Hunting for humans in forest ecosystems: are the traces of Iron-Age people detectable?

An investigation into the importance of Iron-Age slash-and-burn agriculture in KwaZulu-Natal forests using compositional and demographic data and carbon isotope techniques.

by

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Acknowledgements

- ***Field work***

Field data were collected in four field trips to KwaZulu-Natal and two to the Southern Cape over the period June 1996 – July 1998. In total, I spent roughly 5 months in the field. I am indebted to all my field assistants, but most noticeably to the incredible Ronnie Stiles without whose eagerness and knowledge I could not have managed and to Bruce Anderson who was injured in the line of duty.

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- ***Laboratory work***

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Samples for isotopic analysis were run in the Archaeometry Unit, Archaeology Department, UCT. Pilot samples were combusted offline and gases distilled cryogenically. The main bulk of the samples were run online. Many thanks to Dr. Julia Lee-Thorpe and John Lanham for assistance and laboratory space.

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- ***General***

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Lastly, thanks to Don, Lol, Mark, Ronnie, Bruce and Andrew, my fellow post-grads in the Eco-Lab for making the last two and half years the most enjoyable and rewarding experience.

Plates

(overleaf)

Plate A

A tree-fall gap in Hilltop Forest, Hluhluwe Umfolozi Game Reserve. Note the small gap-size (approx. 15m diameter) and the striking lack of regeneration.

Plate B

A recently abandoned crop field in communal forests adjacent to Hluhluwe Umfolozi Game Reserve. This is an example of a typical study site for the examination of $\delta^{13}C$ isotopes of soil organic matter and the regeneration of woody forest species.

Plate C

An aerial view, northwards, of the coastal dune cordon at Cape Vidal. The forests shown here formed part of the Cape Vidal study area.

Plate D

An aerial view of coastal forest near St. Lucia showing gaps associated with subsistence forest dwellers. Gaps of this scale may facilitate the regeneration of certain forest canopy species in several KwaZulu-Natal forests.


A


B


C


D

1

General Introduction

To what extent are humans responsible for the biological landscapes that we see today? We relate to recent phenomena such as urban environments and commercial farmlands as anthropogenically created landscapes, however historic anthropogenic influence may have been a lot more extensive than previously accepted (Gómez-Pompa & Kaus 1992, Bird 1995, Motzkin *et al* 1996). In southern Africa we are surrounded by landscapes influenced by humans to some degree (Hoffman 1997). It is now accepted that even wilderness landscapes previously labelled as "pristine" or "natural" are subject to constant change (Botkin 1990) and could well have been generated, or at least influenced, by humans in the past (Gómez-Pompa & Kaus 1992, Foster *et al* 1996, Bird & Cali 1998). This is certainly the case for many forest systems (Binford *et al* 1987, Balée 1989, Northrop & Horn 1996, Noble & Dirzo 1997, Ogden *et al* 1998, Lindbladh & Bradshaw 1998, Foster *et al* 1999).

This thesis attempts to answer, for forest ecosystems, the question posed almost 20 years ago by Feely (1980): "Did Iron Age Man have a role in the history of Zululand's wilderness landscapes?" In doing so, I hoped to address the larger issue of "ecosystem virginity" and to what extent landscapes with a lengthy history of human habitation are dependant on human-generated disturbance.

Why KwaZulu-Natal Forests?

KwaZulu-Natal forests present a suitable arena to test for human-dependent ecosystems. The extensive archaeological record of the region and current forest dynamics indicate the potential for demonstrating this phenomenon.

♦ *Human history in the region*

There is a long history of human habitation in KwaZulu-Natal. Evidence from Border Cave suggests that *Homo sapiens sapiens* was present in the region up to 115 000 years ago (Beaumont *et al* 1978) and may even have evolved there. These Stone Age people seem unlikely to have caused significant impact on the vegetation before 40000 years BP (Siegfried & Brooke 1995), due to low population numbers and the use of mainly “extensive” fire regimes (Hall 1984). Significant anthropogenic impacts most likely began with the advent of the Iron Age, which saw an increase in technological expertise and consequent demands on the land.

Iron Age agropastoralists moved into the northeastern coastal lowlands of KwaZulu-Natal from the North (Hall 1983) and spread southwards from there (Hall 1987). The initial farming settlement is dated at AD 200 (Hall 1984) and by AD 500 the colonisation of the eastern and southeastern savanna regions of southern Africa by early Iron Age farmers was essentially complete (Maggs 1984, Hoffman 1997). At about AD 900 – 1000 there was a change in settlement pattern over much of southern Africa (Hall 1984), which is viewed as the boundary between the Early and Late Iron Age (Maggs 1984). Farming communities expanded from the coastal lowlands via river valleys into the higher lying areas within the valley systems and the high grasslands of the interior plateau (Hall 1984). It has been suggested that this movement was associated with an increase in domestic livestock numbers that resulted in a shift from a predominant emphasis on crop farming to a primary interest in livestock herding (Hall 1981). Nevertheless slash-and-burn farming, first practised in AD 200, still continues in KwaZulu-Natal today.

The introduction of iron smelting may also have had significant impacts on the vegetation of KwaZulu-Natal (Hall 1980, Hall 1984) and the Transkei (Feely 1985). The production of charcoal, necessary for the smelting of iron, requires considerable quantities of suitable timber (van der Merwe & Killick 1979). Thus Iron Age communities were likely to have had a high consumption rate of wood, a demand which may have altered the surrounding biota (Hall 1984, Feely 1985).

The potential effect of Iron Age farmers and smelters on the environment has been demonstrated in other areas. The demand for timber and subsequent deforestation as a direct result of fuel procurement for iron smelting has been cited in West Africa (Goucher 1981), and Europe (Darby 1951, Darby 1956, Lindsay 1975). However, recent evidence suggests that the extent of this impact in Europe may not have been as severe as originally thought (Mighall & Chambers 1993).

Thus evidence shows that Iron Age people have inhabited various regions of KwaZulu-Natal for between 900 and 1700 years. Practices such as slash-and-burn agriculture and wood harvesting for iron smelting are likely to have significantly impacted the forest and woodland vegetation in these regions.

◆ *The forest dynamics dilemma*

Work in several KwaZulu-Natal forests has shown a lack of regeneration of many canopy species (Midgley *et al* 1995a). A similar finding of arrested regeneration has also been reported in Uganda (Chapman *et al* 1999). In the KwaZulu-Natal forests these canopy species seem unable to recruit under the current disturbance regime of small-scale treefall disturbances. The canopy species are thought to be shade-intolerant, requiring large-scale disturbance in order to regenerate. However, the typical causes of large-scale disturbance, such as fire, hurricane blowdowns and elephants have not been documented in these forests. Thus the mechanism for recruitment in these forests is at present unknown.

Due to the lengthy history of human habitation in the KwaZulu-Natal region, it seems plausible that Iron Age peoples may well have created the disturbance regime that allowed the establishment of these forests. Certainly, a low density, slash-and-burn farming strategy within a forest would create large-gaps that would be conducive to the recruitment of shade-intolerant forest species.

The hypothesis central to this thesis, that Iron Age peoples may have helped to perpetuate the KwaZulu-Natal forest systems, is unusual. In most studies of human impacts on forests, human impacts are purely negative, involving the clearing of forest vegetation and the resultant loss of biodiversity (Corlett 1984, Forester & Machlis 1996, Lindbladh & Bradshaw 1998, Carcaillet 1998). This thesis investigates the possibility that low-density human impact is essential for the regeneration of some canopy species dominant in these forests, a positive interaction not often seen in the literature.

Finding the human "footprint": Questions and techniques

The archaeological evidence suggests that humans are likely to have played a role in the forest systems of Zululand, as outlined above. How does one go about demonstrating this from an ecological perspective? I was interested in seeing if one could show the influence of people using forest compositional, spatial and demographic data or isotopic tests.

I set about testing potential human impacts by attempting a variety of techniques in two different forest systems. The questions I hoped to answer with these techniques were:

1) Is a specific suite of tree species, or functional types, associated with human disturbance of this nature?
2) Can one easily detect human disturbance with artefacts, such as charcoal or pottery?
3) Can one find a simple manner to identify old fields (or large-scale disturbance) in forest systems?

I felt that answering these questions would greatly advance the study of human-generated, or impacted, ecosystems.

The methods used in this study were a combination of techniques from different disciplines. The majority of the methodology employed was standard botanical ecological sampling involving data collection on forest composition and tree demography. These data indicate the nature of these forests and provide much of the analyses on human impacts. However I felt that these data alone would be insufficient to show the historical presence, and therefore impacts, of humans conclusively. A diffuse "footprint" such as the one I was searching for, would require a battery of approaches. With this in mind, I searched for artefacts, such as pottery and charcoal in sites of known human disturbance in order to examine whether this corroborated the ecological data. I also used stable carbon isotopes, firstly in soil organic matter and secondly in tree cores, to infer the presence of humans.

I considered the combined information gathered from these techniques to be sufficient to indicate the feasibility of detecting the "footprint" of humans or not.

Thesis structure

This thesis is presented in paper format (Chapters 2-5). Each paper is intended to be independently comprehensible. I have presented maps of my study sites at the end of this introduction (Figures 1-3) and these are referred to in Chapters 2-5.

Chapter Two explores the dynamics of Hilltop Forest in Hluhluwe-Umfolozi Game Reserve. This forest is an old-growth KwaZulu-Natal forest that shows the lack of regeneration of canopy dominants mentioned earlier. This chapter examines compositional, demographic and spatial data and demonstrates the potential importance of large-scale disturbance in coarse-grained forests.

Chapter Three is based on data collected in the coastal dune forests of Cape Vidal. At Cape Vidal several methodologies aimed at detecting the presence of people were tested. The successes and failures of these are discussed in the general conclusion (Chapter 6). This chapter examines the rates of recovery after human disturbance in these coastal dune forests. The chapter was prepared in order to test the predictions made by previous researchers (Mentis & Ellery 1994) that climax dune forest was readily recoverable after dune mining disturbance. As dune mining could potentially impact the entire dune cordon, I felt that this was an important topic to address.

Due to the potential importance of large-scale disturbance in coarse-grained forests, I devised an isotopic test with which to determine the regeneration environments of forest trees. Using the stable carbon isotopes of tree cores, this technique allows one to be able to distinguish between trees that recruited under a forest canopy, in small treefall gaps or in larger forest gaps. This technique, tested in temperate (Diepwalle Forest, Knysna) and sub-tropical forest (Hilltop Forest, Hluhluwe), is described in Chapter Four.

Cereal crops have a different carbon isotopic signal from forest trees due to their different photosynthetic pathways. It is possible to detect this difference in soil organic matter using stable carbon isotope ratios. Previous work has shown that vegetation changes between plants exhibiting C_4 and C_3 pathways can be observed by sampling $\delta^{13}C$ of soil organic matter down soil profiles (see Chapter 5 for references). I was interested to see if one could use this technique to identify old croplands in current forest communities. In Chapter Five, I tested the applicability of this method for this human-scale disturbance.

The general conclusion (Chapter 6) serves to summarise the main findings in terms of the thesis aims, and to evaluate the general success of the methodology employed.

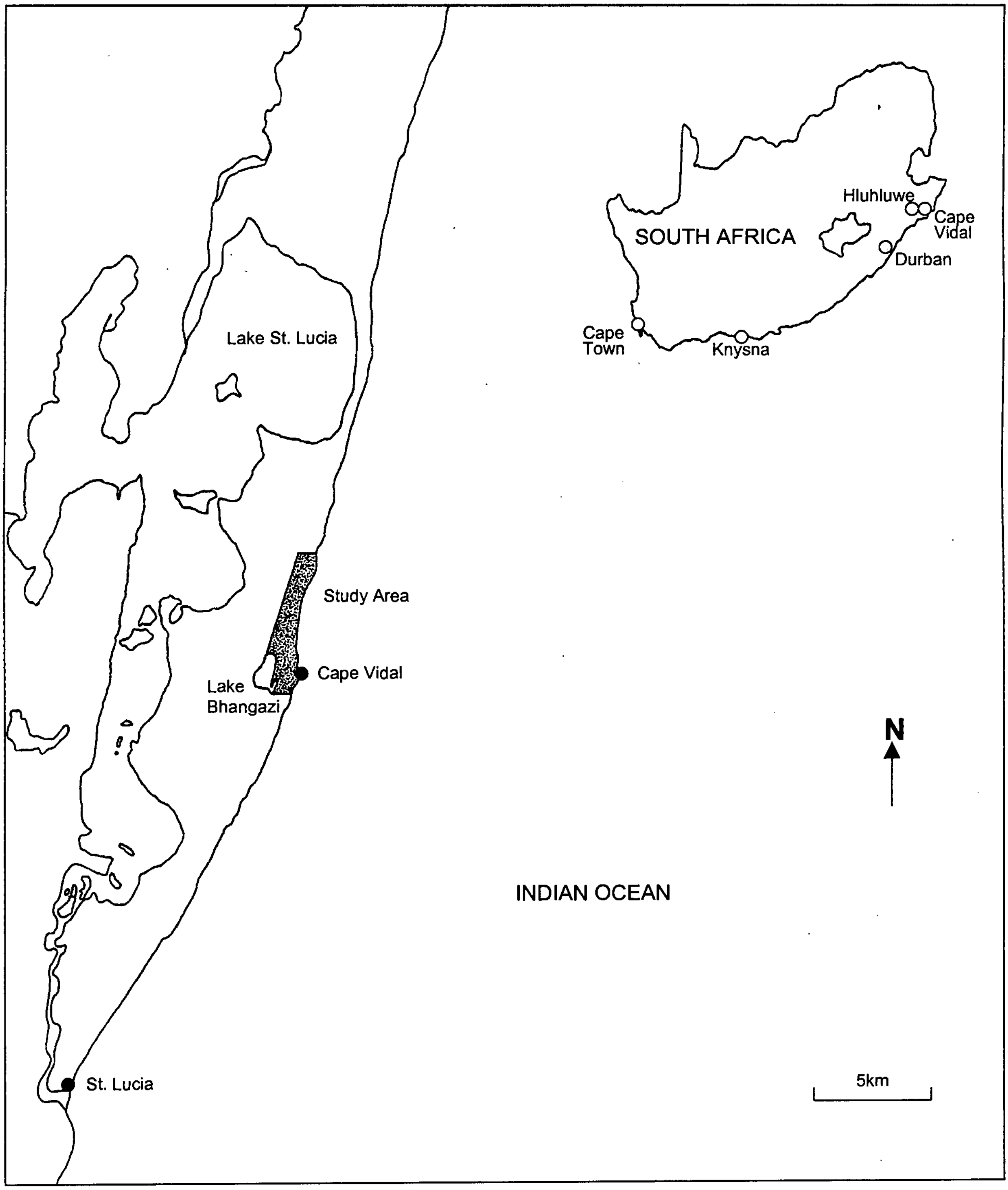


Figure 2: Map of the Cape Vidal area showing the position of the dune forest study area

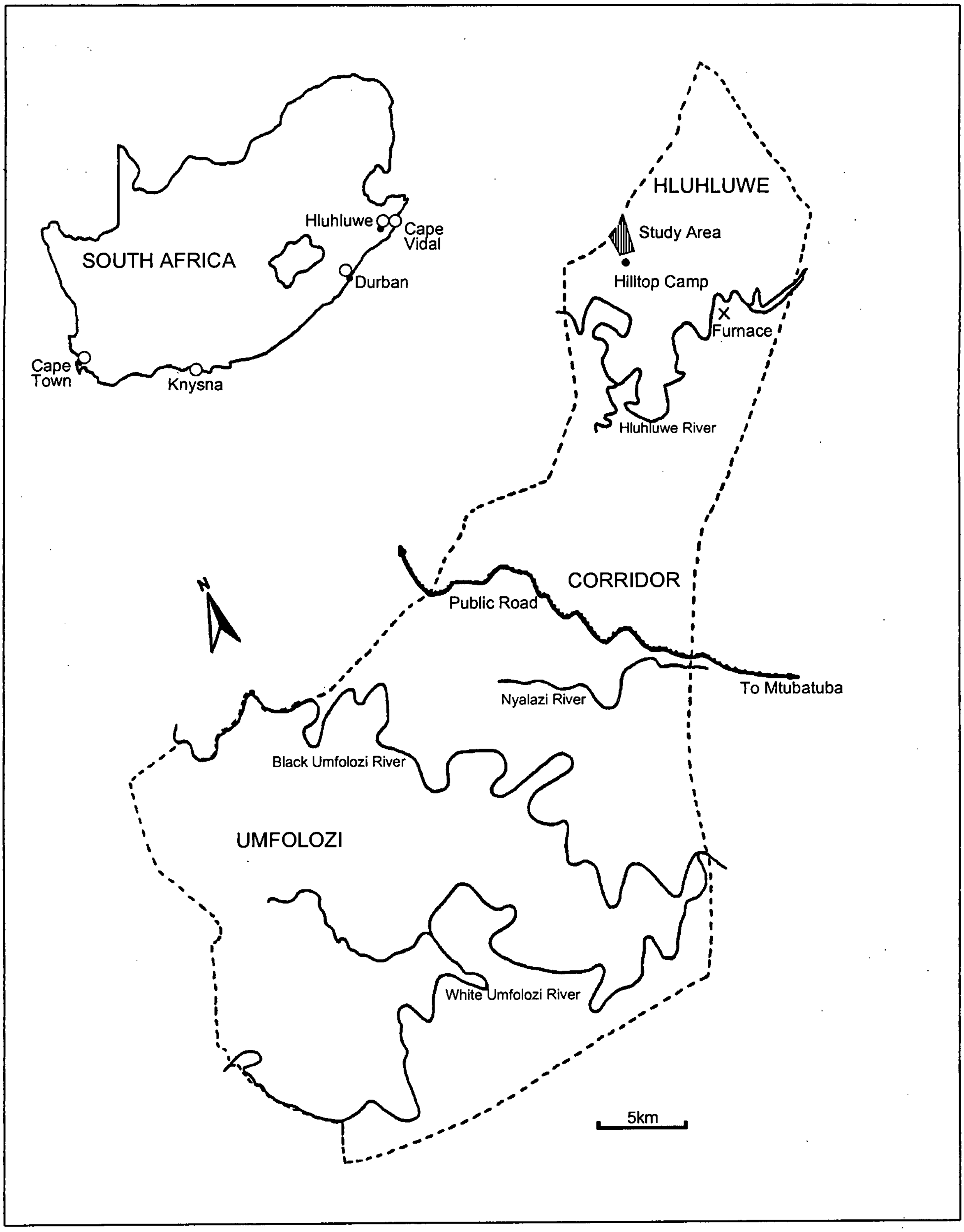


Figure 1: Map of the Hluhluwe-Umfolozi Game Reserve showing the position of the Hilltop Forest study area and the location of an Iron-Age Furnace

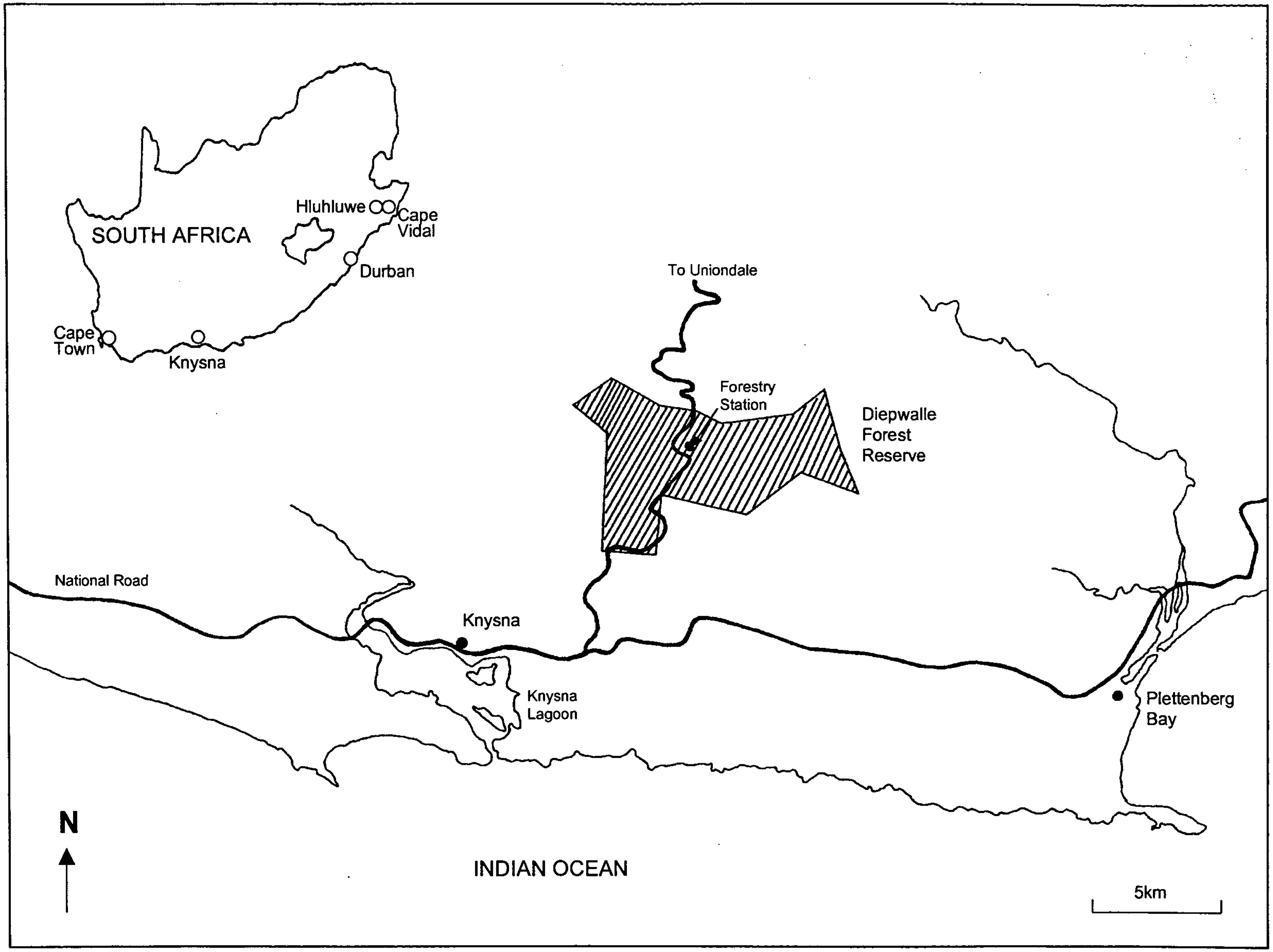


Figure 3: Map showing the position of Diepwalle Forest Reserve, Knysna

2

Dynamics of the forest vegetation of the Hluhluwe-Umfolozi Game Reserve, KwaZulu-Natal

Abstract:

A lack of regeneration of shade-intolerant canopy species has been reported in KwaZulu-Natal forests. The forests of Hluhluwe-Umfolozi Game Reserve, KwaZulu-Natal, were examined in order to determine the extent of this regeneration failure, the forest grain, dynamics and conservation value. Field sampling took the form of recording DBH for all species in twenty-nine 0.04 ha circular plots, walking 5-metre wide transects in mature and marginal forest to record size-classes of important species and analysis of twenty gaps. Data were analysed by the multivariate programs TWINSPAN and CANOCO. Size-class distributions indicate a lack of regeneration and suggest a prevalence of shade-intolerant species. The composition of the canopy and subcanopy is distinct. This forest is coarse-grained and can be classified as coastal scarp forest. Management for conservation of the present species composition should encourage large-scale disturbance. It is hypothesised that swidden agriculture may have resulted in present forest canopy structure. This forest is a fragment of a rapidly diminishing vegetation type and efforts should be made to conserve this valuable resource.

Keywords: coastal scarp forest, grain, human disturbance, large-scale disturbance, management, multivariate analyses, regeneration failure, size-classes

Introduction:

In KwaZulu-Natal, forests patches comprise approximately 100 000 hectares, or 1.05% of the vegetation (Cooper 1985). With increasing anthropogenic pressure on the land, as witnessed worldwide, these forests patches are under threat. As with the protection of other natural resources, the conservation of forests in KwaZulu-Natal has involved the incorporation of these vegetation types into reserves. Here, fenced of from the growing population pressure, forests are seemingly protected. However, it has been noticed that there is a lack of regeneration occurring in many of these KwaZulu-Natal forests (Midgley *et al* 1995a). It would seem that current conditions are not conducive to regeneration, a situation that needs to be addressed if these forest reserves are to remain sustainable functional units.

In the past, the majority of forest research in South Africa has been descriptive, although recently more attention has been given to dynamics and life-histories of constituent species (Everard *et al* 1995, von Maltitz *et al* 1996, van Wyk *et al* 1996). In order for our forests to be managed and utilized in sustainable manner, a thorough understanding of the dynamics and factors involved in successful regeneration needs to be achieved.

♦ *Forest dynamics*

Forest dynamics can be expressed as depending on disturbance regime and the degree of shade-tolerance of constituent species (Midgley & Gobetz 1993, Okitsu *et al* 1995, Hara *et al* 1995).

The disturbance regime can involve both small-scale, autogenic processes such as tree- and branch-fall (Brokaw 1985; review on gaps in Ecology 70, 1989, Uhl *et al* 1988, van Wyk *et al* 1996) and large-scale, allogenic processes such as earthquakes, volcanism, hurricanes and fires (Veblen *et al* 1992, Okitsu *et al* 1995, Akashi & Mueller-Dombois 1995, Batista *et al* 1998, Carlton & Bazzaz 1998). The degree to which these occur has profound impacts on the composition of the forest. The degree of shade-tolerance of constituent species reflects their ability to thrive and regenerate under different grades of canopy closure. Simplistically, one would expect shade-tolerant species to exhibit advanced regeneration under closed canopies, whereas shade-intolerant species would require light gaps in order to reach the canopy (Midgley *et al* 1995).

- ***Grain***

All of these factors and the scale over which they occur can be concisely expressed by the concept of "grain" (see Midgley *et al* 1990, Everard *et al* 1995). In a fine-grained forest, the composition of the canopy is similar to the sub-canopy and consists of predominantly shade-tolerant species. Small-scale disturbance is sufficient to allow regeneration, which occurs primarily by advanced regeneration from a sapling bank. In a coarse-grained forest, the canopy and sub-canopy are markedly different and consist of both shade-tolerant and shade-intolerant species. Both small- and large-scale disturbances occur and the latter enable the regeneration of shade-intolerant species, but not near their adults. All southern African forests can be seen as fitting along a continuum between fine- and coarse-grain extremes (Everard *et al* 1995, van Wyk *et al* 1996). Grain is a useful classificatory measure especially for forest conservation, as forests of similar grain would have similar dynamics and can thus be managed in a like manner (Everard *et al* 1995).

