Revisiting *Aloe dichotoma*'s suitability as an indictor of climate change in southern Africa

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Abstract

Apparent recent population contractions at *Aloe dichotoma*'s equatorward range limit have led this iconic arborescent succulent to be cited as one of the first biological indicators of the impact of anthropogenic climate change in southern Africa. However, prior evidence from historical photography of populations as well as detailed botanical field notes indicated that mortality was already pervasive in the southern and central distribution of the species within the first half of the 20th century. This, as well as possible previous assumptive and interpretive problems prompted a reassessment of the evidence for *A. dichotoma*'s promotion as a climate change indicator species. In the current study, a framework for assessing species vulnerability to climate change was used to determine *A. dichotoma*'s exposure, sensitivity, and adaptive capacity to climate change impacts.

First I evaluated *A. dichotoma*'s exposure to climate change by independently assessing historical rainfall and temperature records of the longest possible duration, and specific to *A. dichotoma*'s distributional extent, in order to evaluate how average conditions and temporal trends might contribute to demographic patterns. I then made use of very high spatial resolution demographic information collected during a roadside mega-transect in order to re-examine the merits of a latitudinal cline in mortality. Subsequently, I related demographic patterns to a detailed contemporary climate surface in order to gauge the strength of the relationship between the two, as well as to determine the relative sensitivity of juvenile and adult life history stages. Additionally, with the aid of detailed population-level sampling and averaged solar radiation values for opposing aspects, I investigated *A. dichotoma*'s adaptive capacity in terms of its ability to recruit to more favourable aspects. In this respect, a new technique was developed to determine the approximate time since death of *in situ* skeletons, as well as the age classes from which they were derived. Lastly, study results were interpreted in relation to *A. dichotoma*'s life history traits to determine the likelihood of a recent response to climate change

Despite a paucity in instrumental records and record length, particularly within the equatorward summer rainfall zone (SRZ), encompassing southern and central-western Namibia, historical climate analyses revealed considerable spatial and temporal variability in temperature and, especially, rainfall, within the distribution range of the species. For the SRZ, average climatic conditions were found to be at least as severe within the Gariep River valley, between 28°S and 29°S, as for the equatorward extreme at approximately 21°S, undermining previous inferences of a simple latitudinal climate gradient. Conversely, average rainfall within the poleward winter rainfall zone (WRZ), and south-western extreme

of the SRZ, was shown to have been historically higher and more consistent than the SRZ to the north. The natural climatic disjunction between northern and southern rainfall zones has likely had a significant influence on the maintenance of relative latitudinal recruitment and mortality rates in *A. dichotoma*, and may have contributed to an erroneous attribution of observed mortality to recent, anthropogenic climate change.

Historical temperature records indicated an almost uniformly increasing trend throughout the distribution, rising more rapidly within the SRZ. However, rainfall trends were more difficult to interpret, being strongly contingent upon record length, segment of time recorded, and initial and terminal conditions under which the record was established. These interpretive difficulties were considerable for Namibian stations, and advocated a cautious interpretation of negative rainfall trends at several summer rainfall stations, while generally more robust records at winter rainfall stations registered mostly positive trends over the last sixty years.

Results from the roadside mega-transect corroborated trends in climatic severity, indicating that proportional mortality had also been greatest within the Gariep River valley between 28°S and 29°S and not at the equatorward range limit as previously suggested. Furthermore, there was only a very weak relationship between age classes and key contemporary climate variables, which suggested an uncoupling between the two. Despite generally poor relationships, juveniles were most responsive to climate and solar radiation gradients, suggesting a greater sensitivity compared to the adult age class, which appeared more resilient. In addition, most mortality was shown not to be recent in origin, but to have occurred several decades ago and to be chiefly derived from larger and, therefore, more climatically-resilient, adult age class rather than smaller, more climatically-sensitive juvenile individuals.

In combination with *A. dichotoma*'s life history traits, including longevity, slow growth and infrequent recruitment, the findings from this study indicate that current demographic patterns reflect longer-term climatic fluctuations rather than recent climate change and that certain climatically marginal populations may be biological relicts of a previously more amenable climate. These findings challenge the view that *A. dichotoma* has responded negatively to recent, anthropogenically-driven changes in climate and reassert the importance of longer term climatic and demographic processes in shaping patterns currently observed within populations of this species.

Coupled with the establishment of a long term ecological research network at key populations spanning the full latitudinal (and longitudinal) range, a greater focus on the regeneration niche and physiological thresholds would help advance our understanding of *A. dichotoma*'s susceptibility to moisture and temperature deficits arising from climate change. Assessment of the suitability of A.

dichotoma as a sentinel of climate change would also be greatly aided by the improved temporal and spatial resolution of historical and palaeo-climatic records within southern Africa. There is an urgent need for this work in the face of possible lagged responses to environmental change within long-lived, infrequently recruiting species, as well as rapidly rising temperatures and uncertainty surrounding future precipitation in the region.

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General introduction: *Aloe dichotoma* as a climate change indicator species

1.1 Background and rationale

1.1.1 Climate change impacts on species distributions

There is now unequivocal evidence that many terrestrial plant and animal species are responding to anthropogenic climate change, mainly as a result of raised global temperatures due to an intensification of the greenhouse effect (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003). While species responses are often complicated by synergistic effects (Walther, 2010), the most common measurable expressions come in the form of phenological and distributional shifts (Parmesan, 2006). The latter are expressed either as poleward shifts in latitude (Hickling *et al.*, 2006) or upward shifts in elevation (e.g Grabherr *et al.*, 1994), or both. While mobile organisms may be more capable of tracking changes in climate (e.g. Graham & Grimm, 1990; Parmesan *et al.*, 1999), sessile organisms, such as terrestrial plant species, face more of a challenge, as many are not able to disperse frequently or far enough to keep pace with a shifting climate envelope (Hill *et al.*, 1999; Foden & Midgley, 2009). The result is typically a shift towards proportionally lower recruitment and higher mortality in the demographic profile of populations at the equatorward end of the geographical distribution (e.g. van Mantgem & Stephenson, 2007; Allen, 2009).

However, most of the empirical studies which document species' range shifts in response to anthropogenic climate change are drawn from European and North American examples, where records of species' distributions stretch further back in time. In this respect the southern hemisphere is comparatively understudied, probably because of a paucity of the historical record and relatively weak institutional capacity (Hughes, 2003; Parmesan, 2006). While there have been efforts to address the shortfall in certain southern hemisphere regions (e.g. Chambers *et al.*, 2005; Gallagher *et al.*, 2009), most have seen little progress. This is worrying situation, given the rate of projected climate change and the posited greater wealth in biodiversity south of the equator (Gaston, 2000; Chown *et al.*, 2004; Haensler *et al.*, 2011).

Southern Africa, for example, has seen several attempts at modelling future regional and sub-regional climate (e.g. Hulme *et al.*, 2001; Hoerling *et al.*, 2006; Boko *et al.*, 2007; Mackellar *et al.*,

2007; Haensler *et al.*, 2011), as well as numerous predictive studies on likely future distributions of species (e.g. Midgley *et al.*, 2001; Erasmus *et al.*, 2002; Midgley *et al.*, 2002; Midgley *et al.*, 2003; Bomhard *et al.*, 2005; Midgley *et al.*, 2005[a]; Midgley *et al.*, 2005[b]; Broennimann *et al.*, 2006; Midgley *et al.*, 2006; Thuiller *et al.*, 2006[a]; Thuiller *et al.*, 2006[b]; Midgley & Thuiller, 2007; Yates *et al.*, 2010). There has also been some progress in experimental work, studying the effects of elevated temperatures on the physiology of arid adapted species (e.g. Musil *et al.*, 2005; Musil *et al.*, 2009). However, empirical studies documenting species responses to recent climate change are rare (but see Botes *et al.*, 2006). It is essential that this knowledge gap is filled, both in light of the unusually biodiverse and highly endemic flora found in the Karoo-Namib region (Cowling *et al.*, 1998; Cowling *et al.*, 1999; Desmet & Cowling, 1999) - a part of which (the Succulent Karoo) has been classified as a global biodiversity hotspot (Myers *et al.*, 2000) – and because of projected increases in temperature and precipitation variability as a result of climate change (Thuiller *et al.*, 2006[b]; Boko *et al.*, 2007; Haensler *et al.*, 2011).

1.1.2   A. dichotoma *as a southern hemisphere indicator species*

One southern African species that has been the target of recent empirical work is the quiver tree, *Aloe dichotoma.* This iconic tree-aloe is distributed across eleven latitudinal and nine longitudinal degrees in the semi-arid regions of Namibia and South Africa (Palgrave, 1977; Reynolds, 1982; Smith & Steyn, 2005). This large area, spanning more than 200,000 km^2 encompasses the Succulent Karoo, Nama Karoo and Namib Desert biomes, with highly variable topography, geology and a sizeable temperature and rainfall gradient associated with two distinct rainfall zones. *A. dichotoma*, a keystone species within its distribution (Midgley *et al.*, 1997), is adapted to survive in arid conditions, storing water in its trunk, branches and fleshy leaves. It has a tall growth-form, is shallow rooted, slow growing and long-lived, with an average life-span estimated at between one hundred and two hundred and fifty years (Vogel, 1974; Kaleme, 2003). Functionally similar to its 'sister' species, *Aloe pillansii* (Duncan *et al.*, 2006), and to several succulent Sonoran Desert species (Turner *et al.*, 1966; Jordan & Nobel, 1981; Jordan & Nobel, 1982), *A. dichotoma* is thought to recruit episodically during high rainfall years, although this may vary depending on the regularity of rainfall.

In a study sampling discrete populations spanning the full geographical range of the distribution, Foden *et al.* (2007) reported large-scale, recent mortality in northern *A. dichotoma* populations, while southern populations had both lower mortality and higher recruitment rates. It was suggested that mortality patterns reflected a recent southward range shift as a result of regional temperature increases and resultant 'water balance constraints', which had forced

northern populations beyond 'critical climate thresholds' (Foden *et al.*, 2007). Because the study was the first to link recent anthropogenic climate change to distributional changes in a southern Africa species , the research received widespread attention both in the scientific literature (e.g. Midgley *et al.*, 2007; Midgley & Thuiller, 2007; Thuiller *et al.*, 2008; Allen, 2009; Cherry, 2009; Jackson & Sax, 2009, Midgley *et al.*, 2009; Musil *et al.*, 2009; Hannah, 2010; Yates *et al.*, 2010) and popular media (e.g. Joubert, 2006; BBC News, 2007; Bruce, 2007). More recently *A. dichotoma* has emerged as the sole terrestrial plant species on the IUCN top-ten list of 'flagship' species potentially threatened by climate change (Foden & Stuart, 2009). While this attention has stimulated much-needed local awareness and debate through its promotion as a 'sentinel' for climate change in southern Africa (Midgley *et al*, 2009), there are nevertheless certain interpretations and assumptions of the previous study that warrant more thorough investigation. This is especially important in light of its potential to influence management and policy decisions.

1.1.3 *Previous interpretations and assumptions*

1.1.3.1 Interpretations

Given the high spatial variability in *A. dichotoma* mortality over relatively short distances and its weak relationship with latitude (Foden *et al.*, 2007; Saillard, 2010), an interpretation that mortality increases linearly in an equatorward direction may be overly simplistic and possibly incorrect. With such a high degree of spatial variability in mortality, studies sampling either discrete populations (e.g. Foden *et al.*, 2007) or sub-regions (e.g. Jankowitz, 1972; Jankowitz, 1977; Molyneux, 1977) might well fail to accurately capture the true pattern in mortality and recruitment. In this case, a more continuous and less intensive sampling effort may be required (Braunisch & Suchant, 2010).

In addition, an interpretation of recent northern mortality as anthropogenically driven appears not to take into account that *A. dichotoma* straddles a major seasonal rainfall divide (i.e. summer versus winter rainfall), governed by fundamentally different atmospheric processes, with likely different responses to anthropogenic CO_2 forcing (Fauchereau *et al.*, 2003). Differences in the spatial and temporal dynamics in rainfall and associated temperatures in winter and summer rainfall zones have in fact resulted in the emergence of very different vegetation communities, associated with different biomes. The Succulent Karoo biome in the south west relies on consistent winter rainfall, while the Nama Karoo and hyper-arid Namib Desert biomes to the north are supplied by more spatio-temporally erratic summer rainfall (Cowling *et al.*, 1998; Cowling *et al.*, 1999). *A. dichotoma*'s distribution across these distinct biomes, with their different rainfall and temperature environments, is relatively unusual (P. Craven, pers. comm.)

and may have led to historically different recruitment and mortality rates in equatorward and poleward populations. In light of this, the argument that different demographic profiles at the northern and southern latitudinal extreme are an artefact of a natural climatic disjunction rather than as a result of recent climate change should be investigated in more depth.

1.1.3.2 Assumptions

Due to its extensive distribution (Palgrave, 1977; Reynolds, 1982; Smith & Steyn, 2005), longevity (Vogel, 1974; Kaleme, 2003), as well as the persistence of skeletons in the landscape (Foden *et al.*, 2007), *A. dichotoma* was assumed to be a good candidate species to reveal longer term shifts in climate, especially in an area with a relatively poor spatial distribution of historical climate data (Midgley *et al.*, 2009). Yet, it is unclear whether these characteristics are necessarily suitable in an indicator species, as most species emerging as indicators of climate change have very different life history characteristics (e.g. Sweeney *et al.*, 1990; Johnson, 1998; Hoegh-Guldberg, 1999; Perry *et al.*, 2005; Broennimann *et al.*, 2006; Jiguet *et al.*, 2007; Lenoir *et al.*, 2008; Sohdi *et al.*, 2008; Munday *et al.*, 2008), which combine to elicit rapid observable responses to small fluctuations in abiotic drivers.

Typical Sonoran Desert species which share *A. dichotoma*'s life history characteristics and grow under similar climatic conditions provide little alternative evidence to support *A. dichotoma*'s suitability as an indicator species, capable of responding to subtle shifts in climate. Recruitment in species such as *Carnegiea gigantea* and *Ferocactus acanthodes* can be rapid, but it is predominantly controlled by infrequently occurring and extended periods of above average rainfall (Shreve, 1917; Steenbergh & Lowe, 1969; Brum, 1973; Jordan & Nobel, 1979; Jordan & Nobel, 1981; Turner, 1990; Bowers *et al.*, 1995). Historical botanical fieldnotes (Acocks, unpublished (see Rutherford *et al.*, 2003)) and repeat photography (Hoffman *et al.*, 2010) from the southern-central parts of *A. dichotoma*'s distribution suggest that conditions conducive to recruitment have not occurred for much of the 20th century. The implication of this is that the more sensitive juvenile age class has probably not contributed significantly to the conclusions that have been drawn about shifting *A. dichotoma* distributions.

In contrast to juveniles, adult *Carnegiea gigantea* and *Ferocactus acanthodes* individuals are far more resilient to climatic perturbations due to the buffering provided by their considerable water storage capacity (Jordan & Nobel, 1982). Mortality in populations of these species has therefore been described as a far more gradual process (Turner, 1990); only escalating in the face of severe and prolonged drought events (Parker, 1993) and freezing, induced by extended periods of sub-zero temperatures in winter (Shreve, 1917; Niering *et al.*, 1963). In the context of

historical changes in southern Africa climate, there has been little evidence of an increase in freeze events, while uncertainty surrounds the cause and incidence of drought within the last few decades (e.g. Rouault & Richard, 2003; Fauchereau *et al.*, 2003; Hoerling *et al.*, 2006; Hoffman *et al.*, 2009).

A further assumption in previous work is that mortality in *A. dichotoma* has occurred primarily as a result of recent, anthropogenically-driven climate change (Foden *et al.*, 2007). However, besides indicating that little or no recruitment had occurred in the early to mid 20th century, detailed botanical field notes (Acocks, unpublished (see Rutherford *et al.*, 2003)) and historical photographs (Hoffman *et al.*, 2010) also suggest that numerous *A. dichotoma* populations where *already* in decline at that stage, and possibly before. If *A. dichotoma* populations follow a episodic recruitment and mortality cycle, as suggested above and found in many long-lived desert succulent species (e.g. Jordan & Nobel, 1979; Goldberg & Turner, 1986; Pierson & Turner, 1998; Bullock *et al.*, 2005) and the closely related subspecies, *A. pillansii* (e.g. Bolus *et al.*, 2004; Duncan, 2006), then the period during which sampling occurs can critically influence the results obtained and, subsequently, the conclusions drawn about population health.

The use of *A. dichotoma* as a potential climate change indicator species is further confounded by potential lags in the response time of such a long-lived species to gradual changes in external stimuli; a concern previously raised for the arid adapted saguaro of south-western North America (Escoto-Rodriguez & Bullock, 2002) and other vegetation types (Colling & Matthies, 2006). In the context of *A. dichotoma*, this means that despite a possible decline in the environmental suitability of certain parts of its range, it may have continued to persist in these areas primarily because of its arid-adapted succulent habit and opportunistic, infrequent recruitment strategy. Equatorward populations, therefore, may be biological relicts (e.g. Magnuson, 1990) and represent a potential extinction debt to be paid in the future (Jackson & Sax, 2009). The implications of this are that contemporary climate may be only partly responsible for observed demographic patterns. In this respect, an assessment of long-term historical climate, as well as the role that palaeo-climates may have played in shaping the contemporary distribution and demographic patterns could yield important insights.

1.2   General objectives

The central objective of this study was to assess critically the promotion and use of *A. dichotoma* as a climate change indicator species and to re-examine its suitability in this role. This involved a detailed assessment of historical climate specific to the distributional extent of the species. In

addition, a sampling methodology was designed for this study to capture spatially-explicit demographic information on both a large and small scale in order to address directly the key assumptions and interpretive problems from previous studies, which have been highlighted above.

Dawson *et al.*, (2011) have developed a useful conceptual framework for interpreting the vulnerability of species to climate change, which has been adopted for this study. They suggest that a species' vulnerability can be interpreted within three different components. The first is a species' *exposure* to climate, as determined by exogenous factors such as its geographical location, the size and connectivity of populations, and the rate and magnitude of predicted climate change within the region (Dawson *et al.*, 2011). The second and third components represent a species' *sensitivity* and *adaptive capacity*, respectively, to changing climate. These facets of vulnerability are governed by endogenous factors such as physiological constraints, phenotypic plasticity, evolutionary potential, dispersal, growth, and biotic interactions (Dawson *et al.*, 2011). I have adopted this framework for interpreting the result of this study, using exposure, sensitivity and adaptive capacity as the three components to evaluate the vulnerability of *A. dichotoma* to climate change.

With this in mind, Chapter 2 explores the degree of exposure of *A. dichotoma* to recent changes in climate within its distribution range (after Dawson *et al.*, 2011). I provide a detailed overview of historical climatic conditions, both in terms of average conditions and trends through time. Rather than derive a composite measure, such as plant water stress (which is limited by the shorter of the two climatic records) the aim is to maximise the number and duration of reliable station records and provide an illustrative account of climate within the distribution. The rationale behind this approach is that, because of the unique life history characteristics of *A. dichotoma*, and its likely slow response to environmental change, longer records will be better suited to elucidating changes that might be having an influence on demographic patterns. Analysis of the climate record will therefore highlight where climatic conditions are most severe within the distribution, as well as where trends indicate the greatest change has taken place. Comparisons between stations will also allow an appraisal of how record length, initial and terminal conditions and specific segment of time influences trends.

As a measure of the sensitivity of the species to climate change (Dawson *et al.*, 2011), Chapter 3 employs a 'roadside mega-transect', to explore large-scale, spatially-explicit demographic information about *A. dichotoma*. It investigates the strengths of relationships between individual age classes and underlying climatic variables within the summer and winter rainfall

zones. This provides insight, both in terms of a general impression of the strength of the relationship between *A. dichotoma* and contemporary climate, as well as possible differences in the climatic requirements of individuals within each respective rainfall zone. If *A. dichotoma* were responding to contemporary shifts in temperature due to recent global warming, then one should expect a reasonably tight coupling between current climate and current demographic patterns – this is the primary assumption made in prior research. A weak link between contemporary climate and demographic patterns would suggest that other factors such as biotic interactions or past climates play a more significant role than previously thought.

Chapter 4, the 'detailed population-level survey', focuses on smaller scale demographic information at the level of the individual and discrete population. This study addresses questions which relate to aspect preference and the effect of solar radiation on individual age classes. This is useful in determining the degree to which a specific age class might be more or less susceptible to small climatic perturbations, such as those wrought by both past and projected anthropogenic climate change. The hypothesis addressed in this chapter is formulated as follows: due to incremental temperature increases as a result of recent climate change, *A. dichotoma* should preferentially recruit to more favourable aspects and that the more vulnerable juvenile age class category (due to a larger surface-area-to-volume ratio and therefore a greater desiccation potential (after, for example, Turner *et al.*, 1966)) should be the first to be affected deleteriously on more unfavourable aspects. This provides a useful test of the susceptibility and adaptive capacity of the species to both current and future climate change (after Dawson *et al.*, 2011).

A related goal was the development of an index of 'time since death' in order to determine if mortality had occurred recently, as suggested by previous work which has promoted *A. dichotoma* as a 'sentinel' of climate change (e.g. Foden *et al.*, 2007; Midgley *et al.*, 2009). It was also deemed necessary to determine mortality in relation to age class, in order to test the hypothesis that juveniles (again, being the more sensitive age class) should have contributed disproportionately towards mortality if it had been predominantly caused by recent climatic change.

Lastly, the degree to which northern and southern aspects contributed to recent and non-recent mortality was investigated. The objective was to determine whether recent mortality was concentrated on more unfavourable northern aspects at the equatorward end of the distribution, as one would expect in light of previous work arguing for a 'progressive exceedance of critical climate thresholds' at the northern limit of the distribution (Foden *et al.*,

2007). Furthermore, given temperature increases, one would also expect populations at the poleward extreme to colonise increasingly favourable southern aspects and for these poleward populations to have a generally low proportion of recent mortality.

Chapter 5 presents a concise synthesis, and begins by outlining the rationale for the study, before summarizing the key objectives. The main findings of each data chapter are then discussed in detail within the framework of the population's exposure, sensitivity and adaptive capacity to climate change in order to arrive at an overall conclusion about *A. dichotoma's* suitability as a reliable indicator of recent climate change. Finally, future research directions are suggested.

1.3   Significance of the study

Anthropogenic climate change is arguably the most pressing problem currently facing humanity. There is much uncertainty in climatic predictions for the future (e.g. Stott & Kettleborough, 2002), and even less certainty about how complex natural systems will respond (e.g. Walther, 2010). However, measurable responses in the form of shifting phonologies, demographic profiles and distributions in more sensitive species provide useful clues as to the magnitude and rate of change we can expect in the future (Parmesan, 2006). It is therefore critical that we identify sensitive species and accumulate as much knowledge about their responses to historical climate change as possible, as this will contribute to our understanding of how larger systems are likely to change, and consequently improve our ability to mitigate against the more pervasive impacts of future climate change. In southern Africa the need for improved empirical knowledge on how species and natural systems are responding to historical climate change is all the more urgent, given the disproportionately high levels of biodiversity (e.g. Gaston, 2000; Chown *et al.*, 2004) and the extent and severity of predicted climate change in the region (Hulme *et al.*, 2001).

Equally essential, however, is the need for a thorough evaluation of the specific merits and demerits in the selection of an indicator species. This is especially salient in the case of *A. dichotoma*, arguably the first southern African species to be promoted as an indicator of climate change by the scientific community. It has consequently become a flagship indicator species within both the public and political realm (e.g. Joubert, 2006; BBC News, 2007; Bruce, 2007; Geldenhuys & Swart, 2009), with implications for policy and management decisions in the region.

1.4 Study limitations

1.4.1 Historical climate

The chief limitation in the construction of both average historical conditions and trends through time is the paucity of instrumental records and the brevity in record length within the distributional extent. The spatial deficiency was most acute at the equatorward extreme, while the temporal deficiency was more widespread within Namibia generally. In addition, the duration of temperature records was invariably considerably shorter than for precipitation. Notwithstanding the above limitations, the quality of the data utilised in terms of the proportion of missing values, was generally very good.

1.4.2 Roadside mega-transect

A. dichotoma's distribution adheres closely to more rugged, mountainous terrain, which made access to certain areas difficult. In addition, the nature of data collection along transects meant that only individuals growing on aspects facing the roadside were recorded, while those out of view were not. This might have skewed observations, especially with respect to proportional aspect preferences if, for example, certain aspects dominated within certain transects. Despite this limitation, it is believed that aspect (and other) biases would be tempered by the high density of roads that were driven within mountainous areas. Access restriction to the Sperregebiet in south-western Namibia precluded data collection in this area and was therefore excluded from the study.

Because of the nature and scale of the roadside sampling approach, errors may have been made in the recording of individual trees, especially those growing further from the roadside. Other vegetation, as well as rocky terrain, may also have led to a systematic under-reporting of the smaller juvenile age class as well as wind-thrown or highly decayed dead individuals. However, it is believed that misclassifications, as well as systematic under-reporting of certain age classes, would have been more or less constant across the latitudinal distribution and would therefore not have skewed the findings in any appreciable way.

1.4.3 Population level survey

The time frame within which the data was collected did not allow for more than fourteen populations to be sampled. Given the characteristic variability in *A. dichotoma* demography, this may not be a sufficiently large sample size to confidently assess relationships between opposing aspects and/or between individual age classes and solar radiation. The problem of an insufficient sample size was made all the more acute by the failure to find sufficient individuals on certain aspects, especially at equatorward and Gariep River valley sites. While limiting the

conclusions we can confidently draw from the data, the comparatively small number or absence of individuals on certain aspects is in itself a strong indication that these aspects were unfavourable. Results should be interpreted bearing this in mind. Despite these shortcomings, the trends in 'time since death' and the age classes from which mortality was derived were consistent enough across sites to justify greater confidence in their accuracy.

Climate trends within the range of *Aloe dichotoma* in the 20th century

2.1 Introduction

The Grinnellian niche concept holds that species' distributions are largely defined by environmental factors, both biotic and abiotic (Grinnell, 1917; Soberon, 2007; Soberon & Nakamura, 2009). However, while biotic factors often have a more fine-scale, localised influence in the form of resource availability, competition, disease, etc., abiotic factors such as climate play a more primary role in establishing the broader distributional limits of species through physiological constraints, typically operating at the range margins, or more marginal areas within the distribution (Pearson & Dawson, 2003). This is especially salient in more arid environments, where biotic impacts may be relatively muted compared to abiotic factors (e.g. Grime, 1977; Goldberg & Novoplansky, 1997 (although not without debate: Chesson & Huntly, 1997; Wilson & Lee, 2000)). For this reason an analysis of historical climate trends can explain current demographic patterns since key processes such as mortality and recruitment are influenced by climatic events such as drought and above-average rainfall periods. Such an analysis also provides an assessment of a species' vulnerability and especially its degree of exposure to climate change (Dawson *et al.*, 2011).

In addition, the importance of historical climate trends may be even greater when investigating the population dynamics of long-lived species, which due to their life history characteristics, generally respond more slowly to changes in climatic conditions (Brubaker, 1986; Chapin *et al.*, 1993). Longer historical climatic records would therefore be preferential in studies investigating demographic change in long-lived species, as these records are more likely to have captured shifts or trends in environmental variables.

Several attempts have been made to describe the trends evident in the historical climate record in the south-western part of Africa, the geographical area within which *A. dichotoma* occurs. Many studies have had a broad geographical scope, being part of continental or regional scale analyses (e.g. Hulme, 1996; Landman & Mason, 1999; Hulme *et al.*, 2001; Nicholson, 2001; Richard *et al.*, 2001; Fauchereau *et al.*, 2003; Hoerling *et al.*, 2006; New *et al.*, 2006; Haensler *et al.*, 2010). Others have had a more detailed sub-regional focus, usually delimited by national

borders and have assessed climatic trends within specified countries or biomes (e.g. Mason *et al.*, 1999; du Pisani, 2001; Rouault & Richard, 2003; Kruger & Shongwe, 2004; Hewitson *et al.*, 2005; Midgley *et al.*, 2005[a]; Midgley *et al.*, 2005[b]; Warburton *et al.*, 2005; Kruger, 2006; Kelso & Vogel, 2007; MacKellar *et al.*, 2007; Hoffman *et al.*, 2009; Hoffman *et al.*, 2011). All studies have had to contend with a generally poor spatial density of instrumental records, especially in more arid areas where low human population densities have decreased the utility of recording historical climate. In addition, temperature records have only been available for a subset of stations, and then for a much reduced period of time (Nicholson, 2001).

This lack of climate stations and often short recording periods has been especially problematic for larger studies which portray general conditions within regions using standardized climatic measurements for defined time series. Most studies have therefore discarded unsuitable station records and have instead adopted techniques for aggregating, interpolating or modelling the remaining historical datasets (e.g. Nicholson, 1985; Legates & Willmott, 1990; New *et al.*, 2002); this despite evidence of sometimes profound spatial and temporal variability within original station records. While simplifying data in this way may be necessary to discern broader regional climatic trends, it is often at the expense of a precise, if spatially complex picture at a sub-regional scale, and consequently of diminished value in studies of local vegetation dynamics or investigations of individual species. Conversely, studies at a more detailed sub-regional level have relied predominantly on original, unaggregated climate data, usually from a greater number of stations, and have reported at spatial scales more meaningful to local-scale studies.

Within this suite of sub-regional climate studies, South Africa has featured more prominently than Namibia, where for historical, political and institutional reasons, less has been published on historical climate. The historical climate of Namaqualand, within the western part of the Northern Cape of South Africa, has probably been most well studied due to the unusually long climate record, as well as its unique biodiversity value (Cowling *et al.*, 1998; Cowling *et al.*, 1999; Myers, 2000). Here, for example, Kelso & Vogel (2007) undertook one of the few studies to investigate climate prior to the 20th century, the approximate start of instrumental records in the region. Using historical documentary sources from 19th century missionaries and travellers, periods of probable drought were highlighted. Droughts were found to be both frequent and severe, and possibly linked to El Nino Southern Oscillation events (Kelso & Vogel, 2007).

While many instrumental records in the Northern Cape were initiated at the beginning of the 20th century, few studies have utilized the complete record. In one such study, Hoffman *et al.* (2009) analysed the rainfall records from six Succulent Karoo stations and found no clear

directional trend in 20th century precipitation (see also Mason *et al.*, 1999). MacKellar *et al.* (2007), investigated climate trends in an area similar to that studied by Kelso & Vogel (2007), using an interpolated climate surface generated by Hewitson & Crane (2005) from several station records and data for the latter half of the 20th century. They reported a general wetting trend in the south-western and north-eastern parts of the Northern Cape, and a drying trend along the escarpment (MacKellar *et al.*, 2007). In another study which sampled stations from a wider geographical area, Kruger (2006) also found evidence for an increase in precipitation in the Northern Cape between 1910 and 2004. Meanwhile, Mason *et al.* (1999) reported a modest decline (20%) in the intensity of high rainfall events between 1930-1960 and 1961-1990 in most of the northern and central Northern Cape, while an increase was apparent in the south-western corner, abutting the Western Cape. None of the above studies were in agreement with previous suggestions that southern Africa had experienced a slight, non-significant drying trend over the 20th century (e.g. Hulme, 1996), or within the last 30 years (Midgley *et al.*, 2009).

Namibian precipitation trends in the 20th century have been comparatively understudied, which is surprising since it has been suggested that Namibia is the driest sub-Saharan country in Africa (du Pisano, 2001). While projections are for drier future conditions in Namibia (e.g. Midgley *et al.*, 2005[b]; Thuiller *et al.*, 2006[b]; Boko *et al.*, 2007; Haensler *et al.*, 2011), only one study has investigated historical precipitation trends (e.g. du Pisani, 2001 (but see also Haensler *et al.*, 2009, who used a modelled historical precipitation surface)). Based on data for the period 1950-2000, du Pisani (2001) reported a general decreasing trend in precipitation throughout Namibia, though the author stressed that the length of record had a profound effect on the result (du Pisani, 2001). For example, Windhoek, with a record of over a century had a flat trend, while most stations with records for only the second half of the 20th century displayed negative precipitation trends. Although historical temperature increases and a water balance index derived from temperature and precipitation data have previously been assessed in terms of climate change risks for Namibia (Midgley *et al.,* 2005[b]) trends in precipitation were not explicitly reported on.

In contrast to rainfall, most historical temperature trends in both South Africa and Namibia appear to be increasing steadily. For example, Midgley *et al.* (2005[b]) found a significant temperature increase at approximately half of Namibian stations with recording periods of between 25 to 60 years, while several studies have reported significant temperature increases within the Cape Floristic Region, just south of the southern distributional limit of *A. dichotoma* (Kruger & Shongwe, 2004; Midgley *et al.*, 2005[a]; Warburton *et al.*, 2005; Hoffman *et al.*, 2011). Maximum temperature trends specific to the Northern Cape are also generally positive for the

period 1950-2000, and the number of frost days have significantly declined over the same period (Warburton *et al.*, 2005). Kruger & Shongwe (2004) had similar results in terms of maximum and minimum temperatures for the Northern Cape, indicating the greatest (significant) mean annual increase for the period 1960-2003. In addition, a more broad-scale analysis by New *et al.* (2006) reported a general increase in the duration of warm spells and a decrease in the duration of cold spells for the Northern Cape. However, the above results for the Northern Cape were drawn from only two instrumental records in the case of Kruger & Shongwe (2004) and New *et al.* (2006), while Warburton *et al.* (2005) also only used two records which broadly overlapped with the contemporary distribution of *A. dichotoma*. This points to the need for a more detailed analysis of temperature trends in the Northern Cape in relation to the distribution of *A. dichotoma*.

Despite the generally good overview of historical climate provided by the above sub-regional studies, particularly those in the Northern Cape of South Africa, their usefulness for understanding the population dynamics of *A. dichotoma* remains limited due to the mismatch between their spatial focus and the distributional extent of the species. In addition, because the objective of historical climate studies was often to compare matching time series' (e.g. du Pisani, 2001; Hewitson & Crane, 2005), instrumental record length was not always maximised. These spatial and temporal limitations in previous historical climate studies are exacerbated by the inherent small-scale spatial variability in demographic patterning, as well as by the longevity of *A. dichotoma* individuals, which can survive for up to 250 years (Kaleme, 2003).

As part of an assessment of *A. dichotoma*'s response to recent climate change, Foden *et al.* (2007) represents the only study to analyse climate specific to the range of the species. However, because the goal was to produce an index of water balance using the Thornthwaite (1948) approach (which has temperature and latitude as input variables), the length of the record was constrained by temperature, which has a relatively short recording history within *A. dichotoma's* distributional area. Notwithstanding the potential insights of a water balance index for gauging plant health, employing this approach effectively limited the average period over which 'water stress' could be measured to approximately 33 and 41 years for Namibian and South African stations, respectively. In addition, the Thornthwaite (1948) technique has been criticised as a means of assessing potential evaporation because of its sole reliance on air temperature (Hobbins *et al.*, 2008; Dai, 2010). Consequently, as temperature has increased due to global warming, so calculated potential evaporation has also risen, along with inferred plant water stress in Foden *et al.* (2007). However, more reliable physical representations of evaporative demand, such as pan evaporation show widespread declines (see Hobbins *et al.*,

2008), including in areas just south of the distributional extent of *A. dichotoma* over the last 30 years (Hoffman *et al.*, 2011).

2.1.1   Objectives and key questions

This chapter will focus on climate history specific to the distributional extent of *A. dichotoma* and assess the exposure of the species to recent changes in climate (after Dawson *et al.,* 2011). However, because of the lack of basic physiological knowledge for the species, as well as possible temperature biases implicit in the in the previously utilized Thornthwaite (1948) equation, the aim will not be to infer physiological thresholds or derive any composite measure of water stress. Instead, the goal will be to illustrate historical climatic trends from as many stations within and surrounding the contemporary distribution, using the longest sets of time series available. The appraisal of historical rainfall and temperature trends in isolation may seem overly simplistic, given that *A. dichotoma* individuals are influenced by a combination of several climatic variables at any one time. However, our still poor understanding of the physiological requirements and responses in *A. dichotoma* to changing climatic stimuli suggest the need for an initially simplified approach, focussing on the most salient climate variables, namely temperature and rainfall. This might lead to the future development of a meaningful composite climate metric specific to *A. dichotoma*, the change in which could be tracked through time. The current overview of historical climate will link with *A. dichotoma* demographic patterns in later chapters to begin exploring some of these ideas.

Here, I address the following specific questions:
- What is the extent of the instrumental recording network if rainfall and temperature data are analysed independently?
- What are the average annual and seasonal rainfall and temperature conditions within the extent of *A. dichotoma's* range?
- How have these values changed over the historical recording period, including the incidence of drought?
- What are the main shortcomings of the historical record and how does this affect our interpretation of the data?

