

**A Demographic Study of *Aloe dichotoma* in the
Succulent Karoo:
Are the Effects of Climate Change Already Apparent?**

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INTRODUCTION

Southern Africa's arid Succulent Karoo region supports an extraordinarily rich and compositionally unusual flora (Cowling et al. 1998). The area is characterised by low but predictable winter rainfall and the dominance of short, leaf-succulent shrubs (Desmet and Cowling 1999). In an area of 100 000 km², it contains 5 000 species (40% endemic) and 730 genera, 67 of which are endemic (Cowling and Hilton-Taylor 1999). This is over three times as many endemic genera as Sahara-Arabian and North American arid lands which exceed its size by orders of magnitude (Cowling and Hilton-Taylor 1999). The Succulent Karoo has been identified as one of the world's 25 biodiversity hotspots, based both on richness and threat criteria (Myers et al. 2000).

While agriculture, overgrazing and mining have traditionally been regarded as a threat to the Succulent Karoo's biodiversity (Myers et al. 2000), a new, more extreme and pervasive threat has recently been identified. Climate change scenarios for South Africa indicate that the Succulent Karoo biome will disappear almost completely from its current range along the western coastal and inland plain by 2050 (Midgley et al 2001, Rutherford et al. 1999). Rutherford et al. (1999) predict that unless the Succulent Karoo can cross the Cape Fold Mountains into the Southern Cape (which is highly unlikely given the distance and terrain), large-scale plant extinctions will occur.

Evidence of biological impacts of climate change across the world continues to accumulate. Several studies in the northern hemisphere have illustrated a clear shift in species' distribution ranges towards the poles in response to warmer climates (Warren et al. 2001, Parmesan et al. 1999, Thomas and Lennon 1999, Parmesan 1996). Other responses include population growth of Arctic shrubs (Sturm et al. 2001), increases in elevation of alpine tree establishment (Pauli et al. 1996) declines in emperor penguin populations in Antarctica (Barbraud and Weimerskirch 2001). Pounds et al. (1999) reported crashes in amphibian populations, as well as changes in bird and reptile communities in Monte Verde, Costa Rica, in response to atmospheric warming. This constitutes one of the very few biological examples of climate change in tropical systems.

Could climate change really have the devastating effects on the tropical Succulent Karoo that scenarios predict? Will species ranges shift polewards, as other studies have found? Temperatures have already risen by 0.6°C this century (IPCC 3rd assessment report). Are these effects already apparent?

One of the most striking and charismatic Succulent Karoo species, *Aloe dichotoma* (Masson), is a giant tree succulent (up to 9m tall) that occurs mainly in dense populations or “forests” in otherwise arid and treeless landscapes. *Aloe dichotoma*’s common name, the “Quiver tree”, comes from the use of its hollowed-out branches by San hunters to carry arrows. It occurs in the Succulent Karoo as well as eastwards into the Nama-Karoo and throughout southern Namibia as far northwards as Usakos (Reynolds 1950). *Aloe dichotoma* has been suggested as a keystone species due to its importance as a source of moisture for a wide spectrum of mammals, birds and insects, as well as for bird nesting sites (Midgley et al. 1997). Its long life span (approximately 200 years (Vogel 1974)) makes it ideal for studying long-term climate trends. This study aims to determine whether *Aloe dichotoma*, important both as a representative of the Succulent Karoo and in its own right, is being impacted upon by climate change.

Time series analysis provides the ideal tool for analysing long-term population changes (Udevitz and Ballachey 1995). Demography data on thirteen *Aloe dichotoma* populations are available from studies conducted in 1987 and 1997 by Rebelo et al. (unpublished data). The fourteen-year time interval between 1987 and the present is, however, not long relative to the estimated 200 year lifespan of *Aloe dichotoma* (Vogel 1974). *Agave deserti*, a functionally equivalent giant succulent in the Sonoran desert, has been shown to have recruited only once in 17 years (Jordan and Nobel 1979). Although the fourteen-year interval investigated in this study is inadequate to draw firm conclusions about long-term population trends, combining it with a study of population demographics is revealing. *Aloe dichotoma* does not resprout and grows only from terminal apices (Midgley 1996). Height therefore provides a surrogate measure of age (Midgley et al. 1997) and hence a useful indication of past growth conditions.

Global circulation models (GCM’s) provide spatially explicit projections of climate responses to changing concentrations of greenhouse gasses (Hewitson 1999). These broad-scale scenarios have been scaled down for South Africa by Schulze and Perks (1999).

Creating species-level projections involves selecting and quantifying the climatic criteria which determine a species' distribution and relocating these tolerance ranges, termed isotherms (Jeffree and Jeffree 1994, Parmesan et al. 1999) or bioclimatic envelopes (Midgley et al. 2001, Rutherford et al. 1996), in future climate scenarios. This method of bioclimatic envelope modelling has been used to create scenarios of plant distribution responses to climate for *Eucalyptus* (Hughes et al. 1996), Proteaceae and *Cladoraphus* (Midgley et al. 2001), *Euclea* and *Burkea* (Rutherford et al. 1995) and a range of other southern African species (Rutherford et al. 1996).

Generalized additive models (GAM's) provide an alternative to generalized linear models (GLM's), sharing many of their strengths, but with added flexibility (Hastie 1992, Hastie and Tibshirani, 1990). Variables are modelled non-parametrically using a scatterplot smoother (Hastie 1992) by local fitting to subsections of data (Thuiller et al., in press). This tool allows the data to suggest non-linearities (Hastie 1992) and avoids the need to estimate the response curve function. In this study GAM is conducted on binomial distribution data for *Aloe dichotoma*, using the same bioclimatic and geological variables used in bioclimatic tolerance modelling. GAM provides an alternative method to bioclimatic modelling for generating climate change scenarios and hence provides a test of projections' robustness.

Bioclimatic modelling assumes that climate and soils are the primary determining factors of an organism's habitat range and success. This study sets out to test this assumption by examining several non-climatic variables that appear pertinent to *Aloe dichotoma*'s success. A previous study of tree succulents in the Richtersveld by Midgley et al. (1997) suggests that herbivory by baboons (*Chachma ursinus*) and porcupines (*Hystrix austro-africanus*) causes mortality of *Aloe dichotoma*, while trampling and herbivory of seedlings and nurse plants by goats limits recruitment (Midgley et al. 1997, Rebelo et al. 1989). Rebelo et al. (1989), Rebelo et al. (unpublished data) and Midgley (1997) suggest that removal of seedlings by collectors is preventing recruitment. "Vanishing disease" and "aloe cancer" are local names for fungal pathogen infections that are reported to cause mortality of *Aloe dichotoma* (B. Wiese, pers. com.). This study attempts to control for the effects of herbivory, removal of seedlings by collectors, fungal pathogens, density dependence and decreased seed set.

If climate change is affecting *Aloe dichotoma* populations, they are likely to show visible signs of climate-induced stress. G. Williamson (pers com.) has observed that, during prolonged droughts, some of the branches of *Aloe dichotoma* lose their leaves, thereby reducing transpiration and water loss. This results in the death of the branch, which does not resprout and hence remains evident throughout the rest of the plant's life (figure 1). This phenomenon is investigated as a potential indicator of long-term climate-induced stress.

Climate change scenarios for the Succulent Karoo look ominous, but they rely on a series of models and assumptions and remain theoretical until biological evidence to support them emerges. This study uses the GCM climate change scenarios for *Aloe dichotoma* over the next 50 years. Scenarios for 2010 identify the regions in which the bioclimate first becomes unsuitable for the species. If climate change scenarios are correct, *Aloe dichotoma* populations occurring in regions outside the 2010 bioclimatic envelope will show greater mortality and reduced recruitment relative to those remaining within the 2010 bioclimatic envelope. This study aims to test the above hypothesis and thereby determine if early signs of climate change in the Succulent Karoo are apparent.

METHODS

Bioclimatic envelope modelling

Five climatically derived environmental parameters play a key role in defining plants' bioclimatic envelopes in South Africa (Midgley et al. 2001). These include, firstly, the mean minimum temperature in the coldest month of the year, as this affects a species' ability to assimilate water and nutrients and maintain basic cell function. It is also a requirement for certain processes such as bud break and seed germination (Midgley et al. 2001). Secondly, heat units, the average sum of daily temperatures exceeding 18°C, affect whether plants can tolerate high temperatures, but are also a requirement for the completion of growing cycles. Annual potential evapotranspiration affects the processes of water flow through plants, as well as xylem vulnerability to cavitation. Lastly, number of soil moisture days in summer (November to February) and winter (May to August) determine the seasonality and intensity of drought stress and affect both plant survival and recruitment (Midgley et al. 2001).

Maps of these bioclimatic variables have been derived for South Africa by Schulze and Perks (1999). In addition, images of South Africa's soil fertility (indexed from 1-9), percentage clay (1-6) and percentage sand (1-6) were obtained from Schulze (1997). Suitably fine-scale bioclimatic data was not available for Namibia and this necessitated that only the South African populations of *Aloe dichotoma* were considered in this study. Climate data was at a minute-by-minute scale (approximately 1.5 X 1.8 km) and hence localised soil patterns and details of aspect could not be included.

The distribution of *Aloe dichotoma* was derived from herbarium specimen labels (National, Bolus and Compton herbaria), data collected by Acocks (1988) and Reynolds (1950) as well as personal observations. Arcview 3.2 geographic information system was used to identify the upper and lower limits of each climate and soil parameter at which *Aloe dichotoma* occurs. These limits were then applied to bioclimatic maps of South Africa and the species' current bioclimatic envelope

determined (Rutherford et al 1996). Sensitivity analysis was conducted by including and excluding various parameters from the analysis.

GCM climate scenarios derived for South Africa include those generated by HadCM2, an ocean-coupled model developed by the Hadley Centre (U.K.), which creates projections both excluding and including the ameliorating effects of atmospheric sulphate aerosols (Hewitson 1999). Scenarios from the CSM model (U.S.A.), a more recent fully-coupled ocean-atmosphere model (Hewitson 1999), were also used. *Aloe dichotoma*'s bioclimatic tolerance limits were used to identify suitable future climate envelopes based each of the three GCM models. GCM scenarios, interpolated to smaller time-steps (assuming linear change), were used to create projections of *Aloe dichotoma*'s distribution at decade intervals from 2010 to 2050.

Generalized additive modelling

Generalized additive modelling (GAM) was conducted using 'S' programming language in the software package Splus version 4.5 (Hastie and Tibshirani 1990, Hastie 1992). Presence and absence data for *Aloe dichotoma* was derived from herbarium specimen data and observations while in the field (110 points).

Biogeoclimatic factors including heat units (htunt) (annual sum of daily temperatures that exceed 18°C), mean minimum temperature during the coldest month (tncold), annual potential evapotranspiration (apan), soil moisture days in summer (smdsum) and winter (smdwin) as well as soil fertility, clay and sand indices were derived for each point. Various degrees of spline smoothing were investigated for the non-categorical variables and these were compared using a pseudocoefficient of discrimination (R^2) (Swartzman et al. 1992).

These variables were used to construct an additive regression equation. Splus 4.5 contains an automatic step-wise variable selection function which produced a second generalized additive model for *Aloe dichotoma* distribution as follows:

$$\text{presence} \sim \text{s(apan)} + \text{s(htunt)} + \text{s(tncold)} + \text{sand}$$

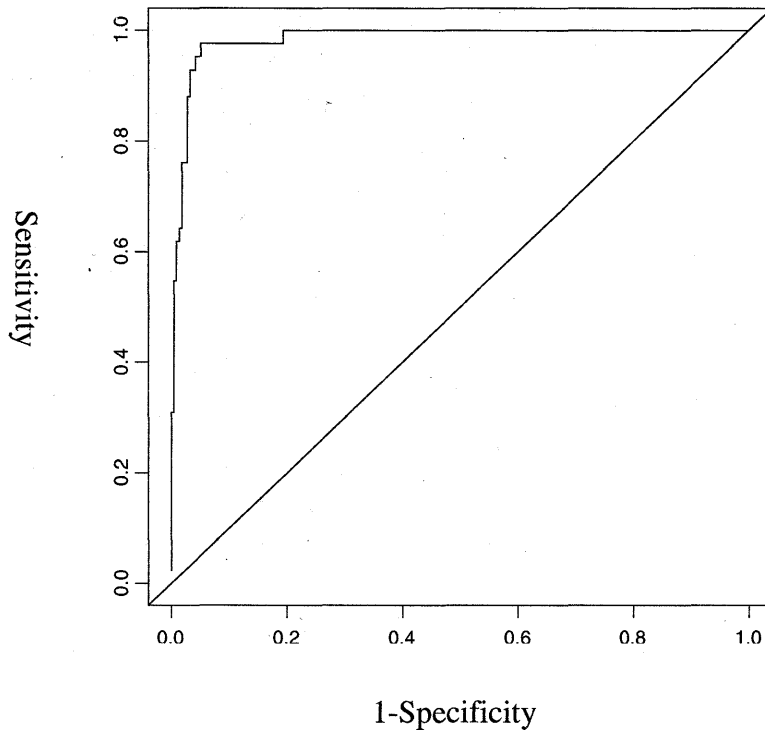


Figure 1: The ROC graph in which sensitivity (true positive proportion) is plotted against the false positive proportion for a range of threshold probabilities for (a) the step-wise GAM of Aloe dichotoma distribution. The 45° line represents the sensitivity and false positive values expected from chance alone.