This aim of this study was to examine the dynamics of the north-eastern forest of the Hluhluwe-Umfolozi Nature Reserve, KwaZulu-Natal, hereafter referred to as Hilltop Forest, in an attempt to assess and address the lack of regeneration of shade-intolerant canopy species.

Study Area:

The Hluhluwe-Corridor-Umfolozi Nature Reserve Complex (28°00'S and 28°26'S; 31°43'E and 32°09'E) (Watson & Macdonald 1983) is situated in KwaZulu-Natal. It covers 900 km^2 with altitude ranging from 60m to 750m above sea level (Whately & Porter 1983). Topography is hilly, with flat areas confined to the floodplains of the larger rivers (Brooks & Macdonald 1983). The main rivers of the reserve are the Hluhluwe River, with its tributaries the Manzibomvu and Nzimane Rivers, the Nyalazi River and the Black and White Mfolozi Rivers (Whately & Porter 1983).

The Hluhluwe Nature Reserve, where this study was based, occupies the north-eastern 225 km^2 of this complex (Whately & Porter 1983). Forest communities are restricted to the high rainfall hillsides or to riverine belts (Brooks & Macdonald 1983). Here the rain falls mainly between October and March with a mean annual rainfall of 990 mm (50 years) and a 27.4% coefficient of variation (Brooks & Macdonald 1983). Although there is great edaphic heterogeneity in the Hluhluwe-Umfolozi Complex (Whately & Porter 1983), the forests occur mainly on basalt outcrops which are found in the north-west and eastern part of Hluhluwe Reserve (Whately & Porter 1983).

This study was conducted in the north-westerly part of the Hluhluwe reserve, in the forests to the North of Hilltop Camp (see Chapter 1, Figure 1 for map).

Methods:

♦ *Vegetation sampling methods*

In order to determine the general composition, dynamics and grain of the forest and to examine specific sites of recruitment, a variety of vegetation sampling was performed. The bulk of the data was collected from sampling vegetation within plots randomly located in the forest community. As the data recorded in the plots includes species, size and canopy position these data contain information on composition, dynamics and grain and formed the basis for most of the analyses. A comparison between plots in the forest core and on the margins provides an indication of forest expansion or decline and potentially allows the analysis of developing forest. Size-class data, a useful tool for determining the dynamics of individual species, were extracted from the plots and bulked up by additional transect sampling. The understory and seedling data collected in the plots provides information on regeneration in closed forest. However, In order to examine recruitment dynamics further, tree-fall gaps were sampled. These data indicate whether gaps provide a site for recruitment and, in doing so, add to the understanding of the dynamics and grain of the forest. Due to my initial observations that regeneration is limited under a closed canopy and in tree-fall gaps in this forest, I searched for evidence of large-scale disturbance as a potential site of recruitment. In order to do this I sampled large, even-aged stands of canopy trees (hereafter referred to as "Clumps") within the forest community. All of the above methods are explained in detail below.

Plot and transect sampling

Plot data was recorded using nineteen 0.04 ha circular plots (radius 11.28m) randomly located in stands of mature forest. A further ten plots were sampled on the forest margins. In all the plots, the total height or stem diameters at breast height (DBH) for all woody species were categorised. Categories used were seedlings 25 cm in height; understory (> 25 cm but <2 m high); subcanopy (> 2 m but clearly not reaching canopy) and canopy (> 2 m and in the canopy). The criterion for canopy status was for a tree to be over two-thirds the mean plot height and have access to unimpeded light from above. In terms of sampling seedlings, one quadrant (0.01 ha) was used as a subsample of the entire plot, excepting in areas of high seedling density where five 1m^2 subsamples were used per 100m^2.

At each of these plots a site description was taken, including aspect, slope, mean canopy height and estimated distance from forest margin. Plant names were derived from Pooley (1994).

Five metre wide transects were also sampled through the mature forest in order to supplement the plot data for species size-class frequency distributions. The direction of these transects was chosen randomly and then strictly maintained in order to prevent biasing the data towards larger, more visible individuals. A similar procedure was used for transects along the forest margins. However here the forest edge served to delimit the course of the transect. Size-classes were created for the eleven most common species and analysed by creating a ratio of small stems (<10cm DBH) to large stems (>10cm DBH) and determining stem density in both the margins and in the mature forest.

Tree-fall gap sampling

Twenty tree-fall gaps were sampled in the mature forest. Data collected included the area of gap, the number and species of seedlings present and the size of all woody species. I attempted to ascertain the gap-maker and potential gap-taker or cause of gap closure whenever possible.

Large-scale recruitment ("Clump") sampling

As mentioned earlier, due to observations indicating low recruitment in shaded areas and tree fall gaps, I searched for evidence of recruitment in large-scale disturbances ("Clumps"). I reasoned that documentation of three elements associated with these clumps would constitute evidence for the existence of regeneration in large-scale disturbances: These elements were, firstly, the existence of clumps of closed forest with a higher than normal abundance of an apparently shade-intolerant canopy species. Secondly, these clumps should have a small range in DBH as a result of establishing as a cohort after large gap formation. Thirdly, these clumps should be significantly larger than forest tree-fall gaps.

All clumps had to meet the criteria of occurring on flat ground and containing individuals that were slightly smaller than the maximum sizes recorded for those specific species. The first criterion ensured that clumps sampled were potentially arable and could thus possibly be of human origin, a factor that was important for further analyses (see Chapter 5). The second criterion was established in order to eliminate the potential problem of recording trees that had converged on the same maximum size and thus falsely appeared as a uniform cohort. In each clump, species and DBH were recorded of all canopy trees over 20 cm DBH. The edges of a clump were determined visually.

Sampling stopped after either recording tree species other than the dominant canopy species of that clump, or individuals noticeably larger than the mean DBH of the clump. The areas of these clumps were noted for comparison to tree-fall gap sizes that were sampled in the forest. Five such clumps within the mature forest community were sampled.

♦ *Multivariate analyses*

Broadly, multivariate techniques allow the grouping of plots into communities based on user-defined importance values. In this study multivariate analyses were used to examine the relationship between forest canopy and subcanopy and the forest margins.

The plot data were initially classified using the hierarchical classification program TWINSPAN (Hill 1979). TWINSPAN is a polythetic divisive method and plots are separated on the basis of total species composition (Kent & Coker 1992). Thus, the dendrogram produced by TWINSPAN provides an indication of which plots are similar in species composition to one another. The program was run with defaults and the number of stems per species per plot were used as the importance values. Only woody plants were used, as data were not complete for other creepers and herbs. The analysis was run for all species and then again with the dominant understory species removed.

Ordinations were performed as detrended correspondence analyses (DCA) by the computer package CANOCO (ter Braak 1988). The programme was run with defaults. Number of stems per plot served as the importance values for species. Environmental data of aspect and slope were analysed simultaneously with the plot data. As for the TWINSPAN analyses, two ordinations were run; one with all species data, and one with the dominant understory species removed. The output of this analysis was graphed; the similarity between samples is reflected by their proximity to one another.

For both the TWINSPAN and CANOCO analyses, the sample plots were separated into a canopy subplot and a subcanopy subplot. This created four plot categories, namely forest canopy (fc), forest subcanopy (fs), margin canopy (mc) and margin subcanopy (ms). By examining how the multivariate analyses separated these plots I could interpret both grain and succession.

♦ *Size-class analysis*

Frequency distributions of the dominant tree species were created by grouping plot and transect data into size classes and graphing these. These curves were then analysed by creating a ratio of small stems (<10cm DBH) to large stems (>10cm DBH). One would expect small stem: large stem ratios to be >1 for species that are successfully recruiting. Ratios of <<1 would indicate species with low recruitment and hence low representation in juvenile size-classes. In mature forest with a low level of disturbance, such as Hilltop Forest, size-class distributions help to indicate whether or not a species is recruiting under the canopy. Under these conditions, species with a high numbers of individuals in the smaller size classes and low numbers in the larger size classes (fitting a negative exponential distribution) are assumed to be shade-tolerant and characteristic of fine-grained forests (Midgley *et al* 1990). Species with flat, unimodal or bimodal curves are assumed to be shade-intolerant and indicative of coarse-grained forests (Everard *et al* 1995).

♦ *Clump analyses*

The abundance of the dominant canopy species in the clump was compared to the same species' abundance in the forest plot data. Differences in the count data of occurrence were tested for by Chi-square tests. Size class distributions were created for each clump from all the trees sampled in that clump. The coefficient of variation was determined for these size-class distributions and compared to that of all trees over 20cm DBH sampled in the forest plots. The median area of the clumps was determined and compared against that of the tree-fall gaps sampled in this study by means of the Kruskal-Wallis ANOVA by Ranks test. This tests whether the samples in the comparison were drawn from distributions with the same median (Zar 1996).

Results:

In total, eighty-seven woody species were recorded during the study, of which eighty were recorded in the sample plots and seven were recorded on transects. Average tree density (>10 cm DBH) was 830 stems/ha, with the maximum number of stems obtained in a plot (0.04ha) being 62 stems.

♦ *Classification and ordination*

For both the TWINSPAN and the CANOCO analyses, understory species *Buxus natalensis*, *Cola greenwayi*, *Englerophytum natalense* and *Rawsonia lucida* were excluded. The abundance and ubiquity of these species, especially *Englerophytum natalense*, hampered the community analysis of potential canopy species. Analyses run with the afore-mentioned species included grouped all subcanopy plots tightly together and precluded any meaningful interpretation.

From the TWINSPAN output, a dendrogram of plot relationships was created (Figure 1). In this figure, one can see selected indicator species and the eigenvalues of the individual divisions. Plot numbers have been replaced with codes designating the area where the plot was located. Labels are Forest Canopy (fc), Forest Subcanopy (fs), Margin Canopy (mc) and Margin Subcanopy (ms). The first division divided samples into subcanopy plots and canopy plots. Within the 30 subcanopy plots of the first group there were 5 misclassified canopy plots. Within the 26 canopy plots of the second group there were 2 misclassified subcanopy plots. These strong groupings are evidence of the significant difference in composition between the canopy and subcanopy layers.

Figure 2 shows the DCA-ordination produced from CANOCO. The eigenvalues of both Axis 1 (0.7814) and Axis 2 (0.5707) are reasonably high, suggesting a fair degree of robustness. However, no strong linear arrangement, suggestive of a successional trajectory, is obvious from this

Figure 1: Dendrogram, from TWINSPAN, of plot relationships showing eigenvalues for each split and selected indicator species. Groups used for community analysis are shown below. Full species name are shown in Table 1.

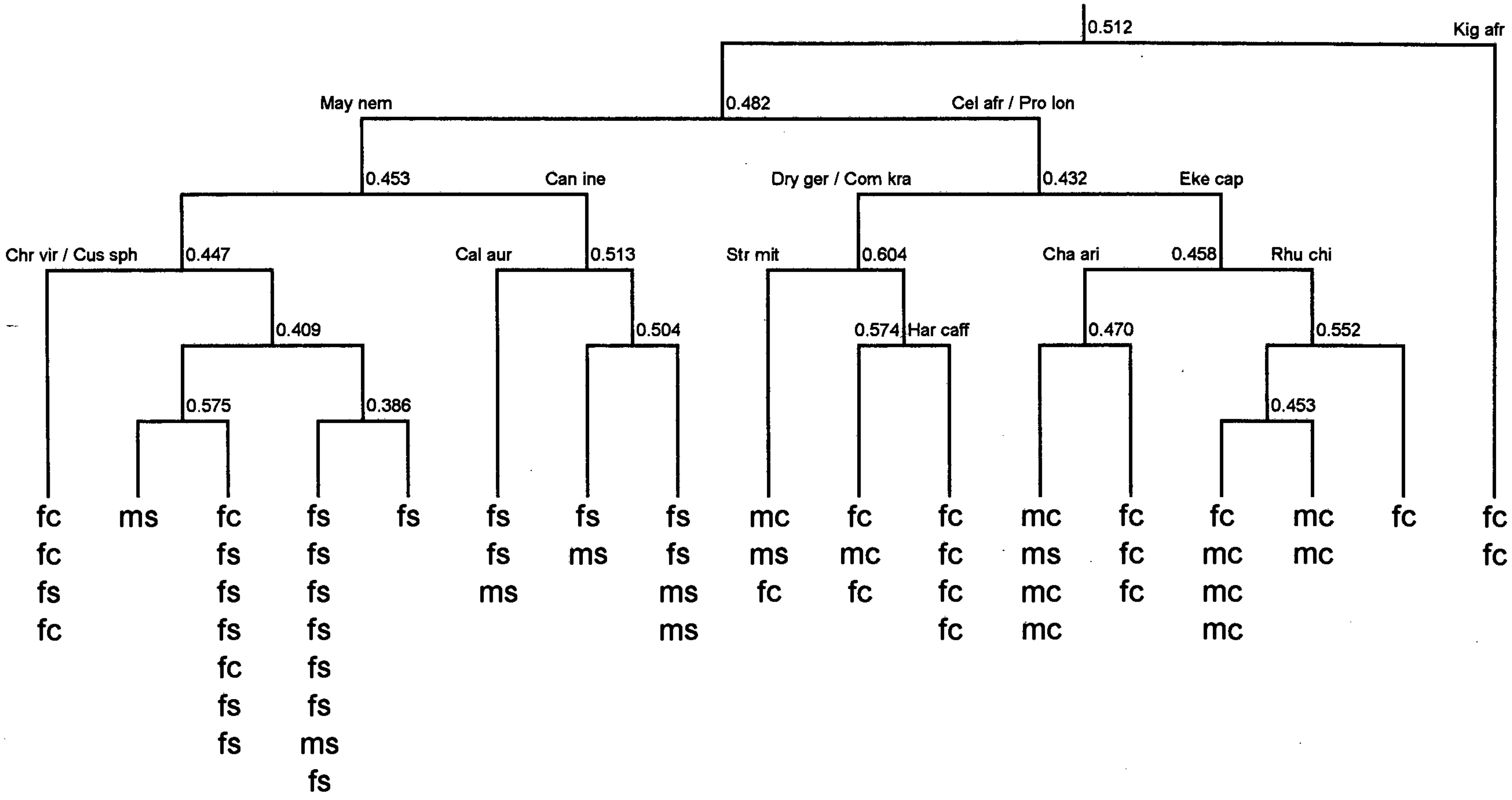
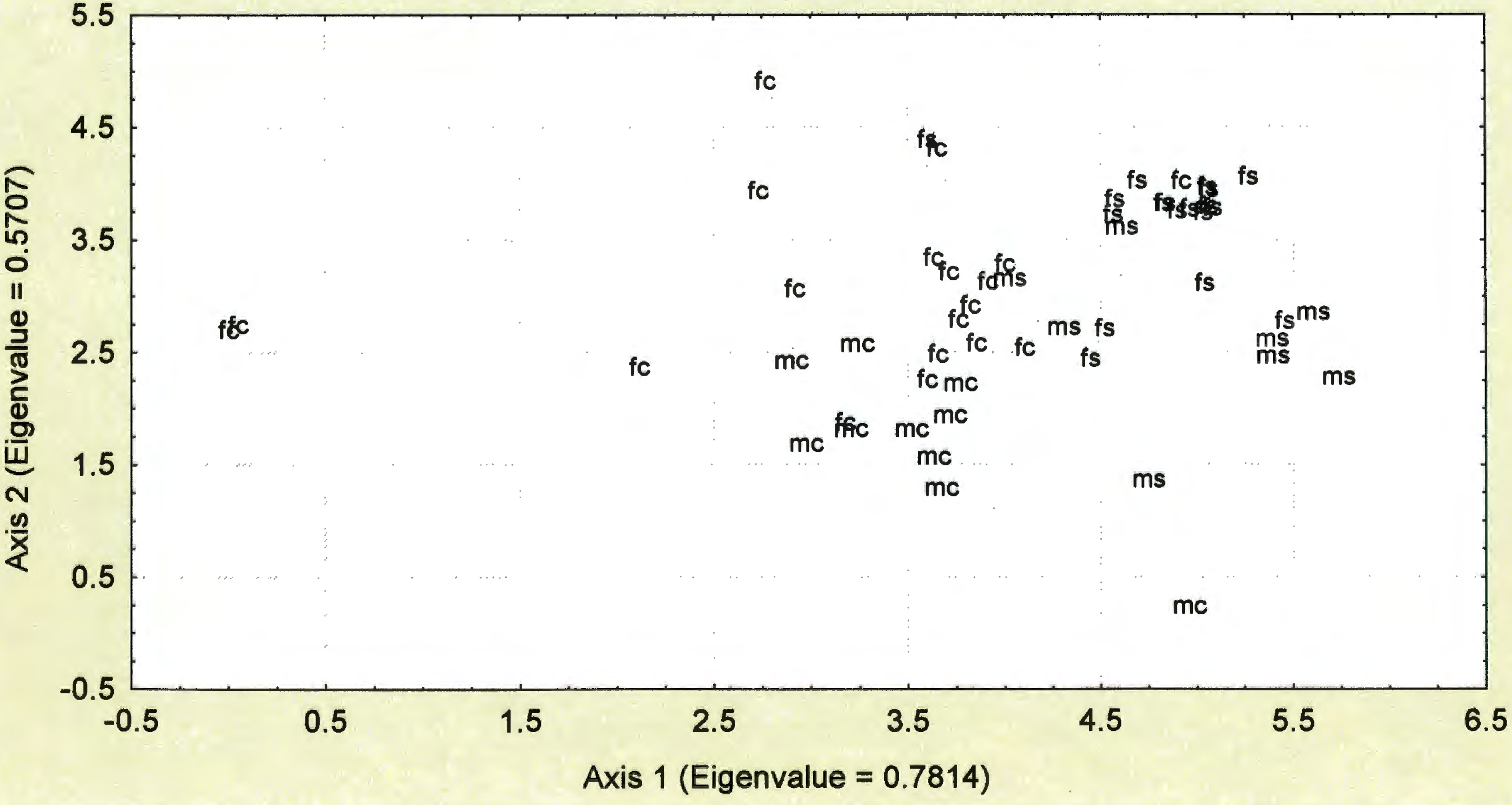


Fig 2. DCA of all plots for Hluhluwe data with no. of stems as importance values
Labels indicate Forest Canopy (FC), and subcanopy (FS) and Margin Canopy (MC) and subcanopy (MS)



ordination. In general, communities do not seen to be sharply defined and groups are linked loosely together across both axes. Canopy and subcanopy components of individual plots proved to be unrelated and were generally distinct from each other.

♦ *Demography*

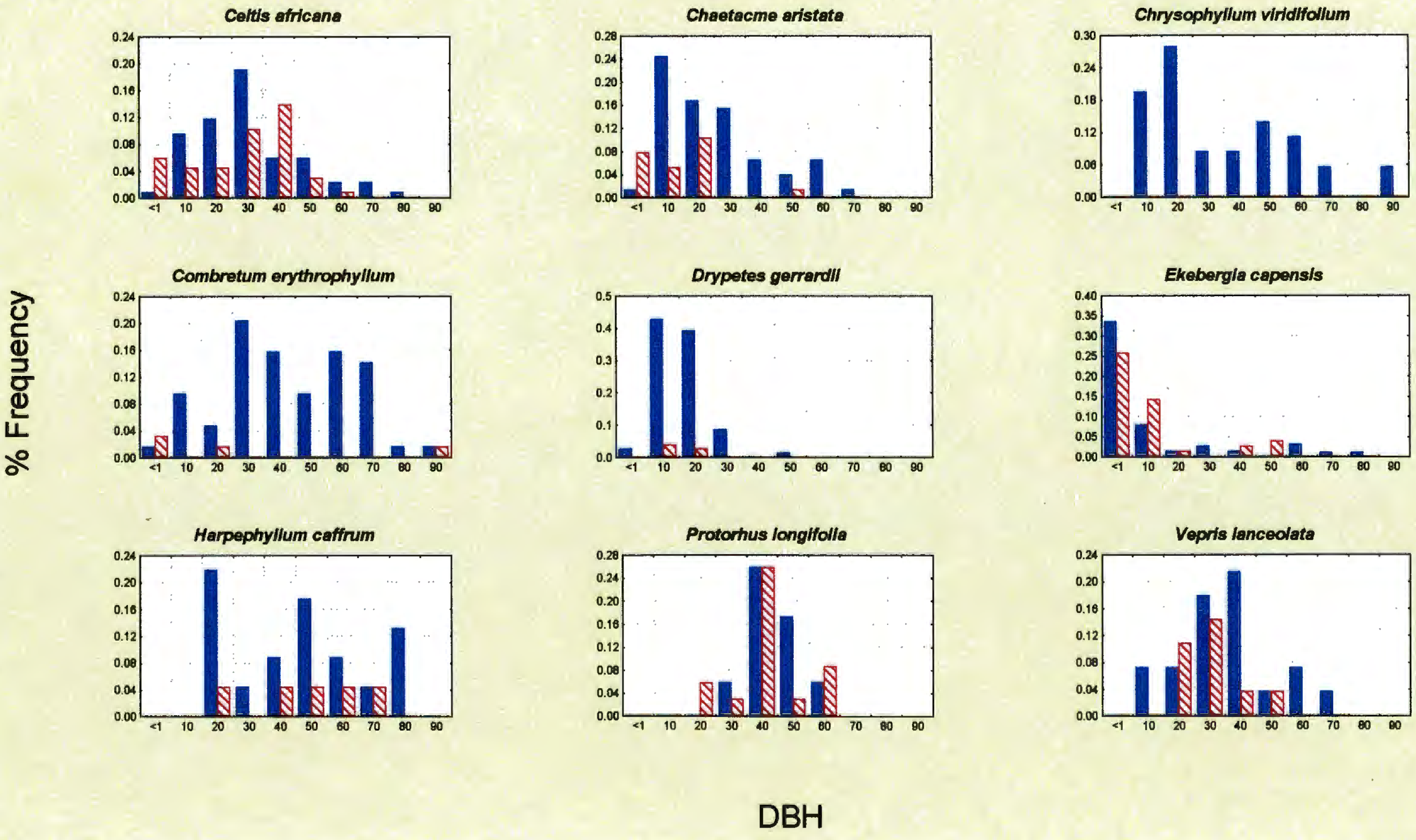
The size-class distributions of the nine most common canopy species are shown in Figure 3. Other species were too rare to create meaningful size-class distributions. The ratios of small stem to large stems (<10cm DBH / >10cm DBH) and stem density are shown for these nine species in mature forest and in forest margins (Table 1). The stem density indicates relative abundance in margins and forest.

Table 1: Ratio of small stems (<10cm DBH) to large stems (>10cm DBH) and density of stems (per ha) for various species in Mature Forest and Forest Margins. Ratios > 1 implying recruitment under current conditions are marked in bold type.

Species	**Mature Forest stems**		**Forest Margin stems**	
	small / large	**density**	**small / large**	**density**
Celtis africana	0.22	53.9	0.32	112
Chaetacme aristata	0.51	42.1	**1.11**	20.0
Chrysophyllum viridifolium	0.26	13.1	-	-
Combretum kraussii	0.13	2.63	1.00	0.00
Drypetes gerrardii	0.93	101	**1.50**	12.5
Ekebergia capensis	**4.05**	31.5	**5.17**	20.0
Harpephyllum caffrum	0.00	13.1	0.00	7.50
Protorhus longifolia	0.00	19.7	0.00	40.0
Vepris lanceolata	0.12	9.21	0.00	10.0

Only one species, *Ekebergia capensis*, has a ratio of >1 in the mature forest and shows a true negative exponential curve indicative of shade-tolerance and successful, subcanopy regeneration. *Chrysophyllum viridifolium*, *Drypetes gerrardii* and *Chaetacme aristata* have distributions that approximate a

Figure 3: Size-class distributions of the 9 most common tree species in Hilltop Forest (Solid Blue = Forest ; Diagonal Red = Margins)



negative exponential curve, but they lack regeneration in the first size-class. All the other species examined here have ratios of <1 in the forest and exhibit unimodal or bimodal shaped curves with very low levels of recruitment.

Three species, *Chaetacme aristata*, *Drypetes gerrardii* and *Ekebergia capensis*, have ratios >1 in the forest margins. However, species like *Chrysophyllum viridifolium*, *Harpephyllum caffrum, Vepris lanceolata* and *Protorhus longifolia*, a common component of margins, do not seem to be recruiting at all in the margins.

♦ *Tree-fall gap dynamics*

In the twenty tree-fall gaps sampled, five species were identified as gap makers. *Combretum kraussii* occurred as a gap maker in five gaps, and was the only species occurring more than once in this role. There were nineteen species of potential gap takers recorded. Of potential canopy species, the most frequently occurring gap takers, *Chrysophyllum viridifolium*, *Combretum kraussii* and *Chaetacme aristata*, appeared three times each. Advanced regeneration from sub-canopy species, such as *Englerophytum natalense*, often filled tree-fall gaps. No specific replacement patterns were observed. In general, recruitment in tree-fall gaps was extremely poor and did not differ substantially from the closed canopy forest. The largest gap sampled was $800m^2$, with the average size being $243m^2$. Creeper choking and lateral infill from canopy trees were common in the smaller gaps.

Due to the low levels of recruitment occurring in the forest and the gaps, only one species, namely *Celtis africana*, was found in sufficient numbers to allow a comparison of recruitment between the forest and tree-fall gaps. This comparison, of density of seedlings (<25 cm high) and understory recruits (between 25cm and 2m high) in gaps and non-gaps, shows that the density of seedlings was much lower, while the density of understory recruits was much higher, in gaps than in non-gaps (Table 2). Thus, for *Celtis africana*, survivorship of seedlings in gaps is higher than in the forest as a greater proportion of seedlings grow into the recruit class from gaps.

Table 2: Differences between numbers and densities of *Celtis africana* seedlings (< 25 cm tall) and recruits (> 25 cm but < 2 m tall) in plots (non-gaps) and gaps.

Celtis africana	**sample**	**area (m^2)**	**no. of stems**	**density**	**Chi-squared**	**p <**
seedlings	plots	8400	4	0.0005	14.70	0.0001
	gaps	4838	15	0.0031	(d.f. = 1)	
recruits	plots	8400	5060	0.6024	2264.68	0.0000
	gaps	4838	100	0.0207	(d.f. = 1)	

♦ *Clumping and Large-scale disturbance*

The relative abundance of the dominant species in all clumps is significantly greater than the average abundance in the forest (Table 3). The frequency distributions of the DBH of clumped trees have lower coefficients of variation than that found for canopy trees over 20cm DBH in the forest (Figure 4). The areas of the clumps are significantly larger than that of the gaps (Table 4).