2.2 Methods

2.2.1 *Rainfall*

A total of thirty stations were chosen to illustrate 20th century rainfall trends within and surrounding the contemporary distribution of *A. dichotoma* in Namibia and north-western South Africa (Fig. 1). The area studied encompassed both the winter and summer rainfall zones within the Northern Cape in north-western South Africa and the predominantly summer rainfall southern and central-western areas of Namibia. In Namibia, climate records were derived primarily from the Namibian Meteorological Office, occasionally from the Daily Rainfall Data Extraction Utility (Lynch, 2003), and sometimes from farmers' private records. In South Africa all records were a combination of original South African Weather Service (SAWS) data and Lynch (2003), itself based primarily on SAWS data.

In order to characterise rainfall trends pertaining specifically to *A. dichotoma*'s distribution, only stations within 100 km of the contemporary distributional extent were selected (Fig. 1). The exception was Okaukuejo in northern Namibia, which was included because of the limited number of long-term stations in the far north of the species range, and also because this station had featured in an important previous study by Foden *et al.* (2007) on *A. dichotoma*. The influence of changes in Okaukuejo's rainfall record should nevertheless be treated with caution, as it is over 230 km removed from the northernmost distributional limit of *A. dichotoma*.

In addition, the minimum length of a continuous rainfall station record was set at 45 years. This was done to try and mitigate against anomalously dramatic trends, which tend to occur more often within shorter rainfall records with unusual initial or terminal values. For this reason, and despite its inclusion in a previous study on *A. dichotoma* (Foden *et al.*, 2007), Sitrusdal in northern Namibia was excluded from the rainfall analysis because its record was only 30 years in duration and the station is located over 200 km from the nearest *A. dichotoma* population.

Data derived from Lynch (2003) was carefully selected to minimise the amount of patched and missing data in each record. Patched data are defined by Lynch (2003) as any daily values which are in-filled by one or more of the following recognised techniques (listed in the order in which they are used by Lynch (2003)): expectation maximising algorithm (Makhuva *et al.*, 1997[a,b]), median ratio method (see Lynch, 2003), inverse distance weighting (Meier, 1997), and the monthly infilling technique (Zucchini *et al.*, 1984). In addition, where patched data were used, trends were assessed visually for continuity with prior and subsequent records. Due to the frequency of outliers and generally high variability in rainfall records, missing data within the Lynch (2003) and SAWS records (i.e. unpatched, blank cells) were replaced by median values.

Patched and median-filled cells were subsequently reported as a percentage of the total number of values in the record.

Average annual rainfall was calculated from monthly means from October to September; summer rainfall from October to March and winter rainfall from April to September, reflecting average conditions during actual growing seasons. The coefficient of variation (CV) in rainfall was calculated for the same time periods, and reflected the spatially comparable variability in rainfall throughout the distribution.

Where enough data were available, the full rainfall record within the period 1900-2010 was divided into early (1900-1950) and more recent (1951-2010) time periods to assess the relative rate of change. The slopes of linear rainfall trends for each station and time period were estimated using the non-parametric Sen's method (Sen, 1968), which is analogous to a linear trend line. Sen's slope estimate requires a time series of equally spaced data and proceeds by calculating the slope as a change in rainfall per change in time. The non-parametric Mann-Kendall test was used to test for the presence of a monotonic increasing or decreasing trend in rainfall. Both techniques were used as part of the MAKESENS software package developed by the Finnish Meteorological Office (Salmi *et al.*, 2002).

Drought frequency and severity was assessed over 24 month time-slices (advancing in one month time-steps) using the standardised precipitation index (SPI) technique developed by McKee *et al.* (1993).The slope values of the resulting indices were calculated using Sen's slope estimate and assessed for significance by means of the non-parametric Mann-Kendall test. Average decadal change in rainfall was calculated for all decades which contained five or more annual average rainfall values. The procedure entailed calculating a decadal rainfall average, subtracting the latter from the prior average, and calculating an overall average from these values.

2.2.2 Temperature

Far fewer stations recorded temperature when compared with the number of stations which recorded rainfall (Fig. 1). This dearth in temperature records, as well as the considerably lower spatial and temporal variability in temperature, prompted the relaxation of a) the maximum station distance from the contemporary distributional limit, and b) the minimum number of years on record. This allowed for the inclusion of 14 stations in total, some with records shorter than 45 years *and* outside the 100 km buffer on the contemporary distributional limit. These included the more spatially removed northern stations of Okaukuejo and Sitrusdal mentioned

previously, as well as Clanwilliam, a station slightly outside of the 100 km buffer to the south west of the southern extremity of the distribution.

Average monthly temperatures derived from daily records missing fewer than ten daily values per month were retained and reported as the percentage of cells with incomplete monthly data. If more than ten daily records were missing, the average for the month was instead derived from the mean of all existing average values for the month in question. The number of cells for which this operation was performed was reported as the percentage of average-filled values.

Average annual and seasonal temperature was calculated in the same way as for rainfall (i.e. annual runs from October to September; summer from October to March and winter from April to September). Sen's slope estimate was used to determine the trend in temperature over time and the non-parametric Mann-Kendall test assessed the significance of the slope for each station.

2.3   Results

2.3.1   Rainfall

The current study utilised seventeen rainfall stations in Namibia and thirteen in the north-western region of South Africa (Fig. 1, Table 1). Most stations in Namibia were, however, concentrated in the southern part of the country, with a comparative dearth in stations in the equatorward tail of *A. dichotoma*'s distribution. Rainfall station coverage was conversely reasonably uniform across the north-western region of South Africa in areas where *A. dichotoma* is known to occur.
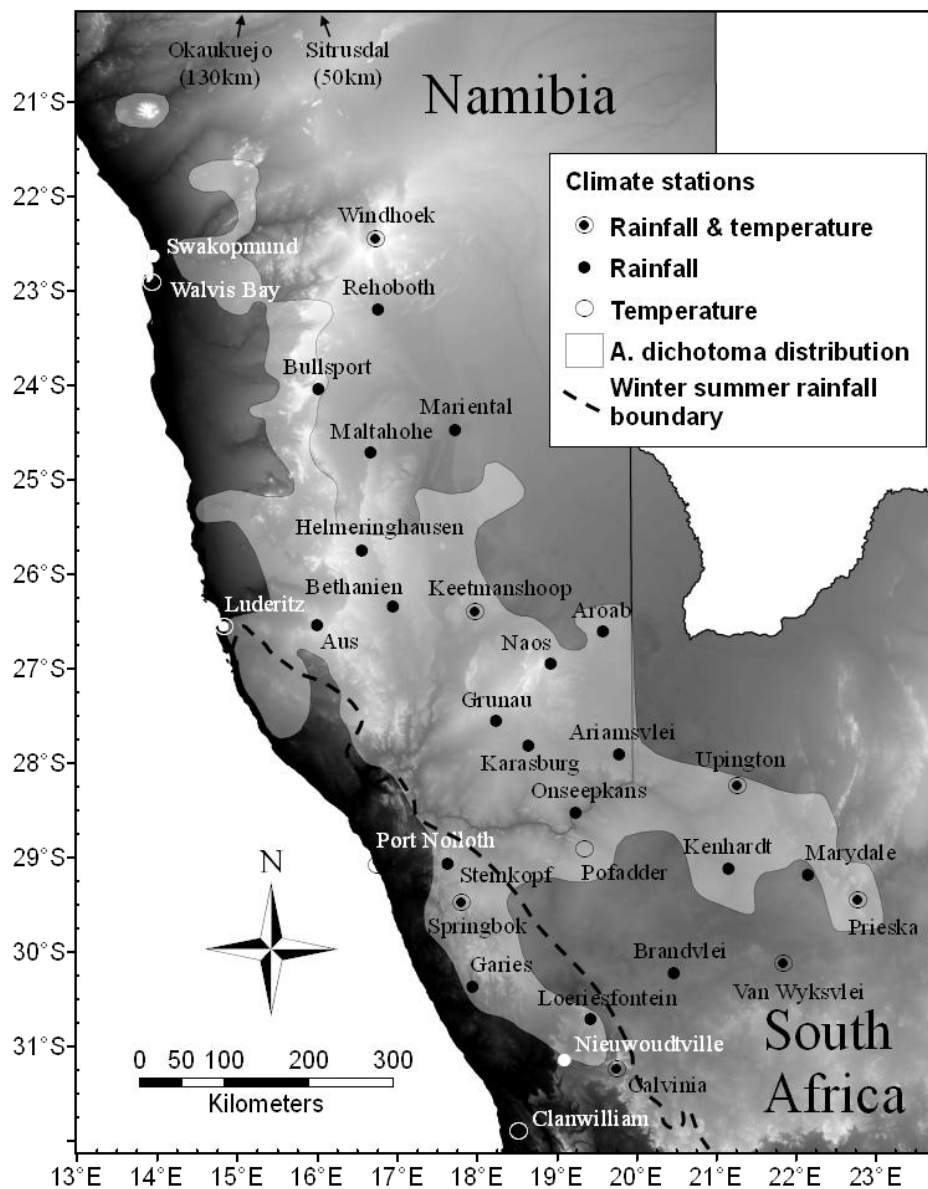
Fig. 1. Map indicating geographical position of climate stations in relation to the contemporary Aloe dichotoma *distribution. Okaukuejo and Sitrusdal climate stations are approximately 235 km and 207 km removed from the closest recorded* Aloe dichotoma *population, respectively, and are included only because of a dearth in climate stations at the equatorward extreme.*

Average rainfall record length was generally shorter in Namibia (±70 years) than in South Africa (±100 years) (Table 1). Records for many Namibian stations were terminated in the mid 1990s or 2000s, leaving only four stations with records stretching to 2010. With the exception of Garies, all South African records ran until 2010. Because of the format in which the data was received, it was not always clear whether Namibian precipitation data had been patched, but where there were indications that this had happened, it was reported. Rehoboth and Aroab accounted for most of the patched data for Namibian stations while other Namibian stations were largely free of patched data. Median-filled precipitation values were slightly more prevalent across Namibian stations, but still only accounted for approximately 2.3% of all values. The general impression was one of a relatively accurate, though incomplete collection of rainfall records for Namibia.

Table 1. A list of all rainfall stations used, including the percentage of patched data and values filled with median scores per station record. The horizontal line between Ariamsvlei and Upington splits South African (below) and Namibian stations (above). Stations located within the WRZ are denoted with an asterisk.

Station name	Latitude	Longitude	Altitude (m)	Start date used	End date used	Total years	Total % patched	Total % median-filled	Total % patched & median-filled
Okaukuejo	-19.1803	15.9215	1102	1934	2010	77	0.0	3.5	3.5
Windhoek	-22.5714	17.0865	1725	1913	2010	98	0.0	0.0	0.0
Swakopmund	-22.6730	14.5322	12	1944	2002	59	0.0	5.3	5.3
Rehoboth	-23.3212	17.0837	1386	1916	2010	95	18.6	2.5	21.1
Bullsport	-24.1590	16.3693	1397	1949	2006	58	0.0	0.4	0.4
Mariental	-24.6286	17.9572	1099	1948	1996	49	0.0	0.2	0.2
Maltahohe	-24.8548	16.9660	1400	1913	1997	85	0.0	2.1	2.1
Helmeringhausen	-25.8890	16.8173	1500	1950	2003	54	0.0	3.0	3.0
Bethanien	-26.5012	17.1608	1150	1916	2007	92	0.0	2.7	2.7
Keetmanshoop	-26.5814	18.1384	1064	1949	2010	62	0.0	1.2	1.2
Luderitz	-26.6501	15.1556	16	1939	2001	63	0.0	0.1	0.1
Aus	-26.6666	16.2604	1421	1913	1996	84	0.0	6.1	6.1
Aroab	-26.8066	19.6518	1000	1920	2003	84	10.2	3.2	13.4
Naos	-27.1404	19.0239	1400	1952	2009	58	0.0	1.4	1.4
Grunau	-27.7460	18.3609	1059	1963	2007	45	0.0	0.2	0.2
Karasburg	-28.0125	18.7464	1013	1922	2006	85	3.5	4.1	7.5
Ariamsvlei	-28.1200	19.8353	774	1927	2007	81	0.0	4.1	4.1
Upington	-28.4630	21.2500	793	1899	2010	112	18.5	0.4	18.9
Onseepkans	-28.7410	19.3030	374	1951	2010	60	4.6	0.0	4.6
Steinkopf*	-29.2500	17.7360	809	1899	2010	112	3.3	0.0	3.3
Kenhardt	-29.3550	21.1530	791	1907	2010	104	5.6	0.8	6.5
Marydale	-29.4060	22.1060	1059	1915	2010	96	2.0	0.0	2.0
Prieska	-29.6670	22.7330	949	1899	2010	112	43.5	0.1	43.5
Springbok*	-29.6710	17.8870	1006	1899	2010	112	1.3	0.0	1.3
Van Wyksvlei	-30.3500	21.8240	962	1899	2010	112	28.7	0.3	29.0
Brandvlei	-30.4640	20.4780	922	1917	2010	94	32.4	0.0	32.4
Garies*	-30.5700	17.9900	240	1899	2008	110	9.5	1.0	10.5
Loeriesfontein*	-30.9500	19.4400	914	1933	2010	78	0.8	0.0	0.8
Nieuwoudtville*	-31.3740	19.1160	719	1922	2010	89	1.8	0.0	1.8
Calvinia*	-31.4820	19.7610	977	1905	2010	106	3.9	1.4	5.3

Precipitation data from South African stations varied in the percentage of patched data contributing to the total from a low of 0.8% for Loeriesfontein to a high of 43.5% for Prieska (Table 1). Despite a high proportion of patched data for several stations in South Africa, data were nevertheless considered reliable due to the established patching techniques employed by Lynch (2003). The continuity provided by patched values allowed for analyses which required a continuous time-series. The percentage of median-filled values was generally lower for South African stations than for those in Namibia. In summary, despite precipitation records having a generally higher proportion of patched values, records were generally considered to be reliable, whilst record length was good for most South African stations.

The two stations which recorded the highest average annual precipitation over the period for which records are available were located in the northern (Okaukuejo) and eastern (Windhoek) part of the species distribution (Fig. 1, 2). However, both of these stations are relatively distant from where *A. dichotoma* occurs and these values are considerably greater than what the species experiences in the northern part of its distribution. In general, average annual precipitation was higher for stations in the winter (and to a lesser extent summer) rainfall zones at the southern end of the distribution.
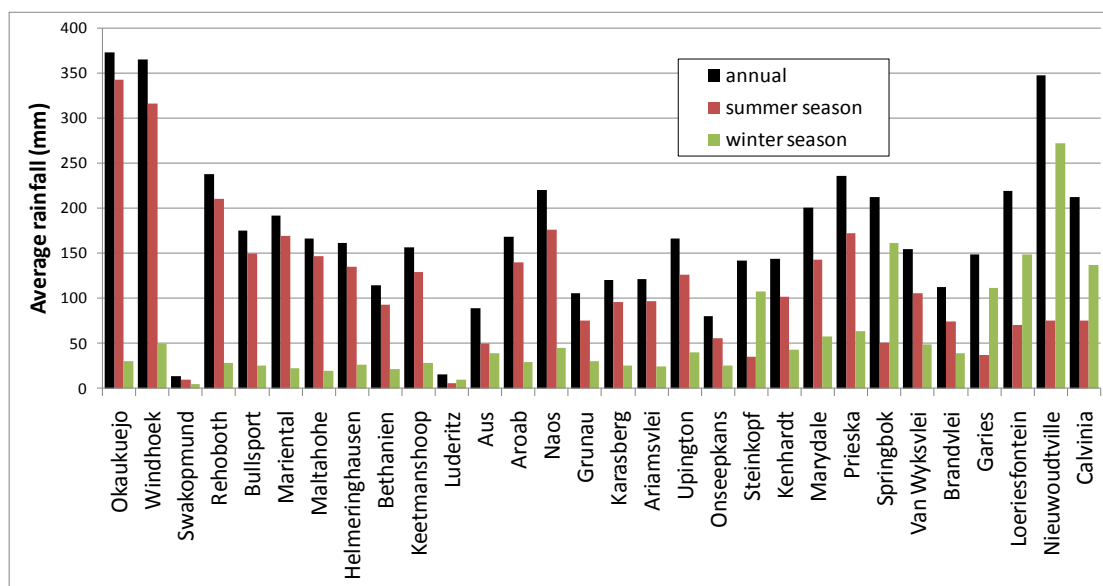
Fig. 2. Average annual (Oct-Sep), summer (Oct-Mar) and winter (Apr-Sep) rainfall for climate stations within or close to the distribution range of Aloe dichotoma*. Stations are arranged according to latitude from north (left) to south (right).*

The lowest average annual rainfall occurred around Luderitz and Swakopmund (Fig. 2) as a result of these stations being located north of the influence of winter frontal rain from the south

west and their separation from the summer rainfall systems to the north east. Average annual rainfall was also relatively low for stations on the Bushmanland plateau (between the western and eastern 'arms' of the current southern distribution) (e.g. Van Wyksvlei, Brandvlei in Fig. 1), and more consistently within the Gariep River valley (e.g. Onseepkans) and north of it in the central-northern parts of *A. dichotoma*'s distribution (e.g. Grunau, Karasberg, Ariamsvlei). Not surprisingly, winter rainfall contributed a high proportion to annual precipitation at stations within the winter rainfall zone (WRZ), such as Steinkopf, Springbok, Garies, and stations further south. Conversely, stations in the summer rainfall zone (SRZ) accumulated most of their precipitation in the summer season, as could be seen for Prieska, and all stations to the north (with the exception of Steinkopf).

Generally, inter-annual and -seasonal coefficient of variation (CV) values were lowest within the WRZ at the southern distributional limit and highest within the Gariep River valley and in the central-northern part of the range, corresponding to the broad area of lowest average annual precipitation (Fig. 3). Winter rainfall at stations located in the WRZ and summer rainfall at Windhoek and Okaukuejo (SRZ stations) had the lowest CV values, the latter due to the seasonal influence of the Intertropical Convergence Zone. Generally CV values were high for summer rainfall in the WRZ and winter rainfall in the SRZ. Both Luderitz and Swakopmund had anomalously high CV values due to their geographic location at the coast and very low and variable annual rainfall totals.
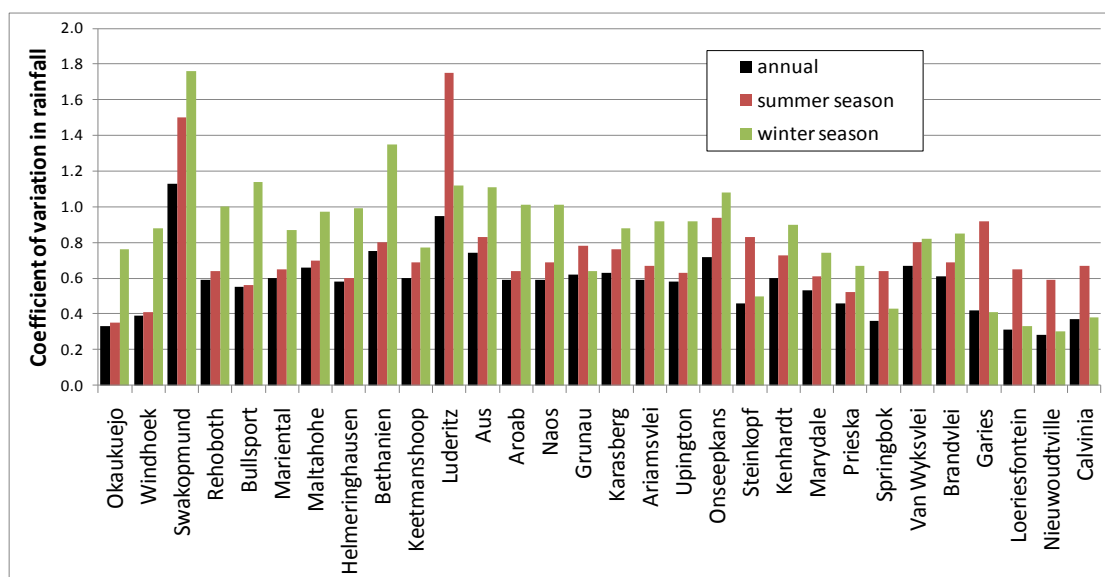
Fig. 3. Coefficient of variation in annual (Oct-Sep), summer (Oct-Mar) and winter (Apr-Sep) rainfall for each station.
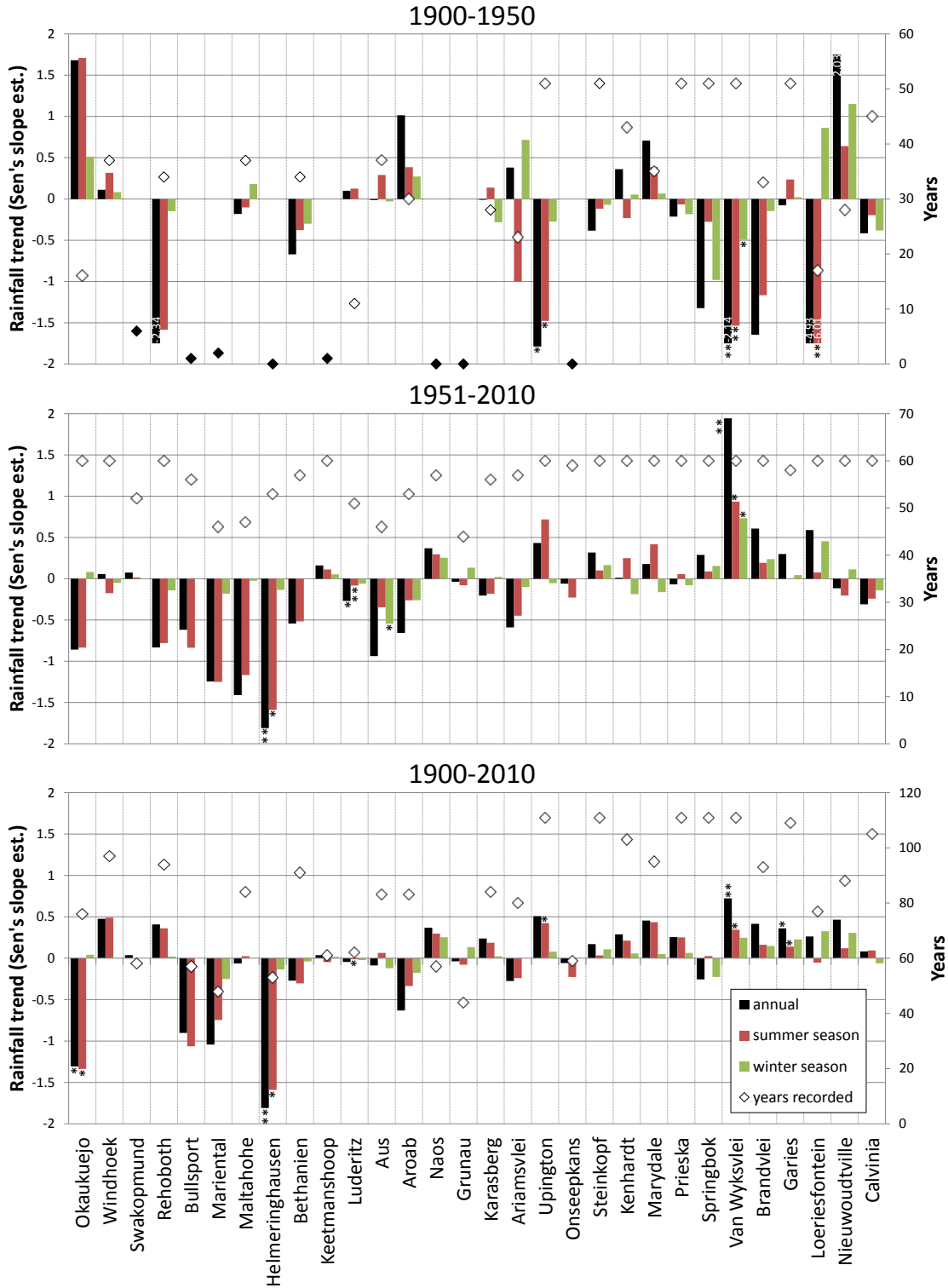
Fig. 4. Trends in annual, summer and winter rainfall, using available data within three time periods: 1900-1950, 1951-2010, and 1900-2010, illustrated by bars representing the slope of the linear trendline (using Sen's slope estimate, on the primary y-axis). Where the slope is greater/less than 2/-2 the value is inserted in the bar in white font. Years of data contributing to the calculation of trends at each climate station are displayed on the secondary y-axis and symbolized with white diamonds where record length was deemed sufficiently long, and black diamonds where stations were omitted due to insufficient record length. (Significance level: *=0.05; **=0.01; ***0.001).

The direction and slope of the trendline in precipitation was heavily dependent upon the length of the record, the particular time period examined, as well as the conditions during the initial and final recording years (Fig. 4). The full rainfall record for all stations (1900-2010) generally resulted in slopes that were less steep, whilst trendlines that were based on shorter records from the periods 1900-1950 and 1951-2010 were generally steeper.

The trends in precipitation for the northern half of the distribution indicated a general decrease over the full time period (1900-2010). However, the slopes of the trendlines for the latter half of the 20th century (1951-2010) were consistently more negative than those in the first half (1900-1950) although the relatively short record for many Namibian rainfall stations influenced this pattern considerably. Trends for the latter half of the 20th century (1951-2010) indicated a consistent decline in rainfall across several stations in the northern parts of the range; the most dramatic being for Helmeringhausen, where declining annual and summer trends in rainfall were classified as significant at the 0.01 and 0.05 level, respectively.

Declines in precipitation were noted at several stations in the southern half of the distribution during the initial half of the 20th century (1900-1950). Stations exhibiting negative trends for this period were located both in summer and winter rainfall zones. The trend for Nieuwoudtville was anomalous but might have been influenced by the relatively short length of the rainfall record. Despite the general initial decline in precipitation, increasing trends over the last 60 years in the south have resulted in an overall modestly increasing trend for the 20th century as a whole. This increase has been significant for both annual and summer rainfall at Van Wyksvlei and Garies.

Decadal rainfall change provided a more interpretable and ecologically relevant measure of the magnitude in change over time (Fig. 5). However, in some cases averages of overall change were derived from data for only five or six decades and should be interpreted with caution. A moderate degree of variability existed between stations in the northern part of *A. dichotoma*'s range. For example, Okaukuejo, Mariental, Maltahohe and Helmeringhausen all indicated an annual average decadal rainfall decline. This loss was as much as 18.8 and 19.2 mm per decade for Helmeringhausen and Mariental respectively, although in both cases these dramatic declines were based on data from only five decades. Conversely, decadal rainfall increase by 10.6 and 11.1 mm in Windhoek and Rehoboth, where records were based on ten and nine decades' worth of records, respectively.

The central part of the distribution had a mixture of increasing and decreasing average decadal change. Here, within the SRZ, both summer and winter precipitation influenced the trend in average decadal rainfall either positively or negatively. While the summer compliment of rainfall in both the SRZ and WRZ of the southern part of the species distribution had declined in most cases, the decadal increase in winter rainfall rendered the annual average decadal change positive. In the south, annual average decadal rainfall had typically increased by up to 7.3 mm at Nieuwoudtville.

Fig. 5. Overall average decadal change in rainfall, calculated for all decades with five or more average annual (Oct-Sep), or seasonal (Oct-Mar/Apr-Sep) values. Bars represent the pooled average of these decadal averages, with the number of decades contributing to each pooled average on the secondary y-axis. Where the average decadal change is greater/less than 15/-15 mm per decade, the value is inserted in white font. In most cases standard deviations are considerable, and have been omitted for the sake of clarity.

Similar to rainfall, trends in the standardized precipitation index (SPI) were heavily influenced by record length (Fig. 6). Generally, the slope of the trendlines for stations with longer records was lower than for stations with shorter records. Irrespective of the length of the record, linear SPI trends in the northern half of the distribution indicated a general increased frequency of below average rainfall. Despite this general trend, three stations at the equatorward extreme (including two with considerable record length) indicated a slight increase in above average rainfall events through time. Considering the brevity of the record, the trend toward wetter events for Grunau should be interpreted with caution. The SPI trends in the southern half of the

distribution mirrored what was found in the north. Notwithstanding a slight increase in dry conditions for Springbok, southern stations indicated a more modest but consistent trend towards above average rainfall.
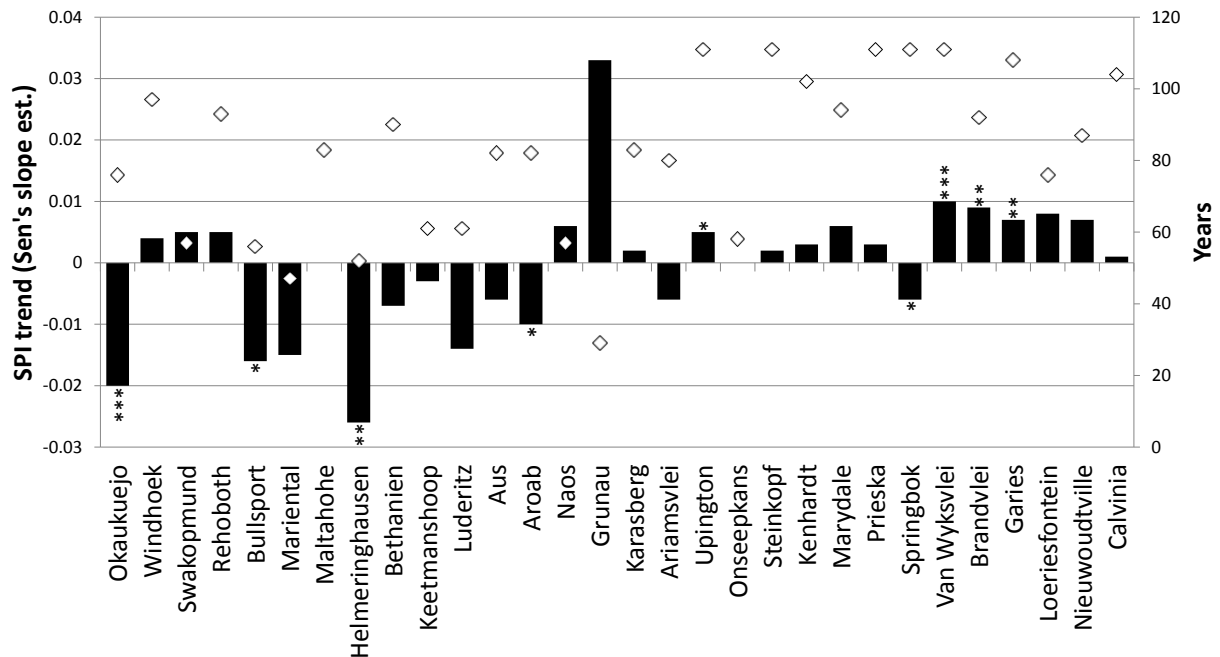
Fig. 6. Standardized precipitation index (SPI) trends for 24 month time slices for the individual stations through time, illustrated by Sen's slope estimates (bars and primary y-axis) and the length of the record from which the linear slope estimates were derived (points and secondary y-axis). Negative slope values indicate an increase in below average rainfall events through time, while positive values suggest an increase in above average rainfall events through time. Significance level: *=0.05; **=0.01; ***=0.001.

2.3.2   Temperature

The number of climate stations with instrumental temperature records were far less numerous than for precipitation (Table 2). Data from only six Namibian and eight South African stations were of sufficient quality to be used. In addition, two of the six stations in Namibia (Okaukuejo and Sitrusdal) were based far to the north east of the current range of *A. dichotoma*. Station records in Namibia were also, on average, generally more than ten years shorter in duration than those from South Africa. Despite the relative brevity of the historical temperature record, the Namibian and South African stations utilized had few incomplete records or missing values; the overall average for incomplete records or missing values for both countries was less than 5%.

Table 2. A list of all temperature stations used, including the percentage of cells with incomplete monthly data (i.e. average monthly temperature values despite daily records missing nine or fewer values) and percentage of cells in which average values were in-filled (due to monthly average being derived from daily records missing ten or more values). The horizontal line between Luderitz and Upington splits South African (below) and Namibian stations (above). Stations located within the WRZ are denoted with an asterisk.

Station name	Latitude	Longitude	Altitude (m)	Start date used	End date used	Total years	Total % cells with incomplete monthly data	Total % average-filled	Total % cells with incomplete monthly data & missing values
Okaukuejo	-19.1803	15.9215	1102	1974	2003	30	0.0	1.7	1.7
Sitrusdal	-19.9333	16.3833	1340	1975	2003	29	0.0	6.0	6.0
Windhoek	-22.5714	17.0865	1725	1959	2010	52	0.0	2.0	2.0
Walvis Bay	-22.9532	14.5020	0	1993	2010	18	0.0	6.9	6.9
Keetmanshoop	-26.5814	18.1384	1064	1969	2010	42	0.0	2.4	2.4
Luderitz	-26.6501	15.1556	16	1959	2000	42	0.0	5.7	5.7
Upington	-28.4000	21.2670	836	1968	2010	43	0.7	0.1	0.8
Pofadder	-29.1300	19.3900	982	1959	2010	52	0.5	0.0	0.5
Port Nolloth*	-29.2500	16.8700	7	1960	2010	51	8.9	3.7	12.6
Prieska	-29.6700	22.7500	932	1959	2010	52	1.4	0.2	1.5
Springbok*	-29.6700	17.8800	991	1959	2010	52	0.5	0.0	0.5
Van Wyksvlei	-30.3500	21.8200	962	1959	2010	52	1.5	0.0	1.5
Calvinia*	-31.4700	19.7700	990	1959	2010	52	0.1	0.2	0.2
Clanwilliam*	-32.1200	18.5200	154	1965	2000	36	1.4	0.7	2.0

Average annual, summer and winter temperatures displayed a very slight increase from south to north and a generally greater increase from west to east within the summer season (Fig. 7). In terms of latitudinal averages, Okaukuejo and Sitrusdal were warmer than all other SRZ stations during the summer season. Average summer temperatures for coastal stations, such as Port Nolloth, Luderitz, and to a lesser degree, Walvis Bay, were relatively low due to their proximity to the Atlantic Ocean and the influence of the cold Benguela Current.
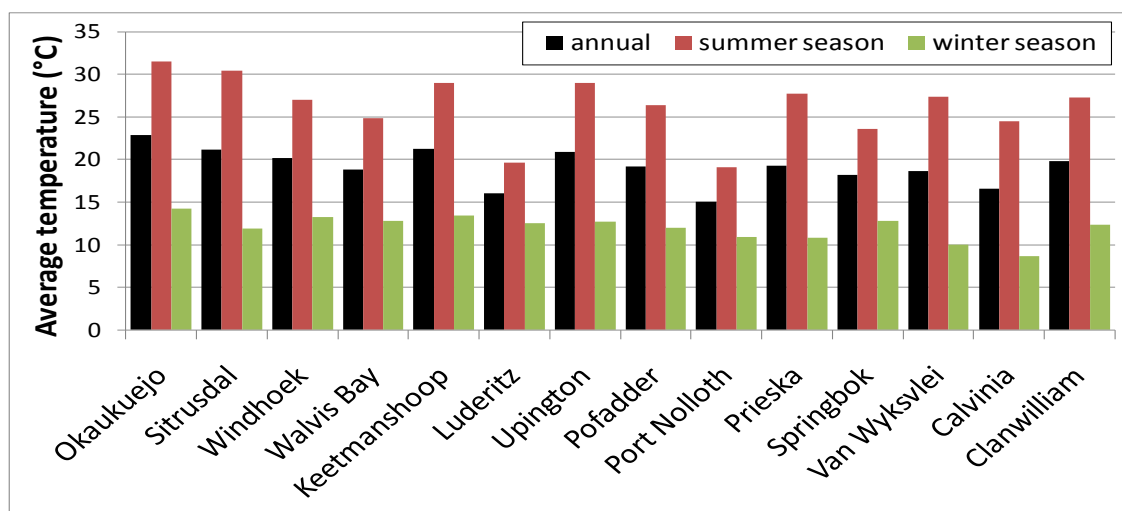
Fig. 7. Average annual (October-September), summer (October-March), and winter (April-September) temperature for each station. Stations are arranged according to latitude from north (left) to south (right).