Both all-variable and step-wise models were used to predict the species' current climatic envelope (Hastie 1992) and the reliability and discrimination capacity of these predictions assessed using relative operating characteristic (ROC) curve. The ROC curve for the step-wise model is shown in figure 1. The ROC curve provides a graphical approach to assessing discrimination capacity of a model, by plotting sensitivity (true positive portion) against the false positive proportion (Pearce and Ferrier 2000). The area under the ROC curve, expressed as the total area of the square defined by the false positive and true positive axes, is regarded as the best discrimination index (Pearce and Ferrier 2000). The all-variable model and step-wise models have discrimination indices of 0.9440 (std. error = 0.0226) and 0.9436 (std. error = 0.0217) respectively. Rates higher than 0.9 have been described by Swets (1988) as indicating "very good discrimination" because the sensitivity rate is high relative to the false positive rate. There was no significant difference between the

discrimination capacity of the two models (i.e. between the areas under the ROC curve) (Chi-square, $p > 0.98$). Being simpler and more parsimonious without compromising discrimination capacity, the stepwise model provides the preferable modelling choice (Huisman et al. 1993), and was used to create the climate change projections.

HadCM2 model (excluding sulphates) projections for 2010 and 2050 were applied to the step-wise GAM to determine *Aloe dichotoma*'s potential distribution. The GAM output consists of a probability of presence for each grid cell. The threshold probability used to distinguish whether cells were included in the suitable envelope was derived using the ROC curve (figure 1). This threshold probability represents the best compromise between correctly predicting the occurrence of the species (true positive) and incorrectly predicting the presence of the species (false positive) (Pearce and Ferrier 2000) and was found to be $P=0.275$ for this model.

Collection of demographic data

During July 1987 a demographic study was carried out by A. Rebelo, P. Holmes and the U.C.T. Botanical Club on eleven populations of *Aloe dichotoma* in the north-western Cape and southern Namibia (figure 2). The first 100 individuals encountered in the densest part of each population were measured and height, basal circumference, height to first branching and number of branches was recorded for each. The number of dead plants encountered was also noted. Aspects of reproductive biology including abundance and viability of inflorescences and fruit were recorded and the mean number of plants flowering was calculated for each population. Site characteristics such as aspect, and grazing intensity were also recorded.

Population density and percentage mortality were estimated by counting live and dead individuals in a 1000m X 3m straight belt transect that bisected the densest part of the population and spanned its topographic gradients. Sampling small populations necessitated that transects were broken into smaller non-overlapping belts, but the total area surveyed remained 3000m².

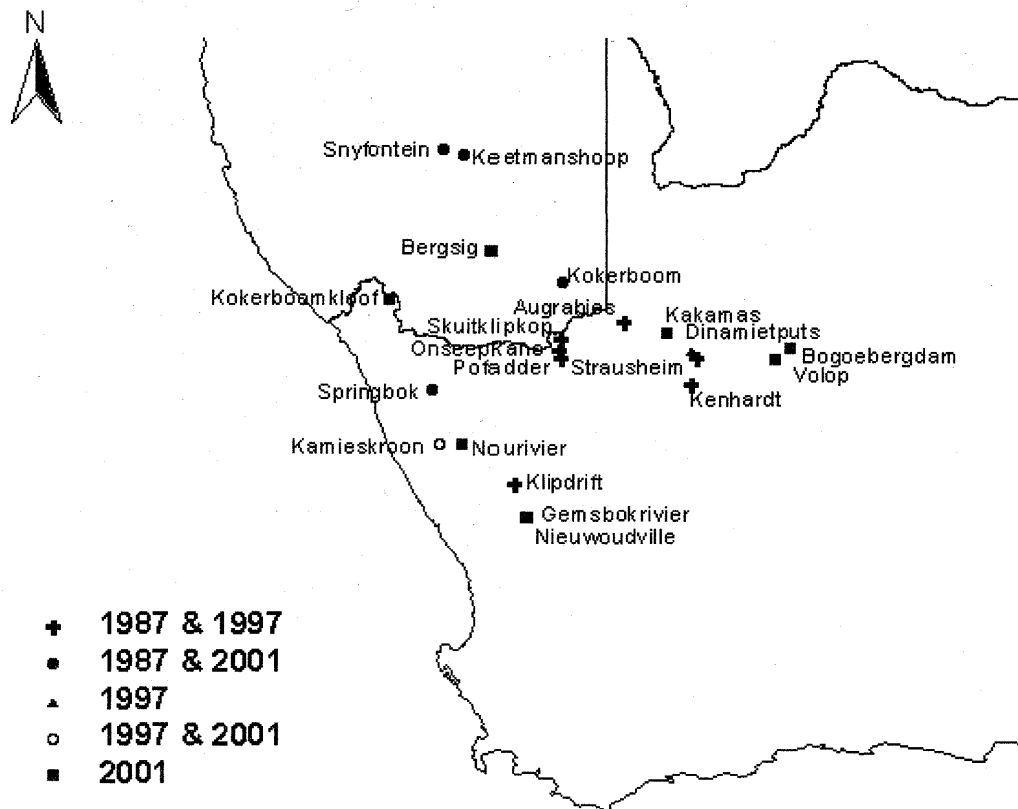


Figure 2: Map showing the distribution of *Aloe dichotoma* study sites as well as the year(s) in which they were surveyed.

During June 1997 A. Rebelo and P. Holmes revisited seven of the 1987 sites (all in South Africa, see figure 2) and two further sites, namely Kamieskroon and Dinamietputs. The sampling methodology used during 1987 was repeated, although belt transect measurements were not carried out.

In November and December 2001 thirteen further sites were surveyed by the author (see figure 2). This included the three Namibian populations studied in 1987 as well as Springbok and Kamieskroon. New study populations were located from herbarium specimen labels and included Nourivier in the West and Gembokrivier and Nieuwoudville (the southern limit for the species (Reynolds 1950)) populations. Populations in the Richtersveld (Kokerboomkloof) and in the Groot Karasberg mountains in Namibia (Bergsig), as well as two eastern sites (Volop and Boegoebergdam) in the summer-rainfall Nama-Karoo region, were also studied.

Although *Aloe dichotoma* was recorded at Posmasberg in the Hay district in 1933 (H. Daniel, herbarium specimen, Reynolds (1950)) a visit to this area suggested that climate and topography were atypical for the species and numerous local inhabitants confirmed that *Aloe dichotoma* was not found in the area. The most easterly populations encountered were 12km west of Prieska, and at Volop and Boegoeberg Dam on the Orange River.

Sampling methodology used in the 1987 and 1997 studies was repeated and belt transect measurements were included. In addition, the percentage of total canopy loss, as well as a score for the severity of damage to the trunk or stem from 0 (no damage) to 3 (severe damage) were estimated for each plant. Fungal infection of the trunk was evident as a grey 'powder' on otherwise yellow bark, and this was recorded as a score from 0 (none) to 5 (completely grey). Leaf fungal infection appeared as small white powdery spots and leaf fungal infection per plant was also scored from 0 (none) to 5 (almost white). Evidence of fruiting (such as fruit capsules and fruit stalks) was noted, as was the incidence of trees growing with completely entwined trunks (Reynolds 1950).

For all dead plants encountered, measurements of basal circumference and height to first branching (where visible) were made, stem damage was scored (0-3) and note was made of whether or not the dead plant was still standing. In order to determine the height (and hence age) of individuals at their time of death, a regression equation was derived from the relationship between stem circumference and height of live individuals. A separate equation was derived for each population so that estimates of dead plant height matched its population's phenotype.

At each site, dung frequency and type were recorded in two 100 X 2m transects. This provided an objective measure of grazing intensity and frequencies were divided into categories (0-5). Further site measurements included aspect, slope and rockiness. Rainfall records for various localities in the Northern Cape were obtained from the South African Weather Bureau.

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In order to relate specific plant height to age, *Aloe dichotoma* individuals of known age from the Van Rhynsdorp nursery in each of the following categories were measured: 8 months (n=30); 20 months (n=30); 3 years (n=30); 25-30 years (n=30) and 40 years (n=16). Vogel (1974) used carbon-dated tissue from a disc of diameter 56-66cm sawn from the trunk of a large, recently dead *Aloe dichotoma* near Kakamas, and determined that its age was 100 years (± 45 years). The linear regression equation for the relationship between trunk circumference and height of plants at the Kakamas study site ($y = 48.294x + 17.093$; $R^2 = 0.6576$) was used to estimate the height of this individual and results were combined to create a height vs. age curve.

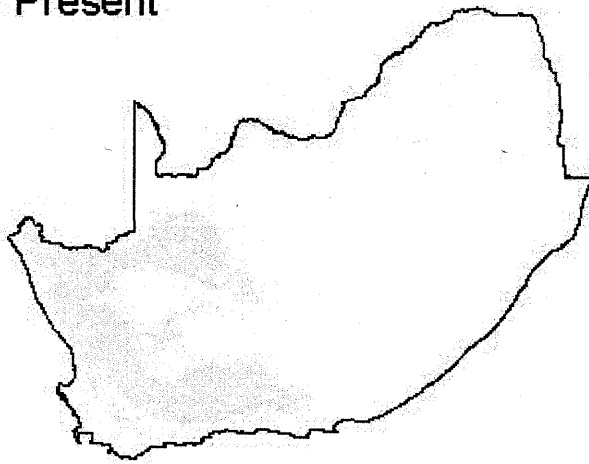
RESULTS

Climate change scenarios

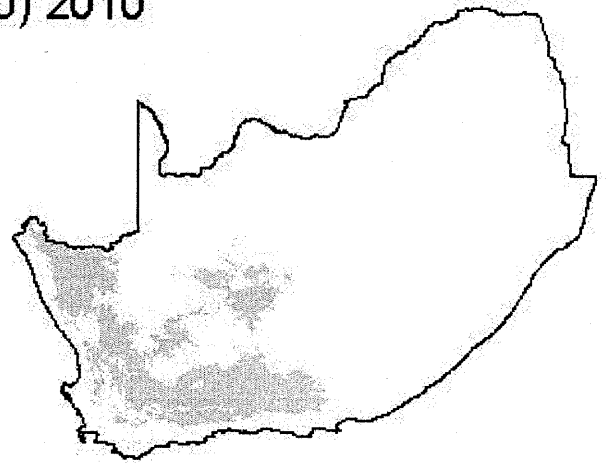
Climate change scenarios created using bioclimatic modelling based on interpolation of HadCM2 models, with and without sulphates, and using the CSM model are shown in figures 3, 4 and 5 respectively. Figures 3 (a), 4 (a) and 5 (a) show *Aloe dichotoma*'s current bioclimatic envelope in South Africa. In all predictions this envelope spans the northern border of the Northern Province, though areas immediately adjacent to the Orange river are excluded. It extends Southwards down the West Coast, never reaching closer than 10km from the coast and as far as Prieska in the North East. Sensitivity analysis reveals that higher altitude Great-Karoo and West Coast regions are excluded from the envelope by minimum temperature requirements. The current bioclimatic envelope extends southwards into the low-lying southern Karoo and little Karoo. A visual interpretation suggests that the current envelope provides a reasonable fit with *Aloe dichotoma* distribution in the northern half of the envelope, but its southern extension into regions where *Aloe dichotoma* does not occur is surprising.

Figures 3, 4 and 5 (b) to (d) indicate that the HadCM2 (with and without sulphates) and CSM models produce scenarios indicating a southward movement of *Aloe dichotoma*'s range and an eastward expansion of its southern parts into the Little Karoo. The suitable bioclimatic envelope retracts from the West Coast and by 2050 is greatly reduced, occurring only in the most southerly regions of the Karoo. No overlap occurs between current envelopes and 2050 scenarios in the two HadCM2 projections, while the CSM model suggests that the higher elevation areas in the western regions of the envelope will remain suitable. The scenarios produced by bioclimatic modelling using the three Hadley model scenarios do not differ markedly from each other, although those from the no-sulphates model show the greatest changes in *Aloe dichotoma*'s range. The HadCM2 (no-sulphates) model (figure 4) incorporates fewer uncertainties than the HadCM2 (no-sulphates) model (Hewitson 1999) and, as it is conventionally regarded as providing the most credible view of climate change, it will be used in further comparisons.

