Acacia karoo and its effects on the succession of Dune Forests in the Eastern Shores, Kwazulu-Natal.

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ABSRACT:

Acacia karoo arises following disturbance in the Dune Forests of Northern KwaZulu-Natal. Patches of *A. karoo* which had arisen as a result of the abandonment of fields by subsistence farmers in a dune forest matrix were studied. Previous authors have considered *A. karoo* to be part of a successional mechanism which leads towards a climax forest canopy (Mentis and Ellery, 1994; von Maltitz et al, 1996). This succession is questioned as a number of the conclusions of these authors were not verified by my own work. The present paradigm holds that the *A. karoo* is even aged and will senesce after 25 years, while recruitment does not occur in the patches. I found no evidence of canopy senescence and microhabitats within which recruitment of *A. karoo* occurred were identified. Further the introduction of other species in the patches is facilitated not through the *A. karoo* canopy but was shown to be facilitated by the presence of multi-stemmed canopy-trees of other species which had not been removed by the farmers. However this introduction of other species into the patches was still limited, with certain species not found in even the very oldest patches (37 years old). No discernable chronosequence could be identified when comparing patches of different age, which casts doubt on the belief that these patches will eventually revert to climax dune forest.

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Introduction:

Acacia karoo Hayne has previously been recognised as a part of succession in Natal Coastal Dune Forests, normally arising as the first canopy tree in areas disturbed by humans (von Maltitz et al, 1996). It has become of great importance recently due to its use in the revegetation of dunes following mining activities. These activities have provoked a storm of controversy and conservationists and the public have demanded that the miners (Richard's Bay Minerals) prove that they can in fact rehabilitate the dunes to their original state following their highly destructive activities (See Kruger et al, 1997 for a review of the debate).

Mentis and Ellery (1994) showed that following mining and some restorative work involving the reshaping of the dunes, the replacement of the topsoil removed before mining as well as the seeding of perennial species to secure the sand surface, a canopy of *A. karoo* arises. The authors concluded that this *A. karoo* canopy was part of a successional pathway that would eventually result in climax dune forest. This conclusion has further been supported by von Maltitz et al (1996) and van Aarde et al (1996). These studies concluded that *A. karoo* was a facultative species which led to the establishment of other species in a successional progression. This falls under the Relay Floristics Model in which certain species colonise following a disturbance and are replaced by others in an orderly succession until a climax state is achieved. This thesis was intended to address concerns as to how *A. karoo* comes to be in the dune community and also to examine the successional dynamics acting on the *A. karoo* patches.

Through the use of chronosequences (patches of *A. karoo* of different ages produced by abandonment of fields by subsistence farmers) I wished to examine the nature of the *A. karoo* presence in the dune forest. Of central importance is the issue of whether the patches will senesce and whether they are facilitators in a successional pathway. If trends can be found which display a time-orientated directional change then succession can be assumed to occur. If however the patches are shown to be largely homogenous with no time-related element. Further if recruitment of *A. karoo* can be shown to be occurring then it is likely that these patches will remain dominated by *A. karoo* for some time and not return to climax forest.

Within this framework of rehabilitation the identification of specific guilds is of vital importance. That other species can penetrate the *A. karoo* patches is not necessarily a sign of succession. It is rather the presence important climax forest guilds which will establish the authenticity of successional claims in the dunes. Ralston (1996) showed that frugivorous birds were not that common in *A. karoo* patches and as a result those species whose seed dispersal is dependant upon such frugivores would be limited in their ability to spread to such *A. karoo* patches. Even if measures such as species richness or diversity or cover of species other than *A. karoo* be shown to increase, this is not sufficient evidence for claims of rehabilitation. That the land is simply revegetated is not enough, both measures of structure as well as functioning of the community must be restored.

Materials and Methods:

Investigations were conducted in the dune forests around Cape Vidal in the Greater St. Lucia Wetland Park. *A. karoo* patches were identified using old aerial photographs and their positions were mapped using GIS. This allowed us to go directly to these patches and prevented selection of the sites by subjective means. Using successions of photographs of the same areas it was possible to roughly date the abandonment of the sites. They were previously used by subsistence farmers for crops, who were relocated. Three basic ages of the *A. karoo* canopy were recognised (1960, 1975, 1988) and three plots from each age were targeted. Three control areas were also determined by selecting areas which had never been altered by human disturbance, but which were both close to previously disturbed areas and were also similar in terms of topography.

At each site a single transect extending from the edge of the *A. karoo* canopy to the middle of the patch was laid. Trees within 7.5m of the transect line were recorded. All *A. karoo* individuals within this zone were noted, either by height (if the individual was less than 2m tall) or by measuring the diameter 10cm above the ground. Size-class distributions for *A. karoo* were produced by working out the percentage of each size class for each plot. For all other species, only those individuals over 2m in height were recorded. The transect was divided up into 10m lengths and individuals within the blocks were recorded. Species other than *A. karoo* did not however have their size recorded, but it was recorded if they were multi-stemmed or single-stemmed. Multi-stemmed was defined as having multiple stems arising from the ground, branching aboveground was considered single-stemmed. If the individual was also part of the canopy, then this information was also noted.

Forest species other than *A. karoo* were analysed both through presence/absence data which was processed by the multivariate package TWINSPAN (Hill, 1979), as well as calculating the percentage that each species contributed to the total number of individuals other than *A. karoo* in the transect. The percentages of trees (per species) which were canopy or subcanopy, as well as multi- or single-stemmed was also calculated as a proportion of the total number of individual trees in the transect. The number of species, and the percentages as calculated here, of the species which were common only to stands of a certain age were also calculated. Correlation coefficients were calculated by comparing the number of multi-stemmed canopy trees in each of the 10m blocks of the transect to the number of individual trees, as well as the number of species in each block. One-way ANOVAs (STATISTICA 5) were also employed to examine the significance of the distribution of the various species according to their percentage in each transect. Before any ANOVAs were performed the data was analysed to ensure that it was normal. This was performed in STATISTICA through the use of Kolmogorov-Smirnov and the data was assumed to be normal if the significance value (p) was not < 0.05.

The percentages of each population greater and less than 30cm in diameter were compared among sites using "Kolmogorov-Smirnov test for equal samples" (Statgraphics 5.0). This Kolmogorov-Smirnov test was also used to determine the significance of differences in mortality of *A. karoo*'s greater or smaller than 30cm in diameter.

A variety of patch conditions were sampled to examine *A. karoo* recruitment. Quadrats 7.5m × 7.5m were examined under two canopy conditions: closed or open (gap). Further, different understorey conditions were also examined. The dominant understorey herb is *Isoglossa woodii* and understorey conditions were thus classified as bare earth, low *Isoglossa* cover or high *Isoglossa* cover. Foliage profiles were made by randomly selecting 2 points in each quadrat. From each point it was then estimated how far away a board 20cm × 20 cm would be 50% obscured by the foliage. This was performed at heights of 25cm, 50cm, 75cm and 100cm looking in 4 different directions away from each point.

The seedbank in the dunes was examined by sifting for the seeds using a fine (5mm) wire sieve. An area of ground one meter by thirty-three centimetres was sieved to a depth of fifteen centimetres. Sieving was conducted at 3 points in each *A. karoo* patch and once in each control site. In the *A. karoo* patches the seedbank was sampled in the middle of the patch under the *A. karoo* canopy, in the ecotone (under the meeting place of the forest and *A. karoo* canopies) and between 5 and 10m into the surrounding forest. A two-way ANOVA (STATISTICA 5) was performed on the resulting data to determine if the seedbank altered with age, or if there were significant changes in the number of seeds in the their distributions within individual sites.