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Trends in historical temperature were consistently positive (Fig. 8); more so in the northern half of the distribution, where the greatest increase was evident. In most cases (in both the SRZ as well as WRZ) average temperature increases during the summer months accounted for the major share of average annual temperature increases, although this was not the case for Okaukuejo and Prieska, where rising winter temperatures were dominant. Temperature increases were generally more muted for stations in the WRZ, with Springbok being the only station to register an overall decrease in temperature over the recording period, mostly due to a significant decrease in average winter temperatures.
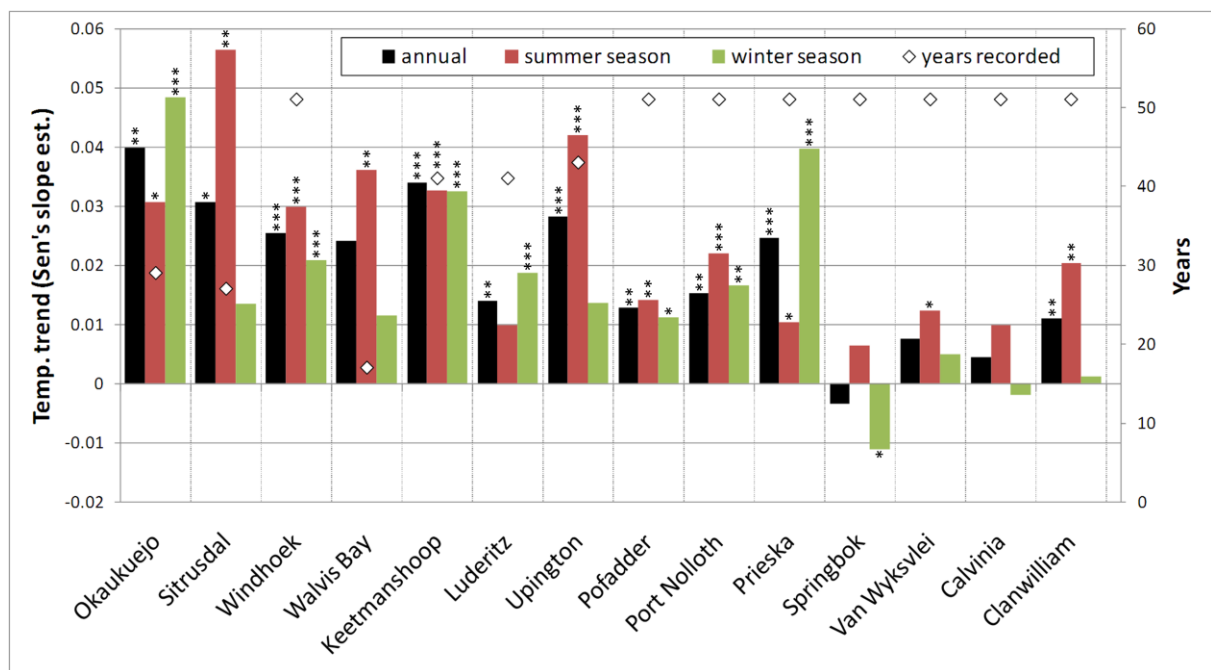
*Fig. 8. Trends in annual, summer and winter temperatures, using longest available records, illustrated by bars representing the slope of the linear trendline (using Sen's slope estimate, on the primary y-axis). Years of data contributing to the calculation of trends at each climate station are displayed on the secondary y-axis. (Significance level: *=0.05; **=0.01; ***=0.001).*

The graph for the average decadal change in temperature was similar to that for historical temperature trends (Fig. 9), and indicated a consistent change in temperature over the recording period. Stations in the SRZ have experienced a decadal increase in average annual temperature of between approximately 0.1 and 0.5°C (average: 0.29°C) or approximately 0.1 to 0.4°C (average: 0.23°C), if the more distant Okaukuejo and Sitrusdal stations are excluded from the analysis. WRZ stations also exhibited a decadal increase in average annual temperature, although this was lower (0.09°C per decade), compared to the SRZ. In both rainfall zones increased temperature in the summer season contributed most to the overall annual increase in temperature.
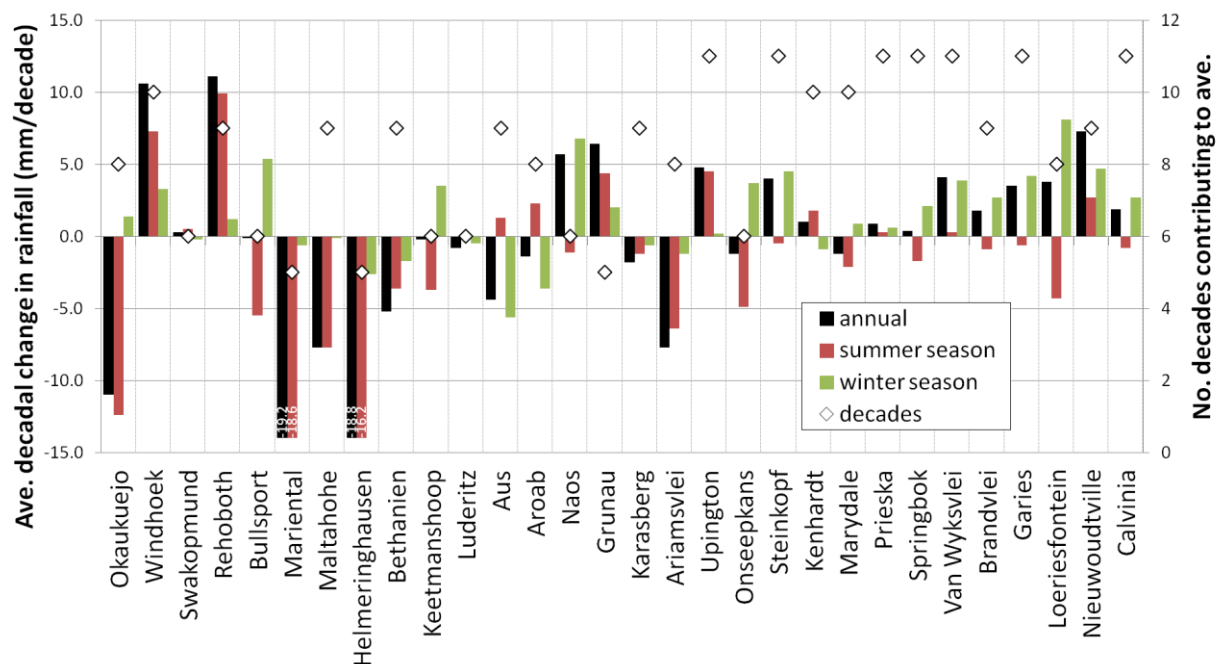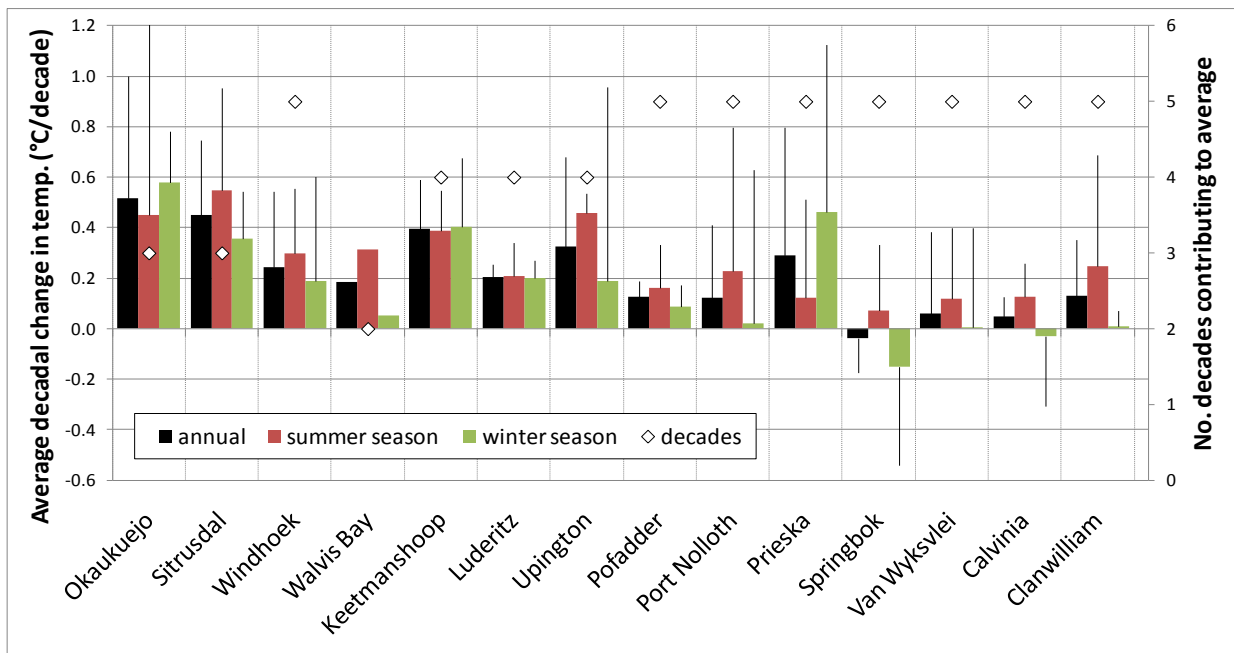
Fig. 9. Overall average decadal change in temperature, calculated for all decades with five or more average annual (Oct-Sep), or seasonal (Oct-Mar/Apr-Sep) values (primary y-axis). Bars represent the pooled average of these decadal averages, with the number of decades contributing to each pooled average on the secondary y-axis. Standard deviation bars are attached. Walvis Bay lacks standard deviation bars because decadal change is based on only two decades, hence only one average decadal change value.

2.4   Discussion

2.4.1   Problems with the climate record

This study found a similar lack of instrumental records within the broad distributional area of *A. dichotoma* in south-western Africa as previously reported by Nicholson (2001). Of specific concern were the brevity of both rainfall and temperature records in Namibia, and more generally, the poor spatial coverage of temperature records. However, by performing independent analyses on rainfall and temperature, the current study removed the temporal and spatial constraints imposed by the latter variable, effectively doubling the number of rainfall stations used in the analysis of historical rainfall patterns within the species' distribution. While this represents a distinct improvement in terms of rainfall coverage in the southern and central parts of the distribution, the equatorward part of the range remains poorly represented, with no stations occurring north of 24°S, which represents approximately the northern third of the distribution. This places an important limitation on our understanding of climate at the northern distributional limit, especially in terms of more spatially variable rainfall trends.

2.4.2   Equatorward to poleward climate gradient within the range of A. dichotoma

Notwithstanding the above limitations, interpretation of available station records within and surrounding the contemporary distribution of *A. dichotoma* confirmed a number of previous findings and also provided some novel insights. Generally, average rainfall was shown to decrease from the poleward extreme towards the central-northern part of the range, as well as from east to west, while the coefficient of variation in average rainfall mirrored these trends.

However, some important discontinuities exist within these generalized gradients, with implications for *A. dichotoma* demographic patterns. For example, stations within the winter rainfall zone (WRZ) were generally characterized by high and consistent average winter rainfall. This was as a consequence of reliable frontal rainfall received in the winter months - a key element in the maintenance of the unusually biodiverse Succulent Karoo within the WRZ (Cowling *et al.*, 1998; Cowling *et al.*, 1999). Similarly, the south-eastern 'arm' of the summer rainfall distribution, near Upington, Marydale and Prieska, also experienced relatively high and consistent summer rainfall. Rainfall declined gradually at first and then more markedly in a northerly and westerly direction, culminating in highly variable and low average rainfall at Onseepkans within the Gariep River valley. However, north of Onseepkans, the consistency and amount of summer rainfall increased again for stations lying east of the escarpment, while stations on the coast and bordering the Namib Desert (e.g. Aus and Bethanien) experienced similar rainfall variability but, notably, slightly greater average rainfall. This trend improved further north at Bullsport, the northernmost station located within the distribution, where

average annual rainfall increased to an even greater degree, with a concomitant reduction in variability. This indicated more benign local conditions relative to rainfall stations immediately to the south.

Given the steep east-west climate gradient in Namibia as a result of the western oceanic influence on atmospheric processes (Mendelsohn *et al.*, 2002), average rainfall probably decreased (and variability increased) slightly toward the equatorward distributional extreme in the north west (Wittneben, 2003). Conversely, station records outside the distribution to the east and north east (i.e. Windhoek and Okaukuejo) indicated a steady increase in average rainfall, and a decrease in variability.

The shortage of instrumental records at the equatorward extreme makes it difficult to say conclusively whether the amount and consistency of rainfall is greatest at the north-western extremity of the distribution, or within the Gariep River valley. However, station records illustrate that latitudinal rainfall patterns are more complex than previously inferred from a linear gradient in *A. dichotoma* mortality (e.g. Foden *et al.*, 2007). The data suggest that the equatorward extreme is not significantly drier or more variable than other sites within the distribution. In fact, present evidence would favour Onseepkans, situated within the Gariep River valley, as the latitude where the driest conditions prevail, as this station receives lower average rainfall than all inland stations further north, and the variability in rainfall is only matched by the central-northern stations of Aus and Bethanien.

With respect to the strong longitudinal climate gradient in northern Namibia (Mendelsohn *et al.*, 2002), the inclusion of stations located a considerable distance to the east and north east of the distribution (i.e. Windhoek, Okaukuejo and Sitrusdal) may provide a misleading impression of climatic conditions at the equatorward extreme of the range. These stations are strongly influenced by atmospheric processes that give the impression of much higher and more consistent average summer rainfall, and substantially elevated summer-time temperatures in the north than is likely the case in equatorward populations of *A. dichotoma* (e.g. around the Brandberg and near Omaruru). This eastern difference is due to the influence in summer of warm, moist air being forced south by a regular southerly movement in the Intertropical Convergence Zone (ITCZ), which brings considerable amounts of rain to north-eastern Namibia (Mendelsohn *et al.*, 2002). With respect to Windhoek, elevation also plays a role in increasing rainfall and lowering temperatures. However, the tropical system described above has a greatly diminished influence on the climate at the north-western extremities of *A. dichotoma*'s

distribution, which is likely controlled to a greater degree by the influence of the Atlantic Ocean and the cold Benguela Current on coastal atmospheric processes.

In addition, while coastal stations such as Luderitz and Swakopmund illustrate the steepness of the west-east climatic gradient, they should be regarded as climate outliers, due to their proximity to the Atlantic Ocean and the cold waters of the Benguela Current. This ocean current effectively cools coastal air to such a degree that it remains trapped below an overlying layer of warmer air, preventing the formation of rain bearing clouds and resulting in extremely low year-round rainfall at the coast (Mendelsohn *et al.*, 2002).

While average climatic conditions illustrated in the current study were in broad agreement with previous work (e.g. Shulze, 1997; du Pisani, 2001; Mendelsohn *et al.*, 2002), the advantage of focussing on those stations within the distributional extent of *A. dichotoma* meant that a more detailed analysis was possible. For example, some of the subtleties inherent within the rainfall and temperature gradients were highlighted and important discontinuities which could influence *A. dichotoma* health and survival were also identified. The process of selecting specific climate stations also allowed an assessment of the relevance of their records on *A. dichotoma* growth and survival, based on their distance from the contemporary distribution.

2.4.3 Historical trends in rainfall and temperature

With respect to historical *trends* in rainfall and temperature, the results of the current study indicated an almost uniform increase in temperature across the distribution and a mixed, though generally positive rainfall signal in the Northern Cape, and a general decrease in rainfall in Namibia. For some climate stations trends in rainfall and temperature were even steeper than previously reported, while in others the opposite was true. For example, the current study calculated average decadal temperature increase at Okaukuejo to be as much as 0.5°C per decade for the last three decades, as opposed to 0.21°C per decade reported by Foden *et al.* (2007). Using a similar methodological approach, Kruger & Shongwe (2006) found mean annual decadal temperature to have increased by approximately 0.25°C and 0.3°C at Upington and Van Wyksvlei, respectively. While results from the current study suggested a similar increase for Upington, a far more modest increase of <0.1°C was found for Van Wyksvlei.

Not surprisingly, the clearest trends were for temperature, which has increased most rapidly at the far north-eastern stations of Okaukuejo and Sitrusdal, more moderately within the remainder of the SRZ, and to a lesser degree in the WRZ. If the north-eastern stations were included, the average SRZ temperature increased by 0.29°C per decade. This constituted a

greater increase than the global average of 0.2°C per decade for the last 30 years (Hansen, 2006). However, the actual increase experienced within the SRZ distributional extent probably falls somewhere between this higher value and the lower average of 0.23°C, which excludes the abovementioned stations, but then suffers from a coastal station bias, where temperatures have not increased as much as inland, due to the ameliorative influence of the Atlantic Ocean and the cold Benguela Current.

Average decadal temperature increases were an order of magnitude lower at stations within the WRZ when compared to the SRZ, possibly due to the longer length of records within the WRZ, though other explanations are possible. For example, cool coastal air driven inland by the circulation of the South Atlantic Anticyclone may act as an ameliorative influence on summer temperatures within the WRZ. Conversely, higher summer temperatures within the SRZ may result in increased evaporation and therefore an increase in insulating summer cloud cover. One station within the WRZ (Springbok) displayed a decrease in average annual temperature over the five recorded decades. In all other cases average decadal temperature increase in the WRZ was attributable to an increase in temperature within the summer season. While reasons for this remain unclear, the trend towards greater increases in maximum temperatures may find more expression in the summer season, when temperatures are generally much higher and cooling coastal breezes more infrequent. This conclusion is supported by studies that have found good evidence for greater increases in maximum temperatures within the region (e.g. New *et al.*, 2006). However, there may be other explanations for this trend.

Spatial and temporal trends in rainfall were found to be far more variable than temperature. Their direction and (especially) magnitude appeared to depend greatly on the length of record, segment of time recorded, and initial and terminal conditions under which the record was established (e.g. du Pisani, 2001). This has contributed to the emergence of several subtly different views of historical rainfall trends for the Northern Cape (e.g. Mason *et al.*, 1999; MacKellar *et al.*, 2007; Kruger, 2006). In this respect, the comparatively short Namibian rainfall record and the paucity of climate stations in the north is problematic. So too are the initial and terminal conditions at most Namibian rainfall stations. For example, the extremely high rainfall received in the summer rainfall region during the 1974-1976 period (e.g. Washington & Preston, 2006), followed by severe droughts in the early 1980s and 1990s (Richard *et al.*, 2001; Fauchereau *et al.*, 2003) established a strong negative trend through time at many Namibian rainfall stations and effectively removed any less prominent rainfall signals in the trend. This is despite the fact that these highly unusual wet or dry periods comprise only a fraction of the temporal extent of the record.

To some degree the Standardized Precipitation Index (SPI) mitigates against this bias by averaging rainfall over longer time periods (i.e. 24 months) and normalising rainfall data so that wet and dry spells have equal weighting, but the problem of record length remains. For example, many Namibian station records were terminated in the mid-1990s and early 2000s, just before an extended period of above average rainfall (Menges, 2009; Menges, 2011), reminiscent of the wet 1974-1976 period. Out of a total of seventeen Namibian rainfall records, seven were terminated prior to 2005, and only four extend to 2010. Most stations have therefore not captured the recent high rainfall years between 2008 and 2010, which would undoubtedly have influenced the slope of the trends in historical rainfall.

While the above challenges and shortcomings in Namibian rainfall data do not preclude an interpretation of rainfall trends, they do highlight the limitations of the record when making an interpretation. Weaknesses in respect of record length and initial and terminal conditions are partially offset by the number of Namibian stations within the SRZ indicating a similar drying trend in the latter half of the 20th century. This point is reinforced by broadly decreasing SPI trends at SRZ stations, which also indicate a gradual shift towards conditions in which below average rainfall events increase in frequency, making the occurrence of droughts more likely. The downward trend in rainfall has translated into a decadal loss of roughly 19 mm for Helmeringhausen and Mariental, though these results were from only five decades of data. Longer data records at Bethanien and Maltahohe suggest a smaller decadal loss of between 5 and 7.5 mm. Countering these declining trends, and increasing the spatial complexity of the rainfall signal, are two rainfall stations with lengthy records situated to the north of those mentioned above, but no further east (i.e. Rehoboth and Windhoek). Rainfall and SPI trends from these stations are positive for the entire record length and showed a decadal increase in average annual rainfall of more than 10 mm per decade.

Generally longer record duration at stations in the southern half of the distribution allow for greater confidence in the trends derived from the data. Indications are that after a particularly dry first half of the 20th century, rainfall has increased at most stations, resulting in an average decadal increase in average annual precipitation of between zero and 7.5 mm. This is supported by SPI trends, which suggest an almost uniform increase towards above average rainfall conditions at both WRZ and south-eastern SRZ rainfall stations.

Possible drying trends in the SRZ of Namibia and wetting trends in the southern half of the distribution may be real (in a long-term sense, given short recording periods in some cases), but there are several reasons why it remains difficult to ascertain to what degree these trends are

due to anthropogenic climate change. While rising global and regional temperatures can easily be explained through a direct mechanistic link between atmospheric CO_2 concentrations and the greenhouse effect (e.g. Hansen *et al.*, 1981; Stott *et al.*, 2001), the indirect nature of the relationship between greenhouse gas forcing and rainfall change make interpretation far more complex (e.g. Fauchereau *et al.*, 2003; Hewitson & Crane, 2005; MacKellar *et al.*, 2007). In addition, southern Africa's geographical location between contrasting oceanic systems and steep orographic gradients have led to different climate regimes and highly complex seasonal and spatial rainfall patterns (Fauchereau *et al.*, 2003), making accurate modelling of regional climate a complex and computationally taxing task.

Nevertheless, a northern hemisphere study did make such a comparison between model simulated and actual historical climatic trends for the second half of the 20th century (Kiktev *et al.*, 2003). Their results indicated that explicit anthropogenic radiative forcing was required to reproduce observed temperature trends, but there was no evidence that the climate model could detect an anthropogenic signal for precipitation extremes (Kiktev *et al.*, 2003). Similarly, Hoerling *et al.* (2006) concluded that an ensemble of greenhouse-gas-forced climate models employed by the Intergovernmental Panel on Climate Change were not able to simulate 20th century drying trends in Africa, suggesting instead that drought conditions were of natural origin and were well within recorded variability (deMenocal, 2004).

There have been recent rapid advances in the development of regional climate models (RCMs) in southern Africa, which provide significant improvements in the resolution of modelled past, present and future climate (e.g. Haensler *et al.*, 2011). This will prove more useful to biologists and ecologists studying change within systems at small spatial scales. However, downscaled RCMs are based on larger models of global climate, which despite their formidable complexity, still contain numerous assumptions, oversimplifications and uncertainty (Murphy *et al.*, 2004; Knutti, 2008). For example, our understanding of coupled ocean-atmosphere processes driving phenomena such as El Niño or La Nina is still poor and, therefore, inadequately incorporated into global climate models. There is an urgent need to improve our understanding of these and other regional processes in order to develop more accurate and precise models.

Whether of natural, anthropogenic or mixed origin, observed historical rainfall trends seem to have diverged in the summer and winter rainfall zone during the latter half of the 20th century. Taken at face value, results suggest recently declining precipitation in the SRZ, and increasing WRZ precipitation. However, a more spatially detailed analysis of climate has revealed important limitations and caveats to this simplistic interpretation, instead advocating a cautious

interpretation. Temperature, however, appears to have increased across the distributional range over the course of the 20th century. The species has, therefore, clearly been exposed to changing climatic conditions over the last century, although the degree, form and duration of exposure is different across the distributional range of the species. To what degree *A. dichotoma* is sensitive or able to adapt to these changes (after Dawson *et al.*, 2011), are topics for the remainder of the thesis.

How tightly coupled is *Aloe dichotoma* to contemporary climate?

Insights from a roadside mega-transect

3.1   Introduction

3.1.1   *Niche concepts and species distributions*

The concept of the fundamental niche is based upon the well-established theory that species have tolerance thresholds for abiotic variables such as rainfall, temperature, geology, etc., which combine to define their hypothetical limits to distribution within environmental space (Hutchinson, 1957). Biotic variables provide additional constraints, through competition, predation, parasitism and disease, to determine the *actual* extent of the species, both in space and time. This is termed the realised niche, and its geographical size and position can fluctuate temporally as individual species respond to changes in physical environmental conditions (such as climate) and the nature of ecological interactions with other species (Hutchinson, 1957; Pearson & Dawson, 2003).

Palaeo-environmental studies have shown that phenological and distributional shifts in species' fundamental niche space have been the primary response to changing environmental conditions in the past (e.g. Clark *et al.*, 2001; Rosen *et al.*, 2001; Williams *et al.*, 2004) and are thus likely to be the chief responses to current and future anthropogenically-driven climate change (Clark *et al.*, 1998; Jackson & Overpeck, 2000; Davis & Shaw, 2001). The rapid rate of current and projected climate change makes this all the more likely, as the ability of most species to keep pace through evolutionary adaptations alone will probably be overwhelmed (Davis & Shaw, 2001; Jump & Penuelas, 2005).

In this respect a species' sensitivity, defined as the "degree to which the survival, persistence, fitness, performance, or regeneration are dependent on the prevailing climate" (Dawson *et al.*, 2011, p. 53), has a critical bearing on its vulnerability to changing climatic conditions. Highly sensitive species are expected to respond rapidly to smaller climatic perturbations through reductions in fecundity or survival, while comparatively little or no change would be evident in a less sensitive species (Dawson *et al.*, 2011). Moreover, sensitivity does not only vary *between*

species, but also *within* individuals of a species and particularly within different age classes. Due to their larger surface-area-to-volume-ratio and smaller resource acquisition potential, juveniles for example, are usually thought to be a more sensitive age class (e.g. Turner *et al.*, 1966), which has led to the development of a body of theory around the regeneration niche (e.g. Grubb, 1977; Jackson *et al.*, 2009). This has important implications for studies of species in relation to climate change, where determining which age class is most sensitive to climatic perturbations can direct research efforts.

Numerous studies have now documented contemporary phenological and distributional responses in terrestrial species in response to anthropogenic climate change (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003). In terms of distributional shifts, species have been found to be moving poleward in latitude (e.g. Hickling *et al.*, 2006) and upward in elevation (e.g. Grabherr *et al.*, 1994). However, examples of these shifts are drawn mainly from the northern hemisphere, while the southern hemisphere has remained comparatively understudied and subsequently underrepresented in terms of documented species shifts (Hughes, 2003; Parmesan, 2006). This is a worrying situation, given the rate of change documented in certain northern hemisphere species (e.g. Parmesan *et al.*, 1999), as well as recent evidence that the southern hemisphere might contain higher levels of biodiversity (Chown *et al.*, 2004).

In this context, *A. dichotoma* has emerged as an important 'flagship' climate change indicator species in southern Africa (Foden *et al.*, 2007), an area containing the Cape Floristic Region and the Succulent Karoo biome, both recognised as having unusually high levels of biodiversity and endemism (Cowling *et al.*, 1998; Cowling *et al.*, 1999; Desmet & Cowling, 1999; Myers *et al.*, 2000). It has been suggested that *A. dichotoma*'s fundamental niche might be shifting polewards as a result of anthropogenic climate change (Foden *et al.*, 2007), which has seen the western arid region become warmer and drier over the last thirty years (Midgley *et al.*, 2009). Based on decadal increases in average temperature, water balance constraints are hypothesised to have caused a 'progressive exceedance of critical climate thresholds' in equatorward populations (Foden *et al.*, 2007). This is thought to have resulted in a higher percentage of observed mortality (and lower recruitment) in equatorward populations, while the converse has been found in poleward populations.

3.1.2   *Grounds for further investigation*

While the Foden *et al.* (2007) study has been instrumental in drawing attention to the negative effects that climate change will have on biodiversity in a southern African context, there is still

some doubt surrounding the suitability of *A. dichotoma* as an indicator species. This was highlighted by detailed historical botanical fieldnotes (Acocks, unpublished (see Rutherford *et al.*, 2003)) and repeat photographs (Hoffman *et al.*, 2010), which indicated that low recruitment and high mortality rates were already ubiquitous in the southern and central parts of the distribution in the early to mid 20th century. This is contrary to Foden *et al.'s* (2007) assertion that mortality has increased in recent decades primarily in response to rising temperatures, as a result of anthropogenic climate change.

Mortality was interpreted as increasing linearly in an equatorward direction, however there was a high degree of spatial variability between populations in close proximity to one another and a weak relationship between latitude and observed mortality (Foden *et al.*, 2007; Saillard, 2010). Variability in the demographic profile of adjacent populations suggested that the scale at which sampling occurred could critically influence the results obtained. Studies that have previously sampled either discrete (e.g. Foden *et al.*, 2007) or district-wide (e.g. Jankowitz, 1972; Jankowitz, 1977; Molyneux, 1977) populations might therefore not have captured the true demographic pattern across the species' geographical range. Indeed, there is some evidence from data collection for broad-scale species distribution modelling which suggests that where a trade-off between sampling effort and spatial extent is necessary it is better to record less precise data more consistently over a broader area rather than more precise data over a smaller cumulative spatial extent (Braunisch & Suchant, 2010). Thus a more continuous fine scale sampling design may shed more light on the role of smaller scale biotic impacts previously discounted, and provide a better test of the strength of the relationship between demographic patterns and contemporary climate.

Previous studies also did not acknowledge and account for the fact that *A. dichotoma* straddles a major seasonal rainfall divide, which might have contributed to the overly simplistic conclusion that mortality followed a linear latitudinal gradient. Summer and winter rainfall zones differ markedly from each other. The winter rainfall zone (WRZ) in the south-western corner of the distribution is dominated by low but annually consistent frontally-derived rainfall, while the extensive summer rainfall zone (SRZ) to the north and south east is supplied by more spatially and temporally variable convective rainfall. These climatic differences have had a considerable effect on the evolution and maintenance of vegetative communities and have ultimately lead to the classification of winter and summer rainfall zones as separate biomes (Rutherford & Westfall, 1994). The Succulent Karoo biome in the south west is associated with winter rainfall, and the Nama Karoo and hyper-arid desert biomes to the north and east with summer rainfall (Cowling *et al.*, 1998; Cowling *et al.*, 1999).

Differences in the spatio-temporal consistency of rainfall in summer and winter rainfall zones highlighted above are likely to have played a key role in shaping and maintaining broad demographic patterns in *A. dichotoma* populations. 'Healthier' winter rainfall zone populations in the south and more 'marginal' summer rainfall zone populations to the north could therefore be an artefact of the rainfall disjunction, and not as a consequence of recent changes in temperature. An appraisal of the strengths of the relationships between seasonal rainfall zones and associated *A. dichotoma* demographic patterns is therefore required to shed more light on this issue.

A final point which requires more consideration is to what degree *A. dichotoma*'s unique life history characteristics make it an appropriate climate change indicator species. *A. dichotoma*'s widespread distribution (Palgrave, 1977; Reynolds, 1982; Smith & Steyn, 2005), longevity (Vogel, 1974; Kaleme, 2003), and the fact that dead skeletons decay slowly *in situ* (thus providing a record of past mortality), have all been cited as benefits in the species' use as a climate change indicator (Foden *et al.*, 2007; Midgley *et al.*, 2009). However, these traits are not necessarily beneficial in the context of a species required to respond to subtle shifts in climate. In fact, a host of species that have emerged as indicators of climate change have very different life-history characteristics when compared with those of *A. dichotoma*. These include restricted distributions (e.g. Johnson, 1998; Broennimann *et al.*, 2006), high temperature sensitivity, short life-spans, frequent recruitment intervals and smaller size at maturity (e.g. Sweeney *et al.*, 1990; Hoegh-Guldberg, 1999; Perry *et al.*, 2005; Jiguet *et al.*, 2007; Lenoir *et al.*, 2008; Munday *et al.*, 2008; Sohdi *et al.*, 2008). These characteristics combine to elicit a more rapid response to small changes in environmental conditions.

Furthermore, well studied Sonoran Desert species, such as *Carnegiea gigantea* and *Ferocactus acanthodes*, which grow under similar climatic conditions and are functionally similar to *A. dichotoma* (e.g. succulent, long-lived, infrequently recruiting) have been shown - for the adult age class - to respond relatively slowly to fluctuations in climatic conditions. This resilience has been ascribed to the buffer provided by water stored in the succulent plant tissue of adult plants (e.g. Turner, 1990). Mortality in adult *Carnegiea gigantea,* for example, only escalates during severe and prolonged drought events (Parker, 1993) and during periods of unusually low minimum temperatures, which can result in freezing and a loss of turgor pressure (Shreve, 1917; Niering *et al.*, 1963). In a southern African context, there is little evidence for an increase in freeze events, while uncertainty surrounds the link between drought and anthropogenic climate change (Fauchereau *et al.*, 2003; Hoerling *et al.*, 2006).

Interestingly, saguaro (common name for *Carnegiea gigantea*) population level mortality might also occur *en masse* when even-aged cohorts reach senescence simultaneously (Goldberg & Turner, 1986). Synchronised mortality events could be a feature of *A. dichotoma*'s life history, as the species also appears to recruit episodically. Without a more comprehensive understanding of *A. dichotoma* life history characteristics, population level mortality events are not easily attributed to a specific cause, be it the effects of recent climate change or natural aging and death of a population which has been unable to replace itself.

In contrast to the resilience of adults, the recruitment and young juvenile phase in saguaro has been shown to be far more sensitive and responsive to climatic drivers (e.g. Shreve, 1917; Turner *et al.*, 1966; Steenbergh & Lowe, 1969; Brum, 1973; Nobel, 1980; Pierson & Turner, 1998). Rather than being influenced by temperature though, recruitment events were almost invariably coupled to infrequent periods of above average rainfall (Shreve, 1917; Turner *et al.*, 1966; Steenbergh & Lowe, 1969; Brum, 1973; Jordan & Nobel, 1981; Turner, 1990; Bowers *et al.*, 1995) and their mortality linked to extended droughts (Jordan & Nobel, 1982).

3.1.3   Objectives and key questions

The first objective in this chapter was to produce the most detailed, continuous and spatially explicit map to date of demographic patterns across the full geographical range of the species. This information could then be used to more fully assess broad demographic patterns and highlight obvious discontinuities, such as might be visible between the summer and winter rainfall zones. In addition, mortality patterns were investigated for the degree to which they adhered to a linear latitudinal gradient.

Spatially referenced demographic data captured during the roadside mega-transect also allowed for the extraction of the most spatially accurate and detailed set of climatic variables to date for *A. dichotoma.* This was done by matching *A. dichotoma* presence localities with climate data derived from the high resolution Worldclim database, developed by Hijmans *et al.* (2005). Underpinning the second objective was the construction of a detailed latitudinal climate gradient, unique to the distribution of *A. dichotoma*. This further helped to determine the extent to which summer and winter rainfall zones differed from each other in terms of key climate variables. The strength of the relationships between single or multiple climate variables and demographic age class categories was then tested within each rainfall zone. Notwithstanding possible sampling errors and modelling assumptions, a weak relationship between contemporary climate and demographic patterns could imply that *A. dichotoma* was not in equilibrium with current environmental conditions (after Sprugel, 1991). This might mean that,

in certain parts of its range, *A. dichotoma* may be surviving as a biological relict (after Magnuson, 1990) whose distributional extent and demographic attributes have been shaped to a greater degree by factors other than recent climate.

Specifically, the following questions are addressed in this chapter:

- What are the proportional density patterns in *A. dichotoma,* with respect to individual age classes and is there evidence for increased equatorward mortality?
- What are the latitudinal gradients in *A. dichotoma* age classes, both in terms of absolute and proportional density in the summer and winter rainfall zones and are these gradients similar to those found previously?
- Is there any single or combination of contemporary climatic variables that adequately account for the current *A. dichotoma* demographic pattern?

3.2 Methods

3.2.1 Roadside mega-transect

Data were collected over the course of several field trips to Namibia and the Northern Cape in South Africa during 2008 and 2009. An extensive network of roads was driven, covering the entire geographical distribution of *A. dichotoma* in as much detail as possible. Due to access restrictions at the time of sampling, the Sperregebiet in Namibia was the only major area not covered. A total of about 280 000 trees were recorded in over 3 000 transects covering 15 000 km. Previous published and unpublished *A. dichotoma* distribution records in local and national herbaria (e.g. PRECIS, 2010), field guides and atlases (Palgrave, 1977; Reynolds, 1982; Curtis & Mannheimer, 2005), fieldnotes (e.g. Acocks, unpublished (see Rutherford *et al.*, 2003)), and studies (e.g. Jankowitz, 1972; Jankowitz, 1977; Molyneux 1977; Foden *et al.*, 2007) all helped direct our data collection efforts to areas where *A. dichotoma* was known to occur.

Data were captured within five kilometre long transects, marked at their beginning and end points by geographical co-ordinates recorded on a handheld Garmin GPS60. *A. dichotoma* individuals within each transect were counted with the aid of a pair of Nikon Monarch 8x42 CFD binoculars and assigned to age class and aspect categories. When transects contained a prohibitively large number of trees (typically more than a thousand), a representative number from each age class and aspect were counted and used to establish a ratio for each. This was done by dividing the number counted for a specific age class or aspect by the total. Subsequent block-counts in the immediate vicinity were then multiplied by the ratio in order to obtain a number for that age class or aspect. If necessary, this method was used repeatedly within a transect, each time taking care to establish a new ratio if the populations were in any way separate from each other.

