Regional differences in the long-term population dynamics of a succulent tree, *Aloe dichotoma* in the semi-arid Karoo, South Africa as revealed by repeat photography

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Abstract

Aloe dichotoma is a succulent tree up to 9 m, which is widely distributed in the drier western parts of South Africa and Namibia. The dramatic collapse in some populations in the last several decades has recently been used as evidence for climate change in the region. This study aimed to 1) analyze the growth dynamics and life history of *A. dichotoma* and 2) to assess the extent and rate of change in several *A. dichotoma* populations. Research was carried out at nine sites in both summer and winter rainfall areas in the Karoo. Methods used were matched photographs, combined with transects in the field to record the size class distributions. Although little is known about the growth of *A. dichotoma*, anecdotal information and matched photography show that the growth rate of the species is higher in the juvenile stage which lasts for approximately 50 years. The adult stage, lasting about 150 years, is characterized by a relatively small increase in plant volume with few major changes in the external architecture of the plant. The senescent stage may last for as long as 50 years and the life span of the species is thought to be approximately 250 years although considerable variation exists. Analysis of photograph pairs taken 41 – 98 years apart reveals a significant difference between populations occurring in the summer and winter rainfall areas in terms of the mortality rate, the recruitment rate and in the percentage change in the population. Transect data confirm these patterns. Lower recruitment, higher mortality and a decrease in population size were observed in the summer rainfall areas supporting the hypothesis of climate-induced effects, particularly extended drought, on *A. dichotoma* populations occurring in these areas. Populations in the winter rainfall area on the other hand, show a different pattern with relatively high recruitment, lower mortality and an increase in the number of individual trees in the population over time. Populations occurring in areas which receive both winter and summer rain appear to be healthiest. These results confirm earlier reports and interpretations of the population dynamics of *A. dichotoma* in the region and provide clear evidence for both an increase and a decrease in population size in different parts of the country.

Keywords: degradation, demography, drought, environmental history, vegetation change

1. INTRODUCTION

Some of the mysteries surrounding desert population dynamics have been solved by recent studies showing that communities in arid regions may experience short-term climatic variation within certain narrow limits (Goldberg & Turner 1986, Turner 1990). While successional processes might be present they are often difficult to detect and evidence is often inadequate to support the theory (Turner 1990). Long-term monitoring of plant communities is an essential prerequisite for understanding and eventually predicting the response of vegetation to both long-term climate change and short-term anthropogenic or natural disturbance and to understanding the possible selective forces that shape the demography of populations (Goldberg & Turner 1986).

Matched photography has been widely used to track vegetation change. Examples include studies in a North American grassland community (Buffington & Herbel 1965), long-term changes in Zambezi riparian woodland as revealed by photopanoramas (Dunham 1989), vegetation change in the Sonoran Desert (Goldberg & Turner 1986 and Turner 1990), long-term changes in the vegetation of the semi-arid Karoo (Hoffman & Cowling 1990), changes of desert plant populations of the Grand Canyon in Arizona, USA (Bowers et al. 1995), interpretation of vegetation change in western Namibia (Rohde 1997), the floristic biodiversity and history of African arid regions (Jurgens 1997) and many others. While information in matched photographs is often of high quality, it is also relatively limited, and field visits are therefore important in that additional observations can be made at the sites where the photograph pairs were taken.

The Karoo has a poor tree richness and comprises only 35 tree species, but this paucity is offset by the presence of charismatic endemics such as the quiver tree, *Aloe* *dichotoma*, the bastard quiver tree, *Aloe pillansii*, and the halfmens, *Pachypodium namaquanum*. These succulent tree species and several succulent shrubs are often the only perennial plants able to grow in this arid environment (Midgley et al. 1997).

Aloe dichotoma Masson (Liliaceae), known locally as Kokerboom (quiver tree), can reach a height of 9 m and occurs either as isolated individuals or in dense populations or "forests" in arid and treeless landscapes of the southwestern part of southern Africa. It is mainly found in the Succulent Karoo biome, eastward into the Nama-karoo biome and throughout southern Namibia as far as Usakos (Reynolds 1950, Foden 2002). Demographic data and life history information for this species are generally lacking.

A. dichotoma is among the keystone species pollinated by birds and plays an important role in providing food to sunbirds and other species and water to some animals during extremely arid times (Midgley 1996, Foden 2002). As is the case for many long-lived species, it depends on highly variable climatic events where germination and recruitment is episodic (Shreve, 1917, Beatley 1974, Ackerman 1979, Sherbrooke 1989, Bowers et al. 1995). To survive the dry period, seedlings must develop sufficient water storage tissue during the previous wet seasons, since slow growth limits water storage capacity. Seedling survival is therefore greatly influenced by drought (Jordan and Nobel 1979). Recruitment into populations is infrequent and requires a series of favorable climatic events, a suitable microhabitat location and escape from predation or competition (Sherbrooke 1989, Parker 1993).

Foden (2002) and Midgley (1996 & 1997) suggested that some populations of *A. dichotoma* have suffered from high levels of mortality and low levels of recruitment during the last several decades. These changes were said to have occurred in areas where a reduction in rainfall and an increase in rainfall variability have been predicted by several climate change models (Midgley et al. 2001). The projections of human-induced climate change and the evidence of a recent rapid shift in prevailing climatic conditions suggests that patterns of biodiversity may change on a landscape scale over time frames as short as decades (Hannah et al. 2002, Midgely et al. 2001, Midgey et al. 2002). *A. dichotoma* could be an important indicator species. It could be used to monitor the impact of long-term climate change including changes in physiology, reduced productivity and growth, and changes in species distribution and abundance due to migration and range shifts under different climatic conditions (Parmesan 1996, Parmesan et al. 1999, Midgley et al. 2002).

Previous observations show that herbivory by baboons (*Papio ursinus*), gnawing by porcupines (*Hystrix africaeaustralis*) and fungal infection are among the most important causes of mortality of *A. dichotoma*, while trampling and predation of seedlings and their nurse plants by goats may prevent recruitment (Reynolds 1950, Coates Palgrave 1977, Midgley 1996, Midgley et al. 1997, Foden 2002). Since *A. dichotoma* (as is the case for other aloes) is an obligate out-crosser, isolated plants may have reduced seed set and thus a reduction in the number of recruits (Hoffman 1988, Miggley 1996). Given these alleged adverse recruitment conditions and predictions of climate change, this study set out to analyze the growth dynamics, life history and the extent as well as the rates of change in several *A. dichotoma* populations using repeat photography.

2. METHODOLOGY

2.1. Study area

Research was carried out in the magisterial districts of Calvinia, Carnarvon, Hay, Kenhardt and Namaqualand, in the Northern Cape Province of South Africa during October and November 2002 (Fig. 1 and Appendix 1). Two of the districts (Calvinia and Namaqualand) receive rain predominantly in the winter months (April to September) while the others receive summer rainfall. Site selection was determined by the image quality of the archival photo, the occurrence of at least five *A. dichotoma* individuals in the image and site accessibility.

The area is dominated by rugged landscapes with low treeless vegetation (Dean & Milton 1999). The soil is lime-rich, weakly developed over rock (Low & Rebelo 1999) and is home to species within the families Mesembryanthemaceae (predominantly in the west), Euphorbiaceae and Asteraceae (Cowling et al. 1999). In the summer rainfall area, the vegetation has strong subtropical affinities, dominated by low trees such as *Acacia mellifera* and *Boscia albitrunca* and shrubs such as *Eriocephalus spinescens*, *Felicia filifolia* and *Pentzia incana* and grasses such as *Eragrostis lehmanniana*, *Fingerhuthia africana* and *Stipagrostis* spp. Strong Cape (temperate) affinities occur in the winter rainfall areas toward the southwest (Cowling et al. 1999, Cowling & Hilton-Taylor 1999, Werger 1978b, Low & Rebelo 1999) where the vegetation is dominated by leaf and stem succulent species such as *Ruschia* spp, *Drosanthemum* spp, *Zygophyllum morgsana*, *Euphorbia mauritanica*, *E. burmanii*, and asteraceous shrubs such as *Pteronia pallens*, *Tripteris sinuatum*, *Hirpicium alienatum* and many others.