Dormancy of the seeds was investigated by attempting to induce germination in 100 seeds collected from the dunes. Fifty of the seeds were soaked in sulphuric acid for two minutes to break the seed coat. The other fifty were not treated at all. All of the seeds were then placed in petri-dishes and placed in a dark cupboard (T. Wilson, pers. comm). Germination rate was determined by observing the number of seeds which had germinated at regular intervals.

Results:

Figs. 1,2 and 3 are representative size class distributions from three of the transects. Fig. 1 shows the typical structure of the patches as expected from the work of Mentis and Ellery (1994) and von Maltitz et al (1996), showing no recruitment in a relatively even-aged stand. Fig.2 describes the situation in a more mature plot, but which differs from Fig. 1 in that the distribution is more spread and despite the fact that the plot is 37 years old there is no large mortality of the large size classes. Fig. 3 indicates a plot which has seen a large amount of mortality in the large size-classes, but has also shown that recruitment is occurring in the gaps.

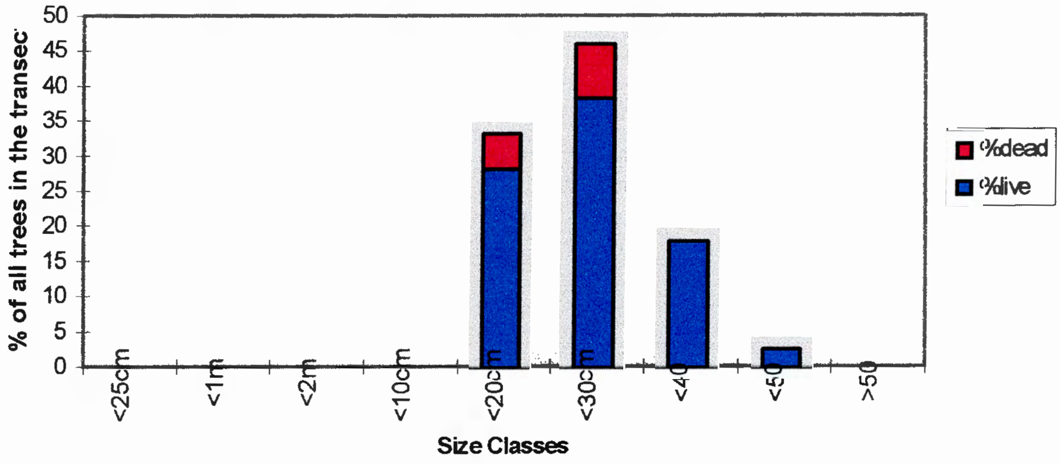


Fig 1: Size class distribution of *A. karoo* in Site 19 (1988). (First three size classes are heights, the rest are diameters)

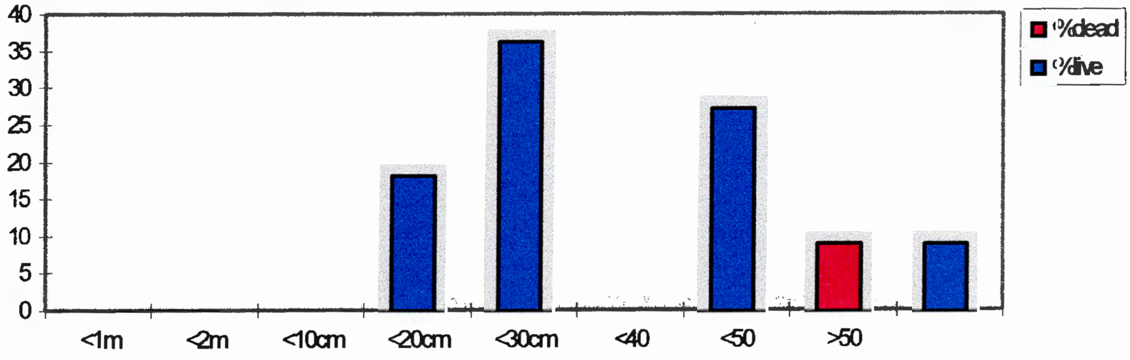


Fig 2: Size class distribution of *A. karoo* in Site 29 (1960). (First two size classes are heights, the rest are diameters)

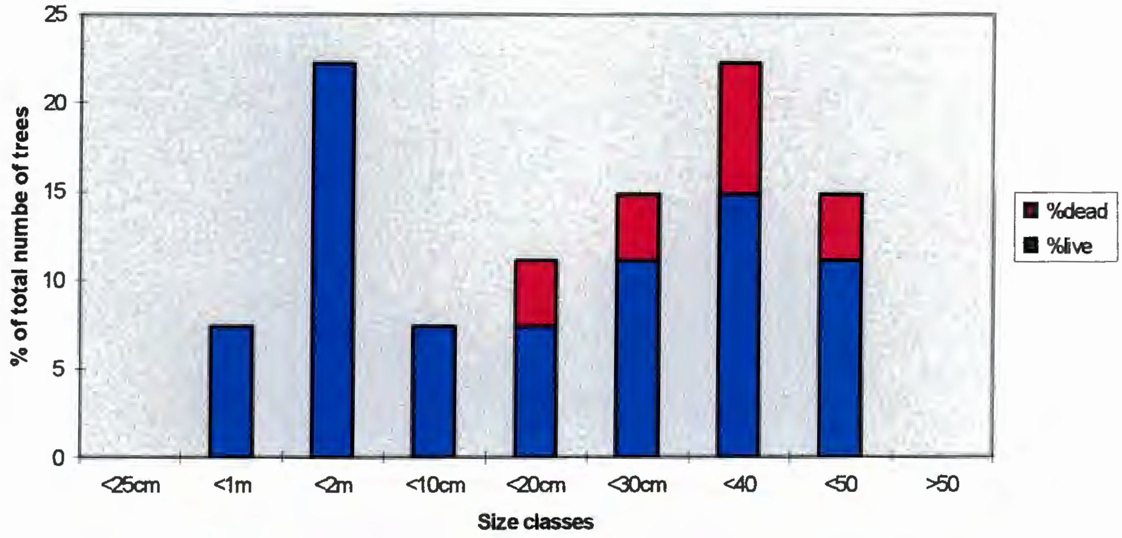


Fig 3: Size class distribution of *A. karoo* in Site 30 (1960). (First two size classes are heights, the rest are diameters)

From the results of Table 1 and Fig. 4 below it is clear that canopy cover as well as foliage density are the two defining factors for potential recruitment microhabitats. Although the same number of sites were sampled under the *A. karoo* canopy as in gaps, only two of the sites under the canopy contained woody seedlings (each had two recruits) and both of these sites had very little *Isoglossa* understorey.

Table 1: Correlation coefficients relating foliage density at a height of 25cm from the ground for the two canopy conditions against the number of *A. karoo* seedlings found. Significance is indicated by * ($p < 0.05$).