Several other variables were also recorded at the 5 km interval to supplement the demographic and aspect information pertaining to *A. dichotoma*. Altitude at road level was recorded (GPS recording), as well as an estimate of the difference between the altitude at road level and the elevation of the highest *A. dichotoma* individual in the transect. This was necessary to establish the altitudinal range of *A. dichotoma* individuals per transect. An estimate of the average width of the transect, ranging between 200 m (e.g. a road through a narrow rocky gorge) and a maximum of 2 km (e.g. a flat, receding plain) was recorded in order to compute a density value for each transect. For the sake of consistency and accuracy, lateral (binocular assisted) observations were limited to what was estimated to be up to 1 km from the roadside. Populations were excluded if there was any obvious recording bias towards larger age classes,

due to other vegetation or extreme rockiness, or if visibility was compromised, due to glare or poor light.

3.2.2 Age Classes

All recorded *A. dichotoma* individuals were assigned to one of five age class categories in the field, namely juvenile, adult 1, adult 2, senescent and dead (Table 1). This was a necessarily subjective classification used to generate a demographic profile of the species within each transect. While there was some overlap between categories, the full suite of criteria used to assign age classes allowed for a reasonable degree of separation.

Table 1. Age class categories for Aloe dichotoma *individuals based on a suite of architectural and reproductive characteristics*

Original age class	Modified age class	Height (m)	Canopy diameter (m)	Dichotomous branching nodes	No. of leaf rosettes	Reproductively mature
juvenile	juvenile	generally < 1.5	~0.60	none	1	n
adult 1		variable, generally 2-3	1-1.5	1-3	2-8	y
adult 2	adult	variable, generally 3-5.5	2-3.5	6-10	> 10	y
senescent	dead	generally > 4	2-4	8-12	> 20	y
dead		n/a	n/a	n/a	n/a	n/a

Juvenile/adult 1 and senescent/dead age class categories were subsequently merged to provide a more simplified and easily replicable analysis and will hereafter be referred to as 'juvenile' and 'dead' age classes, respectively. The rationale behind this was that both juvenile and adult 1 individuals would likely have recruited within the last 30-50 years (Kaleme, 2003) which is the period during which *A. dichotoma* has reportedly been responsive to the effects of anthropogenic climate change (Foden *et al.*, 2007; Midgley *et al.*, 2009). Senescent and dead categories were combined because senescent individuals were effectively 'the living dead'. Their characteristically spindly and frail architecture usually bore little in the way of reproductive structures, and they were also prone to breakage from strong gusts of wind (Hoffman *et al.*, 2010).

3.2.3 Worldclim (Bioclim)

Bioclim is a set of biologically meaningful bioclimatic variables derived from the Worldclim dataset (Hijmans *et al.*, 2005). It provides a suite of monthly rainfall and temperature values for a spatially continuous interpolated surface for all terrestrial areas on Earth (excluding Antarctica). A subset of 13 Bioclim (henceforth referred to as 'bioclimatic') variables was chosen for their applicability to the current study. In addition, an aridity index (AI) and measure of

potential evapotranspiration (PET) (also derived from Worldclim data) were added for their relevance to the species under study. These indices were defined in the following way:

Aridity Index:

Aridity Index (AI) = MAP / MAE

Where MAP = Mean Annual Precipitation and MAE = Mean Annual Potential Evapotranspiration

Potential evapotranspiration:

PET = 0.0023 * RA * (Tmean + 17.8) * TD0.5 (mm / day)

Where Tmean = mean monthly temperature, TD = mean monthly temperature range, and RA = mean monthly extra-terrestrial radiation at the top of the atmosphere.

3.2.4   *Absolute and proportional density and latitudinal averages*

Transect area was used in conjunction with log-transformed count data to calculate total and individual age class densities. The tree count data were log-transformed because of the large range (one to five orders of magnitude) in absolute values between neighbouring transects. This initial density analysis was carried out for all transects containing one or more trees (i.e. for wherever *A. dichotoma* individuals occurred). Proportional density was calculated by first filtering for transects with a total tree count of twenty or more (to guard against proportional biases in transects with very low numbers from a single category), and then dividing each of the three age classes by total density. Non log-transformed versions of these data were used to generate spatially explicit GIS layers, using ESRI ArcMap 9.3 (ESRI, 2010) software.

It soon became apparent that, while absolute and proportional density maps were useful in understanding the broad spatial distribution of age classes, the high degree of variability between transects made it difficult to recognise latitudinal trends in recruitment, persistence and mortality. Absolute and proportional density data were therefore averaged across half degree latitudinal bands and represented as scatterplot trends with standard deviation bars. The same procedure was followed to generate a latitudinal profile for the 13 bioclimatic variables, as well as AI and PET. These variables were displayed as scatterplot trends with standard deviation bars and arranged into precipitation and temperature groups for ease of comparison.

3.2.5   Seasonal rainfall divide

One of the bioclimatic variables (mean temperature of the wettest quarter (TwetQ)) was used to separate the winter rainfall zone (WRZ) from the summer rainfall zone (SRZ). Transects with a mean TwetQ greater than 15°C were classified as summer, and those less than or equal to 15°C, as winter. This method of separation was in almost perfect spatial agreement with Schulze's (1997) map of precipitation seasonality in South Africa, which separated winter from summer rainfall regions.

In all spatial, graphic and tabular representations summer and winter rainfall zones were either illustrated with different symbols, or the seasonal division indicated by a dashed line. This was done to highlight potential differences in climatic or demographic patterns between the rainfall zones. An additional benefit of the separation of rainfall zones was the resultant reduction in the longitudinal spread - and therefore variability in the data - when averaged into half degree latitudinal bands.

3.2.6   Single and multiple climatic interactions

Initially, an average value was computed for altitude and all key bioclimatic variables within summer and winter rainfall zones, respectively. Differences between the rainfall zones were then tested for significance using a two-tailed Student's t-test assuming unequal variance.

The range in each bioclimatic variable was then subjectively partitioned into a number of bins and individual age class categories averaged within these. Cross-validated R^2 (xR^2) values derived from the Hyperniche software package (version 2.09; McCune and Mefford, 2009) indicated the relative strength of the relationship between bioclimatic variables and age class categories for summer and winter rainfall zones, respectively.

In the multivariate analysis, four bioclimatic variables with the strongest individual xR^2 relationships with age classes in the summer and winter rainfall zones were selected. These four initially selected bioclimatic variables were then assessed for co-correlation using Spearman's rho and Kendall's tau. Starting with the two bioclimatic variables with the strongest xR^2 values, if the correlation coefficient was greater than 0.6, then the variable with the weaker of the two xR^2 values was discarded and replaced by the bioclimatic variable with the next strongest xR^2 value. This stepwise elimination process was repeated until a xR^2 threshold (for the single variable relationship between a bioclimatic variable and an age class) of 0.05 was reached, whereupon the set of selected non co-correlated variables (the predictors) was subjected to the model building process described below.

Multivariate analysis was performed using non-parametric multiplicative regression (NPMR; McCune, 2006) within the Hyperniche software package (version 2.09; McCune & Mefford, 2009). Contrary to most traditional modelling approaches, NPMR makes no prior assumptions about model form. Instead, complex predictor interactions (in different areas of the *n*-dimensional environmental space) are captured by combining predictors multiplicatively in an iterative local model building process, which searches for the best single or combination of predictor variables to account for response variable occurrence. A local mean estimator was used in conjunction with a Gaussian kernel function (Bowman & Azzalini, 1997), which places greater weight on data points falling nearer the target point in predictor space. The form of this Gaussian weighting function is based on the standard deviation (or 'tolerance') of each predictor variable. In each model, the minimum average neighbourhood size (i.e. the maximum distance searched from the target point for inclusion in the estimate) was set at 10% of the number of samples. This was a compromise between the recommended default setting of 5% and the more conservative setting of 20%. It was chosen to force broader tolerances so that fitted curves did not tightly track individual or clusters of points. Model quality, or fit, was appraised by mean of a leave-one-out cross-validated xR^2. This is a more conservative and parsimonious method when compared to a conventional R^2, as the sample point being estimated is excluded from the data when an estimate for that point is made (McCune, 2006).

Besides xR^2 values, Hyperniche 2.09 has several built-in techniques for evaluating the predictive success of models. Monte Carlo randomization tests were performed (1,000 runs per model evaluated), to determine if the fit of the models was better than what could be achieved by chance alone, given the same number of predictor variables. A randomization test works by shuffling the response variables, thereby breaking the individual relationships with the predictor variables and then attempting to fit the best model.

Sensitivity analyses provided a measure of the relative importance of individual predictors in each model. Sensitivities were generated by nudging the values of individual predictor variables up and down in 5% increments and assessing the change elicited in the response variable, measured as a fraction of the observed range in the response variable. The accumulated sensitivities are averaged across all data points and expressed as a proportion of the range of the response variable. The greater the sensitivity, the more influence that variable has in the model. For example, a sensitivity value of 1.0 implies a change in the response variable of equal magnitude to the change in the predictor, whereas a response of 0.0 means that nudging a predictor has no effect on the response. 3D projections were generated to give a visual

illustration of the relationship between primary and secondary predictor variables and proportional density of individual age classes within each seasonal regime.

3.3. Results

3.3.1   The distribution and abundance of A. dichotoma *in southern Africa*

A. dichotoma is confined to a long, narrow tail in the extreme north, from 21°S to approximately 25.5°S, after which its distribution expands both east and west into the main body between Helmeringhausen and Pofadder (Fig. 1). At approximately 29°S the distribution splits into two 'arms' which flank either side of the arid, flat Bushmanland plateau, within the Northern Cape. The westerly 'arm' is largely confined to the winter rainfall region of south-western Africa while the easterly arm falls within the summer rainfall zone (SRZ). The South African distribution of *A. dichotoma* surrounding Noenieput between 26°S and 28°S and east of 20°E was not visited due largely to the inaccessibility of the area and the improbability of finding *A. dichotoma* there.
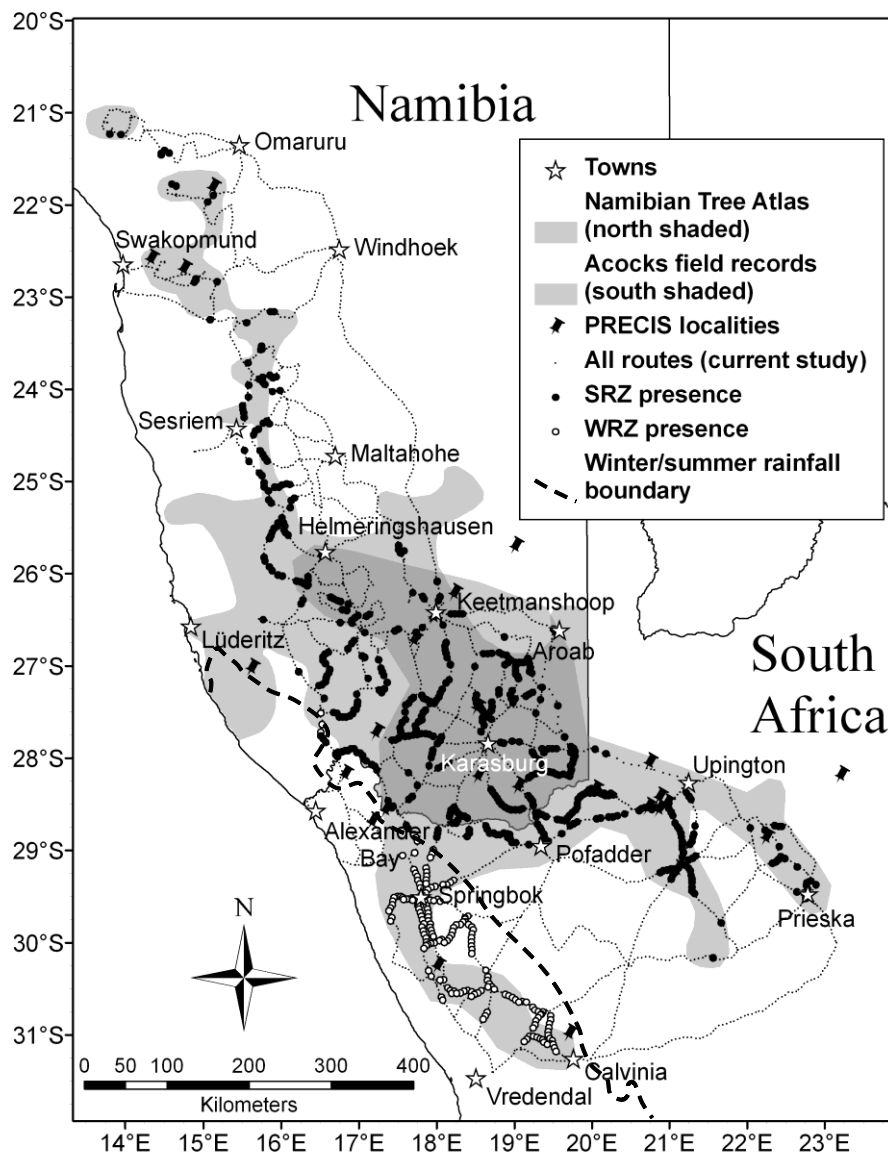
Fig. 1. The extent of the roadside survey and recorded occurrence of Aloe dichotoma *in the current study (for the summer and winter rainfall zones) in relation to past distribution maps and PRECIS records.*

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Although there were some minor discrepancies, the area mapped by the current study corresponded well with previous mapping efforts. Important new distribution records included a population between the Brandberg and Spitzkoppe and between *ca.* 25°S and 23°S the distribution was found to be wider than previously documented. A significant number of new populations were recorded to the south east of Springbok while several smaller populations were also recorded for the first time south of Upington and in central Bushmanland. Two PRECIS localities, both dating from 1933, fell well outside of the eastern margins of the main distribution and were not visited.
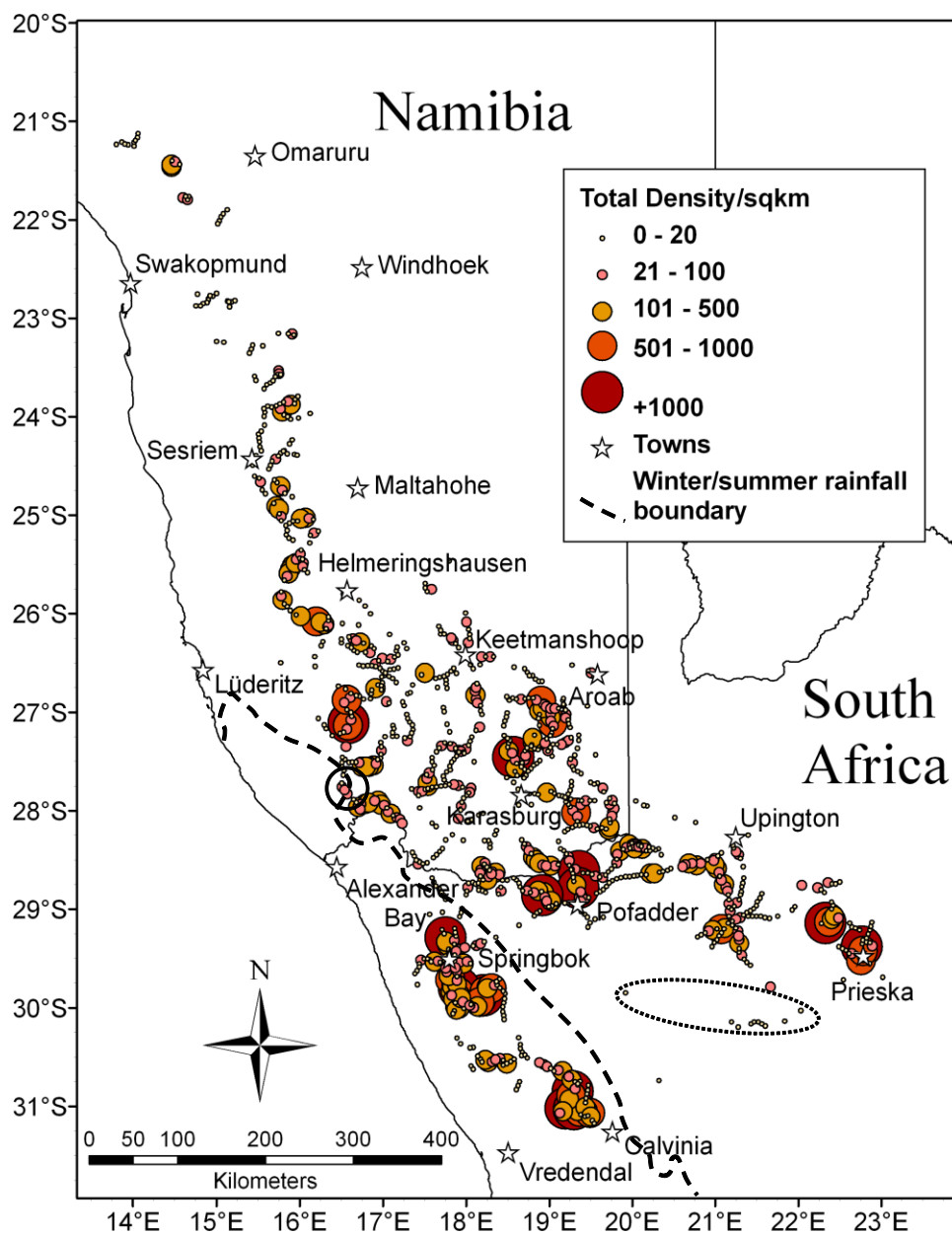
Fig. 2. Graduated symbols indicating the total density of Aloe dichotoma *per square kilometre. The dashed ellipse and solid circle indicate outlier populations when averaging winter and summer rainfall zone populations across half degree latitudinal bands.*

A. dichotoma density generally increased from north to south although there was considerable variability even between adjacent transects (Fig. 2). The density of individuals within different age classes was similarly variable with a high standard deviation for each half degree of latitude (Fig. 3). In the SRZ there were relatively few plants south of 30°S and the density of all age classes dropped significantly in this region. Conversely, there was a slight increase in the density of all age classes at the northern extreme of the range. In the winter rainfall zone (WRZ) the density of all age classes generally increased southwards with a consistent decline at 31°S in the flat plain which exists between the Kamiesberg mountains and Nieuwoudtville escarpment.
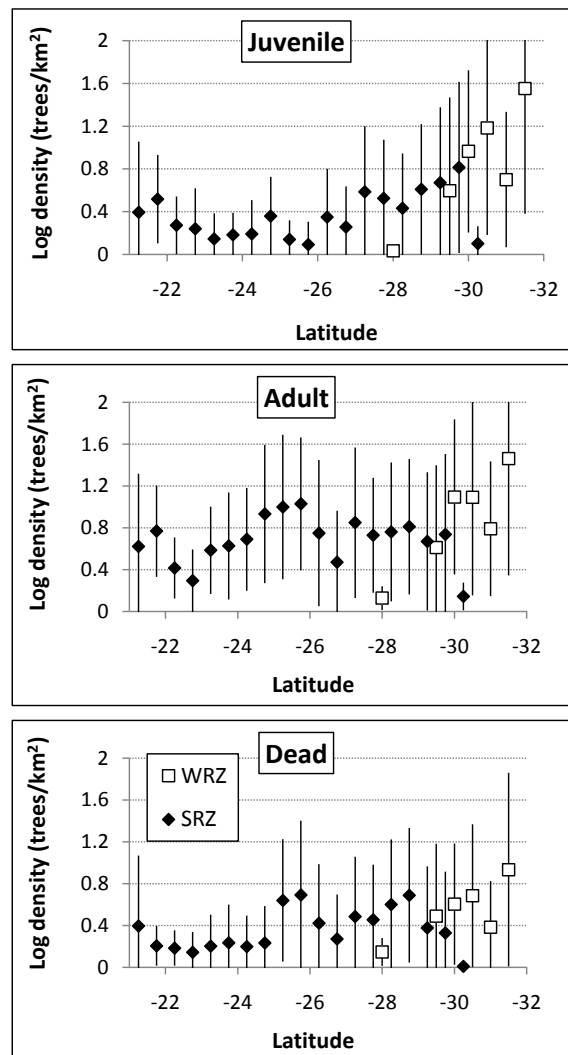
Fig. 3. Juvenile, adult and dead Aloe dichotoma *density within the summer and winter rainfall zones, averaged by half degree latitudinal bands, with standard deviation bars attached.*

3.3.2   *The proportional density of age classes*

The proportional density of individual age classes differed markedly from each other, both in terms of broad spatial patterning (Fig. 4) and latitudinal trends (Fig. 5). When rainfall seasons were considered together, the proportional density of juveniles and adults in a population
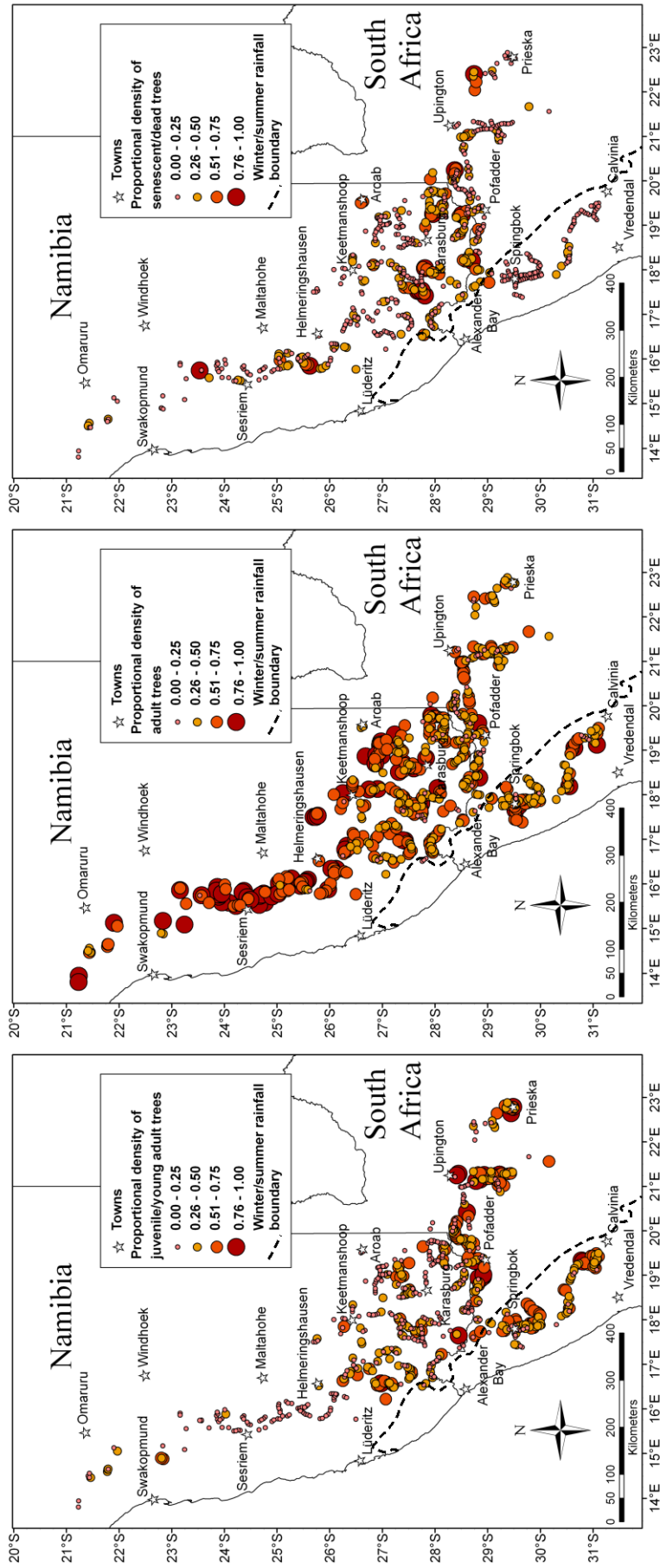
Fig. 4. Graduated symbols indicating the proportional density of juvenile, adult and dead Aloe dichotoma *individuals per transect for all transects with ≥20 trees.*

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mirrored each other, with the former increasing in a southerly and easterly direction and the latter increasing in a northerly and westerly direction. The pattern for the proportional density of dead individuals in a population was patchier and appeared greatest in the Gariep River valley and east and west of Karasberg (i.e. between approximately 28°S and 29°S).
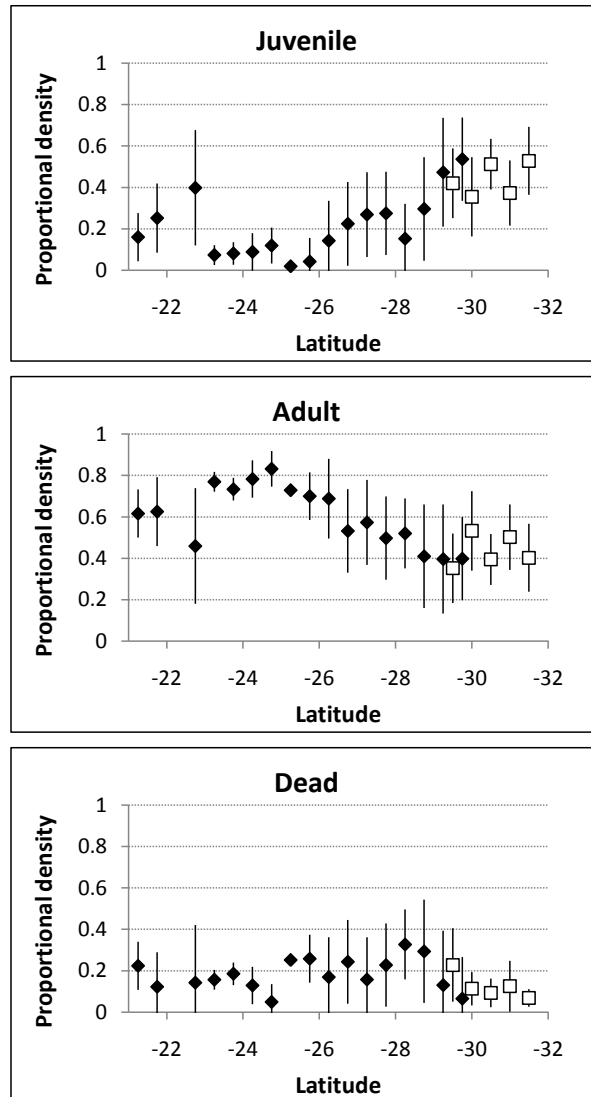
Fig. 5. Juvenile, adult and dead Aloe dichotoma *proportional density within the summer (black diamonds) and winter (open squares) rainfall zones, averaged by half degree latitudinal bands, with standard deviation bars attached.*

Averaging the proportional density of individual age class categories into half degree latitudinal bands and separating summer and winter rainfall zones, gave a clearer indication of latitudinal demographic trends within and between rainfall zones (Fig. 5). The average proportional density of adult *A. dichotoma* individuals was often more than three times that of the other two age class categories in the northern and central parts of the species distribution. Juvenile and adult age class categories had similar proportional densities south of 29°S (40% of total

density), while dead individuals were only a third as dense. As was the case for measures of plant density, the separation of rainfall zones highlighted important non-linear trends within the SRZ. For example, the proportional density of juvenile plants in the SRZ displayed an anomalous pattern in the extreme north, increasing steadily from 21°S to 23°S, where it comprised an average of 40% of the total density. It then dropped to its lowest levels between 23°S and 26°S, before increasing again in the southern part of its distribution within the SRZ.

The proportional density of juveniles in the WRZ fluctuated between 40-50% of total density, which was similar to that of the southern extreme of the SRZ. In contrast, the proportional density of adult plants in the SRZ was greatest between 23°S and 25°S where it comprised, on average, three quarters of the total density. This value declined on either side of this peak, reaching its lowest level at the southern end of its distribution in the SRZ. The average proportional density of adult plants in the WRZ remained relatively constant between 40-60%. The proportional density of dead individuals in the northern half and southern extremity of the SRZ was mostly below 20%. It was slightly above this level at the extreme northern end of the SRZ distribution and at its highest levels further south, between 25°S and 29°S. The proportional density of dead individuals decreased rapidly at the southern extreme of the SRZ and was consistently low across the latitudinal extent of the WRZ.

3.3.3   Altitudinal and climatic characteristics associated with the distribution of A. dichotoma

A latitudinal profile through the distribution of *A. dichotoma* revealed complex altitudinal and climatic gradients, both within and between summer and winter rainfall regimes (Fig. 6). Mean values for several bioclimatic variables and altitude indicated significant differences between summer and winter rainfall zones (Table 2). For example, in terms of altitude, individuals in the SRZ were found, on average, over 230 m higher than those in the WRZ. Individuals at 24°S had the highest average altitude (1500 m), while those in the extreme south were found at a little more than 500 m above sea level (Fig. 6). MAP was significantly lower (by 44 mm) in the SRZ when compared to the WRZ, while precipitation seasonality (i.e. coefficient of variation) was significantly greater (Table 2). MAP was greatest south of 29°S and to a lesser extent between 23°S and 24°S (Fig. 6). MAT was significantly higher in the SRZ, where it peaked at the northern extreme of the range and in the Gariep River valley between 28°S and 29°S.

The trends for precipitation and temperature seasonality mirrored each other in the SRZ (Fig. 6). The former was most variable in the north and decreased south of this, while the latter became increasingly variable in a southerly direction. These trends indicated consistently warmer conditions in the far north, while cooler, more variable SRZ temperatures

Table 2. Average altitude and climatic conditions for Aloe dichotoma *individuals within the winter and summer rainfall zones. Differences between rainfall zones were significant in all cases but for precipitation of the wettest quarter.*

	SRZ	Std. dev.	WRZ	Std. dev.	df	t-stat	p-value (2-tailed, unequal var.)
Altitude (m)	1016	291	780	231	290	11.998	0.0000
MAP (mm)	137.1	47.2	181.5	34.5	312	-14.790	0.0000
Precip. seasonality (coeff. var.)	0.832	0.229	0.525	0.081	775	32.188	0.0000
Precip. wettest quarter (mm)	80.0	28.7	78.4	14.3	483	1.149	0.2512
Precip. driest quarter (mm)	7.3	5.1	16.7	5.0	248	-23.046	0.0000
Precip. warmest quarter (mm)	57.3	24.6	22.5	6.6	1013	37.258	0.0000
Precip. coldest quarter (mm)	8.9	6.4	77.3	14.4	189	-62.354	0.0000
Aridity index	0.081	0.028	0.118	0.022	290	-19.605	0.0000
MAT (°C)	18.9	1.6	17.3	0.8	463	19.645	0.0000
Temp seasonality (coeff. var.)	0.459	0.094	0.410	0.040	599	11.439	0.0000
Temp. wettest quarter (°C)	23.4	2.2	12.5	0.9	651	113.955	0.0000
Temp. driest quarter (°C)	13.9	2.5	21.8	1.4	421	-61.270	0.0000
Temp. warmest quarter (°C)	24.4	2.3	22.3	1.1	534	19.198	0.0000
Temp. coldest quarter (°C)	12.7	1.6	11.9	0.9	445	9.859	0.0000
Temp. range (°C)	28.8	4.0	26.2	2.2	418	12.464	0.0000
PET (mm)	1694	148	1540	84	412	19.425	0.0000

predominated in the south. Precipitation was both more erratic and generally lower in the far north of the SRZ, while the converse was true for the southern end of the SRZ. Precipitation seasonality in the WRZ was clustered at the lower end of the range in variability, indicating a consistently reliable yearly rainfall supply, while mean temperature in the WRZ was low to moderately variable in relation to the range in the SRZ. Temperature range was well correlated with temperature seasonality. There was a clear separation between the temperature range experienced by individuals in the SRZ and WRZ at comparable latitudes.

Mean precipitation of the wettest, driest, warmest and coldest quarter reflected differences in how and when summer and winter rainfall zones received their rain (Fig. 6). Of these four precipitation measures, three were significantly different between rainfall zones. The amount of precipitation falling in the wettest and warmest quarter of the SRZ suggested virtually the entire annual rainfall complement was received within the summer rainfall season, while precipitation of the driest and coldest quarter indicated virtually no rain fell outside of this period, especially north of 25°S, where it was exceptionally dry during winter. The modest amount of supplementary rainfall received at the southern extremity of the SRZ in winter helped elevate the MAP in the south above that found between 23°S and 24°S. Converse to the SRZ, the WRZ received the majority of its rainfall in the coldest quarter and considerably less in the warm summer months, although this minimum still equated to roughly the maximum received by the SRZ during its dry season.
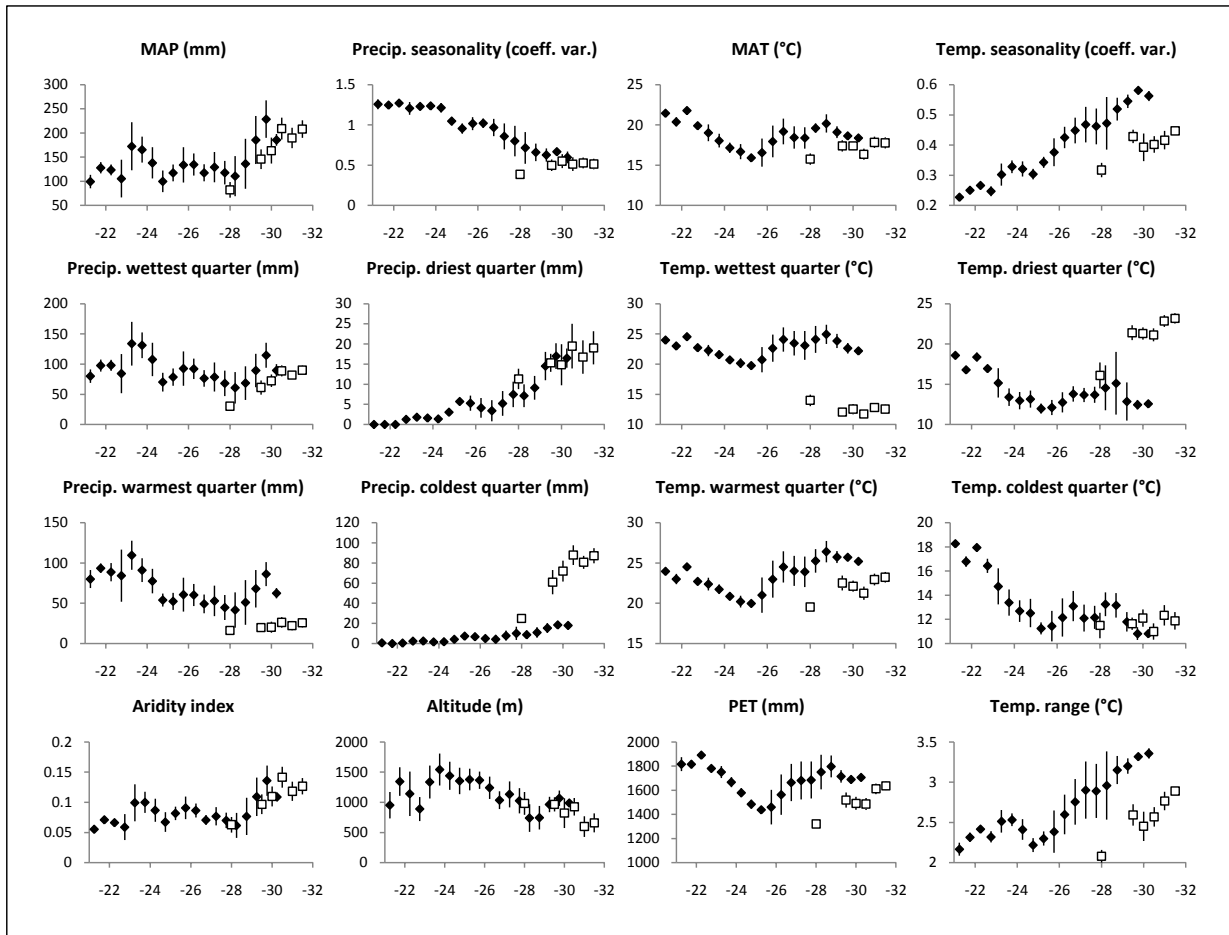
Fig. 6. Gradients in selected bioclimatic variables and altitude, based on averages for half degree latitudinal bands, within summer (black diamonds) and winter (open squares) rainfall zones, with standard deviation bars attached.

Mean temperature of the wettest, driest, warmest and coldest quarter reflected differences in the temperatures associated with different rainfall seasons (Fig. 6). All four of the temperature measures were significantly different between rainfall zones (Table 2). Similar to precipitation of the coldest quarter, temperature of the wettest and driest quarter clearly separated winter and summer rainfall regimes. Temperature of the warmest quarter indicated that summer temperature extremes in the SRZ were greatest in the latitudes surrounding the Gariep River valley (i.e. between 28°S and 29°S), while those at the northern limit of the SRZ distribution were comparable with summer temperatures in the WRZ. While still moderate (i.e. less than 20°C), the temperature of the coldest quarter in the northern extreme of the SRZ was notably higher than found further south. This was undoubtedly the cause of MAT peaking in the far north of the range, as well as for the equatorward decline in temperature seasonality and range. Average temperatures in the WRZ displayed little latitudinal variation in the colder, wetter months, while in the summer months they tended to increase in a southerly direction.