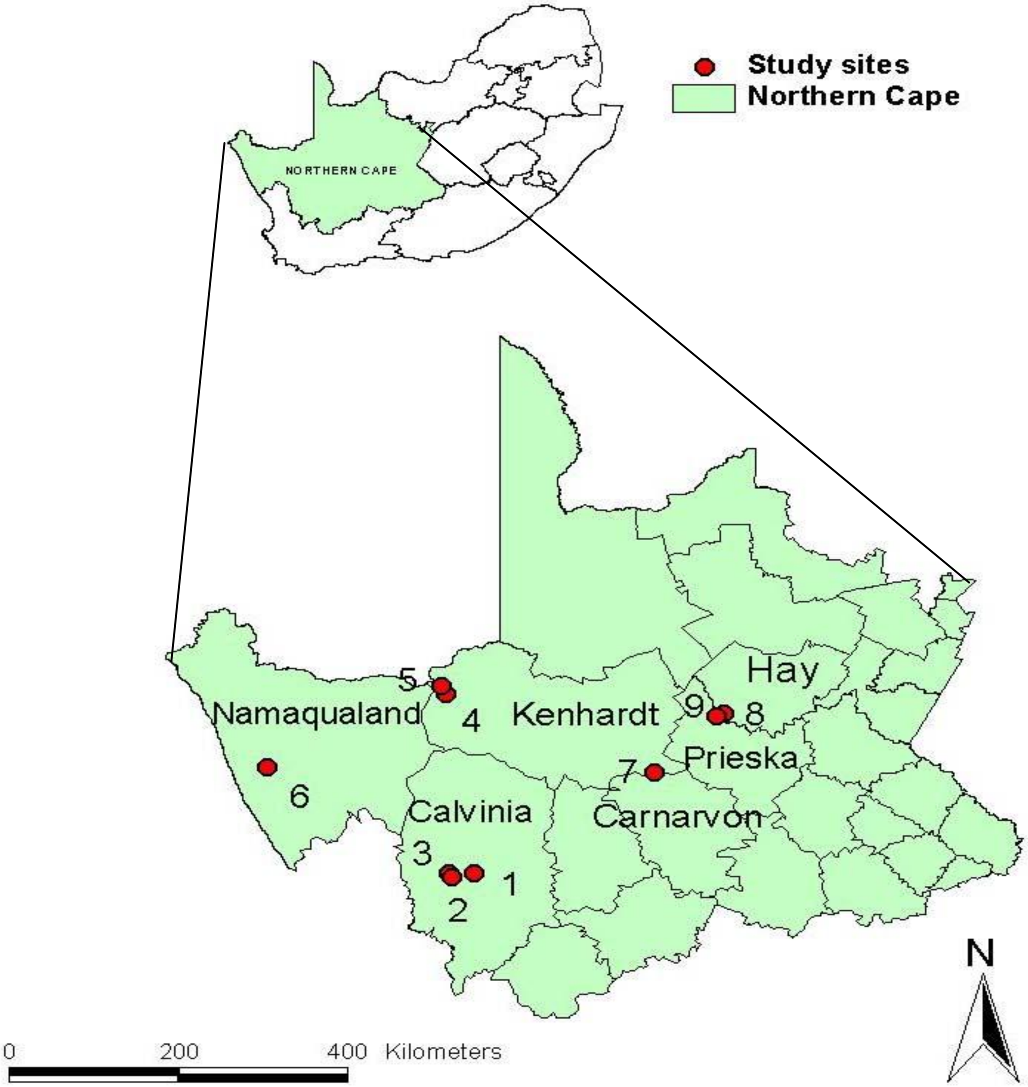

Figure 1. Location of the study sites within key magisterial districts of the Northern Cape Province, South Africa. 1 = Windkraal, 2 = Middelpos, 3 = Jangora, 4 = Kabas, 5 = Coboop, 6 = Vaalheuwel, 7 = Strondberg, 8 = Koegas, 9 = Westerberg.

2. 2. Methods

2.2.1 Life history and growth rate of *A. dichotoma*

Little is known about the growth rate and life history of *A. dichotoma.* Anecdotal information collected from farmers, literature and the tracking of individuals in matched photographs were the primary data sources used to reconstruct, in a reliable manner, the life history and life span of this species. At several sites across the study area the number of fruits on adult trees were counted. Individual inflorescences were collected and the number of seeds in each fruit determined so as to calculate the potential average annual reproductive output for adults of the species.

2.2.2 Population growth rate

Matched photography

This method, used as a means of provoking relevant questions about environmental change in a specific location, is a powerful tool in providing high quality comparative information of change over time. Twenty-one photographs which contained at least five identifiable individual *A. dichotoma* plants were selected for analysis (Appendices 1 and 2). Data sheets were drawn and information collected as suggested by Rohde (1997). Four cameras were used for the purpose of this study. Images were taken in black and white film, color slides and a digital camera to minimize the risk of spoiled films. Two exposures of each photograph were taken.

In the laboratory, all early and repeat photographs were scanned and printed in A4 format with a caption for each image comprising the location, the date of the photograph, the photographer, the location (with GPS coordinates), and notes on the major changes.

The file is kept at the Institute for Plant Conservation, Botany Department, University of Cape Town.

Analysis of photograph pairs was performed using Adobe Photoshop where the matched photograph was overlaid digitally on top of the earlier photograph. The first step was to reduce the opacity of the top photograph and adjust the two photographs to match each other using identifiable features in the image such as rocks, hill slopes or trees. A number was then assigned to each individual tree in the early photograph and recorded. The final step was to make the matched image opaque and record the presence or absence of individuals. Individuals present in the original photograph but missing in the repeat were tallied as deaths. Those present in the repeat but not in the original photographs were counted as recruits. Only individuals appearing to occupy the same spot, and of appropriate size were counted as survivors (Bowers et al., 1995).

The total number of individuals in the original, in the repeat, and the number of survivors, number of dead and number of recruits were calculated. Deaths and recruits were tallied and expressed as a gain or loss. Mortality and recruitment were calculated as suggested by Bowers et al. (1995).

$M = [D/(D+S)]\ [n/\ 100yrs]\ [100\ \%];$ where:

M = mortality rate expressed as the fraction of deaths in percent of observed individuals per century;

D = number of dead individuals;

S = number of surviving individuals; and

n = number of years between photographs.

$R = [N/(N + S)]\ [n/100\ yrs]\ [100\ \%]$ *where:*

R = recruitment rate expressed as a fraction of recruits in percent of observed individuals per century; and

N = number of new individuals.

The percent change in a population (ΔP) was calculated as:

$$\Delta P = [(S + N)(100)/(D + S)] - 100.$$

Size class distribution

While repeat photography is useful in recording changes in a relatively small pie-shaped slice of landscape, it is limited in interpreting broader trends in the environment. At each site, a transect was made to collect demographic data. Two or more transects were surveyed at each site and the data lumped in this analysis. Ten size classes of *A. dichotoma* were used in the field (Appendices 3 and 4) but lumped for analysis into four major classes:

a. *Juvenile*: individual of less than 2 m and no more than three branching events which is reproductively immature;
b. *Adult*: more than 2 m height with at least three branching events, and reproductively mature;
c. *Senescent*: very old individual with some broken branches and less leaves at the end of branches but which is often still reproductive;
d. *Dead*: individual of any size class standing or lying down, but not alive.

Rangeland condition, notes on the major changes on the landscape, dominant species, and threat or damage to trees including the effects of grazing, diseases or human interference were also recorded at each photographic station.