Canopy condition	**Correlation coefficient (r)**
Open	0.90*
Closed	0.57

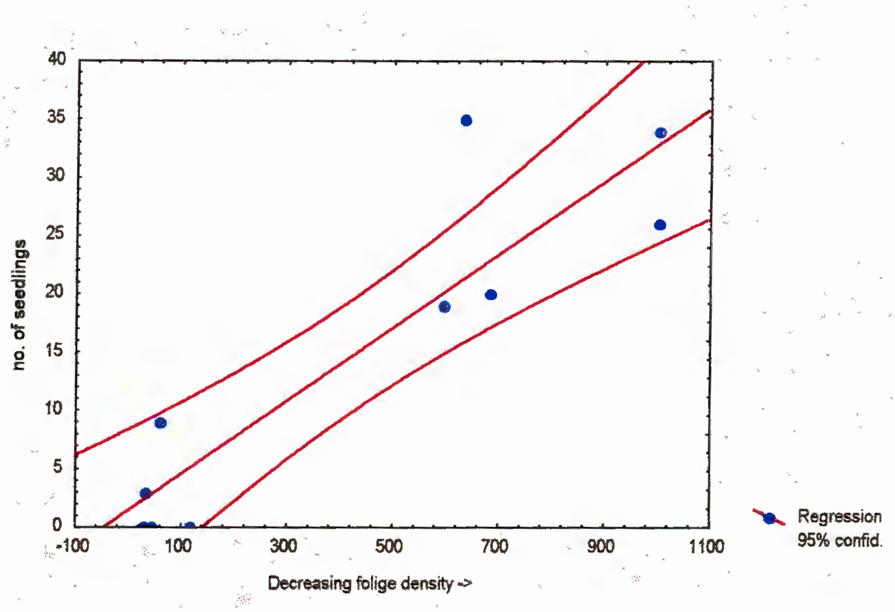


Fig. 4: Graph indicating correlation between decreasing foliage density and the number of woody seedlings under open canopy ($r = 90$, $p < 0.05$). (X-values are the average distance at 25cm derived from the foliage estimation method.)

The percentage contribution of each species found only in certain age classes and the controls was calculated and expresses as the percentage of individuals of each transect (See Fig. 5).

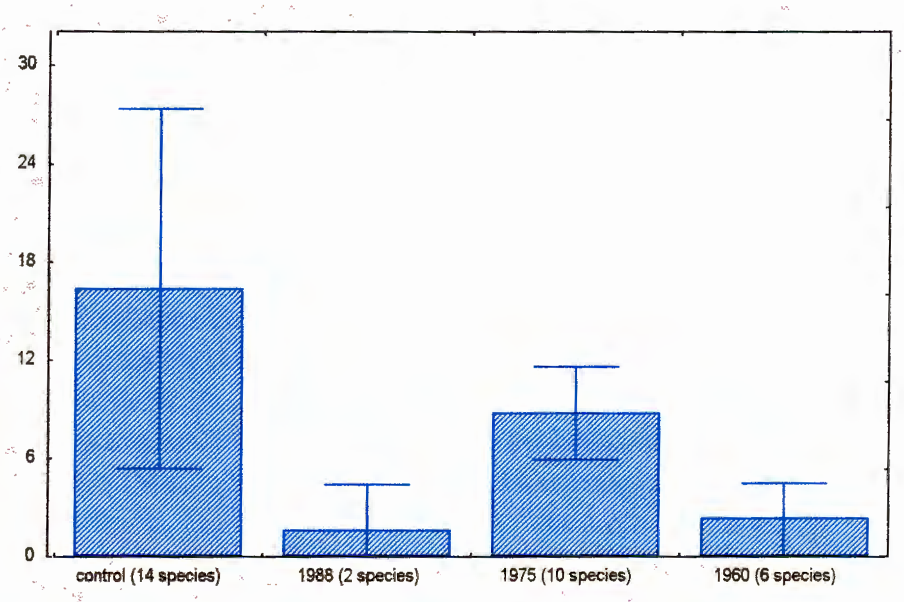


Fig 5: Average % of all individuals which belong to species found only in one age-group per transect. The number of species contributing is included in brackets after the age of the group.

When the age groups in Fig. 5 are compared to one another to determine if there is a significant difference among all of the age-groups, the result comes close to being significant(one-way ANOVA: F = 4.066, p = 0.0527). However when the test was altered so that it compared only the controls against all of the *A. karoo* patches, the result was highly significant (F = 8.792, p = 0.014*).

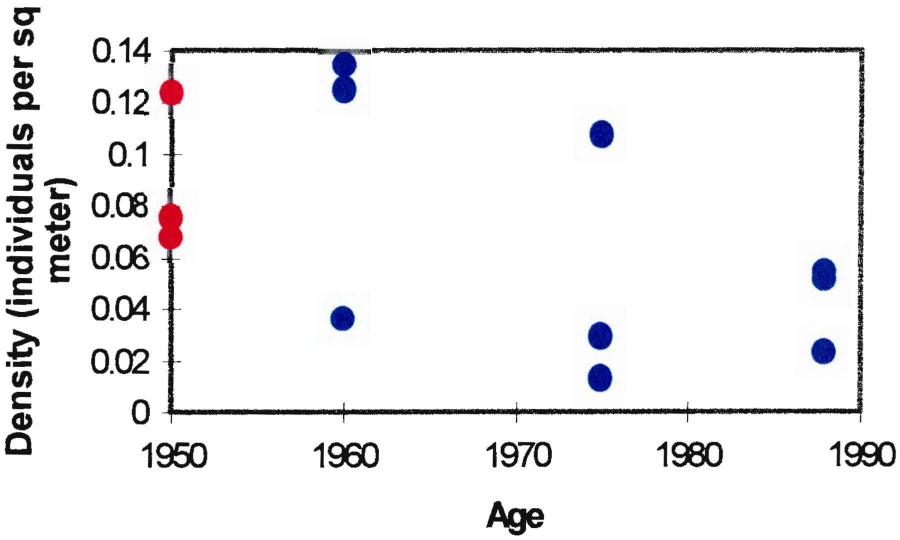


Fig 6: Density of species other than *A. karoo* compared with age for each site. Control values are represented by the red data points.

No clear change in species density could be shown for Fig. 6 as the data was too variable. This appears to indicate that the site conditions are more important than the age of the patch in determining species density.

Dividing the dead skeletons of *A. karoo* up by classing them as either greater or less than 30cm diameter did not provide any significant results (Kolmogorov-Smirnov, DN = 0.556, K-S = 1.18. p = 0.124). Kolmogorov-Smirnov also did not assign significance to the distribution of living *A. karoo* when classed as greater or less than 30cm diameter for each site (DN = 0.44, K-S = 0.943, p = 0.336) (see Fig. 7).

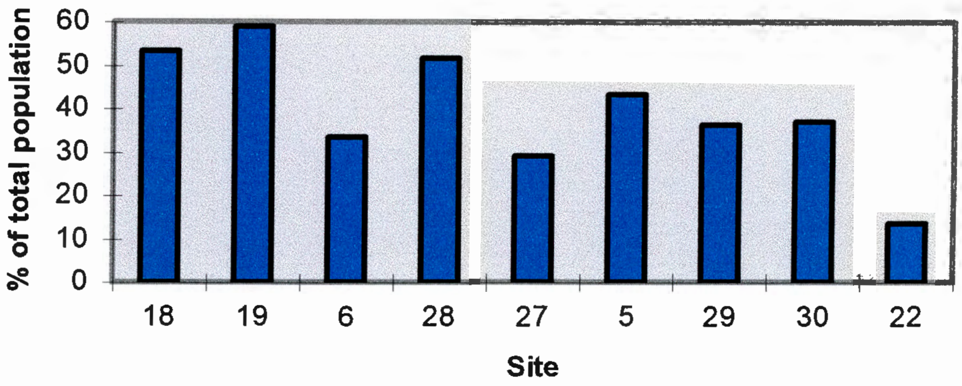


Fig 7: Graph showing the percentage of living *A. karoo* in each site with a diameter >30cm.

Table 2: Results of a two-way ANOVA (Statgraphics 5.0) performed on the *A. karoo* seedbank data, comparing both age of site and the distribution of seeds within the site, i.e. according to position in either the thicket, ecotone or neighbouring forest. (* indicates significant value, $p < 0.05$).