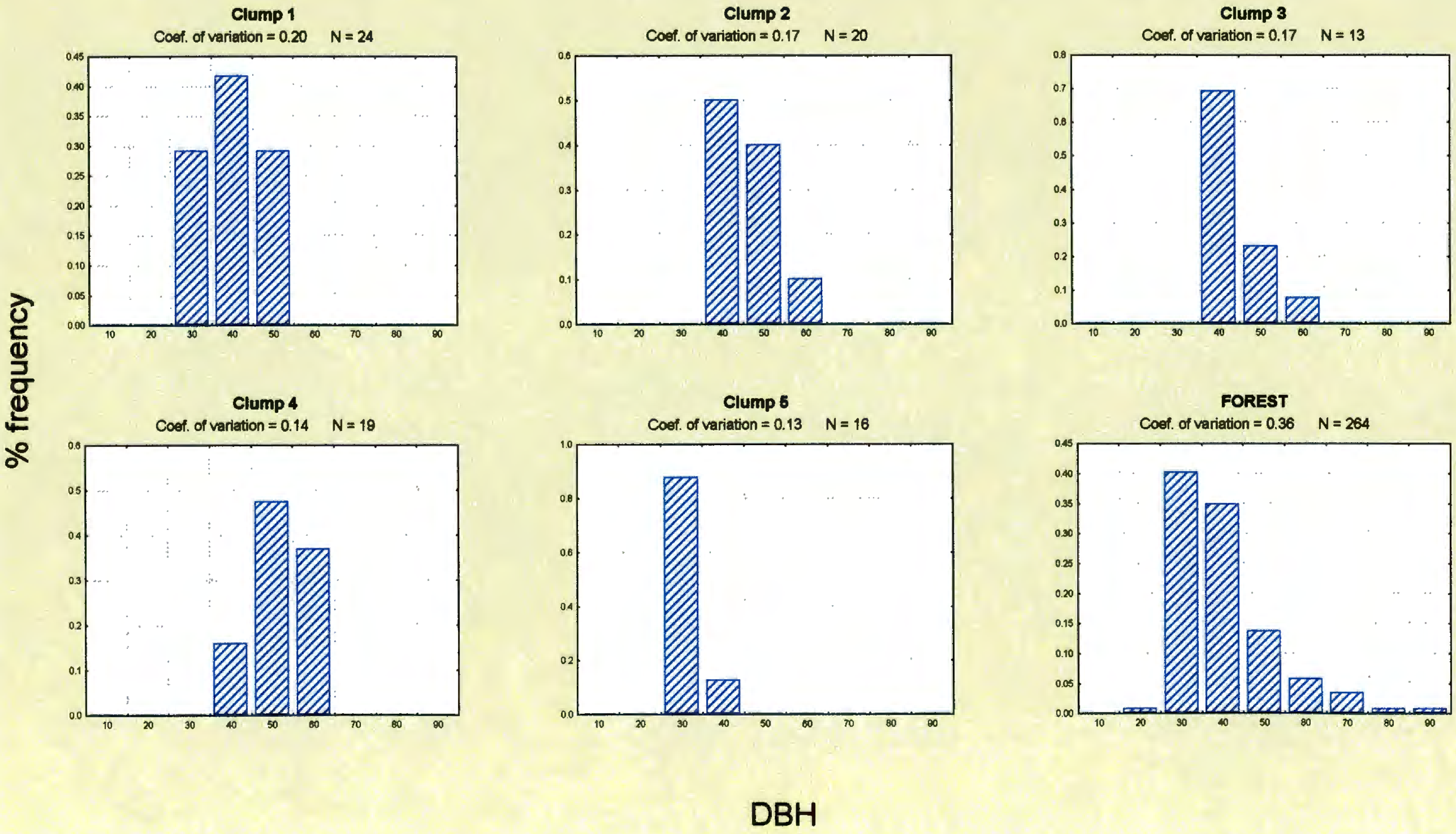
Table 3: Comparative test of abundance's of the dominant species in each clump versus all forest plot data. Percentage of total composition is shown, with number of samples in parentheses. Significant difference of count data tested for by Chi-square.

Clump	**Species**	**% of clump (n)**	**% of forest (n)**	**Chi-square**	**p <**
1	*Protorhus longifolia*	63% (24)	4.0% (261)	32.62	0.0000
2	*Calodendrum capense*	32% (19)	0.0% (261)	63.98	0.0000
3	*Protorhus longifolia*	62% (13)	4.0% (261)	39.88	0.0000
4	*Harpephyllum caffrum*	16% (19)	1.0% (261)	15.45	0.0001
	Protorhus longifolia	47% (19)	4.0% (261)	34.53	0.0000
5	*Margaritaria discoidea*	25% (16)	11% (261)	27.52	0.0000

Table 4: Comparison of median area between clumps and forest gaps. Means tested for significant difference by Kruskal-Wallace analysis of variance by ranks.

	Median (m^2)	**n**	**Chi-square**	**p <**
Clumps	2100	5	6.77	0.0093
Gaps	200	20	(d.f. = 1)	

Figure 4: Frequency distribution of DBH of all canopy trees over 20cm DBH sampled in Clumps and in Forest plots.



Discussion:

◆ *Grain*

The classification and ordination show canopy and subcanopy components of individual plots to be distinct from one another (Figures 1 and 2). This is indicative of a coarse-grained forest (Midgley *et al* 1990) and reflects the situation of light-demanding canopy species and shade-tolerant understory species. In a fine-grained forest, canopy and subcanopy should be extremely similar (Midgley *et al* 1990).

◆ *Size-class distributions*

In forests in which gaps comprise a small aerial part of the forest, such as Hilltop Forest, shade-tolerant species should exhibit negative exponential curves (Everard *et al* 1995). This negative exponential curve reflects the situation of many small individuals and few large individuals. A forest species with this type of frequency distribution would appear to be successfully regenerating under the canopy. In shade-intolerant species, recruits cannot develop under the canopy and regeneration is limited to sprouting and gap recruitment. This type of species would typically have a greater number of large than small individuals, and would thus exhibit a much flatter, or even bell-shaped, curve (Everard *et al* 1995) under conditions of infrequent gap disturbance.

The size-class distributions shown in Figure 3 are typical of a coarse-grained forest. In the forest, *Harpephyllum caffrum*, *Protorhus longifolia* and *Vepris lanceolata* all display low ratios of small:large stems (Table 1), indicating a lack of regeneration in the smaller size-classes. These species would seem to be persisting in the form of a few large individuals until large-scale disturbance enables them to recruit once again. In the prolonged absence of this disturbance, one would predict these species would be lost.

Combretum kraussii also displays a low ratio of small:large stems (Table 1). However, *Combretum kraussii* is able to sprout (pers. obs.). It seems likely that established individuals will just persist, resulting in a preponderance of large size-classes composed of several large stems belonging to one individual rather than one immensely tall canopy stem. Kruger *et al.* (1997) hypothesise that sprouters should be at a disadvantage in tall forests and this may account for the relatively large proportion of gaps caused by fallen *Combretum kraussii.*

Chrysophyllum viridifolium, *Drypetes gerrardii* and *Chaetacme aristata* have higher small:large stem ratios (Table 1), and hence greater regeneration potential, however they lack recruits in the first class (<1 cm DBH) and are not visibly recruiting under the canopy. This could be due to browsing of seedlings by herbivores such as Nyala, or Red Duiker, in this forest. Certainly, regeneration failures due to grazing impacts have been documented in other forests (Tilghman 1989). Evidence of browsing is visible in the Hluhluwe forests, and this is an avenue for future research.

In the mature forest, only *Ekebergia capensis* has more small sized individuals than large, hence a small:large stem ratio of >1 (Table 1). *Ekebergia capensis* shows the negative exponential curve typical of a shade-tolerant species regenerating under the canopy. Given the same disturbance regime as present, one would expect species like *Ekebergia capensis* to become more common with time.

In the forest margins, recruitment levels are not uniformly different from the closed forest (Table 1). This suggests that forest expansion of currently dominant canopy species is not occurring in the margins. In fact, the TWINSPAN classification (Figure 1) and DCA ordination (Figure 2) do not distinguish between margin and forest plots. No significant forest margin regeneration is seen in *Protorhus longifolia*, *Harpephyllum caffrum*, *Vepris lanceolata* and *Chrysophyllum viridifolium. Combretum kraussii* and *Drypetes gerrardii* have small:large stem ratios of >1 in the margins, however these are probably just an artefact of small sample size, and these species cannot be considered to be recruiting in the margins.

Celtis africana, a fast growing, pioneer type species definitely shows an increase in the smaller size-classes in the margins. Other increases in margin regeneration are not seen in the shade-intolerant canopy species as one might expect, but rather in the more shade-tolerant species, *Chaetacme aristata*, and *Ekebergia capensis.*

One would expect to see this pattern in a receding forest margin. As the forest is receding, the canopy on the margin has the same composition as in the closed forest, however there are increased levels of light. This should allow greater rates of growth and recruitment, and as the canopy species are unable to regenerate *in situ.*, shade tolerant species are able to respond to this. Hilltop Forest borders on grassland and it is possible that these are burnt too frequently for the spread of forests into their margins.

These size-class distributions indicate that Hilltop Forest has similarities to both coastal scarp and coastal lowland forest types as presented by Everard *et al.* (1995). However, the coarse grain, species composition and size-class distributions of Hilltop Forest, together with its geographic location and disturbance regime classify it as coastal scarp forest.

♦ *Tree-fall gap dynamics*

From the analysis of the tree-fall gap data, there do not seem to be any fixed replacement patterns. Certainly, there do not seem to be any examples of intra-specific facilitation, where the adult of a species makes way for its recruit, or succession, where one species is commonly succeeded by another. Instead, there seems to be much variability in gaps sampled. This suggests random replacement in gaps.

It is apparent that unless the disturbance has created a gap sufficiently large, the canopy will be filled by advanced regeneration from shade-tolerant subcanopy species, or by lateral infill from surrounding trees. This was seen on numerous occasions and further supports the coarse-grain designation for this forest, as coarse-grained forests typically require large-scale disturbances in order to maintain species diversity.

Tree-fall gaps unquestionably influence the reproductive success of certain species. For *Celtis africana* there is an increase in understory sized plants in gaps compared with non-gaps (Table 2). There is also far lower density of seedlings in these gaps (Table 2). This implies that survival and growth to the following size-class of the seedlings is greatly enhanced in gaps. The numerous seedlings produced under intact forest canopy, presumably below con-specific adults, rarely attain size of over 5 cm (pers. obs.). Thus dispersal of the seed away from parents into gaps is extremely important. One would expect this to apply to other species in this forest.

Despite this apparent success, gaps seem to be relatively unimportant in terms of regeneration success in the Hluhluwe forests. Most of the dominant canopy trees of this forest are apparently shade-intolerant species incapable of advanced regeneration and many species do not seem to be recruiting at all. These species are not able to establish in the small gaps created by standing tree death or branch fall. Much larger gaps, such as those caused by multiple tree fall or fire, might allow regeneration of these species. However, no direct evidence of large-scale disturbance was seen in the forest under the current disturbance regime. Nevertheless, by employing indirect methods, old areas of large-scale disturbance could be detected.

◆ *Clumping and large-scale disturbance*

Three lines of evidence support the existence of large-scale gaps filled by clumped, even-aged canopy species. Firstly, the abundances of the dominant shade-intolerant species were significantly higher in clumps than in forest (Table 3). Secondly, these clumps had a median area of 2100m^2, which is significantly larger than normal forest gaps (Table 4). Thirdly, there was a small range in DBH sizes of canopy trees in the clumps compared with the rest of the forest (Figure 4).

In addition to the evidence above, an isotopic study was performed on trees cored in these clumps. This isotopic study was aimed at creating a technique by which to examine the past regeneration environments of trees and is presented in full in Chapter 4. In this study, it was demonstrated that tree cores could be used to differentiate between trees that grew up under a canopy or in small gaps and those that recruited in open areas or large gaps. The results showed that the trees from the Hilltop clumps differed significantly from trees in the closed forest (and hence small gaps), indicating that they recruited as a cohort in a large clearing.

Thus, it appears as if large-scale disturbance played a part in the establishment of the current shade-intolerant canopy communities of Hilltop Forest. Establishing the potential cause of this disturbance is an extremely interesting problem and is discussed later.

♦ *Management implications*

Hilltop Forest is coarse-grained. The size-class analyses (Figure 3, Table 1) indicate that of all the species shown, only *Ekebergia capensis* is able to recruit in mature forest. Thus, under present conditions, there seems to be a general recruitment failure for most of the canopy species. If no active management is pursued in these forests, one would forecast the loss of certain shade-intolerant species and the gradual increase in shade-tolerant species. Of course this change is not necessarily detrimental. If the desired management strategy is the maintenance of the present species composition, the clearing of large gaps could facilitate shade-intolerant species regeneration. Reduction in browsing stock numbers in the forest could also enhance recruitment and this is an avenue for future research.

As has been pointed out by Everard *et al.* (1995), the maintenance of coarse-grained forests requires the preservation of as much area as possible. This is due to the fact that regeneration of several important species in this forest does not occur on the small-scale, but rather at a distance from the parent. By conserving too small a patch, the forest may lose its ability to remain a sustainable functional unit (Everard *et al* 1995). This certainly applies to Hilltop Forest. In addition to this, the Forest seems to be receding from its margins. A reduction in the frequency of burning in the adjacent grasslands might promote forest expansion in these areas, or at least prevent grassland encroachment.

At present, human utilisation of this forest is prohibited, although some evidence of harvesting was visible near the periphery of the reserve. It seems likely that South African nature reserves shall, at some point in the future, be forced to be of direct benefit to their surrounding rural communities. If local communities were allowed limited harvesting rights in Hluhluwe Reserve, only shade-tolerant species should targeted. Everard *et al.* (1995) explain that the removal of saplings of shade-intolerant species could lead to their extinction from the forest. The removal of the large size-class individuals would be equally disastrous. However, shade-tolerant species are able to regenerate under an existing forest canopy with ease, thus it would be hard to eliminate them with casual harvesting. In fact, the harvesting of certain shade-tolerant understory and subcanopy species could promote species diversity in the forest, as their removal may well aid the recruitment of shade-intolerant species. An example of a species that could be harvested for rural use is *Rawsonia lucida*, an abundant, shade-tolerant understory species that is targeted for its bark at present (pers. obs.).

♦ *Hypothesis on the origins of coarse-grained forest in Hluhluwe*

The forest of Hluhluwe Reserve does not seem to undergo any major disturbance at present. Human impacts are minimal. Lightning induced fires are rare, and ineffectual in creating large gaps. Hurricanes occur extremely infrequently and are not effective in creating blow-down disturbance. Multiple tree fall gaps were not observed in this study. There does not seem to be any evidence for extremely intensive grazing occurring, nor do elephants occur in this forest. Thus, the question arises of how clumps of light-requiring canopy species originated and still exist, as it is clear that the regeneration levels of many canopy dominants are inadequate to maintain the present composition in an area without periodic, large-scale disturbance such as Hluhluwe. It would seem that disturbance was more prevalent in the past than at present, and the most probable cause for this would be anthropogenic impacts.

The Hluhluwe Reserve was proclaimed in 1895 (Brooks & Macdonald 1983). Before that, the area was utilised by indigenous peoples for swidden agriculture and iron-smelting, dating to roughly two thousand years ago (Hall 1981, Deacon 1992, Scholes & Walker 1993). This iron-age lifestyle required a large timber supply, and has been identified as a potentially landscape transforming epoch (Feely 1980, Hall 1984). Swidden agriculture, also known as "slash-and-burn" farming, involved the clearing of forest or woodland patches for crop fields. These fields would be used for a few years, until infertile, and then abandoned. After abandonment, these old fields, situated in or near forest vegetation, would be suitable for recruitment of shade-intolerant species. The discovery of an iron-smelting site in Hluhluwe Reserve (Hall 1980) not more than 7 kilometres from the forest (see map in Chapter 1) supports this suggestion.

I suggest a possible model for the development of coarse-grained forest in these areas. Two thousand years of low-density swidden agriculture, and associated iron-age practices, induced a patchy forest composed of fast-growing, shade-intolerant species. When the reserve was proclaimed in 1895, the anthropogenic impacts were phased out. This allowed the maturation of these species into the closed canopy community seen today. However, as disturbance is no longer a regular factor, these shade-intolerant species are unable to regenerate, and shade-tolerant species are able to establish and increase in dominance. Thus, with time, these coarse-grained forests may become finer-grained.

This model is, of course, merely a hypothesis and would require additional evidence to test it. Apart from additional archaeological evidence, which would prove invaluable to this hypothesis, isotopic techniques could be used. The analysis of soil carbon isotopes has been used to show vegetation change (Ambrose & Sikes 1991, Bond *et al* 1994, Pessenda *et al* 1996, Desjardins *et al* 1996, Connin *et al* 1997). The possibility for application of this technique to human generated disturbances and old agricultural lands is an exciting point for further research (see Chapter 5).

It would seem likely that this model could apply to other coarse-grained forests on the Eastern seaboard of South Africa. Forests where present disturbance is minimal and there is a history of human settlement would be ideal for further investigation into this hypothesis. The implications for conservation are enormous, especially concerning utilisation of these reserves by local peoples and for what we perceive as "natural" vegetation.

Conclusion:

The forests of Hluhluwe Nature Reserve are coarse-grained and can be classified as coastal scarp forest. There is substantial difference between the composition of the canopy and subcanopy layers. This reflects the fact that canopy species are not regenerating beneath their adults. The most common canopy species are shade-intolerant species that require relatively large-scale disturbance in order to become established. At present these species are mainly represented by large individuals. Very few saplings of these species are regenerating.

Normal treefall gaps do not play a large role in allowing shade-intolerant species to recruit. However, recruitment of certain species, such as *Celtis africana*, is enhanced in these gaps. The larger the gap the better, for these shade-intolerant species, as creeper choking and lateral infill often closes the smaller gaps. The presence of large clumps of even-aged trees indicates that large-scale disturbance is important in proving recruitment opportunities for shade-intolerant canopy species.

Management for conservation of this speciose forest involves two aspects. Firstly, the forest is being encroached upon and regular burning of the forest margins should not be encouraged as any reduction in area of the forest could result in a loss of species diversity. Secondly, the creation of large, man-made gaps in the mature forest may prove necessary in order to maintain shade-intolerant species. The forest provides habitat for amongst others Nyala, Red Duiker, Buffalo and Black Rhino as well as numerous birds and insect species. It represents a fragment of what is a rapidly diminishing vegetation type. Conservation of this resource is of importance.

It is hypothesised that the existence of coarse-grained forest in Hluhluwe, and possibly elsewhere, can to some extent be explained by iron-age anthropogenic impacts. The removal of anthropogenic disturbance, with the creation of the reserve, allowed the development of a predominantly shade-intolerant canopy. Ironically, without this “unnatural” disturbance, these species seem unable to recruit. If this hypothesis can be proven in this and other areas, the implications for conservation are enormous.

Preface to Chapter Three:

In order to identify ecological indicators for anthropogenic effects I looked at successional changes after the abandonment of old fields. I reasoned that species present at different successional stages, if largely confined to old fields, would be markers of anthropogenic influence in these forests. Also by dating time since abandonment I could determine rate of return to primary forest composition giving an indication of how long anthropogenic effects could be seen. I did this work in the coastal dune forest of KwaZulu-Natal.

Coincidentally, successional changes in dune forest have been at the centre of controversial ecological impact assessments with regard to open-cast dune mining. Protagonists have agreed that forest succession is rapid after dune mining is completed, opponents argue that forests do not recover.

This chapter was written as a paper that will be submitted in the context of the dune mining controversy. Key points relating to the use of forest succession information for tracking anthropogenic effects are noted here briefly, and in the concluding chapter.

3

Reassessing the effects of human disturbance in the dune forests of Cape Vidal, KwaZulu-Natal.

Abstract

I investigated the effects of swidden agricultural disturbance in dune forest communities near Cape Vidal on the north-eastern coast of KwaZulu-Natal. Three disturbed and two undisturbed categories of dune forest were identified from aerial photographs from 1937 to 1996. Three communities in a successional sequence were identified; *Acacia karroo* woodland, Secondary dune forest and Climax dune forest. Species diversity was found to be highest in Climax dune forest, with 30% of the species found in the study being restricted to this community. Succession to climax dune forest was estimated to take 80 to 130 years post-disturbance. Functional type analysis indicates that certain species might not recover post-disturbance. In light of these results, previous findings of successful rehabilitation after open-cast dune mining are questioned.

Keywords: *Acacia karroo*, coastal dune cordon, distance analysis, dune mining, Iron Age habitation, rare species, recovery, rehabilitation, succession, swidden agriculture

Introduction

The proposal for dune mining of heavy minerals in the St. Lucia area (CSIR Environmental Services 1993) has been a contentious issue for sometime. Deposits of Ilmenite, Rutile and Zircon exist in commercially exploitable quantities from a depth of 3 to 52m in these dunes. In order to commercially extract these minerals, all vegetation is cleared, the topsoil removed and the dune topography destroyed (Lubke *et al* 1996). Richards Bay Minerals (RBM), the company behind the proposal, are committed to rehabilitation of these areas. Amongst other factors, this rehabilitation would involve recreation of topography and aiding the recovery of dune forest communities. However, questions have been raised as to whether the latter is in fact possible or readily achievable.

Previous studies (Mentis & Ellery 1994, Lubke *et al* 1996, Mentis & Ellery 1998) suggest that dune forest is easily rehabilitated after dune mining disturbance. These studies showed that mined sites did not differ significantly from unmined sites in successional trajectories and the recovery of these sites was adequate and was heading to a climax condition relatively rapidly. However, there are several problems with the underlying assumptions on which these studies were based.

- ***Previous rehabilitation studies (Mentis & Ellery 1994, Mentis & Ellery 1998)***

1) Comparisons between successional trajectories on mined and unmined land were used to indicate acceptable ecosystem recovery after mining. However, the unmined lands selected as a control were also heavily disturbed, having undergone "bulldozing for industrial or urban development" (Mentis & Ellery 1998). This leads to a comparison of disturbed versus disturbed successional tracks, which heavily weights the chances of congruence in forest development.

2) Mentis and Ellery (1994, 1998) used species richness as their main measure of ecosystem recovery. However a measure of species richness, by not identifying the type of species involved, does not discriminate between species of primary forest and weeds of recently disturbed lands. Comparisons of species composition are much more appropriate measures when the objective is to recover a community resembling the primary community in composition.

3) Mentis and Ellery (1994, 1998) measured successional progress towards a "climax" by comparing sample plots with plots they considered to be successional endpoints. The outcome of such an analysis clearly depends on the choice of endpoints. In this regard, the inclusion of *Acacia karroo* woodlands as a successional end point is unjustified. Previous work has shown *Acacia karroo* woodlands to be early precursors in a lengthy successional sequence after disturbance (Weisser & Marques 1979, Weisser 1980). Indeed it has been questioned whether *Acacia karroo* woodlands are in fact natural states in the dune forest community (MacDevette & Gordon 1991). Nevertheless, three primary forest plots and three *Acacia karroo* woodlands were used by Mentis and Ellery (1994) to create a goal endpoint for succession in a distance analysis. Their use of endpoints is also not consistent. In analyses involving time since disturbance, climax forest plots were excluded, as their exact disturbance histories were unknown, and the *Acacia karroo* woodlands were used as the sole endpoints. Since mining produces *Acacia karroo* woodlands, this choice of endpoint biases the results towards indicating successful rehabilitation.

The aim of this chapter is to examine the recovery of these dune forests after agricultural disturbance and compare this to mining disturbance. As noted by Mentis and Ellery (1994, 1998) there is a long history of farming by Iron Age cultivators in these forests. I aimed to determine which species returned after abandonment of old fields and which, if any, did not. I also aimed to determine the rate of forest recovery after this agricultural disturbance. This comparison, I felt, would be an appropriate benchmark of whether the dune forest could recover after the more extreme case of dune mining disturbance. In order to allow fair comparison I have employed the methods used in the previous rehabilitation studies (Mentis & Ellery 1994, Mentis & Ellery 1998), attempting to eliminate the problems outlined above.

Site description:

Sampling was undertaken in the coastal dune forest from Cape Vidal, KwaZulu-Natal (28°07'S, 32°33'E) for several kilometres Northwards (see Chapter 1, Figure 2 for map). This area forms part of the Zululand coastal dune cordon. Average rainfall is 1300mm per annum (von Maltitz *et al* 1996). These dunes rank as the second highest vegetated dunes in southern Africa (Tinley 1985) and reach an altitude of 166m above sea level within a kilometre from the shoreline.

The Zululand coastal dune cordon was formed during the last glacial period, 18 000 years ago, when the sea level dropped to approximately 125 metres below its current level and exposed a large sandy plain (Maud 1991). A series of dunes were built up from this sandy plain, and with the establishment of the sea-level at present levels, the present dune cordon took shape, probably by parabolic blow-out dune-building processes (Tinley 1985). Ecologically, these dunes are a young formation (von Maltitz *et al* 1996), possibly less than 10 000 years old (Maud 1991).

The vegetation, classified by Acocks as veld type 1d, Dune Forest (Acocks 1953), consists of a mosaic of mature dune forest, secondary dune forest and grassland (von Maltitz *et al* 1996). The floristics and successional change of these forests have been described (Venter 1976, Weisser 1980, Tinley 1985), although much work is in the form of unpublished reports. Basic succession has been documented in the dune forests (Moll 1972, Weisser & Marques 1979, Weisser 1980, Weisser 1991). This has been used to show potential for rehabilitation after the effects of dune mining disturbance (Mentis & Ellery 1994, Mentis & Ellery 1998). However, it would seem that the analysis and interpretation of this succession have not been examined carefully enough, as recently, complexities in the dune forest successional sequence have been demonstrated (von Maltitz *et al* 1996).

It is possible that stone-age peoples were present in the Zululand coastal dune cordon since its formation (Beaumont *et al* 1978). However, significant anthropogenic impacts only occurred with the advent of iron-age economies and practices, around the third century AD (Feely 1980, Hall 1981, Hall 1983, Hall 1984). Initially, these practices included swidden agriculture and fuelwood harvesting, but the arrival of cattle around AD 1000, led to increased burning to create grazing areas (von Maltitz *et al* 1996). These practices continued until recently. Cattle were pastured up until 1975 on the Eastern Shores of Lake St. Lucia (Feely 1980), when the subsistence farmers were removed and a nature reserve was proclaimed. Aerial photography shows that the dune slacks, found between the fore dune and hind dune, were favoured for agriculture. It seems likely that these areas could have undergone roughly 1600 years of shifting agriculture (Hall 1981).

