that populations of long-lived desert plants do not fall below a critical threshold between large, episodic recruitment events. This critical threshold relates to extinction due to environmental stochasticity and the Allee effect, where density-dependent effects such as

low genetic diversity and the attraction of fewer pollinators accelerate the population's decline (Ashman et al. 2004). A lack of both episodic and continuous recruitment over prolonged periods therefore suggests an increased risk of extinction (Wiegand et al. 2004). Populations in the summer rainfall zone with a unimodal distribution and pronounced peak, i.e. Kenhardt, Richtersveld, Keetmanshoop and Kokerboom appear to have been established during large episodic events, which have not reoccurred. Rates of recruitment from repeat photographs are low at Kenhardt, Richtersveld and Kokerboom, suggesting that these sites have the highest risk of extinction if another episodic recruitment event does not occur before mortality pushes their numbers below a critical threshold.

4.4 THE INFLUENCE OF CLIMATE SEASONALITY ON THE DEMOGRAPHY OF *A. DICHOTOMA*

The influence of winter and summer rainfall seasonality on *A. dichotoma* has emerged as an important factor in each of the analyses in this study. The effect of biotic and anthropogenic factors such as herbivory, nurse plant associations and theft cannot be discounted, but are likely to play a secondary role in moderating observable patterns as opposed to being primary drivers. A closer examination of the climatic factors likely to be driving differences in the response *of A. dichotoma* in these two rainfall zones is therefore required.

Rainfall, and therefore available moisture, was shown to influence recruitment and mortality trends in *A. dichotoma*. Palaeoclimatic reconstructions of rainfall in southern Africa over the last 200 years have revealed differences within the winter and summer rainfall zones (Neukom et al. 2013), which are likely to be important in explaining contrasting responses of the species in different parts of its range. The winter rainfall zone showed no significant change in mean rainfall between the 19th and 20th centuries, although a significant increase in rainfall variability was detected (Neukom et al. 2013). The summer rainfall zone, on the other hand, showed a decrease in mean rainfall over this period. The recruitment curves suggest that this is likely to have contributed to the lack of recruitment at many summer rainfall sites, although these broad-scale patterns may vary considerably at the site scale. The relationship between high temperatures and associated mortality due to moisture stress has been established on a correlative basis for adults (Foden et al. 2007) and juveniles (Jack 2011).

However, the lack of observable change in rainfall in the winter rainfall zone over the last 200 years, apart from an increase in variability, is unlikely to have exclusively driven

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the high recruitment and low mortality in the winter rainfall zone. Limitation of recruitment in the winter rainfall zone imposed by cold temperatures during the Little Ice Age of the 17th to mid-19th centuries (Tyson et al. 2000) has not been assessed. Conversely, the increase in temperature in the winter rainfall zone in the second half of the 20th century could explain recent population expansions in this region. Mortality of the functionally similar *C. gigantea* (especially seedlings) is caused by periodic freezes in colder parts of its range (Steenbergh and Lowe 1976; Turner et al. 1995; Drezner 2004). Winter temperatures in the Sonoran desert are cool and only occasionally fall below freezing (Drezner 2004), and are therefore comparable to the temperature regimes of the winter rainfall zone in southern Africa. For example, daily minimum winter temperatures for Nieuwoudtville (near Gannabos) are almost always below 10°C and drop below freezing intermittently, although Springbok (near Bulletrap) experiences slightly higher temperatures that seldom drop below freezing. Significant temperature increases, detected by Foden et al. (2007) over the last 25 to 60 years, are likely to have enabled this species to establish in areas where it may previously have been cold-limited. Drennan and Nobel (2000) suggest that the combined influence of increasing temperatures and improved photosynthetic efficiency (due to CO_2 enrichment) is likely to result in range expansions of freezing-sensitive CAM species, such as *A. dichotoma*. Experimental testing is required to determine the extent of *A. dichotoma's* sensitivity to low temperatures and confirm this relationship.

Longer-term changes in *A. dichotoma's* distribution, as inferred from genetic evidence, and supported by palaeoclimatic proxy data, also appear to support the assertion that temperature extremes (and associated aridity) have influenced the species. Populations in the middle of its latitudinal range showed the highest genetic diversity (and the longest history of establishment), with populations in the south thought to be the most recently established (Midgley et al. 2009). The winter rainfall zone was colder and wetter and extended further north soon after the last ice age, approximately 15 000 years ago (Chase & Meadows 2007). *A. dichotoma* populations are thought to have established in the south only after warming occurred (Midgley et al. 2009), suggesting that colder and wetter conditions have limited its southerly distribution in the past. Around the time of the Holocene Altithermal (approx. 8700–3500 years ago) warm, humid conditions characterised the northern parts of *A. dichotoma*'s distribution (Chase et al. 2009). Increasing aridity, particularly within the current summer rainfall region, was a feature of the subsequent 3200 years (Chase et al. 2009) and is likely to have influenced the current distribution of this species (Midgley et al. 2009; Jack 2011).