Effect	**F**	**p**
Age of site	1.235	0.314
Position in Site	7.002*	0.005*

Table 4 shows the results of tests performed to determine the significance of the distribution of *A. karoo* seeds in the seedbank. The number of seeds in the seedbank varied quite considerably (Table 3). On average the highest numbers of seeds were found under the *A. karoo* canopy. The ecotone also had a large number of seeds. Numbers of seeds appeared to decline as one moved out of the *A. karoo* patch and the surrounding forest generally had few seeds. However no seeds whatsoever were found in the forest controls. All of the averages are for the same amount of sieving effort.

Table 3: Averages and Variations of the number of seeds found in each position in the patches of *A. karoo*.

	Forest	**Ecotone**	**Thicket**
Average	3.67	35.33	73.67
Variation	12.75	778.75	3430

The treating of the *A. karoo* seeds with Sulphuric acid appeared to be successful and caused the germination of 30 out of the 50 seeds (60%). In contrast not one of the untreated seeds germinated, or even appeared to show signs of absorbing water, this despite a 36 day experimental period. All of the treated seeds that germinated had done so in only 17 days.

Table 4: Comparison of multi- and single-stemmedness between *A. karoo* patches and controls (Kolmogorov-Smirnov, $p < 0.05$ for significant result).

	DN	**Significance level**
Canopy	0.857	0.091
Sub-canopy	0.857	0.091
Total ms:s for transect	1.000*	0.022*

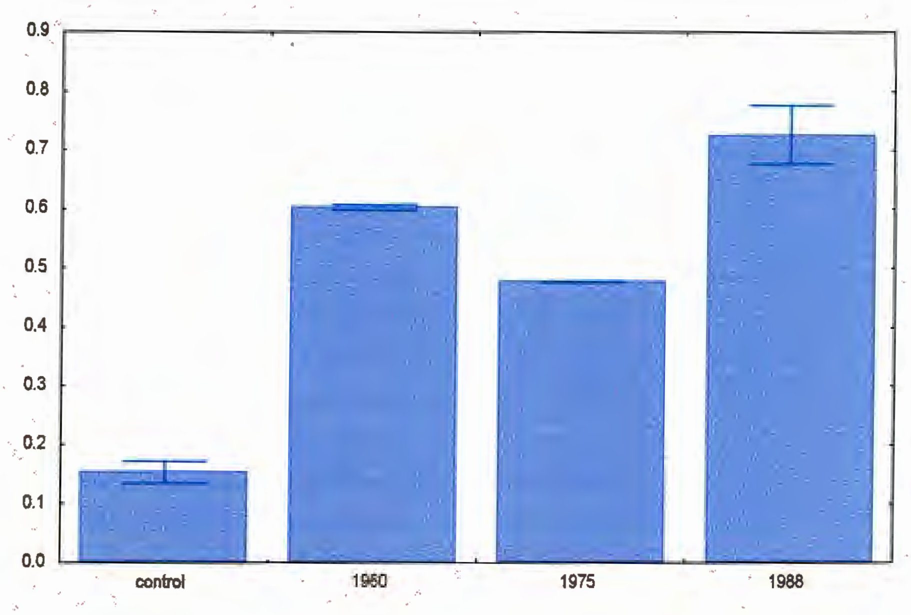


Fig. 8: Graph displaying the average ratio of multi-stemmed to single-stemmed trees in each age-group (DN = 1, p = 0.022*).

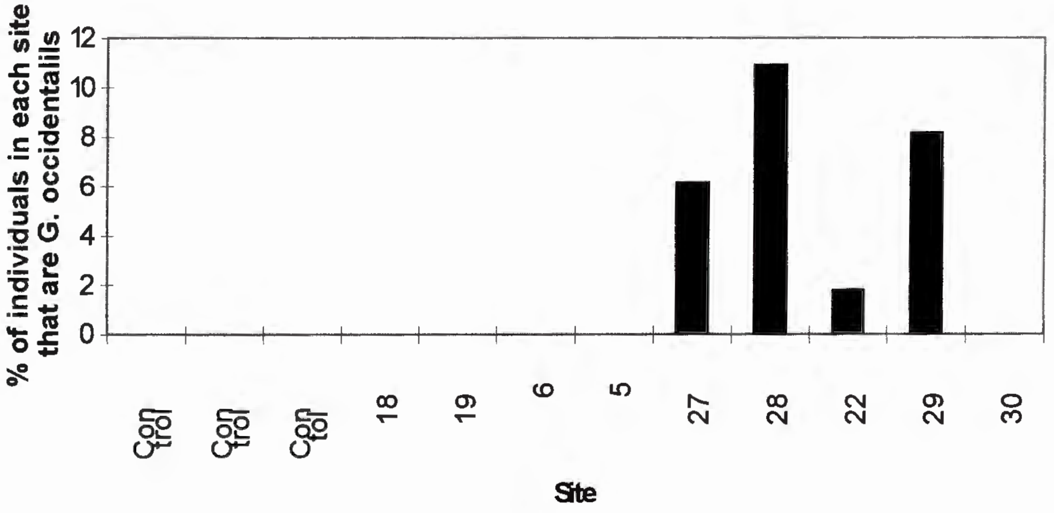


Fig 9: Graph showing the percentage of individuals in each plot which were *Grewia occidentalis*.

(ANOVA comparing all sites: F = 1.909, p = 0.207)

(ANOVA comparing distribution in controls with distribution in *A. karoo* patches: F = 1.392, p = 0.265)

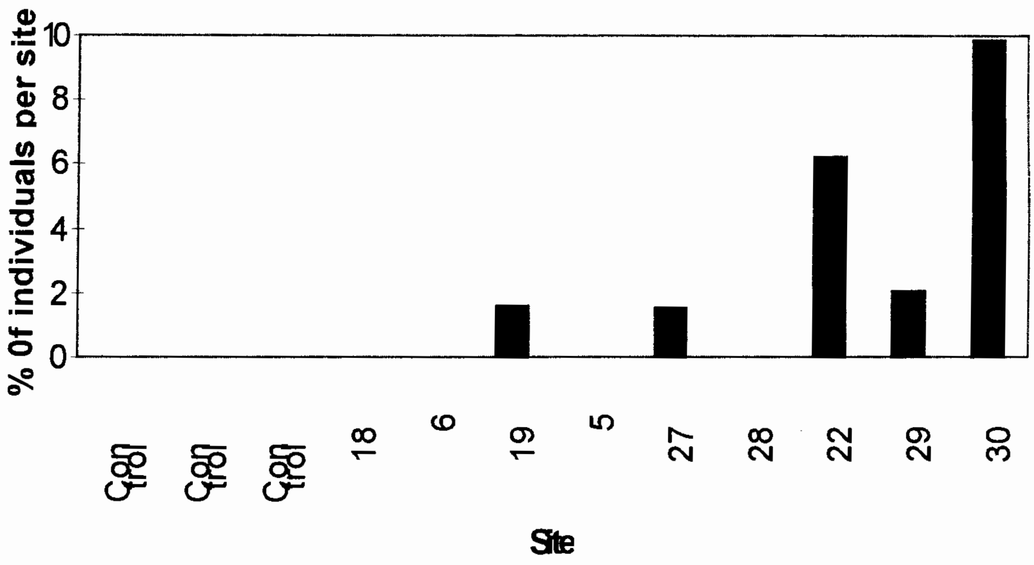


Fig 10: Graph showing the percentage of all individuals in each plot which were *Clausenia anisata*.