Potential evapotranspiration (PET) and the aridity index (AI) were well correlated with mean annual temperature and mean annual precipitation values respectively. In the SRZ, PET was at its lowest level between 25°S and 26°S and increased steadily north and south of this latitude. PET was significantly lower in the WRZ and increased southwards. In the SRZ the AI indicated that aridity was greatest (i.e. lowest AI value) in the extreme north and in the Gariep River valley between 28°S and 29°S. The southern end of the SRZ and the majority of the WRZ were the least arid, while an area in the SRZ between 23°S and 24°S (corresponding to an area of higher rainfall) were also relatively less arid than surrounding latitudes.

3.3.4 *The proportional density of age classes in relation to single bioclimatic variables*

Low xR^2 values and large standard deviations were generally indicative of highly variable and generally weak relationships between single bioclimatic variables and the proportional density of different age classes in both the summer and winter rainfall zones (Fig. 7). Despite this variability, which was generally greater in the SRZ, the relative strength, form and direction of relationships between individual climatic and demographic variables was nevertheless useful in forming a broader understanding of which climate variables were most important and in which rainfall zone relationships where stronger.

Juvenile proportional density was generally better correlated with climatic variables in the WRZ, despite reasonably good correlations for some variables in the SRZ. When compared to the suite of temperature variables, those derived from precipitation were generally better related to juvenile density, especially in the WRZ. While MAP and precipitation seasonality were significantly related to juvenile proportional density in the WRZ, the two strongest single variable interactions for this age class in the WRZ were precipitation of the warmest quarter and precipitation of the driest quarter. For the SRZ, juvenile proportional density was best related to temperature and precipitation seasonality and was positively related to the former and negatively related to the latter. Precipitation of the coldest and driest quarters (i.e. winter rainfall in the SRZ) both indicated clear positive linear relationships with juvenile proportional density in the SRZ.

Converse to the juvenile age class category, adult proportional density had, on average, stronger associations with climate variables in the SRZ when compared to the WRZ. However, the suite of precipitation variables remained generally dominant as explanatory variables across both rainfall zones. In the SRZ, precipitation seasonality was positively correlated with adult proportional density and explained the greatest percentage of the variance (xR^2 = 0.23). Adult proportional density was significantly negatively related to precipitation of the driest and

coldest quarters (i.e. winter rainfall in the SRZ). In addition, the correlation of adult proportional density and temperature of the warmest and wettest quarters (i.e. summer conditions in the SRZ) suggested adults preferred cooler summer average temperatures of approximately 21°C.

	Juvenile	xR^2	Adult	xR^2	Dead	xR^2
MAP (mm)		0.062		0.039		0.060
		0.168		-0.016		-0.006
Precip. seasonality (coeff. var.)		0.118		0.230		0.025
		0.120		0.106		-0.033
Precip. wettest quarter (mm)		0.015		0.041		0.064
		0.085		0.006		-0.063
Precip. driest quarter (mm)		0.098		0.165		0.024
		0.192		0.104		0.059
Precip. warmest quarter (mm)		0.032		0.049		0.059
		0.202		0.077		0.105
Precip. coldest quarter (mm)		0.107		0.139		0.016
		0.048		0.003		-0.063
Aridity index		0.031		0.047		0.091
		0.063		0.008		0.030

Fig. 7. The relationship between single climate variables (x-axes) and the proportional density of juvenile, adult and dead age classes (y-axes). A subjective number of bins were chosen based on the range between lowest and highest values for each climatic variable. Black diamonds represent the summer rainfall zone; open squares the winter rainfall zone, and standard deviation bars are attached. xR² values to the right of each graph (summer rainfall zone above and winter rainfall zone below) are a measure of the strength of the relationship between climate variable and proportional density. For ease of reference, a white background signifies a xR² value of 0.05 or less; a light grey background a xR² value of between 0.05 and 0.1; and a dark grey background a xR² value of greater than 0.1.

	Juvenile	xR^2	Adult	xR^2	Dead	xR^2
MAT (°C)		0.029 / −0.084		0.075 / −0.047		0.078 / −0.045
Temp. seasonality (coeff. var.)		0.129 / 0.069		0.134 / 0.069		0.026 / 0.060
Temp. wettest quarter (°C)		0.049 / 0.022		0.100 / 0.006		0.028 / −0.046
Temp. driest quarter (°C)		0.008 / −0.001		0.006 / 0.050		0.005 / −0.010
Temp. warmest quarter (°C)		0.032 / −0.037		0.121 / −0.041		0.042 / 0.003
Temp. coldest quarter (°C)		0.015 / 0.074		0.001 / 0.038		0.093 / −0.024
PET (mm)		0.052 / −0.006		0.078 / 0.042		0.082 / −0.011
Temp. range (°C)		0.057 / 0.113		0.098 / 0.139		0.045 / 0.052

Fig. 7. (continued).

Adult proportional density was generally poorly related to climatic conditions in the WRZ. However, adult individuals did tend to occur more frequently in populations where temperature range and summer rainfall was lower and precipitation seasonality was higher. This suggested that adults were generally more numerous at the northern end of the WRZ.

Of the three age class categories, the proportional density of dead individuals was most poorly related to recorded climatic conditions in both summer and winter rainfall zones, although it was generally slightly better for the SRZ. Generally, temperature was again the slightly better explanatory variable for mortality in the SRZ. Here mortality was weakly positively related to

both MAT and PET, suggesting higher mortality in areas with higher temperature and evaporative demands. Mortality was also significantly correlated with temperature of the coldest quarter (i.e. winter conditions in the SRZ), though the trend was non-linear and difficult to interpret. With respect to the suite of precipitation variables, the AI, MAP and measures of summer rainfall in the SRZ (themselves co-correlated) were all weakly, but negatively correlated with mortality. This suggests that mortality was greater where conditions were more arid and there was less summer rainfall.

In the WRZ precipitation was marginally better at accounting for the variance in mortality, solely due to the strength of the negative correlation between precipitation of the warmest and driest quarters (i.e. summer rainfall in the WRZ). Temperature seasonality and range were also weakly correlated with mortality, but the direction of the trend was difficult to interpret.

3.3.5   The proportional density of age classes in relation to multiple bioclimatic variables

Combining the best non co-correlated bioclimatic variables in a multivariate modelling procedure explained between 20 and 30% of the variance in the proportional density of juvenile and adult age classes (Table 3). The dead age class category was, however, relatively poorly represented by current bioclimatic variables with only about 15% of the variance explained in the models.

Table 3. Multivariate non-parametric multiplicative regression (NPMR) models describing the strongest relationships between each of the age class categories in the summer rainfall zone (SRZ) and winter rainfall zone (WRZ) and a suite of non co-correlated bioclimatic variables (above a xR^2 interaction threshold value of 0.05). The variables are arranged in order of importance based on sensitivity scores (Sens.). A randomization test (RT) indicated that, in all cases, the fit achieved in the modelling procedure was significantly better than what could be achieved by chance alone.

Seasonal rainfall regime	Size class	RT (p-value)	xR^2	First var.	Sens.	Second var.	Sens.	Third var.	Sens.
SRZ	Juvenile	0.000	0.229	Tseason	0.661	PET	0.445	Pseason	0.426
	Adult	0.000	**0.283**	Pseason	1.188	Tseason	0.351		
	Dead	0.000	0.152	TcoldQ	0.877	PET	0.783	AI	0.528
WRZ	Juvenile	0.000	**0.267**	PwarmQ	1.078	PwetQ	0.276	Trng	0.177
	Adult	0.000	0.191	Trng	1.719	Pseason	0.561		
	Dead	0.002	**0.154**	Tseason	1.208	PwarmQ	1.174		

Juvenile proportional density in the WRZ was strongly positively correlated with precipitation of the warmest quarter (i.e. the drier of the two seasons). The 3D graph indicated that juvenile densities were higher where there was more summer precipitation (Fig. 8d). Precipitation of the wettest quarter and temperature range both had a much smaller influence with the former not showing a clear directional trend in the 3D graph (Table 3 and Fig. 8d). The relationship

between the juvenile age class and climatic conditions in the SRZ was not as strong as for the WRZ, but variability in temperature and precipitation, as well as PET, appeared to be important (Table 3). In the SRZ, juveniles were proportionally more numerous when PET was low and temperature seasonality was high (Fig. 8a).

Adult proportional density in the SRZ had the strongest xR^2 value of all models, mostly due to the influence of precipitation seasonality, which had a much higher sensitivity score than temperature seasonality (Table 3). The adult age class is clearly proportionally dominant in the SRZ where precipitation is most variable. This is illustrated in the 3D graph by a strong positive relationship between precipitation seasonality and adult density (Fig. 8b). Despite a relatively weak xR^2 value, adult proportional density in the WRZ was greatest where the range in temperature was narrowest and rainfall more variable. This is indicative of more marginal, mountainous environments on the northern periphery of the winter rainfall zone (e.g. Fig. 6).
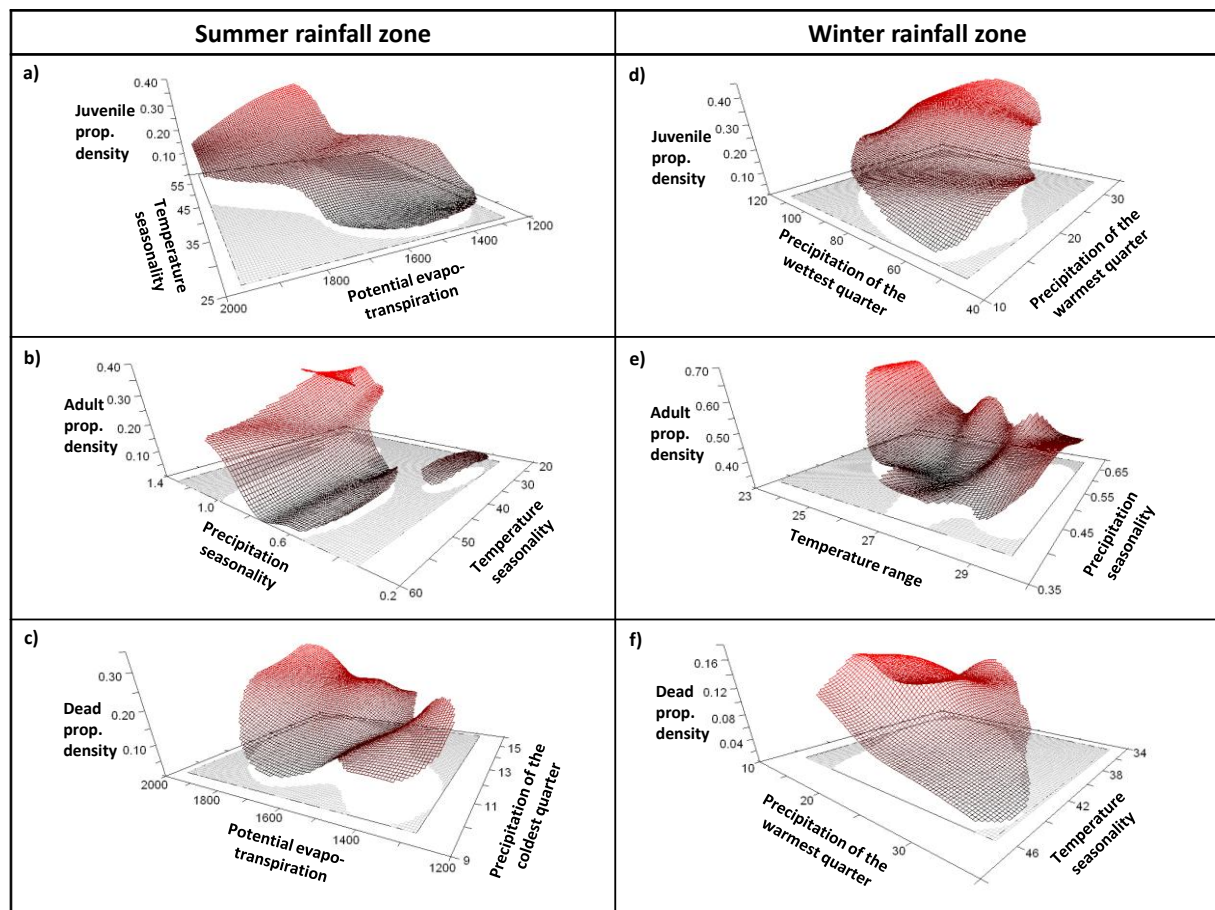
Fig. 8. Three-dimensional graphs of relationship between age classes in the summer/winter rainfall zones and bioclimatic variables of primary and secondary importance.

Both summer and winter rainfall zones had equally weak xR^2 values for the dead age class category (Table 3). There appeared to be no dominant single bioclimatic variable to account for mortality in the SRZ. However, there was a generally positive relationship between PET and proportional mortality in the SRZ, while the relationship with precipitation of the coldest quarter was less clear (Fig. 8c). In the WRZ both temperature seasonality and precipitation of the warmest quarter (i.e. summer rainfall) played an important role in the model, but did not account for much of the variation in mortality. Summer rainfall (i.e. PwarmQ) appeared to be negatively correlated with proportional mortality in the WRZ, whilst the direction of the relationship with temperature seasonality was not clear (Fig. 8d).

3.4. Discussion

3.4.1   The value of the roadside mega-transect

The current study has produced the most detailed and spatially explicit map of *A. dichotoma's* distribution and demographic patterns to date, and probably represents one of the highest resolution sampling efforts for a species occurring at a similarly large geographical scale. Because the mega-transect sampled continuously at a 5 km interval, a much larger number of observations were captured, improving the spatial representivity of the data and making it possible to calculate half-degree latitudinal averages for individual age classes. This allowed for a fuller and more nuanced interpretation of demographic patterns with respect to current biotic and abiotic drivers.

Previous discrete (Foden *et al.*, 2007) and district level (Jankowitz, 1972; Jankowitz, 1977; Molyneux, 1977) sampling efforts captured greater detail at sampling foci, but were spatially discontinuous, especially at the equatorward end of the distribution. For example, of the 53 populations sampled by Foden *et al.* (2007) within the full 1100 km latitudinal extent of the distribution, only six populations were recorded within the northernmost 450 km (or 2/5th's) of the distribution, despite considerable variation in mortality evident even within these six northern populations.

While Foden *et al.* (2007) and the current study both illustrated the high degree of spatial variability in mortality, the current continuous sampling at a high spatial resolution has resulted in different observed mortality patterns, particularly with regard to the previously described linear gradient in equatorward mortality.

3.4.2   Latitudinal and altitudinal trends in mortality, recruitment and persistence

Half-degree latitudinal averages indicate that the proportional density in observed mortality is in fact highest just north east of the winter rainfall zone (WRZ) and occurs within the summer rainfall zone (SRZ) of the Gariep River valley, and east and west of Karasberg. This places the peak in relative mortality between approximately 28°S – 29°S, in the southern third of the latitudinal distribution. From here, latitude mortality declines sharply in a southerly direction, and more gradually towards the north. While the proportional density in mortality remains consistently low within the WRZ, it does appear to increase again towards the northern extremity of the SRZ, where there is a smaller secondary peak, accompanied by a great deal of variability. This pattern is different and more complex than the linear equatorward mortality cline reported previously in Foden *et al.* (2007). It also highlights the considerable variability that exists at the equatorward extreme and between 26-29°S. The latter band of variability

occurs primarily as a result of the longitudinal expansion of the distribution and the additional environmental variability that this introduces, which has not been taken into account in previous studies.

In addition to the above trend in mortality, latitudinal trends in recruitment and persistence offer little additional support for the hypothesis that equatorward sites have recently become less climatically favourable. If this were so, juveniles, typically thought of as the most vulnerable - and therefore responsive - life history stage in functionally similar arid-adapted species (e.g. Shreve, 1917; Turner *et al.*, 1966; Steenbergh & Lowe, 1969; Brum, 1973; Nobel, 1980; Pierson & Turner, 1998), would theoretically be at their lowest levels at the equatorward limit. This is shown not to be the case, both in terms of absolute and relative juvenile densities which, notwithstanding considerable variability, increase north of their lowest levels between 26-23°S. Furthermore, adult proportional density is shown to be far higher in the equatorward, rather than climatically benign, poleward, half of the distribution, again going against the trend one should expect under the assumption that equatorward climate is progressively more hostile.

If the above revised trends of *A. dichotoma* mortality are interpreted as having resulted from a recent exceedance of physiological thresholds, then it would be more appropriate to argue that such environmental conditions occur predominantly within the Gariep River valley and just north of it and, if a critical absence of juveniles are taken to mean climatic unsuitability, in the 'tail' of the distribution between, approximately, 23-26°S. This is a somewhat different interpretation when compared to previous assertions that the greatest proportion of mortality was to be found at the equatorward limit (e.g. Foden *et al.*, 2007).

To some extent altitude accounted for the abovementioned trends in mortality and recruitment (e.g. higher elevation populations experienced less mortality). However, one low altitude northern population (at approximately 23°S) displaying very low mortality was excluded from the previous analysis, due to the suspect removal of dead individuals by park rangers (W. Foden, pers. comm.)). In the current study the same low elevation population was found to be recruiting prolifically (pers. obs.), underscoring the inherent variability in the health of the species, even at equatorward latitudes. The use of altitude as the chief explanation for demographic profiles in equatorward populations is further complicated by the poor relationship between altitude and juvenile density (Foden *et al.,* 2007). In addition, a counterintuitive *negative* relationship between altitude and juvenile proportional density was found in the current study for individuals growing north of 24°S. Previous studies on a closely related sub-species, *A. pillansii*, have also made reference to a weak or non-existent relationship

between altitude and recruitment (Bolus *et al.*, 2004; Duncan *et al.*, 2006). So, whilst there may well be an ameliorative effect from altitude, it is unlikely to have systematically confounded latitudinal trends in proportional density of mortality or recruitment.

3.4.3   *Demographic patterns and contemporary climate*

An assessment of the strength of the relationship between *A. dichotoma* demographic patterns and climate has thus far remained coarse, due largely to the lack of high resolution datasets, but also because of an unusual distribution that straddles a major seasonal rainfall divide and three biome boundaries. For example, a previous study which generated climatic surfaces for sites at which *A. dichotoma* was sampled used the New *et al.* (2002) interpolated climatic surface, at a spatial resolution of 10 arc minutes, or approximately 18.5 km (Foden *et al.*, 2007). It is likely that this spatial resolution masked considerable climatic variability (Hijmans *et al.*, 2005), especially in the more mountainous terrain characteristic of much of *A. dichotoma*'s distribution. However, the overarching limitation in linking climate to *A. dichotoma* demography was the previously relatively low population sampling resolution, which, at 53 sites (Foden *et al.*, 2007) over a distributional area of more than 200 000 km^2, may not have fully described *A. dichotoma*'s highly variable climatic envelope.

The development of a detailed roadside mega-transect at 5 km intervals has created a spatially explicit network of *A. dichotoma* localities for which a suite of climatic variables at 1 km spatial resolution could be extracted (Hijmans *et al.*, 2005). This is a significant improvement in resolution. A visual assessment of these climate-distribution patterns reveal complex, non-linear latitudinal trends (especially within the more extensive SRZ part of the distribution), as well as discontinuities between summer and winter rainfall zones. This is at odds with previous interpretations which imply, for example, through their association of mortality with latitude, that a linear climatic gradient exists from equatorward to poleward populations (e.g. Foden, 2002; Foden *et al.*, 2007).

Differences in the mean value (as well as variability) of key climate variables in the summer and winter rainfall zones have not previously been emphasized. The WRZ had significantly less variability across most rainfall and temperature variables, highlighting the stability and consistency of contemporary climate in the south-western part of the distribution. This is as a result of the proximity of the Atlantic Ocean and the arrival, primarily in the winter months, of predictable frontal rains brought on by circumpolar westerly winds (Hoffman & Cowling, 1987; Cowling *et al.*, 1999). The climatic variability in the SRZ is partly due to the longitudinal extension of the distribution between 26°S and 29°S. However, rainfall is also inherently more

variable in the SRZ since it is determined to a large degree by localised and spatially discrete convective thunderstorms (Mendelsohn *et al.*, 2002, Henschel *et al.*, 2005).

These findings are in agreement with those of the previous chapter and suggest that *A. dichotoma* individuals in the WRZ exist under fundamentally different climatic conditions to those of the SRZ, with potential implications for both current and long-term *A. dichotoma* recruitment, persistence and mortality trends. Indeed, there is good support for this hypothesis from several sources. For example, in an analysis of nine repeat photographs of *A. dichotoma* populations in the Northern Cape of South Africa, Kaleme (2003) found that populations re-photographed in the WRZ had consistently low mortality and high recruitment rates, whilst the converse was true for populations in the SRZ. Kaleme (2003) ascribed this to differences in the consistency of seasonal rainfall. Bolus *et al.* (2004) analysed the distribution and population structure of the closely related species, *A. pillansii*, which occupies a much smaller distribution in the rugged and arid Richtersveld National Park in South Africa and the adjacent mountains in south-western Namibia. Similar to Kaleme (2003), he found that the consistent nature of winter rainfall and the presence of coastal fog were critical determinants of the numbers of juvenile individuals in a population (Bolus *et al.*, 2004).

There are many other examples of species-climate associations from similar winter rainfall deserts (e.g. Esler & Rundel, 1999). Good examples can be found in the climatically similar Sonoran Desert in south-western North America (Drezner, 2004; Schwinning *et al.*, 2004), where the consistency of seasonal rainfall is related to growth rates and recruitment success in functionally similar species such as *Carnegiea gigantea*, *Stenocereus thurberi* and *Lophocereus schottii* (e.g. Parker, 1988; Drezner, 2003).

In the current study the response of *A. dichotoma* to climatic conditions in the winter and summer rainfall zones was very different *between* age classes, while in most cases the responses *within* age classes was similar. This indicated two things. Firstly, specific *A. dichotoma* life history stages have broadly similar climatic requirements, irrespective of their geographical location within the summer or winter rainfall zone, and secondly, that specific life history stages respond fundamentally differently to climatic stimuli. While the above points have interesting implications for understanding the relative sensitivity of specific age classes in relation to climate change (after Dawson *et al.*, 2011), one should nevertheless be mindful of generally low model xR^2 values.

Of the three age class categories, patterns in juvenile proportional density were generally better related to contemporary climatic data than the other age class categories. This should not be surprising, given that juveniles have necessarily been exposed to contemporary climate for a greater proportion of their lives than older individuals and are thought to be more sensitive to environmental perturbations. Specifically, increased dry season rainfall (i.e. winter rainfall in the SRZ and summer rainfall in the WRZ) and low precipitation variability emerged as important determinants of juvenile density in winter and summer rainfall zones, respectively, while temperature measures generally performed poorly as single explanatory variables. Despite being the primary variable in the multivariate analysis for the SRZ, the low sensitivity score and anomalous positive relationship with juvenile density suggested that temperature seasonality was not as important as indicated in the multivariate model. Instead, a weak correlation between temperature seasonality and precipitation of the driest quarter indicated that the latter variable – and possibly precipitation seasonality - were more likely to have a greater influence on juvenile density in the SRZ.

Since water uptake and storage limitations affect the survival of juveniles in functionally similar desert succulents such as *Carnegiea gigantea* (Turner *et al.*, 1966) and *Ferocactus acanthodes* (Jordan & Nobel, 1981), the availability of water in the dry season could, therefore, be critical to the survival of young *A. dichotoma* individuals. The greater spatial and temporal stochasticity of rainfall within the SRZ could be a possible explanation for the lack of recruitment within the northern part of the distribution. Conversely, higher and more consistent rainfall in the WRZ could explain why recruitment and establishment rates are so much greater at the poleward range limit. Crucially, neither of these explanations need invoke recent climate change for the patterns evident in the respective rainfall zones. These results improve upon a previous generalized linear modelling exercise and question the prevailing idea that a temperature driven increase in evaporation rates within the last 30 years has been the primary determinant of patterns in *A. dichotoma* recruitment (e.g. Foden *et al.*, 2007; Midgley *et al.*, 2009).

Adult proportional density was well correlated with measures of precipitation seasonality and winter rainfall within the SRZ. However, the direction of the relationships indicated that the adult age class was proportionally dominant in areas receiving *more* variable and *reduced* winter rainfall in the SRZ, which already experiences extremely low rainfall in the winter months. While generally more poorly related to climate variables in the WRZ, the direction of relationships indicated a similar association between adult individuals and more severe climatic conditions.

The above results are difficult to interpret in the context of contemporary climatic patterns. Since juveniles have been shown to be vulnerable to dry season drought stress, it would appear that climatic conditions where adults currently dominate are currently too harsh for the recruitment of significant numbers of new individuals. One hypothesis, discussed in more detail later, is that climatic conditions must have been sufficiently benign at some point in the past to have resulted in the recruitment and establishment of one or more cohorts in the central and northern parts of the SRZ. Based on our understanding of *A. dichotoma* longevity (Vogel, 1974), inferred growth rates (Kaleme, 2003), and evidence for infrequent recruitment intervals, these recruitment episodes would certainly have occurred well before the middle of the 20th century and likely before the beginning of the 20th century. The recruitment interval would also have needed to last a considerable amount of time (or happen repeatedly) for large populations to establish in the areas where the trees are now found.

If the above hypothesis is true, it would imply that climatic conditions have subsequently become less favourable, and probably have been so over much longer time scales than suggested in previous studies. The affect of this would have been to curtail or preclude further recruitment in the central and northern parts of the distribution, where climate is more variable. The resultant picture from a present-day viewpoint would be of aging and gradually shrinking adult populations, unable to adequately replace themselves and only able to persist in an inhospitable climate due to extraordinary water storage capacities which provide a buffer against frequent, prolonged dry spells.

The relationship between contemporary climatic variables and proportional mortality was the weakest of the three age class categories, registering xR^2 values of 0.15 for both summer and winter rainfall zones. In addition, the selection of several different climatic variables in the modelling procedure, and their similar sensitivity scores within rainfall zones, indicated that there was not a single stand-out climate variable which could explain mortality patterns. Despite this, the presence of PET in the multivariate model and the weak positive correlation between PET and MAT for single climate variable interactions in the SRZ may provide some support for the assertion that mortality and evaporative demand are related (Foden *et al.*, 2007). However, while the possibility exists that the relationship between PET and *A. dichotoma* mortality patterns is real, the xR^2 values are so poor that they warrant cautious interpretation.

In summary, the application of the most spatially explicit and detailed climatic and demographic datasets to date have produced some key new insights, such as a non-linear latitudinal mortality gradient resulting from different recruitment and mortality patterns within the respective

rainfall zones; a link between increased and more consistent dry season rainfall and greater juvenile density; and the ability of adults to persist in areas where contemporary climate has arguably become unsuitable for recruitment. These findings illustrate the range in sensitivity of different age classes. In addition, they suggest that, with respect to recent climate change impacts, the juvenile age class should be investigated further, as it appears to be the most sensitive to abiotic influences.

The sensitivity of *A. dichotoma* to climate change needs also to be viewed in terms of its entire life history strategy. This includes the ecophysiological ability of adult individuals to persist for long periods of time during conditions unfavourable to younger, smaller age classes, as well as the species' infrequent, opportunistic recruitment strategy. This strategy enables climatically resilient, reproductively mature individuals to take advantage of rare, but favourable, above average rainfall events, and microhabitats provided by nurse plants and rocks (Foden *et al.*, 2007). It also ensures that the species is able to persist in areas where average climatic conditions may have become unfavourable (such as in large parts of the SRZ) over long periods of time. Despite prior inferences based on observed mortality, this age class had the *weakest* relationship with contemporary climate, which is not surprising, given that slowly decaying skeletons accumulate *in situ* and obscure the signal of recent climate change on population level mortality.

The generally poor relationship between contemporary climate and broad demographic patterns suggests that *A. dichotoma* is not in close equilibrium with climate. This raises doubts about the suitability of the species as an indicator of recent climate change. Instead, results suggest that explanations for the species' distribution and demographic patterns are more complex and probably include many other poorly understood biotic and abiotic factors. These influences affect recruitment, persistence and mortality dynamics at a range of temporal and spatial scales and ultimately shape demographic patterns over longer timescales.

The influence of aspect and solar radiation on recruitment, persistence and mortality of *Aloe dichotoma* populations across a latitudinal gradient

4.1   Introduction

4.1.1   The role of aspect and the influence of climate change

Plant cover, species composition and biomass have all been shown to differ on northern versus southern aspects, especially at mid latitudes, due to differential heat loading from solar radiation (e.g. Ayyad & Dix, 1964; Holland & Steyn, 1975; Armesto & Martinez, 1978; Sternberg & Shoshany, 2001; Mata-Gonzalez *et al.*, 2002; Fekedulegn *et al.*, 2003; Gitlin *et al.*, 2006). In the southern hemisphere for example, this means that north facing slopes generally receive higher average annual solar radiation, thus increasing ambient and soil surface temperatures and affecting soil moisture and nutrient levels, which in turn affect the vegetation (Holland & Steyn, 1975; Sternberg & Shoshany, 2001). Conversely, lower average annual solar radiation on south facing slopes lowers evapotranspiration rates, as well as daily maximal temperatures during peak summer water stress periods. This difference in heat loading between aspects has an important selective influence on plant communities, especially in arid and semi-arid areas, where water availability is a limiting factor (Noy-Meir, 1973; Sternberg & Shoshany, 2001), and also at range margins or within marginal areas of a species' distribution, where environmental pressures are greater and microsite selection more important (Lennon *et al.*, 2002).

Recent expressions of this response to environmental gradients have been shown to be the result of anthropogenic climate change. For example, numerous species have shifted their geographical distributions latitudinally (e.g. Hickling *et al.*, 2006) and altitudinally (e.g Grabherr *et al.*, 1994) in response to incremental increases in temperature (McCarty, 2001). Where species have not been able to keep pace with changing climate, local or regional extinction has been the result (McLaughlin *et al.*, 2002). Under projected future changes, species are expected to further shift their ranges poleward or upward in response to rapidly shifting climate

envelopes (e.g. McCarty, 2001; Bakkenes *et al.*, 2002; Iverson *et al.*, 2004; Jetz *et al.*, 2007), or face likely extinction (Thomas *et al.*, 2004).

Sessile species, which are long-lived and recruit infrequently, may be especially at risk of being overwhelmed by projected rates of change, as their life-history strategy is not designed for keeping pace with a rapidly changing climate. In other words, sessile species may have a poor capacity to adapt to change (after Dawson *et al.*, 2011). However, traits have evolved which allow populations to persist *in situ*, despite changing environmental conditions. These include phenotypic plasticity, genetic diversity and dispersal and colonisation ability through the use of microhabitats (Dawson *et al.*, 2011).

In this respect, recruiting to a proximal cooler aspect may represent one of the few ameliorative opportunities for a long-lived, infrequent recruiter against an increasingly hostile climate (e.g. Parmesan *et al.*, 1999; Lennon *et al.*, 2002). However, despite being a potentially easily testable phenomenon, few studies have actually investigated the role that aspect may play, in the context of climate change, in providing a) more favourable slopes for species to recruit to, and b) a repository of recent mortality on unfavourable slopes in response to anthropogenic climate change (e.g. Thuiller *et al.*, 2005). This is surprising, given that many studies documenting species' equatorward range contractions are located in the mid to high latitudes (e.g. Badeck *et al.*, 2004; Parmesan; 2006; Parmesan, 2007), where the difference in solar radiation levels between northern and southern aspects is high, and the potential expression of these differences would be most pronounced (Holland & Steyn, 1975).

4.1.2   A. dichotoma *as a climate change indicator species*

As previously discussed, the iconic arborescent succulent species, *A. dichotoma,* has recently been promoted as an indicator of anthropogenic climate change in temperate southern African. However, some debate surrounds this conclusion. For example, an analysis of repeat photography of populations in the southern and central distributional region suggest that *A. dichotoma* populations were already undergoing significant mortality and no visible recruitment in the first half of the 20th century, and perhaps earlier (Hoffman *et al.*, 2010). This is corroborated by detailed historical botanical fieldnotes from the same time period (Acocks, unpublished (see Rutherford *et al.*, 2003)), which also describe pervasive mortality and no recruitment in populations around Karasberg and Keetmanshoop in southern Namibia. Despite this historical evidence, previous studies linking *A. dichotoma* mortality with climate change have not distinguished between recent and non-recent mortality. The inclusion of this

consideration may change the previous interpretation that mortality is predominantly a consequence of recent climate change.

That individual life history stages often have different response thresholds with respect to climatic gradients must also be taken into consideration. Juveniles typically have narrower niches than adults, due to their limited root, water storage and photosynthetic capacities (Grubb, 1977; Jackson *et al.*, 2009), as well as their greater exposure to desiccation as a result of greater surface-area-to-volume ratios (e.g. Turner *et al.*, 1966). There are, for example, many instances in which seedlings have succumbed to drought, flooding or temperature extremes that present no deleterious effects to conspecific adults (e.g. Donovan *et al.*, 1998). This is especially true for succulent desert species such as *Carnegiea gigantea*, *Ferocactus acanthodes*, and *Agave deserti* (Steenbergh & Lowe, 1969), which are functionally similar to *A. dichotoma*. Given the above, if *A. dichotoma* mortality has escalated recently as a result of climate change, one should expect that this mortality be skewed to juvenile individuals.

If, conversely, mortality is predominantly derived from the adult age class, one would need to consider whether recent temperature increases (over approximately the last 30 years (Foden *et al.*, 2007; Midgley *et al.*, 2009)), as a result of climate change, have been sufficient to cause this. Again, indications from well studied and functionally similar Sonoran Desert species are that mortality in adult individuals typically only escalate in the face of severe and prolonged drought events (Parker, 1993); extended periods of sub-zero winter temperatures (Shreve, 1917; Niering *et al.*, 1963); and even-aged cohorts reaching the end of their life-spans at a similar time (Bowers & Turner, 2001).

While unequivocal evidence exists for a generally increasing temperature signal in southern Africa (Kruger & Shongwe, 2004; Midgley *et al.,* 2005[a]; Midgley *et al.*, 2005[b]; Warburton *et al.*, 2005; Hoffman *et al.*, 2011), debate surrounds the incidence and severity of recent drought (Fauchereau *et al.*, 2003; Rouault & Richard, 2003; Hoffman *et al.*, 2009), as well as its causal mechanisms (Fauchereau *et al.*, 2003; Hoerling *et al.*, 2006). Conversely, there is little support for an increase in frost events due to a general increase in both maximum *and* minimum temperatures in the region (New *et al.*, 2006). As far as synchronous death is concerned, little is known about recruitment and mortality dynamics in *A. dichotoma*, but indications are that individuals recruit in cohorts (e.g. Kaleme, 2003; Hoffman *et al.*, 2010) and therefore, assuming similar rates of aging, might senesce and die at similar times. This may give the impression that

mortality has resulted from a recent shift in climate, when the actual cause may simply be death as a result of old age.

4.1.3   Objectives and key questions

Here I first document the latitudinal pattern of aspect preference, utilizing data from both the roadside mega-transect and population level study. I then establish if differences in solar radiation (a proxy for temperature) on northern and southern aspects has resulted in different proportional representation (in terms of juvenile, adult and dead age classes) on these opposing aspects. For example, if recent climate change has impacted the species, one should expect younger, and more recent mortality on more climatically severe northern aspects at the equatorward extreme, and comparatively higher rates of recruitment on southern aspects at a similar latitude. In order to test this, I develop a novel technique for dating the approximate 'time since death' of dead individuals and - along with information about the median girth of age classes at death – comment on when the majority of mortality most likely occurred, as well as from which age class it was derived.

I address the following specific questions in this chapter:

- Are there aspect preferences across the latitudinal extent of the distribution and which aspects are preferred at the latitudinal extremes?
- Does solar radiation differ between northern and southern aspects, and if so, do these differences translate into a consistently observable aspect preference within age classes?
- When did most of the observed mortality occur and from which age class category was this mortality predominantly derived?
- Is there a relationship between aspect and recent mortality, specifically at the equatorward extreme?

4.2   Methods

4.2.1   General patterns in aspect preference

The roadside mega-transect (Chapter 3) provided an initial appraisal of relative aspect preference across the distributional extent by recording the number of individuals on each of N, S, E, and W slopes at an interval of 5 km (see Chapter 3 for more details on the mega-transect). For each interval, the proportion of individuals on each aspect was calculated, assigned to bins and mapped as graduated symbols using ESRI ArcMap 9.3 (ESRI, 2010).

4.2.2   Detailed population survey: site sampling technique

Fourteen sites were sampled over two consecutive winter seasons in Namibia and the Northern Cape in South Africa during 2008 and 2009 (Fig. 1). As far as possible, sites were chosen at roughly equal intervals spanning the latitudinal extent of the distribution. In addition, sites were selected for having populations on as many aspects as possible. Conspicuous populations along busy transport routes easily accessed from the roadside were avoided, due to the likelihood of prior removal of young individuals and the effect that this would have on relative demographic measures.