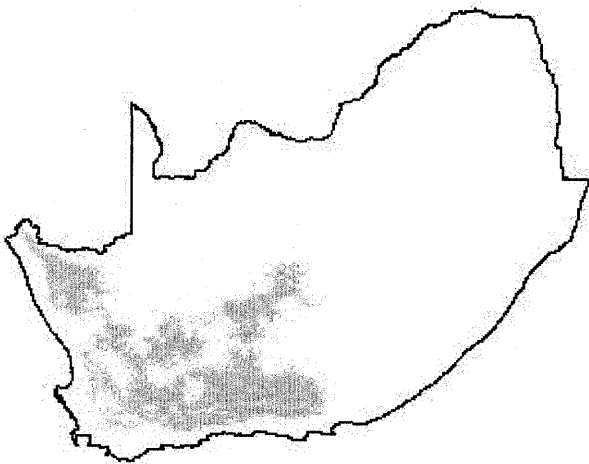
a) Present



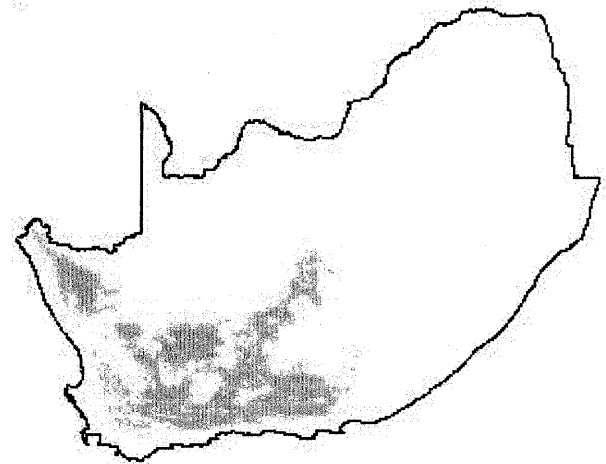
b) 2010



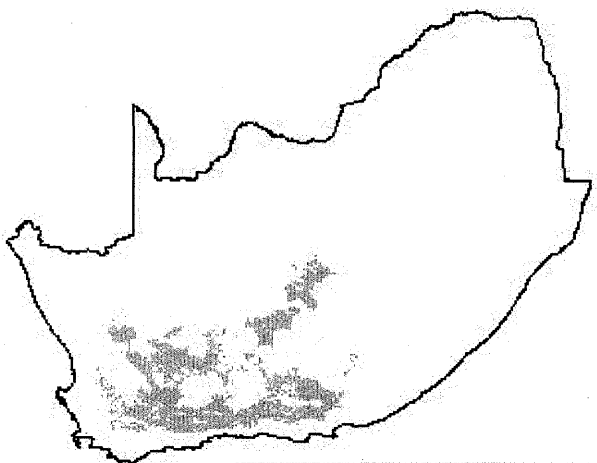
c) 2020



d) 2030



e) 2040



f) 2050

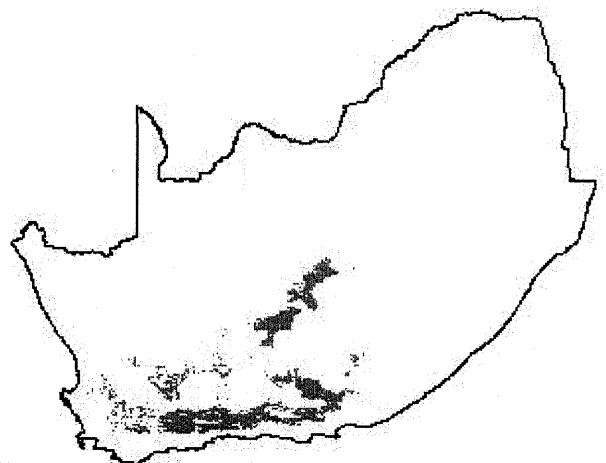
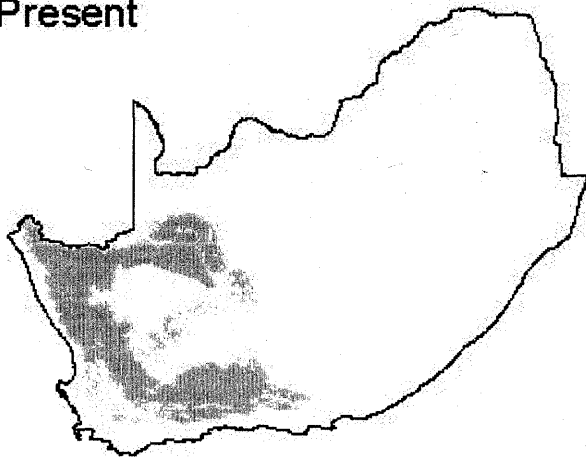
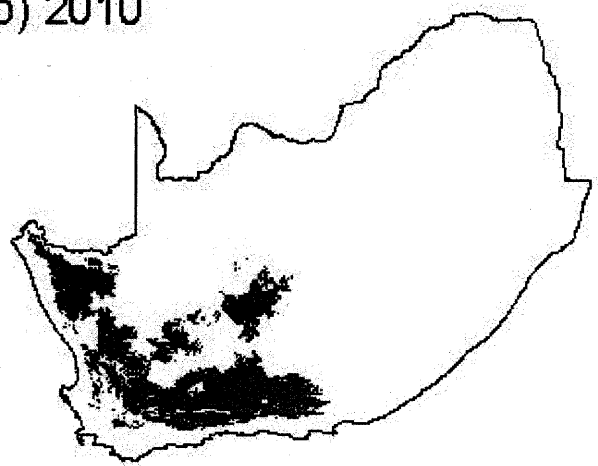


Figure 3: Maps showing bioclimatic envelope projections for *Alo dichotoma* in South Africa based on the HadCM2 (sulphates) model for a) the present, b) 2010, c) 2020, d) 2030, e) 2040 and f) 2050. Blue points show the current distribution.

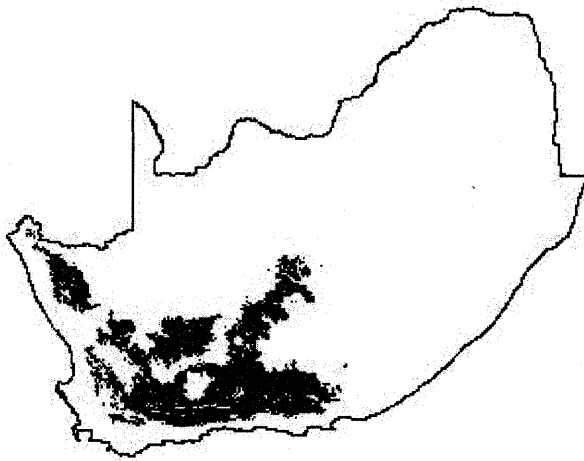
a) Present



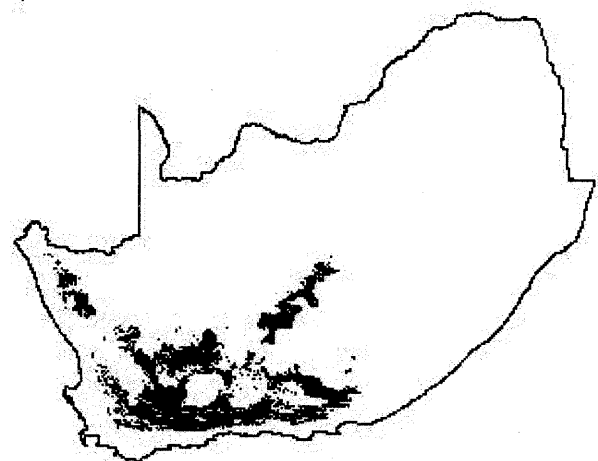
b) 2010



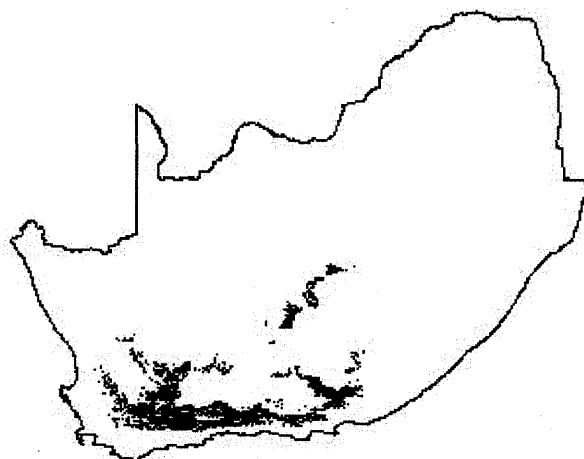
c) 2020



d) 2030



e) 2040



f) 2050

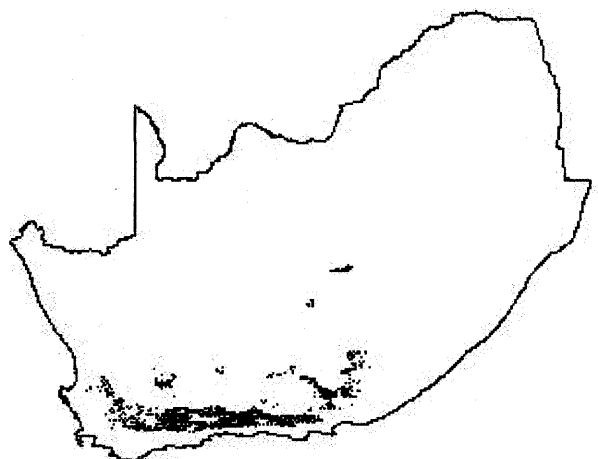
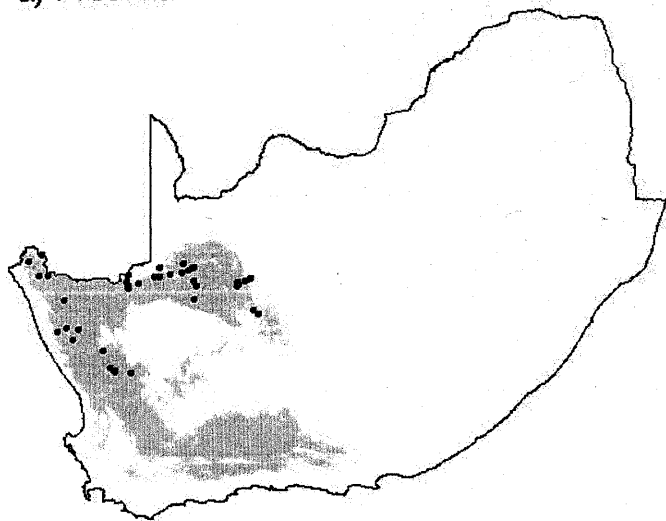
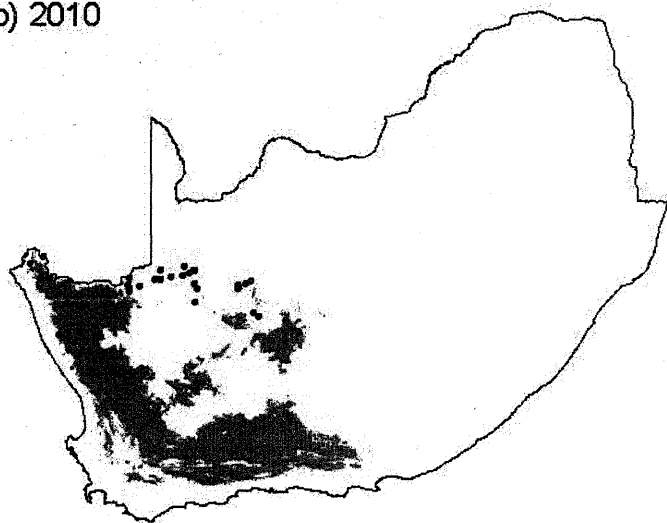


Figure 4: Maps showing bioclimatic envelope projections for *Aloe dichotoma* in South Africa based on the HadCM2 (no-sulphates) model for a) the present, b) 2010, c) 2020, d) 2030, e) 2040 and f) 2050. Red points show the current distribution.