(ANOVA comparing all sites: F = 5.757, p = 0.21)

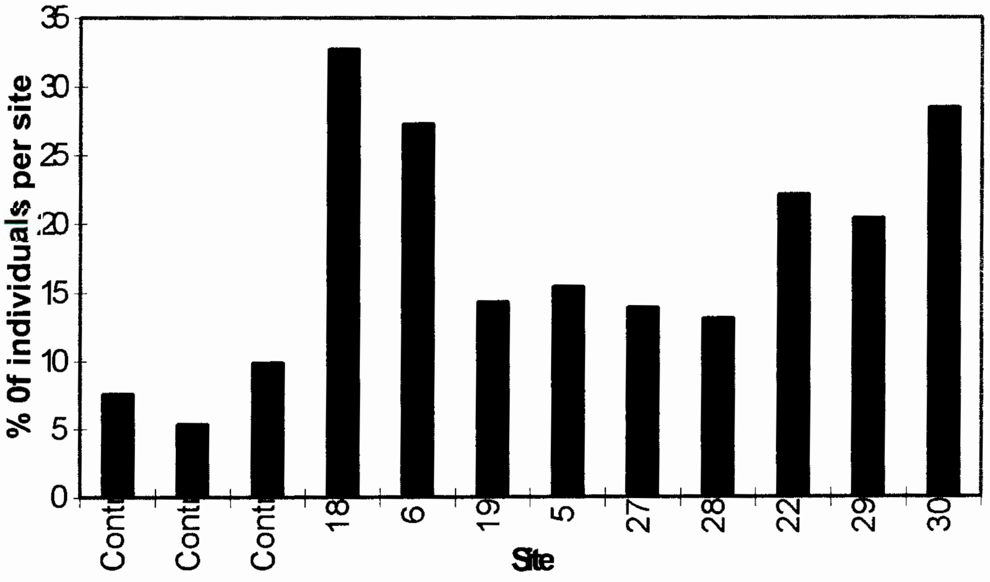


Fig 11: Graph showing the percentage of individuals in each plot which were *Celtis africana*.

(ANOVA comparing all sites: F = 7.056, p = 0.012)

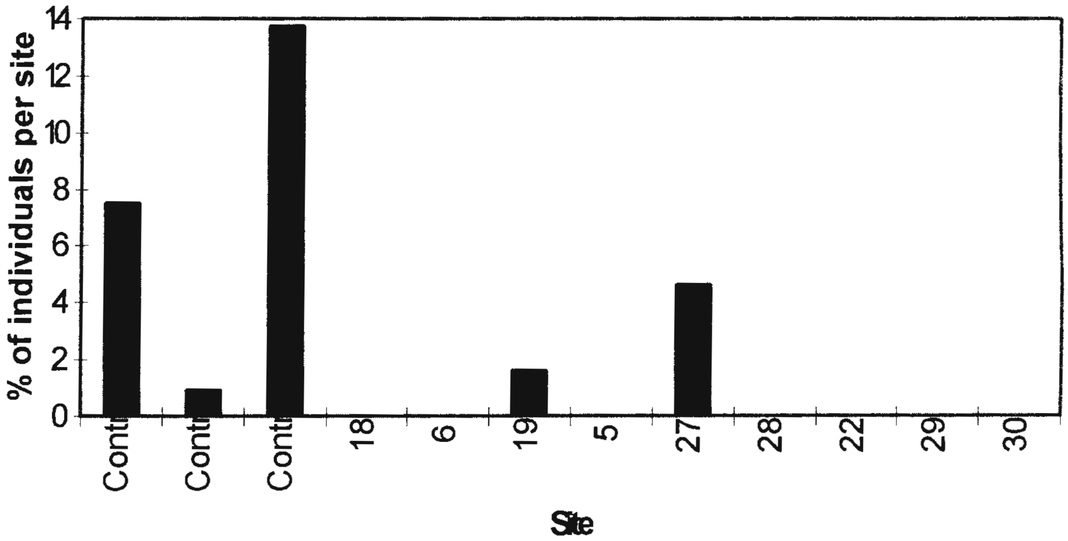


Fig 12: Graph showing the percentage of individuals in each plot which were *Strychnos mitis*.
(ANOVA comparing all sites: F = 2.820, p = 0.107)
(ANOVA comparing controls with *A. karoo* patches: F = 9.885, p = 0.011)

Figs. 9 -12 are representatives of the species distribution results which were subjected to ANOVAs. Species were first subjected to a one-way ANOVA which compared the relative percentage of each species between all 12 sites. *Celtis africana* (Fig. 11) and *Clausenia anisata* (Fig. 10) were found to have significant distributions, while the others, with distributions like *Grewia occidentalis* (Fig. 9), were found to be non-significant. However, when the distributions in the control sites were compared to all the *A. karoo* patches as a single group, another species was found to have a significant distributions: *Strychnos mitis* (Fig. 12).

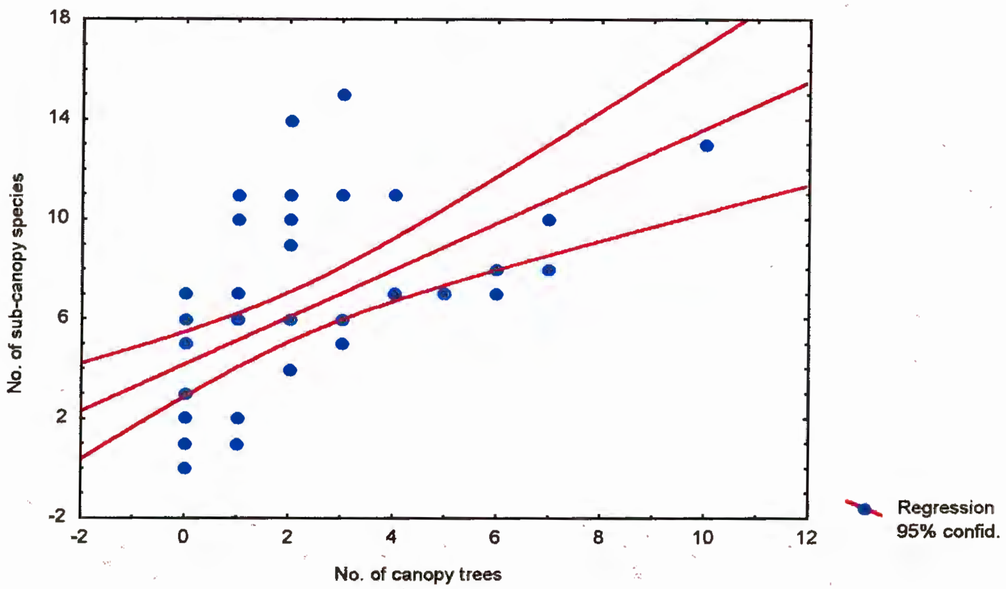


Fig 13: Graph showing the correlation between the number of canopy trees and the number of species in each 10m x 15m block (not considering *A. karoo*). (p = 0.001*)