4.5 FURTHER RESEARCH

The main limitations of this study were the number of sites and individual trees sampled, as well as the availability of high-resolution climatic data. Climatic variables could not be added to the population dynamics and growth GLMs separately due to limitations imposed by the number of observations, which made it difficult to decouple the influences of individual climatic variables and detect differences between sites. It is suggested that this is easier near the environmental optimum of the species (Drezner 2004), where population densities are highest (Niering et al. 1963). Additional study sites should therefore be sampled within the winter rainfall zone. The scale of future studies is also important. Knowledge of the coarse-scale dynamics of the species has been improved by this, and other prior studies. Fine-scale patterns, for example the recruitment niche for this species, are still poorly understood. This study has shown that while micro-climatic conditions may be important for recruitment, biotic influences, including herbivory, pollination and the importance of nurse plants need greater consideration. Findings from this crucial period in the life history of *A. dichotoma* may highlight other important drivers of population change.

4.6 CONCLUSION

By assessing responses at the population and individual scales, this study has provided multiple lines of evidence confirming the very different influences of winter and summer rainfall zones on *A. dichotoma* and its distribution.

Winter rainfall sites were generally characterised by much lower mortality and higher recruitment than summer rainfall sites, with demography reflecting these patterns. In addition, overall population change was positive at all of the winter rainfall sites and negative at all of the summer rainfall sites. This provides strong evidence that conditions within the winter rainfall zone are more favourable for the recruitment and persistence of *A. dichotoma*. The mechanisms driving these patterns were more challenging to identify: while rainfall was not as closely tied to mortality and recruitment as might have been expected, the influence of temperature appeared important, with recruitment constrained by maximum and likely also minimum temperatures.

Growth data revealed some interesting patterns: contrary to expectations, change in height of adults was faster at summer rainfall sites. The influence of aridity, as opposed to rainfall alone, was thought to explain the observed patterns, with architectural differences to minimize water loss influencing the perceived growth rates. Rates of growth in juveniles

were highly variable due to their greater sensitivity to biotic influences. The relationship between growth and climatic influences was complex. The recruitment curves derived from growth data again highlighted differences between winter and summer rainfall sites: relatively recent recruitment peaks (and lower-level recruitment prior to that) were observed at winter rainfall sites, while summer rainfall sites showed more varied recruitment patterns. These findings also suggested that episodic recruitment is occurring in most populations, with little continuous recruitment evident, and provided an indication of whether the populations were likely to persist into the future.

These considerable differences in demography, mortality, recruitment (both spatial and temporal patterns), population change and growth between winter and summer rainfall zones (and the general agreement of these patterns with climate modelling) have improved our understanding of long-term drivers of change and their effects on *A. dichotoma*. It has become clear that *A. dichotoma*'s response to climate change may be more complex than the negative responses previously projected. This study has confirmed population declines, likely to be linked to increasing moisture stress in the more arid summer rainfall parts of this species' distribution, but has also shown that warming associated with climate change may also be contributing to population expansions in cold-temperature-limited parts of the winter rainfall zone. The advancement of knowledge of broad spatial and temporal patterns in *A. dichotoma* and the likely causes, coupled with fine-scale future studies, will enable more detailed prediction of the species' response to future global change.

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APPENDICES

A. POPULATION DYNAMICS

Table A.1. Results of pairwise least-squares means test of GLM to determine differences in the mean annual mortality of ten Aloe dichotoma *populations (n=70). P values displayed have been corrected using the Bonferroni method. * = sign*ificantly different from mean (at significance level of 0.05).