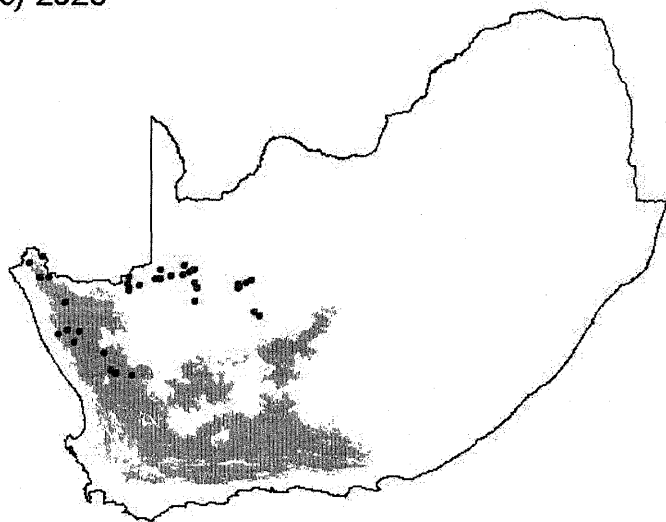
a) Present



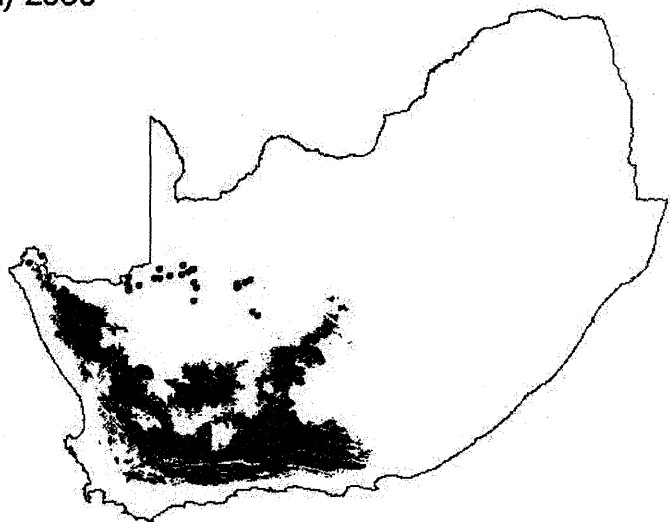
b) 2010



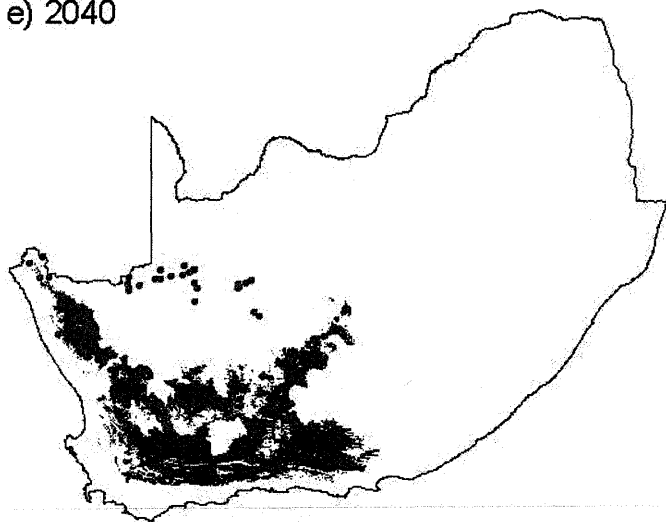
c) 2020



d) 2030



e) 2040



f) 2050

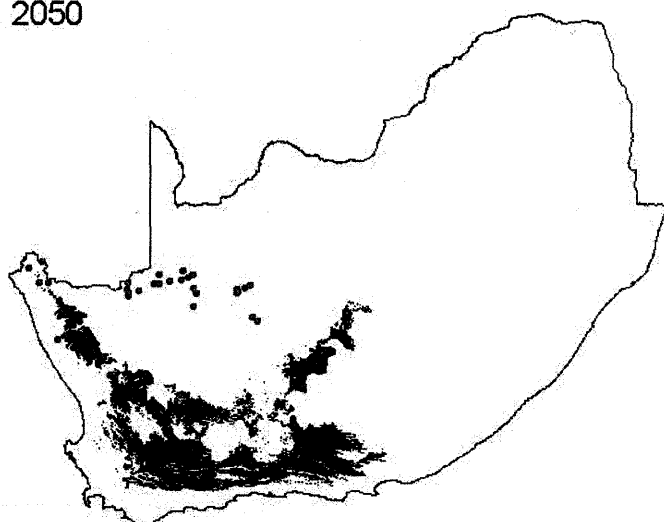
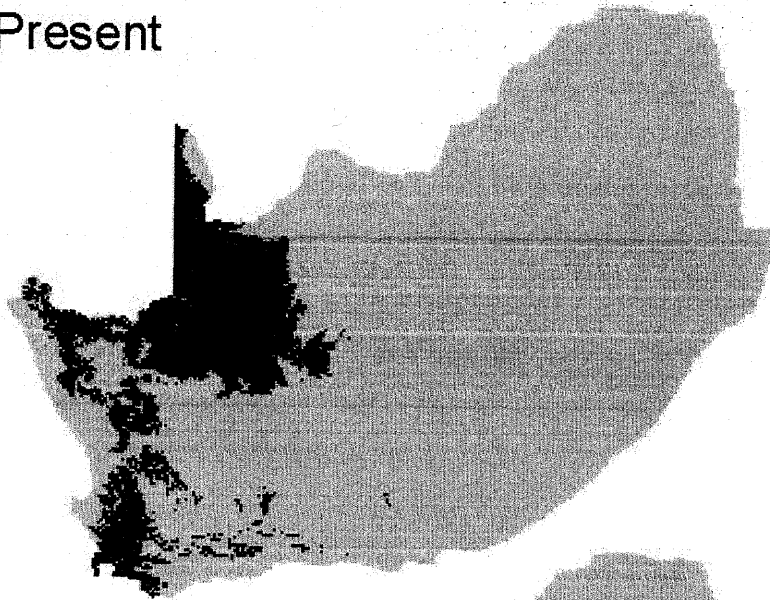
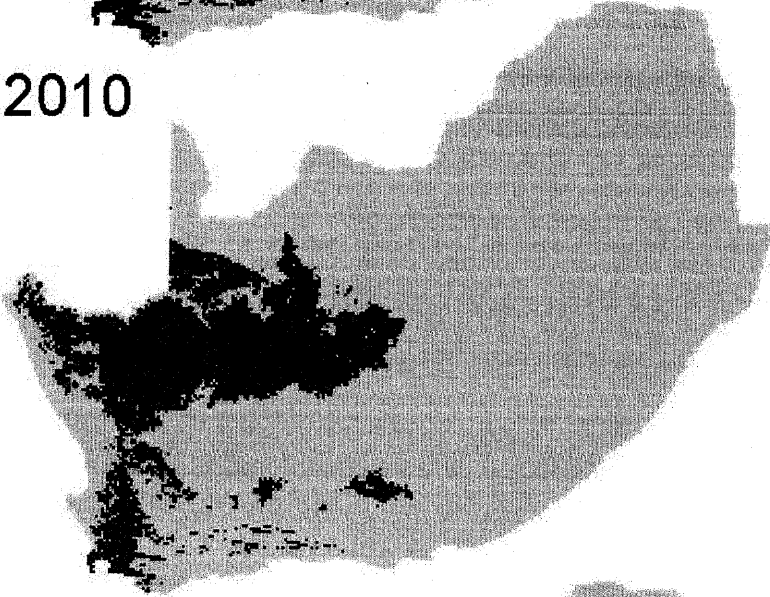


Figure 5: Bioclimatic envelope predictions for *Aloe dichotoma* based on CSM predictions for a) the present, b) 2010, c) 2020, d) 2030, e) 2040 and f) 2050. Red points show the current distribution.

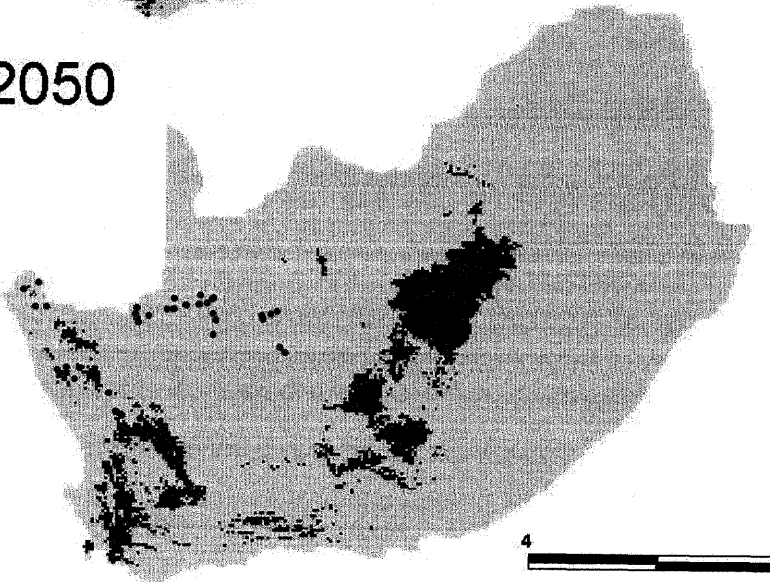
a) Present



b) 2010



c) 2050



absent
present
current
distribution

4 0 4 Kilometers

Figure 6 : Maps showing the results of generalized additive modelling of *Aloe dichotoma* distributions for (a) the present, (b) 2010) and (c) 2050. (Red points show the current distribution).

GAM projections of *Aloe dichotoma*'s distribution change show similar trends to those of bioclimatic modelling (figure 6) and, like bioclimatic models, suggests that the current envelope extends far south of its current distribution. Interestingly, the GAM envelope indicates that there is a disjunction in the envelope immediately south of the species' southernmost distribution, and this may be the cause of *Aloe dichotoma*'s failure to disperse southwards. Future GAM climate envelopes suggest that this disjunction disappears and dispersal southwards could become possible.

The current envelope predicted using GAM differs from the bioclimatic models in that it includes northern Bushmanland as well as extending northwards into the Kalahari-Gemsbok region. Sensitivity analysis shows that these areas are excluded from the bioclimatic modelling due to excess heat units and high soil fertility respectively. The 2050 GAM bioclimatic envelope, like the CSM bioclimatic scenarios, suggests that some suitable climate will still exist in the high altitude western parts of *Aloe dichotoma*'s current range as well as in the southern Cape Fold Mountains. Its 2050 range is predicted to extend eastwards into the Free State Province, again similar to predictions by the CSM bioclimatic model. Sensitivity analysis reveals that if, as in the step-wise GAM model, soil moisture days (summer and winter) are excluded from the bioclimatic modelling, south-eastern sections of the 2050 bioclimatic envelopes also extend further East.

Testing the predictions: spatial analysis

Unmatched sites measured in 1997 and 2001 showed no significant difference in recruitment, establishment or mortality (Mann-Whitney U-test). As a result, data from these sampling periods were combined for use in spatial analyses. In all analyses, $p < 0.05$ was considered the threshold for significance.

The percentage of mortality in each population is shown in figure 7. Greatest mortality occurs at sites in the northwest of *A. dichotoma*'s South African range (Kenhardt, Pofadder), along the Orange River valley (Augrabies, Volop, Onseepkans), as well as in the Richtersveld (Kokerboomkloof). Least mortality occurs in the Western and Southern parts of *Aloe dichotoma*'s range, although Strausheim in the North West also has low mortality.

Dead (%)
 Live (%)

Present envelope
 2010 envelope

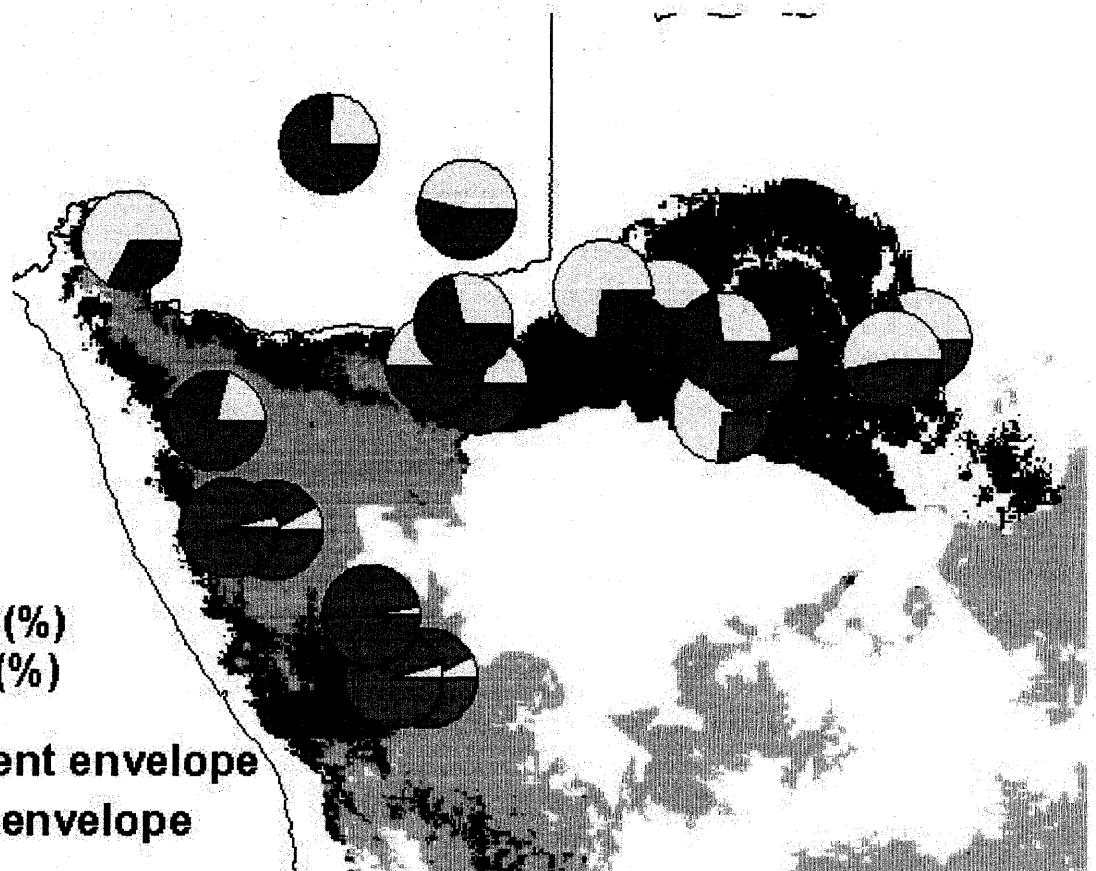


Figure 7: locations and percentage of live and dead individuals in 1997 and 2001 study populations. The red area shows the current bioclimatic envelope and the superimposed pink area shows the predicted 2010 envelope (HadCM2 no-sulphates model).