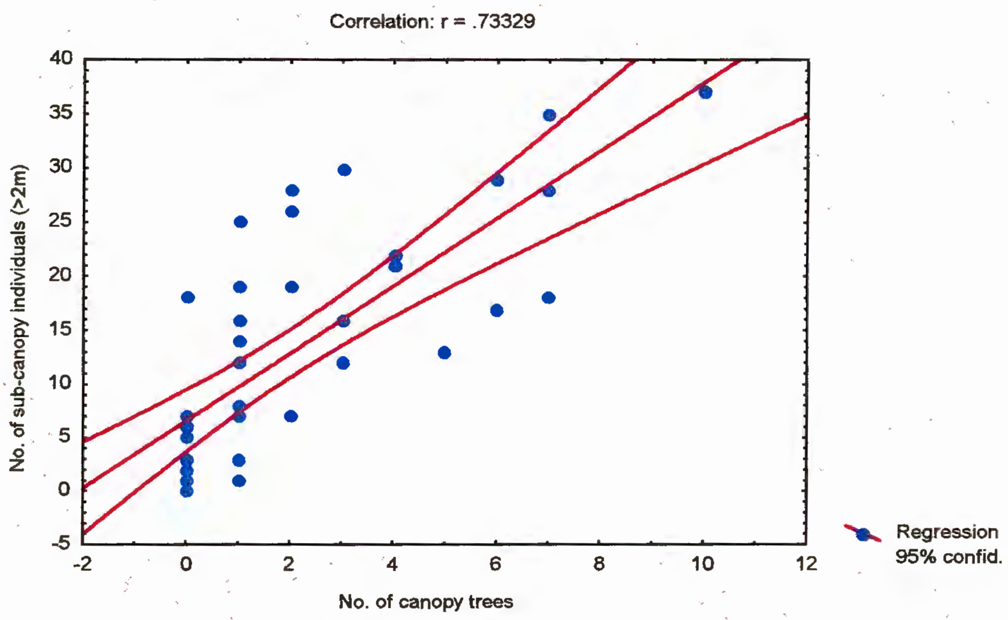


Fig 14: Graph showing the correlation between the number of canopy trees and the number of sub-canopy trees (>2m) for each 10 x 15m block (not considering *A. karoo*) (p = 0.00001*)

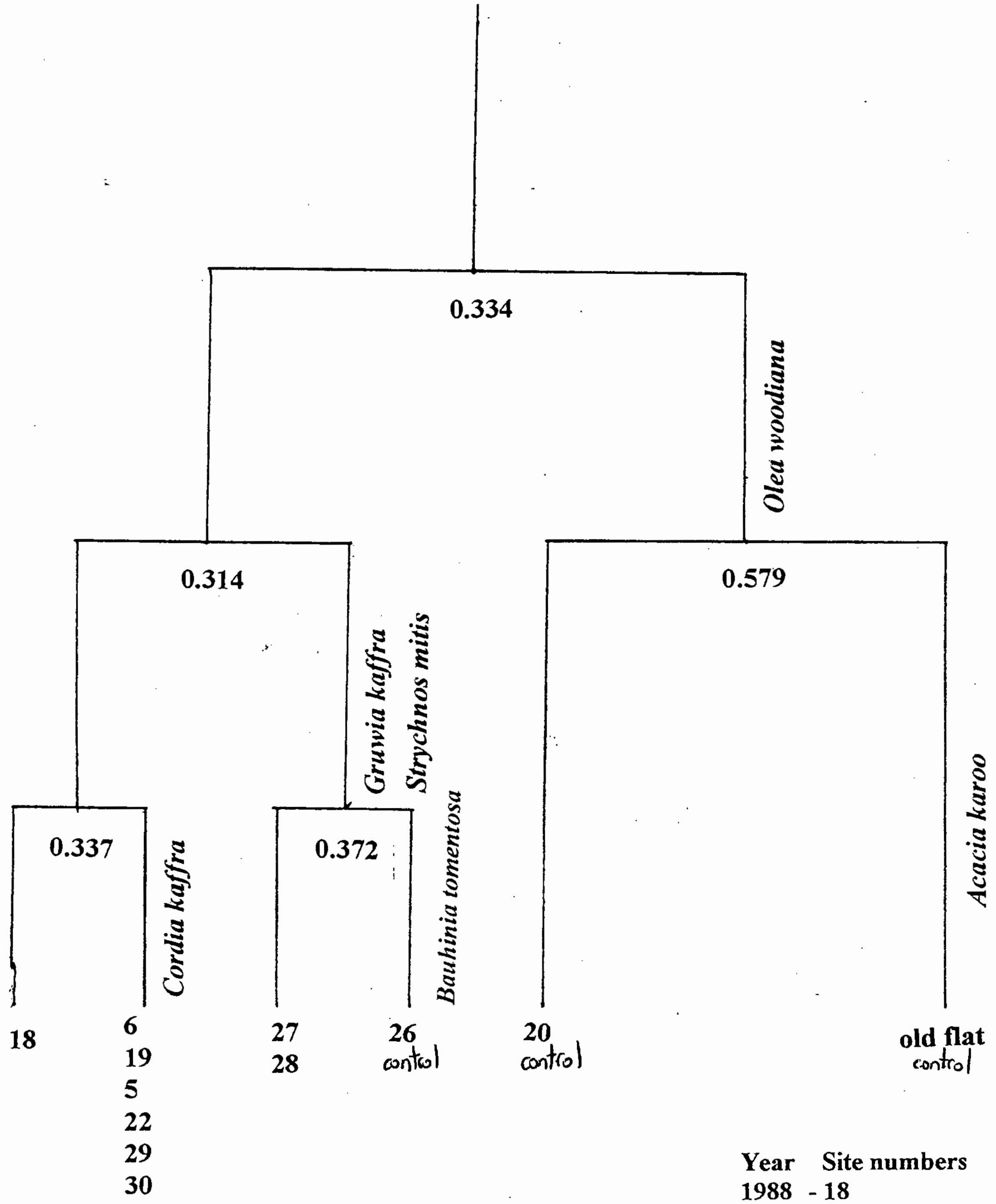
Figs 13 and 14 reflect the increase in the number of species and trees in the *A. karoo* patches in association with an increase in the number of canopy trees other than *A. karoo*. However when the correlation coefficients are calculated for the relationships between the number of canopy

Figs 13 and 14 reflect the increase in the number of species and trees in the *A. karoo* patches in association with an increase in the number of canopy trees other than *A. karoo*. However when the correlation coefficients are calculated for the relationships between the number of canopy trees and the number of sub-canopy species and individuals in each patch age-group an interesting trend of decreasing relatedness emerges. Table 5 displays this information.

Table 5: Comparison of correlation coefficients obtained for the relationships between the number of canopy trees and a) the number of sub-canopy species and b)the number of individuals, for each age-group. Significant results ($p < 0.05$) are indicated by *.

	Correlation coefficients:	
	a) Sub-canopy trees	b) No. of subcanopy species
1988	0.85*	0.83*
1975	0.79*	0.60*
1960	0.56*	0.42

Fig. 15 is the results of the TWINSPAN analysis showing the similarity of the plots based on presence/absence data of all of the species. The control sites are labelled as Old Flat, 26 and 20. Although the control sites are isolated from the *A. karoo* sites, there does not appear to be much difference in the species composition of the patches, despite the difference in ages of the patches.



Year	Site numbers
1988	- 18
	- 19
	- 5
1975	- 6
	- 27
	- 28
1960	22
	- 29
	- 30

Fig. 15: results of TWINSPAN (Hill, 1979) analysis of presence/absence data of tree species from all transects

Discussion:

Population Ecology of the *A. karoo* Patches:

The *A. karoo* patches around Cape Vidal appear to consist for the most part of only one cohort of trees. Recruits are either very low in number or do not occur. While seedlings were often noticed, slightly older saplings were generally absent. Woody seedlings and young trees up to the height 2m tended to occur in specific localities and were relatively rare within the patches. It was observed that they were normally clumped and existed in old gaps caused by treefall of an adult *A. karoo*. As can be seen in Fig. 30 trees in the smaller size classes are capable of making up a large proportion of the total number of trees. Adults tend to be large trees (diameter > 20cm) with branches that reached up into the canopy. However it was noted that thinner trees (with diameters 7cm and larger) were capable of bearing a crown in the canopy. In some sites with an apparently large percentage of trees in the lower size classes, these trees would all be classified as adults as they were all reproductive and their branches were capable of reaching the canopy, despite their high density.