Methods

♦ *Sampling strategy:*

I sampled tree and shrub vegetation in 39 sites of varying ages since disturbance. These sites were identified by examining aerial photographs of the area from 1937, 1960, 1975, 1988 and 1996 and locating areas within the forest that had been cleared for cultivation by swidden agriculturists. I was able to determine at which period the sites started to re-vegetate from the sequence of photographs. I labelled three ages of disturbance: 1) recovered between 1937–1960 (1960), 2) recovered between 1960-1975 (1975), 3) recovered between 1975-1988 (1988). Thus, assuming at least 5 years are required to form a canopy that is recognisable on aerial photographs, I sampled sites with minimum (and possible maximum) post-disturbance ages of 42 (60), 27 (36) and 14 (21) years. Obviously, due to the uncertainty in the exact age since land abandonment, a certain degree of overlap between categories is to be expected.

I identified two control groups. The first control group consisted of sites that were topographically similar to the disturbed sites (i.e. in the dune slacks) but showed no sign of agricultural disturbance in any of the aerial photographs. These sites were labelled slack controls (SC). It is possible that these sites were farmed at sometime in the past. However if this were the case, the minimum age of the stands would be well in excess of 60 years as they were covered by mature forest in the 1937 aerial photographs. I reasoned that these slack controls might well represent the climax state of anthropogenically disturbed forest. The second control group was chosen in order to control for any form of agricultural disturbance, however ancient. These topographic controls (TC) were located on flat ground on the tops of dunes as opposed to the dune slacks where all other sites were located. I reasoned that these sites would be least likely to have experienced any agricultural disturbance, due to their topographic isolation, and would thus provide an effective comparison to the slack controls.

Thirty-nine plots (50m x 15m) were laid in the five different categories of disturbance (7x1988, 6x1975, 6x1960, 10xSC, 10xTC). The species name, diameter at breast height (DBH) and number of stems of all plants over 2 metres tall, rooted in the plot, were recorded.

♦ *Data analysis:*

In order to examine the appearance and disappearance of species through the successional sequence, transect data was transformed into a plot by species matrix. By ranking plots by age since disturbance and species by occurrence and biomass in plots of various ages, a visual representation of the species composition through the successional sequence was obtained. The groupings within this matrix were derived by manual sorting.

Size-class distributions of the 23 most abundant species were extracted from the plot data. These were separated into size-classes in control plots (SC, TC) and disturbed plots (1960, 1975, 1988). From these size-classes one can determine which species are able to persist through agricultural disturbance. I regarded any individuals in the disturbed sites that were larger than 30cm DBH as having persisted through the agricultural disturbance either through being left as shade trees or coppicing after abandonment.

Specific leaf area (SLA) was determined for 22 of the most abundant tree species in Cape Vidal. SLA, measured in $cm^2.g^{-1}$, provides a measure of leaf longevity, rates of photosynthesis and conductance (Reich *et al* 1991, Reich *et al* 1992) which in turn relates to life history. Shade-tolerant trees are predicted to have low SLA values and shade-intolerant trees to have high SLA values (Midgley *et al* 1995b). Leaves were collected at Cape Vidal, in October 1997, by which time most species had produced a new set of fully expanded leaves (Midgley *et al* 1995b). Several well-lit branches were collected from each species and from these, 10 young, fully expanded leaves were sampled and pressed in the field. Leaves were dried at 35°C for 48 hours and their area measured on a leaf area meter. SLA was determined for each leaf by dividing area by mass and a mean was obtained for each species.

♦ *Succession*

Succession was examined following the methods of Mentis and Ellery (1994), and involved a direct (distance analysis) and an indirect (ordination) analysis.

Distance analysis

The direct analysis of succession was achieved by examining the distance of each plot from a previously defined successional end-point. Following Mentis and Ellery's approach (1994), I calculated a Euclidean distance dissimilarity matrix for plots based on species abundance, using the computer programme Relevé Manager (ter Braak 1988). Two separate analyses were performed; the first with all species included and the second with rare species (single occurrences) deleted. I created an average climax plot by averaging the distances obtained for each plot from the 10 topographic control sites. This average plot was seen to represent the end-point of succession. By analysing the distances away from putative primary forest plots one could see if the vegetation was converging on this climax state. Since this end-point is user-defined, the validity of this analysis hinges largely on the appropriateness of this definition and this should be borne in mind when interpreting analyses of this nature. Corroboratory evidence from indirect analyses, such as an ordination, can provide support for direct analyses and the selection of end-points.

Using the Multidimensional Scaling Module of STATISICA (StatSoft 1996), distances for plotting on a two-dimensional plane were obtained. These distances were graphed against total plot biomass. Total plot biomass (calculated from basal areas) was used as a surrogate for age since disturbance as the age categories were discrete and exact ages for undisturbed sites were unknown. The regression of biomass against age was determined and examined for significance.

Ordination

Ordinations provide an indirect analysis of a successional trajectory by examining the similarity of each plot to all other plots on the basis of species composition. Thus, in an ordination, the position of any one plot is determined relative to all other plots simultaneously, as opposed to just one end-point as in the distance analysis. This is an indirect method of examining succession as the ordination can separate out plots on the basis of any factor, such as environmental variables or edaphic features, and not necessarily successional time. It is therefore useful as independent evidence of succession, as at no stage are user-defined climax end-points introduced into the analysis.

For the ordination, the data were initially classified using the hierarchical classification program TWINSPAN (Hill 1979). The program was run with defaults and presence and absence of species per plot were used as the importance values. As TWINSPAN is a polythetic divisive method (Kent & Coker 1992), plots are separated on the basis of total species composition. Thus, the groupings produced by TWINSPAN provide an indication of which plots are similar in species composition to one another. This gives insight into possible community affiliations within the samples. The clustering produced by this analysis can then be superimposed on to ordinations of the same databases.

A detrended correspondence analysis (DCA) was then performed using the computer programme CANOCO (ter Braak 1988). The programme was run with defaults. The presence/absence of species in a plot served as the importance values as the occurrence of rare species were interpreted as important indicators of plot recovery. All species were included. The first two axes of the ordination were graphed, the proximity of the plots indicating similarity. Groupings based on the TWINSPAN analysis were superimposed on the graph.

Timing of succession

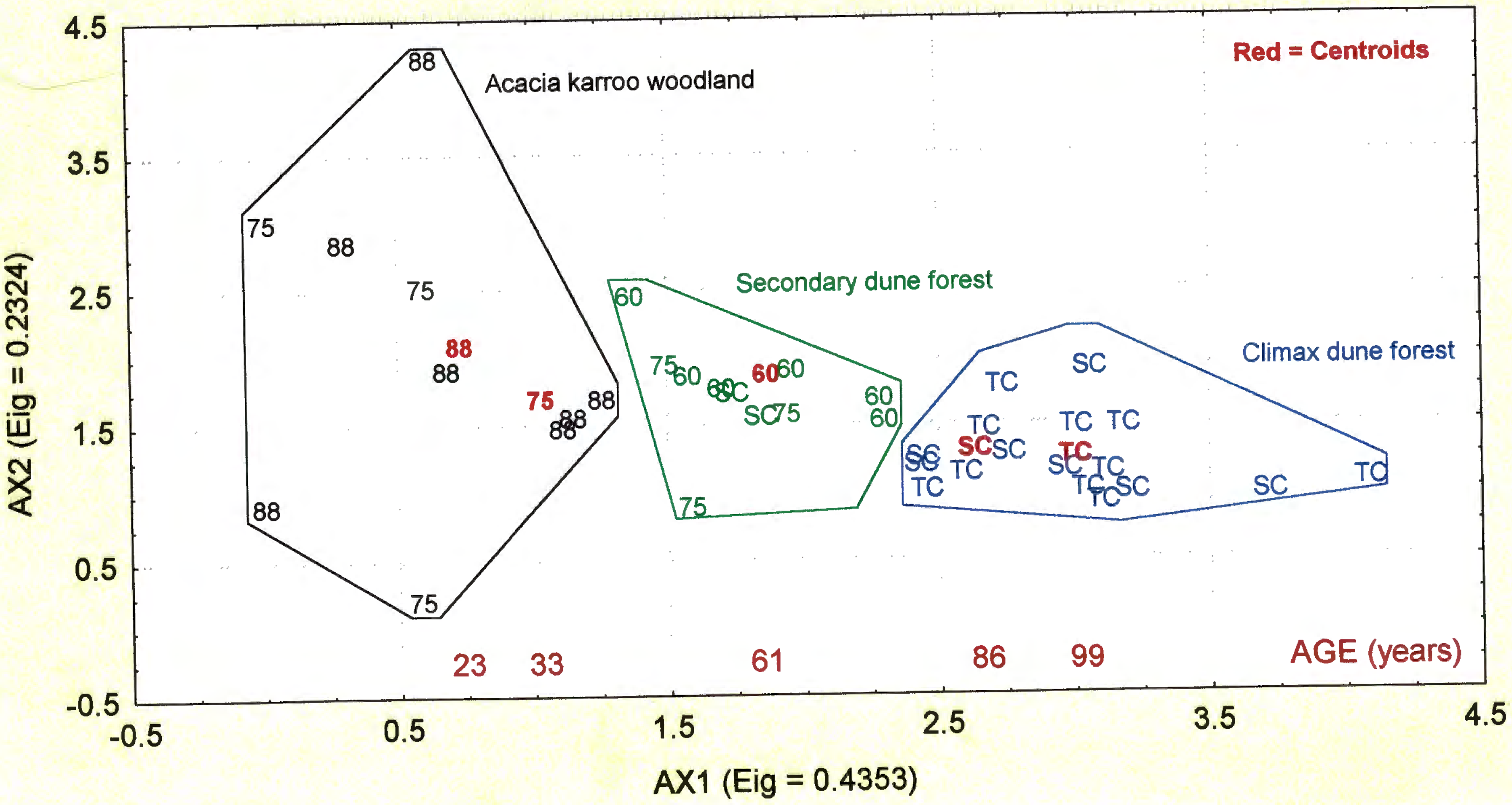
The timing of the successional sequence was determined by regressing the centroid of each disturbed category (1988, 1975, 1960) from the first axis of the DCA ordination against maximum age for that category. This was then extrapolated to the control sites of unknown age. The maximum age of each disturbed category was used in the regression so that a slightly conservative estimate of time to climax forest was obtained. A conservative estimate of rate of succession is desirable in this instance as it leads to a greater degree of confidence in obtaining complete recovery by the estimated time.

Results

♦ *Communities and diversity*

The TWINSPAN communities correlate well with the perceived trajectory of succession shown in the DCA ordination (Figure 1). It is possible to distinguish three main communities in this sequence. Following previous descriptive work (Weisser & Marques 1979, Weisser 1980, Weisser & Müller 1983) these communities can be labelled 1) *Acacia karroo* woodland, 2) Secondary dune forest and 3) Climax dune forest. Detailed community descriptions can be found in these texts.

Fig 1: DCA of Cape Vidal plots based on presence/absence of species
Groupings based on TWINSPAN community analysis.
Symbols represent site age categories (see text)



Species diversity per site, total richness and endemism within communities increase through the successional sequence (Figure 2). Endemics, in this instance, are defined as species that occur in only one of the three communities. A large proportion of the species richness and diversity is contained within the climax dune forest and there is a high level of endemism. Failure to recover this community would lead to a loss of 30% of the total species sampled (Figure 3).

♦ *Functional types*

A table of species occurrence and abundance per plot (Appendix 1) shows the change in species composition with plots of increasing time since disturbance. Groups of species have been highlighted according to their appearance in the successional sequence and labelled as potential functional groupings. In particular, species groups can be identified that are limited to disturbance and those that are limited to undisturbed areas. Analysis of the life-attributes of these species in an attempt to classify functional types is a subject for further work.

Size-class distributions of the 23 most abundant species have been included in Appendix 2. A close examination of these size-class distributions, reveals that *Acacia karroo*, *Celtis africana*, *Sideroxylon inerme*, *Teclea gerrardii* and *Ziziphus mucronata* all have large individuals in disturbed sites that exceed 30cm DBH. In fact, these individuals range from 35cm DBH to 78cm DBH, with the exception of *Acacia karroo*, which has several trees in the 30-35cm DBH class. As it is unlikely that these individuals attained such size from seed in the limited time since disturbance, I regard these as persisters through agricultural disturbance. This persistence could take two forms. Either the trees were left in fields to provide shade or fruit (Cunningham 1988) or the trees coppiced after abandonment. It is likely that the presence of these larger individuals in recently abandoned sites would have effected rates of recovery and this is discussed later.

Fig 2: Total number of species and endemics recorded and mean species richness per site within communities

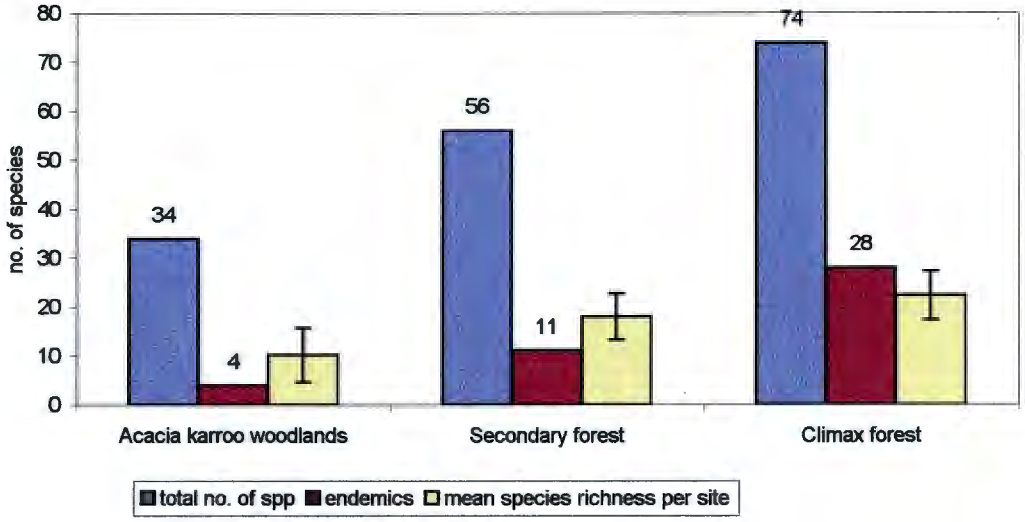
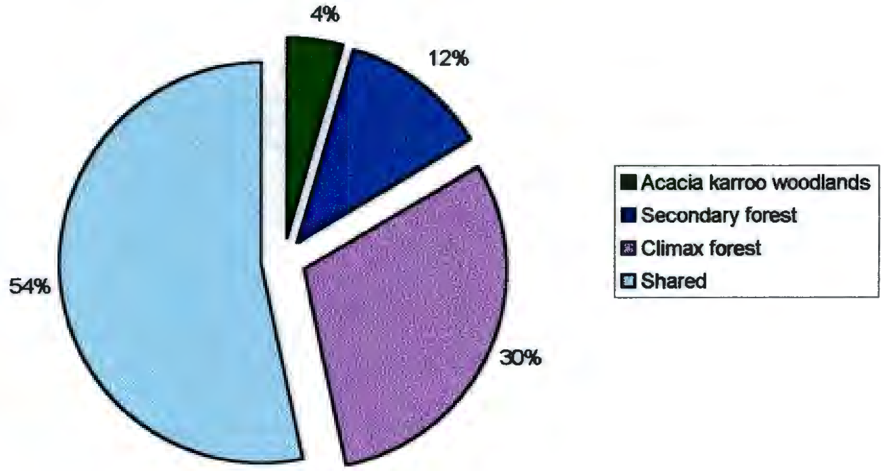


Fig 3: Proportion of total flora endemic to each successional community and those shared between communities



Average specific leaf area decreases from *Acacia karroo* woodland to Climax forest (Table 1) indicating a shift to a predominance of more shade-tolerant, climax species with time. All three communities have significantly different means ($F_{(2,2830)}$= 210.65; p<0.0000).

Table 1: Means of specific leaf area in each community

community	Mean ± std. dev.
Acacia karroo woodland	104.86 ± 31.63
Secondary forest	87.73 ± 27.53
Climax forest	74.26 ± 28.98

♦ *Succession*

The successional trajectory plotted in the ordination (Figure 1) indicates a progression from young *Acacia karroo* woodland sites through to undisturbed climax forest sites and thus supports the choice of topographic controls as successional end-points in the distance analysis.

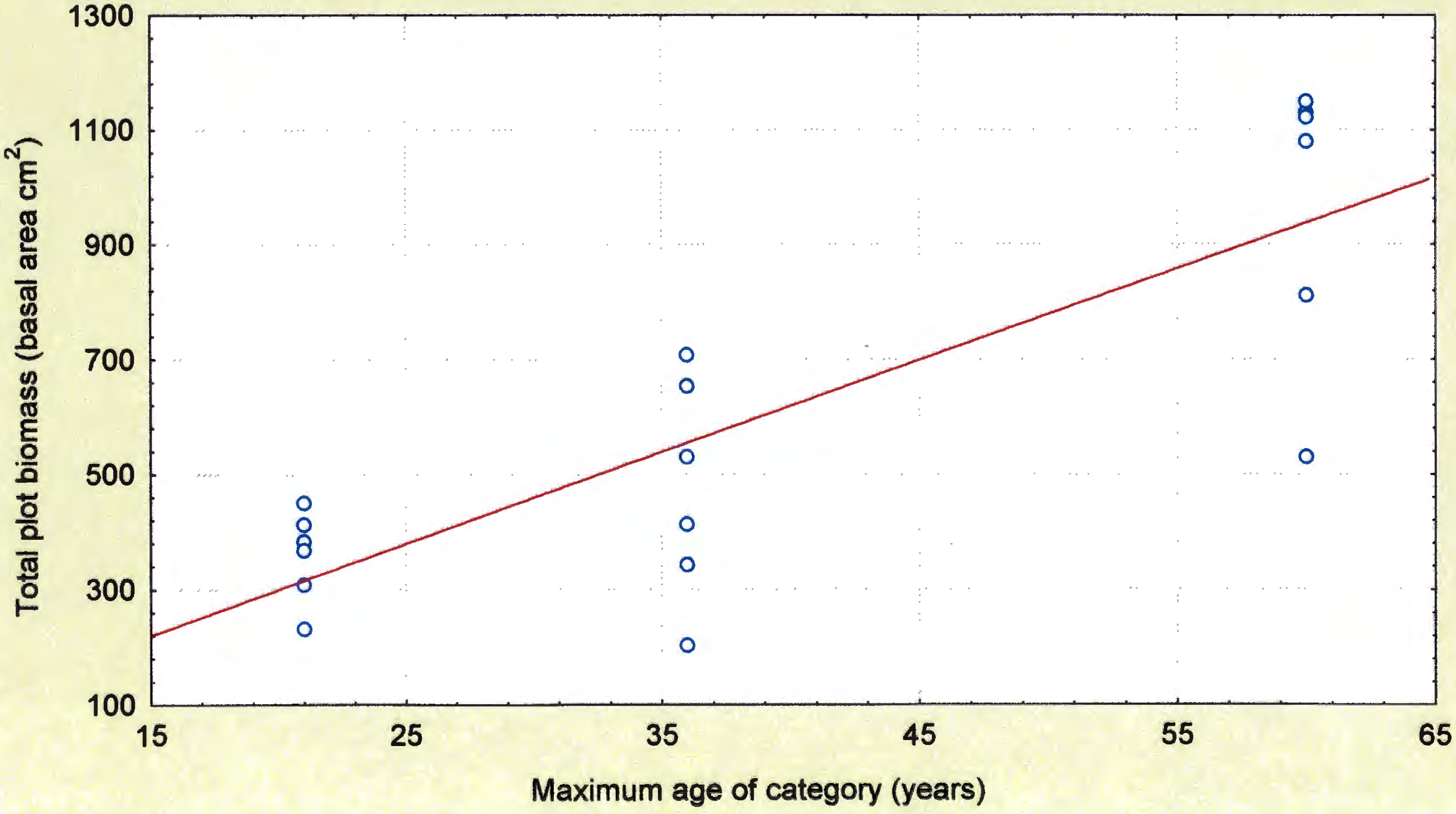
In order to create a successional trajectory from the distance analysis, Euclidean distance from the end-point was plotted against time since disturbance. As the age categories sampled in this study are artificially discrete, it is not desirable to plot them in a x-y plot versus a continuous variable such as Euclidean distance. Using a continuous variable such as total plot biomass as a surrogate for age circumvents this problem. A surrogate can only be legitimately used, however, if the two variables are well correlated. I tested this correlation by regression. The regression between total plot biomass (derived from summed basal area) and age since disturbance is

$$B = 1.190 + 21.78T \quad (R^2 = 0.651, \text{d.f.} = 17, P < 0.0000) \qquad (1)$$

where B is total biomass and T is years since disturbance (Figure 4).

Fig 4: Regression between maximum age of categories and total plot biomass

B = 1.190 + 21.78T (R^2 = 0.651, d.f. = 17, P < 0.0000)



This regression indicates that a good relationship exists between age and biomass despite the discrete nature of the variable T detracting from the fit of the regression. Thus, I feel that total biomass can be confidently used as a surrogate for age.

The Euclidean distance of plots from the successional end-points is shown plotted against biomass, as a surrogate for age (Figure 5). Two regressions were calculated and the data plotted. The first regression used data with all rare species (single occurrences) excluded. The second regression included all species. These two regressions, shown below, indicate the importance of regarding rare species, as their inclusion and exclusion greatly alters the results obtained in the distance analysis. With rare species excluded, the regression between distance and biomass is

$$D = 2.829 - 0.002B \quad (R^2 = 0.903, \text{d.f.} = 39, P < 0.0000) \qquad (2)$$

where D is Euclidean distance and B is the total biomass per plot.

With the rare species included, the regression is

$$D = 1.873 - 5.029e^{-4}B \quad (R^2 = 0.174, \text{d.f.} = 39, P < 0.0074) \qquad (3)$$

where D is Euclidean distance and B is the total biomass per plot.

Both regressions are significant, but the R^2 changes from 0.903 to 0.174 with the inclusion of rare species. The poor fit of the second regression (equation 3) indicates that the appearance of rare species in the successional sequence is not smooth and predictable. The trajectories of the regressions also change with the inclusion or exclusion of rares. In the first regression (equation 2), the trajectory of the slope converges on the average climax plot, indicating that common species follow a smooth successional trajectory towards climax forest. This trajectory changes and moves away from the average climax plot when rare species are included, indicating a breakdown in the targeted successional sequence. Thus, if one regards rare species as vital components of successful rehabilitation, late successional plots are still substantially

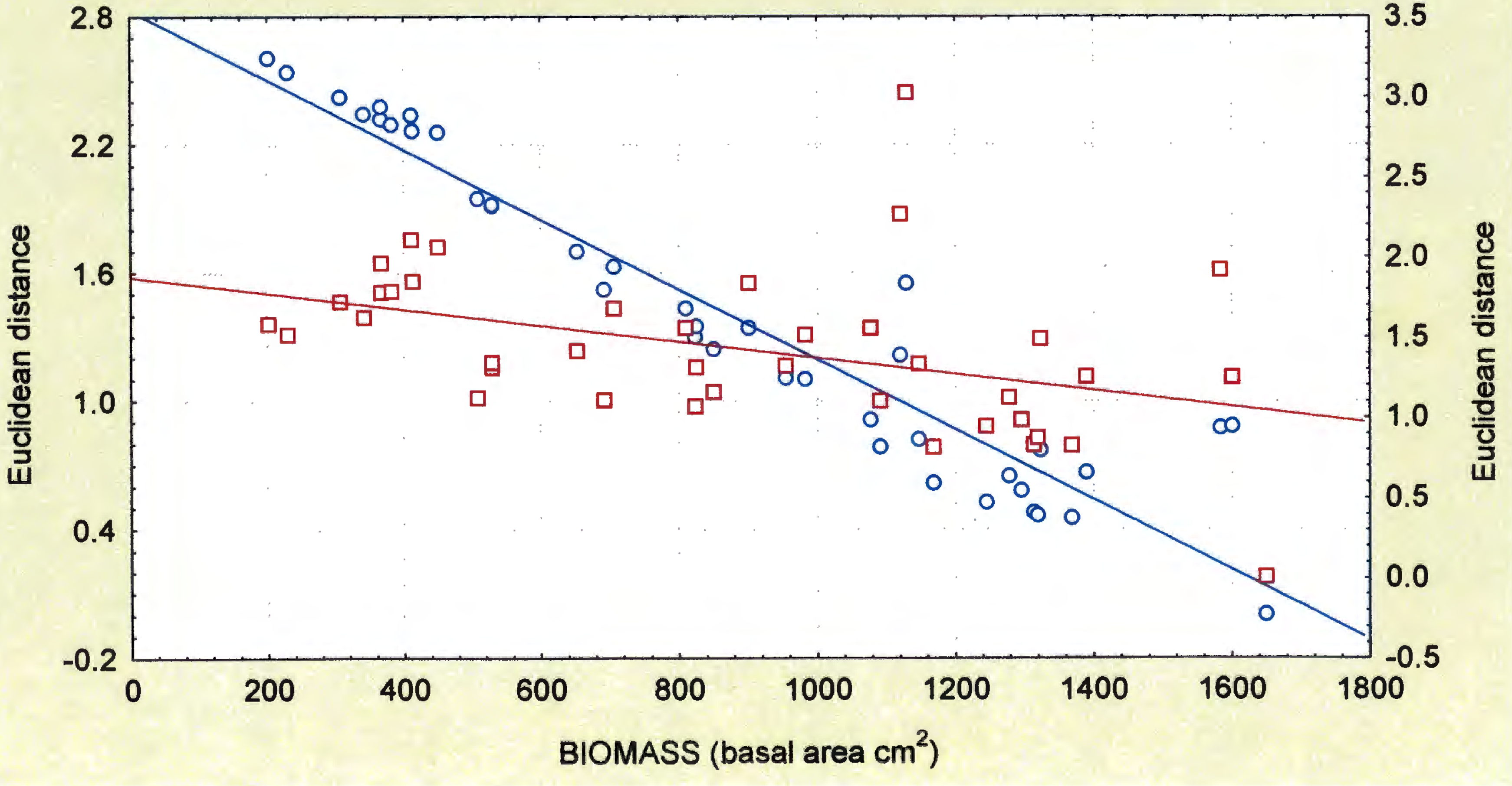


Figure 5: Euclidean distances from a putative CLIMAX plot vs. total plot biomass

Left axis (Blue) = rares excluded $R^2 = 0.903$

Right axis (Red)= all data, rares included $R^2 = 0.174$

different from the average climax plot and this successional "goal" does not seem likely to be obtained.