Height Classes

0-0.3m
 0.3-0.6m
 0.6-1m
 1-2m
 2-3m
 3-4m
 >4m

Present envelope
 2010 envelope

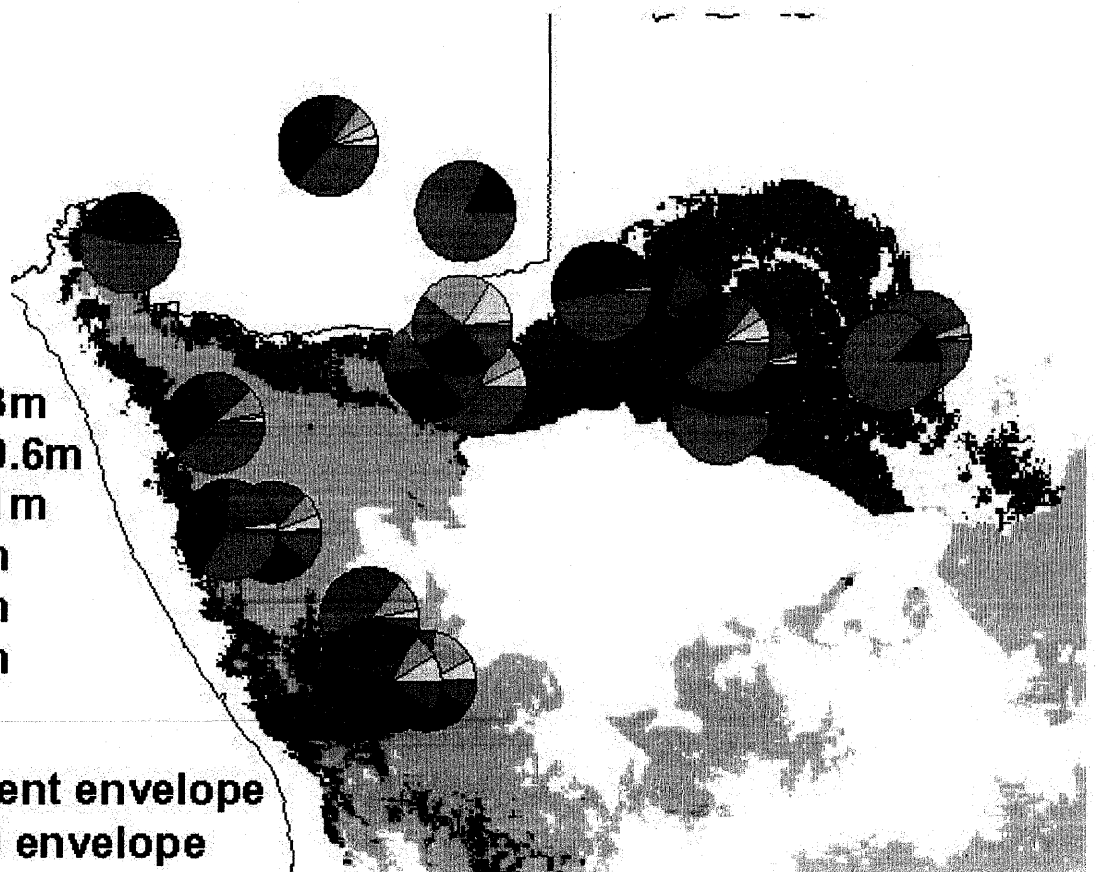


Figure 8: locations and size structure in 1997 and 2001 study populations. The red area shows the current bioclimatic envelope and the superimposed pink area shows the predicted 2010 envelope (HadCM2 no-sulphates model).

Aloe dichotoma's current bioclimatic envelope and, superimposed on it, the envelope predicted by the HadCM2 (no-sulphur) model for the year 2010 are shown in figure 7. *Aloe dichotoma* populations with current distributions outside the predicted 2010 envelope show a significantly higher mortality than those remaining within the 2010 envelope (Kolmogorov-Smirnov, $p < 0.05$). There was no significant difference in the heights of dead individuals between the two groups. Table 1 shows the results of comparisons between mortality and at each 1997 and 2001 study site and the mean of all populations combined (Chi-squared 2-tailed test) and groups sites according to their position relative to the 2010 climate envelope. This illustrates a clear pattern of below-average mortality in sites in or bordering with the 2010 climatic envelope, and a general trend of above-average mortality in sites outside the 2010 envelope.

Population demographics at each study site are shown in figure 8. A summary of comparisons between recruitment and frequency of >4m height plants at each site with mean recruitment for all sites (Chi-square test) is shown in table 1. There is little pattern, however, in deviances from the inter-population mean of recruitment and while the >4m height comparisons show what appears to be a trend of fewer older plants associated with the 2010 envelope, this is not significantly less than at sites outside the 2010 envelope (Kolmogorov-Smirnov Test). A comparison of recruitment (plants <1m in height) inside and outside the 2010 climatic envelope also revealed no significant difference (Kolmogorov-Smirnov Test). No difference was found between plant densities within and outside the 2010 envelope (Kolmogorov-Smirnov Test).

Testing the predictions: temporal analysis

The demographics of sites that were observed during 1987-1997 and 1987-2001 intervals are shown in figure 9. Minimal recruitment between 1987 and 1997, detected as decreases in plants in the <1m height class, were found at four of the eight revisited sites (Fisher's exact test), namely at Klipdrift ($p < 0.000$), Onseepkans ($p < 0.05$), Augrabies ($p < 0.002$) and Strausheim ($p < 0.05$). During the interval 1987-2001 significant decreases in the frequency of <1m high plants were found at Springbok ($p < 0.001$) and Snyfontein ($p < 0.001$) but not at Keetmanshoop or Kokerboom. With the

exception of Springbok, all South African sites showing decreased recruitment fell outside the 2010 bioclimatic envelope.

Table 1: Summary of the deviances of each 1997 and 2001 study population's mortality, recruitment and establishment frequencies from the means of all populations. + 's and - 's represent population means above and below expected inter-population means respectively. Non-significant differences ($p > 0.05$) are indicated by a "0". Comparisons were made using a Chi-squared 2-tailed test and the probability that the difference results purely from chance (P) are given in each case. Sites are divided into those falling outside the 2010 climate envelope, close to its border and inside it.

Relationship with 2010 envelope	Site	MORTALITY		RECRUITMENT		>4m HEIGHT	
		Difference from mean	P	Difference from mean	P	Difference from mean	P
Outside	Kakamas	0	0.237	-	0.032	-	0.000
	Skietskipkop	0	0.820	+	0.000	-	0.002
	Kenhardt	+	0.000	0	0.812	+	0.002
	Dinamietputs	0	0.609	0	0.965	0	0.341
	Kokerboomkloof	+	0.000	-	0.033	+	0.005
	Volop	0	0.176	0	0.216	0	0.540
	Boegoebergdam	+	0.003	-	0.001	+	0.000
	Strausheim	-	0.003	0	0.166	-	0.000
	Pofadder - North	+	0.020	0	0.305	0	0.228
	Pofadder - South	+	0.006	0	0.866	+	0.047
Onseepkans	0	0.075	+	0.000	-	0.004	
Border	Klipdrift	-	0.000	0	0.607	-	0.000
	Gemsbokrivier	-	0.002	0	0.090	-	0.000
	Nieuwoudville	-	0.000	0	0.322	-	0.003
Inside	Springbok	0	0.087	0	0.874	0	0.440
	Kamieskroon	-	0.005	-	0.016	0	0.720
	Nourivier	-	0.001	0	0.953	-	0.001

Mortality increased between 1987 and 1997 at Pofadder (South)($p < 0.05$) (outside 2010 envelope) and between 1987 and 2001 at Keetmanshoop ($p < 0.02$) and Snyfontein ($p < 0.001$) (Fisher's exact). A decrease in frequency of mature plants (>4m) was found at Kenhardt (Fisher's exact, $p < 0.05$) (outside 2010 envelope).

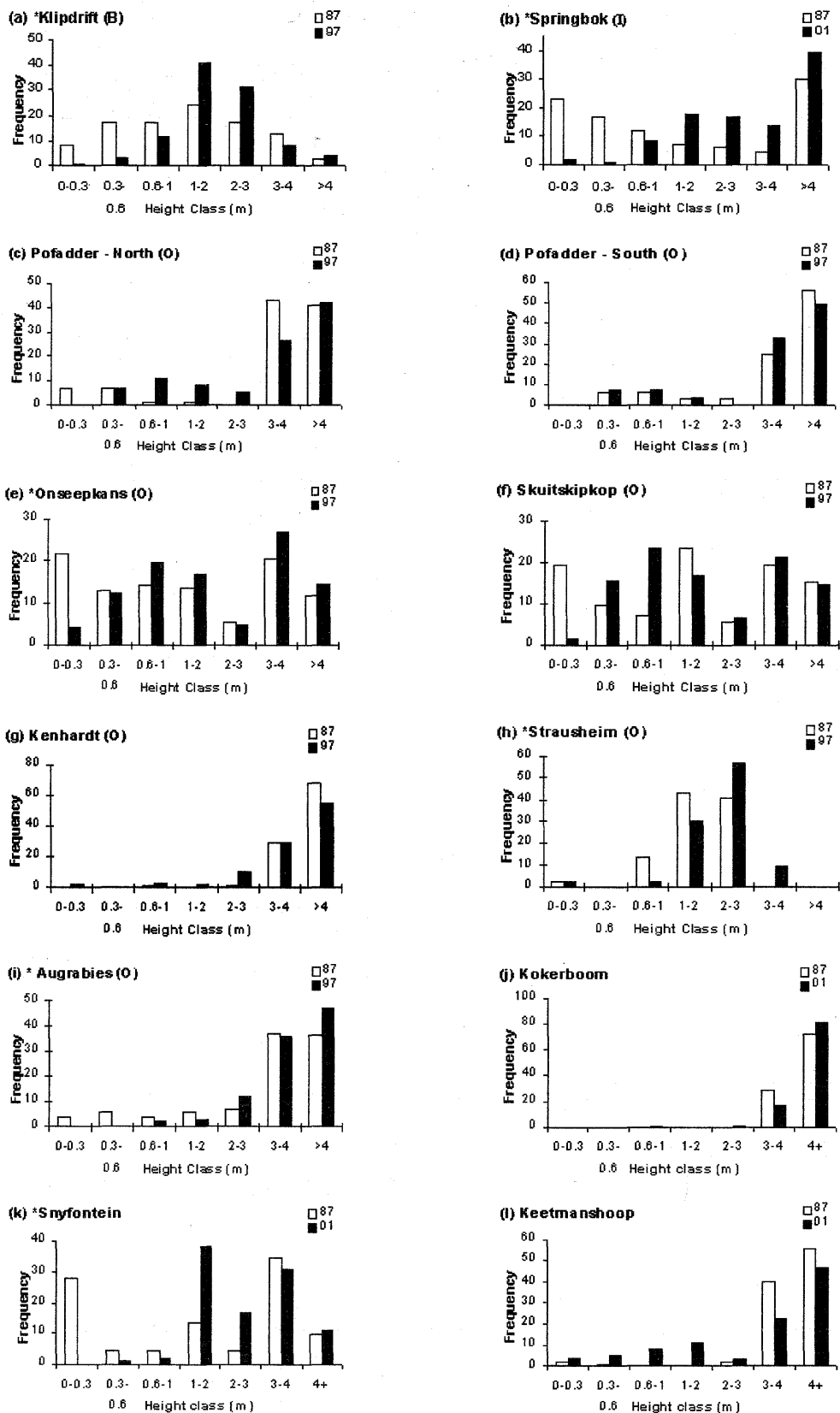


Figure 9: Histograms showing the demography of *Aloe dichotoma* populations in 1987 and either 1997 or 2001. Sites in which a significant decrease in recruitment occurred are marked (*), as are the population's position relative to the 2010 bioclimatic envelope (I=inside, B=Border, O=outside). Unmarked sites occur in Namibia were not

included in model predictions. Probability values are given where there is a significant decrease in recruitment (number of plants of <1m height). (a) Klipdrift ($p<0.000$), (b) Springbok, (c) Pofadder (North), (d) Pofadder (South), (e) Onseepkans ($p<0.05$), (f) Skuitskipkop, (g) Kenhardt, (h) Strausheim ($p<0.05$), (i) Augrabies ($p<0.002$), (j) Kokerboom, (k) Snyfontein and (l) Keetmanshoop.

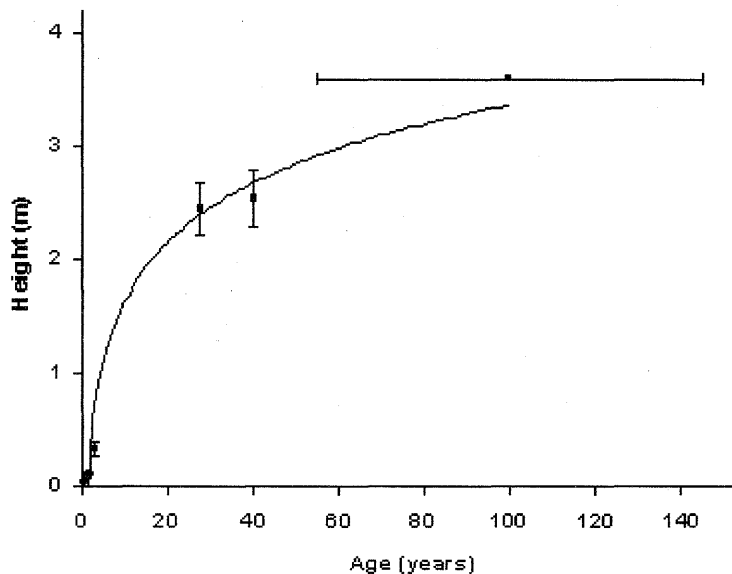


Figure 10: Graph showing the relationship between plant height and age, derived from plants of known age at the Van Rhynsdorp nursery (data points 1-5) and from carbon dating of a trunk segment (datum point 6; Vogel 1974) (regression equation: $y = 0.7507\text{Ln}(x) - 0.0882$).

