The distribution and population structure of *Aloe pillansii* in South Africa, in relation to climate and elevation.

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Abstract

South Africa comprises almost 10% of known plant species and also has the only arid zone "hotspot" defined worldwide, namely the succulent Karoo. Anthropogenic climate change predictions for South Africa suggest rapid climate change in the next 50 years will have adverse affects on its vegetation biomes. This study shows how the aborescent succulent, *Aloe pillansii*, has a limited distribution due significantly to environmental and climatic variables and therefore it is potentially at risk given anthropogenic climate change predictions. The total South African *A.pillansii* population investigated is made up of 1202 individuals and is found in the Richterseld, which is part of the Succulent Karoo. The *A. pillansii* individuals were sampled in terms of their height and geographical position and then defined into sub-populations by a distance of 2 kms of separation. The sub-populations were then evaluated in terms of their respective environmental and climatic variables acquired from a CCWR database for South Africa using Arc View 3.2. The sub-population size class distributions were also constructed so that population dynamics and recruitment could be investigated. The results show how the *A.pillansii* sub-populations are limited to a specific environmental and climatic range. The sub-populations group along similar environmental and climatic variables with the healthiest sub-populations found at lower elevation, higher temperatures and higher Potential Evapo-Transpiration. The climatic range of *A.pillansii* is also evident from the range of its environmental and climatic variables and the associated unhealthy sub-populations that lie on the extremes of this range. Recruitment was found to correlate strongly with the environmental and climatic variables, % winter rainfall and elevation, suggesting it is moisture limited. The evidence found in this study of *A.pillansii's* specific environmental and climatic distribution may have negative implications for its future survival and conservation especially with present indications of anthropogenic climate change.

Key words: aborescent succulent, bioclimatic envelope, anthropogenic climate change

Contents:

Introduction

Aloe pillansii is commonly known as the 'Bastard quiver tree" because it is closely related to the 'Quiver tree" *Aloe dichotoma* (Powell et al., 2003). Its name does not give it complete justice as it is a striking species of 'kingly' nature and is a distinctive element of the succulent Karoo flora which is part of the arid areas of southwestern South Africa (Midgley et al., 1997). It is only found in South Africa and Namibia in a very limited range of environments with the South African population restricted to the Richtersveld (Powell et al., 2000), which is part of the Succulent Karoo. The Succulent Karoo is the only arid zone that has been identified as one of the global biodiversity hotspots (Myers et al., 2000) and makes up almost a third of succulent species diversity world wide (Rogers, 2004). It is known for its astounding richness and for the uniqueness of its plant species with over 40% of the 4849 species endemic to the region (Myers et al., 2000). As *Aloe pillasii* has a very limited distribution and may be in population decline (Powell et al., 2000) it has the potential to be impacted negatively by anthropogenicaly driven climate change and therefore could be used as an 'early warning' indicator species for climate change impacts on the biodiversity of the Succulent Karoo.

This is especially pertinent since climate is considered to be the most important factor for the regeneration and population expansion of flora in the severe climate of the Richtersveld (Powell et al., 2000). Environmental and climatic variables influence the physiology, distribution, phenology and adaptation of organisms (Hughes, 2000). A plant's distribution is influenced by its environmental and climatic tolerances which can be defined in terms of a bioclimatic envelope (Midgley et al, 2001). Identifying the critical range of tolerances for particular environmental variables of a species is useful when assessing the potential influence of environmental and climatic change on plants. This in effect determines a bioclimatic envelope for the species by defining the environmental and climatic variables that define its distribution. This is important because of the current threat of anthropogenically driven climate change and its potential influence on plant and animal distributions (Hughes, 2000, Midgley et al., 2001, Foden, 2002).

There has been much interest in *A.pillansii* since its discovery in 1926 by Nevill S. Pillans (Reynolds, 1950). A number of studies have raised concern about the population health of the species. Since early estimations of its population number of 200 by Midgley et al. (1997) its population estimate has soared significantly. A study by Powell et al. (2000) looked at 920 individuals of the South African population categorized into 19 sub-populations and concluded that *A.pillansii* is under serious threat because of insufficient seedling and juvenile recruitment (Powell et al., 2000). There are still only 1202 known *A.pillansii* individuals in South Africa at present and approximately1500 known individuals in Namibia (Loots et al., 2004), which together make up its total population. Consequently *A.pillansii* is ranked on the IUCN's red list as endangered (Rogers, 2004). Possible causes for its decline and derelict health are highlighted as collecting (Midgley et al, 1997), climate change, plant disease (Powell et al., 2000, Foden 2002) and herbivory (Midgley et al., 1997). However the predominant cause has not yet been isolated.

Investigating seedling recruitment and the factors that influence it, is a way of evaluating *A.pillansii's* population viability. A lack of juveniles suggests that the species may be suffering a population decline (Condit et al., 1998) and factors, which limit recruitment, are therefore critical to population viability. Environmental and climatic parameters are found to limit recruitment frequencies in other desert succulents. Recruitment of *Saguaro* seedlings in the Sonoran desert, for example, is limited by moisture (Drezner, 2004). *Agave deserti* seedling establishment is largely affected by water stress and consequently drought following germination limits recruitment to only one out of 17 years (Jordan et al., 79). Climatic influences are also seen on woody desert plants along the Colorado River in the Grand Canyon, where recruitment and mortality patterns are the product of climatic fluctuations over the past century (Bowers et al., 1995). It is evident that seedling establishment of succulent species in different parts of the world is significantly influenced by environmental and climatic factors. The environmental and climatic factors of influence on seedling establishment are therefore also important to population viability.

Seedling survival can however also be limited by non-climatic influences as found in aborescent semi-succulents in the Zapotitlan de las Salinas Valley, Mexico, which were negatively influenced by predation (Flores, 2004). It is possible that there are a number of influences on seedling recruitment and identifying the most important influences needs to be done because of the importance of recruitment on population viability.

Environmental and climatic variables have various potential influences on plant responses (Shulze, 1997) and can therefore limit plant distribution. Even though climate is not the only factor that can limit plant distributions (Midgley et al., 2001) it is a dominant limitation on *A.pillansii* distribution as shown in this study and as suggested by Williamson (1998). The dominant view in the past has been that in deserts survival is ultimately dependant on the elements however other factors are begining to be noted too (Barbour, 1981). For *A.pillansii* however there is growing evidence of its sensitivity to climate.

A closely related species, *A.dichotoma* (Reynolds, 1950) whose ranges also enter the Richtersveld, is suggested to be already experiencing the impacts of anthropogenic climate change (Foden, 2003). Bioclimatic modeling techniques and mortality assessments done on *A.dichotoma* found that the most northern populations in its range are experiencing increased mortality (Foden, 2003). Kaleme (2003) also found regional differences in long-term population dynamics for *A.dichotoma* using repeat photography. This correlates with future climatic predictions from GCM's (Global Climate Models) of anthropogenic climate change in South Africa (Foden, 2003). The influence of non-climatic variables was also found to be small in comparison to climate influences on the health of *A. dichotoma* populations. Given the morphological similarity between *A.pillansii* and these two species there is a good possibility that similar responses may occur or are already occurring on *A.pillansii* if it is sensitive to a specific climatic environment because of its apparent population decline.