2.2.3. Climate data

Climate data comprising the mean annual precipitation (MAP), the coefficient of variation (CV) in rainfall, mean annual temperature (MAT), percentage summer and winter rainfall and annual potential evapotranspiration (PET, equivalent of A-Pan) for each site were obtained from the National Botanical Institute (NBI) Kirstenbosch, Cape Town. Schulze (1997) and Midgley et al. (2002) provide a description of these climate factors. The climate data for each photographic station were plotted against the observed recruitment and mortality rates and the percentage change in a population over 100 years to explore the relationship between these variables.

3. RESULTS

3.1. Life history and growth rate of *Aloe dichotoma*

3.1.1 Description of growth

Case studies recorded from anecdotal information and matched photographs are presented to estimate the growth rate at different stages and the life span of *A. dichotoma*.

Case study 1: Evidence (Fig. 2 A) is provided by van Heerde (2001) on individuals from his Springbok garden (Namaqualand) where a young individual of ± 80 cm in 1938 was re-photographed at about 4 m in 1978 at the adult stage.

Case study 2: A photograph taken by Acocks (Fig. 2 B) in 1952 in the Strondberg, near Vanwyksvlei depicts two individuals at the juvenile stage (± 50 - 60 cm) that were observed in the field as adults in 2002. The first (foreground) was 3.20 m high, 98 cm diameter at base, with a crown diameter of 1.84 m, and 7 branching events. The second (upper right background) was 3.5 m high, 84 cm diameter at base, with a crown diameter of 2.45 m, and 8 branching events.

Case study 3: The last example was provided by Mr William Maree, a farmer in the Westerberg region of the Northern Cape (Fig. 2 C). A young plant that was ± 85 cm in 1953 was photographed at the adult stage in 2002 and was measured as 3.5 m height, 76 cm diameter at base and with 9 branching events.

These anecdotal observations suggest that the juvenile stage of *A. dichotoma* trees is characterized by fast growth during the first 50 years, which then slows down. The growth rate can be influenced by external environmental factors such as soil type and architecture, climate (drought or a decrease in rainfall and changes in temperature), diseases (scales or other of insect origin) and grazing by livestock or wildlife.

The adult stage (Fig. 3) is characterized by little increase in volume and almost no change in the external architecture of the plant. Evidence is provided by Acocks' photograph No. 5400 (Fig. 3 A 1) which depicts a tree for which no major change could be observed between the original photograph taken in 1948 and the matched photograph taken in 2002. Marloth's photograph taken in 1904 at Windkraal near Calvinia (Fig. 3 B 1) shows an adult tree which was senescent in 2002. Although there is not enough data to adequately substantiate this view, the adult stage may last for as long as 150 years.

The senescent stage could be estimated to last about 50 years. During the adult and senescent stages a plant is reproductively active and because of its volume can usually resist a prolonged drought or water stress.

Taken together, this evidence suggests that the life span of *A. dichotoma* could be as long as 250 years, although considerable variation is likely to exist between sites and between individuals within a site.

3.2. Population growth rate

3.2.1. Basic survival and mortality analysis

The distribution of survival and mortality rates across sites through matched photographs shows that during the last 100 years or so, populations in the winter rainfall areas have grown more than those in the summer rainfall areas (Table 1 and Appendix 5). An increase in the number of individuals was observed in the sites of the Calvinia district (Windkraal, Middelpos and Jangora) while populations at the other sites have declined over time.

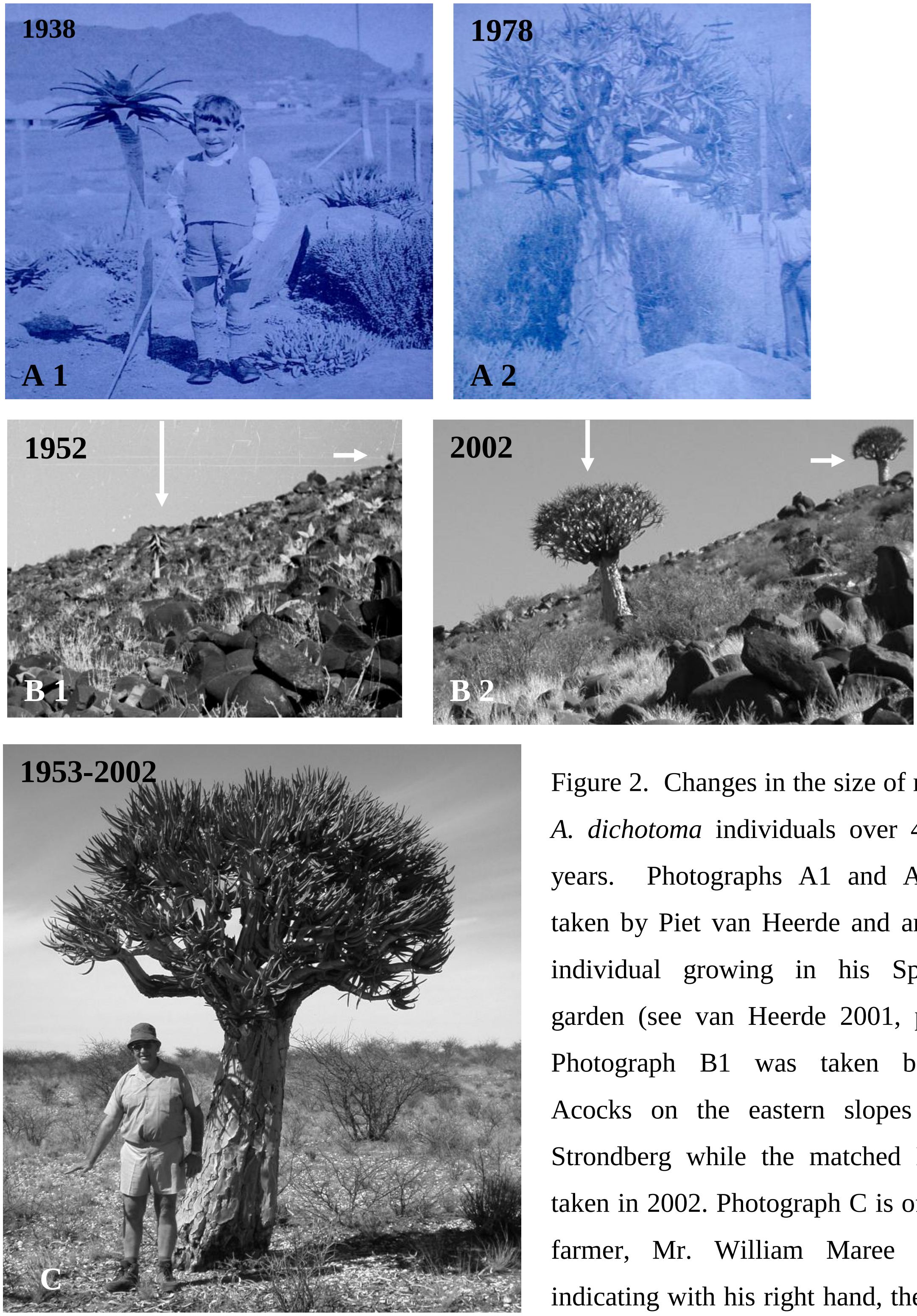

Figure 2. Changes in the size of matched *A. dichotoma* individuals over 40 – 50 years. Photographs A1 and A2 were taken by Piet van Heerde and are of an individual growing in his Springbok garden (see van Heerde 2001, pg. 70). Photograph B1 was taken by John Acocks on the eastern slopes of the Strondberg while the matched B2 was taken in 2002. Photograph C is of a local farmer, Mr. William Maree who is indicating with his right hand, the size of the *A. dichotoma* individual behind him in 1953