For each of the four aspects (N, S, E and W) an estimate was made of the transect width which would be required in order to sample approximately 60 individuals, spanning the full altitudinal extent of the population. This transect was then sampled. If the target of 60 individuals per aspect was not initially achieved, the transect was either widened or neighbouring populations on the same aspect were sampled to supplement the initial recording. A sample of less than 60 individuals was accepted only once an exhaustive search in the near vicinity of the originally sampled population yielded no further trees.

Individuals were placed into age class categories using the same classificatory methods established in Chapter 3 (see Table 1 in Chapter 3) and then, to simplify analyses, subsequently merged into three age class categories, namely juveniles (comprising juvenile and adult 1 age classes), adults, and dead (comprising senescent and dead individuals).

The geographical position and altitude of each individual was recorded by means of a handheld Garmin GPS60, resulting in a total of 3368 individuals sampled across 14 populations. A range of allometric measurements were then taken for each live individual, including measures of tree height, canopy diameter, basal circumference, number of dichotomous branches, live and dead leaf rosettes, broken or abscised leaf rosettes, inflorescences containing either flowers or fruit,

and an overall canopy and stem health score. Basal circumference was measured for each dead individual (or estimated from root remains) and the individual subsequently classified into a 'time since death' category.
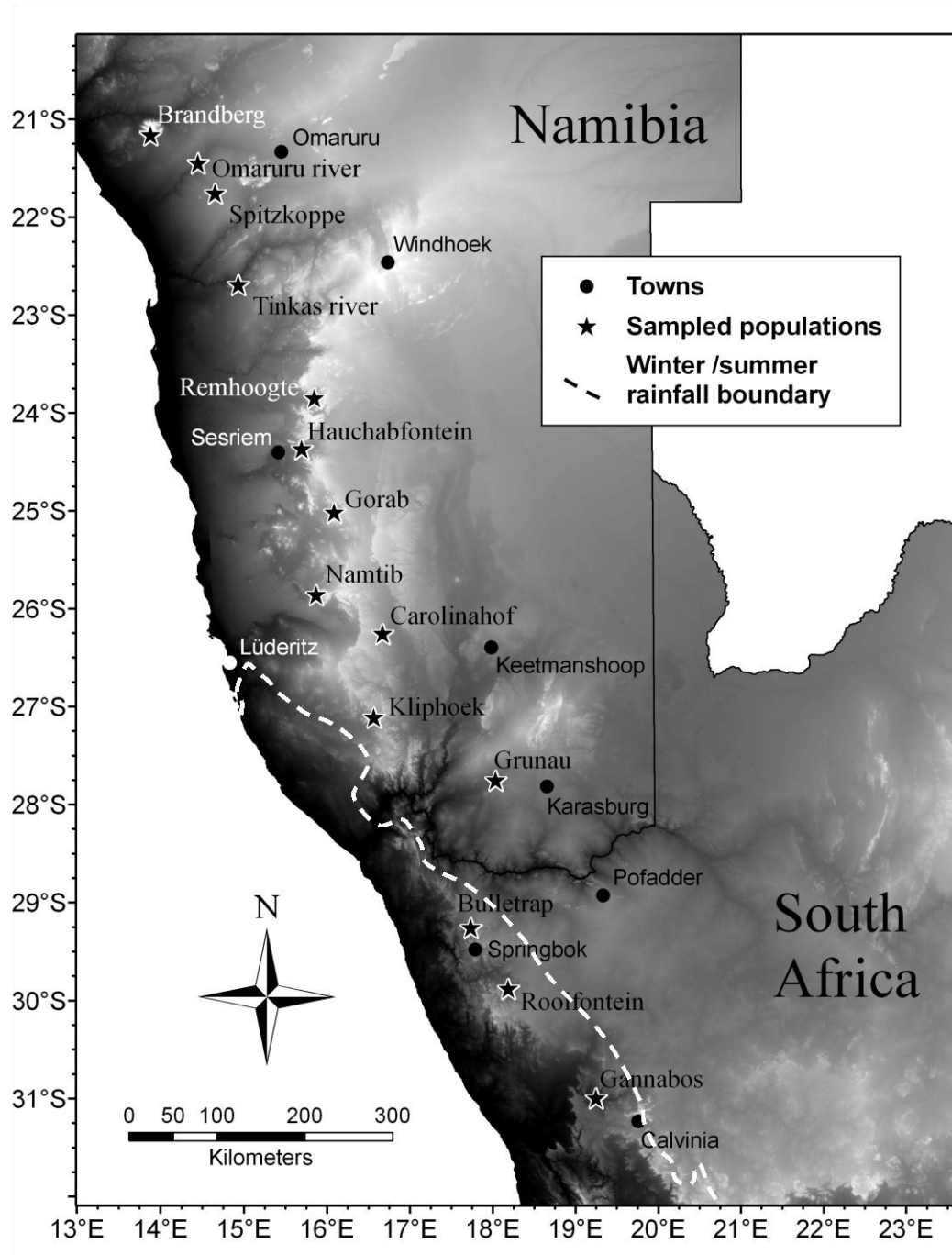
Fig. 1. Geographical map of the distribution of sampled Aloe dichotoma *populations.*

4.2.3   Time since death classification

'Time since death' was estimated based on the decay rates observed in several repeat photographs from different parts of the distribution (e.g. Fig. 2; Table 1) and from repeated visits by researchers within the Plant Conservation Unit at the University of Cape Town to individuals which had died since 2002. While there are obvious assumptions implicit in this technique (such as constant temporal and spatial decay across a considerable latitudinal distance and two different rainfall zones), it is nevertheless a useful guide for gauging approximate ages of dead individuals. At the very least, the technique can be used to confidently differentiate recent from non-recent mortality. Histograms were drawn for each site, illustrating the frequency of each 'time since death' category. Figure 2 and Table 1 outline the main criteria used in determining the 'time since death'.

Fig. 2. An example of how repeat photography aided the development of a 'time since death' classification. The Aloe dichotoma *skeleton in the 1908 Marloth image was still visible 100 years later, and would - as a conservative estimate - have fallen within category 5 or 6. (Photo: T. Hoffman & S. Jack)*

Table 1. Criteria used for categorizing time since death for dead individuals.

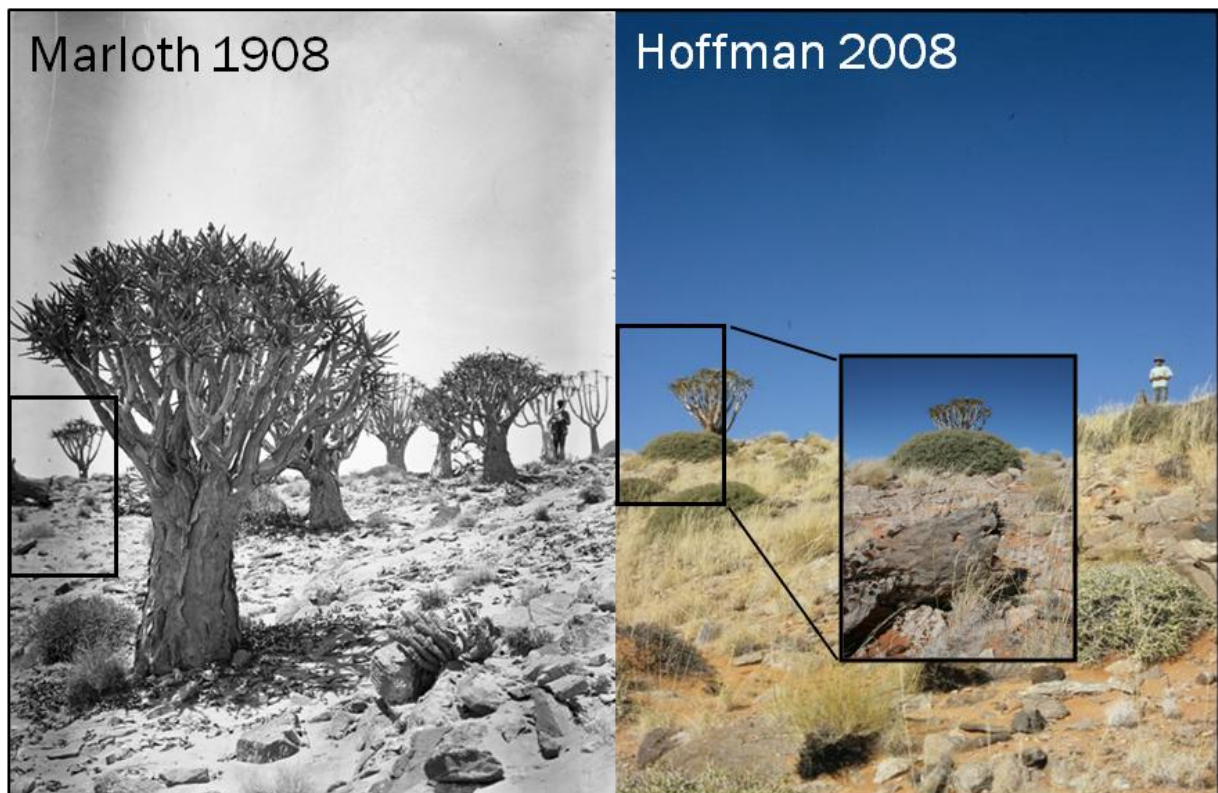| Category	Estimated yrs since death	Leaves	Bark remaining	Branches	Stem circ. Integrity	Growth rings	% plant remaining	Description
1	1-5	Present	> 95% and present on branches and trunk; may be easy to peel away	All present and intact	Whole	Not visible	100%	The tree appeared to have died recently. Leaves were still present and in some cases at least partially green (*A. dichotoma* dies predominantly from bottom upwards). Branches and at least 95% of the bark also remained, as did white bloom and/or black scale. The tree still had a solid feel, sometimes containing water in its pithy core.
2	6-10	Sometimes present, but always dried out and often only a fraction remaining either on the tree or, more usually, on the ground surrounding the tree	50% > 75% disproportionately present on branches	All present, but not necessarily intact (i.e. all/fraction may have collapsed due to mechanical failure)	Whole	Not visible	95%	The tree had been dead long enough for the trunk and leaves to dry out completely. Some of the dried leaves may be retained on the tree. At least a fraction would still be visible on the ground surrounding the tree. Bark may be peeling off, though normally more than half would still be present
3	11-20	Absent	<40%	All present, but not necessarily intact (i.e. all/fraction may have collapsed due to mechanical failure)	Very slight decay	Not/barely visible	~80% - 90%	The leaves would no longer be present, although the branches may have remained intact. The trunk may have started to decay from exposure to elements due to absence of bark.
4	21-40	Absent	< 5%	< 50%, some primary lower branches may remain	Beginning to break/disintegrate	Becoming visible	~50%, usually trunk	Few branches remain and almost all bark is now gone. Growth rings are starting to show on parts of the trunk. The trunk itself may have started to disintegrate due to earlier mechanical failure of one or more of the main branches.
5	41-60	Absent	Absent	< 10%, first 1-2 dichotomous nodes may remain in larger trees	Usually (but not always) 25% > 50% broken/disintegrated	Clearly visible	~20% - 40%, usually section of trunk	All terminal branches are gone and only branches that may remain are first or second dichotomous node in larger trees. Growth rings are completely exposed and the trunk is often broken and in a moderate stage of disintegration.
6	61+	Absent	Absent	Absent	> 80% disintegrated	Clearly visible	< 5%, lower section of trunk or roots only	Very little remains of the tree - usually only a small section of the lower trunk or roots. The trunk is more than 80% disintegrated and growth rings are clearly visible.

4.2.4   Average distance matrices and altitudinal range

Because it was impractical to keep effort (analogous to area or time) constant in the sampling of each aspect at a site, another measure was required to determine relative aspect preference for the population level sampling approach. Typically, the most favourable aspects at a site were well populated with comparatively short distances between live individuals. Conversely, more marginal aspects had fewer live individuals with larger spacing between trees. This characteristic patterning was analysed using ESRI ArcMap 9.3 (ESRI, 2010) in order to derive a measure of relative suitability between aspects. The procedure is described below.

Aspect populations were individually inspected for isolated live individuals, obviously separate from the main population cluster and not reflective of the general density of the rest of the population. These individuals, as well as all dead trees, were removed from the analysis. The reason for excluding the latter category was to derive a distance measure based on conditions experienced more recently (i.e. amongst live individuals). The distance between each individual and all remaining individuals in the population was then calculated and averaged, to achieve a single average distance value for each aspect, at each site. If large, but separately occurring clusters of trees were present on a single aspect at a site, average distances were calculated separately for each individual cluster and combined to form an overall average. Average distances on northern and southern aspects were then graphed side-by-side for each site. Sites were excluded only if there was an absence of trees on an opposing aspect at a comparable altitude.

Altitude was also captured for each individual by means of a handheld Garmin GPS60 and averaged for each aspect and site. This value was subsequently used to draw box and whisker plots using STATISTICA (Statsoft, 2009).

4.2.5   Solar radiation, proportional age class representation and aspect

Adjusted incoming solar radiation was calculated for trees at each site by means of individual geographical co-ordinates and altitude values, specific aspect slope angles, a solar position algorithm (Reda & Andreas, 2008) and a formula for direct irradiance (Campbell & Norman, 1998), which incorporated seasonal changes in extra-terrestrial flux density, atmospheric transmittance and an optical air mass number (Young, 1994). Adjusted incoming solar radiation values were recorded for individual trees at 20 minute time-steps (as recommended by Schulze, 1997) between sunrise and sunset, and averaged daily for a single leap year. Cumulative average daily values were then divided by the number of days in the year to derive an average

annual adjusted incoming solar radiation value in MJ.m^{-2}.day^{-1}, which will henceforth be referred to simply as 'solar radiation'.

The difference in solar radiation on northern and southern aspects at comparable latitudes was analysed for statistical significance using a non-parametric, unpaired Mann-Whitney U test. Proportional representation of individual age classes on northern, southern, and all aspects, was then graphed against solar radiation and simple linear trend lines fitted (with associated R^2 values). Lastly, the proportional contribution of each age class to the total number of individuals on northern and southern aspects was calculated and graphed for each site, based on a minimum of twenty individuals for each age class per aspect.

4.2.6   *Mortality: age class and aspect*

Basal circumference measurements for individual age classes were used to draw box and whisker plots using STATISTICA (Statsoft, 2009) and analysed for statistical significance using a non-parametric, unpaired Mann-Whitney U test.

'Time since death' categories were split into recent (0-20 years ago) and non-recent (21-60+ years ago) dead classes and the proportional contribution to northern or southern aspects calculated. These were then graphed side-by-side. Aspects represented by dotted bars were illustrated as such due to the opposing aspect either failing to meet the minimum requirement of ten dead individuals for inclusion, or because of a complete absence of dead trees on that aspect.

4.3 Results

4.3.1 Aspect preference inferred from roadside mega-transect and average distance matrix

The roadside mega-transect (Chapter 3) indicated that *A. dichotoma* had a clear preference for north facing slopes within the winter rainfall zone (WRZ), as indicated by a higher proportional density on northern aspects in the south-western part of the distribution (Fig. 3). Conversely, south facing slopes were generally favoured at the northern end of the distribution and along the central and south-eastern margins of the summer rainfall zone (SRZ).

The proportional density pattern on western and (especially) eastern aspects was less obvious. Proportional density was generally lowest on eastern aspects, without any clear pattern being present. Western aspects were better represented and appeared to favour the western margins of the distribution, but this pattern was not as clear as that of either northern or southern aspects. As a consequence of this, it was decided to focus solely on the aspects with the clearest patterns, namely northern and southern aspects.

Individuals in the central 'body' of the distribution (i.e. Karasberg and surrounds) grew predominantly on flat or very gently sloping ground, while the northern half of the distribution as well as the WRZ in the south west contained comparatively few such examples (not shown).

For populations sharing comparable altitudinal ranges (see Fig. 4), average distances between live individuals on northern or southern aspects provided a proxy measure of the suitability of that aspect, which could be compared to findings from the roadside mega-transect (Fig. 5). Populations on aspects with *smaller* average distances between live individuals indicated a denser habit and typically more favourable conditions. Conversely, *larger* average distances between live individuals indicated that trees were more spaced out, suggesting more unfavourable aspects.

Despite some variability, southern aspects appeared preferable to individuals growing at equatorward sites and northern aspects were favoured by individuals growing at the poleward end of the distribution. The former statement may seem spurious as it is based on the difference in average distances from only two northern populations. However, at a *comparable* altitude, both the Brandberg and Tinkas River sites had no *A. dichotoma* individuals present on the northern aspect, despite a similar geology and no obvious dispersal barrier between aspects. *A. dichotoma was* present on northern aspects at the Brandberg, but only above 1700m, while no individuals were present on the northern aspect at Tinkas River. These two sites can therefore
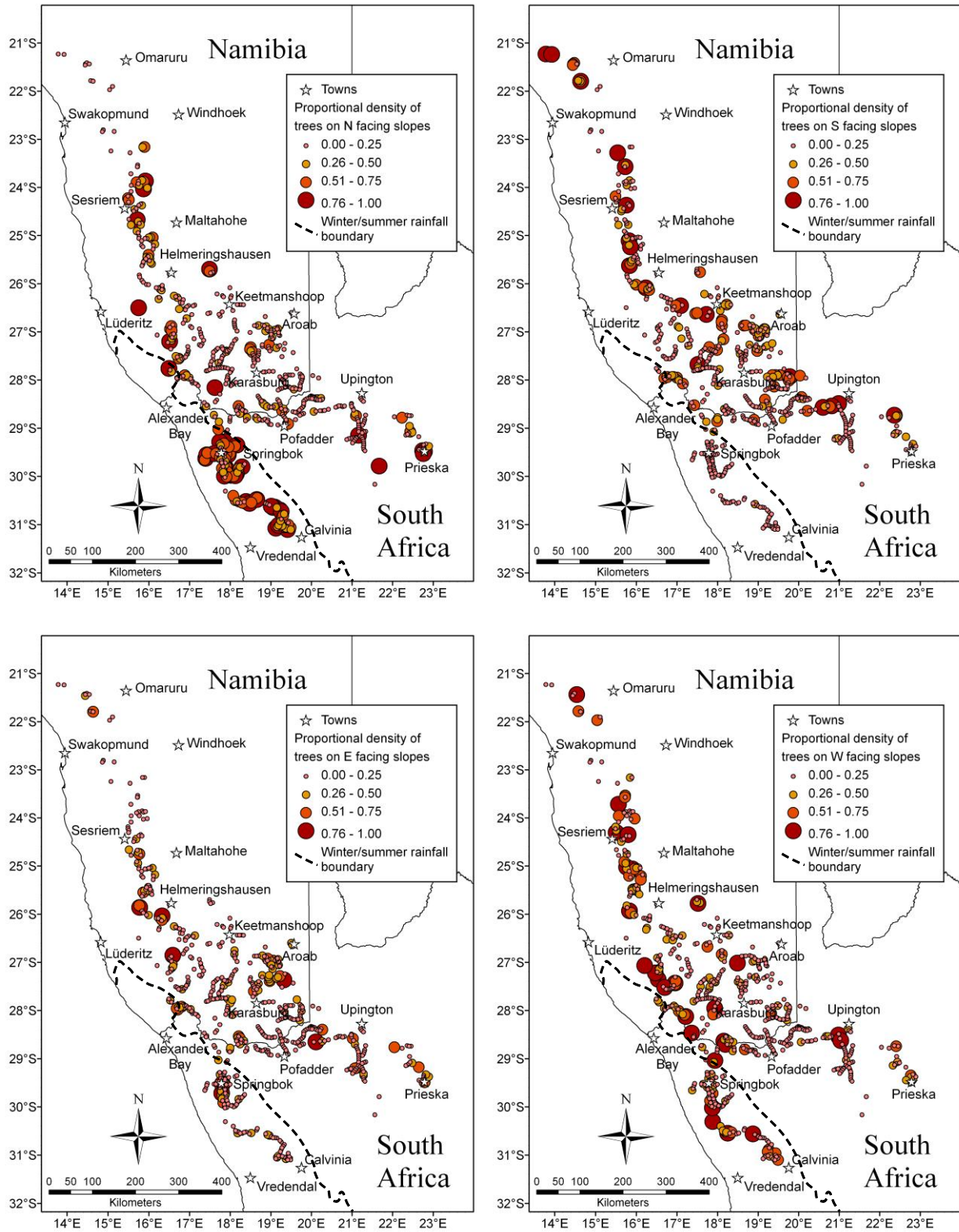
Fig. 3. Map from the roadside survey indicating the proportional density of Aloe dichotoma *individuals on each aspect.*
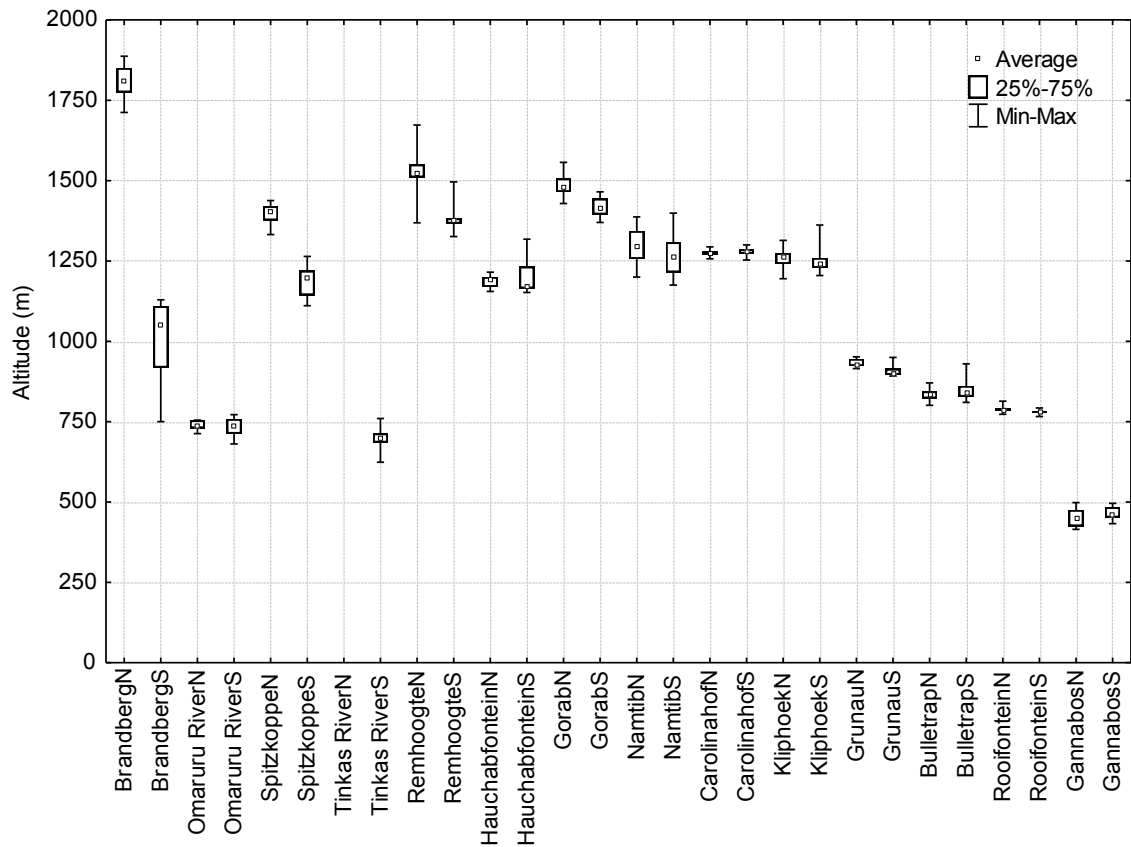
Fig. 4. Box and whisker plots indicating median (small box), 25th-75th percentile (large box), and maximum and minimum values (whiskers) for altitudinal range of populations on northern and southern aspects.
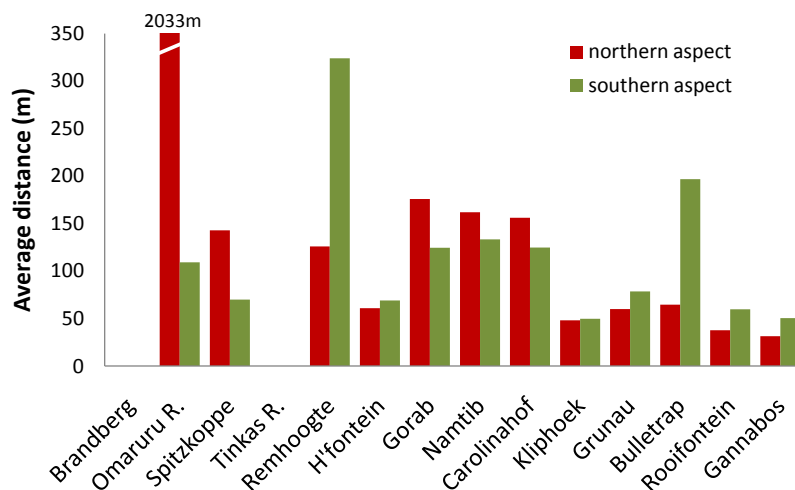
Fig. 5. A measure of aspect suitability based on averaged distances between individuals on northern and southern slopes. A larger average distance indicates a more disparate population and therefore less favourable conditions. Brandberg and Tinkas River sites were excluded due to an absence of specimens on the northern aspect at comparable altitudes, possibly suggesting more favourable southern aspects at these sites.

be interpreted as having comparatively favourable southern aspects. While northern and southern aspects were of similar suitability at Hauchabfontein, Remhoogte was an anomaly, displaying a strong preference for the northern aspect.

4.3.2   Solar radiation, age class relationships and aspect

Solar radiation values on the northern and southern aspects at each site (arranged in north-south latitudinal order) indicated that a significant difference existed in all instances where opposing aspects could be compared ($p < 0.001$; Mann-Whitney U Test). The exception was Tinkas River, which had no individuals growing on the northern aspect (Fig. 6). Northern aspects received, on average, over 6 MJ.m^{-2}.day^{-1} more solar radiation than southern aspects. This is roughly double the difference in solar radiation between the same aspects at either end of the latitudinal distribution.
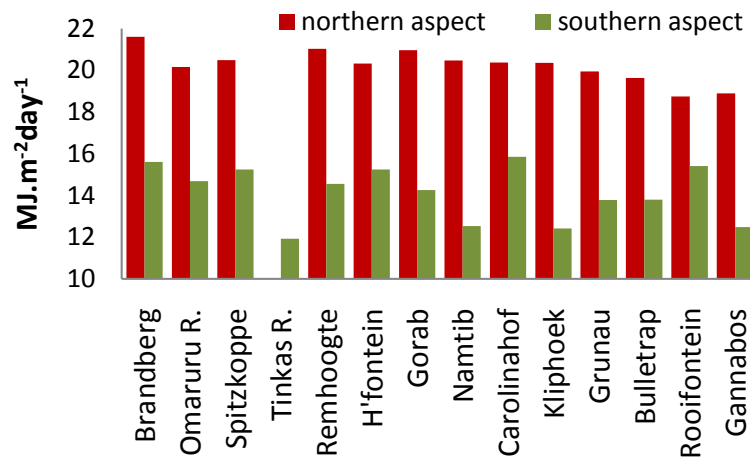
Fig. 6. Solar radiation on northern and southern aspects at each site.

When considered as a continuous variable (i.e. including all aspects) solar radiation exhibited no clear relationship with any age class (dotted linear regression and very low R^2 values) (Fig. 7). However, when considering only aspect extremes, corresponding to solar radiation values below 16 MJ.m^{-2}.day^{-1} and above approximately 19 MJ.m^{-2}.day^{-1}, there emerged a fair relationship with the juvenile age class category, and a weak relationship with the dead age class category. On cooler southern aspects juveniles responded positively to higher solar radiation, while on hotter northern aspects the relationship was slightly stronger and negative.
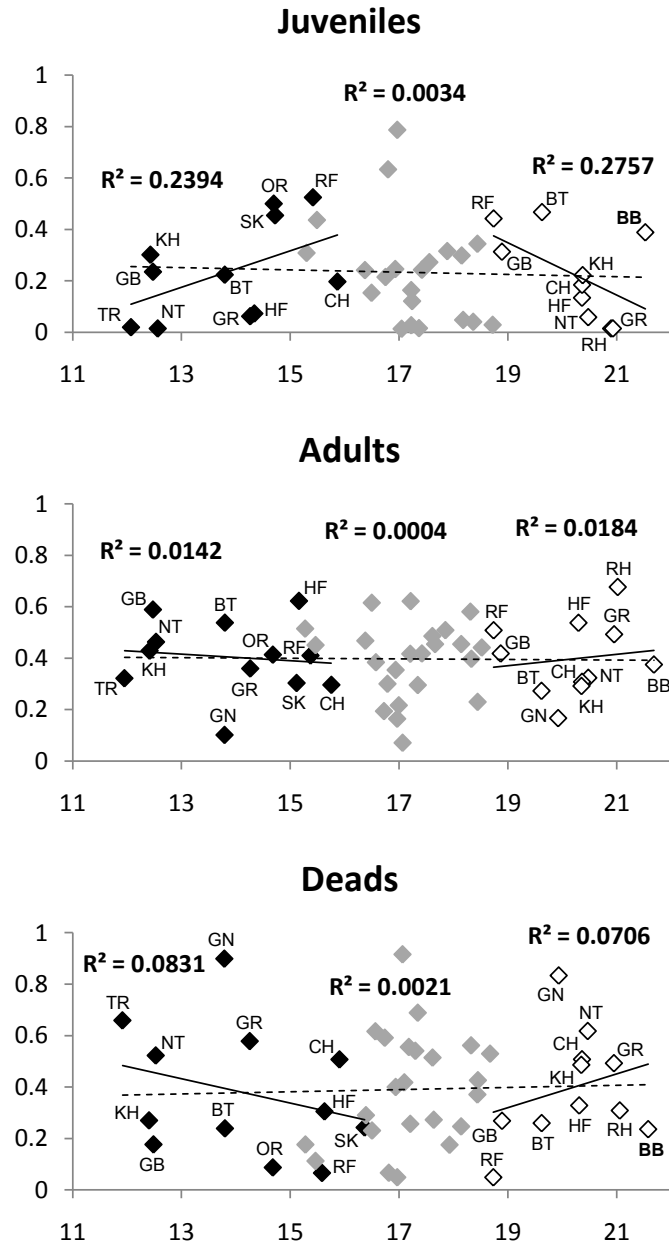
Fig. 7. The relationship between solar radiation (x-axis: MJ.m^{-2}.day^{-1}) and proportion of each age class (relative to other age classes on the same aspect) (y-axis). Black diamonds (and associated R^2 and solid trend line) = southern aspect; white diamonds (and associated R^2 and solid trend line) = northern aspect; grey diamonds = other aspects. Dotted trend line is the regression for all aspects and is associated with the middle R^2 value. Abbreviated names of sites accompany each value for northern and southern aspects.

The opposite trends were evident for the relationship between mortality and solar radiation on southern and northern aspects, though in both cases R^2 values were poor. However, the relationship strengthened considerably for both juvenile and dead age class categories when the anomalously high altitude northern aspect population at the Brandberg (BB) was excluded from

the analyses; northern aspect R² values improving to 0.75 and 0.23 for juvenile and dead age classes, respectively. Adults appeared uncoupled from solar radiation, even at the extremes, exemplified by very poor relationships on northern (white diamonds) and southern (black diamonds) aspects.
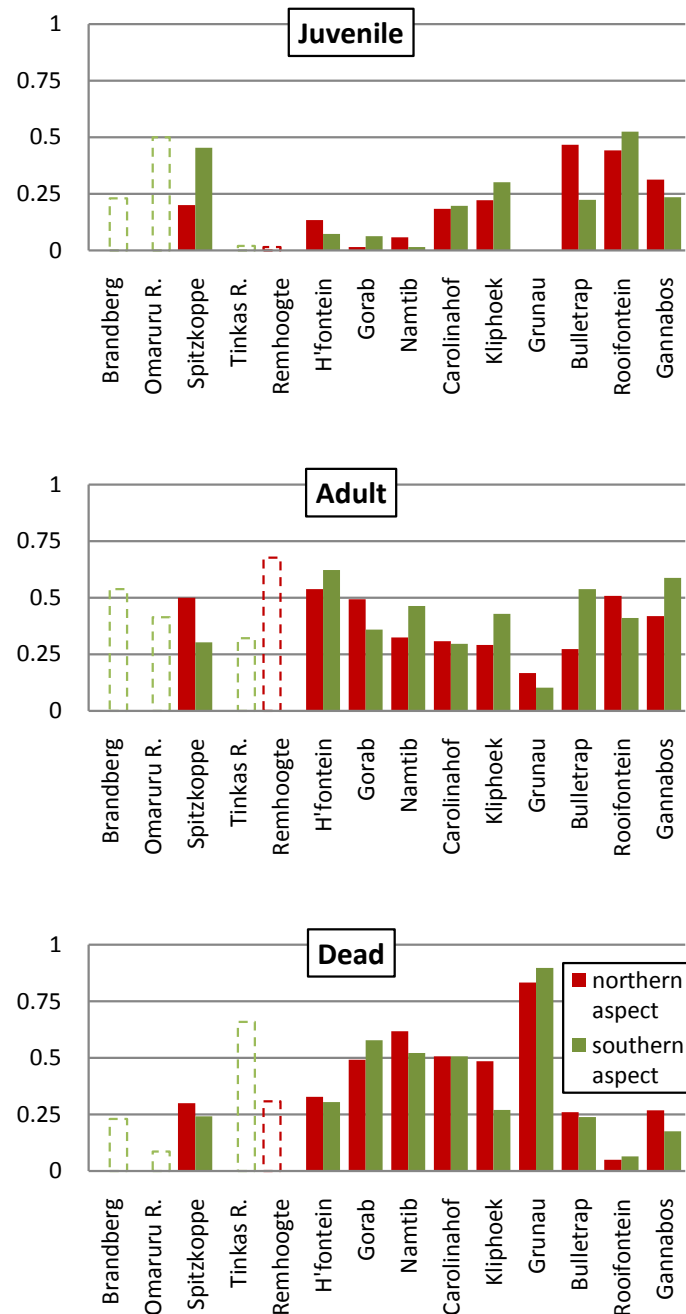
Fig. 8. The relationship between proportional representation of age classes (relative to other age classes on the same aspect) (y-axis) on northern and southern aspects at sampled populations. Dashed bars indicate proportional representation of age classes on an aspect which did *meet the minimum requirements for inclusion (≥20), but for which the opposing aspect was too poorly represented (at a comparable altitude) to qualify for inclusion.*

Proportional representation of age classes at each site was in general agreement with the proportional density pattern found in the roadside mega-transect (see Chapter 3, Fig. 5). However, poor representation on certain (usually northern) aspects at equatorward sites and Grunau led to the exclusion of several populations from the proportional analyses. For example, the northern populations at the Brandberg, Omaruru River and Tinkas River sites either had insufficient numbers, or no trees at all on northern aspects at equivalent altitudes. The same was true for Remhoogte in the central-northern part of the latitudinal range, but in its case numbers were insufficient on the southern aspect. Grunau, the site closest to the Gariep River valley, had no juveniles on either northern or southern aspects; the bulk of the population being comprised of dead individuals.

In terms of proportional representation on northern versus southern aspects, there were no clear patterns for any of the age classes (Fig. 8). Instead, northern and southern aspects appeared to have a similar representation at most sites, with the exception of Spitzkoppe and Bulletrap for juvenile and adult age classes, and Kliphoek for the dead age class category.

If, however, one included sites omitted as a result of a dearth or absence of trees on an opposing aspect (at comparable altitudes), and took this dearth or absence to infer a preference for the more populated aspect, then interpretation would be somewhat different. There would then be some justification in interpreting a juvenile preference for southern aspects at equatorward sites (given that juveniles already appear to favour the southern aspect at Spitzkoppe). However, adult proportional dominance on northern aspects at Spitzkoppe made interpretation more difficult for this age class. It was similarly unclear what the trend was for mortality, due to an absence of populations on northern aspects.