In this study I investigate the environmental and climatic variables that influence the distribution and health of the *A.pillansii* population so that its sensitivity to these variables can be assessed. I hypothesize that the health and distribution of the *A.pillansii* sub-populations are strongly associated with a few critical environmental and climatic variables that define its limited range in South Africa. To test this hypothesis I will answer the following questions:

1. What is the distribution, range and population size of the main *A. pillansii* population and sub-populations in the Richtersveld, South Africa?

2. How are the size class distributions and health of all the sub-populations dispersed along environmental and climatic gradients?

3. How do seedlings and juveniles (plants <2 m) relate to the climatic and environmental variables and what does this suggest about the long-term viability of *A.pillansii* in the Richtersveld, South Africa?

Methods

Study site

The study on *A.pillansii* took place in the Richtersveld's where the geographical range proceeds from the Orange River mouth southward to Port Nolloth, eastward along the main road to Steinkopf and then Northward again to the Orange River at Vioolsdrif (Powell et al, 2000).

Species description

Aloe pillansii is a tree aloe that grows up to a height of 10m with a stem diameter that varies from 1-2 meters at the base and gets narrower upwards (Reynolds, 1950). It has a diversity of branching which ranges from having no branches to having many simple or dichotomous branches around the middle of the plant. Leaves are densely rosulate at the apices of the branches with inflorescences produced laterally from axils on the lowest leaf. This clearly distinguishes it from *A.dichotoma* and *A.ramisissima* (Reynolds, 1950). Its flowering season is in September and October with some plants sometimes flowering as late as November. Flowering does not occur annually for every plant but is sporadic. Pollination is done by nectar seeking birds. (Powell et al, 2000). Its seeds are 33mm long and 25mm in diameter (Reynolds, 1950) and have wings, which show that it is likely dispersed by wind.

Data and subpopulations definition

The data on *A.pillansii* individuals for the South African population was compiled from 2 separate databases. The largest database was from Howard Hendricks at the South African National Parks and the second database for the Cornell's Kop population was from Timm Hoffman at the IPC (Institute for Plant Conservation), University of Cape Town.

The data used for the study, contained information on the geographical co-ordinates, identification number and the height for each of the *A.pillansii* individuals found in South Africa. The number of *A.pillansii* individuals in this study was 1202, but 110 of the individuals did not have height data and were excluded from some of the analyses. This database represents the most rigorous and up to date representation of all the *A.pillansii* individuals found in South Africa.

To map the *Aloe pillansii* individuals Arc View 3.2 was used (ESRI, 1998). The population was then defined into sub-populations on the assumption that a sub-population is a group of individuals less than 2 kilometres away from their nearest neighbour. Therefore the distance between sub-populations is greater than 2 kilometres but the distance between nearest neighbour individuals within a population is less than 2 kilometres. This criterion was defined because *A.pillanssi* seeds are dispersed by wind as they have wing like structures and are small in size. Therefore it is unlikely they will disperse further than a radius of 2km. Also the sub-populations may be clumped as they are because of an adaptation to bird pollination since they cannot self-fertilize and therefore rely heavily on pollinators for reproduction (Midgley et al., 1997).

Climatic variables

Eight environmental and climatic variables that are likely to influence the distribution and survival of *A.pillansii* were used in the study. The variables extracted for each sub-population were mean elevation [elevation (m)], mean slope [slope (°)], mean aspect [aspect (°)], mean annual rainfall [MAR (mm)], mean % winter rainfall [% winter rain (%)], mean annual maximum temperature [MAMaxT (°C)], mean annual minimum temperature [MAMinT (°C)] and the annual sum of Potential Evapotranspiration [PET $(\mathrm{mm.yr^{-1}})$]. These variables were summarized for each sub-population in GIS from 1'x1' grid coverage's contained within the South African Atlas of Agro hydrology and Climatology (Shultze, 1997).

The environmental and climatic variables were chosen because of their known influences on plants and potential to limit plant distributions. Elevation has a major influence on climate and consequently hydrological and biological responses. Aspect and Slope are very important in ecological processes because of their relationship with solar radiation budgets that influence plant communities. For example different vegetation types can be found on different slopes corresponding with cooler or warm slopes. Temperature (MAMinT, MAMaxT) is a vital control and limiting factor for certain distributions of plants and crops. MAR represents the long-term quantity of water received by an area and therefore is an indication of water availability. Percent Winter rain is a measure of the proportion of total MAR that falls during the 4 winter months May, June, July and August. Finally PET is a measure of the atmospheric demand on water from evaporation at the surface and of transpiration from stomata. (Shulze, 1997)

The climatic and environmental variables were extracted for each *A.pillansii* population using Arc View 3.2 (ESRI, 1998). The environmental variables (mean aspect, mean slope and mean elevation) were derived from a Digital Elevation Model that was created using a 20m contour map obtained from the Department of Land Affairs in Mowbray, Cape Town.

Climatic variables and sub-populations

To determine the relationship between the sub-populations and their associated environmental and climatic variables a non-parametric Kruskal-Wallis One-Way ANOVA test was done. This gave a result showing which sub-populations are significantly different from each other in terms of each environmental and climatic variable (at the $p \leq 0.05$ level). A Spearman Rank Correlation matrix was also produced to examine the relationship between the environmental and climatic variables used.

To determine how the sub-populations are described in terms of their environmental and climatic variables an ordination was done using Non Metric Scaling with a Bray Curtis distance measure (McCune et al., 1999). This was done on the ordination programme PC ORD (McCune et al., 1999). An ordination arranges items as a way of graphically summarizing complex relationships and extracting one or a few dominant patterns from an infinite number of possible patterns (McCune et al., 2002). Therefore the statistical analysis summarized the patterns between the sub-populations in relation to their eight associated environmental and climatic variables. A cluster analysis was done on the sub-populations and their associated variables so that the sub-populations could be grouped according to the similarity of their environmental and climatic variables. To interpret the central axes on the ordination further statistical analysis was done using a Spearman Rank Correlation to determine which environmental and climatic variables significantly correlate with the axis 1 and axis 2 scores of the ordination result. Significance was determined by correlations that have a $p \leq 0.05$.

Population structure and recruitment

An analysis was then done on *A.pillansii* to investigate its population dynamics. The population analysis consisted of constructing frequency size class distributions of 1m intervals for the entire *A.pillansii* population and defined sub-populations in the Richtersveld. This was done using the available height data on each *A.pillansii* individual.

Static size class distributions may not be a good predictor of evaluating future population trends (Condit et al., 1998) but sub-populations can still be compared critically to see which have more seedlings in comparison to adults to evaluate potentially healthy populations. Therefore the % seedlings and juveniles [% seedlings (<2m)] were calculated for each sub-population. This was used as a surrogate for health status because of the importance of recruitment (Condit et al., 1998) for population viability. Percent seedlings represents a ratio of non-reproductive individuals [% seedlings (<2m)] against reproductive individuals [adults (>2m)]. A scatter plot of the log of the number of seedlings and juveniles (<2m) against the log of the number of adults (>2m) was done to investigate the relationship between reproductive and non-reproductive individuals in the *A.pillansii* sub-populations.