There did not appear to be any great difference in size class distributions among the different ages. Further density of trees was not significantly altered according to patch age, as the percentage of old *A. karoo* individuals (those in the larger size classes, >30cm in diameter) remained similar for all ages of patch (Fig 7). It would thus appear that the structure of the patches is constant over the timescale measured here (maximum of 37 years). This would indicate a single cohort of trees which arose following abandonment of the fields by farmers. The finding of even aged stands with restricted recruitment would suggest that they will eventually pass out of the system, however there are two concerns which follow on to this conclusion.

The first is that recruitment does occur, albeit in specific microhabitats (see later for discussion) and that as such young trees were seen to make up a large proportion of the trees in some transects. In Site 30 (Fig 3) gaps had been opened by the death of three large canopy trees (all had diameters greater than 35cm) which had been filled by a large number of recruits.

The second concern is that although these cohorts were presumed to have a limited life-span, no large-scale senescence was observed, despite the age of some of the plots. If one presumes that at some future, as yet undetermined, date the entire cohorts will begin to die, it is likely that only small patches of *A. karoo* canopy will remain. However if mortality is more random (i.e. not simultaneous across a whole patch) there exists the likelihood that a sufficient number of microhabitats will be established for recruitment. At present it seems that despite the age of some of the plots, no large-scale mortality is occurring. For example Fig. 2 reveals that very limited recruitment has occurred in that patch, despite it being approximately 37 years old. Further, mortality was not shown to be confined to the larger size-classes, where one would expect senescence to occur. Thus it appears that mortality of the patches is not linked to the age or size of the trees within the patch, despite the fact that some of the trees are nearly 50 years old.

Von Maltitz et al (1996) stated in their paper on dune forest succession that such even-aged stands would start to senesce after 25 years. This despite the fact that they sampled *A. karoo* individuals in patches which were 59 years old. Their methods refer to all of the *A. karoo* patches that they sampled as consisting of even-aged trees, thus one must presume that these very old patches had still retained their canopy.

Despite this the senescence of the *A. karoo* canopy was seen by von Maltitz et al (1996) to be the mechanism whereby other species were able to invade and dominate the canopy. In fact I would argue that mortality is not be size-specific due to a lack of significance in the distribution of mortality between trees less than 30cm in diameter versus trees greater than 30cm in diameter. Rather it would appear that mortality occurred in similar proportions in all of the adult size classes. Thus it appears that the belief that canopy succession in the patches would be facilitated by senescence of the *A. karoo* canopy is false.

While recruitment to woody seedlings is possible only in areas with no canopy and at least low *Isoglossa,* preferably bare earth (which was presumed to arise through some form of disturbance of the soil). Such conditions did appear in the patches and the recruits preferences are shown in Fig 4 and Table 1. Treefall was often associated with recruitment patches. In both sites 18 (1988) and 30 (1960) (Fig 3) large treefalls had opened up large canopy gaps which allowed for the growth of woody seedlings up to the height of 2m. Although tiny seedlings were often found under the canopy and even under dense *Isoglossa*, there was a distinct lack of seedlings with woody tissue in these circumstances. The development of woody tissue was taken to be a sign that the seedling had survived at least one full year of growth. The lack of such developed seedlings under dense *Isoglossa* and the *A. karoo* canopy is presumed to be due to a lack of light or competition for nutrients with the *Isoglossa.*

von Maltitz et al (1996) state that the gaps in the *A. karoo* canopy are seldom filled by *A. karoo* seedlings or saplings, however this is the area in which the seedlings were shown to recruit most actively by this study. One presumes that as von Maltitz et al (1996) do not mention the condition of the understorey, they had not recognised its importance in preventing recruitment. If past authors have discounted claims that *A. karoo* can recruit it is disturbing in light of this information. As a result of the lack of cohort-wide mortality and the observation of gap-filling by *A. karoo* recruits it appears that the previously published papers on *A. karoo* succession have missed vital points in the population ecology of this species.

The characteristics of the *A. karoo* seedbank are of importance when considering the claim made by Mentis and Ellery (1994), van Aarde et al (1996) and von Maltitz et al (1996) that *A. karoo* is part of the natural dune system in light of centuries of human-induced. Based on this belief *A. karoo* dominated plots have been nominated as part of the climax state in previous studies (Mentis and Ellery, 1994). The fact that it appears to produce only a slight seedbank in the forest surrounding the patches (Table 3), with no seeds observed in climax forest sites indicates that *A. karoo* is more likely maintained in the dune forest community through the human-mediated means. The method of seed dispersal is not known for *A. karoo*. The seed is too heavy for wind dispersal, but it has been shown to pass through the digestive system of domestic livestock and be disseminated by them (O'Connor, unpublished work, as cited by O'Connor 1995).It does not however have as thick a seed coat as those *Acacia*'s which are eaten and dispersed after passing through the digestive tracts of ungulates.

If one were to consider *A. karoo* as a natural part of the dune forest one would probably be inclined to judge it as a species dependant on treefall to provide the disturbance in the canopy it needs for recruitment. Many *Acacia* species have been shown to be dependant on disturbance for germination (Smith and Shackleton 1988).This would also explain the apparent dormancy shown by its seeds. However despite the dormancy shown in the laboratory, young *A. karoo* seedlings were often noted in the patches, irrespective of canopy condition. Further, not only does *A. karoo* not seem to accumulate a seedbank over time (Table 2), probably as a result of germination rate equalling the rate at which the seedbank is produced, but there was also no sign of a seedbank in the climax forest. It thus seems unlikely that the seeds remain dormant in the soil waiting for a cue to indicate the presence of a gap in the forest canopy. Although some seeds were found in the neighbouring forest, no seedlings were observed there. But the fact is that a seedbank does exist in the soil. Precisely how old the seeds in the soil are is not known. It is possible that the seeds have a slight dormancy with a light cue. von Maltitz et al consider *A. karoo* to be highly likely of lasting in the soil due to its hard seed coat.

The germination experiment was conducted in a dark cupboard on the advice of T. Wilson (pers. comm.) who had worked with *A. karoo* from the Northern Province. Many different forms of *A. karoo* are being recognised (Brain 1989), and this could be a form-specific character evolved specifically for survival in the dune forest. It may be possible that the reason that none of the untreated seeds germinated was because they lacked a light stimulus. Thus the hypothesis is that the seeds are dispersed by domestic livestock into the disturbed fields. The slight dormancy allows for the accumulation of *A. karoo* seeds in areas which had previously been forest, and which had contained no *A. karoo* seedbank. During the time in which the fields were in use, the seedlings would have been weeded out, but following abandonment of the fields *A. karoo* was able to successfully recruit.

It is clear that on average, the number of seeds under the *A. karoo* canopy is greatest and the number declines as one moves successively into the ecotone and then the forest. This decline was shown to be significant. One should also note that no seeds were found in the control plots, although the sample number was low. Dispersal into the forest may also be dependant on a gap-specific dispersal agent. Considering the work of O'Connor (1995) indicating that viable seed can be disseminated by domestic livestock, it is possible that *A. karoo* in the dunes is at present limited by the lack of a dispersor due to the exclusion of such livestock from the Greater St. Lucia Wetland Park. This would explain why the seedbank of *A. karoo* was so high in the patches and yet was not found elsewhere.