An estimation of the relationship between *Aloe dichotoma*'s height and age is shown in figure 10. These results must, however, be interpreted with caution as the curve is based on sampling of the very limited number of known-age individuals available. The estimated age shown in datum point 6 (100 years old) by carbon dating has an uncertainty value of 45 years (Vogel 1974). Data points 1-5 are derived from sampling at the Van Rhynsdorp nursery where plants receive regular water throughout the wet and dry season and are therefore likely to grow faster than plants in their naturally arid environments (B. Wiese, pers. com.). Further, *Aloe dichotoma* was observed to show a large amount of phenotypic variation between (and even within) populations. Plants from the Kamieskroon and the Richtersveld areas are an extremely tall (up to 9m), relatively narrow-stemmed phenotype (Williamson 2000a), while plants in the southern populations (Nieuwoudville, Gembokrivier and Kliprand) are a short (seldom over

4m), very thick-stemmed phenotype. The curve shown in figure 10 utilises all information available at this time, and despite these drawbacks, it provides some help in the interpretation of height-based demographic studies.

Are the apparent decreases in recruitment over the past 14 years attributable to climate? The height vs. age curve was used to reclassify demographics of a spectrum of populations into broad age classes which are useful in determining when recruitment was likely to have occurred. Comparisons between these and rainfall records for corresponding areas are shown in figure 11. Rainfall medians are shown for summer, winter and total annual rainfall. In years when rainfall exceeded the limit of the upper quartile range, deviance from this limit (mm of rainfall) was plotted and these years appear as peaks on the graphs.

Comparison between rainfall for populations in figure 11 clearly show that populations encounter very different rainfall regimes. Klipdrift and Springbok populations frequently encounter wet years with peaks in both summer and winter rainfall. Populations at these sites have individuals spread through all age classes and recruitment appears to occur regularly. Little recruitment is evident between 1987 and 1997, but recruitment following the high rainfall in December 1996 at both sites is not likely to have been visible in the mid-1997 survey.

Pofadder rainfall records suggest that no suitable window of recruitment has occurred over the last 50 years and this is reflected in the low frequencies of individuals in the lower age classes. Age structure of the Kenhardt population shows that very little recruitment has occurred in approximately the last 60 years. This is despite a series of peaks in the mid 1970's which would be expected to have resulted in a cohort of individuals in the 8-20 year age class in both 1987 and 1997. An investigation of the relationship between rainfall and recruitment was conducted by regressing the height of populations' youngest cohort (>5 individuals) against the number of years since the last rainfall peak. This produced a weakly positive, though non-significant correlation (Spearman, $N=9$, $R=0.605$, $p=0.084$), while correlations with summer and winter rainfall were weaker. This analysis, as well as the failure of the Kenhardt population to recruit following successive rainfall peaks suggests that other climate factors such as

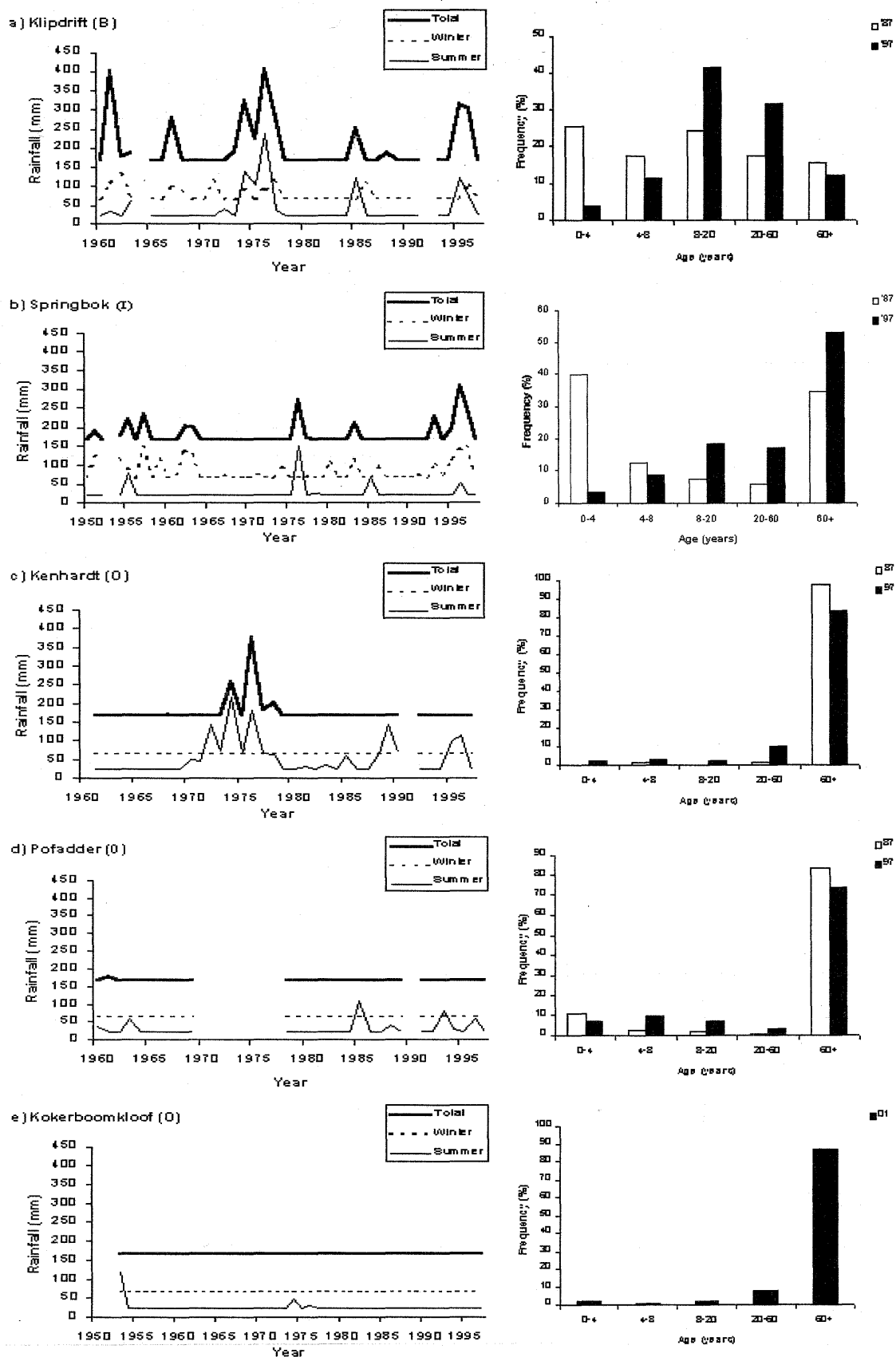


Figure 11: Graphs showing median summer, winter and total annual rainfall at 5 sites over a 50-60 year period. Deviations from the medians show rainfall (mm) in excess of the upper quartile limit. Histograms indicate the frequency of *Aloë dichotoma*

populations in age classes (derived from figure 10) at corresponding study sites, namely (a) Klipdrift with rainfall data from Calvinia, (b) Springbok (c) Kenhardt, (d) Pofadder (North and South) and (e) Kokerboomkloof (Richtersveld) with rainfall data from Vioolsdrif. Populations' positions relative to the 2010 H2N bioclimatic envelope are shown as (I)(inside), (B) (bordering with) and (O)(outside the envelope).

temperature may interact with rainfall in determining the conditions suitable for recruitment.

Finally, the Kokerboomkloof population shows again that very little recruitment has occurred during the last 60 years. In fact, the single individual in the 4-8 year age class was growing in a small crevice in a boulder and is likely to be an old plant with stunted growth. While localised climate is extremely variable in the Richtersveld region and fog plays an important role (Williamson 2000a), rainfall records from nearby Vioolsdrif

are likely to give an idea of the overall moisture pattern. These suggest that climate may indeed be the factor limiting recruitment in this population. The fact that one extremely rare high rainfall period 50 years ago seems to be responsible for the bulk of recruitment does not bode well for the survival of the Kokerboomkloof population.

Canopy loss

A photograph showing an example of branches that have lost their leaves and died appears in figure 12. Canopy loss and mortality were significantly correlated (Spearman; $R=0.59$; $p<0.05$) (figure 13) suggesting that canopy loss does provide an indication of population stress. For this to be a useful measure of climate change a link must be established between climate stress and canopy loss. No correlation was found between mean canopy loss and any climatic variable. The interactive effects of climate variables as well as climate variability, rather than mean climate, are more likely to cause stress, however, and these factors have not been investigated in this study.

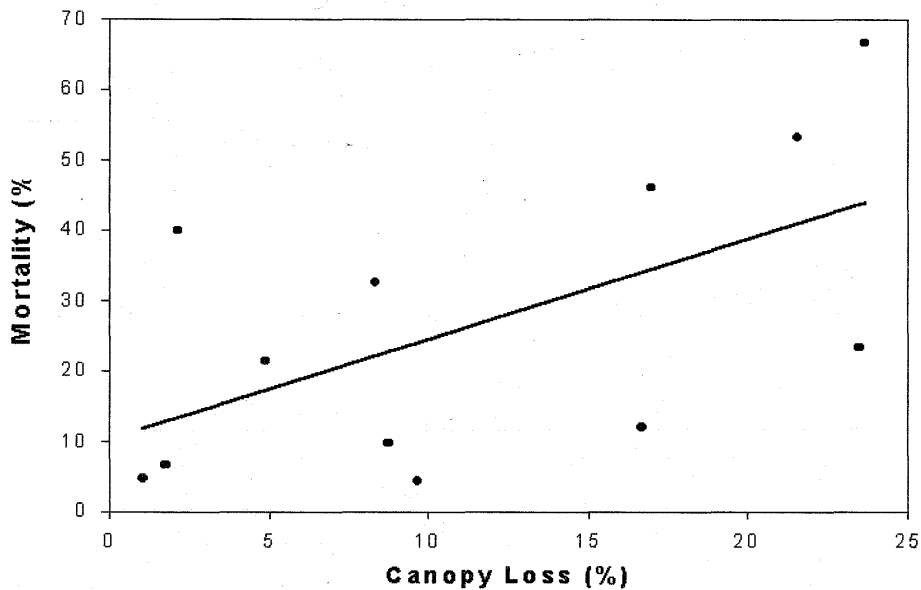
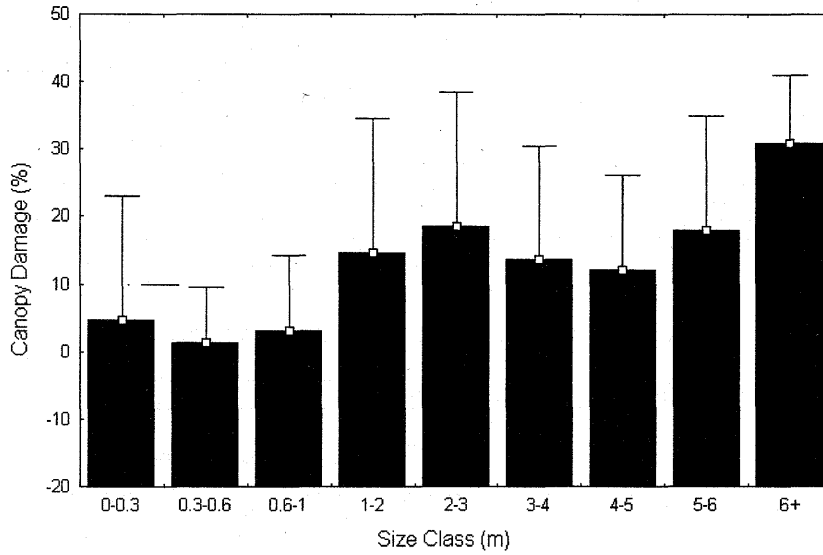


Figure 13: Graph showing the relationship between mean population canopy loss and mortality (Spearman, $N=9$, $R=0.59$, $p<0.05$)

There is no correlation between canopy loss and either dung frequency (Spearman, $N=12$, $R=-0.07$, $p>0.8$) or stem damage (Spearman, $N=10$, $R=0.30$, $p>0.4$) and this rules out the possibility that animal damage is the cause of canopy loss. Furthermore, no baboon dung was encountered at any sites during dung frequency counts.