Timing of succession

The regression of the centroids of disturbed categories versus axis 1 of the DCA regression is

$$A = -1.16 + 33.24x \quad (R^2 = 0.98;\ d.f. = 2;\ P < 0.08377) \qquad (4)$$

where A is the age of the plot in years since disturbance and x is the co-ordinate from axis 1 of the ordination. Despite the high R^2 value, the regression itself is not significant ($P>0.05$), but this is an artefact of the very low degrees of freedom. Ideally, one would not regress three data points, however this was unavoidable due to the discreet ages of the categories sampled.

The regression ages the centroid, or average plot, of each category from most recently disturbed to topographic control as 23, 33, 61, 86 and 99 years old (Figure 1). The oldest climax forest plots are estimated to be between 115 and 130 years old since disturbance (Figure 1).

Discussion

♦ Acacia karroo *woodlands as successional endpoints*

It would seem that using *Acacia karroo* woodlands as successional endpoints is inappropriate. Instead of being endpoints, *Acacia karroo* woodlands are in fact the start of a potentially very lengthy successional sequence. In addition to this, they are extremely depauperate in terms of species diversity, when compared with true climax communities. Post-disturbance restoration aimed at reaching this state can not be deemed rehabilitation, but rather revegetation to an earlier seral stage.

♦ *Timing of successional sequence*

From the regression of known age category versus ordination axis 1 (equation 4), it is possible to extrapolate to the unknown aged climax sites. Time, in years since disturbance, is plotted on the x-axis of Figure 1. Climax forest is estimated at between 80 and 130 years old. These ages are similar to other estimations that have given ages of 25 to 60 years for the establishment of *Acacia karroo* woodlands and a further 30 to 150 years for the replacement of the woodlands by secondary dune forest (Weisser & Marques 1979).

Succession does seem to occur in the dune forest, but it is a relatively slow process. As most of the species diversity is contained in the climax dune forest, it can take up to 80 years post-disturbance to retrieve 60% of the original species composition of the forest and a further 50 years to recover the remaining 30% (Figures 2 and 6). Furthermore, this study was based in Cape Vidal wilderness area, where bird, mammal and primate dispersers were in abundance. Thus, propagule dispersal into disturbed sites was at an optimum, a factor that most likely accelerated the process of succession. In areas where these dispersers, especially mammals and primates that are important for the later stages of development, are absent or scarce, succession may not proceed as rapidly.

Another factor that may lead to faster recovery in old fields than in mined dunes is the ability of certain species to persist through the disturbance, namely, in this study, *Acacia karroo*, *Celtis africana*, *Sideroxylon inerme*, *Teclea gerrardii* and *Ziziphus mucronata*. The persistence of larger sized forest species in recently abandoned land is likely to aid recovery of these sites (Kammesheidt 1998). Propagule dispersal should be enhanced, by both direct (individual's own seeds) and indirect (providing perch sites) means. Large forest trees could thus act as nurse plants to other forest species leading to rapid compositional recovery through the development of bush clumps (von Maltitz *et al* 1996). Mining and bulldozing do not allow persistence of any trees through the disturbance which would cause a potentially longer time to recovery.

♦ *How important are rare species and is complete recovery possible?*

The inclusion of rare species into the distance matrix greatly alters the outcome of this analysis (Figure 5). In most phytosociological studies, rare species are excluded from the analyses so as to maximise the integrity of community groupings and eliminate noise from hypothesised successional trajectories. This is also done as small sample size can create "pseudo-rares" from species that are actually abundant but were not sampled sufficiently. However, when assessing the progress of succession, especially from a conservation point of view, the rares should be of special concern within the community.

My data supports the hypothesis that succession is occurring towards a putative climax plot when regarding common species. However, when including rare species into the matrix, this successional trajectory deviates from this endpoint. It would appear that certain species are not able to recover after disturbance and this leads to a different successional endpoint from that of undisturbed climax forest. Whether or not the potential loss of rare species is regarded as important depends on the objectives of management.

♦ *The importance of functional types*

Regarding only species richness as a measure of successional progress is a mistake. Classification into functional groups is becoming increasingly important in terms of predicting ecosystem changes and response to climate change (Smith *et al* 1997). The same holds true for response to disturbance. It has been notoriously difficult to classify species into functional groups (Noble & Gitay 1996), although advances are being made in this field (Westoby 1998). With the establishment of a practical and generic method for functional type classification and subsequent identification of these functional types, it may become easier to predict the effects of disturbance and aid rehabilitation.

Conclusions

The finding of Mentis and Ellery (1994, 1998), that dunes were rehabilitating successfully after mining disturbance, needs to be viewed with circumspection. Their analysis of succession was based on the assumption that *Acacia karroo* woodland was a suitable target for rehabilitation and that once this target was achieved, succession to climax dune forest would be rapid. My study not only indicates that the successional timeframe from these woodlands to climax dune forest is, at best, extremely lengthy, but also that complete rehabilitation from *Acacia karroo* woodlands may not occur at all. It has been suggested that two separate successional pathways occur in the dune forest ecosystem (von Maltitz *et al* 1996), one involving *Acacia karroo* woodlands and the other based on bush clumps of forest species. It seems, therefore, that one cannot conclude that the establishment of *Acacia karroo* woodlands ensures certain succession to climax dune forest.

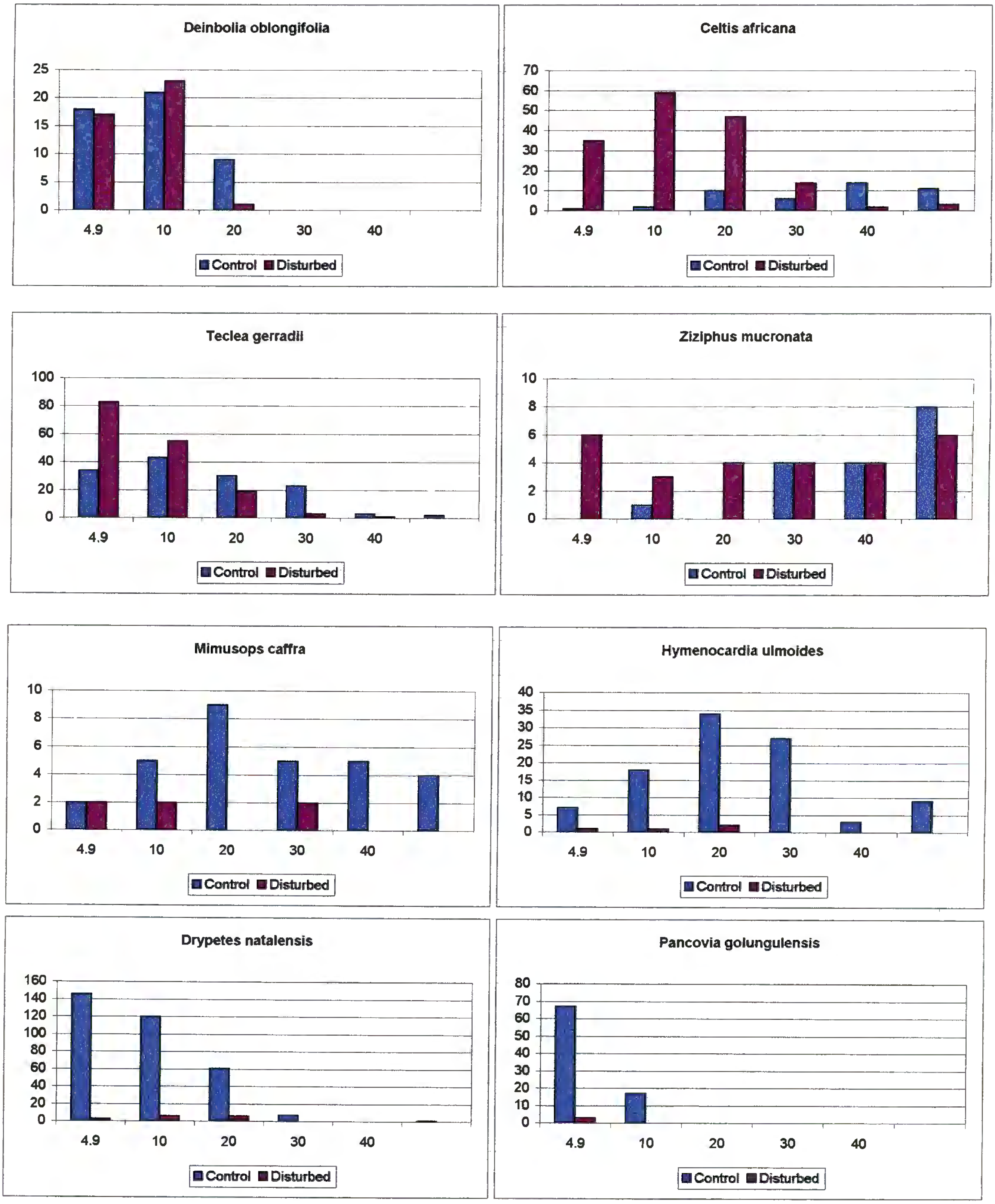
In addition to this, mining disturbance is more severe than that generated by swidden agriculture, as examined in this study. Sprouting species have a chance to persist as coppicing adults through swidden agriculture and can act as nurse plants to other forest species thus potentially generating bush clumps (von Maltitz *et al* 1996) and enhancing compositional recovery. Mining eliminates this possibility. The degree of soil disturbance is also vastly greater from mining disturbance and this could have substantial effects of the abundance, longevity and vigour of forest propagules and seed banks. It also seems unlikely that the fauna of the dunes would remain unaffected by mining and this could well have consequences for dispersal and colonisation, especially of late successional species (van Aarde *et al* 1996). With this in mind, estimates of recovery from mining disturbance should be more conservative than those presented for swidden agricultural disturbance in this study.

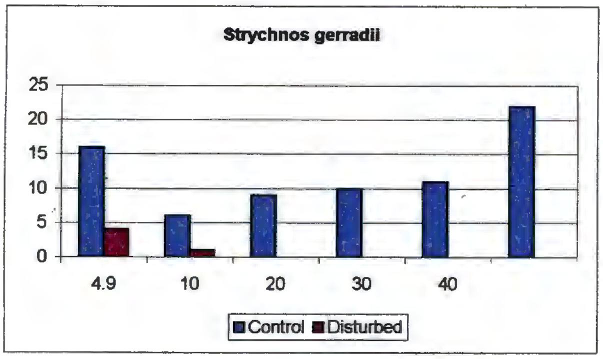
Thus, current dune rehabilitation measures advocate intervention in the form of stabilising and seeding dunes only in the immediate post-mining phase (Camp 1987). Recovery to *Acacia karroo* woodland and then to closed forest is supposed to happen without further intervention in a relatively short time frame, following Mentis and Ellery's (1994) model of succession. My study indicates that many species of forest trees (30% of all tree species) do not re-colonise *Acacia* woodlands. Even closed forest communities that showed signs of having emerged after lands were abandoned in past centuries lacked many species found in primary forest. The slow rate of recovery of forest by natural successional processes does not necessarily remove the possibility of effective forest rehabilitation after dune mining. Introduction of seedlings of relevant species and functional types unable to establish in disturbed sites may promote forest recovery. Without more active intervention in forest rehabilitation, dune mining in coastal dune forests will leave a legacy of dramatically depleted forests well into the next millennium.

Appendix 1: Species occurrence and abundance (summed DBH) per plot at Cape Vidal. Groupings were visually determined and interpreted to represent potential functional groups

plot	6	5	13	I	18	21	19	B	A	K	4	U	W	29	30	25	24	22	27	H	F	AD	Y	OF	M	26	N	C	Z	P	AA	S	AC	X	NC	AB	T	END	V
age category	88	88	88	88	88	88	88	75	75	75	75	75	75	60	60	60	60	60	60	fc	fc	fc	fc	fc	fc	fc	fc	fc	fc	tc	tc	tc	tc	tc	tc	tc	tc	tc	tc
Cler glab	13				5					4.3	15																												
Tric dreg									17																												
Cari wyli												3.5						3.5																				
Psyd obov		species limited to disturbance													13																								
Stry decu																	2.5																					
Roth fisc																		9.6																				
Acac karr	165	353	289	397	389	290	265	201	221	322	110	97	7.5	49	171	201	2.5	630	66				33													12			
Allo nata										2.5	16		30		58		24					9										2.5						
Vepr lanc			10	8				57		2.5	19			17																			13					
Clau anis												26		33	58	18	26	61				11					7.5						2.5		11			
Tric sond					early successional species										18		11		6															5					
Ficu nata	5										12																10												
Eryt berb											12	11	39	8.4	22	34	9.9	4.3			2.6	34	9			3.5	18					5	4.3		19			
Bauh torne				11								5			30		26					34			23														
Cant iner								29		2.5				5					8.6													16							
Ekeb cape						8.5				2.5									30																			
Pedd afri														7.1													5													
Ent? spp?															10												156														
Euge cape															2.5	disturbance generated late successionals													2.5													
Brid cath																		14										10													
Zant cape		ubiquitous species													9	71	47		43				34																		
Celt afri			88		15	28	6			17	27	117	315	90	160	128	518	187	70	20			72	170		108		168	343	9		52			70	136	217		
Zizi mucr	35	14				9.5	17		7	16		161	158	192	31		76	2.5	68			107	66			141		50	149					31		41	110		
Tecl gerr	2.5		2.5		18	9.1	7.8				78	51	54	16	172	75	218	80	186	2.6	34	198	250	140	2.5	88	2.5	36	146	42	5	152	81	225	5	36	119		42
Dios inha			2.5								15	61	77		32	15	13	66	7.5	51		79	49	49	2.5	19	2.5	32	35	13	19	44	7	6	50	71		13	38
Brac disc				4.3		mid successionals																				2.5			6						3.5			
Dios nata												29	5	14	99	99	78	2.5	332	51	68	124	123	59	3.5	89	10	169	120	36	79	331	27	74	72	123	206	7	187
Dein oblo						17					12	16	38	30	8.5	5	5	44	33	21		13	50		5	28	2.5	9.5	18	8	6	31	9	13	8.5	17	63		8.5
Mayt nemo					6.1						29					24							13	5									49		9	6.4	34	7	6.4		51
Ochn nata						7					6			58		119	2.5	5.7	46	178	45	64	7.5	35	27	17	8.5		208	2.5	29	227	121	90	35	29	267		263
Cord caff						5.6									2.5					44						2.5						40							
Dovy long							2.5					36							2.5			2.5	5	2.5	2.5			80		13	109			74	40			178	37
Catu spin												12				4.3			14	3.5		24		22	20		12	18		9.5	23	13	41	80	7.8				
Plec arma																2.5			10						2.5								7		5					7
Pave spp?														5	5	8.2		3.5	2.5				2.5	14	2.6	9.5	7				5		14	6	5	7			
Gard thur															15	2.5	29								10					20					21					60
Side iner											18	14	7.4			27	19	11	109						2.5		46	28		11	62		2.5	43	114	187			17
Eucl natn																46			5								36	8			13	42	74			63		10	111
Euge wood									29	4.3		late successionals							13			12	5		2.5	2.5		14	25		10	143	2.6		7.5		84		46
Xylo krau																5					3.5				2.6		31				15					5		11	
Inha henr												5		2.5					2.5			18					2.5	45			3.5				20	41	8	12	
Dryp nata											118								23		3.5	147		56	55	29	100	72	205	146	88	65	40	237	349	112	133	28	436
Olea wood																21					31			125	22		2.5	15							102	176	49	106	3.5	
Panc gofg											7.5									7.5			12	11		37	27	8	74	67	2.5	5	5	7.5	7.5	8	24	2.5
Hyme ulmo										32		3.5								217				496		414			287			195			23		336	
Stry gerr											11								8.5	68	194			39	16		18	318	39	190	387	37	315	155	44	250		82	77
Eucl racs															5	14	19							7			45	20		5	30		65	2.5	72	2.5	40		45
Mimu caff																15	43		5		17	3.5	36	43	35	96				17	144		49		127	60		60	10
Pave revo												5																					2.5			8.4	5		
Gard spp?														3.5	6																								40
Stry spin																				7																			
Anti veno																					18																		
Albi adia																					2.5																		
Cass pera																						2.5																	
Garc livi																								2.5															
Mayt cord																									13		22													
Scol zeyh																										143													
Mimu obov																				14							2.5					56							
Olea cape																								35											17					36
Bala maug																											35					137						73
Cass papi																					3.5															14				
Milk rube																												2.5			2.5					2.6			
Mani conc																					2.5									49			28		14			153	
Cari bisp																					2.5						4.3		3.5	3.5		5	5	2.5	3.5			
Cass aeth																				5				10	15			27	7		14		29	53	25	12		24	2.5
Mani disc																									114		46			104					15			44	
Eryt emar																					36				24		23			17			12	2.5			6	6	2.5
Tric cape																					7.9				24		45				6.1		8.5					2.6	
Tric dela																														3.5									
Euph inge																														47									
Krau flor																														2.5				8.4					6
Cola gree																															3.5								
Comm negl																						Climax species									52		10						
Rube spp?																																2.5					13		
Dios scab																																			8				
Cola nata																																						347	
Crab zimm																																						80	
Ture obtu																																						3.5	
Acok oppo																																							5

Appendix 2: Size-class distributions for the 23 most common species in Cape Vidal. Distributions are seperated into "Control" (categories FC & TC) and "Disturbed" (categories 88, 75 & 60). See text for detailed explanation of categories. Axes are % Frequency (y) and DBH size class (x).





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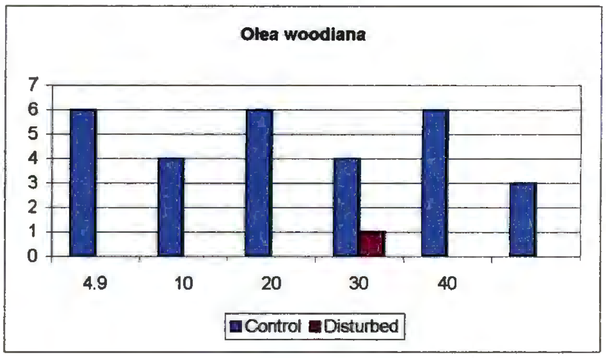

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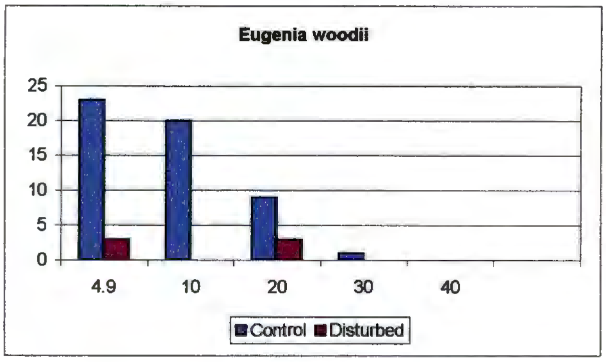

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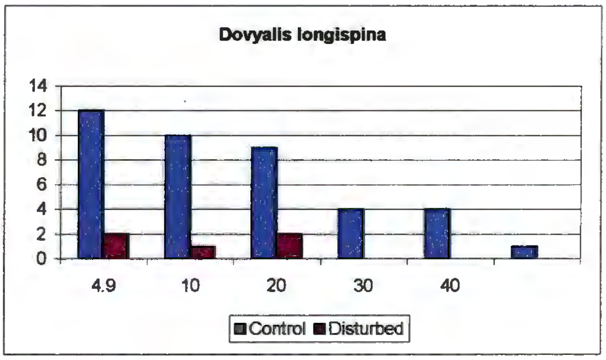

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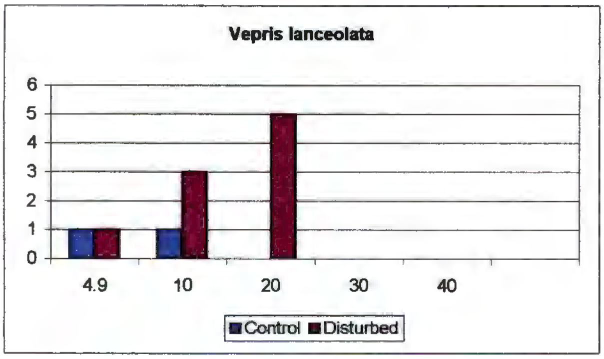

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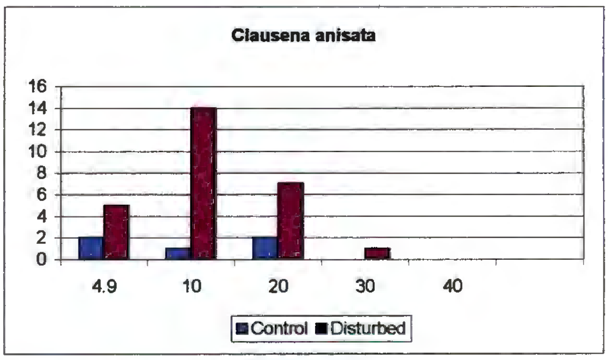

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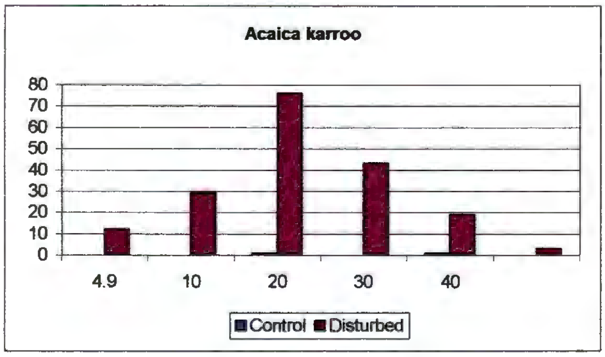

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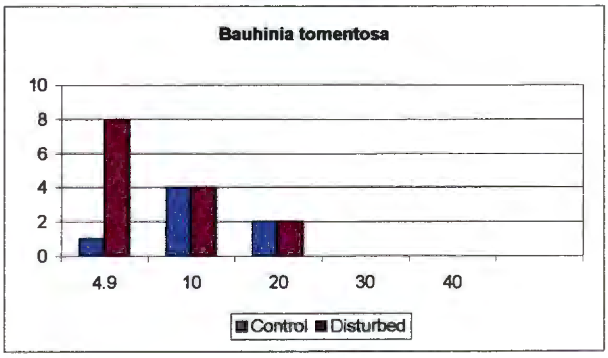
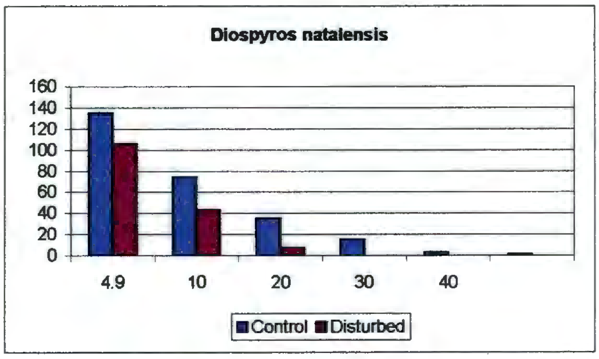


Bauhinia tomentosa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160
140
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80
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20
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4.9
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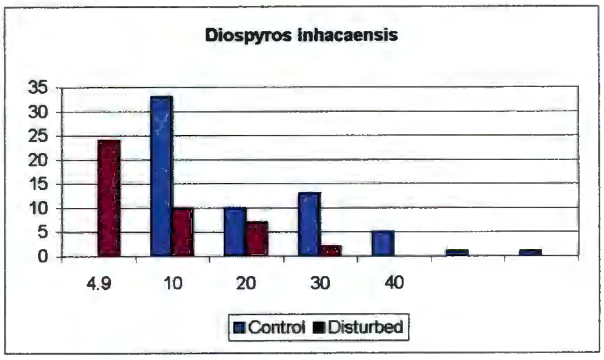
■ Control ■ Disturbed


Diospyros inhacaensis
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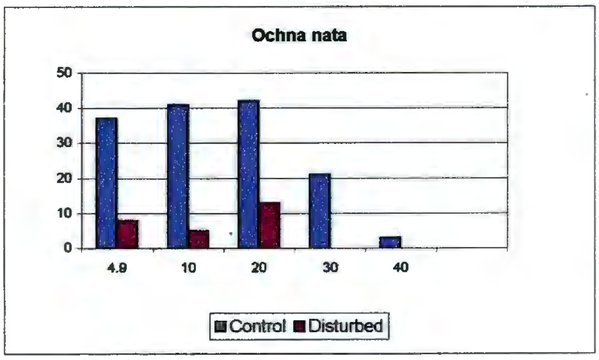
Ochna nata
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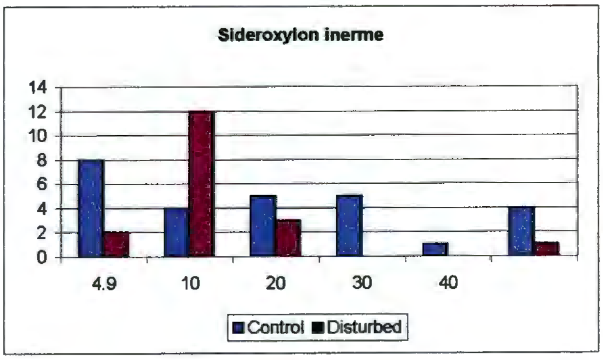
Sideroxylon inerme
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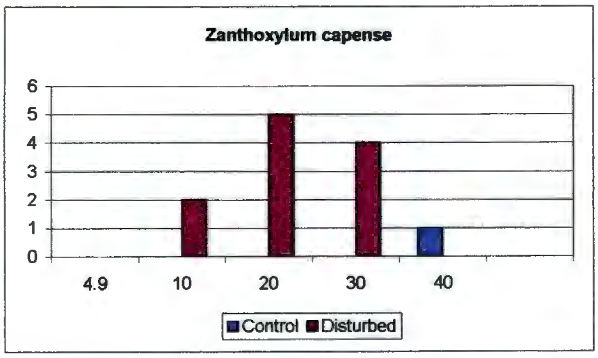
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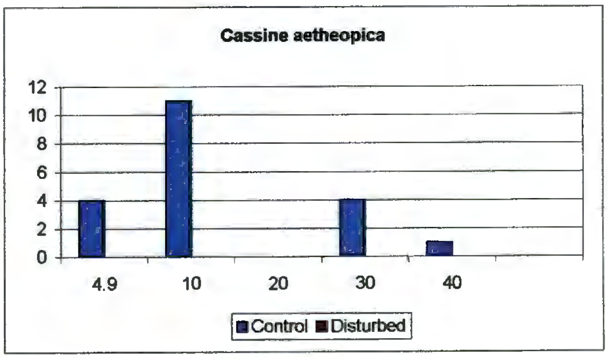
■ Control ■ Disturbed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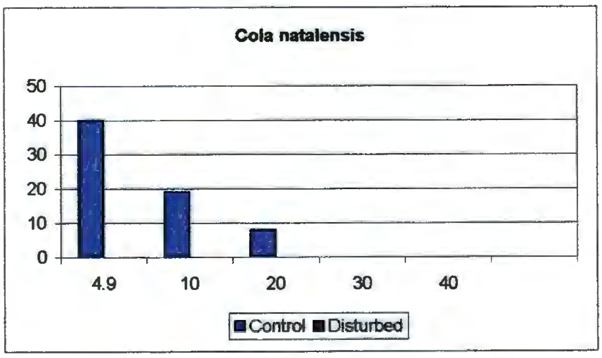
Cola natalensis
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■ Control ■ Disturbed

The evaluation of δ^{13}C isotopes of trees to determine past regeneration environments

4

Abstract

The effects of past regeneration environments and canopy position on δ^{13}C signals in leaf and wood tissue were examined. Leaves were collected from various canopy positions both inside and outside of closed forest and from gaps ranging in size from 75 to 829m^2. Trees of known life-histories were cored and wood was extracted from the outer rings and from the centre of the tree. Whole tissue was converted to holocellulose for isotopic analysis. An elevation of ~1$^{o}/_{oo}$ in δ^{13}C was associated with conversion to holocellulose. A regression of whole tissue vs. holocellulose produced R^2=0.84. A significant depression in δ^{13}C values of leaf tissue was observed in areas under a closed canopy. Leaves sampled from open areas, or from a well-lit canopy position, had more positive δ^{13}C values. In gaps, δ^{13}C of the leaves increased with increasing gap size. The difference between δ^{13}C of inner and outer wood within a tree was compared. Results indicate that it is possible to distinguish between differing life-histories with this technique. The data indicate that the regeneration environment confers a specific isotopic signal on a tree that can be detected later in its life-history. The method can be used to determine recruitment environments and should allow for grouping of species into accurate functional types. The potential uses of this ecological tool are important for restoration ecology and the management of forest ecosystems.