Higher rather than lower % seedlings and juveniles (<2m) in a sub-population are assumed to be a sign of better health. To investigate % seedlings and juveniles (<2m) and its relation with the eight environmental and climatic variables, a Spearman Rank Correlation was done. This determined which variables are most significantly correlated with % seedlings and juveniles (<2m) from the sub-populations.

Results

The distribution of *A.pillansii* in relation to environmental and climatic variables

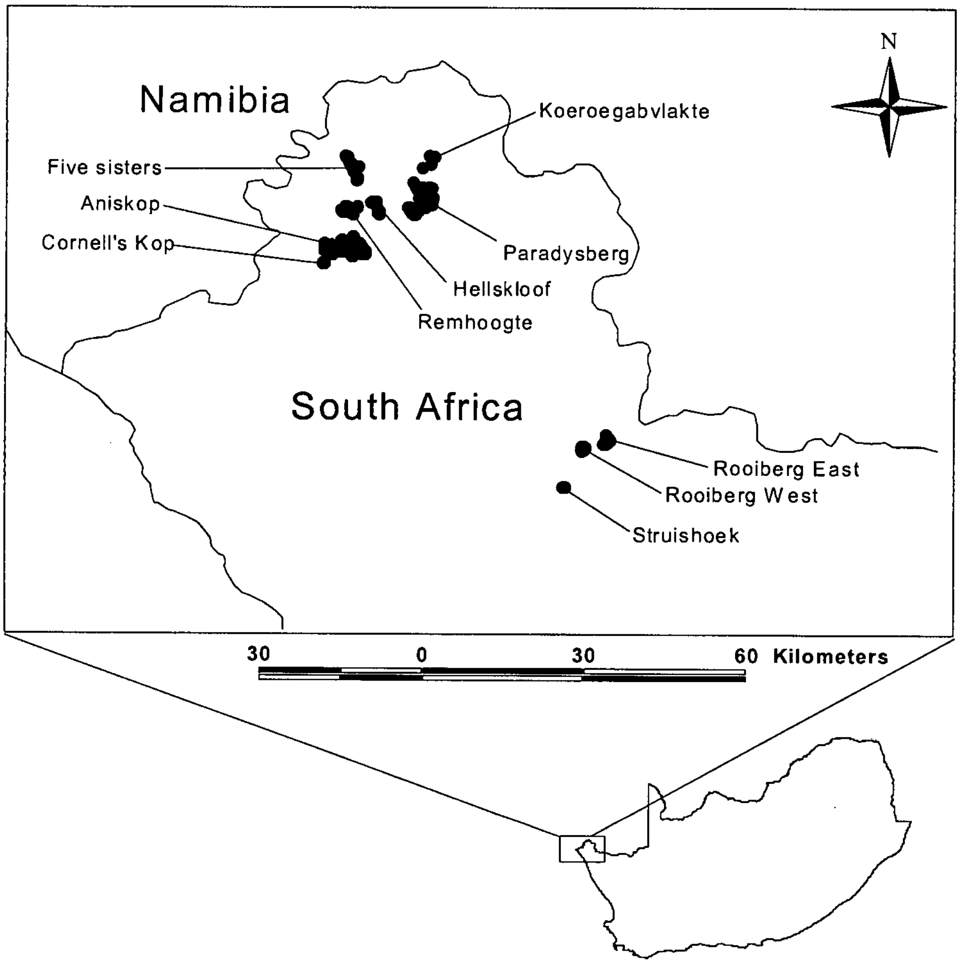

Fig 1. The geographical distribution of 1202 *Aloe pillansii* individuals located in 10 main sub-populations in the Richtersveld, Northern Cape, South Africa.

The sub-populations are dispersed geographically across the Richtersveld with the southern sub-populations (Rooiberg East, Rooiberg West and Struishoek) separated from the Northern sub-populations (Aniskop, Five sisters, Remhoogte, Cornell's Kop, Koeroegabvlakte, Paradysberg and Hellskloof) by a distance of approximately 60 km (Fig1).

The sub-populations are influenced by different environmental and climatic variables at their geographical positions (Table 1). The results from the Kruskal-Wallis One-Way ANOVA test show the sub-populations that have significantly different environmental or climatic variables (Table1).

The sub-population sizes range from 6 individuals in the Koeroegabvlakte sub-population to 556 individuals in the Aniskop sub-population. The mean elevation for the sub-populations ranges from 148 m at the Cornell's Kop sub-population to 657 m at the Struishoek sub-population. The mean slope for the sub-populations ranges from 12.3 degrees to 26.0 degrees. Paradysberg, Remhoogte and Rooiberg East all have positive mean aspect values (northerly slopes) with all other sub-populations having negative mean aspect values, indicating a predominance of more southerly slopes.

The most southern sub-populations Rooiberg East, Rooiberg West and Struishoek have the highest MAR. The rest of the sub-populations have a MAR that ranges from 22mm.yr^{-1} for Koeroegabvlakte to 30mm.yr^{-1} at Cornell's Kop. The % winter rainfall ranges from 50% in the Koeroegabvlakte sub-population to 75% for the sub-populations Cornell's Kop, Five sisters and Remhoogte. Both the mean annual minimum and maximum temperature for the sub-populations have a range of approximately 2 °C from the lowest to the highest value. The MAMaxT ranges from the lowest of 24.0°C at Struishoek to 26.6°C at Five sisters. The MAMinT ranges from the lowest of 9.0°C for Struishoek to a maximum of 11.0°C at Cornell's Kop. The mean PET ranges from 1677mm.yr^{-1} for Struishoek to 1793 mm.yr^{-1} for Koeroegabvlakte (Table1).

Table 1. Mean values for each of the eight associated environmental and climatic variables (± Standard Deviation) for the 10 *Aloe pillansii* sub-populations. The Kruskal-Wallis One-Way ANOVA results represented by subscript letters show which climatic or environmental variables are significantly different between populations. Significance is at the $p \leq 0.05$ level. % Seedlings and juveniles ($\leq$ 2m) are also represented for each sub-population.