Individual plant age was strongly positively correlated with canopy loss (Spearman, $N=1177$, $R=0.57$, $p<0.001$) (figure 14 (a)). It is not clear whether this indicates that canopy loss is simply a result of senescence, or that climate-stress effects accumulate over time. The high canopy loss in the 2-3m height class did not correspond to an increase in mortality in this or smaller height classes (figure 14 (b)) and could indicate a response to a particular drought period in the past. Results may also be clouded by the difficulty in retrospectively distinguishing branch damage by caused by herbivores, birds burrowing nests in branches and branches simply becoming too heavy with age from spontaneous branch loss. In summary, the results of this study are unsuccessful in determining whether *Aloe dichotoma* canopy loss can be used as an indicator of climatic stress.

a



b

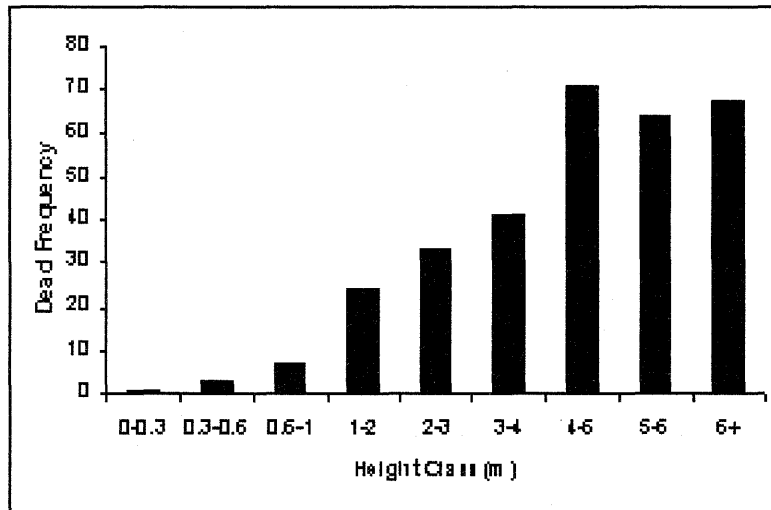


Figure 14: (a) Box and whisker plot showing the mean canopy loss per size class (boxes indicate the standard error and error bars represent the standard deviation) and (b) the frequencies of dead plants in corresponding size categories.

Non-climatic influences on distribution

Competition & seed availability

Plant density may affect recruitment both at low densities, by the reduction of seed availability, and at high densities due to competition. Live plant density was not significantly correlated with recruitment (Spearman rank order, $N=24$, $R=0.21$; $p>0.3$) (figure 15), suggesting that competition between seedlings and adults is not affecting

recruitment. Live density was, in fact, significantly negatively correlated with mortality (Spearman, $N=24$, $R=-0.519$; $p<0.01$), indicating that competition between adults is also negligible. There was also found to be no correlation between the number of plants growing with merged trunks and mortality (Spearman rank order; $N=12$, $R=0.01$; $p>0.9$). These results suggest that within-species competition is not impacting on *Aloe dichotoma*'s success.

The percentage of adult plants (>2m in height) producing fruit was not found to be correlated with mortality (Spearman, $N=12$, $R=0.01$, $p>0.9$). Rebelo et al. (unpublished data) found no significant correlation between recruitment and mean number of flowers per plant, number of viable fruits per inflorescence or parasitized fruit per inflorescence (Spearman, $R=0.25$ and 0.19 respectively; $p>0.05$). This provides further evidence that seed availability is not a limiting factor in recruitment.

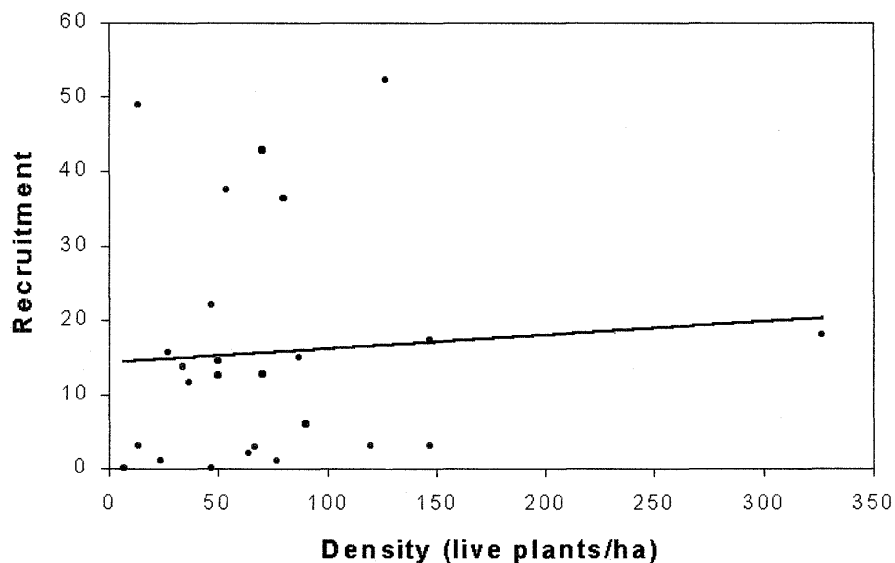


Figure 15: Graph showing the relationship between density of live plants and recruitment (Spearman, $N=24$, $R=0.21$; $p>0.3$).

Herbivory

An example of severe stem damage is shown in figure 16. Although stem damage was positively correlated with mortality, this relationship was not significant (Spearman, $N=10$, $R=0.57$, $p=0.084$) (figure 17). There is also no relationship between stem damage and recruitment (Spearman, $N=10$, $R=-0.46$, $p>0.15$). This, coupled with the lack of correlation between grazing score and recruitment (Spearman, $N=25$, $R=0.05$;

$p > 0.8$) (figure 18), suggests that recruitment is not severely affected by herbivory of either *Aloe dichotoma* juveniles or nurse plants.

When mortality and trunk damage to plants $> 1\text{m}$ in height only is considered, the correlation with mortality was much weaker (Spearman, $N=10$, $R=0.4316$, $p > 0.3$). This result was expected since the conducting tissue of these monocotyledonous trees is extremely robust when structural damage is not sustained. Trees completely ring-barked in the past by porcupines in the Nieuwoudville population were still growing and showed no canopy loss or sign of senescence. Tree succulents are a source of moisture to a host of animals in arid areas (Midgley et al. 1997) and hence the positive relationship between mortality and animal damage may be more an indication of mutual drought stress, than of a causal relationship.

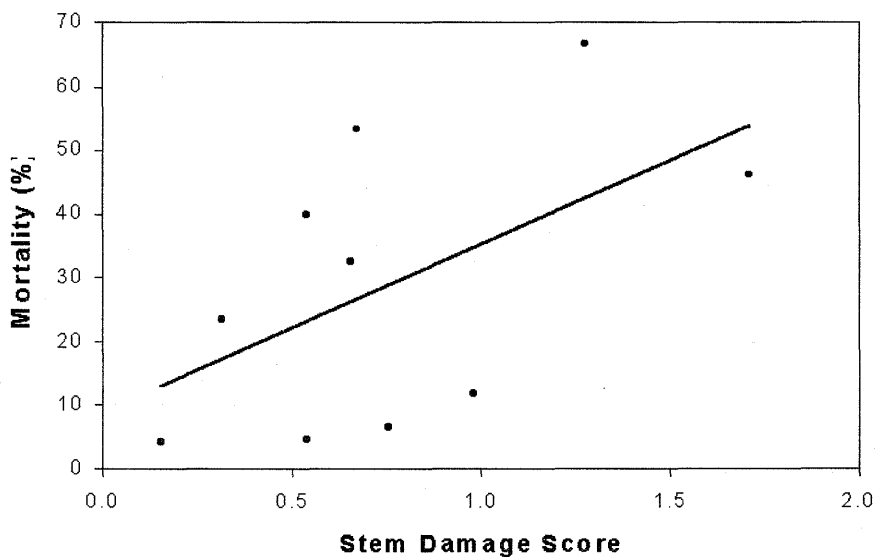


Figure 17: Graph showing the relationship between live stem damage and mortality (Spearman, $N=10$, $R=0.57$, $p=0.084$).

There was no correlation between the trunk scars of dead trees and mortality (Spearman, $N=10$, $R=0.23$; $p > 0.5$). Grazing score and mortality were not significantly correlated. These results provide further support for the conclusion that herbivory does not have a significant impact on *Aloe dichotoma* population adult survival.

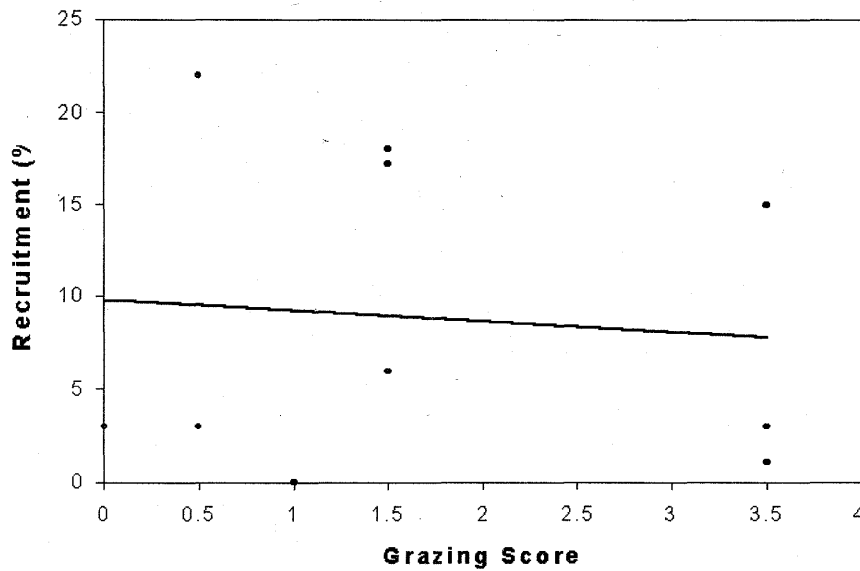


Figure 18: Graph showing the relationship between grazing and recruitment (Spearman, $N=10$, $R=0.05$; $p=0.820$).

Removal of seedlings by plant collectors

Recruitment at sites advertised as tourist attractions showed significant difference in frequency of <1m height individuals relative to less-visited populations (Mann-Whitney, $N=21$, $U=31.00$, $p>0.5$). Further, no correlation was found between distance of populations from tar roads and recruitment (Spearman, $N=21$, $R=0.081$, $p>0.7$). This suggests that removal of seedlings by plant collectors is not having a significant impact on *Aloe dichotoma* recruitment.

Fungal pathogens

Neither trunk nor leaf fungus showed significant relationships with either mortality or recruitment, indicating that they are not important in determining the distribution of the species and are unsuitable as population health indicators. A strong positive correlation was found, however, with winter soil moisture (Spearman, $N=8$, $R=0.97$, $p<0.001$), and negative correlations with summer soil moisture (Spearman, $N=8$, $R=-0.80$, $p<0.02$), heat units (Spearman, $N=8$, $R=-0.99$, $p<0.001$) and potential evapotranspiration (Spearman, $N=8$, $R=-0.71$, $p<0.05$) were indicated. These strong fungal climate affinities, while not impacting on *Aloe dichotoma* population health, should be investigated for their effect on decomposition rates of dead plants.

DISCUSSION

Bioclimatic modelling

Bioclimatic models present disturbing scenarios of the effects of climate change on *Aloe dichotoma*. If predictions are correct then escalating dieback and failed recruitment can be expected in all South African *Aloe dichotoma* populations in the next 50 years. Unless the species is able to disperse relatively quickly into the southern Karoo, Little Karoo and Free State it is unlikely to survive in South Africa in the future.

But how reliable are these predictions? Criticism has been levelled at bioclimatic models for their assumption that climate limits plant distribution, as well as for assuming that species are able to occupy their fundamental niches (Brereton et al. 1995). Realised niches may be smaller than fundamental niches due to the interactive effects of herbivores, interspecies competition and ecosystem processes such as fire. This study investigates non-climatic variables pertinent in *Aloe dichotoma*'s environment and establishes that herbivory, pathogen infection, seed availability and plant collection do not have significant effects on survival or distribution. The apparent restriction of recruitment to favourable years makes inter-species competition effects unlikely. Further, the high discrimination capacity of the GAM model based on just 3 climate and 1 soil variable provides strong support for the conclusion that macroclimate determines *Aloe dichotoma*'s distribution. This is in agreement with the conclusions of Rutherford et al (1999, 1996), Brereton et al (1995), Woodward (1988), Thuiller et al. (in press) and Midgley et al. (submitted).

Bioclimatic modelling has been criticised for placing undue emphasis on individuals at the fringe of bioclimatic zones instead of on the bulk of the population (Jeffree and Jeffree 1994). The use of minimum and maximum tolerances in modelling may, however, be more biologically meaningful than mean tolerances. The fact that South African climate change studies fail to include land transformation and habitat fragmentation effects has been raised as an issue (van Jaarsveld and Chown 2001). This criticism is valid and other studies have included these variables in bioclimatic

modelling scenarios, but it must be noted that their inclusion is unlikely to change overall trends and will make bioclimatic envelopes even smaller.