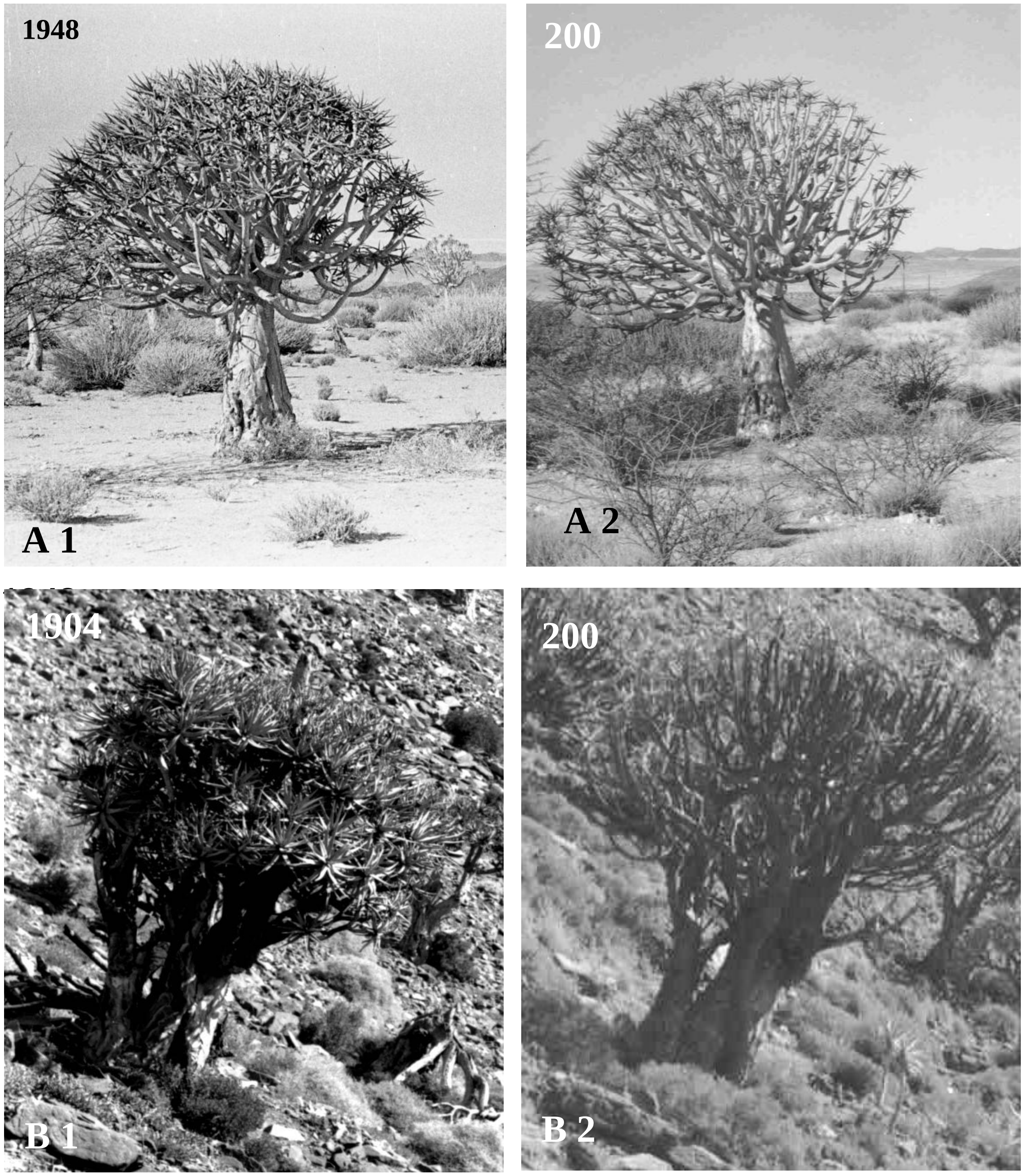

Figure 3. Two matched photographs showing the relatively slow rate of change in adult *A. dichotoma* individuals. Photograph A1 was taken by John Acocks near the farm Coboop, Kenhardt District in 1948. Rudolph Marloth took photograph B1 near the farm Windkraal, Calvinia District in 1904. The repeat photographs were taken in 2002.

There was a sharp decline in the proportions of survivors and recruits when moving east or northwards, while southern and western populations showed a high proportion of survivors and recruits. The proportion of dead individuals also increased east and northwards.

Mortality rates calculated over a hundred years range from 11 – 67 % and are generally greater for sites in the north and east (Tables 1 and 2). Recruitment rates over a hundred years for the species span a wide range (0 – 69 %). Only the three sites of the Calvinia district (sites 1-3) have higher recruitment rates than mortality rates. Although patterns of recruitment and mortality vary considerably from site to site, overall the first four winter rainfall sites (sites 1 – 3, 6, see Appendices 1 & 2) are generally less negatively affected than the remaining summer rainfall sites.

3.2.2. Specific size class distribution

Transect data recorded in the field depict the proportions of individuals of each size class (Fig. 4). Juveniles are relatively abundant in the Calvinia and Namaqualand sites, located in the winter rainfall region. The proportion of adults at each site does not show large differences except at Kabas and Coboop where adults appear relatively less abundant. The two northern populations at Kabas and Coboop have the lowest number of live individuals and populations are skewed toward dead individuals.

3.2.3. Climate factors

The percentage change in a population over 100 years was significantly negatively related ($p<0.01$) to the potential evapotranspiration at a site (Fig. 5). The %

recruitment and % mortality over a hundred years were not significantly related to any of the environmental variables measured. However, when Vaalheuwel was excluded from the analysis, the % recruitment per 100 years at a site was significantly negatively related to PET ($y = -0.002x + 5.7002$, $R^2 = 0.7208$, $p < 0.01$)

4. DISCUSSION

4.1. Individual plant growth rates

The association among different life history characteristics can be used to develop more detailed questions and hypotheses about the life history and population dynamics of individual species as well as trade-offs among these characteristics (Goldberg & Turner 1986). The growth rates of succulent species vary considerably (Jordan & Nobel 1981). Although little is known about the life history and growth rate of *A. dichotoma*, information used to construct it using matched photographs and anecdotal information does support our estimates of fast growth during the first 50 years of the life of the plant. The method of estimating the growth using the relationship between age and height (Midgley 1997, Foden 2002) with individuals from nurseries seems difficult to apply in a natural environment where water is a limiting factor. A tree of ± 2m high could be in the juvenile or adult stage, depending on the environment it grows in, its development and reproductive stage making it difficult to accurately predict its age. Environmental factors such as the degree of rockiness, soil type and moisture play a major role in the plant's growth. *A. dichotoma*, similar to other very long-lived plants, possesses the following main life history traits: long maximum life span, high early survival after the first year, high long-term survival, large size at maturity, low density, erratic recruitment, and/ or

Table 1. Change in the number of individual *A. dichotoma* trees surviving, dying and recruiting at 9 sites in the Karoo over the time period of the matched photographic pairs.

Site No.	Site name	No. of years between photographs	Total No. of Aloes in the original photographs	No. of Aloes surviving to 2002	% survival	No. of Aloes not surviving to 2002	% mortality	Total No. of Aloes in repeat photographs	No. of new Aloes in 2002 photographs	% new recruits
2	Middelpos	84	13	7	54	6	46	35	28	80
1	Windkraal	98	128	78	61	50	39	268	190	71
3	Jangora	84	15	12	80	3	20	22	10	45
6	Vaalheuwel	45	20	15	75	5	25	17	2	12
7	Strondberg	50	50	13	26	37	74	30	17	57
9	Westerberg	65	404	141	35	263	65	213	72	34
8	Koegas	84	353	70	20	283	80	173	103	59
4	Kabas	41	74	23	31	51	69	35	12	34
5	Coboop	54	41	3	7	38	93	3	0	0

Table 2. The average mortality rate (%), recruitment rate (%) and the % change in the population of *A. dichotoma* calculated over 100 years at 9 sites in the Karoo from an analysis of repeat photographs. Sites are arranged from the greatest increase in percentage change in the population to the lowest. Calculations for determining the mortality rate, recruitment rate and the % change in the population are indicated in the methods section.