Keywords: canopy position, forest ecology, functional types, gaps, holocellulose, leaves, life-history, stable carbon isotopes, tree cores

Introduction

In tropical and sub-tropical forests, regeneration requirements of trees are central to understanding forest dynamics. Trees vary in their ability to establish in shade or in gaps of different sizes. Identification of gap requirements is not always possible from analysing the distribution of young trees. This is the case in Southern African sub-tropical forests, where one often sees a lack of regeneration of canopy trees (Midgley *et al* 1995a). In this study, I explore the use of stable carbon isotopes as a tool to determine the regeneration history of forest trees and its application in interpreting patch-scale dynamics in sub-tropical forests.

The $^{13}C/^{12}C$ ratio of plant tissue varies according to a variety of factors including carbon source, CO_2 concentration, O_2 concentration, light intensity and water use efficiency (Smith *et al* 1976, Ehleringer *et al* 1986, van der Merwe & Medina 1989, Farquhar *et al* 1989, Leavitt & Long 1991, Hanba *et al* 1997, Buchmann *et al* 1997). In forest ecosystems, three main factors governing variation in $\delta^{13}C$ are carbon source, CO_2 partial pressures internal and external to the leaf and water-use efficiency (Berry *et al* 1997). As carbon is cycled under the canopy, it becomes isotopically lighter (depleted in ^{13}C) than normal atmospheric CO_2 (Vogel 1978). Plants that photosynthesise below the canopy and utilise this sub-canopy CO_2 become isotopically light. Plants with their leaves in or above the canopy draw on CO_2 from the atmospheric pool, which is richer in ^{13}C, and thus differ from sub-canopy plants.

The ratio of the partial pressures of CO_2 internal and CO_2 atmospheric (c_i/c_a) is also responsible for the isotopic differences seen in forest communities. These differences can be strongly correlated to light intensity (Leavitt & Long 1991). As light intensity drops, so c_i/c_a increases, leading to a discrimination against the heavier isotope and an isotopically lighter plant. Water-use efficiency also contributes to c_i/c_a and works in a similar direction to that of light intensity. As water stress increases, so stomatal conductance decreases, enhancing water-use efficiency (Farquhar *et al* 1989, Schulz & Adams 1995). This causes a decrease in c_i/c_a which favours the heavier isotope and leads to an increased (less negative) $\delta^{13}C$ signal (Leavitt & Long 1991). Thus, in a forest community one can envision trees in well lit, open areas being isotopically heavier than shaded, sub-canopy trees due to the combined effects of carbon source, light intensity and water-use efficiency.

These factors lead to the pattern seen in forests of decreasing $\delta^{13}C$ down the canopy profile (Vogel 1978, Medina & Minchen 1980, Ehleringer *et al* 1986, van der Merwe & Medina 1989, Medina *et al* 1991). This effect has been shown with regards to canopy structure (Buchmann *et al* 1997), irradiance clines (Ehleringer *et al* 1986, Hanba *et al* 1997) and to a limited extent in cleared forest areas (van der Merwe & Medina 1989).

In this study, three lines of evidence were examined. Firstly, $\delta^{13}C$ signals from shaded and well-lit leaf tissue were examined. This tested for expected differences between $\delta^{13}C$ signals in leaves, in shaded or open positions during different stages in the life history of a tree. Secondly, the effects of gap size on $\delta^{13}C$ variation in leaf tissue were examined. Thirdly, the $\delta^{13}C$ signals of early and late wood in tree cores were examined in trees of various histories (shaded and open) to test for changing growing conditions during the life of a tree.

Materials and Methods

♦ *Sites*

Sampling was undertaken in mature forest and neighbouring open areas at Diepwalle Forest Reserve in Knysna and Hilltop Forest in Hluhluwe Game Reserve, South Africa (see Chapter 1, Figures 1 & 3 for maps). The study sites represent two very different forest types in South Africa, Diepwalle being temperate and Hilltop sub-tropical forest (Table 1). These forests have also been labelled fine-grained and coarse-grained respectively (Midgley *et al*

1990)(see Chapter 2), with reference to their regeneration patterns, characterised by shade-tolerant and shade-intolerant species respectively. For this study, six species were sampled: *Podocarpus latifolius*, *Afrocarpus falcatus* and *Olea capensis subsp. macrocarpa* (Diepwalle), *Protorhus longifolia*, *Chrysophyllum viridifolium* and *Celtis africana* (Hilltop). *P. latifolius*, *O. capensis macrocarpa* (Midgley *et al* 1990) and *C. viridifolium* (West, unpublished data) are described as shade-tolerant. *C. africana* is a facultative species (Everard *et al* 1995). *A. falcatus* (Midgley *et al* 1990) and *P. longifolia* (see Chapter 1) are described as shade-intolerant.

Table 1: Site characteristics and species sampled

Site name	Temperate forest Diepwalle Forest	Sub-tropical forest Hilltop Forest
Latitude	33°58' S	28°00' S
Longitude	23°05' E	31°43' E
Elevation	519 m a.s.l.	750m a.s.l.
Precipitation p.a.	1187 mm*	990 mm**
Canopy height	20-30 m	12-20 m
Species sampled	P. latifolius	P. longifolia
	A. falcatus	C. africana
	O. capensis macrocarpa	C. viridifolium

* (Midgley *et al* 1990)

** (Brooks & Macdonald 1983)

♦ *Sample collection*

Sampling took the form of leaf collection and tree coring during the period from March to July 1998.

Leaf samples

Leaves were collected from fully shaded juveniles and from the top of emergent canopy trees in the closed canopy forest. Outside of the forest, in open areas, comparable sampling was performed. Here the juveniles were fully lit, as were the mature trees. In all cases five trees were sampled from each category with *circa* 20 fully expanded new leaves being collected from all four cardinal points of the individual.

Leaf samples – Gaps

Thirty-one gaps of various sizes (75-829 m^2) were sampled for juvenile sun leaves. The gaps sampled were part of an experiment by the Department of Forestry. These gaps were cleared in the Diepwalle forest and in the Tsitsikamma Nature Reserve in 1994 and their exact size, position and contents were noted. Thus, it was possible to sample, with confidence, individuals that established after the creation of the gap.

Tree Cores

I first tested the values of $\delta^{13}C$ for identifying recruitment conditions by coring trees of known history. I then applied this method to trees of unknown regeneration history. For trees of known history, one group encompassed trees that recruited and grew up completely in the open, never having been shaded for any length of time. This group is hereafter referred to as "open". Trees for this category were selected from an arboretum (Temperate forest) where trees were planted in cleared forest areas.

The section of the arboretum used in this study was created in 1931, when 1.23ha of forest was cleared and monospecific stands of forest trees were planted in 0.28ha (2800m^2) areas (Lübbe & Geldenhuys 1991). These areas were repeatedly cleared of all other plants until 1969 (Lübbe & Geldenhuys 1991). The arboretum enabled the collection of genuine "open" samples of shade-tolerant species, effectively an artificial situation, which could then be contrasted against the natural scenario of recruitment under a closed canopy.

In the sub-tropical forest, "open" samples were obtained from expanding forest margins.

The "open" trees were compared with trees that recruited and grew up in the shade and subsequently emerged though the canopy to be fully lit. This category is hereafter referred to as "closed". As detailed records of individual trees in these forests are not available, trees were selected by choosing an individual presently in the canopy that was surrounded by larger individuals on all sides. It was then inferred that these older trees would have shaded the selected tree until it eventually reached the canopy. This assumption is valid for the shade-tolerant species. However, for shade-intolerant species, caution must be exercised when interpreting such "closed" situations as it is unlikely that these species would establish and grow in the shade. Nevertheless, for the sake of consistency these cores were labelled as "closed".

The method was then applied to trees of unknown regeneration history. These trees were suspected of recruiting in abandoned agricultural fields within the sub-tropical forest. These trees formed an apparent cohort of similar sized stems grouped on roughly a hectare of level ground within a much larger forest. Isotopic analysis of the soil carbon in these areas showed the existence of C_4 plants at some stage in the past (Chapter 5). This group is hereafter referred to as "field".

Sampling tree cores

Tree coring was performed with borers of two different sizes. The larger borer (24mm diameter) was used to remove the first two centimetres of wood from the tree, the bark and phloem being discarded. The borer was then drilled in further to stop one and a half centimetres short of the estimated centre of the tree. The large borer was then removed and a stainless steel pipe (20mm diameter) was inserted and held against the drilling face. Into this pipe the small borer (19mm diameter) was inserted, and three centimetres of wood removed. The wood was then pulled out through the pipe thereby preventing contamination with wood along the core. Wounds were then filled with dowel and sealed. Cores were taken as low on the trunk as possible.

Care was taken to accurately estimate the centre of the tree, but it can be assumed that this was not always achieved, hence the larger section of wood being taken from the centre of the tree in order to maximise the chance of striking the centre. This is an inherent weakness of the method but unfortunately seems unavoidable if a principle of non-destructive sampling must be adhered to, as was the case in this study.

- ***Sample analysis:***

Samples were oven dried at 70°C for 48 h and then ground in an electric mill to fine powder. Cellulose (holocellulose) was isolated from the samples using a toluene-ethanol solvent and acidified sodium chlorite solution (Leavitt & Danzer 1993). A 0.05mg subsample of this holocellulose was then combusted on-line in a VG Micromass 602E mass spectrometer and the isotopic ratio of the CO_2 was determined relative to the PDB standard [$\delta^{13}C = ((R_{sample} / R_{PDB})-1 \times 1000$, where R is the ratio of ^{13}C to ^{12}C].

- ***Data analyses and statistics:***

All statistical tests were performed with the software package "Statistica" (StatSoft 1996).

For leaf samples, differences between categories were tested by ANOVA. Homogeneity of variance was tested with a univariate test (Cochran, Hartley and Barlett) and ANOVA only run if no significant difference was obtained. Means were tested with the Tukey Honest significant difference test.

ANOVAs were also used to test for a significant difference between $\delta^{13}C$ signals from small (<400m^2) and large (>400m^2) gaps. Comparisons of $\delta^{13}C$ signals from closed forest, small gaps, large gaps and open areas were performed by ANOVA, where the variance was homogeneous. Where variance was not homogeneous (*O. capensis macrocarpa* and *P. latifolius*), the Kruskal-Wallace test was employed.

The means and standard deviation of the difference between $\delta^{13}C$ of inner and outer wood within a tree core were calculated and plotted. ANOVAs were performed between "open" and "closed" cores within the same species.

ANOVAs were also performed between "open" and "closed" cores within shade-tolerant and shade-intolerant categories. These categories were based on previous knowledge of these species' traits as mentioned earlier.

Results

♦ *Holocellulose versus whole tissue*

One hundred and twenty-four samples were run both as whole tissue and as holocellulose. Eighty-one of these samples were leaf tissue and forty-four were core wood. The overall regression of holocellulose plotted against whole tissue (Fig 1a) produced an R^2=0.84. For leaf tissue (Fig 1b) and core wood (Fig 1c) the R^2 was 0.74 and 0.84 respectively. For each case, the regression line was elevated by approximately $1^{o}/_{oo}$ from a one to one relationship. The residuals of each group of samples were examined for specific trends. There was no apparent trend of consistent elevation or depression away from the regression amongst any of the categories sampled.

♦ *Carbon isotope ratios of foliage*

Within a species, sun leaves from canopy trees in closed forest, leaves from similar sized trees located outside of the forest and leaves from juvenile trees located outside the forest all had similar $\delta^{13}C$ values (Figure 2). In all species, leaves from juvenile trees located under a closed forest canopy were consistently and significantly more negative than all other cases (Figure 2).

An increase in $\delta^{13}C$ is seen with increasing gap size (Figure 3). This increase is linear; however, one would expect an asymptotic relationship with $\delta^{13}C$ tending to a maximum at the larger gap sizes.

Fig 1a: **Regression of whole tissue vs. holocellulose, all leaf and core samples included (R^2=0.84 n=124)**

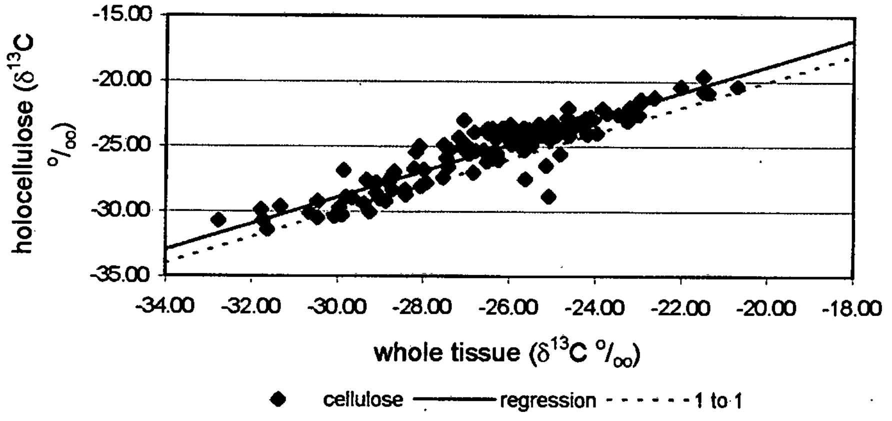


Fig 1b: **Regression of whole leaf tissue vs holocellulose (R^2=0.74 n=81)**

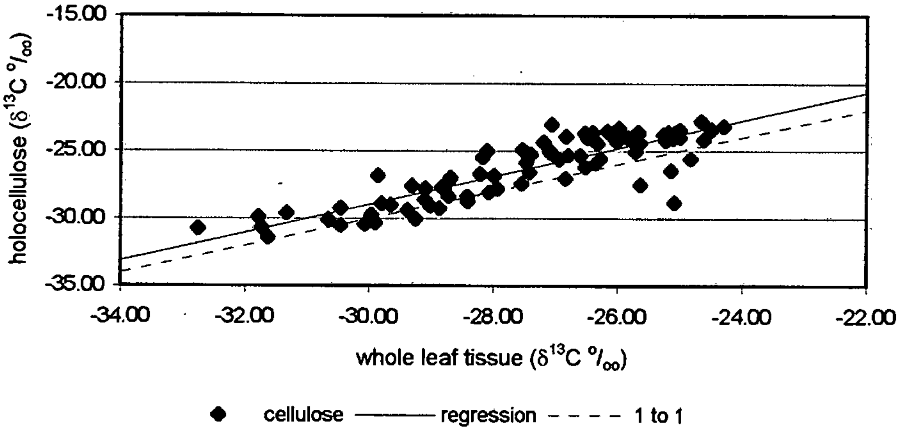


Fig 1c: **Regression of whole core wood vs. holocellulose (R^2=0.84 n=44)**

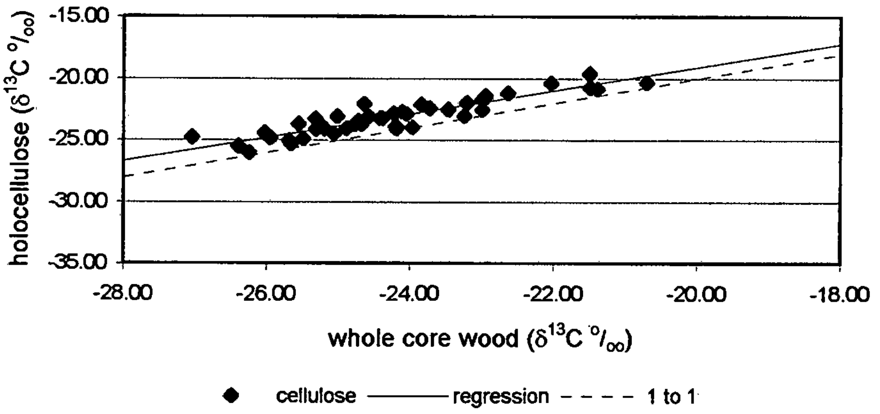
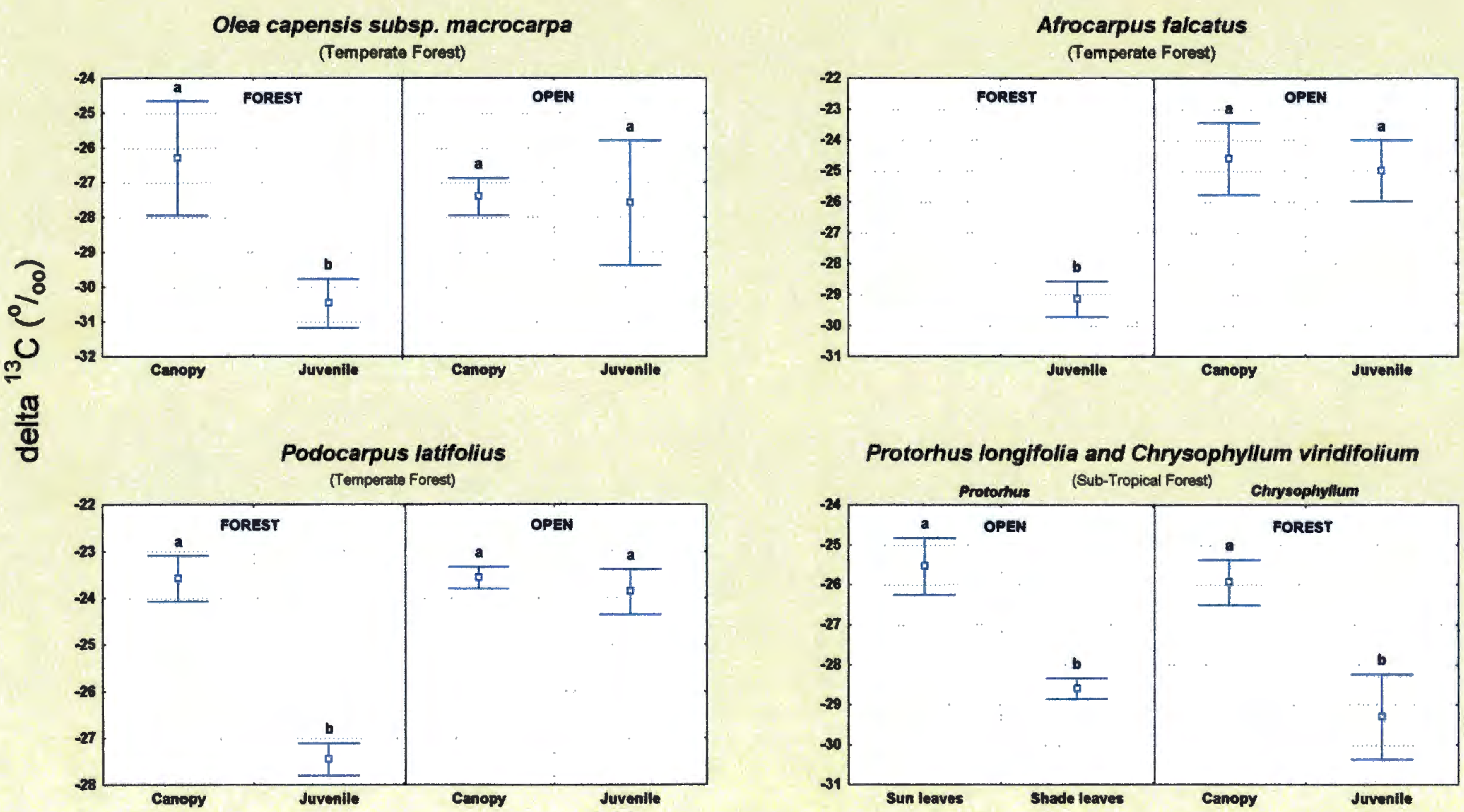


Figure 2: $\delta^{13}C$ values for holocellulose extracted from leaf tissue of showing the effect of habitat and canopy position in temperate and sub-tropical forests. "Forest" and "Open" indicate habitat. Where not specified, all "Open" and "Forest" canopy leaves were fully lit. All "Forest" juveniles were fully shaded. Letters indicate significantly different means (Tukey HSD test).



Figures $3_{a\text{-}c}$: $\delta^{13}C$ of leaf holocellulose vs gap area, in a temperate forest, for *Olea capensis subsp. macrocarpa* (3a), *Podocarpus latifolius* (3b) and *Afrocarpus falcatus* (3c). Individuals sampled were well lit and located in the centre of the gap. All individuals were of similar size (30cmH - 1mH).

Fig 3a: ***Olea capensis subsp. macrocarpa***
($R^2 = 0.47$)

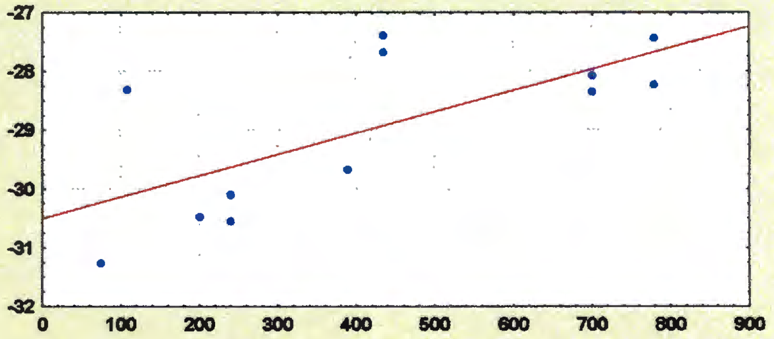


Fig 3b: ***Podocarpus latifolius***
($R^2 = 0.46$)

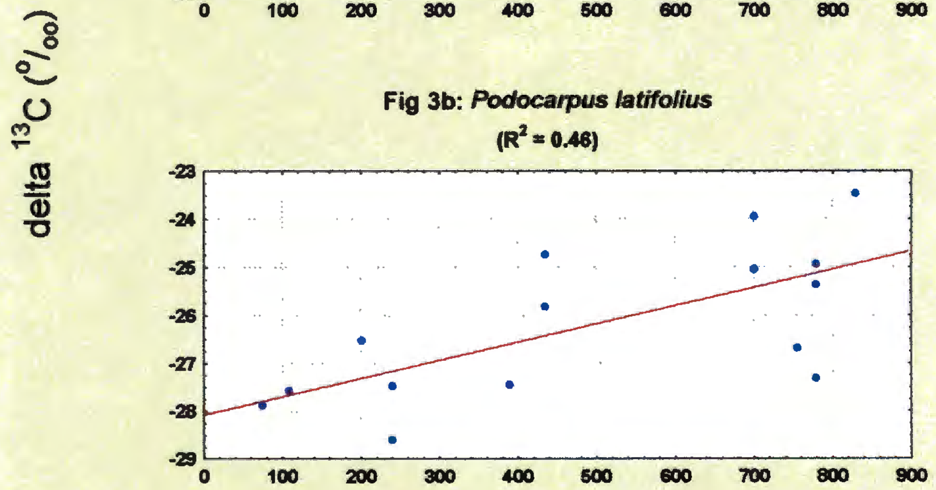
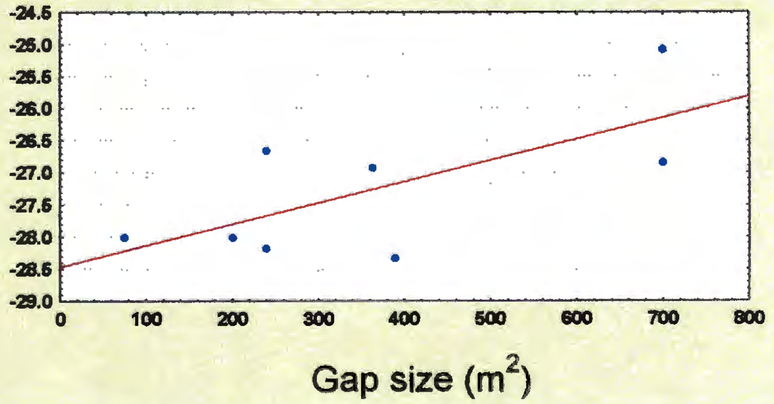


Fig 3c: ***Afrocarpus falcatus***
($R^2 = 0.48$)



I determined that 400m^2 was an appropriate area above and below which it was possible to distinguish between regeneration in large and small gaps. The difference between $\delta^{13}C$ values above and below 400m^2 was significant for all three species (*P. latifolius*: $F_{(1,13)}= 17.67$, $p < 0.0010$; *O. capensis macrocarpa*: $F_{(1,10)}= 24.52$, $p < 0.0006$; *A. falcatus*: $F_{(1,6)}= 6.58$, $p < 0.0426$). There is a trend of increasing $\delta^{13}C$ with increasing area of exposure to both light and atmospheric CO_2 (Figure 4). Large and small gaps generally induce a $\delta^{13}C$ closer to the open and closed environments respectively, than to each other (Figure 4, Table 3).