Sub-Population	**N**	**% Seedlings ($\leq$ 2m)**	**Elevation**	**Slope**	**Aspect**	**MAR**	**% Winter Rain**	**MAMaxT**	**MAMinT**	**PET**
			(m)	**(degrees)**	**(radians)**	**($mm.yr^{-1}$)**	**(%)**	**(°C)**	**(°C)**	**($mm.yr^{-1}$)**
Aniskop	556	40	208 ±49^{b}	12.3 ±9.0^{a}	-0.73 ±0.37^{a}	30 ± 2^{e}	0.72 ±0.06^{c}	26.3 ±0.6^{d}	10.9 ±0.3^{f}	1780 ±15^{d}
Cornell's Kop	79	42	148 ±10^{a}	19.9 ±7.9^{b}	-0.83 ±0.07^{a}	35 ± 0^{f}	0.75 ±0.00^{d}	26.0 ±0.0^{c}	11.0 ±0.0^{g}	1777 ±0^{c}
Five sisters	104	59	217 ±37^{c}	26.0 ±11.9^{b}	-0.66 ±0.43^{a}	25 ±0^{a}	0.75 ±0.00^{d}	26.6 ±0.5^{e}	10.6 ±0.5^{e}	1786 ±18^{e}
Hellskloof	31	30	461 ±56^{d}	23.1 ±9.8^{b}	-0.10 ±0.73^{c}	28 ±2^{d}	0.71 ±0.07^{c}	25.8 ±0.4^{c}	9.8 ±0.4^{bc}	1738 ±12^{b}
Koeroegabvlakte	6	0	547 ±48de	17.2 ±8.5^{ab}	-0.71 ±0.24^{ab}	22 ±2^{a}	0.50 ±0.00^{a}	26.5 ±0.5^{de}	10.0 ±0.0^{b}	1793 ±7^{e}
Paradysberg	114	21	565 ±113^{e}	21.9 ±12.5^{b}	0.09 ±0.70^{cd}	26 ±1^{b}	0.72 ±0.07^{c}	25.7 ±0.8^{c}	10.1 ±0.5^{c}	1761 ±20^{c}
Remhoogte	41	44	380 ±43^{d}	16.2 ±9.8^{a}	0.72 ±0.43^{e}	27 ±1^{c}	0.75 ±0.00^{d}	26.5 ±0.5^{de}	10.5 ±0.5^{d}	1779 ±10^{d}
Rooiberg East	153	31	651 ±41^{f}	24.3 ±8.3^{b}	0.26 ±0.55^{d}	83 ±7^{g}	0.59 ±0.02^{a}	25.1 ±0.3^{b}	9.1 ±0.3^{a}	1720 ±9^{a}
Rooiberg West	107	17	590 ±27^{e}	19.4 ±8.4^{b}	-0.56 ±0.34^{b}	78 ±3^{g}	0.65 ±0.01^{b}	26.0 ±0.0^{c}	10.0 ±0.0^{bc}	1726 ±0^{b}
Struishoek	11	0	657 ±21^{f}	17.4 ±7.8^{ab}	0.42 ±0.30^{de}	105 ±0^{h}	0.66 ±0.01^{b}	24.0 ±0.0^{a}	9.0 ±0.0^{a}	1677 ±0^{a}
Mean Value			442.80	19.82	-0.21	46	0.68	25.9	10.1	1754

Correlation between environmental and climatic variables

The relationship between the environmental and climatic variables used is shown in the correlation matrix (Table 2).

Table 2. Spearman rank correlation matrix of the environmental and climatic variables. Significance levels are as follows: * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$. NS = not significant.

Variables	**PET**	**MAR**	**%Winter Rain**	**MAMinT**	**MAMaxT**	**Slope**	**Elevation**
MAR	-0.8424**						
% Winter rain	0.3497^{NS}	-0.2147^{NS}					
MAMinT	0.6809*	-0.4012^{NS}	0.7693**				
MAMaxT	0.8754***	-0.6930*	0.4616^{NS}	0.6616*			
Slope	-0.2485^{NS}	-0.0182^{NS}	0.0061^{NS}	-0.1885^{NS}	-0.2188^{NS}		
Elevation	-0.7091*	0.4303^{NS}	-0.7547**	-0.9058***	-0.6809*	0.1394^{NS}	
Aspect	-0.5515*	0.2485^{NS}	-0.1411^{NS}	-0.6261*	-0.3830^{NS}	0.0545^{NS}	0.6485*

Elevation was found to be highly correlated with MAMinT and % Winter rain with significant values of $p \leq 0.001$ and $p \leq 0.01$ respectively. Elevation is correlated with both MAMinT and MAMaxT negatively, which indicates that as elevation increases the average temperature decreases. The correlation with % Winter rain is also negative which means that in general at higher elevation there is less % Winter rain. Elevation is also significantly correlated with PET, MAMaxT and Aspect (Table 2). Aspect has a negative significant correlation with PET, MAMinT and Elevation (Table2).

PET was found to correlate with MAR and MAMaxT with significant values of $p \leq 0.01$ and $p \leq 0.001$ respectively (Table 2). The correlation with MAR is negative (Table 2) which means that higher MAR is associated with higher PET. This suggests that areas getting less rainfall are under greater atmospheric water demand and are subsequently more arid. The correlation of PET with both the temperature variables MAMaxT and MAMinT are positive (Table 2) meaning that areas with higher temperatures on average also have higher water demands on plants and surface water. Finally % Winter rain had a highly positive correlation with MAMinT (Table 2) and therefore areas with higher minimum temperatures get more winter rainfall than areas with less winter rainfall. This may be due to the strong influence of elevation on both % Winter rain and the temperature variables.

Ordination result

Fig 2a shows the ordination result with the 4 groups derived from the cluster analysis superimposed. The sub-populations were grouped at the 0.5 linkage distance in the cluster analysis. Aniskop, Cornell's Kop and Five sisters are in the 1st group. Hellskloof, Paradysberg and Remhoogte are in the 2nd group. Struishoek, Rooiberg East and Rooiberg West are in a 3rd group while Koeroegabvlakte is in its own 4th group. The correlation of the environmental and climatic variables with the ordination axis scores is shown in Table 3. Seven of the environmental and climatic variables emerged as central axes on the ordination result (Fig2b). The climatic variables PET, MAMaxT, MAMinT and % Winter rain all had negative significant correlations with axis 1 (horizontal axis on Fig2). Elevation and Aspect had positive significant correlations with axis 1 while aspect also had a positive significant correlation with axis 2. Slope and MAR did not have any significant correlation with either axis 1 or 2. This means that slope and aspect have little influence on the groupings formed by the ordination.