4.3.3   Mortality: when, where, and to whom?

'Time since death' histograms for each site, which combined all aspects, illustrated that mortality was generally left-skewed, indicating a greater frequency of non-recent rather than recent dead individuals (Fig 9). This can be more clearly seen in a single histogram (bottom right of Fig. 9), incorporating *all sites*. Moreover, there was no tendency towards recent/non-recent mortality at one or other end of the latitudinal extent of the distribution. Notable exceptions to the left skewed pattern were Spitzkoppe, which was bimodal, and Omaruru River and Bulletrap, which were both approximately normally distributed.
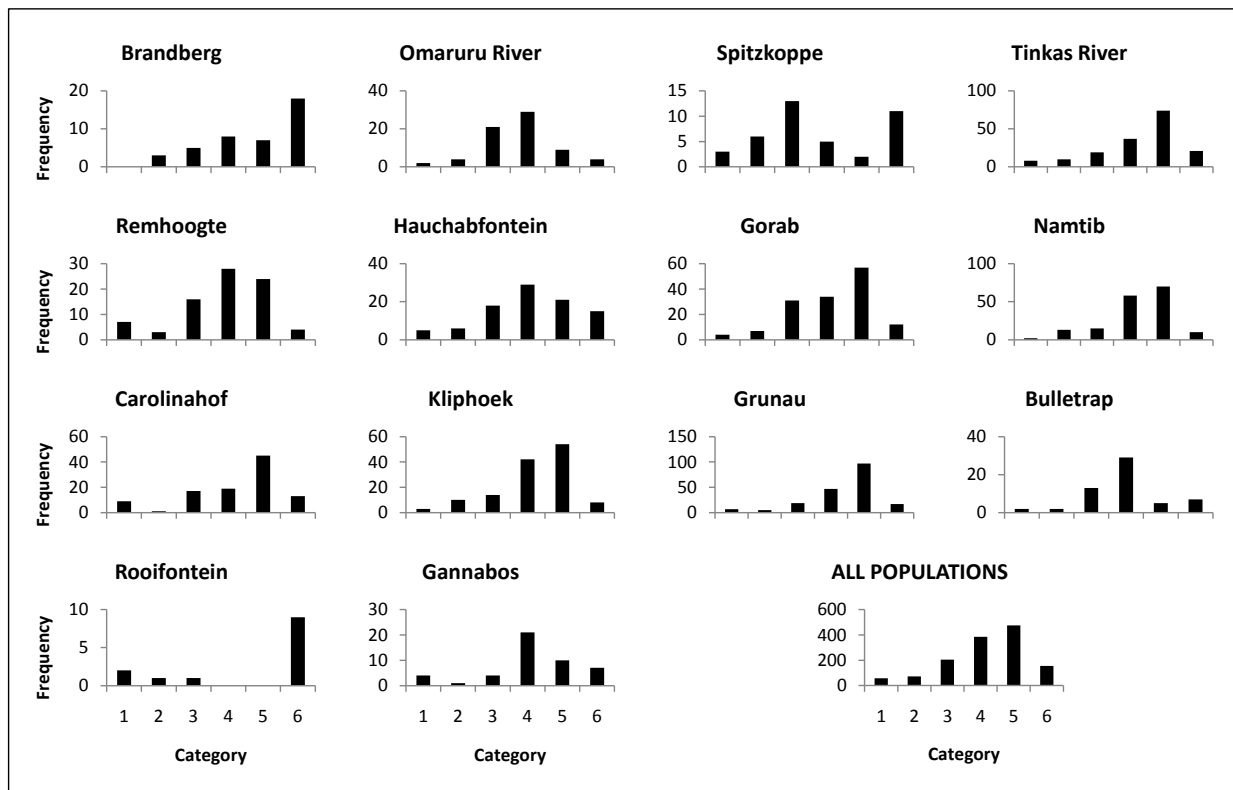
Fig. 9. Approximate 'time since death' histograms for each site and all *sites combined. Cat. 1 = 1-5yrs; cat. 2 = 6-10yrs; cat. 3 = 11-20yrs; cat. 4 = 21-40yrs; cat. 5 = 41-60yrs; cat. 6 = 60+yrs. Graphs arranged in latitudinal order from north to south, read horizontally (i.e. top left to bottom right).*

Despite a considerable range between minimum and maximum basal circumference values (particularly for the dead age class), comparisons between age classes indicated adult and dead categories were of a similar size (with broadly overlapping 25th-75th percentiles) and not significantly different from each other at *all* sites except Gannabos, where dead individuals were significantly *larger* than adults (p<0.001; Mann-Whitney U Test) (Fig. 10). Conversely, the juvenile age class was significantly smaller than both adult and dead age classes at *all* sites except Grunau, for which there were only two juvenile individuals (p<0.001; Mann-Whitney U Test). This pattern was consistent throughout all sampled sites and across the latitudinal distribution, indicating that mortality was derived almost entirely from the adult, as opposed to juvenile, age class category.
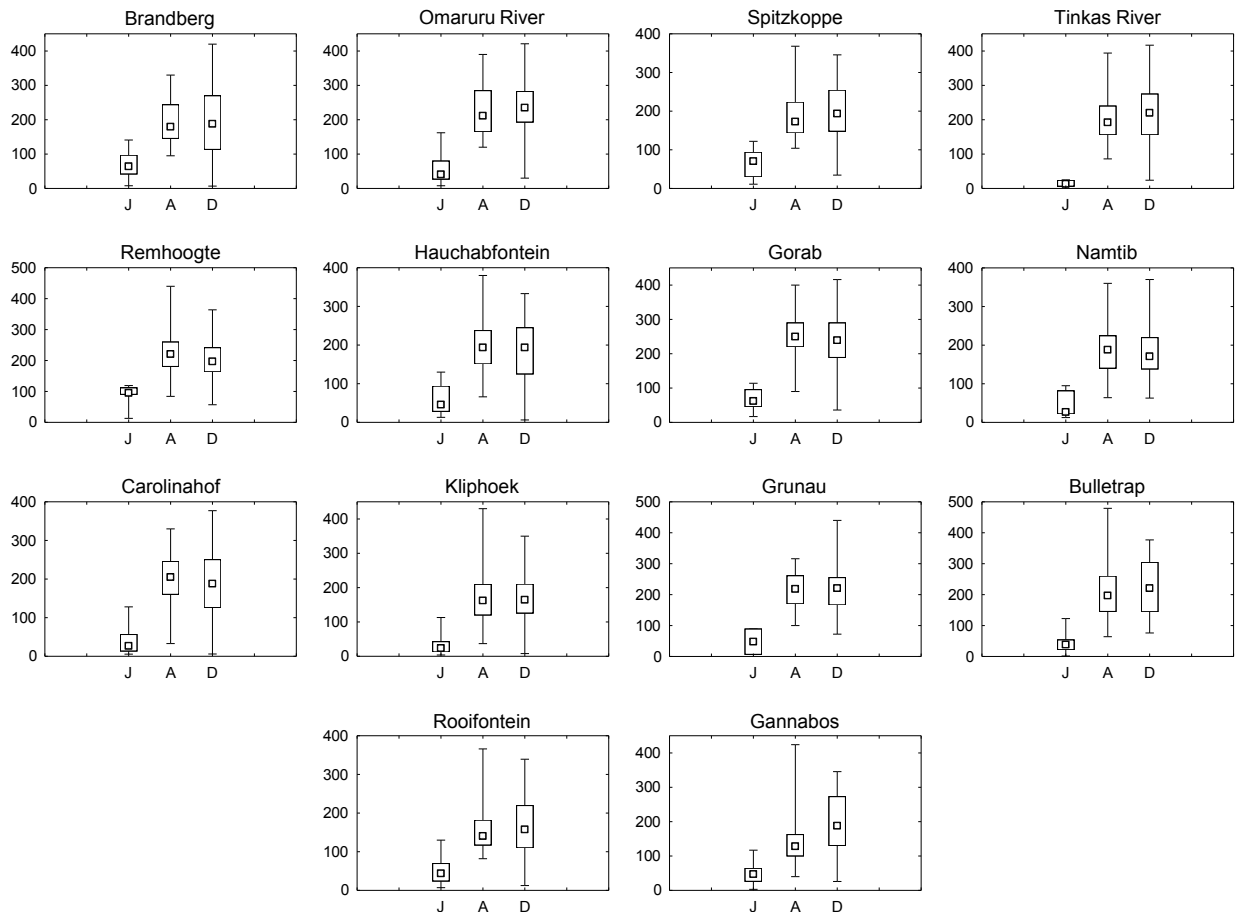
Fig. 10. Box and whisker plots indicating the median (small box), 25th and 75th percentile (large box), and maximum and minimum values (whiskers) for the basal circumference (in cm on y-axis) of each of the three age classes (x-axis: J=juvenile; A=adult; and D=dead) at each site. Graphs arranged in latitudinal order from north to south, read horizontally (i.e. top left to bottom right).

In an analysis of recent and non-recent death on opposite aspects (Fig 11), several equatorward sites either failed to meet the minimum number of dead individuals required on either northern or southern aspects, or had a total absence of dead trees on one of these aspects. This meant that it was not possible to determine which of northern or southern aspects contributed most to mortality at equatorward sites.

Nevertheless, Fig. 11 again illustrated that mortality fell predominantly into the non-recent 'time since death' category. In addition to this, recent mortality was generally dominant on southern aspects at poleward sites, while non-recent mortality was greater on northern aspects in the southern-central part of the distribution.

Recent death (cat. 1-3)

'Non-recent' death (cat. 4-6)
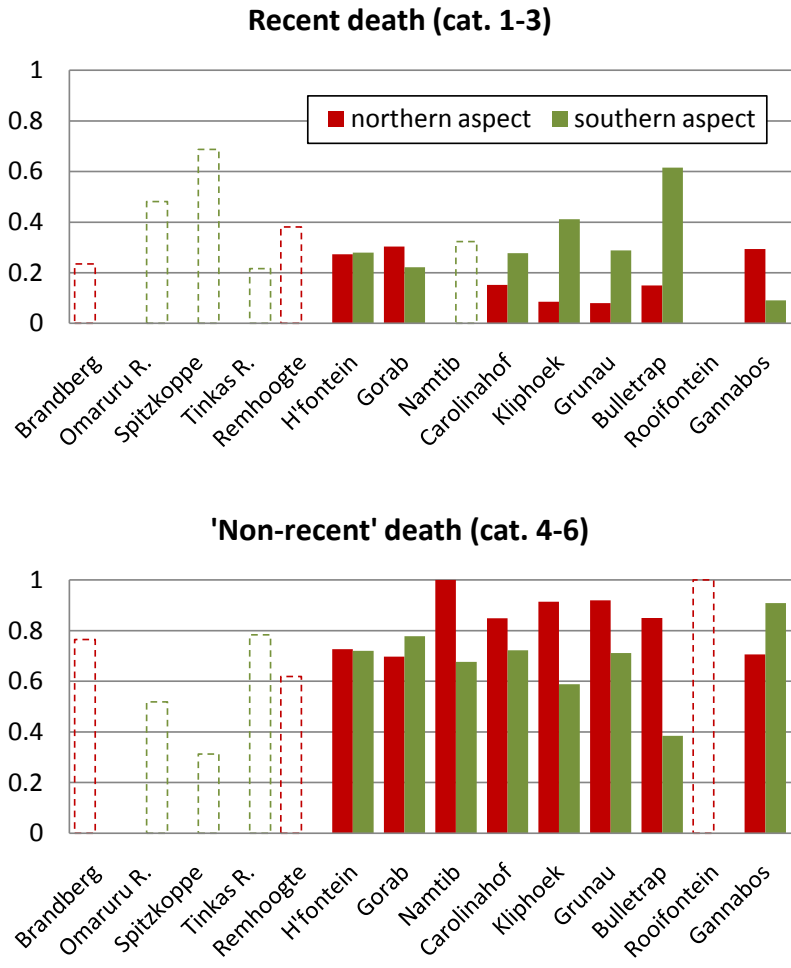
Fig. 11. Proportional representation of 'time since death' on northern and southern aspects categorised into recent (cat. 1-3 or 0-20 years old) and non-recent (cat. 4-6 or 21-60+ years old) death. Dashed bars represent aspect populations which did *meet the minimum requirement for inclusion (≥10), but for which the opposing aspect failed to satisfy this requirement.*

4.4 Discussion

4.4.1 Aspect preference

Data from both the roadside mega-transect and the population level survey suggests a clear pattern of *A. dichotoma* preference for cooler southern aspects at the equatorward limit and along the eastern margins of the distribution, as well as warmer northern aspects at poleward sites. In addition, the low density or absence of individuals on northern aspects at several equatorward sites, as well as the disparity in average distance between individuals growing on northern versus southern aspects at these latitudes, is evidence that the direct and indirect effects of solar radiation are more acutely felt at equatorward sites. This observation is supported by an analysis of average altitude, which indicates that, for equatorward sites, northern aspect populations are often at higher elevations than those found on southern aspects.

Conversely, whilst displaying a consistent preference for northern aspects, poleward populations within both summer and winter rainfall zones, do not vary greatly in terms of average distances between individuals on either northern or southern aspect (with the exception of Bulletrap), or indeed in terms of altitude between opposing aspects. This suggests that while northern aspects are still more favourable for poleward populations, it would appear that the ameliorative effect of cooler southern aspects provide a comparatively greater advantage to equatorward populations. These observations of aspect preference lend credence to Foden *et al.*'s (2007) assertion that equatorward populations are closer to their 'critical physiological thresholds'. In addition, the different altitude at which certain north and south facing populations occur suggests that this factor plays an important ameliorative role for *A. dichotoma* at climate extremes.

The beneficial effect of cooler southern aspects at the equatorward extreme (with a consequently reduced evaporative demand) is not unique to *A. dichotoma*, having been reported for many plant species across several vegetation types (e.g. Holland & Steyn, 1975; Rolland & Schueller (1996) in Theurillat & Guisan, 2001; Lennon *et al.*, 2002; Lesica & McCune, 2004). For example, commenting on vegetation patterns near Pietermatirtzburg at 30°S, Aitken (1922) noted that closed canopy bush was restricted to southern aspects, while open tree veld characteristic of drier conditions, occurred on northern aspects.

Similarly, northern hemisphere succulent species such as *Carnegiea gigantea* and *Ferocactus acanthodes*, and others growing in a comparably arid environment, indicated a preference for

warmer equatorward aspects at poleward range margins (e.g. Ehleringer & House, 1984; Pierson & Turner, 1998; Bullock *et al.*, 2005). Pierson & Turner (1998), for example, suggested that *Carnegiea gigantea* preferentially colonised southern aspects at their northern range margins, due to the increased frequency of freeze events. However, studies spanning the full latitudinal range of species - especially as widespread as *A. dichotoma* - are rare, and consequently comparisons between relative aspect preferences at latitudinal range margins are uncommon (Parmesan, 2006), making this study quite novel.

In certain respects, the above observations of aspect preferences in *A. dichotoma* at the extreme margins of the distribution are incongruent with findings from the previous chapters, which suggest climate extremes not only at range margins, but also within the Gariep River valley in the southern third of the distribution. This discrepancy can be accounted for by the coarse sampling resolution in the population level survey and the absence of any suitable populations to sample within the more rugged areas of the Gariep River valley. However, the closest sampled population to the Gariep River, Grunau, had a highly left-skewed demographic profile (Fig. 8), suggesting that it faced similarly deleterious conditions to those at the equatorward extreme.

The roadside mega-transect didn't indicate an obvious preference for any aspect within the Gariep River valley, except perhaps a slight favouring of west facing slopes. Reasons for this also relate to the extreme ruggedness of the terrain and the lack of a road network sufficient to capture a representative number of populations on all aspects. However, observations suggest that most populations are old and scraggly, thinly scattered and occurring at high elevations (relative to the road). This indicates a preference for cooler conditions (analogous to colonization of southern aspects), but the general age of individuals suggests that this up-slope shift has not occurred recently.

4.4.2   Solar radiation, age class relationships and aspect

Despite some variability, the difference in solar radiation on northern and southern aspects does not change markedly with latitude; the difference between aspects for populations at the same latitude being twice as great. Yet, for *A. dichotoma*, there are clearly observable aspect preferences at the equatorward and poleward limit of the distribution. This suggests that, while important, solar radiation is probably not the primary cause for differential aspect suitability evident at latitudinal extremes. Instead, it is likely that solar radiation acts in concert with other factors, such as local climate and biotic influences, and that the effects of solar radiation are only

expressed when these additional environmental factors force *A. dichotoma* closer to its threshold tolerance limits. Moreover, the importance of these additional factors are likely to vary across a species' geographical range, making it possible for different suites of climatic and biotic factor to control the species' equatorward and poleward range limits (e.g. Theurillat & Guisan, 2001; Lennon *et al.*, 2002).

Despite the likely influence of factors other than solar radiation on demographic patterns, juveniles did emerge as having a reasonably strong relationship with solar radiation, but only below and above threshold values corresponding to southern and northern aspects, respectively. The juvenile relationship with higher levels of solar radiation was even stronger when the anomalously high elevation, high rainfall, Brandberg population was removed from the analysis (improving the R^2 value from 0.28 to 0.75). This tighter coupling between solar radiation and juvenile proportional representation was not surprising, as the juvenile life history stage has also been recognized as the most climatically sensitive within similarly arid systems (Shreve, 1917; Steenbergh & Lowe, 1969; Jordan & Nobel, 1979; Jordan & Nobel, 1981).

Historically, water limitation in arid systems was seen as the primary control in seedling germination and establishment (Noy-Meier, 1973). However, in subsequent work, temperature minima and maxima have been found to exert an important influence on seedling survival in functionally similar species, both in terms of physiological tolerance limits but, more importantly, in terms of the indirect implications for plant water relations (e.g. Jordan & Nobel, 1979; Nobel, 1984; Drezner, 2004). For example, due to the small size of juveniles, their surface-area-to-volume ratio is high, thus exposing them to potentially faster evapo-transpiration rates compared to larger individuals (Turner *et al.*, 1966; Jordan & Nobel, 1979; Jordan & Nobel, 1981). Water stress due to higher temperatures is also exacerbated by the proximity of juvenile individuals to the soil surface, where maximum temperatures can be several degrees higher than half a metre above the surface (Nobel, 1984). This is likely why microhabitats such as rock crevices and nurse plants are so critical to juvenile survival directly after germination and during drought events, as has been reported for functionally similar species in arid environments (e.g. Turner *et al.*, 1966; Steenbergh & Lowe, 1969; Jordan & Nobel, 1979).

Juvenile sensitivity, specifically to maximum temperatures, points to the likelihood of the juvenile *A. dichotoma* age class responding disproportionately to the effects of recent, anthropogenically driven temperature increases and the impact that this would have on soil moisture and evaporative demand. However, the distinction in the response of different age

classes has not been made explicitly. Future studies would therefore do well to assess the physiological thresholds of the juvenile age class in more detail.

A positive response to higher levels of solar radiation at the lower end of the spectrum suggests that minimum temperatures have also constrained recruitment and establishment on cooler southern slopes. This is accentuated by generally steeper slope angles on which southern populations occur (not shown), which further reduced levels of received solar radiation. Freeze related mortality is well documented for juveniles in functionally similar Sonoran Desert succulent species (Steenbergh & Lowe, 1969; Nobel, 1980; Parker, 1993), especially at the poleward extreme (Niering *et al.*, 1963). The same enlarged surface area that makes juveniles vulnerable to desiccation also makes them more prone to freezing than adult individuals (Nobel, 1980; Pierson & Turner, 1998). Interestingly, Drezner (2007) found that nurse plants, commonly thought to protect seedlings against maximum temperatures, also help raise minimum temperatures, thereby affording seedlings some protection from freeze events. While frequent or prolonged periods of sub-zero temperatures are uncommon anywhere within the distributional range of *A. dichotoma*, frosts do occur along the southern and eastern range margins (Schulze, 1997). And while mortality, as a result of freeze events, has not been previously reported for the species, it is likely that minimum temperatures, as a result of local climate and low solar radiation, help delineate the southern, and possibly eastern, range limits.

Given the resilience displayed by adult *A. dichotoma* in the preceding chapter, it was not surprising that the adult *A. dichotoma* age class was comparatively unresponsive across the full spectrum of solar radiation values. This suggests that the contribution solar radiation makes to elevating temperature, and consequently lowering plant water balance, has little effect on this age class. This is likely due to the buffering provided by greater water storage capacity and reduced surface-area-to-volume ratio in adult individuals, which reduces evapo-transpirational water loss relative to juveniles (e.g. Turner *et al.*, 1966). The shallow rooting characteristic of the succulent growth form is another advantage in that it enables the rapid capture and storage of a disproportionate amount of rainfall from both light and heavy showers (e.g. Chesson *et al.*, 2004; Ogle & Reynolds, 2004). This has contributed to the characteristic 'uncoupling' of adult individuals from small climatic perturbations, as has been reported for the closely related sub-species, *A. pillansii* (Duncan *et al.*, 2006) and for the functionally similar saguaro of south-western North America (Jordan & Nobel, 1979; Turner, 1990; Bowers & Turner, 2001).

Trends in mortality with respect to solar radiation were intuitive in the sense that mortality was proportionally higher at extremely low and high solar radiation levels. When the Brandberg population was removed the R^2 value again improved (from 0.07 to 0.23), and the trend line steepened, suggesting that mortality was more tightly coupled to temperature maxima, rather than minima. However, variation between populations meant that R^2 values were generally low, making it difficult to interpret results.

While a relationship between solar radiation and the proportional representation of juveniles or dead individuals may seem reasonable, one need bear in mind the potential confounding influence arising from a disparity between the relative abundance of juvenile or dead individuals within populations in respective rainfall zones. For example, winter rainfall zone (WRZ) sites generally have higher juvenile densities and lower mortality, while the opposite is generally true for summer rainfall zone (SRZ) sites. However, a higher proportion of juveniles, for example, could be due to other factors, such as winter rainfall consistency, and not solar radiation. A similar argument could be made for low proportional mortality values. However, this explanation fails to account for strong aspect preferences at range margins, as local climate (e.g. rainfall) is unlikely to result in the favouring of one aspect over another.

4.4.3   *Effect of solar radiation on demographic patterns*

Despite a good relationship between solar radiation and juvenile proportional representation and a weaker relationship for mortality, these associations were not obvious in an assessment of the relative proportions of the different age classes on northern and southern aspects across the full range of solar radiation values. This is suggestive of a poor capacity in *A. dichotoma* to adapt to recent changes in climatic conditions (after Dawson *et al.*, 2011). This is also surprising, given the significant difference in solar radiation received on opposing aspects at comparable latitudes. Interpretation of equatorward aspect preference was also rendered more difficult by the absence or relative scarcity of individuals on one of either southern or - more frequently - northern aspects at several sites. If, however, one makes the reasonable assumption that absence or scarcity on an aspect implies aspect unfavourability, and one considers the more populated aspect more favourable, then there is some justification for concluding that southern aspects are generally more preferable at the northern latitudinal extreme.

Remhoogte, just north of 24°S, represents a singular and obvious puzzling reversal of the above trend. The population is located on a north facing slope within a deep escarpment valley. A road bisecting the north and south facing slopes in the valley also divides land ownership. There are

several possible explanations for the anomalous aspect preference, including a) an unusually cool microclimate, which may restrict recruitment on cooler southern aspects due to frost, b) consistently greater showers on northern aspects resulting from an interaction between the local orography and the direction of arrival of rain-bearing clouds, and c) a possible anthropogenically mediated disequilibrium, arising from an inability to recruit on southern aspects (e.g. grazing pressure due to different land use/stocking rates on opposing aspects).

At the poleward end of the distribution there was no consistent preference for aspect amongst individual age classes in the population level survey, despite a clearly observed preference for northern aspects in the roadside mega-transect, and a reasonable relationship between solar radiation and (especially) juvenile proportional representation. This is puzzling, but probably has to do with the low number of sampled WRZ populations and the inherent variability across small spatial scales. However, it should also be noted that the WRZ climate has been shown to be relatively benign in comparison to the SRZ (e.g. Kaleme, 2003), resulting in a more uninterrupted *A. dichotoma* distribution, and generally less of a disparity between the suitability of northern versus southern aspects (as can be seen in Fig. 5, with the exception of Bulletrap). In light of this, one should expect to see more muted responses in the preference for opposing aspects from individual age classes when compared to the SRZ.

The effect of solar radiation appears to be especially important at climatic extremes, but in many cases it is difficult to make a comparison between opposing aspects because the more climatically deleterious aspect is not populated (e.g. Brandberg, Tinkas River). This could be because a shift to a more benign aspect, and/or a contraction on an unfavourable aspect, could have been catalysed long ago. In this respect, *A. dichotoma* life history characteristics have the potential to further confound interpretations of aspect preference trends by introducing lag effects and disequilibria. For example, because the duration of the adult age class can span 150 years or more (Kaleme, 2003), and is considerably more resilient to environmental perturbations than the juvenile age class, it can persist in a landscape or on an aspect which has become climatically unsuitable for recruitment.

Moreover, given a 'trickle' of background recruitment due to the presence of suitable microsites (e.g. Lennon *et al.*, 2002; Matthes & Larson, 2006) and nurse plants, or occasional recruitment of larger cohorts during good rainfall seasons, this persistence can last for many generations, resulting in populations in a state of prolonged disequilibrium (e.g. Sprugel, 1990) or very gradual decline (Magnuson, 1990; Jackson *et al.*, 2009). This persistence might also be the result

of evolved adaptive capacity, where traits such as genetic diversity, phenotypic plasticity and dispersal and colonizing ability, which promote *in situ* persistence, have been preferentially selected (after Dawson *et al.*, 2011). This might also help explain why there is so much variability in demographic patterns and aspect preferences which remains unaccounted, and also highlights the risk in snap-shot sampling, which may give the misleading impression that the demise of populations has been a recent phenomenon.

4.4.4   Mortality: when, where, and to whom?

The temporal element to *A. dichotoma* mortality was a notable omission in previous studies (e.g. Foden *et al.*, 2007), which made no distinction between recent and non-recent mortality, effectively assuming all dead individuals were the result of recent climate change. In this respect, the development of a 'time since death' index in the current study provides a novel and useful, though approximate, technique for gauging the temporal nature of mortality, and hence to what degree recent changes in climate have contributed to mortality. This technique has been given some credence through its use in classifying recent versus non-recent mortality in a similarly arid adapted species in the Sonoran Desert (Bowers & Turner, 2001).

While previous estimates have suggested that skeletons can persist *in situ* for several years, or even decades (e.g. Foden *et al.*, 2007; Midgley *et al.*, 2009), new evidence from repeat photographs indicate that in certain instances skeletons can remain visible for much longer periods of time; sometimes more than a century. This is perhaps not surprising when one considers that the hot, dry environment which characterizes much of *A. dichotoma's* range would necessarily produce very slow rates of decay (Foden & Stuart, 2009). With the aid of the 'time since death' classification, the persistence of dead skeletons makes it possible to link pervasive mortality with known periods of drought, for example.

Results from the current study indicate quite clearly that recent mortality has contributed very little to overall mortality at most sites across the latitudinal distribution range and that the highest proportion of dead individuals fall within categories 4 and 5 (i.e. died between 20 and 60 years ago). Contrary to previous findings increased recent mortality at the equatorward end of the distribution was not observed.

In addition to this, the median girth of dead individuals was found to match closely with that of the adult age class and differ significantly from the juvenile age class in all but one population. The implication of this is that mortality is derived predominantly from the adult age class and

not the juvenile age class. This is contrary to what one would expect if climate change was having an impact, as the juvenile age class has been shown to be more sensitive to environmental perturbation in this species (current study), as is the case with the closely related sub-species, *A. pillansii* (Duncan *et al.*, 2006), and other functionally similar species in arid environments (e.g. Shreve, 1917; Steenbergh & Lowe, 1969; Brum, 1973; Jordan & Nobel, 1979; Nobel, 1980; Pierson & Turner, 1998).

Besides inherent assumptions about decay rates in the 'time since death' technique, there exist possible alternative explanations for the observed higher frequency of non-recent deaths and the resultant significant relationship between adult and dead girth measurements. These alternative explanations are addressed below. Because of the larger size and smaller surface-area-to-volume ratio of adult individuals relative to juveniles, they probably persist for longer periods of time in the landscape, effectively accumulating whilst smaller individuals decay more quickly. This might have led to the result in the current study indicating mortality skewed towards the adult age class. However, while the accrual of larger dead individuals through time is likely, the 'time since death' index provides an assessment of whether observed mortality – adult or juvenile - is of recent origin or not. Despite the likelihood of a persistent signal from slowly decaying adults, one should nevertheless expect a recent surge in mortality if anthropogenic climate change was the primary cause, but there was little evidence for this.

Furthermore, given the sensitivity of the juvenile age class when compared to adults, one should perhaps expect a steadily increasing accumulation of juvenile (rather than adult) *A. dichotoma* mortality in light of a recent progressive deterioration in climate. 'Time since death' and mortality age class derivation datasets, as well as detailed field observations, simply did not support this, yielding virtually no examples of juvenile mortality due to rosette abscission and very little recent adult mortality. With respect to juvenile deaths, only a very small proportion could *not* be confidently attributed to damage caused by herbivory or disease.

A further explanation for the lack of a juvenile mortality signal was that there had not been any significant recruitment events over several preceding decades, possibly in response to temperature increases due to climate change. There is mounting evidence in support of the prior view (e.g. Acocks, unpublished (see Rutherford *et al.*, 2003); Hoffman *et al.*, 2010), but little evidence for a causal link to the latter, unless the effects of anthropogenic climate change were already having a profound effect on recruitment dynamics prior to the 1950s, which seems unlikely.

While instrumental records indicate that temperatures in the region have been increasing steadily from the 1960s (e.g. Kruger & Shongwe, 2004; Midgley *et al.,* 2005[a]; Midgley *et al.,* 2005[b]; Warburton *et al.*, 2005; Hoffman *et al.*, 2011; this study), there are few records prior to this (see Chapter 2), although Hansen *et al.* (2006) suggests a global temperature surge only post 1980 (Hansen *et al.*, 2006). Moreover, attribution of rainfall variability within the first half of the 20th century has not been ascribed to climate change (Fauchereau *et al.*, 2003; Hoerling *et al.*, 2006). It may therefore be more parsimonious to argue that natural climatic fluctuations, which likely precluded recruitment in the first half of the 20th century, or before, have persisted during the second half of the 20th century, with a possible additional influence of increased temperatures.

Lastly, despite the exclusion of several equatorward sites due to insufficient numbers on aspects under investigation, the relationship between northern/southern aspect and 'time since death' was fascinating in the sense that it was entirely counter-intuitive. As mentioned previously, there was a general predominance of non-recent deaths (21-60+ years ago), but this was concentrated on northern aspects, while southern aspects at the poleward end of the distribution almost invariably contained more recent deaths (0-20 years ago). This was contrary to expectations, given that an increase in temperature during the 20th century would theoretically have made south facing slopes at the poleward end of the distribution increasingly favourable. There was no clear explanation for this aspect pattern in mortality, but it did suggest that recent temperature increases have not catalysed a southward expansion of the species.

In summary, the above findings indicate that while it is possible for water stress resulting from incremental temperature increases to have resulted in widespread mortality in equatorward (and other marginal) populations, there is very little evidence from both climate and demographic data to suggest that this has occurred recently. The characteristic 'spikes' in the frequency of mortality in certain non-recent 'time since death' categories suggests instead that adult mortality could be a result of old age, when populations which have recruited in cohorts age and die synchronously, possibly in response to severe drought spells. Pulsed recruitment that would result in this kind of synchronous death has been suggested for *A. dichotoma* (Kaleme, 2003; Hoffman *et al.*, 2010), as well as its sister species, *A. pillansii* (Duncan *et al.*, 2006), and is well documented for certain arid adapted species in the Sonoran Desert of south-western North America (Jordan & Nobel, 1982; Parker, 1993; Bowers & Turner, 2001; Bullock *et al.*, 2005).

In addition, adult *A. dichotoma* mortality which could *not* be ascribed to old age was observed to be predominantly the result of physical damage or disease (personal observation). Geldenhys & Swart (2009) similarly attributed mortality in the quiver tree forest at Kenhardt, in the Northern Cape, to insect damage and disease, while Midgley *et al.* (1997) and Jankowitz (1972) suggested physical damage by baboons and porcupines were important. In the current study the characteristic 'shoot-shedding' phenomenon associated with plant water stress in previous studies (Foden *et al.*, 2007) could often be ascribed to physical damage by baboons, ungulates and – especially - one or more species of aphid and/or borer beetle (E. Swart, pers. comm.; personal observation). Aphids and borer beetles are common and attack the fleshy base and heart of the rosette and eventually cause it to abort, leaving damage which often heals into a smooth, tapering stump. While it is possible that insect or pathogen attack could result indirectly from impaired plant defences due to, for example, water stress, this was deemed unlikely due to the ubiquity of these factors in populations throughout the latitudinal range. However, little seems to be known about the mechanisms underlying rosette abscission, and it would be useful for future research to investigate this phenomenon more thoroughly.

While the above findings do not support a recent response in *A. dichotoma* to anthropogenic climate, our poor understanding over the exact nature of physiological responses to temperature and moisture gradients in different life history stages is a critical limitation. Given the myriad abiotic and biotic influences operating within the geographical distribution of *A. dichotoma* at different spatial and temporal scales, natural populations are probably not ideal for studying subtle physiological thresholds in different age classes. Instead controlled experiments under a gradation of moisture and temperature regimes would provide a better platform through which to gain insight into the relative importance of these climatic variables, and consequently, the likelihood of a response within natural populations to recent climate change.

Synthesis

5.1   Rationale for the study

In the context of a rapidly changing global climate due to temperature increases resulting from anthropogenic CO_2 emissions, the iconic arborescent succulent, *A. dichotoma*, has emerged as a southern African indicator species (Foden *et al.*, 2007). It has been cited as the first such example for the region, and one of very few in the southern hemisphere (Hughes, 2003; Parmesan, 2006). This is cause for concern, not only because of the wealth of biodiversity within south-western Africa (e.g. Cowling *et al.*, 1998; Cowling *et al.*, 1999; Desmet & Cowling, 1999; Myers *et al.*, 2000) which is potentially under similar threat, but also because of high rates of predicted future climate change in the region (Thuiller *et al.*, 2006[b]; Boko *et al.*, 2007; Haensler *et al.*, 2011).

Foden *et al.* (2007) suggested that *A. dichotoma* populations at their equatorward range limit were closer to their physiological tolerance limits than more southerly populations and were being pushed beyond critical climate thresholds due to increased temperatures and a concomitant reduction in water balance, resulting in higher equatorward mortality rates (Foden *et al.*, 2007). Although this was counterbalanced by burgeoning poleward populations under a more benign climate, northern decline was reportedly exceeding southern expansion due to slow dispersal rates, resulting in a latitudinal constriction of the distribution, and consequently, concern over the long-term future of the species in the region (Foden *et al.*, 2007).

However, several strands of evidence suggest that the role of recent anthropogenic climate change may not be central in the apparent decline of *A. dichotoma* at northern range margins and elsewhere within the distribution (e.g. Jurgens *et al.*, 1997; Burke, 2004). Historical photographs from the early to mid 1900s (Hoffman *et al.*, 2010) and detailed botanical fieldnotes (Acocks, unpublished (see Rutherford *et al.*, 2003)) from *ca.* 1950 suggest that many populations within the southern-central part of the distribution experienced significant mortality and little to no recruitment prior to or during this period.

The skeletons of many *A. dichotoma* individuals which died during this early period of the 20th century are likely to have persisted *in situ* as a result of their highly fibrous composition and slow rate of decay in a generally arid environment (e.g. Foden *et al.*, 2007; Midgley *et al.*, 2009). It therefore seems plausible that much of the mortality recorded by Foden *et al.* (2007) might

have originated prior to the 1950s, possibly in response to severe drought conditions in the 1930s and 1940s (Hoffman *et al.*, 2010), or even before this. By expanding the sampling effort and distinguishing between recent and non-recent mortality, and between more resilient adults versus more climatically sensitive juveniles, the current study can achieve a clearer understanding of the role of recent anthropogenic climate change in relation to *A. dichotoma* mortality.

The previously reported linear increase in mortality from the poleward to equatorward extreme of the distribution was based on a limited sample of northern populations, and does not represent the high degree of latitudinal variability in mortality. Similarly, climate was implicitly assumed to follow the same gradient, becoming progressively more unfavourable as one moved northwards (Foden *et al.*, 2007), which is not necessarily the case. In addition, a water balance deficit – thought to be the main cause of equatorward mortality – was derived from a dataset with a relatively short duration (average of 32.6 years for Namibian stations), and by means of the controversial Thornthwaite (1948) equation, which relies solely on temperature to derive a measure of evaporative demand (Hobbins *et al.*, 2008; Dai, 2010). Finally, the effects of water stress on *A. dichotoma* physiology with respect to critical thresholds or rosette abscission - proposed factors accounting for mortality - remain unstudied.

The current study was thus prompted by the need to further investigate interpretations and assumptions made in previous studies, given the significant policy and management implications of declaring a species as an indicator of climate change. By taking into account evidence from the historical record and a more detailed investigation of demographic patterns, it is hoped that we can advance our understanding of the patterns and processes involved in shaping them.

5.2   Summary of key objectives

In revisiting *A. dichotoma*'s suitability as a climate change indicator, the current study had three main objectives. The first was an assessment of historical climate, both in terms of average conditions as well as trends through time. This was done to gauge the exposure of *A. dichotoma* to recent climate change (after Dawson *et al.*, 2011). Whilst the historical climate of the region has been investigated, large-scale studies have either been insufficiently detailed, or the geographical focus not well aligned with the current extent of *A. dichotoma*'s range. My approach focused on the contemporary distribution and aimed to characterise climatic trends rather than produce a composite measure of plant water stress, for which the requisite climatic variables (for the calculation of an unbiased metric) are not available in the region in which *A.*

dichotoma occurs. This approach allowed for the use of a greater number of climate stations, as well as longer records, resulting in a more comprehensive illustration of climate within *A. dichotoma*'s distribution.