Site No.	Site name	% mortality	% recruitment	% change in the number of Aloes in the population
2	Middelpos	39	67	169
1	Windkraal	38	69	108
3	Jangora	17	36	40
6	Vaalheuwel	11	5	-15
7	Strondberg	37	28	-40
9	Westerberg	42	22	-47
8	Koegas	67	50	-51
4	Kabas	28	14	-52
5	Coboop	43	0	-80

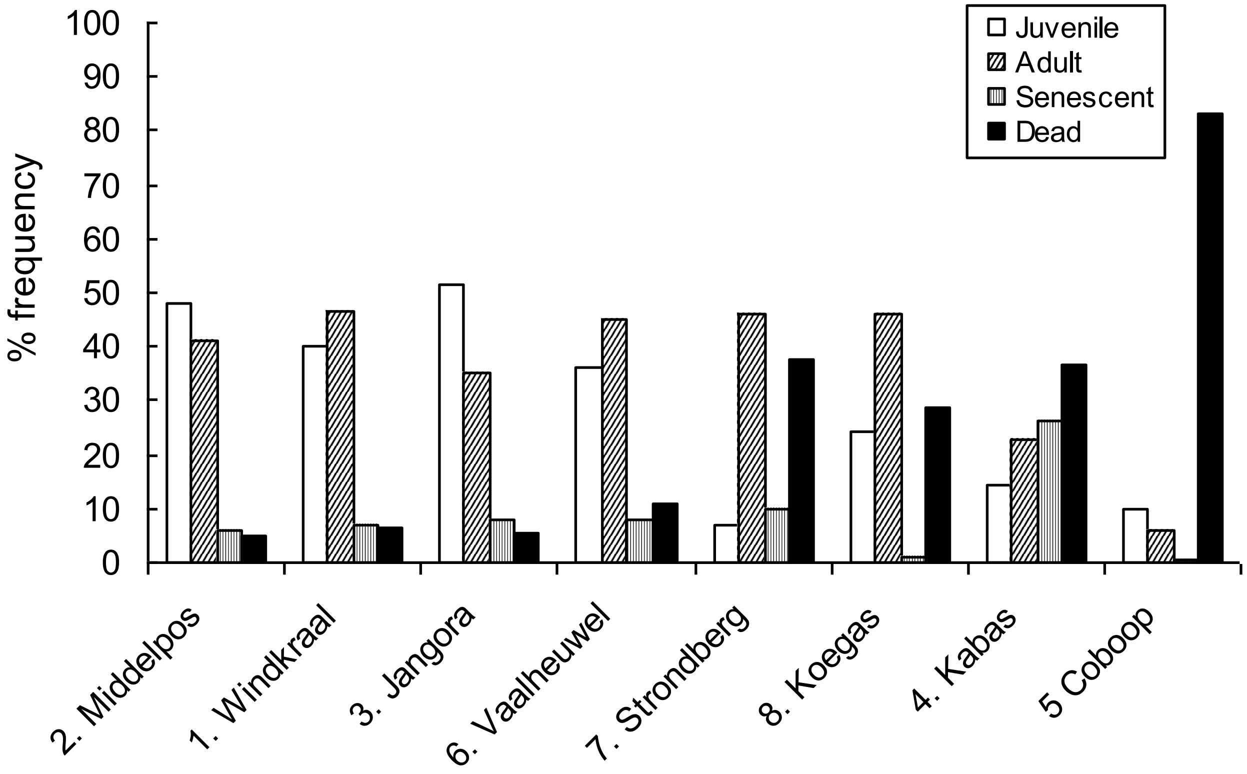

Figure 4. The percent frequency of four size classes of *A. dichotoma* plants recorded along transects at eight sites in the Karoo. It was not possible to sample the site at Westerberg which has therefore been excluded from this analysis.

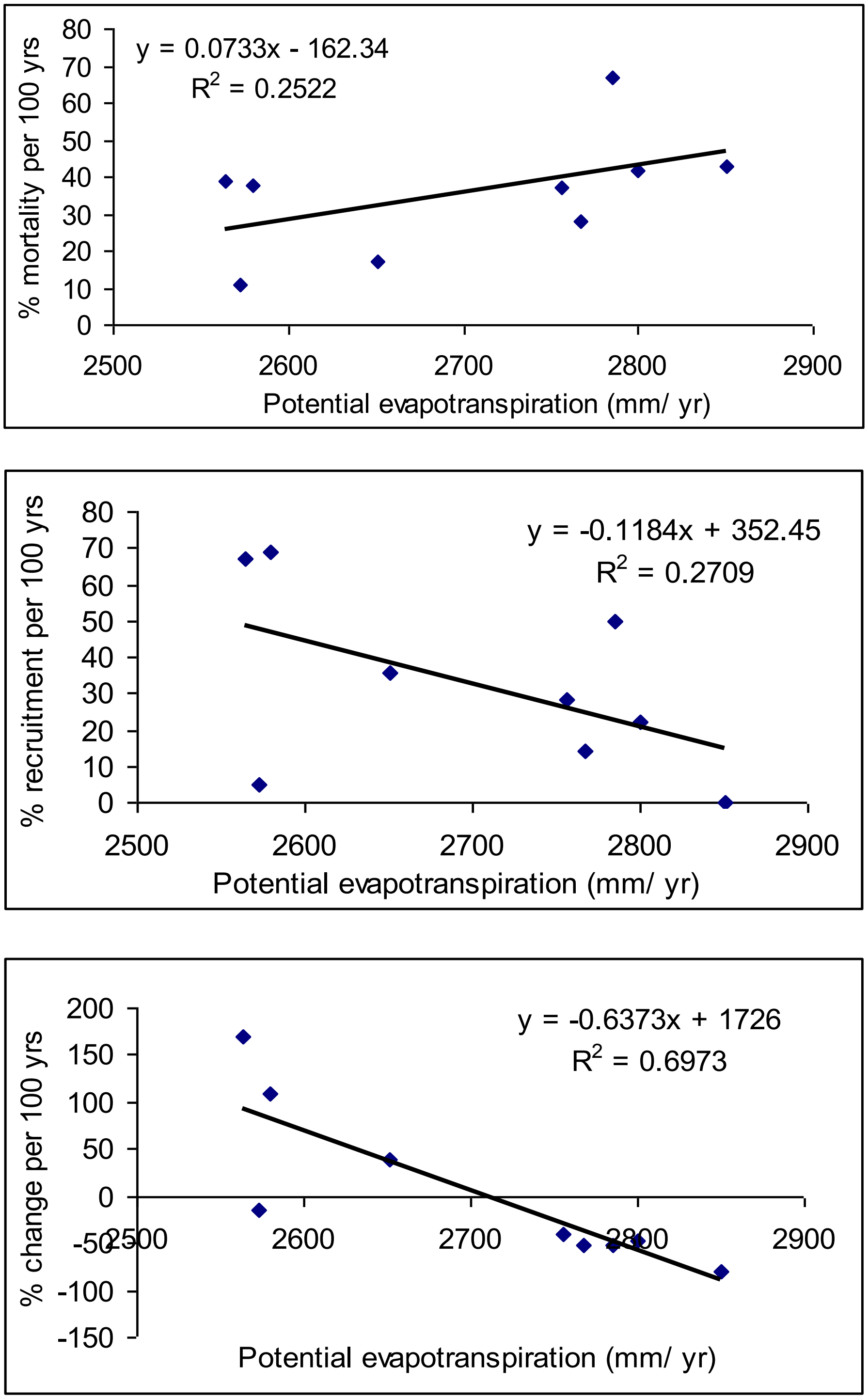

Figure 5. Correlation between annual potential evapotranspiration (mm/ yr) and recruitment rate, mortality rate and the percentage change of *A. dichotoma* over 100 years.

age structure skewed towards older plants (Goldberg & Turner 1986). At the adult stage in particular, the plant accumulates enough water to survive extended periods of water stress or drought.