Table 3: Results of statistics performed on leaf data from closed forest, gaps and open areas. Within a species, different letters indicate significantly different means. (Kr-W = Kruskal-Wallace test)

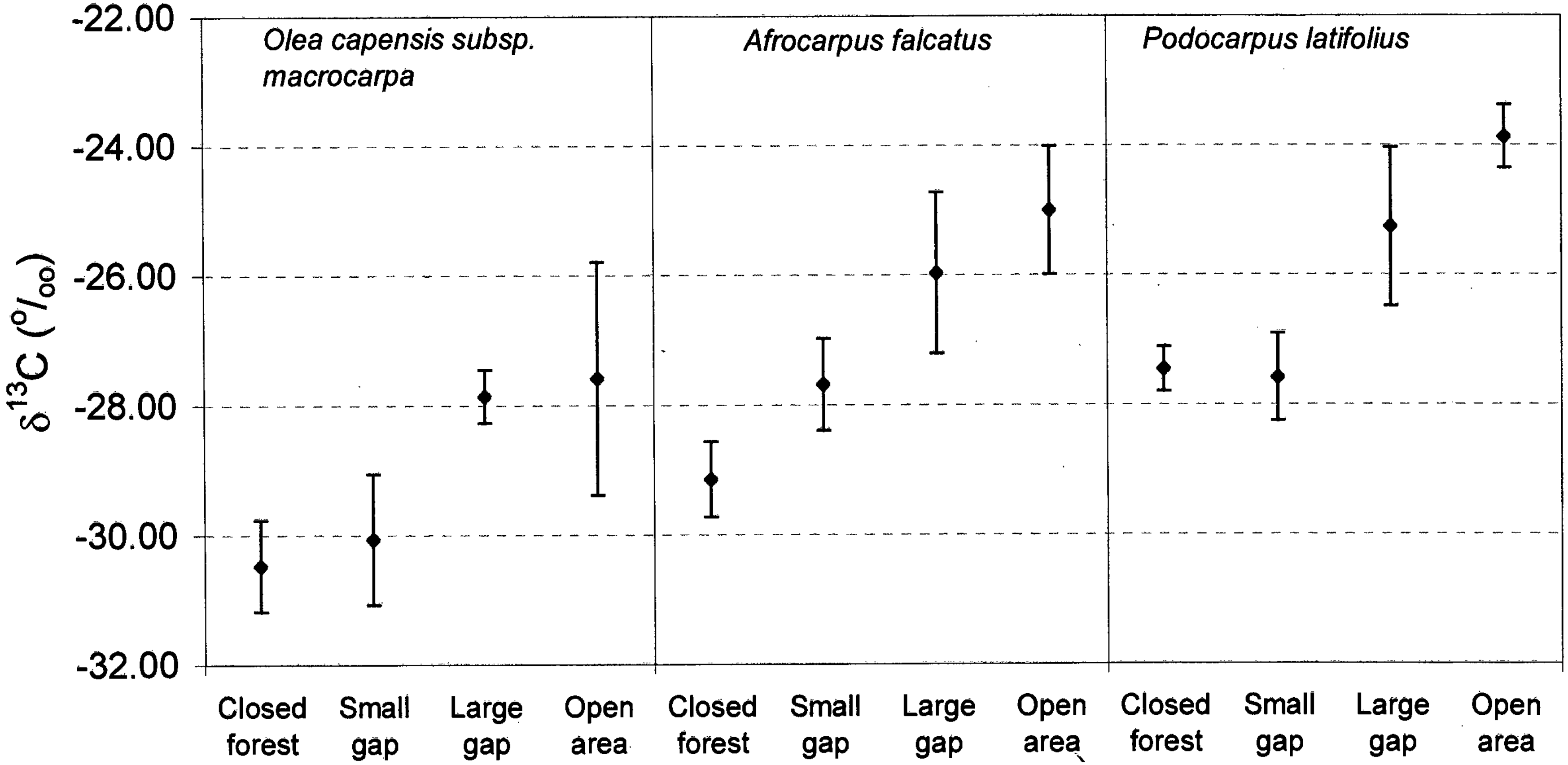
Species	Closed forest	Small gap	Large Gap	Open area	Test used
P. latifolius	a	a	b	b	Kr-W
O. capensis macrocarpa	a	a	b	b	Kr-W
A. falcatus	a	b	b/c	c	ANOVA

◆ *Carbon isotope ratios of tree cores*

I used the difference in $\delta^{13}C$ between inner wood and outer wood as a measure of ontogenetic change in growing conditions. Since shaded leaves have more negative $\delta^{13}C$ than exposed canopy leaves, plants that regenerate in the shade should show a more negative difference between inner and outer wood than plants that established in open or large gap environments.

The means of the differences between the $\delta^{13}C$ of inner and outer wood are shown in Figures 5 and 6. For the shade-tolerant species (Figure 5), namely *P. latifolius*, *O. capensis macrocarpa*, *C. africana* and *C. viridifolium*, there is a

Figure 4: Comparison of δ^{13}C of holocellulose from juvenile leaves from closed forest, small gaps (<400m^2), large gaps (>400m^2) and open areas



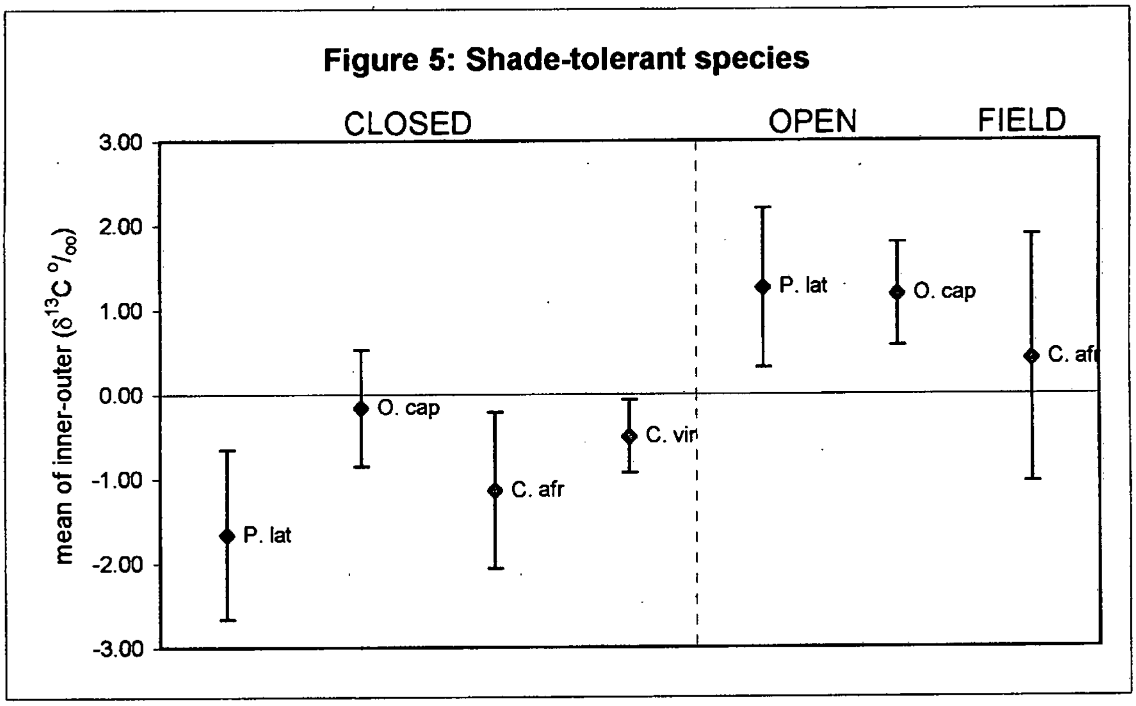
relatively clear distinction between "closed" trees, which have a negative differential, and "open" and "field" trees, which have a positive differential.

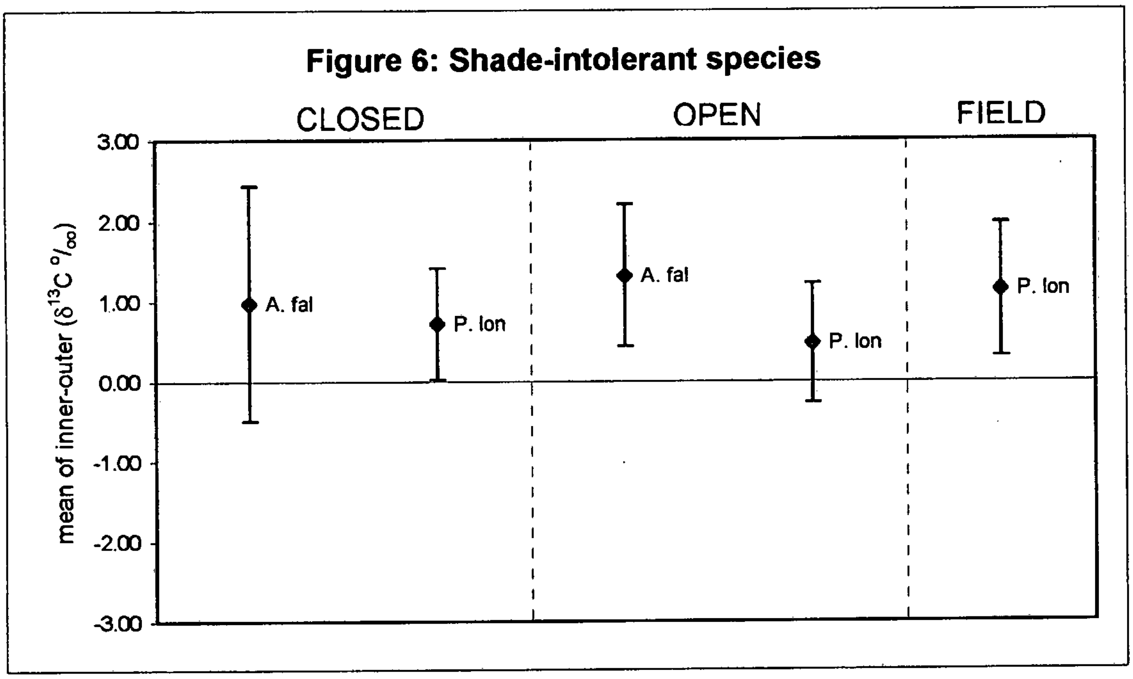
For the shade-intolerant species, *A. falcatus* and *P. longifolia*, all means are positive for "closed", "open" and "field" categories (Figure 6).

There was a significant difference between "open" and "closed" core categories for the shade-tolerant species *P. latifolius* ($F_{(1,8)}= 22.46$; $p < 0.0015$) and *O. capensis macrocarpa* ($F_{(1,8)}= 10.67$; $p < 0.0114$). There was no significant difference between the "open" and "closed" categories for the shade-intolerant species *A. falcatus* ($F_{(1,8)}= 0.56$; $p < 0.4738$) and *P. longifolia* ($F_{(1,8)}= 0.20$; $p < 0.6659$).

"Open" and "closed" categories were compared against each other for both the shade-tolerant species (Figure 5) and the shade-intolerant species (Figure 6). A significant difference was seen between "open" and "closed" for the shade-tolerant species ($F_{(1,26)}= 35.37$; $p < 0.0000$), but not for the shade-intolerant species ($F_{(1,18)}= 0.02$; $p < 0.8927$).

Figures 5 - 6: Means of the differences between $\delta^{13}C$ of inner wood – $\delta^{13}C$ of outer wood for canopy trees. Groups on the x-axis refer to the recruitment environment of the tree. "Closed" indicates recruitment beneath a canopy, "Open" indicates recruitment in open areas and "Field" indicates recruitment in abandoned fields. Shade-tolerant species, P. latifolius, O. capensis macrocarpa, C. africana and C. viridifolium. Shade-intolerant species, A. falcatus and P. longifolia.





Discussion

My results indicate that it is possible to determine past regeneration environments of mature trees by using a simple isotopic test. The method is based upon the fractionation of ^{13}C due to changes in source CO_2, light intensity and water-use efficiency.

◆ *Cellulose versus whole tissue for isotopic study*

This study examines small changes in $\delta^{13}C$ during the individual's life-history, a signal that is contained in the cellulose laid down at that time. Whole tissue contains mobile compounds, such as lipids, starch and sugars, that have characteristically different $\delta^{13}C$ signals (Benner *et al* 1987, Boutton 1996) and can thus obscure the cellulose signal. I was interested to know if, practically, extraction of cellulose (holocellulose) was a necessary procedure for this study. The regressions of whole tissue to holocellulose (Figures 1a-c) showed a good fit, and a positive shift of $1^{0}/_{00}$ for whole tissue would calibrate it to the holocellulose regression. However, there is no pattern in the dispersion of residuals away from the regression and this prohibits the use of whole tissue $\delta^{13}C$ especially if sample size per category is low, as was the case for this study. I concluded that extraction of holocellulose from whole tissue is required for accurate results in studies with low sample size examining small $\delta^{13}C$ shifts.

◆ *Testing the hypothesis: leaf tissue*

The study on leaf tissue served to test for the effects of the factors outlined above on $\delta^{13}C$ signals. The results supported the *a priori* hypothesis that the combined effects of shading, water-use efficiency and CO_2 recycling under a canopy should produce a more negative isotopic signal. All "closed" juveniles had a significantly more negative $\delta^{13}C$ signal than did juveniles in gaps or in open areas (Figures 2, 4). This was the case in both temperate and subtropical forests.

The results also showed a distinct difference between leaf isotope composition in small gaps ($<400m^2$) and large gaps ($>400m^2$) (Figure 3). Small gaps and large gaps were found to be more similar to closed forest and open areas respectively, than to each other (Figure 4), a result that concurs with work done in Puerto Rico (Medina *et al* 1991). These results indicate a gradient of increasing $\delta^{13}C$ with increasing gap size. More importantly, they indicate the relative lack of importance of small gaps in affecting the $\delta^{13}C$ signal of the vegetation. Average gap sizes reported in other forests are generally below $400m^2$ (Midgley *et al* 1995, Kneeshaw & Bergeron 1998). In Hilltop forest, of twenty gaps sampled, average gap size was $265m^2$ (see Chapter 2). Thus it could be that most treefall-generated forest gaps are relatively inconsequential in terms of significantly influencing the $\delta^{13}C$ of the plant. This has important consequences for the interpretation of $\delta^{13}C$ signals in tree cores. Trees that recruit and grow up through a canopy should maintain a low $\delta^{13}C$ regardless of whether they are periodically lit by the small gaps that often puncture a continuous canopy. Thus, any positive deviation of $\delta^{13}C$ within a tree core cannot be linked to release via small gaps in a closed forest community.

I deduce, from the leaf data, that the analysis of tree cores is feasible and should contain meaningful information regarding past regeneration environments.

- ***Tree cores as records of past regeneration environments***

Despite the inherent difficulties of sampling and interpreting $\delta^{13}C$ signals of tree cores, it is possible to derive useful ecological data from them. Using the method developed in this study, it is possible to distinguish between different life-histories of individual trees and, in doing so, to determine their past regeneration environments and hence their current regeneration requirements.

Tree cores were analysed by subtracting the $\delta^{13}C$ value of the oldest (outer) wood from that of the youngest (inner) wood. This creates a relative measure, or differential, per tree can then be compared with other individuals. I discovered that trees that had recruited in the shade, beneath a closed canopy, and then subsequently reached the canopy ("closed") displayed a negative differential (Figure 5). Trees that recruited in open environments that were separate from the forest ("open") displayed a positive differential (Figures 5-6).

At first sight, the values for "closed" shade-intolerant trees (Figure 6) seem to be an exception to the rule. These trees were categorised as "closed" because they were smaller canopy individuals surrounded by larger canopy individuals. However, being shade-intolerant they are incapable of recruiting and actively growing in the shade. These are therefore examples of trees that recruited in similar situations to their "open" neighbours, but have subsequently been out-competed. This history is known to be the case for *A. falcatus* in the Diepwalle Arboretum. I regard the fact that these "closed" trees return the same differential as their "open" counterparts as a vindication of the method.

The negative differential seen in trees recruiting below the canopy conforms to the patterns seen in the leaf data. The youngest wood has a more negative $\delta^{13}C$ signal as it is a product of sub-canopy photosynthesis. The oldest wood is primarily a product of full sun photosynthesis by canopy leaves, hence the more positive signal.

The positive differential of the "open" trees denotes that the oldest wood had a more negative signal than the youngest wood. As the source CO_2 is constant in this case, this indicates that the tree experiences a greater degree of shading and/or decreased water-use efficiency with age. Both of these factors are possible as self-shading of leaves and reduced water stress are likely to occur in mature trees. In fact, seedlings recruiting in open environments are likely to be highly water stressed and experience almost no shading, hence the more positive $\delta^{13}C$ signal in the youngest wood.

◆ *Application: Regeneration in a southern African sub-tropical forest*

I investigated the regeneration habitats of canopy dominants in Hilltop Forest, Hluhluwe Game Reserve. Sub-canopy recruitment and gap replacement do not occur in these forests (see Chapter 2). Large-scale disturbance is suspected to trigger recruitment in these forests. However, large-scale disturbance does not occur naturally in the forest, as blow downs, elephants and fire do not play a role.

Using the method developed in this study, I showed that large-scale disturbance is crucial for the regeneration of these canopy dominants. An analysis of tree cores from within the forest showed a prevalence of positive differentials, indicating recruitment in open areas or large gaps (Figures 5, 6). These cores were labelled “field” as they came from areas suspected of being old agricultural lands within the forest.

I hypothesised that swidden agriculture could have provided this large-scale disturbance. The removal of farmers over 100 years ago, when the reserve was proclaimed, could have led to the stagnation in regeneration seen today.

Conclusions

The isotopic test for determining past regeneration environments developed in this study is effective. It is possible to distinguish between shade-tolerant and shade-intolerant species as well as the life-histories and past regeneration environments of individual trees. More precise sampling of the tree cores would enhance the accuracy of this method.

Applications for this method are primarily in forest dynamics and restoration ecology. The method is useful for reconstructing past environments and determining regeneration requirements of species and could be applied anywhere were stochastic or infrequent regeneration occurs. It can also be used as a technique to determine degree of shade-tolerance of individual trees and, from this, to classify species into functional types. Possibly, this method could be extended and used to distinguish between sprouting and seeding forest trees.

5

Investigating historic slash-and-burn agriculture in two KwaZulu-Natal forests using $\delta^{13}C$ from soil organic matter: Can one only detect landscape-scale disturbance?

Abstract

It has been hypothesised that many KwaZulu-Natal forests have been impacted by slash-and-burn agriculture over the last 1600 years. I tested whether stable carbon isotopes in soil organic matter (SOM) could be used to detect these impacts. Twenty-four soil profiles in two different forests were sampled and examined for $\delta^{13}C$ changes with depth. The forests represented sites of known disturbance (Cape Vidal) and of inferred disturbance (Hluhluwe). The results indicated that slash-and-burn agriculture could not be satisfactorily detected by this isotopic technique. Instead, the results showed a large-scale shift, at Hluhluwe, from past vegetation dominated by C_4 species to present C_3 vegetation. This adds weight to the theory that KwaZulu-Natal grasslands are in fact older than originally thought.

Keywords: C4-C3 vegetation shift, human disturbance, shifting agriculture, stable carbon isotopes, vegetation change

Introduction

Worldwide, rural people subsist and subsisted by slash-and-burn farming in woodlands and forests (Dejong 1997, Holscher *et al* 1997, Rawat 1997, Raman *et al* 1998, Lindbladh & Bradshaw 1998, Panda 1999). In southern Africa, this form of farming has been prevalent for roughly 1600 years (Feely 1980, Hall 1984) and still continues today. Slash-and-burn farming involves the felling and burning of patches of established vegetation, often woodland or forest. The ash from the burnt wood provides the nutrients necessary to enable successful crop growth for a few years, after which the field is abandoned. The farmers then move on to a new patch, leaving the abandoned field to recover its natural vegetation. After several field cycles have been completed, farmers may return to previously farmed lands that have recovered sufficiently to ensure productivity for another crop interval of several years.

All traditional African cereals exhibit the C_4 photosynthetic pathway (Hattersley & Watson 1992, de Wet 1992). Thus this shift from forest vegetation to croplands involves a shift from C_3 (forest) to C_4 (crops) vegetation. Could one use soil organic matter (SOM) isotopic techniques to identify these old fields and show human-scale disturbance?

♦ *Soil organic matter (SOM) carbon isotopic studies*

C_3 and C_4 plants have different ratios of ^{13}C to ^{12}C and produce very different isotopic signatures (O'Leary 1993). The mean $\delta^{13}C$ for C_3 plants is –27‰ and for C_4 plants is –13‰, with considerable variation about the mean (O'Leary 1988, Boutton 1991). The $\delta^{13}C$ signal of the vegetation is conveyed to the SOM with decay (Guillet *et al* 1988, Stock *et al* 1993, Wedin *et al* 1995, Boutton 1996) and may persist for decades to millennia (Balesdent *et al* 1988, Cerling *et al* 1997). Under stable conditions the $\delta^{13}C$ of the surface SOM will be in equilibrium with the vegetation it is derived from (Bird & Pousai 1997). Older SOM, lower down the soil profile, should also reflect the $\delta^{13}C$ signature of the parent vegetation (Witt 1997). Thus, under conditions of vegetation change, the $\delta^{13}C$ of the soil profile should offer a record of the dominant vegetation type through time. However, enrichment of $\delta^{13}C$ of SOM does occur with time (Mariotti & Balesdent 1990, Desjardins *et al* 1996). This is attributed to recent changes in the ^{13}C content of atmospheric CO_2 (February & van der Merwe 1992, Bird *et al* 1996), the differential preservation of SOM components with different isotopic signals (Le Roux *et al* 1996, Desjardins *et al* 1996, Boutton 1996) and isotope fractionation during decomposition and mineralization (Deines 1980, Balesdent *et al* 1988, Becker-Heidmann & Scharpenseel 1992, Mariotti & Peterschmitt 1994). Nevertheless, this technique has been successfully used to document vegetation changes in a variety of locations world-wide (DeLaune 1986, Guillet *et al* 1988, Ambrose & Sikes 1991, Stock *et al* 1993, McPherson *et al* 1993, Bond *et al* 1994, Mariotti & Peterschmitt 1994, Pessenda *et al* 1996, Desjardins *et al* 1996, Connin *et al* 1997).

♦ *Aims of this study*

The SOM isotopic technique has been used successfully to show large-scale vegetation changes. I was interested to see if it could be applied to short-term human-generated changes such as those created by slash-and-burn agriculture. The ability to identify human-generated C_4 signals within forest communities would allow detailed analysis and reconstruction of past anthropogenic disturbance regimes and regeneration conditions.

Methods

♦ *Study sites and sampling strategy*

Two sites were sampled in this study. The first site was located in the coastal dune forest from Cape Vidal, KwaZulu-Natal (28°07'S, 32°33'E) for several kilometres Northwards (see Chapter 1, Figure 2 for map). This area forms part of the Zululand coastal dune cordon. Average rainfall is 1300mm per annum (von Maltitz *et al* 1996). These dunes rank as the second highest vegetated dunes in Southern Africa (Tinley 1985) and reach an altitude of 166m above sea level within a kilometre from the shoreline. The soil consists of sand with a humic layer on the surface. Due to the high productivity of the system, organic matter turnover is fast and bioturbation is significant.

Cape Vidal is an area of known historic anthropogenic impacts. Aerial photography shows that the dune slacks, found between the fore dune and hind dune, were favoured for agriculture. It seems likely that these areas could have undergone roughly 1600 years of slash-and-burn agriculture (Hall 1981).

By examining aerial photographs from 1937 to 1996, abandoned fields of various ages since disturbance were located. I sampled three soil profiles in each of 5 disturbance categories. These categories were: 1) last disturbed in 1988, 2) last farmed in 1975, 3) last farmed in 1960, 4) undisturbed in photographic record (since 1937), 5) undisturbed in photographic record and topographically isolated from other farmed sites. This gave sites with a range of ages from 9 years since farming to those potentially never farmed.

The second site sampled was Hilltop Forest in Hluhluwe-Umfolozi Nature Reserve, KwaZulu-Natal (28°00'S; 31°43'E) (see Chapter 1, Figure 1 for map). The reserve covers 900 km^2 with altitude ranging from 60m to 750m above sea level (Whately & Porter 1983). Topography is hilly, with flat areas confined to the floodplains of the larger rivers (Brooks & Macdonald 1983). The forest communities are found to the northwest of the reserve, restricted to high rainfall hillsides or riverine belts (Brooks & Macdonald 1983). Rainfall occurs mainly between October and March with an annual mean of 990 mm (50 years) and a 27.4% coefficient of variation (Brooks & Macdonald 1983). Soils are fine textured clays and evidence of bioturbation is low.

There is no present evidence of human disturbance in Hilltop Forest. However, indirect evidence of the role of large-scale clumping indicates that humans may well have played a role in disturbing this forest (see Chapter 2). Evidence of an ancient iron-smelting site not more than 7 kilometres from the forest (Hall 1980) supports this. Soil samples were taken from three flat areas within the forest reserve where clump-analysis indicated the potential of synchronous tree recruitment over large areas and hence human cultivation (see Chapters 2, 4). Samples were also taken from three steeply sloped areas within the forest reserve in order to act as controls. These areas were chosen as they were too steep to have been used for cultivation.

In neighbouring farmlands adjacent to the reserve, three current slash-and-burn fields were sampled. The first field was relatively new and had only been cultivated within the last two growing seasons with a mixed crop of predominantly beans (C_3) and maize (C_4). This field had been hollowed out of the forest and was surrounded by mature forest trees on all sides. The other two fields were older, inhabitants merely indicated that they had been using these fields for some time. These fields had had a pure maize crop (C_4). Both fields were surrounded by other fields and were relatively distant from the nearest forest patches.