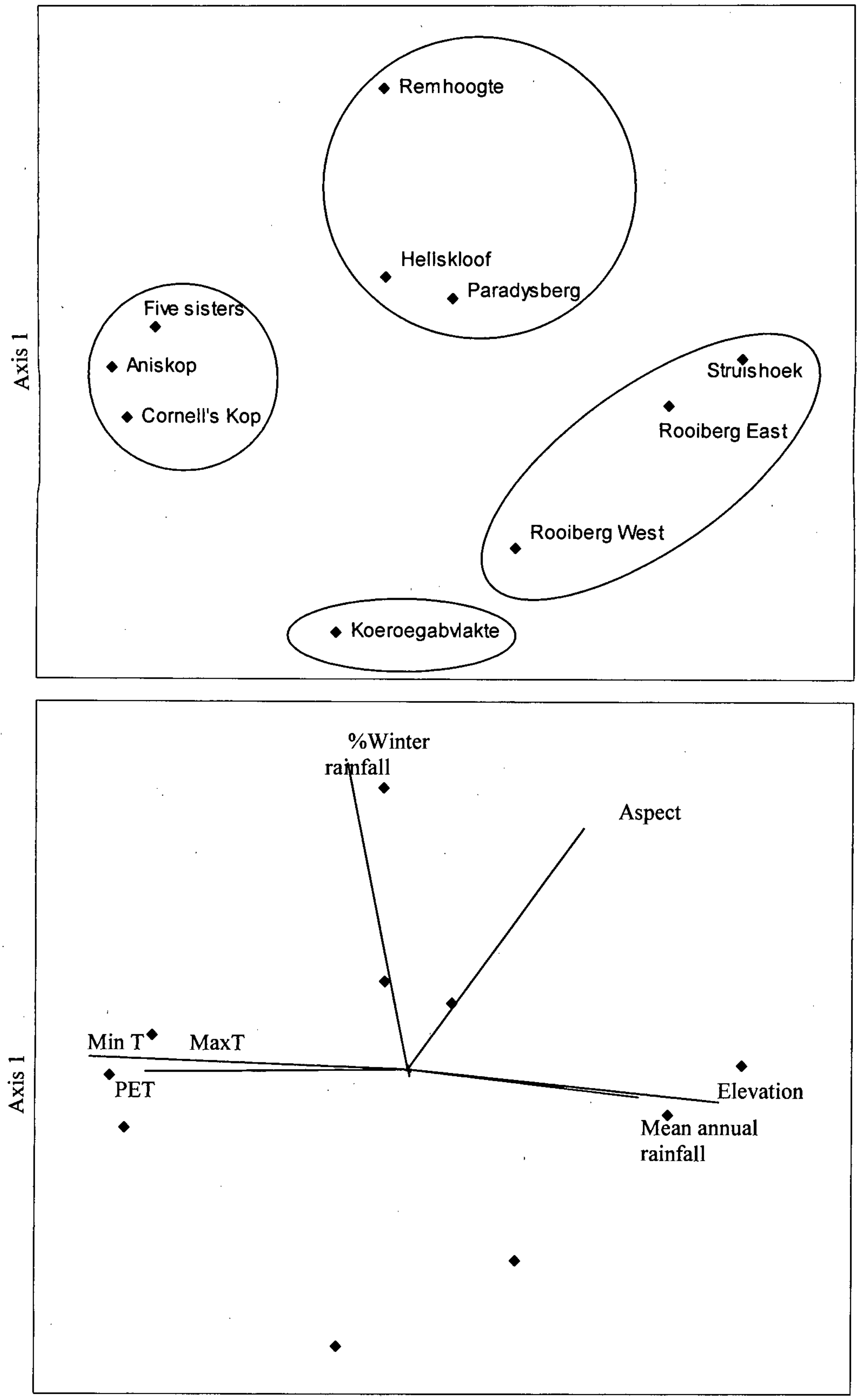

Figure 2. (a) NMDS ordination of the 10 *Aloe pillansii* sub-populations based on their climatic and environmental variables. Clusters derived from a cluster analysis based on Sorrenson/Bray Curtis distance measure have been superimposed. (b) Biplot illustrating the major environmental correlates with the ordination.

Population structure

The frequency size class distribution for the whole of the *Aloe pillansii* population (Fig 3) shows a rapid decline in size class frequency between the 0-1 m height interval and the 4-5 m height interval. At the 4-5 m height interval the size class frequency increases again and then gradually declines toward the 9-10 m interval. This represents a bimodal distribution.

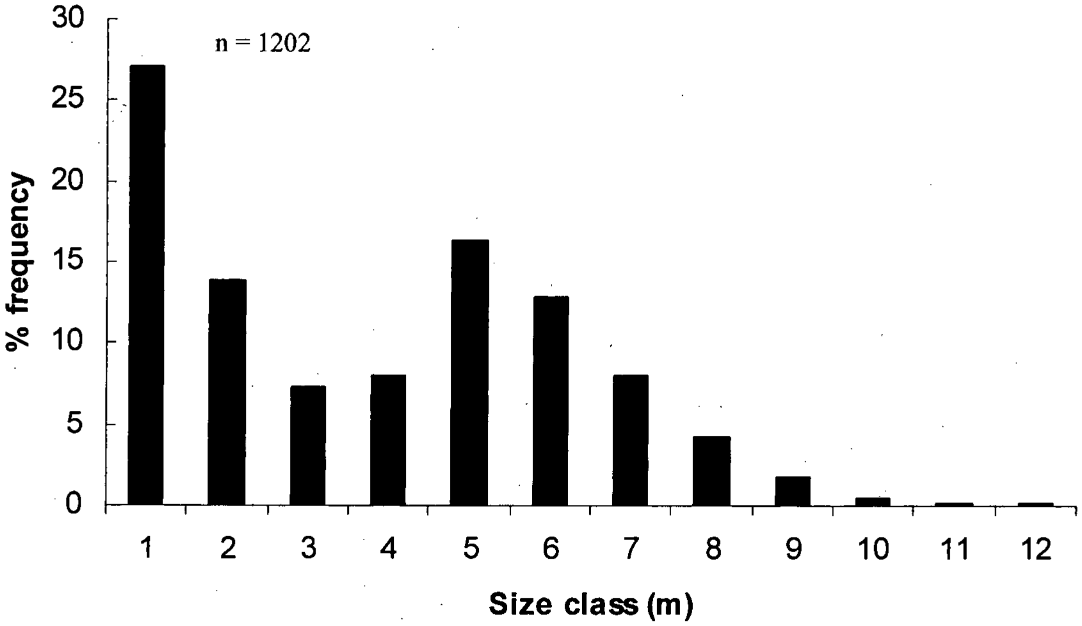

Figure 3. The percentage frequency of *Aloe pillansii* individuals for the recorded South African population within twelve 1m size class intervals.

The sub population frequency size class distributions (Fig 4) have missing intervals below the 9 m interval at Cornell's Kop, Hellskloof, Koeroegabvlakte, Paradysberg and Struishoek. The 4 sub-populations with the highest % seedlings and juveniles (<2m) are Five sisters, Remhoogte, Cornell's Kop and Aniskop with values of 59 %, 44 %, 42 %, and 40 % respectively (Table1). These sub-populations all have % seedlings and juveniles (<2m) ≥ 40 % (Table1). Rooiberg West has the lowest % seedlings and juveniles (<2m) with a value of 17 %, excluding Koeroegabvlakte and Struishoek, which have no individuals in that category (Table1).