	Gan	Kam	Bul	Ken	Ons	Aug	Ric	Kok	Sny	Kee
Gan	-									
Kam	1.000	-								
Bul	1.000	1.000	-							
Ken	0.005*	1.000	1.000	-						
Ons	0.004*	1.000	1.000	1.000	-					
Aug	< 0.0001*	1.000	0.176	1.000	0.774	-				
Ric	1.000	1.000	1.000	0.394	0.431	0.003*	-			
Kok	0.423	1.000	1.000	1.000	1.000	0.363	1.000	-		
Sny	< 0.0001*	1.000	0.002*	1.000	0.000*	1.000	< 0.0001*	0.002*	-	
Kee	1.000	1.000	1.000	0.033*	0.007*	0.000*	1.000	1.000	< 0.0001*	-

*

Table A.2. Results of pairwise least-squares means test of GLM to determine differences in the mean annual recruitment of ten Aloe dichotoma *populations (n=70). P values displayed have been corrected using the Bonferroni method. * = significantly different from mean (at significance level of 0.05).*

	Gan	Kam	Bul	Ken	Ons	Aug	Ric	Kok	Sny	Kee
Gan	-									
Kam	1.000	-								
Bul	1.000	1.000	-							
Ken	0.098	1.000	0.371	-						
Ons	1.000	1.000	1.000	0.038*	-					
Aug	1.000	1.000	1.000	1.000	1.000	-				
Ric	0.083	1.000	0.359	1.000	0.004*	1.000	-			
Kok	0.060	1.000	0.262	1.000	0.007*	1.000	1.000	-		
Sny	1.000	1.000	1.000	0.441	1.000	1.000	0.215	0.177	-	
Kee	1.000	1.000	1.000	1.000	1.000	1.000	0.603	0.503	1.000	-

Table A.3. Results of pairwise least-squares means test of GLM to determine differences in the mean annual population change of ten Aloe dichotoma *populations (n=70). P values displayed have been corrected using the Bonferroni method. * = significantly different from mean (at significance level of 0.05).*

	Gan	Kam	Bul	Ken	Ons	Aug	Ric	Kok	Sny	Kee
Gan	-									
Kam	1.000	-								
Bul	1.000	1.000	-							
Ken	0.005*	1.000	0.048*	-						
Ons	0.839	1.000	1.000	0.429	-					
Aug	0.005*	1.000	0.049*	1.000	0.443	-				
Ric	0.512	1.000	1.000	1.000	1.000	1.000	-			
Kok	0.175	1.000	0.935	1.000	1.000	1.000	1.000	-		
Sny	0.000*	1.000	0.013*	1.000	0.045*	1.000	0.372	1.000	-	
Kee	1.000	1.000	1.000	0.147	1.000	0.152	1.000	1.000	0.011*	-

B. GROWTH

Table B.1. Results of pairwise least-squares means test of GLM to determine differences in mean change in height of adult trees within ten Aloe dichotoma *populations (n=200). P values displayed have been corrected using the Bonferroni method. The number of individuals measured is displayed in brackets next to the site name. * = significantly different from mean (at significance level of 0.05).*

	Gan	Kam	Bul	Ken	Ons	Aug	Ric	Kok	Sny	Kee
Gan (24)	-									
Kam (4)	1.000	-								
Bul (28)	1.000	1.000	-							
Ken (13)	0.512	1.000	0.021*	-						
Ons (29)	1.000	1.000	1.000	0.599	-					
Aug (12)	1.000	1.000	1.000	0.010*	1.000	-				
Ric (33)	< 0.0001*	0.092*	< 0.0001	0.082	< 0.0001	< 0.0001	-			
Kok (15)	1.000	1.000	0.111	1.000	1.000	0.053	0.001*	-		
Sny (9)	1.000	1.000	1.000	0.007*	1.000	1.000	< 0.0001	0.036*	-	
Kee (33)	0.815	1.000	0.004*	1.000	0.956	0.003*	< 0.0001*	1.000	0.003*	-

Table B.2. Results of pairwise least-squares means test of GLM to determine differences in mean change in height of juvenile trees within eight Aloe dichotoma *populations (n=98). P values displayed have been corrected using the Bonferroni method. The number of individuals measured is displayed in brackets next to the site name. * = significantly different from mean (at significance level of 0.05).*