4.2. Population growth rates

Bowers et al. (1995) suggest that associated factors other than climate (such as nurse plants, availability of recruitment sites, predation refuges, etc.) are likely to play a significant role in the survival of long-lived arid plant populations. In the case of *A. dichotoma*, some of the most important influences on the dynamics of the populations include:

a. Herbivory by baboons (*Papio ursinus*). Foden (2002), Midgley (1996, 1997), Midgley et al. (1997), Coates Palgrave (1977) and Reynolds (1950) claim that baboons constitute a big threat for this species by tearing flowers and stripping the trees although no corroborating evidence was provided by this study.

b. Grazing by goats, sheep and donkeys. Although Foden (2002), Midgley (1996, 1997), Midgley et al. (1997) have reported evidence of this, there was no indication that plants were grazed by domestic livestock. Grazing effects on seedlings, however, could have devastating consequences for the long-term viability of populations.

c. Diseases. As reported by Foden (2002), there were cases of scale insects recorded in this study, but no conclusive evidence was found to support the idea that disease plays a significant role in the population dynamics of this species.

Interpretation of plant abundance in terms of climatic variables are complicated by the lack of photographs for the period between the two sets of photographs analyzed. This poses difficulties in identifying the causes of observed changes. However, evidence presented in the transect data analysis converges with that seen in the photographs. There is a clear difference in the dynamics of populations of the winter and those of the summer rainfall areas. The relatively high proportions of juveniles recorded in the winter rainfall areas could be explained by the presence of predictable winter rain, with fog and dew-ameliorated summers (Cowling et al. 1999) providing conditions for regular recruitment and high survival rates. Increased mortality in the summer rainfall areas is not a recent event and was reported by earlier researchers such as Acocks (1988), Moll (1985) and Jurgens (1997). It could be attributed to the long-term effects of climate, particularly a reduction in rainfall. Acocks' photographs, taken in 1948 for example, depict a dying population of *A. dichotoma* at Coboop farm near Pofadder. In his caption to this 1948 photograph, Acocks explains this condition with reference to the droughts of the 1930's and 1940's in the region.

In an attempt to explain the observed mortality rates, recruitment rates and the percentage change in populations, climate factors were correlated with these parameters. PET had a negative correlation with the percentage change in populations across the study area. The other climatic factors showed only weak and non-significant correlations with recruitment, mortality and the percentage change in populations. Vaalheuwel, near Springbok in a predominantly winter rainfall area, was a consistent outlier in these analyses. While the photographic evidence points to low levels of recruitment at this site, the transect data suggest that there is, in fact a large number of newly-recruited juveniles in the population that were not observed in the analysis of the repeat photograph. When excluding Vaalheuwel as an outlier, there is generally a stronger relationship between PET and recruitment over the last 100 years. The fact that PET incorporates temperature, rainfall and evaporation, demonstrates that climatic factors might have played a significant role in the dynamics of this species. An increase in aridity will probably have a negative impact on the populations.

The expanding populations of the predominantly winter rainfall areas near Calvinia might be due to a generally less variable rainfall regime and a greater incidence of sporadic precipitation during the summer months. Jordan & Nobel (1981) suggest that the duration of tolerable drought varies with the age of individual plants, depending on the size of the leaves, stems and roots.

Recruitment in an arid desert environment is usually rare and episodic for long-lived tree species. In the Sonoran Desert, only one seed of *Agave deserti* out of 1.2 million apparently led to a mature plant (Jordan & Nobel 1979). Our observations show that an adult *A. dichotoma* tree can produce an average of 146 (range = 18 to 280) fruits and about 7 300 (range 900 – 14 000) seeds. The small total number of seedlings (14) in the transect data collected in this study suggest that recruitment for *A. dichotoma*, as for the other desert succulents, is episodic and localized to a period where the soil moisture is adequate as a result of climatic factors particularly high rainfall events. Observations from an isolated population (less than 100 years old) at Kenhardt show that recruitment is episodic with only three recruitment events over the time period.

As observed on the desert plants in the Grand Canyon (Turner 1990 & Bowers 1995), overall gains and losses in plants show high responsiveness to climate fluctuations.

It appears likely that climatic events are also largely responsible for the patterns of recruitment, mortality and the percentage change of *A. dichotoma* in the Karoo.

Patterns of high recruitment in the southern populations of *A. dichotoma* and a decline east and northwards could be explained by models of climate change (Midgley, 2002). According to a model developed by Midgley *et al* (2002), outcomes of climate change predict range dislocation or shift, and it appears likely that the rate of climate change will exceed the potential of populations to track the climate change by migrating to favourable areas. If spatially explicit predictions of mortality can be made and ascribed to a particular cause, field monitoring strategies and protocols can be put into place to detect the early signs of climate change in plants (Midgley et al. 2002).

From this study, it seems likely that *A. dichotoma* is alive and well in the southern populations – perhaps the migration suggested by Midgley et al. (2001) has already begun! At least they appear to be under much less threat from climate change here than in the summer rainfall areas. Low recruitment, high mortality and negative percentage change of populations observed in the summer rainfall areas corroborate the hypothesis of climate-induced effects on *A. dichotoma* for the northern and eastern populations, while the winter rainfall areas show a different scenario, perhaps indicating an increase in moisture conditions. Where winter rainfall exists with a smaller proportion of summer rainfall such as in the Calvinia district, *A. dichotoma* plant populations appear to be healthiest.

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Appendix 1: Details of photographic stations and photographs used in this study. All repeat photographs were taken by M.T. Hoffman and P. Kaleme.

No	Ref. Photo	Location	Latitude	Longitude	Region	Magisterial district	Date 1st photo	Photographer	Date repeat
1	Marloth 1025	Windkraal 1	31 12 5.6	19 42 58.7	Calvinia	Calvinia	ca. 1904	Rudolph Marloth	15/10/2002
2	Marloth 1026	Windkraal 2	31 12 31.5	19 43 18.0	Calvinia	Calvinia	ca. 1904	Rudolph Marloth	15/10/2002
3	Pole Evans CF 25	Middlepos	31 15 35.9	19 29 41.8	Calvinia	Calvinia	ca. 1918	I.B. Pole Evans	16/10/2002
4	Pole Evans CF 28	Jangora	31 12 14.8	19 27 09.5	Calvinia	Calvinia	ca. 1918	I.B. Pole Evans	17/10/2002
5	Acocks 6414	Kabas 1	29 03 40.7	19 25 54.1	Pofadder	Kenhardt	5/02/1961	John Acocks	29/10/2002
6	Acocks 6412	Kabas 2	29 03 40.7	19 25 21.3	Pofadder	Kenhardt	5/02/1961	John Acocks	29/10/2002
7	Acocks 6411	Kabas 3	29 03 40.7	19 25 21.3	Pofadder	Kenhardt	5/02/1961	John Acocks	29/10/2002
8	Acocks 6413	Kabas 4	29 03 40.7	19 25 21.3	Pofadder	Kenhardt	5/02/1961	John Acocks	29/10/2002
9	Acocks 5400	Coboop 1	28 57 59.4	19 23 21.3	Pofadder	Kenhardt	8/10/1948	John Acocks	30/10/2002
10	Acocks 5401	Coboop 2 a	28 56 05.1	19 20 34.0	Pofadder	Kenhardt	8/10/1948	John Acocks	30/10/2002
11	Acocks 5402	Coboop 2 b	28 56 05.1	19 20 34.0	Pofadder	Kenhardt	8/10/1948	John Acocks	30/10/2002
12	Acocks 6091	Vaalheuwel	29 23 26.4	17 32 17.5	Steinkopf	Namaqualand	24/8/1957	John Acocks	31/10/2002
13	Acocks 5576	Strondberg 1	30 00 22.6	21 38 45.7	Vanwyksvlei	Carnavon	25/5/1952	John Acocks	16/11/2002
14	Acocks 5577	Strondberg 2	30 00 22.7	21 38 46.7	Vanwyksvlei	Carnavon	25/5/1952	John Acocks	16/11/2002
15	Acocks 5578	Strondberg 3	30 00 24.8	21 28 49.0	Vanwyksvlei	Carnavon	25/5/1952	John Acocks	16/11/2002
16	Acocks 5579	Strondberg 4	30 00 24.8	21 28 49.0	Vanwyksvlei	Carnavon	25/5/1952	John Acocks	16/11/2002
17	Acocks 5580	Strondberg 5	30 00 25.2	21 38 50.7	Vanwyksvlei	Carnavon	25/5/1952	John Acocks	16/11/2002
18	Pole Evans CF 48	Koegas 1	29 18 07.2	22 22 03.6	Koegas	Hay	4/8/1918	I.B. Pole Evans	17/11/2002
19	Pole Evans CF 49	Koegas 2	29 18 15.7	22 22 12.5	Koegas	Hay	4/8/1918	I.B. Pole Evans	17/11/2002
20	Acocks 396	Westerberg 1	29 20 09.2	22 18 00.6	Westerberg	Hay	9/11/1937	John Acocks	18/11/2002
21	Acocks 397	Westerberg 2	29 19 52.8	22 18 30.5	Westerberg	Hay	9/11/1937	John Acocks	18/11/2002

Appendix 2. Twenty-one photograph pairs of *Aloe dichotoma* populations in South Africa which have been used in this study. Appendix 1 provides additional information for each photograph pair and the captions below detail the major changes observed in each population. Appendix 5 also presents details of the number of *Aloe dichotoma* individuals in the populations at each time period.