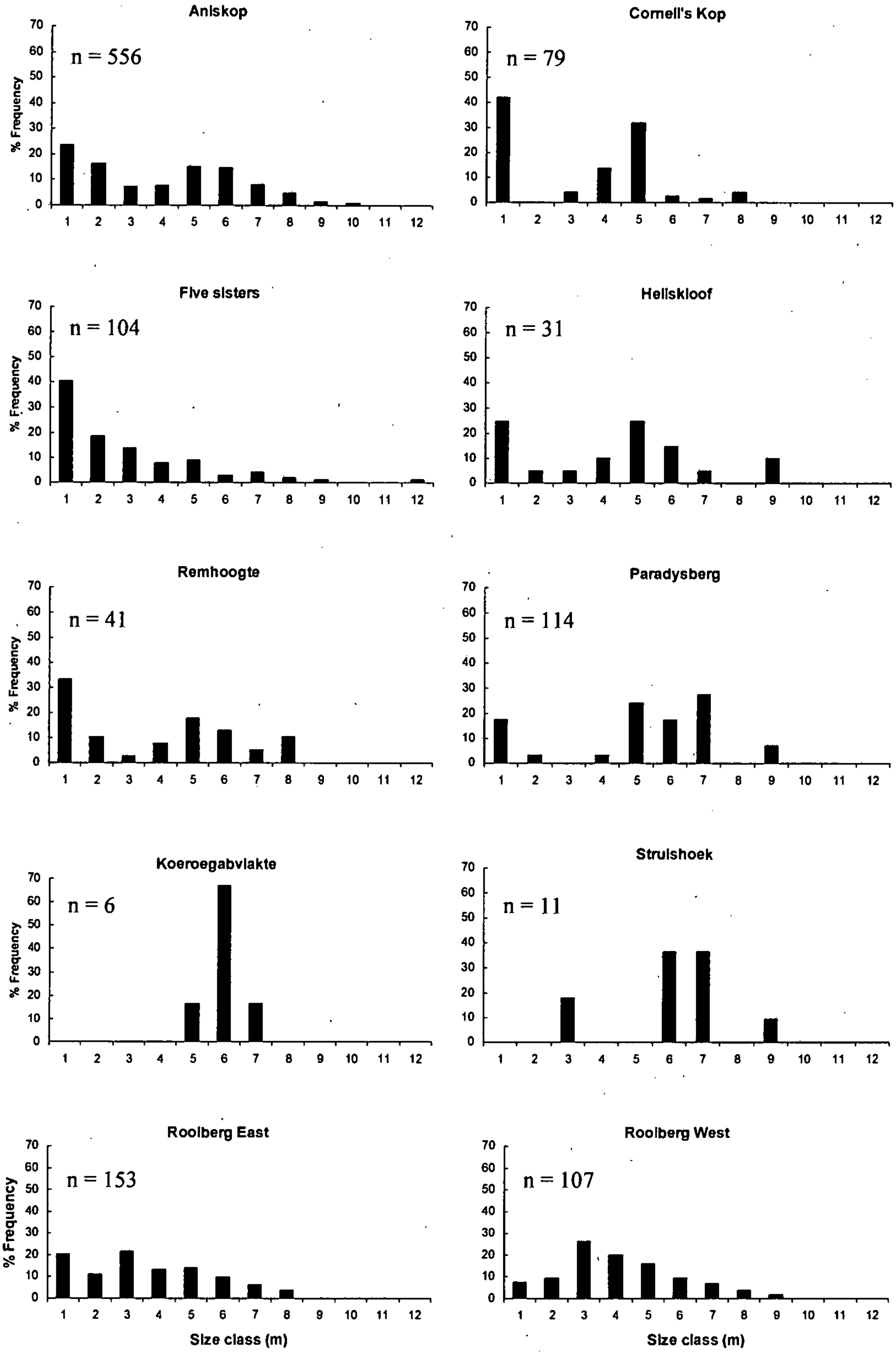

Figure 4. The size class frequency distribution of *Aloe pillansii* individuals within 12 1m size classes is represented for the 10 defined sub-populations in South Africa. (n) is the numbe of individuals in a sub-population .

Recruitment

The environmental and climatic variables that are most significantly correlated with % seedlings and juvenile (<2m) of the sub-populations (Table 3) are Elevation, % Winter rainfall and MAMinT. Elevation had the best correlation with a p value of 0.0025. The relationship is negative which implies that the higher % of seedlings and juveniles (<2m) are found in sub-populations at lower elevations rather than at higher elevations. The log of the seedlings and juveniles (<2m) plotted against log of the adults (>2m) showed a significant relationship with an r^2 value of 0.777 (Fig 4) and therefore a $p < 0.001$.

Table 4. Correlations of the 8 climatic and environmental variables with the % seedlings (<2m) of the *Aloe pillansii* sub-populations. Significance levels are as follows: * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$.

Variables	r
Elevation	-0.8050**
Slope	0.2985
Aspect	-0.1394
Mean Annual Rainfall	-0.5096
% Winter Rainfall	0.7387**
Mean Maximum Annual Temperature	0.4794
Mean Minimum Annual Temperature	0.6735*
Potential Evapo Transpiration	0.5123

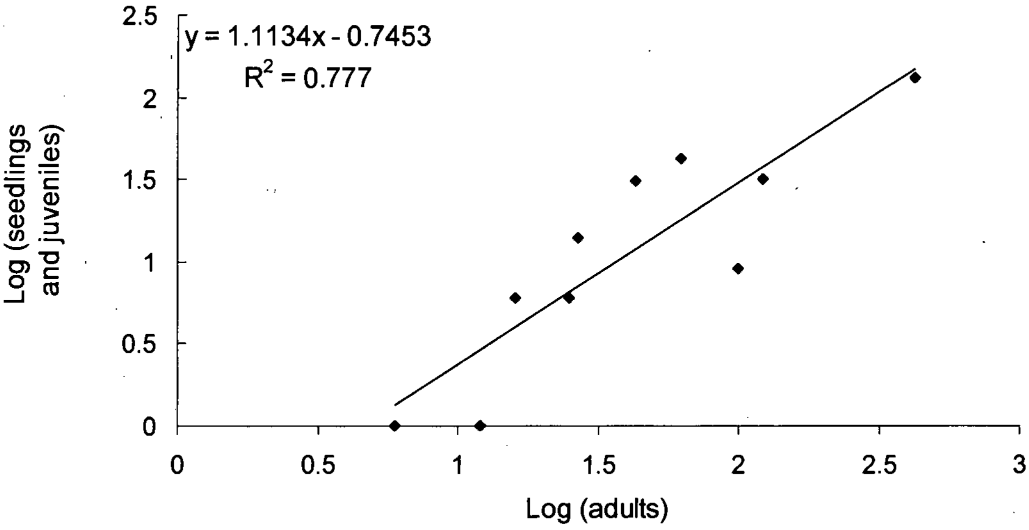

Figure 5. The relationship between seedlings and juveniles (<2m) and adults (>2m) on a log-log scale for all 10 sub-populations. The relationship is significant at the 0.001 level.

Discussion

Distribution of *A.pillansii* in relation to environmental and climatic variables

The 1202 individuals making up the sub-populations of *A.pillansii* are narrowly distributed in the Richtersveld (1% of the total area) (Powell et al., 2000). The species extends northward into Namibia where a further 1500 individuals make up more sub-populations (Loots et al, 2004). *Aloe pillansii* has been of great conservation concern due to its low population size and high mortality evident from dead skeletons and low recruitment (Powell et al., 2000). In addition to this, evidence of the potential influences of human impact, climate change, plant disease and herbivory (Powell et al., 2000) on the health of the *A.pillansii* population have been highlighted.

The focus of this paper is on the environmental and climatic influences on the health of the populations. Population health is defined in this study by % seedlings and juveniles (<2m) because of the important role of non-reproductive individuals in replacing the reproductive adults for future population viability. Static information on size class distributions may not be a good predictor of future populations trends (Condit et al., 1998) and therefore % seedlings and juveniles (<2m) is a broad assumption of probable health. However comparing sub-populations in terms of % seedlings and juveniles (<2m) is useful in determining which populations are more likely to replace aging adults assuming consistent seedling mortality between sub-populations. This does not verify health but rather 'healthier' sub-populations. Healthier sub-populations can then be evaluated in terms of their environmental and climatic parameters. In this discussion I will show how the environmental and climatic variables selected in this study relate to *A.pillanssii's* population's distribution and health.