Why does *Aloe dichotoma*'s current climate envelope extend southwards into the Southern Karoo and Cape Fold mountains when the species clearly does not inhabit this region? The first possibility is that, while the current climatic envelope was interpolated from *Aloe dichotoma*'s distribution in the Northern Cape and the envelope provides a good fit in this area, it cannot necessarily be extrapolated to other regions and habitats (Brereton et al. 1995). An environmental variable specific to the southern regions may prevent *Aloe dichotoma* from establishing here. Although fungal pathogen infection was suspected to be such a variable, the results of this study confirm that this is not the case. Herbivory and plant collection have been eliminated as possible explanations. The type of herbivory experienced by *Aloe dichotoma* in the past, however, may have been more severe than at present. In his journal (15 September 1778), the traveller, Wikar, noted that the area in which he was hunting elephants was called "the Kalagas". Kalagas is from the Nama word meaning *Aloe dichotoma* and has been identified as 20 miles north-east of Pella (Reynolds 1950). Megaherbivores, abundant in pre-colonial times, may have had greater impacts on *Aloe dichotoma* than herbivores today and thereby have prevented *Aloe dichotoma* from establishing in the Southern Karoo.

A second consideration in understanding *Aloe dichotoma*'s distribution is its evolutionary past. Over the last 20 000 years, summer and winter rainfall regions of the subcontinent have advanced and retreated several times (Midgley et al. 2001, Cockroft et al. 1998) and this may explain *Aloe dichotoma*'s tolerance for both summer and winter rainfall. Cool, dry and arid periods occurred in the region during the last glacial maximum, as well as between 14.4-12.5 and 10.9-9.3 K before the present (Shi et al. 1998) and the resulting contraction of flora into highland refuges such as the Richtersveld (Midgley 2001) may have been the cause of allopatric speciation of *Aloe pillansii* and *Aloe ramosissima*. The warmest and wettest of all conditions occurred between 6.3 and 4.8 K before present (Shi et al. 1998) and this may have been the period of *Aloe dichotoma*'s extension into the drier parts of its range and a retraction from areas in the south. The large recruitment in the southern study populations suggests that they are relatively young and possibly a recent return

of the species' to its southern range, as the climate once again becomes more arid in the north.

Finally, GAM modelling of the current climate envelope suggests that a disjunction in the bioclimatic envelope may be responsible for the failure of *Aloe dichotoma* to disperse into potentially suitable southern regions. This raises the question of effectiveness of *Aloe dichotoma*'s dispersal mechanisms and hence how will *Aloe dichotoma* respond to the need to rapidly disperse into new areas due to climate change. Individuals produce a large number of small (15 x 8mm), light, 3-winged seeds, which appear to be dispersed by wind, both through the air and along the ground. The large phenotypic variation between populations suggests that dispersal distances are typically short, yet many populations as well as lone individuals have been able to colonise isolated hills and ridges. Hughes et al. (1996) suggest that long-lived species will battle to relocate to new envelopes because they cannot migrate fast enough and the long interval (12-15 years) between recruitment and reproductive maturity (B. Wiese, pers. com.) will slow dispersal.

The similarity in trends predicted by general additive modelling with those of the three bioclimatic models strengthens confidence in these predictions. The discrepancies between them, however, highlight the differences in the basic theoretical model assumptions. The tolerance limit approach of bioclimatic modelling can result in sites being rejected, despite suitable climatic conditions if, for example, soil fertility is outside the tolerance range. GAM predictions would, however, include this area, as soil fertility was not found to be an essential variable for determining distribution. This discrepancy raises a fundamental question about plant distribution response to environmental variables: do plants respond in an absolute (all-or-nothing) fashion (as bioclimatic modelling assumes) or are they able to tolerate some compromise (as the probability calculations in GAMs assume)? Small-scale microhabitat variation makes this a difficult question to resolve using bioclimatic data at this scale.

GAMs, like bioclimatic models, face difficulties when distributions within a small area must be extrapolated to a much larger area. Step-wise GAMs are extremely useful for highlighting which of a given set of variables are important in predicting

distributions and show their effects on distribution, but they give no information about variables' optimum or tolerance values (Thuiller et al., in press). GAMs also have the advantage of using both presence and absence data, thereby increasing data points and strengthening the model's predictive capabilities.

Tests of Spatial and Temporal Patterns

The null hypothesis that no difference occurs between populations inside and outside the future bioclimatic envelopes is conclusively rejected by the results of the spatial mortality analysis. The greater mortality experienced by populations outside the 2010 climate envelope compared with those inside provides strong support for predictions made by climate change models.

Very little recruitment has occurred at any South African site during the 14 year time interval of this study. This, in itself, is not necessarily disturbing since long recruitment intervals are expected for this and other giant desert succulents (Jordan and Nobel 1979, Nobel 1988a). Size class distributions suggest, however, that several populations have not recruited significantly in over 50 years. Similar size structures have been described for two other Richtersveld *Aloe dichotoma* populations, as well as for all populations of *Aloe pillansii* (Midgley et al. 1997). In the Spergebied, a few hundred kilometres North of the Richtersveld, hundreds of dead *Aloe dichotoma* individuals exist in what would once have been a population, but in which no live plants now remain (Jurgens 1997, G. Williamson, pers com.). Rainfall records suggest that recruitment responds to climatic events and that, in areas where populations show little recruitment, suitable climatic windows have been extremely rare. The dramatic population declines of these long-lived, persistent succulents suggest that areas once colonised by *Aloe dichotoma* have become unsuitable. The findings of this study suggest that this is due to a change in climate.

Improvements and Further Studies

Direct effects of herbivory are not correlated with mortality, but indirect effects of grazing on current and potential nurse plants are more difficult to determine. Dung frequency indicates the amount of biomass lost, but as *Aloe dichotoma* grows in

habitats ranging from *Acacia karoo* grasslands to arid deserts it provides little insight into remaining biomass or nurse plant potential of a site. Nurse plants provide the necessary traps for the collection of wind-blown seeds. They create special microhabitats for seedlings by shading, hence reducing short wave irradiation and lowering maximum soil surface temperature by 10-20°C (Nobel 1988a, Jordan and Nobel 1979). It is often low temperatures, rather than high, to which seedlings are most vulnerable (Nobel 1988b). Nurse plants affect incident long wave radiation thereby raising air temperature and have been shown to increase stem apical temperatures of *Carnegiea gigantea* by up to 2°C (Nobel 1988a, 1988b). Their interception of photosynthetically active radiation, however, can drastically reduce seedlings' growth rates (Nobel 1988a). The importance of nurse plants for the recruitment of *Aloe dichotoma*, as well as the impacts of land use and climate change on nurse plants and seedling physiology require further investigation.

Mean percentage loss of canopy appears to provide a good indication of population health but this study has failed to establish whether or not this is due to climate-induced stress. It has, however, highlighted the prevalence of a previously unreported phenomenon. The large potential benefits of finding an easily observable measure of plant climate stress make this a worthy topic for further research. The inability of *Aloe dichotoma* to resprout or for growth to continue following the death of a branch apex mean that a comparison between the length of dead and live branches could reveal how long ago the branch death occurred and hence valuable information about past climatic conditions.

The disparity between the results of the temporal study, in which recruitment appeared to be the response to climate stress, and the spatial analysis, in which mortality emerged as the climatic response is puzzling. A dead individual may take over 10 years to completely fall over in its typically arid environment (Midgley et al. 1997) and even longer to disintegrate. A photograph taken of *Aloe pillansii* in the Richtersveld by G.W. Reynolds before 1950 was matched by a photograph of the same plants in 1995 (Midgley 1997). Dead individuals in the first picture were still evident in the second, approximately 50 years later. It is therefore possible that mortality differences detected in the spatial analysis occurred before the time interval included in the temporal study, resulting in no difference being detected. This, as

well as the strong climatic effects of climate on fungal pathogens, highlights the high priority of further studies on decomposition rates of dead *Aloe dichotoma* individuals.

While the climate variables identified by Midgley et al. (submitted) are certainly critical and provide a useful generic model, the Succulent Karoo possesses its own novel climate characteristics. Fog from the Atlantic seaboard drifts many kilometers inland, condensing mainly in elevated areas such as the Richtersveld and Kamiesberg mountains. Areas receiving rainfall of as little as 25-50mm annually are able to support diverse, completely fog-dependent plant communities (Williamson 2000b). Biodiversity follows a trend of higher fog condensation in the Richtersveld National Park (Williamson 2000c) and its role in supporting dense plant communities is often underestimated (Williamson 2000b). Understanding, mapping and incorporating the effects of Atlantic fog as a climatic variable supplementing rainfall would help to refine climate change predictions of Succulent Karoo species.

Demography study results are confused by the phenotypic variation in *Aloe dichotoma*'s height. Interpretation of differences in frequencies of plants >4m in height is particularly difficult. This may be resolved by replacing height classes with volume classes calculated using basal circumference and height to first branching as variables in the equation for cylinder volume. This will equate the more biologically meaningful measure of water storage potential with age, and hopefully allow a better comparison of disparate phenotypes.

The ideal method of monitoring long term population changes is by individual based time series monitoring for use in matrix-based population viability analysis (Krebs 1999, Udevitz and Ballachey, 1995). Although meaningful results from individual-based studies of *Aloe dichotoma* are only likely to be available after several decades, the importance of this species as an indicator of climate change, a keystone and flagship species, as well as for its own inherent value make the initiation of a long-term individual-based monitoring program advisable.

Conservation Implications

Climate change is likely to result in an increase in extreme stochastic events (Easterling et al 2000). While this is conventionally regarded as increasing extinction risk, Higgins et al (2000) suggest that for plants with high survivorship of reproductive individuals, increased environmental stochasticity may promote recruitment. This potential positive effect of climate change is balanced, however, by the fact that the seedling stage is more sensitive to high temperatures (Nobel 1988b). The example of failed recruitment in the Kenhardt population, despite consecutive years of good rainfall, suggests that climate variables have interactive effects. This makes anticipating and planning for plants' responses to the effects of climate change even more difficult.

Infrequently recruiting, persistent species such as *Aloe dichotoma* rely on rapid reproduction in favourable years while individuals simply survive during unfavourable years. Therefore even in populations where recruitment has never been observed, the population may not be in decline (Higgins et al. 2001). In light of this strategy, the mortality of *Aloe dichotoma* adults shown in this study, is all the more concerning. The loss of each reproductive individual represents significant loss of 'storage' of the population's future reproductive potential (Higgins et al. 2000). The results of this study suggest that, in the face of climate change, there is cause for concern about the conservation of *Aloe dichotoma* and particularly for rare and closely related *Aloe pillansii*.

What other challenges will climate change introduce to the conservation of *Aloe dichotoma* and the Succulent Karoo? Migration routes may be blocked by land transformation or areas of unsuitable habitat such as the fertile central Bushmanland. New species ranges may not coincide with those of their bird, mammal or insect pollinators. Migrating species will encounter new competitors and pathogens and these interactions play important roles in determining survival (Harrington et al. 1999). These predictions have not incorporated the direct effects of elevated CO₂ and increased UV radiation on *Aloe dichotoma*'s physiology which may cause further disruptions. Non-linear climate responses and climatic 'surprises' are likely to lie ahead (Hewitson 1999). Organisms may respond by developing novel adaptations

(Hughes 2000), but this is an unlikely scenario for long-lived species such as *Aloe dichotoma*. Different phenotypes may have a tolerance narrower than that of the species as a whole (Hughes et al. 1996), further limiting dispersal and future genetic diversity. Bowers and Harris (1994) suggest that under conditions of environmental change, communities will become increasingly dominated by generalist species.

Conservations face the challenge of trying to plan for a future in which a force of unknown magnitude will affect ecosystems in ways not yet fully understood. Climate change models help to predict impacts, but how should conservationists use these and respond to the need to protect the remarkable diversity of species, patterns and processes of Succulent Karoo? Trends of potential range shifts should be incorporated in reserve networks. Metapopulation dynamics, interactions between species as well as with climate variables need to be better understood and the guilds and species traits most vulnerable to climate change effects identified. Biodiversity refugia, migration corridors and 'stepping stone' reserves (Cowling and Pressey 2001) must be identified and incorporated and in extreme circumstances, plant translocations should be considered. Climate change provides one of the greatest challenges that conservationists have faced. Given the likely increases in global aridity due to climate change, warm deserts become even more valuable as the source of genetic stock essential for evolution and diversification (Cowling et al. 1999).

Conclusion

This study has provided a test, not only of climate change predictions themselves, but also of the ability of bioclimatic modelling to translate these correctly into the impacts on biota. Projections need to be tested on a broad range of organisms, but these preliminary results suggest that bioclimatic modelling provides a useful tool for conservation planners for identifying areas vulnerable to the effects of climate change.

Aloe dichotoma, a long-lived, giant succulent occurring in both summer and winter rainfall zones, is likely to have a relatively high tolerance of variation in climate conditions. The long-term population trends highlighted by this study suggest therefore, that the climate changes they are currently encountering are more than simply normal fluctuations or cycles. In addition to this, the spatial pattern of

population decline shows a marked similarity to those that GCM's project due to greenhouse gas emissions. While *Aloe dichotoma* has survived climate fluctuations in past millennia, the changes predicted to occur over the next 50 years are far faster than anything previously encountered.

No single study can provide unequivocal evidence of global climate change (Hughes 2000), but this study adds to the growing number of examples showing trends consistent with climate change predictions. The findings have vital implications for the conservation of both a keystone species and the unique Succulent Karoo biome in which it exists. These results constitute some of the earliest biological evidence of climate change in the tropics, arid areas as well as in Africa.

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