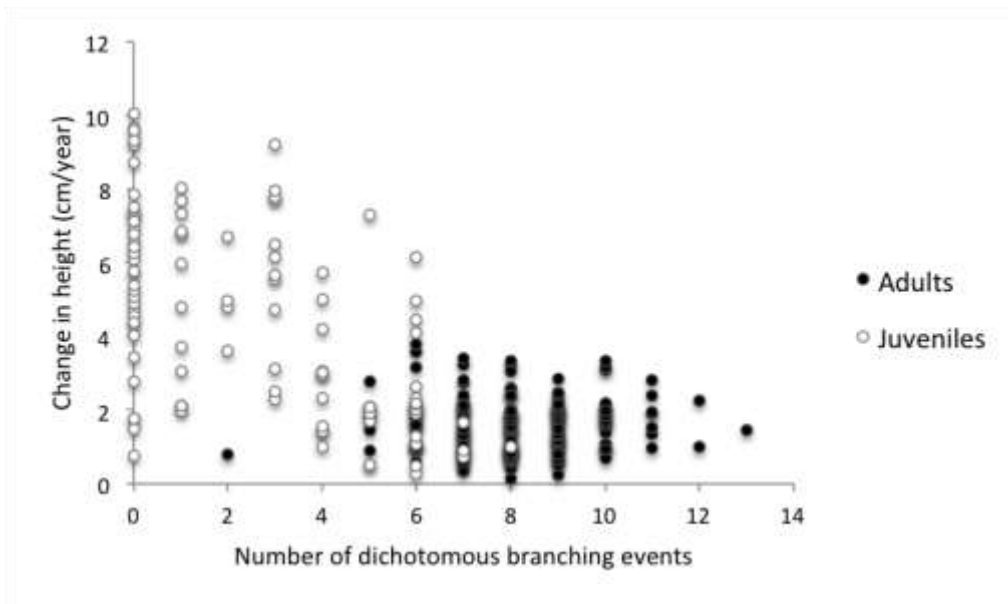|	Gan	Kam	Bul	Ons	Ric	Kok	Sny	Kee
Gan (27)	-							
Kam (1)	1.000	-						
Bul (53)	< 0.0001*	1.000	-					
Ons (9)	0.020*	1.000	< 0.0001*	-				
Ric (1)	1.000	1.000	1.000	1.000	-			
Kok (1)	1.000	1.000	1.000	1.000	1.000	-		
Sny (1)	1.000	1.000	1.000	1.000	1.000	1.000	-	
Kee (5)	0.001*	1.000	1.000	0.049*	1.000	1.000	1.000	-

Figure B.1. Scatterplot showing the relationship between the number of dichotomous branching events and the annual change in height (cm/year) of all individuals. A cluster analysis based on Bulletrap and tested across all other sites suggested that a height of 3 m could be used as a threshold between adult and juvenile change in heights.
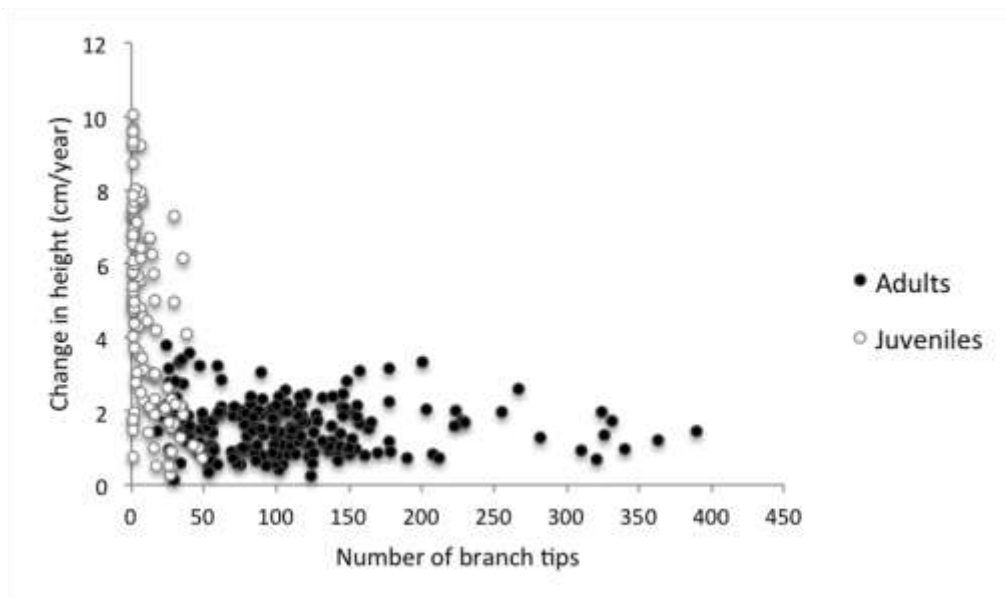

Figure B.2. Scatterplot showing the relationship between the number of live heads and the annual change in height (cm/year) of all individuals. A cluster analysis based on Bulletrap and tested across all other sites suggested that a height of 3 m could be used as a threshold between adult and juvenile change in height.