Environmental variables as surrogates

The environmental and climatic variables that are used in this study must be interpreted cautiously as they are potential surrogates for other environmental and climatic influences. Correlations of the environmental and climatic variables (Table2) give a broad idea of how the variables relate to each other.

Elevation is a central variable that emerges strongly in the results. The 4 healthiest sub-populations Aniskop, Cornell's Kop, Five sisters and Remhoogte comprise 65% of the total population and are found at the 4 lowest elevations defined (Table1). However elevation cannot be looked at on its own because it is a surrogate for other environmental and climatic variables. For example elevation correlates significantly with PET, % winter rain, MAMinT, MAMaxT and aspect (Table2). Elevation can be a surrogate for temperature (Pausas, 2001), as higher altitudes are a general cause of lowered temperatures (Shulze, 1997). Increased elevation is also a surrogate for climatic characteristics such as acting as a barrier to rain bearing masses, forcing moist air to rise through orographic lifting or increasing thunderstorm activity (Shulze, 1997). This is dependent on the local topographical environment. In addition, fog which consists of moist air and is common to the Richtersveld, moves up major valleys and rivers that allow it to infiltrate far inland along valleys and foothills (Dean et al., 1999). Changes in altitude can also lead to increased frost incidence due to air drainage in valleys (Shulze, 1997) leading to lower temperatures in valley bottoms. Elevation therefore represents many different climatic characteristics all of which potentially have an influential role on *A.pillansii's* distribution and health. This is shown by the healthy sub-populations which are found at low elevations.

Grouping of sub populations along climatic gradients

The sub-populations were evaluated to investigate how they grouped in terms of their similar environmental and climatic variables. Fig 2 shows the groups of sub-populations that inhabit similar climatic niches. Aniskop, Cornell's Kop and Five sisters are grouped together in the ordination (Fig 2a) showing that they are at a lower elevation, lower MAR, higher MAMinT, higher MAMaxT and higher PET in general compared to the other sub-populations. These are also the healthier sub-populations defined by their % seedlings and juveniles (<2m) which are greater than 40% (Table1).

Extrapolating the variables directly, a high PET means there is potentially higher relative water loss from evaporation at the surface and from transpiration in plants (Shulze, 1997) in the healthier sub-populations. This means there is higher water stress on plants in these sub populations assuming there are no alternative water sources for the plants other than MAR. Higher MAMinT and MAMaxT also means these sub-populations experience higher temperatures on average. Therefore this suggests these sub-populations inhabit hotter, dryer and low altitude environments in comparison to the other sub-populations and therefore would most likely experience more droughts. This is counter intuitive considering these are the healthier sub-populations and seedling recruitment in other succulents has been found to be limited by water stress (Jordan et al., 1979) and seasonal temperatures (Drezner et al., 2004). Elevation is correlated to all these variables except for MAR (Table2) suggesting that it is a surrogate for them. It is also a surrogate for other climatic characteristics of the Richtersveld region such as fog. The influence of fog is not evident from the environmental and climatic variables used in the correlation (Table2) but is associated with the Orange river which is found at a lower elevation than the surrounding. topography (Dean et al., 1999).

Climatic range

The environmental and climatic variables determined for each population reveal a climatic range for *A.pillansii*. To assess the climatic range the most threatened sub-populations were examined. The two sub-populations that are most threatened are Koeroegabvlakte and Struishoek. Geographically Struishoek is the most Southerly sub-population while Koeroegabvlakte is the most North Easterly sub-population (Fig1). It is evident that they are threatened because of their low population sizes of 6 and 11 respectively (Table1) and also because they have no seedlings and juveniles (<2m). This suggests these two populations are suffering population decline.

Both these sub-populations are at the opposite extremes of the environmental and climatic variables found, and illustrates *A.pillansii's* limited environmental and climatic range. When interpreted directly from the variables this range extends from Koeroegabvlakte's climate where it is potentially dryer and hotter toward Struishoeks' climate where it is potentially cooler and wetter. The ideal climate for the species therefore lies between these two environmental and climatic variable extremes.

Population size class distributions and recruitment

Total population size class distribution

The total *A.pillansii* population and sub-population size class distributions were evaluated to investigate the population viability and showed that the entire population has a bimodal size class distribution similar to plant species in forests where seedling survival is dependant on gaps from disturbance events (Everard, 1994). Illegal collecting (Powell et al., 2000) may be a factor altering the total size class distribution. The extent of the graduated bimodal distribution suggests that collecting would have occurred generally across the sub-populations. This is a possibility because up to 70 % of the individuals are found in unprotected areas in the Richtersveld (Powell et al., 2000).

Infrequent recruitment from unusually wet years occurs in other succulents such as *Agave deserti* (Jordan et al., 1979) and is also likely to influence *A.pillansii.* Rainfall events in the Richtersveld can create similar 'gaps' of opportunity, as rainfall can be rare or non-existent in some years (Powell et al., 2000), for *A.pillansii* to recruit. Natural fluctuations in productivity are a character of the succulent Karoo due to dry and heavy rainfall periods (Hoffman et al., 1990). This produces infrequent recruitment events that create a bimodal distribution because of the delayed frequency and rarity of rainfall events that allow for successful recruitment.

There is good evidence of successful recruitment in the total population, with 41 % seedlings and juveniles (<2m) found (Fig 3). This is not far removed from the ideal inverse J curve size class distribution that exhibits many more small individuals than larger individuals (Everard, 1994). An inverse J curve size class distribution implies that there are enough non-reproductive individuals to replace the adult generation assuming a low rate of seedling mortality. The total population therefore does not appear to be in dire population decline judging from the relatively high number of seedlings and juveniles (<2m) that will replace the adults. However, the low total *A.pillansii* population number of 1202 in South Africa is a reason for concern. This may be an expression of incomplete collection (Powell et al., 2000) of the existing population as it inhabits an often inaccessible area in the Richtersveld and because of the difficulty of finding seedlings under nurse plants. Even if the collection is incomplete, the fragmentation of the population into spread out sub-populations (Powell et al., 2000) is an additional concern for the well being of the entire *A.pillansii* sub-population. Therefore the population appears to be healthy but is potentially at risk.

Sub-population size class distributions

The sub population size class distributions are varied and affected by different factors because of their diverse geographical, environmental and climatic characteristics. The *A.pillansii* sub-populations Koeroegabvlakte and Struishoek have the most damaged size class distributions of all the sub-populations (Fig4) and this is likely due to their position on *A.pillansii*'s environmental and climatic extremes. Five sisters has a J curved size class distribution with 59 % seedlings (> 2m). Therefore Five sisters represents the 'healthiest' sub-population, as there is little evidence of disruptive influences causing it to have an irregular size class distribution. Five sisters is the closest sub-population to the Orange River and is approximately 60 km along the river from the ocean. This gives Five sisters more access to potential fog moisture, which moves up the Orange River coarse (Dean et al., 1999) providing a more reliable alternative moisture supply for it than the other sub-populations found further inland.