The second objective was the construction of a comprehensive demographic map for the species by means of roadside sampling (i.e. the mega-transect). This provides a more detailed account of demographic patterns across the latitudinal gradient and investigates whether mortality, for example, follows a linear latitudinal gradient, as previously suggested by Foden *et al.* (2007). The spatially referenced demographic map also allows for the extraction of a very high resolution interpolated climate surface (Hijmans *et al.*, 2005) for the species' distributional area. This climate surface is then used to gauge the latitudinal linearity of climate variables, as well as the strength of the relationship between key biologically relevant climate variables and individual age classes, in order to analyse sensitivity of *A. dichotoma* age classes to climatic conditions (after Dawson *et al.*, 2011). A generally poor relationship between contemporary climate and *A. dichotoma* demographic patterns would suggest an uncoupling with modern climate, including anthropogenic impacts, and indicate a possibly greater influence from other factors not previously considered.

The third aim was to investigate the influence of different solar radiation intensities on opposing aspects to determine its influence on the adaptive capacity in *A. dichotoma* with respect to recent climate change (after Dawson *et al.*, 2011). If, for example, recent mortality was noted in a population on a more deleterious aspect, and no recruits found on the more benign aspect, this would suggest a limited capacity to adapt to changes in climate in terms of dispersal or colonisation. Similarly, a failure to identify a shift in demographic indicators might suggest the capacity in *A. dichotoma* to cope with the effects of the most recent climate changes through, for instance, genetic diversity, phenotypic plasticity or life history traits (Dawson *et al.*, 2011). To identify possible recent changes in mortality, a technique was developed for gauging the approximate 'time since death' of skeletons. In addition, girth measurements were recorded on living and dead individuals to determine which age class contributed most to mortality.

5.3   Summary of key findings

5.3.1   *Historical climate within* A. dichotoma's *distribution*

5.3.1.1 Rainfall

The pattern in average rainfall and rainfall variability within *A. dichotoma*'s distribution is spatially complex, with no clear latitudinal gradient, even *within* rainfall zones. The equatorward extreme of the distribution is not obviously drier when compared to more

southerly latitudes, as previously inferred by Foden *et al.*, (2007). For example, Onseepkans, located within the Gariep River valley, has rainfall variability similar to inland stations further north east, but *lower* average annual rainfall, making it the inland station with the most critical moisture deficit across the full latitudinal extent.

Historical trends in rainfall are generally difficult to interpret because of considerable spatial and temporal variability, especially within the Namibian section of the SRZ. This is generally less of a problem within the winter rainfall zone (WRZ) and South African section of the SRZ, due to a more consistent annual climate and slightly better station coverage. Southern stations in both the summer and winter rainfall zones appear to have rebounded from an initially dry first half of the 20th century, to end with a positive rainfall trend over the full length of the record. This switch from drier to wetter conditions was reflected in the SPI analysis, which registered a modest positive trend for all South African stations, with the exception of Springbok. Average decadal rainfall change also increased modestly at most South African stations (in both the SRZ and WRZ) by virtue of increased winter rainfall, while in most cases summer rainfall decreased.

Data were insufficient to get a clear picture of rainfall trends in the first half of the 20th century for the northern part of the SRZ, while a general declining trend is evident across several northern stations for the latter half of the century (du Pisani, 2001). However, trends were found to be highly dependent upon the length, specific period of time, as well as initial and terminal conditions of the record (du Pisani, 2001). In this respect, it should be noted that a key wet spell occurred during the mid 1970s, followed by two successive droughts in the early 1980s and 1990s. Declining northern summer rainfall may therefore be an artefact of these climatic events, which determine the linear trend over this short time-frame. The above point is well illustrated by a study investigating climate trends within the same area for the period 1981-2006, which concluded that there had been a general *wetting*, rather than drying trend (Haensler *et al.*, 2010). In addition, the arrival of widespread, unusually wet conditions in Namibia since 2005 (e.g. Menges, 2009; Menges, 2011), which are not well reflected in Namibian rainfall records – many of which terminate in the mid-1990s and early 2000s - add further complexity to understanding the long-term rainfall trajectory for the northern SRZ.

5.3.1.2 Temperature

Average historical temperature patterns do not vary as markedly as rainfall, though changes were often quite dramatic over short distances. Generally, the cooling influence of the Atlantic Ocean caused temperature clines to be significant along a west to east axis, while latitudinal temperature change was more muted across the distributional range. The combination of these

two gradients suggested a broad pattern of increasing average temperature as one moved inland and northwards. Records from Clanwilliam and Windhoek were notable exceptions to this pattern; the latter due to high elevation. However, in addition to these exceptions, the paucity in stations recording temperature may conceal other areas of extreme temperatures. This was illustrated by the latitudinally averaged interpolated climate surface extracted from Bioclim (Hijmans *et al.*, 2005), which indicated peaks in temperature within the Gariep River valley and at the equatorward limit.

Almost all stations registered a steady increase in temperature over the recording period (e.g. Midgley *et al.*, 2005[b]; Foden *et al.*, 2007). Decadal increases were often quite pronounced within the SRZ (between 0.23°C and 0.29°C) and more muted for the WRZ (0.09°C), although the latter increase was derived predominantly from increases in summer temperatures. It was not obvious why there should be such a disparity between decadal increases in the summer and winter rainfall zones, but these finding were consistent with studies that have indicated greater increases in maximum temperatures, which typically occur in summer (e.g. New *et al.*, 2006).

5.3.1.3 *A. dichotoma* exposure to climate change

In light of *A. dichotoma*'s posited northern demise due to recent climate change, a pertinent question would be to what degree observed changes in rainfall and temperature can be attributed to anthropogenic CO_2 forcing. Although a comprehensive answer to this question is outside the scope of the current study, present evidence suggests that changes in southern African precipitation cannot be attributed to an anthropogenic cause with much confidence (Hoerling *et al.*, 2006). However, the same is not true for temperature, which is more directly linked to anthropogenic CO_2 emissions and has been rising steadily as a consequence (e.g. Hansen *et al.*, 1981; Stott *et al.*, 2001). Rising temperatures may exceed the thermal tolerance of plants (e.g. Musil *et al.*, 2005; Musil *et al.*, 2009), but the link with water balance through evaporative demand appears to be more complex. For example, Hoffman *et al.* (2011) found that, in spite of increased temperatures, A-pan evaporation had actually declined within the Cape Floristic Region in South Africa between 1974 and 2005, in spite of significant decadal increases in temperature.

The complex nature of rainfall trends and declining A-pan evaporation associated with rising temperatures make it difficult to interpret the results in the context of *A. dichotoma*'s exposure to climate change (after Dawson *et al.*, 2011). Conditions are predicted to become increasingly hot and dry, especially in Namibia (Haensler *et al.*, 2011). For *A. dichotoma*, this is likely to result in increased exposure to climate change within climatically marginal areas like the Gariep River

valley and possibly at the equatorward extreme. However, the spatial and temporal coverage of instrumental records informing this analysis and used in making future predictions (e.g. Haensler *et al.*, 2011) remain poor, especially in mountainous, hyper-arid areas in Namibia identified as key marginal *A. dichotoma* habitats. These shortcomings in the historical record will continue to make it difficult to link changes in climate with shifts in demographic indicators such as recruitment and mortality. A more extensive network of climate stations within more marginal areas of *A. dichotoma*'s distribution would therefore greatly aid our understanding of species' exposure and response to climate change.

5.3.2 *Demographic patterns and contemporary climate*
5.3.2.1 Latitudinal mortality gradient
The roadside mega-transect revealed that mortality does not follow a straightforward equatorward latitudinal cline as had previously been suggested by Foden *et al.* (2007). Instead, averaged half degree bands emphasise a pattern of considerable latitudinal (and longitudinal) demographic variability and indicate that proportionally, mortality is greatest within the Gariep River valley, within the southern third of the distribution, and not at the equatorward extreme. This is in agreement with the findings of the historical assessment of climate in Chapter 2, which indicates that the Gariep River valley is likely to be the most climatically deleterious area within the distribution. In addition, while high WRZ juvenile densities illustrate the favourability of the poleward range extent, there is not a simple equatorward latitudinal decrease. For example, juvenile proportional density falls sharply within the Gariep River valley and within the northern 'tail' of the distribution before recovering at the equatorward extreme.

Altitude undoubtedly provides some ameliorative effect for *A. dichotoma* individuals occurring at latitudes which experience high heat and water stress. However, there are instances in which altitude cannot account for the more complex patterns in *A. dichotoma* demography. For example, within the SRZ the relationship between proportional juvenile density and altitude is counter-intuitive: juvenile density is lowest where altitude is greatest. Moreover, an equatorward population at approximately 23°S previously sampled by Foden *et al.* (2007), registered very low mortality despite occurring at a low elevation. (It was unfortunately excluded from their analysis due to suspected removal of dead skeletons by park rangers (W. Foden, pers. comm.)) In addition, populations which *do* currently occur at higher elevations at climatically marginal latitudes (such as within the Gariep River valley and at the Brandberg) are unlikely to have retreated upslope in response to recent climate change because these shifts would necessarily be very slow, given *A. dichotoma* growth and recruitment rates. Instead,

demographic profiles strongly suggest that high elevation populations have been established at these altitudes for some time.

The non-linearity of latitudinal demographic patterns is an important observation, which illustrates that habitat favourability should not be assumed to follow smooth clines from the centre to range margins. Instead, it should be recognised that environmental gradients accompanying large distributions are often complex, resulting in variable species density and health in space and time (e.g. Sagarin & Gaines, 2006; Sagarin *et al.*, 2006). As a result, factors that control the geographical limit of a species at one range boundary may not necessarily be the same factors that control species distributional limits in other parts of its distribution.

5.3.2.2 The summer-winter rainfall divide

The winter and summer rainfall zones dividing *A. dichotoma*'s distribution represent an important climatic disjunction which has not previously been considered when interpreting demographic patterns. Differences in, for example, the amount and consistency in rainfall between these two geographical areas are well established (Hoffman & Cowling, 1987; Cowling *et al.*, 1999) and were shown to be significant in the current study, resulting in a clear difference in the demographic profiles within each of the different rainfall zones. The SRZ typically has high mortality and declining juvenile density, while the opposite is true for the WRZ. These results are echoed in previous analyses of repeat photographs, which indicate a very different ratio of recruitment to mortality in populations on either side of the seasonal rainfall divide (Kaleme, 2003). This climatic disjunction and the confounding role that it might play in interpreting latitudinal mortality and recruitment dynamics was not considered in previous interpretation of demographic patterns in Foden *et al.* (2007), and may have resulted in different conclusions being drawn. For example, generally higher mortality rates and more infrequent recruitment in equatorward SRZ populations may not be the result of recent changes in climate, but rather due to a generally more hostile SRZ climate when compared to more benign climate experienced by poleward WRZ populations.

5.3.2.3 Demographic patterns, contemporary climate, and sensitivity in *A. dichotoma*

Despite employing the most spatially explicit demographic and climatic datasets (i.e. Hijmans *et al.*, 2005), and performing independent analyses for the climatically distinct summer and winter rainfall zones, the relationship between both single and multiple non co-correlated contemporary climatic variables and *A. dichotoma* age classes remains poor. Similarly, despite a strong observed aspect preference at the latitudinal distribution limits, the relationship between solar radiation (a proxy for temperature) and age classes, is weak. This is especially

true for patterns in mortality, which consistently have the poorest relationship with both climatic variables and solar radiation. This weakens the case – based on proportional mortality patterns, as in Foden *et al.* (2007) - for *A. dichotoma*'s use as an indicator of recent climate change.

Notwithstanding generally poor relationships, differing correlational strengths between individual and combined climate measures and juvenile and adult age classes *were* useful for investigating the comparative resilience of *A. dichotoma* during specific life history stages, as well as assessing broad strengths of association with measures of precipitation and temperature. The juvenile age class emerged as having the strongest and most significant relationships with contemporary climate variables and measures of solar radiation.

Operating at different spatial scales, the two sampling strategies indicated that both rainfall and temperature are important controls on juvenile abundance, especially at climatic extremes. However, results from the more detailed roadside mega-transect suggests that the amount and consistency of rainfall during the dry season (i.e. winter season in SRZ/summer season in WRZ) is especially important in maintaining juvenile abundance. Indeed, the importance of regular moisture inputs in juvenile survival is well documented in the literature on arid ecosystems (e.g. Noy-Meir, 1973), while unusually high rainfall events are known to promote recruitment pulses in functionally similar species in the Sonoran Desert (Shreve, 1917; Steenbergh & Low, 1969; Jordan & Nobel, 1979; Jordan & Nobel, 1981; Jordan & Nobel, 1982; Turner, 1990; Parker, 1993; Pierson & Turner, 1998; Drezner, 2004; Drezner, 2006). The same moisture-mediated recruitment pulse strategy is also suspected to be true for *A. dichotoma*'s sister species, *A. pillansii*, which has a significantly smaller distribution range within the westerns confines of the Gariep River valley (Duncan *et al.*, 2006).

In contrast to the juvenile age class, adult *A. dichotoma* density is generally greatest in areas in which climate is relatively harsh (e.g. higher rainfall variability and lower precipitation of the driest quarter). In addition, adult *A. dichotoma* individuals appear to be unresponsive to a gradient in solar radiation values, even at climatic extremes. This indicates a higher physiological tolerance threshold in adult individuals for unfavourable climatic conditions, and hence a reduction in sensitivity relative to the juvenile age class (after Dawson *et al.*, 2011). The resilience displayed by adult *A. dichotoma* individuals is not surprising, given significant water storage capability in succulent stem, branches and leaves, and life history traits which promote persistence. These characteristics ultimately allow adult individuals to survive through periods

in which climate is unfavourable (and in which juvenile individuals would likely succumb), affording these individuals the future chance to set seed and recruit into the next generation.

Given the above evidence, it is not surprising that juveniles display a greater sensitivity to contemporary climate. This response is aided by the fact that juveniles have necessarily been exposed to contemporary climate for a greater proportion of their life-spans when compared to adults, which can persist for up to 150 years (Kaleme, 2003). In addition, juveniles are generally known to be more sensitive to environmental perturbations such as drought or excessive temperatures, due to a high surface-area-to-volume ratio, shallow rooting depth, lower carbon reserves and reduced photosynthetic capacity (after Grubb, 1977; Jackson *et al.*, 2009), as has been found in other succulent and arid-adapted species, such as *Carnegiea gigantea* (Turner *et al.*, 1966) and *Ferocactus acanthodes* (Jordan & Nobel, 1981).

The current study therefore draws attention to the greater sensitivity of the juvenile age class and the likely influence of dry season moisture inputs in regulating juvenile health and recruitment pulses. However, because of generally poor relationships between climate variables and demographic indicators, uncertainty surrounding the exact influence of temperature and moisture gradients on juvenile *A. dichotoma* survival remains. Given the degree of variability in natural populations, a controlled experimental investigation of physiological thresholds in juvenile *A. dichotoma* individuals will greatly aid our understanding of the species' likely response to future climate change.

5.3.3   *The timing of mortality*
5.3.3.1 Time since death

If either direct or indirect effects of progressive warming due to recent climate change have catalysed *A. dichotoma* mortality, one would arguably expect a recent spike in mortality, as well as a disproportionate amount of this mortality to be derived from the more sensitive juvenile age class. However, an index developed specifically to gauge the 'time since death' of *in situ* skeletons clearly indicates that the majority of mortality occurred at least two decades ago, and in most cases well before this. Moreover, there is little proof that mortality has been any more recent within equatorward populations, which were considered more climatically marginal by Foden *et al.* (2007). These results improve upon and clarify previous work, which made no distinction between recent and non-recent mortality.

5.3.3.2 Age at death

In addition, basal circumference measurements (median, 25th and 75th percentile) of dead individuals were found to be significantly larger than live juveniles in all sampled populations (with the exception of Grunau, for which only two, relatively large juvenile individuals were present). Conversely, with the exception of Gannabos, the basal girth of dead and live adult individuals matched closely. (At Gannabos dead individuals were significantly *larger* than live adults.) These findings suggest that almost all death is derived from the larger, more climatically resilient adult age class; contrary to expectations, given narrower resilience thresholds and greater sensitivity in juveniles.

It is possible that higher decay rates of juvenile compared to adult skeletons (because of smaller size and larger surface-area-to-volume ratios in juveniles) would confound the 'age at death' interpretation by skewing results in favour of adult mortality. However, in a region which has supposedly seen a recent deterioration in climate favourable for *A. dichotoma* (i.e. within the last 30 years (e.g. Midgley *et al.*, 2009)), one should arguably expect an accumulation in juvenile mortality. There is little evidence for this, as juvenile skeletons were rarely observed. Moreover, in only a fraction of cases could juvenile death *not* be attributed to some form of physical damage such as uprooting or decapitation by animals.

An alternative explanation for the paucity in juveniles (both living and dead) might be because the 'bottleneck' within *A. dichotoma*'s life cycle is not the juvenile period *per se*, but conditions at germination and for a short, critical establishment period thereafter. This is possible, given what is known about the sensitivity of the recruitment phase from similarly arid systems (Jordan & Nobel, 1979). However, if climatic conditions within the SRZ area of *A. dichotoma*'s distribution have only recently become deleterious, there *should* nevertheless be juvenile cohorts which emerged prior to the most recent period of rapid warming (e.g. Hansen *et al.*, 2006). However, besides isolated examples linked to stochastic rainfall events as a result of a highly variable rainfall regime in the SRZ (e.g. Hoffman *et al.*, 2010), this appears not to be the case. In fact, there is little evidence to suggest that recruitment conditions have been favourable within the SRZ throughout the 20th century.

5.3.4   The value of a long-term view

The lack of evidence for recent mortality, the poor relationship between contemporary climatic conditions and *A. dichotoma* demography, and the species' unique life history traits, all highlight the need for an understanding of the species which take into account longer term abiotic, and biotic processes (i.e. historical contingencies (*sensu* Jackson *et al.*, 2009)). Specifically, an

interpretation of demographic patterns which consider climatic fluctuations on longer, millennial timescales is needed, but has thus far seen only a cursory inspection (e.g. Foden, 2002). This is fundamentally important in investigations of a species with a considerable lifespan (Vogel, 1974; Kaleme, 2003), slow growth and an infrequent recruitment regime - traits that allow *A. dichotoma* to persist, despite potentially deteriorating environmental conditions (e.g. Magnuson, 1990).

This final section of the synthesis will therefore explore some more speculative ideas surrounding the likely roles that longer term climatic fluctuations and biotic impacts have played on shaping the current distribution and density patterns in *A. dichotoma*. It will also introduce a novel way of conceptualizing *A. dichotoma* expansion and contraction, incorporating aspects of the regeneration niche previously not given full consideration. Lastly, given an improved understanding of the species, possible future research directions will be suggested.

5.3.4.1 Palaeo-climatic insights

A synthesis of several southern African palaeo-environmental studies (e.g. Chase & Meadows, 2007), as well as the recent discovery of very sensitive palaeo-climatic proxies (e.g. Chase *et al.*, 2009; Chase *et al.*, 2010) at the equatorward *A. dichotoma* range limit have led to a much improved understanding of climatic fluctuations in southern Africa since the last glacial maximum (LGM). For example, several palaeo-climatic proxies of both terrestrial and marine origin have revealed a coherent pattern of a significantly expanded WRZ during the LGM between 32-17 ka (Chase & Meadows, 2007). The likely reason for this expansion was a northward movement in rain-bearing westerlies off the south-western coast of southern Africa, driven by an increase in the extent of Antarctic sea ice (Chase & Meadows, 2007). This finding highlights the dynamic nature of southern African climate on millennial and even centennial timescales (Chase & Meadows, 2007; Chase *et al.*, 2009).

Climatic conditions which prevailed during and subsequent to the Holocene Altithermal (HA) (*ca.* 8000-4000 cal yr BP) are of potential significance to understanding contemporary demographic patterns in *A. dichotoma* within the current extent of the SRZ (i.e. the area previously reported to be suffering higher rates of mortality due to current climate change (Foden *et al.*, 2007)), as well as the south-western WRZ. Exceptionally high resolution fossilised hyrax midden records, recently collected from a site adjacent to the population at Spitzkoppe in the far north of the distribution, indicate that warm, humid conditions prevailed there intermittently from 8700-3500 cal yr BP (Chase *et al.*, 2009). Subsequently, the area experienced an extended period of aridity, which only abated approximately 300 years ago

(Chase *et al.*, 2009). These results were supported by several other more temporally discontinuous climate proxies (see Chase *et al.* (2009) for additional references), including pollen data from the Brandberg at the northern extremity of the range (Scott *et al.*, 2004). Conversely, several palaeo-studies suggested that the present-day WRZ experienced highly arid conditions during the HA (Chase & Meadows, 2007), becoming more variable and wetter during the Little Ice Age between 1300-1850 AD (Tyson & Lindesay, 1992).

Conceptual niche models provide a useful tool for illustrating how these long-term trends in climate may have affected population structure within the summer and winter rainfall zones (Fig. 1 (after Jackson *et al.*, 2009)). The transition from one 'climatic state' to another (defined as a shift in climate that elicits some noticeable change in a species' spatial population structure) need not be sudden, but are depicted as such within the models for simplicity sake. Indeed, Jackson *et al.* (2009) argue that directional climatic trends are themselves not a prerequisite for a biotic response, as an increase in the amplitude of environmental variability can have the same effect. By incorporating the regeneration niche, the models also illustrate how lower threshold environmental tolerances can influence population establishment and maintenance through time.
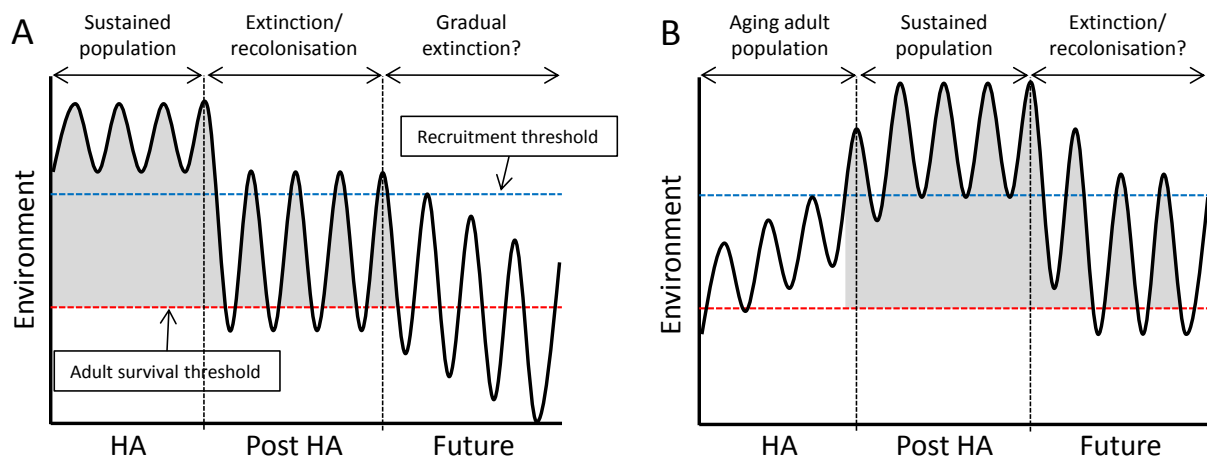
Fig. 1. Conceptual niche models for A) summer and B) winter rainfall zones illustrating likely phases in Aloe dichotoma *population dynamics during the Holocene Altithermal (HA), post HA, and for future conditions under projected warming and possible drying trends. The solid black line represents fluctuating environmental conditions through time and grey shading beneath the line represents periods during which colonisation can take place. Changes in the amplitude of the black line reflect either increasing or decreasing environmental variability. The red dotted line indicates the adult survival threshold beneath which localised extinction occurs. The blue line represents the more sensitive juvenile survival threshold beneath which recruitment cannot occur. Changes in the amplitude of the curve reflect fluctuations in environmental conditions. (See Jackson* et al. *(2009) for a more generalized conceptual framework of such niche models).*

Assuming that growth in current WRZ populations is linked to contemporary climatic conditions (i.e. a warm climate with consistent annual moisture inputs), the palaeo-environmental data suggested that climate within the current SRZ extent was likely to have been conducive to an expansion in the range of *A. dichotoma* during much of the HA (Fig. 1A, sustained population). However, aridification subsequent to *ca.* 3500 cal yr BP would then have initiated a gradual contraction in this expanded range, ultimately resulting in localised extinction and recolonisation events and the typically fragmented and isolated 'island' population structure in the SRZ distribution today (Fig. 1A, extinction/recolonisation). It could be argued that a recent history of deleterious climatic conditions has resulted in an abundance of non-recent dead skeletons and very infrequent recruitment. However, the evidence suggests that SRZ population dynamics vary considerably across both temporal and spatial scales and might therefore be characteristics of the species' sensitivity and adaptive capacity to climate in these highly variable conditions. Conversely, a return to more regular warming and wetter climatic conditions after a period of marked cold during the Little Ice Age (*ca.* 1300-1800AD) (Tyson *et al.*, 2000) or the aridity of the HA (Fig. 1B, aging adult population), would help explain the more contiguous distribution and higher recruitment rates apparent in populations within the current WRZ (Fig. 1B, sustained population).

While the above interpretation of population dynamics through time is necessarily speculative and imprecise due to the lack of evidence of *A. dichotoma*'s past range extent, it nevertheless provides a plausible and intuitive alternative explanation for current distributional and demographic patterns, especially within the SRZ, where palaeo-environmental data have a higher temporal resolution. The interpretation suggests that *A. dichotoma*'s past range boundaries were likely to have been highly dynamic, expanding and contracting in response to shifting winter and summer rainfall zone boundaries (and associated temperatures).

5.3.4.2 Lagged responses and adaptive capacity in *A. dichotoma*

However, because *A. dichotoma* is long-lived, slow growing and an infrequent, opportunistic recruiter, there are also likely to be substantial time-lags between shifts in climate and widespread population extinction and/or (re)colonisation (after Jackson *et al.*, 2009). More specifically, because of *A. dichotoma*'s longevity and resilience in the adult age, it may be able to persist through adverse climatic conditions and then take advantage of rare periods in which climate is favourable in order to recruit. Other long-lived desert species have been able to maintain viable populations in this way by recruiting as infrequently as between 2.2 and 3.7 times a century (Wiegand *et al.*, 2004). In addition to the above recruitment strategy, the climatically ameliorative influence of nurse plants or rocks are likely to further aid *A. dichotoma*

seedlings through the initial vulnerable establishment phase (Foden *et al.*, 2007), as has been shown for the saguaro (Nobel, 1980) and other desert-adapted species in North America (Bowers *et al.*, 1995).

The abovementioned life history traits give adult and juvenile *A. dichotoma* individuals some capacity to withstand rapidly changing or fluctuating environmental conditions by persisting *in situ* (after Dawson *et al.*, 2011). Adults are buffered against desiccation through large water storage capacity, while juveniles limit water loss by utilizing micro-niches. However, if climatic conditions deteriorate below levels required for the regeneration niche to function, the result will be a gradual shift in the demographic profile in favour of adult and dead individuals, rather than juveniles.

Indeed, the dominance of adult individuals and non-recent dead skeletons derived from the adult age class (and often complete absence of juveniles) within isolated, often high elevation, climatically marginal SRZ populations is an indication that these populations are likely to be biological relicts of a previously more amenable climate. In this interpretation, it follows that negative population replacement rates previously reported for a small sample of SRZ populations (Kaleme, 2003; Foden *et al.*, 2007; Hoffman *et al.*, 2010) are more likely to be a function of long-term natural decline, rather than one catalysed by recent climate change. Another explanation for adult skewed demographic profiles in SRZ populations (see Fig. 5 in Chapter 3) is that this more resilient age class is able to persist over long periods when conditions promote mortality over recruitment, but only two or three recruitment episodes per century are needed to reverse that trend. The very high rainfall in the SRZ since 2005 might well constitute such periodic recruitment event in the SRZ. Conversely, the recruitment surge within WRZ populations may represent a release from previous natural climatic constraints and is suggestive of a population in relatively closer equilibrium with contemporary climate.

Operating in conjunction with broader climatic drivers are biotic impacts such as disease, insect and animal damage, and windthrow, which appear to have a more localised impact (Foden *et al.*, 2007), but which have nevertheless been shown to exert considerable influence on population persistence (Jankowitz, 1972; Midgley *et al.*, 1997; Geldenhuys & Swart, 2009). Disease and insect damage are ubiquitous throughout the distribution and have, for example, been implicated in the decline of a sizable mature population at Kenhardt (Geldenhuys & Swart, 2009). Increased baboon and antelope damage were equally common, and possibly on the increase, due to the installation of fixed water points, predator suppression and (with respect to increased baboon roosting sites) riverine bush encroachment. Windthrow too, resulted in

considerable localised mortality, usually of large adults bearing a disproportionate amount of the seed-producing potential in a population.

Extensive field observations across the distribution suggested that, in combination, these biotic influences significantly reduced species health and reproductive output. In addition, in the majority of cases these impacts were thought to be the likely cause of 'shoot-shedding' previously attributed to water stress by Foden *et al.* (2007). A more thorough evaluation of the impacts from these factors is needed, both in order to establish whether their influence is broader in scale, as well as to help separate the noise that they generate from the underlying climate signal.

In summary, the current study found little evidence for a link between recent anthropogenic climate change and equatorward *A. dichotoma* decline, despite a possible increased exposure in equatorward populations to deleterious climate. Instead, distributional and demographic patterns, as well as the time since mortality and age class from which mortality was derived, all seem better aligned with an explanation which incorporates longer term climatic fluctuations and noise generated from biotic impacts and windthrow. A further reason for the uncoupling between age classes and contemporary climate is thought to be due to *A. dichotoma* life history traits, which likely result in the persistence of populations and consequently, lagged responses to changes in climate.

If climate change in southern Africa involves further temperature increases and decreasing or more erratic rainfall (e.g. Hulme *et al.*, 2001; Haensler *et al.*, 2011), it is likely that *A. dichotoma* persistence will ultimately be negatively affected. Under the above future climate scenarios, episodic recruitment associated with more marginal populations within the SRZ is likely to decline further, leading to a gradual aging of adult cohorts and eventual extinction of these populations (Fig. 1A, gradual extinction). However, in a different analysis based on projected changes in total monthly rainfall derived from six statistically downscaled general circulation model rainfall estimates, a slight increase in MAP with an extended late summer rainfall period and more extreme rainfall events is predicted (Dirkx *et al.,* 2008). The implications of such a scenario would be the continuation of population dynamics in the SRZ similar to those recorded in this study. Furthermore, climate trajectories are likely to be different within the respective rainfall zones (Fauchereau *et al.*, 2003; Haensler *et al.*, 2011). If climatic conditions within the WRZ become increasingly variable and/or arid, it is possible that this might catalyse a shift from the current condition of sustained populations to one in which episodic recruitment or even extinction and re-colonisation become the norm (Fig. 1B, extinction/re-colonisation).

In this respect the contrasting population dynamics in the SRZ and WRZ provide a useful indication of the species' sensitivity and adaptive capacity across a broad range of climatic conditions. However, it remains difficult to predict the pace and extent of future change in *A. dichotoma* recruitment, persistence and mortality, as this is largely dependent on future rates of climate change, which are themselves uncertain (e.g. Hulme *et al.*, 1999; Stott & Kettleborough, 2002). Furthermore, due to the species' life history traits (and the relative insensitivity of the adult age class) and resultant lag-effects of climate change on existing populations, *A. dichotoma* is unlikely to be useful as a climate change indicator species, although it could be useful for studying longer-term palaeo-climatic variations.

5.4   Future research directions

5.4.1.   *A valuable* long-term *indicator of change*

Despite mounting evidence that *A. dichotoma* responds relatively slowly to change, studies of the species have, to date, been of relatively short duration, capturing only 'snapshot' views of population health, while current knowledge of *A. dichotoma*'s life history highlights the need for a longer term monitoring effort. Some recent progress has been made in this regard (e.g. Midgley *et al.*, 2009; Conrad Geldenhuys, pers. comm.), though data spanning much longer temporal scales is needed to establish reliable trends in growth and decline for the species. This will reduce the likelihood of erroneous conclusions based on anomalous short-term biotic or abiotic trends (e.g. Matthes & Larson, 2006).

There has been both local (e.g. Midgley *et al.*, 2007) and international (e.g. Lepetz *et al.*, 2009) recognition of the need for such long-term ecological research (LTER) to aid detection of the effects of climate change on biota. Indeed, Jackson & Sax (2009) stress that long-term monitoring programs are urgently required across all natural systems due to the possibility that extinction in many species may lag forcing events, resulting in the phenomenon of 'extinction debt', to be paid in the future. Depending on the species, this 'repayment' could happen over decades, centuries, or even longer (Jackson & Sax, 2009), as may be the case for a long-lived and resilient species such as *A. dichotoma*. These findings should hasten the establishment of LTER networks, which should be aligned with sites for which historical climatic data is available, and preferentially positioned close to ecotones or across strong climatic gradients, where the greatest change is likely to be observed. The first such initiative in southern Africa was the highly successful BIOTA project which, over a ten year period, described biodiversity change through time along major latitudinal and longitudinal axes in South Africa and Namibia, and indentified major drivers of change, both biotic and abiotic (Jurgens *et al.*, 2010).

However, in selecting species for study within a LTER framework, a distinction should to be made between those species which are more likely to respond slowly to changes in climate and those with attributes that would facilitate a more rapid observable response to subtle climate shifts (e.g. Matthes & Larson, 2006). The fact that *A. dichotoma* fails to satisfy criteria for a rapid response to climate change does not necessarily exclude it from consideration. Instead, the species' longevity and the slow decay of dead skeletons mean that it could provide important longer term insight into changing environmental conditions.

5.4.2   Palaeo- and historical climate records

Greater spatial and temporal resolution within the palaeo- and historical climate records would compliment long-term ecological data collected through the establishment of a LTER program. Specifically, this would improve our understanding of how past climates may have shaped current distributional and demographic patterns, and may be useful for predicting how future climate might affect species. However, despite important recent advances in temporal resolution for certain areas (e.g. Scott *et al.*, 2004; Chase *et al.*, 2009), the spatial resolution of palaeo-environmental records remain coarse within south-western Africa, due to widespread aridity and the resultant lack of preservation of traditional proxy data sources (Chase & Meadows, 2007). Nevertheless, exciting opportunities exist to (for example) expand the network of high resolution hyrax midden archives, or to develop other novel proxies for reconstructing palaeo-climates.

While the resolution and accuracy of interpolated climate surfaces is improving (e.g. New *et al.*, 2002; Hijmans *et al.*, 2005) due to advances in digital elevation models and spatial interpolation techniques (e.g. Hewitson & Crane, 2005), such approaches are still heavily constrained by a paucity in instrumental data in southern Africa (Nicholson, 2001). An urgent expansion is therefore required in the network of climate recording stations, especially within the drier, more climatically variable regions of Namibia and the Northern Cape. Without detailed, spatially explicit climate data it will remain difficult to confidently assign trends in climate to changes in recruitment or mortality rates in such a spatially variable species as *A. dichotoma*.

5.4.3   Physiological thresholds of age classes

In addition to long-term monitoring of natural populations and climate, there is also an urgent need to better understand physiological thresholds in different *A. dichotoma* age classes with respect to gradients in key climatic variable. This would be a considerable improvement upon current inferences based solely on (often poor) correlations and undermined by inherent variability in natural populations. In the context of climate change, an understanding of the

specific point at which individual age classes succumb to either moisture or temperature stress would be a critical step forward in our physiological understanding of the species. This could be achieved either through the manipulation or 'forcing' of moisture and temperature conditions within natural populations (e.g. see Musil *et al.*, 2005; Musil *et al.*, 2009) or, perhaps more feasibly, under controlled laboratory conditions in which these variables can be varied experimentally. Results from these analyses would provide critical insight into the likely trajectories of populations at different latitudinal positions, and within different rainfall zones, in the face of climate change. Coupled with accurate climate projections, this would greatly inform management strategies by providing an indication of which populations are most at risk and allow for possible mitigatory action.

The rate of current and future climate change threatens to outpace the collective efforts of climatologists and ecologists (Solomon *et al.*, 2009; Haensler *et al.*, 2011). Urgency is therefore required to understanding how regional and local climate will change and how species are likely to respond, both individually and collectively. These are complex issues which require rapid resolution and for which the margins between success and failure are slim. However, we need to be certain about the species we select as indicators of anthropogenic change, both because of the need for consistency and reliability of science presented for public consumption, and because our findings might have important management implications for the species and region in question.

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