1. Windkraal 1. On the farm Windkraal in the Hantamsberg, near Calvinia. Ninety four years have elapsed since Rudolph Marloth took his photograph on this north-facing scree slope. There has been a significant increase in the number of Aloes on the slope and several individuals in the background, evident as small plants in 1904, have matured into large adults. The individual in the right centre foreground has died and its remains are still evident down slope. A 25 m wide x 100 m long transect, surveyed perpendicular to the photostation, revealed that 48 of 100 individuals were juveniles (see Appendices 3 and 4), 41 were adults, 6 were senescent and 5 plants were dead.

2. Windkraal 2. Taken below Windkraal 1, this photograph pair reveals an influx of *Prosopis* on the bank of the river in the foreground and a significant increase in the number of Aloes on the hill slope. The size class distributions of 208 Aloes in a 25 m wide x 450 m long transect from the base of the slope to the rocky outcrop at the top of the mountain at right show the following patterns: juveniles = 43 %, adults = 44 %, senescent = 5 %, dead = 8 %.

3. Middelpos. Located on Middelpos farm, on the road between Calvinia and Loeriesfontein. This population of Aloe dichotoma was relatively small around 1920 when Pole Evans took his photograph, comprising just 13 plants. The population has grown to 35 individuals and is skewed towards juveniles. Thirty six percent of the 99 individuals on the entire hillslope (including a broader area than covered by the photograph view) are juveniles, 50 % are adults, 6 % are senescent and 7 % are dead.

4. Jangora. On the farm Jangora located on the road between Calvinia and Loeriesfontein. The number of Aloes in the photograph has increased from 15 to 22 individuals since Pole Evans took his initial photograph in 1920. The total of 33 individuals surveyed on the slope show that 58 % are juveniles, 33 % are adults, 3 % are senescent and 6 % were dead.

5. Kabas 1. On the farm Kabas about 11 km N of Pofadder on Onsepkaans road. John Acocks sampled the northern slope of this quartzite hill in 1961 and took several photographs looking in different directions but from the same general location (Kabas 1-4 are represented here). The number of Aloes currently on the northern slope totals 174 of which 17 % are juveniles, 20 % are adults, 18 % are senescent and 44 % are dead. This image (Kabas 1) highlights the general decline in the population size since 1961 which has shrunk from 35 to 16 individuals. The dead aloe in the right foreground in 1961 has fallen over but is still evident on the ground. The two adults in the left foreground have also died. The number of Aloes in the field of view has declined from 35 to 16 individuals. The foreground vegetation looks the same and is dominated by

Sarcostemma viminale, *Euphorbia* sp., *Rhigozum trichotomum* and *Ceraria namaquanum*.

6. Kabas 2. All three Aloes in the centre foreground and the individual in the left background have died since 1961. The group of Aloes in the right background were outside the field of view in 1961 and do not, therefore reflect an increase in the population since this period. The initial tally of 19 Aloes counted in the first photograph has now declined to 9 individuals including a few individuals present on the hillslope in the distance.

7. Kabas 3. All 7 adults present in the field of view in 1961 have now died and just two individuals, one of which is a juvenile evident in the left foreground are present.

8. Kabas 4. This repeat view is poorly matched with the original photograph but shows the general decline of the population from 14 to 8 individuals. The tall individual in the right foreground has died as has the forked Aloe in the centre. This individual has only recently died since green leaf material was still evident on the fallen tree.

9. Coboop 1. Coboop farm, about 23 km north of Pofadder Hotel on Onsepkaans road. John Acocks visited this site in 1948 as part of his work on the Desert Encroachment Committee. The population in the field of view has declined from 12 to three individuals although the tree in the left foreground is the same individual as photographed by Acocks. Three transects of 100 m wide and 200 m long each recorded a total 181 individuals with 24 % assessed to be juveniles, 11 % adults, 2 % senescent and 62 % dead. The cover of *Euphorbia dregeana* seems to have remained fairly constant with little difference between 1948 and 2002 while *Acacia mellifera* and *Stipagrostis* spp. appear to have increased in cover.

10. Coboop 2a. Near farm Coboop on old road which runs next to the telephone line, looking to Orange River about 30 km further N. Acocks' field notes indicate that the Aloes in the field of view died during the prolonged drought evident in the region during the 1930's and 1940's. A 100 m wide by 400 m long transect in the field of view returned 89 individuals in total of which one was a juvenile and two were adults. *A. dichotoma* has not rebounded since 1948. Foreground grass cover has shown a dramatic increase to ± 30 %, which is dominated by *Stipagrostis ciliata*, *S. brevifolia* and *S. obusta*. *Acacia mellifera* seems also to have increased in abundance.

11. Coboop 2b. This photograph was taken at the same location as Coboop 2a and shows a similar trend. The *A. dichotoma* population has nearly completely collapsed while grass cover (*Stipagrostis* spp.) and *Acacia mellifera* have increased significantly. A 100 m wide by 400 m long transect recorded a total of 86 individuals of which 5 % were juveniles, 2 % were adults, 0 % were senescent and 93 % were dead.

12. Vaalheuwel. This site is located on a quartzite hill, 3 km west of the farm Vaalheuwel along the river course. The number of Aloes in the photographs has

declined from 20 to 15 in 45 years, with only 2 new individuals and 75 % of individuals in the original photograph have died. However, a 160 m wide and 500 m long transect recorded a total of 164 individuals of which 35 % were juveniles, 46 % were adults, 8 % were senescent and 11 % were dead. The comparison of the photograph pairs thus significantly underestimated the number of juveniles in the population probably because many were less than 1 m in height. The cover of shrubs was very low and *Galenia africana* was common, if not dominant in place suggesting that the area has been heavily grazed in the past.

13. Strondberg 1. This site is located on the east-facing slope of the Strondberg, north of Vanwyksvlei, on the road to Kenhardt. The photographs labelled Strondberg 1 – 5 were all taken by Acocks in 1952. In the foreground, 11 of the 16 Aloes have died and 5 are still alive although half of these either have been damaged around the base of their trunks or have many dead branches. Three transects of 50 m wide and 150 m long each recorded 143 individuals of which, 8 % were juveniles, 50 % were adults, 10 % were senescent and 41 % were dead.

14. Strondberg 2. This picture is taken just in front of Strondberg 1 and shows a similar view. Ten out of 12 Aloes present in 1952 have died, 2 are still alive and 4 new individuals are evident. Of these four, one is an adult and the other 3 are juveniles.

15. Strondberg 3. Of the 5 Aloes in the earlier photograph, 3 have died and one new seedling has appeared (left midground). The low rosette Aloe species in the right foreground, is *Aloe striata* subspecies *karasbergensis*. It has completely disappeared from the Strondberg and we did not see it anywhere on the hillslope during our survey. Grass cover appears similar in the two photographs.