Successional Dynamics in the Patches:

The species composition of the different sites is of particular interest with regard to the Mentis and Ellery's (1994) proposed method of succession. Where they found that species richness increased, they were including in their species counts all of the herbaceous species. Of more relevance to managers attempting the restoration of a climax community is the species composition of the canopy. In terms of tree cover I found a significantly greater proportion of the control site species are endemic. Further a total of 13 species out of 71 in all of the sites (or 13 out of the 41 species found in all the control sites) were found only in the controls. Ralston (1996) suggested that species with a poor seed dispersal ability, specialised pollination systems or poor seed regeneration were likely to struggle to colonise the *A. karoo* patches. That such species are not found in even the oldest of the *A. karoo* patches suggests that whatever successional changes are occurring in the *A. karoo* stands, some species will probably find themselves unable to invade these areas. If one considers that the restoration of such species, as well as their natural distribution within the plots, is part of the definition of "rehabilitation", then the fact that 35% of the total number of species found in the control plots have as yet not found their way onto the successional pathway raises serious questions as to the validity of the rehabilitation process. Some of the *A. karoo* patches have lasted more than 37 years, yet these species are still missing.

Succession towards the climax forest should be characterised by finding successively greater numbers of species as plot age increases and the trend line should point towards the species number of the climax areas. No such trend can be found in Fig.6. The number of species in each plot appears highly variable and although the plots appear to have similar numbers to the climax plots, the argument in the paragraph above dismisses any claim that might hold this as a sign of rehabilitation. Rehabilitation does not appear to be a simple addition of species in a step-wise transformation in these patches. Instead the above data indicates that even following 37 years of undisturbed succession there are barriers which are preventing the climax community from establishing. It is not simply a case of waiting for the accumulation of species in the patches, species richness appears roughly similar, thus it is the composition which defines the process as either rehabilitation, or just revegetation.

This conclusion as to the difference in the composition of the different sites is confirmed through the use of TWINSPAN (Fig. 15). The cladogram indicating the relationships between sites (based on shared species) isolates two of the 3 control sites out first. The third control is also fairly distinct from the main collection of *A. karoo* patches. No apparent distinction can be made between most of the *A. karoo* patches and 6 out of the 9 are grouped together. There does not appear to be an age-specific effect which would indicate a transformation of the patches as not only is there little distinction between the patches, but the most likely patches to be linked with the controls if there was such an effect, those belonging to the 1960 age-grouping, are not very close at all.

Effects of Multi-stemmed trees on successional processes in the patches:

What succession has arisen in the patches appears to result from the effects of trees already in the canopy. Due to non-mechanised farming methods employed by subsistence farmers in the fields while they were under cultivation, the farmers were presumably unable to remove large stumps or trunks from the fields. As a result some of the trees would have been capable of resprouting from the base and would have formed multi-stemmed individuals. The hypothesis is that as a result these trees would be able to grow up and form a canopy at the same time, if not before, the establishment of the *A. karoo* canopy. While *A. karoo* are poor attractors of such seed dispersers as birds (von Maltitz et al 1996, Ralston, 1996), the multi-stemmed trees would presumably still attract these dispersal vectors. This would enable the transport of forest species propagules into the patches. These would grow up as single stemmed individuals. This is in fact reflected in Fig 2. The appearance of multi-stemmed trees in the control sites is probably the result of natural grazing and acts as a baseline from which to judge the other results. In the youngest plots there is a large proportion of multi-stems which then shows an overall decline as the patches age and more and more single-stemmed individuals are introduced. The graphs showing that both species number as well as the number of individual trees present in the understorey are positively correlated with the number of trees (not *A. karoo*) in the canopy is encouraging (Figs. 13 and 14).

Such a “nurse tree” mechanism was shown to operate in the succession from grassland to forest for the flat areas near to the dunes by von Maltitz et al (1996). These bush-clumps also arose in old field sites, thus it appears likely that such a method could be very influential in the successional dynamics of the *A. karoo* patches. But what is of most concern in dealing with this hypothesis, is that the dune mining undertaken by Richard's Bay Minerals is highly mechanised and destructive. As a result propagules such as stumps which can resprout cannot survive (Mentis and Ellery, 1994). Thus succession in these mined areas must occur without the accelerating input of these facilatative multi-stems. An indication of this slower successional rate is provided by Mentis and Ellery (1994). The authors examined 3 sites which had been recovering following mining for 11 years. The number of tree species (designated as woody species over 2m in height as in my method) for each site was found to be 4, 10 and 11. In my plots the nearest aged sites (those belonging to the 1988 group) which were the youngest that I studied contained 15, 18 and 19 species, despite being 3 years younger than the plots used by Mentis and Ellery (1994). When compared through the use of a one-way ANOVA the result is significant ($F = 13.018$, $p = 0.023$).

Analysis of Species Distributions:

The compositional characteristics were examined in order to detect whether there were any species which reflected either low tolerance for disturbance, or which appear to be advantaged by it. *Grewia occidentalis* (Fig. 9) is representative of most of the species which did not show a significant distribution. Very few trees in fact were found to have a significant distribution. *Clausenia anisata* (Fig. 10)was shown to have a significantly skewed distribution with being represented mainly in the younger, more recently disturbed sites. *Celtis africana* (Fig. 11)was found in every site, however its appears to be present in much larger numbers in *A. karoo* sites. In contrast *Strychnos mitis*'s distribution (Fig. 12) was found to be significant only when comparing the controls to the *A. karoo* patches as a whole. *Strychnos mitis* is probably one of those species which is limited by its seed dispersal vector as suggested by Ralston (1996). *Celtis africana* has small seeds which were relatively plentiful in the *A. karoo* patches' seedbank. They are distributed by a wide variety of birds (the fruit are small) as well as monkeys (Palgraves, 1984) and as a result dispersal into the patches is probably quite easy for this species, thus it is more competitive than other species in terms of the ability to invade the *A. karoo* patches and thus becomes very common.

Ralston (1996) found that most species which have colonised the *A. karoo*-dominated mined areas around Richard's Bay are wind-dispersed, with very few other methods of dispersal present. For example it was found that large frugivorous birds were rare in the patches. Further seed dispersal was identified as the primary factor limiting colonisation when compared with other life-history characters such as resprouting ability (which is linked to seed vigour), specific leaf area (related to shade tolerance) and flower morphology (reproductive specialisation) (Ralston 1996).

Such tree species can be of importance in providing an indicator service, either in their presence or absence as in *C. anisata* and *S. mitis*, or in some measure of their abundance, as in *Celtis africana*. The importance of such indicators is that they can provide useful clues to both researchers and managers alike as to the history of the site. For example a manager encountering an area with a number of *Strychnos mitis* in it could conclude that the area has not suffered disturbance. For most species in this study this kind of disturbance-related relationship could not be determined due to a lack of significance. One might conclude that because of this species by themselves are too random to be indicators of disturbance. Measures such as percentage endemism in an area are probably stronger. However the possibility that a few specific species can be used in this way is worthy of further attention. Perhaps greater numbers of replicates will be able to provide some clarity as to the apparent randomness of the data.

The results of the TWINSPAN analysis demonstrate that there is no clear chronosequence indicating succession in terms of the species composition of the patches. While the controls in general appear as a separate group with little similarity to the *A. karoo* patches, no clumping of the patches according to their age-groups occurs. This indicates that the species distribution of the patches is not altered with time by succession.

Conclusion:

A. karoo has been maintained in the dune-forest system through human-mediated disturbance. However this does not mean that it should be considered as a vital component of the community. Rather it appears to be a barrier in the succession towards the climax dune forest. Past proposals that suggested *A. karoo* was a facultative species which allowed for successional processes to occur underneath its canopy appear to be misguided. These previous studies appear to have overlooked the both the lack of senescence and the occurrence of recruitment within the patches. Further the lack of species guilds within the patches as well as the barriers the patches provide towards fruit dispersal call into question the validity of rehabilitation claims made on the basis of perceived succession under its canopy.

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