Rooiberg East and Rooiberg West are separated from the Northern sub-populations by approximately 60km and have very graduated size class distributions (Fig4). The Northern sub-populations in general have irregular size class distributions with missing size classes and bimodal distributions. This may be due to increased collecting impacts found in the Northern Richtersveld. Five sisters is the exception having a J curve size class distribution (Fig4). On the other hand the southern sub-populations have the highest MAR which may lead to more frequent rainfall events in comparison to the Northern populations and consequently creating more recruitment opportunities. However these recruitment events are not reflected to be as successful as the healthiest populations such as Five sisters, Aniskop, Cornell's Kop and Remhoogte (Table1) that are found in the North. The healthiest sub-populations still lie within the climatic range between Struishoek and Koeroegabvlakte (Table 1) and have a similar combination of environmental and climatic variables (Fig2).

Recruitment and moisture availability

The % seedling and juveniles (< 2m) of *A.pillansii* correlate significantly with the % adult (> 2m) for the sub-populations suggesting that larger populations produce more seedlings (Fig 5). This highlights healthy reproduction in large populations. However, smaller populations may struggle to increase numbers at the same rate with some populations as some populations have no seedlings at all (Fig 4). This is likely due to fragmentation affects on reproduction and environmental and climatic constraints on seedling recruitment.

In arid environments systems can exist under extreme moisture pressures just from the fact that rainfall is much more variable in deserts than mesic environments (Wagner, 1981). The % seedlings and juveniles (< 2m) for each sub-population when correlated against their defined environmental and climatic variables significantly correlate with elevation, %Winter rain and MAMinT (Table 4), illustrating a strong relationship with both environmental and climatic variables. Elevation as mentioned before is a potential surrogate for temperature, rainfall and therefore consequently moisture availability. The three sub-populations Cornell's kop, Aniskop and Five sisters with the highest % seedlings and juveniles (< 2m) are found in environments that have high temperatures, lower elevation and lower MAR. As % Winter rain is significantly and positively correlated to the % seedlings and juveniles (< 2m) it must be an important factor on population health. This means the seasonality of the rainfall is more important than the MAR on successful recruitment because MAR corresponds with the less healthy populations in the ordination. *A.pillansii* seedling survival is likely to be limited by moisture given the strong positive correlation of % Winter rain with % seedlings and juveniles (< 2m). In addition there is strong evidence of seedling recruitment being influenced by summer temperatures (Drezner et al., 2004), drought after germination and water stress during the seedling stage (Jordan et al., 1979) in other succulent plants. However this does not explain why the environmental and climatic variables that are generally surrogates for hotter, dryer and lower elevation environments describe the healthier sub-populations. This can be explained by alternative moisture sources that *A.pillansii* is exposed to.

In addition to winter rainfall, fog is a potential alternative moisture source for plants in the Richtersveld and may explain why the successful sub-populations are found at low elevation and seemingly extreme hot and dry environments. Fog from the sea is a climatic characteristic of the entire West coast of Southern Africa (Desmet et al., 1999). The Orange River, which runs through the Richtersveld, allows fog to penetrate far inland into valleys and foothills (Desmet et al., 1999). The Orange River area is estimated to have up to 75 fog days (Richard et al., 1999) a year and the potential moisture that can be gained from fog can be several times that of MAR in certain instances (Shultze, 1997). This is a substantial amount of water and can be a far more reliable source than MAR in desert environments (Desmet et al., 1999). Therefore fog moisture appears to be benefiting both the Namibian (Loots et al., 2004) and South African populations of *A.pillansii*. The affect of fog and seasonal rainfall events on the *A.pillansii* population health needs to be investigated further to verify its temporal, spatial and biological influence because of the evident influence of additional moisture availability for recruitment.

Conservation and Anthropogenic Climate Change

The potential effect of anthropogenic climate change on *A.pillansii* needs to be mentioned in light of the strong relationship found between the environmental and climatic variables and the sub-population distribution and health. Globally species have the potential to be affected in terms of their physiology, distribution and phenology in response to anthropogenic climate change (Hughes, 2000). Global climate change predictions show that South Africa will become dryer from the West where *A.pillansii* is found and in the next 50 – 100 years the vegetation biomes will be reduced to 35 – 55% of their present area, including the Succulent Karoo, with continued anthropogenic climate change (Midgley et al., 2001). *Aloe pillansii* is a potentially good indicator for climate change influences for other species in the Succulent Karoo because of its evidently discrete evolutionary climatic niche (Williamson, 1998) and limited climatic range in this study. The small population size, fragmentation of sub-populations and limited distribution of *A.pillansii* sub-populations, (Powell et al., 2000) means that its ability to shift its range in response to rapid climate change is also undermined. However these factors mean that the impacts of climate change are likely to be the most obvious on *A.pillansii.*

Modeling which incorporates the bioclimatic envelopes of species needs to be done for *A.pillansii* given its evident sensitivity to environmental and climatic variables with a potential to be impacted by anthropogenic climate change. Predicting species responses to climate change by developing models to assess the potential impacts on them, have already been done in the U.K (Berry et al., 2002). This would be useful for assessing the vulnerability and potential response of *A.pillansii* to anthropogenic climate change. Modeling is useful because of its predictive ability however in terms of conservation prioritizing the results of models need to be at a fine scale to be of value (Berry et al., 2002) especially in light of *A.pillansii's* limited range. GCMs (General Circulation Models) that are used for broader resolution projects (Hannah et al., 2002) of climate change prediction would not incorporate the scale needed to evaluate *A.pillansii* and in the case of *A.pillansii* a regional climatic model will be of greater use.

The current tools of modeling do have criticism because of their assumption that climate is a determining factor of species distribution (Berry et al., 2002). However as the *A.pillansii* distribution and health show a strong relationship with the various environmental and climatic variables used in this study these tools will be useful coupled with field and laboratory studies in determining the sensitivity of *A.pillansii* to climate change. This information is essential if an effective conservation plan for *A.pillansii* is to be formulated. The non climatic influences on *A.pillansii's* health such as illegal collecting, herbivory, plant disease and seed set amongst others (Powell et al., 2000) also need to be investigated to determine the relative significance of their impacts. These factors must then also be incorporated into a complete conservation plan for *A.pillansii*, which will insure its survival.

Conclusion

This study shows that the distribution and potential health of *A.pillansii* in South Africa is influenced strongly by environmental and climatic variables and has the potential to be significantly influenced by eminent anthropogenic climate change. It is therefore consequently a good indicator species for monitoring anthropogenic climate change impacts for the succulent Karoo. This is due to its apparent vulnerability and discrete environmental and climatic niche that it inhabits. To insure the survival of *A.pillansii* further studies into the potential impacts that *A.pillansii* may experience from anthropogenic climate change should be extrapolated to create a conservation framework for the succulent Karoo so that its biodiversity can be protected from predicted impacts. To achieve this an integrated conservation plan needs to be implemented which incorporates known anthropogenic influences, non-climatic influences and anthropogenic climate change for *A.pillansii* and its associated biological diversity. This study has gone forward in highlighting one facet of a number of forces which may be acting in conjunction and leading *A.pillansii* to its decline. In this light *A.pillansii* is a litmus test for conservationists in South Africa in our ability to evaluate vulnerability and respond to anthropogenic climate change and to species which are potentially on the brink of extinction.

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