16. Strondberg 4. This photograph was taken about 2 – 3 m left of from the previous one. Of the 11 *Aloe dichotoma* individuals in the early photograph 10 have died, one has survived and seven new individuals are evident. *Rhigozum trichotomum* occupies the same space in the foreground and has grown thicker. Grass cover appears not to have changed.

17. Strondberg 5. Located about 70 paces down slope from Strondberg 4 and looking south this photograph also indicates high mortality of *Aoe dichotoma* individuals. Located about 70 paces down slope from Strondberg 4 and looking south this photograph also indicates high mortality of *Aoe dichotoma* individuals. Of the 8 individuals in the early photograph 5 have died 3 have survived and 3 new individuals are evident.

18. Koegas 1. This photograph pair was taken a few hundred metres north of the abandoned Koegas mining settlement, north of the bridge over the Gariep River. The number of *Aloe dichotoma* individuals has declined significantly on the mountain slope, especially higher up. Of the 325 individuals counted in the early photograph, 259 have died, 66 have survived and 92 new individuals are present in 2002. Three transects of 50 m wide and 500 m long each recorded a total of 488 individuals of which 22 % were

juveniles, 47 % were adults, 1 % were senescent and 30 % were dead. *Acacia mellifera* has increased significantly in the foreground as well as on the foot slope.

19. Koegas 2. Located on the mountain slope above Koegas farm, looking southwest toward the Gariep River with the Westerberg on the left this photograph pair also shows a dramatic reduction in the number of *Aloe dichotoma* individuals since 1918. Of the 28 individuals recorded in 1918, 24 have died, 4 have survived and there are 11 new individuals present. *Cenchrus ciliaris* is the dominant grass species on this slope and *Acacia mellifera* seems to have increased.

20. Westerberg 1. Near Koegas but south of the Gariep River, looking north to the mountains opposite the Westerberg. The foreground is heavily disturbed and shows an increase in *Acacia mellifera* while the river is dominated by tall alien plants (*Eucalyptus* spp.) Although it was not possible to survey this relatively inaccessible site an analysis of the photograph pairs indicates that of the 278 individuals present in 1937, 185 have died, 93 have survived and 41 new individuals have recruited into the population. The mountain slope reflects a general replacement of Aloes by *Acacia mellifera* except on the quartzite outcrops at the bottom of the slope, which do not seem to have undergone as much of a reduction in Aloes.

21. Westerberg 2. Looking west across the Gariep River to a quartzite hill on the left and gneiss slope on the right. *Acacia mellifera* has largely replaced *Aloe dichotoma* on the gneiss ridge but less so on the quartzite hill. Of the 126 individuals recorded in 1937 78 have died, 48 have survived and 31 new individuals are evident. It was not possible to access this site to survey the *Aloe dichotoma* population across the river.

Appendix 3. Four main size classes of *Aloe dichotoma* with associated sub-categories and their height, branching and reproduction characteristics as recorded along transects in the field. The use of anthropomorphic terms for the size classes greatly assisted in the rapid allocation in the field of individual trees to each size class. Attempts at using alternative approaches based on numbered size classes proved more tedious and less accurate. (See Appendix 4 for a photographic depiction of each size-class sub-division).

No	Size class	Height.	No. Branching events	Reproductively mature
I	*JUVENILE*			
01	Baby	< 30 cm	0	No
02	Toddler	30 cm – 1 m	0	No
03	Pre-adolescent	1 – 2 m	1 – 2	No
04	Teenager	1 – 2 m	2 – 3	No
II	*ADULT*			
05	Young adult	> 2 m	> 3	Yes
06	Mature adult 1	> 2 m	> 3	Yes
07	Mature adult 2	> 2 m	> 3	Yes
08	Old man	> 2 m	> 3	Yes
III	*SENESCENT*			
09	Tired Old Man	> 2 m	> 3	Yes
IV	*DEAD*			
10	Dead	All sizes	All categories	N/A

Appendix 4. Photographs of the different size classes for *Aloe dichotoma* used in this study (see also Appendix 3 for details for each size class).

A. Juvenile stage

Baby

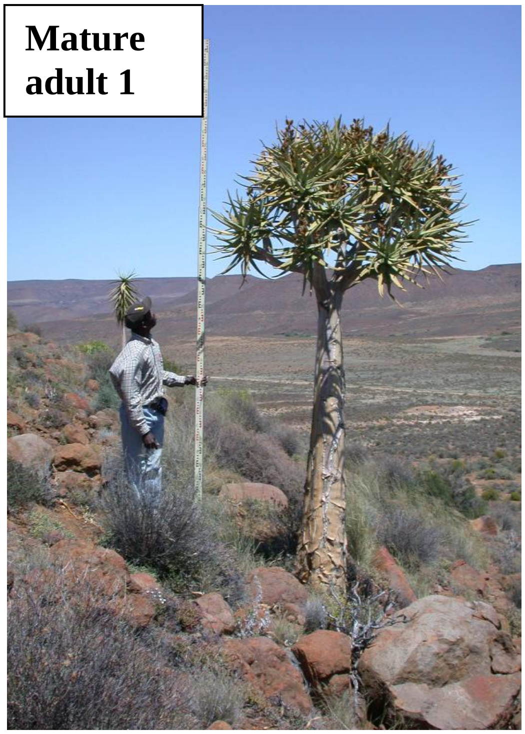
Toddler

Pre-adolescent

Teenager

B. Adult stage


Young adult


Mature adult 1


Mature adult 2


Old man

C. Senescent stage

D. Dead

Appendix 5: Number of individual *Aloe dichotoma* plants in four different size classes (1 = juvenile, 2 = adult, 3 = senescent, 4 = dead). Total values for both photographs as well as the number of individuals surviving, dying and recruiting into the population over time span of the two photographs are also shown. Photographs taken at Koegas1 and Westerberg 1 and 2 were not amenable for the development of a size class analysis. Dead individuals in the original photographs were excluded from analysis.

No	Site No.	Ref. photograph	Original photograph				Repeat photograph				Total in original	Total in repeat	Survivors	Dead	Recruits	Number of years
			1	2	3	4	1	2	3	4						
1	1	Windkraal 1	3	11	2	0	8	25	4	0	16	37	12	4	25	98
2		Windkraal 2	13	95	4	0	34	192	5	0	112	231	66	46	165	98
3	2	Middelpos	1	11	1	0	11	20	4	0	13	35	7	6	28	84
4	3	Jangora	0	15	0	0	2	16	4	0	15	22	12	3	10	84
5	4	Kabas 1	0	30	4	2	0	15	1	0	36	16	16	20	0	41
6		Kabas 2	0	15	2	0	0	9	0	0	17	9	3	14	6	41
7		Kabas 3	0	5	2	0	2	0	0	0	7	2	0	7	2	41
8		Kabas 4	0	11	3	0	2	5	11	0	14	8	4	10	4	41
9	5	Coboop 1	0	10	2	7	0	1	2	0	19	3	3	16	0	54
10		Coboop 2a	0	2	1	8	0	0	0	11	11	0	0	11	0	54
11		Coboop 2b	0	0	0	11	0	0	0	11	11	0	0	11	0	54
12	6	Vaalheuwel	0	18	2	0	0	9	8	0	20	17	15	5	2	45
13	7	Strondberg 1	0	14	2	0	1	4	3	0	16	8	5	11	3	50
14		Strondberg 2	0	12	0	0	1	4	0	0	12	5	2	10	3	50
15		Strondberg 3	3	2	0	0	1	2	0	0	5	3	2	3	1	50
16		Strondberg 4	0	9	2	0	1	7	0	0	11	8	1	10	7	50
17		Strondberg 5	0	8	0	0	0	6	0	0	8	6	3	5	3	50
18		Koegas 1									325	158	66	259	92	84
19	8	Koegas 2	0	28	0	0	3	12	0	0	28	15	4	24	11	84
20		Westerberg 1									278	134	93	185	41	65
21	9	Westerberg 2									126	79	48	78	31	65