♦ *Soil collection*

Soil was collected down a smooth profile of a soil pit. Soil pits were used in order to minimise the chance of sampling areas that had undergone recent bioturbation. Leaf litter was collected from directly above the soil pit prior to digging. Roughly 800 grams of soil was collected at each depth. In Cape Vidal, soil pits were dug to a depth of 90cm. Soil was sampled from depths of 0-10cm, 25-35cm, 50-60cm and 75-85cm. In Hluhluwe, samples were collected from soil pits that were dug to a depth of 55cm (in the forest) and 45cm (in adjacent fields). Soil was sampled from depths of 0-10cm, 15-25cm, 30-40cm and 45-55cm in the forest and from depths of 0-5cm, 10-15cm, 20-25cm, 30-35cm and 40-45cm in the adjacent fields.

♦ *Analytical procedures*

Preparation of samples followed procedures set out in previous studies of soil organic matter (Bond *et al* 1994, Pessenda *et al* 1996, Witt 1997). Surface litter samples were oven dried at 80°C and then ground in an electric mill to a fine powder. Soils were air-dried and sieved through a 2mm sieve in order to remove stones and loose organic matter. From every sample, a 200g subsample was taken and ground in a mortar and pestle. Ten grams were then taken from this 200g subsample and treated with 10% HCl (10M) overnight, in order to dissolve away any carbonates. During this procedure, loose organic matter was also floated off. The samples were then rinsed and centrifuged 5 times to remove the acid and then dried at 105°C overnight. Loose aggregates formed in the drying process were broken up. Depending on organic content, between 0.04 and 0.10mg of sample was loaded into a VG Micromass 602E mass spectrometer and combusted online. Isotopic ratios are expressed relative to the Pee Dee Belemnite Standard [$\delta^{13}C = ((R_{sample} / R_{PDB})-1 \times 1000$, where R is the ratio of ^{13}C to ^{12}C].

Results

- ***Cape Vidal***

All profiles indicated predominately C_3 vegetation with mean SOM $\delta^{13}C$ values all falling between –26.6‰ and –23.2‰ (Table 1). The SOM $\delta^{13}C$ values of the surface litter indicate that the current vegetation is purely C_3 (Table 1).

There do not seem to be any distinct patterns or trends of enrichment specific to any disturbance group (Figure 1). Instead, all profiles show a general trend of enrichment with depth, ranging from 3.4‰ in the most recently disturbed sites to 1.6‰ in the topographically isolated sites (Table 1). There is a greater degree of variation in $\delta^{13}C$ values at the 25-35cm depth than at any other depth for all sites, with the exception of the TC profiles where the greatest variation occurs at the next deepest level (Figure 1, standard deviations shown in Table 1).

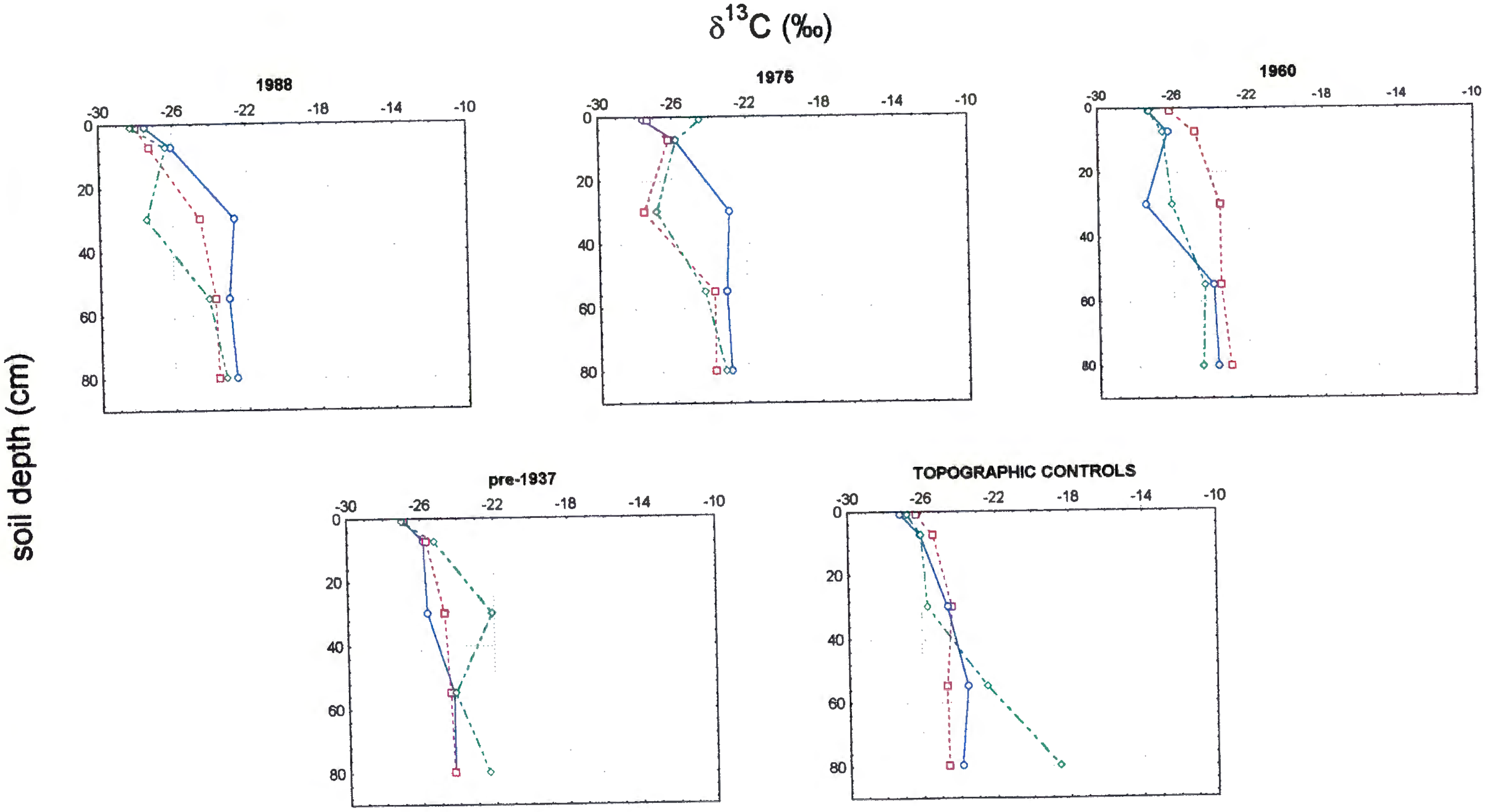


Fig.1: Profile of $\delta^{13}C$ of soil organic matter from Cape Vidal sites. Individual graphs represent replicates in different disturbance categories

Table 1: Mean (± stdev.) of $\delta^{13}C$ values (‰) of soil organic matter at each depth down the profiles from Cape Vidal. Sites are labelled by date since last disturbance. Topographic controls (TC) are interpreted as essentially undisturbed sites. Overall $\delta^{13}C$-shift (‰) from shallowest to deepest soil level is shown.

depth	1988 (n=3)	1975 (n=3)	1960 (n=3)	pre-1937 (n=3)	TC (n=3)
surface litter	-27.9 ± 0.4	-26.5 ± 1.7	-26.9 ± 0.6	-26.9 ± 0.1	-26.7 ± 0.4
0-10cm	-26.6 ± 0.6	-25.9 ± 0.2	-25.9 ± 0.9	-25.6 ± 0.3	-25.8 ± 0.4
25-35cm	-24.9 ± 2.4	-25.8 ± 2.5	-25.7 ± 2.0	-24.2 ± 1.8	-24.9 ± 0.7
50-60cm	-23.6 ± 0.6	-23.7 ± 0.6	-23.9 ± 0.4	-24.3 ± 0.2	-23.6 ± 1.1
75-85cm	-23.2 ± 0.5	-23.3 ± 0.4	-23.7 ± 0.8	-23.7 ± 1.1	-24.3 ± 0.5
$\delta^{13}C$ shift down soil profile	3.4	2.6	2.1	1.9	1.6

In all the above analyses, an outlier was excluded from the 75-85cm depth in the TC profiles. This outlier can be seen in Figure 1 ($\delta^{13}C$ = 18.6‰). This datum was the highest $\delta^{13}C$ value recorded at Cape Vidal and occurred in an exclusively C_3 forest site that had never been exploited agriculturally. Thus, this datum was excluded from the analyses as it was interpreted as being erroneous, possibly through contamination.

♦ *Hluhluwe*

Forest

There is no noticeable difference between the profiles of the two forest categories, namely clumps and slopes (Figure 2). The surface litter for all profiles is indicative of C_3 vegetation. The $\delta^{13}C$ of the top 22.5cm of SOM ranges between 24.1‰ and 22.7‰. The $\delta^{13}C$ of SOM below that ranges from 19.1‰ to 14.8‰. Differences from the top of the soil profile to the bottom are 7.2‰ and 9.3‰ (Table 2).

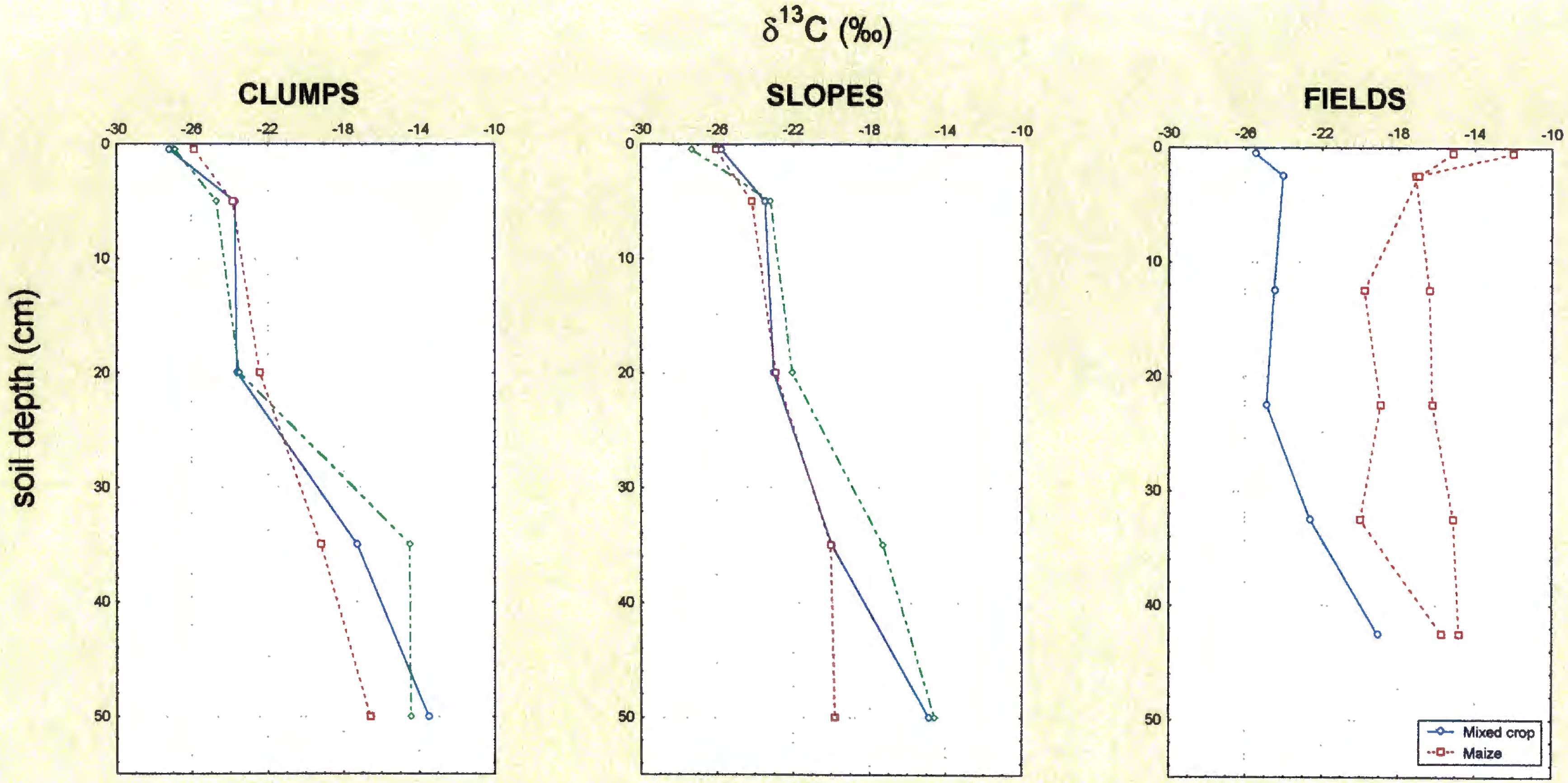


Fig.2: Profiles of $\delta^{13}C$ of soil organic matter from Hilltop Forest, Hluhluwe Nature Reserve, and from neighbouring crop fields. Individual graphs represent replicates in the different categories.

Table 2: Mean (± stdev.) of $\delta^{13}C$ values (‰) of soil organic matter at each depth down the profiles from Hilltop Forest, Hluhluwe Nature Reserve. "Clumps" represent areas of potential human cultivation. "Slopes" represent undisturbed forest areas. Overall $\delta^{13}C$-shift (‰) from shallowest to deepest soil level is shown.

depth	Clumps (n=3)	Slopes (n=3)
surface litter	-26.7 ± 0.7	-26.4 ± 0.8
0-10cm	-24.1 ± 0.5	-23.6 ± 0.5
15-25cm	-23.2 ± 0.7	-22.7 ± 0.5
30-40cm	-17.0 ± 2.4	-19.1 ± 1.6
45-55cm	-14.8 ± 1.6	-16.4 ± 2.9
$\delta^{13}C$ shift down the soil profile	9.3	7.2

Fields

The profile of the mixed crop field is similar to those in the forest (Figure 2). The $\delta^{13}C$ value of the surface litter of this field is –25.5‰. The $\delta^{13}C$ of SOM only becomes greater than –20‰ below 40cm soil depth. The total shift from the top of the profile to the bottom is 5.0‰ (Table 3).

The profiles of the two maize fields are distinct from all profiles recorded. Both profiles decrease in $\delta^{13}C$ from the enriched surface litter and have a very similar first SOM layer (Figure 2). One site then remains relatively constant down the profile, showing only slight enrichment with depth. The second site is similar to this, although it is further depleted in ^{13}C. These maize fields show a mean shift of 1.7‰ down the profile (Table 3).

Table 3: Mean (± stdev.) of $\delta^{13}C$ values (‰) of soil organic matter at each depth down the profiles from current crop fields adjacent to Hluhluwe Nature Reserve. "Mixed crop" indicates bean and maize cultivation. Overall $\delta^{13}C$-shift (‰) from shallowest to deepest soil level is shown.

depth	Mixed crop field (n=1)	Maize fields (n=2)
surface litter	-25.5	-13.6 ± 2.2
0-5cm	-24.0	-17.0 ± 0.1
10-15cm	-24.5	-18.1 ± 2.4
20-25cm	-24.9	-17.6 ± 1.9
30-35cm	-22.6	-17.6 ± 3.4
40-45cm	-19.1	-15.3 ± 0.6
δ13C shift down the soil profile	5.0	1.7

Discussion

◆ ***Cape Vidal***

Present vegetation at Cape Vidal is purely C_3. This surface C_3 signal is slowly enriched down the profile by 1.6 – 3.4‰ (Table 1). This pattern and scale of enrichment has been recorded in temperate and tropical forests before (O'Brien & Stout 1978, Balesdent *et al* 1987, Nadelhoffer & Fry 1988, Martin *et al* 1990, Mariotti & Peterschmitt 1994, Desjardins *et al* 1996) and may be considered a classic pattern for soils in which organic matter is in equilibrium with the C_3 vegetation cover (Desjardins *et al* 1996, Witt 1997). This equilibrium is probably achieved by the fast migration rate of matter through these sandy soils and by the high productivity of the region. Rainfall is also high (1300mm per annum) and this would add to the leaching effect through the soil profile. Thus, at Cape Vidal, the analysis of SOM $\delta^{13}C$ shows no trace of any C_4 vegetation, despite the fact that some of these areas were definitely used as croplands within the last 20 to 60 years.

◆ ***Hluhluwe***

The soils from the Hluhluwe region were much more conducive to SOM isotopic study than the sands of Cape Vidal. The Hluhluwe soils had a much higher clay content and were vastly more stable in terms of bioturbation than at Cape Vidal. Rainfall in the Hluhluwe region is lower (990mm per annum) than that of Cape Vidal. Thus, leaching of organic matter down the profile is less likely to occur in Hluhluwe than at sites in Cape Vidal. Due to the high clay content, more organic matter is bound in the soil and the profile at Hluhluwe should provide a more reliable record of the past vegetation cover.

The Hluhluwe data allow the analysis of two important results, namely the isotopic tracing of croplands and the apparent C_4 to C_3 vegetation shift seen in the entire region. These are discussed in turn.

♦ Using ^{13}C natural abundance to trace slash-and-burn agricultural disturbance in forests

The analysis of three current croplands from Hluhluwe and the Cape Vidal profiles indicate the difficulty in demonstrating the trace of slash-and-burn disturbance with ^{13}C natural abundance studies.

In Hluhluwe, the analysis of the three croplands yielded varied results, due to the inherent heterogeneity in situation of these fields (see Methods). The mixed-crop field showed a $\delta^{13}C$ profile practically indistinguishable from forest profiles. The fact that a large component of this crop was C_3 bean plants, together with the close proximity of the forest and forest generated leaf litter, probably ensured that the majority of organic matter entering the soil was C_3 in origin. Nevertheless, this slash-and-burn field would not have been detected by the SOM isotopic method.

The longer standing maize fields definitely showed strong C_4 signals throughout their profiles, although one field had a larger component of ^{13}C depleted SOM in the middle soil depths (Figure 2). The source of this depleted ^{13}C could be an abundance of C_3 leaf litter from a forest patch that was of close proximity in the past, or inter-cropping with a C_3 crop such as pulses. Thus, even in longer standing fields of current use, isolated from the forest, the credibility of this isotopic test can be jeopardised.

This unreliability is exacerbated in highly productive sandy soils where organic matter seems likely to move quickly down the soil profile. The old fields sampled at Cape Vidal showed no trace of C_4 vegetation in the past (Figure 1) and instead indicated an equilibrium with the covering C_3 vegetation.

The above results indicate that detecting, with confidence, the traces of past slash-and-burn fields is difficult. This was also found to be true for physical and chemical soil properties (Kalisz 1986). Slash-and-burn croplands are only cultivated for short periods, especially on nutrient poor soils, before being left fallow. Results from the fields in Hluhluwe suggest that crop sources of carbon are too small to be detected where the rotation of crops is short. Only where crops have been cultivated for many years, were C_4 signals apparent. Additional factors such as SOM turnover time, vertical movement and mixing down the soil profile, together with the relatively small proportion of C_4 matter that enters the soil and uncertainty over SOM source all serve to hinder this technique. As most slash-and-burn agriculture occurs in productive environments with leached soils, these problems are unlikely to be alleviated in other areas.

♦ *C_4 to C_3 vegetation shift at Hluhluwe*

There seems to be evidence of a general trend from C_4 dominated vegetation at some stage in the past to C_3 dominated vegetation at present in the Hluhluwe Nature Reserve and environs. The forest profiles show a strong trend from C_3 covering vegetation and C_3 derived SOM in the surface layers of the soil (0-25cm) to SOM with a large C_4 component in the deeper soil (30-55cm) (Figure 2). The ^{13}C enriched deeper soil levels are seen in all soil profiles sampled in the Hluhluwe region. The deepest level sampled had $\delta^{13}C$ values ranging from –19.1‰ to –14.8‰, which are typical of arboraceous savanna (Desjardins *et al* 1996) and tussock grasslands (Witt 1997). Thus it would seem that the area presently covered by forest was previously a grassland or grass-dominated savanna.

This raises the question of how old are these forests? The generally accepted view has been that of Acocks (1953), who proposed that forests were the climax vegetation in the KwaZulu-Natal region. Acocks (1953) hypothesised that grasslands existing in this region were "false" grasslands, created by the burning and clearing of forests by iron-age farmers. This hypothesis has been challenged before (Feely 1980, Feely 1985, Feely 1987, Ellery & Mentis 1992). The trends from the Hluhluwe soil profiles support the hypothesis of Ellery and Mentis (1992) that the grasslands are in fact much older than initially thought by Acocks. In addition, this study indicates that grasslands were in fact the precursor to forest vegetation in the Hluhluwe region and that forests are the more recent vegetation cover. It will be interesting to see if further studies support this hypothesis.

Unfortunately, dating SOM is fraught with problems. This is mainly due to the inaccuracies associated with ^{14}C dating, in particular the input of industrially depleted and "bomb" enriched $^{14}CO_2$ effecting dates after 300 BP (Goh 1991, Witt 1997), and the differential rates of decomposition (Vitousek & Sanford 1986) and vertical migration of the various size fractions of SOM (Hoffman *et al* 1995). Using charcoal found at various depths in the profile to date SOM (Desjardins *et al* 1996) also presents problems as bioturbation might result in younger fragments being placed deeper than older fragments. Desjardins *et al.* (1996) found no correlation between depth and charcoal ^{14}C-age. Thus it is difficult to obtain an accurate age for SOM studies. Nevertheless, rough estimates can be obtained using the afore mentioned techniques. This is certainly an avenue to be pursued in future research.

- ***Causes of recent C_4 to C_3 vegetation shifts***

There is evidence of a global expansion in C_4 ecosystems at the end of the Miocene (Cerling *et al* 1993, Quade & Cerling 1995, Cerling *et al* 1997, Cerling *et al* 1997). A similarly widespread shift from these C_4 systems to C_3 dominated systems has been documented in the Holocene (Ambrose & Sikes 1991, Cole & Monger 1994, Pessenda *et al* 1996, Desjardins *et al* 1996, Connin *et al* 1997). This recent increase in C_3 vegetation continues in the present and local climate change and land-use patterns, involving fire regimes and grazing patterns have been invoked to explain these trends (Archer *et al* 1995). However the widespread nature of the Miocene and Holocene shifts suggest that a global cause, possibly changes in global CO_2 levels, is responsible for these vegetation changes.

Several studies have indicated that CO_2 levels are responsible for shifts between C_4 and C_3 dominated ecosystems (Ehleringer *et al* 1991, Cole & Monger 1994, Street-Perrott *et al* 1997). Low CO_2 concentrations are thought to lead to C_4 dominated ecosystems as C_4 plants are favoured under reduced

CO_2 (Ehleringer *et al* 1998). An increase in CO_2 concentration should favour the increase of woody (C_3) plants. The increase in global CO_2 concentrations from ~180ppm (18 000 years ago) to ~275ppm (10 000 years ago) corresponds well with the decrease seen in $\delta^{13}C$ signals (Cole & Monger 1994) and this may in part be due to anthropogenic fires (Bird & Cali 1998). The more recent increase in post-industrial CO_2 concentration to 360ppm (Farquhar 1997) might account for the current woodland expansion witnessed globally.

Nevertheless, it seems likely that on a smaller-scale, land use practices will play a major role in determining the precise vegetation structure and composition. The forest vegetation composition of Hluhluwe is hypothesised as having arisen from slash-and-burn farming practices (see Chapter 2).

Conclusions

The $\delta^{13}C$ SOM technique is useful for detecting broad-scale, long-term vegetation changes, such as the shift from a grass-dominated system to forest as seen at Hluhluwe. However, for studies requiring a more detailed temporal resolution, this method is not appropriate (Witt 1997). Slash-and-burn farming is a short-lived phenomenon that probably doesn't result in much organic matter being incorporated into the soil. In addition, sandy soils that have high productivity, fast organic matter turnover, high levels of bioturbation and rapid leaching, rapidly destroy traces of past $\delta^{13}C$ signals. These factors, together with the difficulty of dating vegetation types reflected in SOM profile studies constrains the efficacy of this technique for identifying old lands that have been re-colonised by forests.

General Conclusion

6

In the 1950's Acocks (1953) hypothesised that many of South Africa's grasslands, especially on the Eastern seaboard, were a product of clearing of bush and forest by Iron Age farmers and smelters. This influential hypothesis was widely accepted and was taken up in the 1980's by Feely (1980) who argued that Iron Age people might have influenced many of Zululand's wilderness landscapes. However, we now have evidence indicating that the KwaZulu-Natal grasslands are in fact much older than the AD1400 date proposed by Acocks (1953) and in fact pre-date Iron Age human impacts quite considerably (Ellery & Mentis 1992, Meadows & Linder 1993). Thus it would seem that the historical impacts of people on KwaZulu-Natal landscapes might have been less extensive than previously perceived. In a similar vein, the accepted notion of widespread historical anthropogenic deforestation in West Africa has recently been challenged (Fairhead & Leach 1996). Despite this it is clear that people have had ample chance and motive to influence ecosystems in Southern Africa and it seems likely that large areas of Southern Africa may have been influenced by humans to some extent in the past (Hoffman 1997). The extent of this anthropogenic disturbance may not be on as grand a scale as of that proposed by Acocks (1953) however this does not diminish the potential importance of understanding and documenting just what the impact was.

Thus this thesis was designed to be an initial attempt at understanding the extent of Iron Age human impacts on wilderness areas in Southern Africa. Specifically, I aimed to detect the potential impacts of Iron Age people in KwaZulu-Natal forest systems. It was felt that KwaZulu-Natal forests represented the best starting point from which to gain experience into studying human impacts of this nature due to the region's extensive archaeological record and current forest dynamics, as outlined in the introduction. I hoped that lessons learned in the forests would aid attempts to study human impacts in other ecosystems. With this in mind, in this conclusion I shall review the techniques used and attempted in this thesis. In particular I shall outline their successes and failures in terms of detecting the human "footprint".

Artefacts: Pottery and charcoal

At the beginning of this study I hoped that the presence of charcoal and pottery sherds would be associated with particular vegetation types, disturbance categories or specific geographic and topographic locations. Furthermore, I hoped to identify the species from which the charcoal was derived and possibly date the pottery sherds. If I was able to show a link in a site of known anthropogenic impacts between the presence of artefacts and specific vegetation, disturbance or topographic types then I could apply this test to other areas with confidence. Such a correlation between disturbed forest and the presence of potsherds and stone axe heads, which are indicative of swidden cultivation, has been shown in the Amazon (Balée & Campbell 1990). I planned to test these techniques at Cape Vidal and then apply them to the forest at Hluhluwe.

To further these aims, I consulted with archaeologists Prof. Martin Hall, Dr. Gavin Whitelaw and Prof. Tim Maggs, and was instructed how to search for and identify pottery sherds. In the field, I conducted surface searches along my vegetation transects and throughout my walking through the forests. Areas such as riverbanks, cutaways from erosion and any form of broken ground were specifically targeted. In addition to this, soil from my soil isotope pits was sieved, primarily for charcoal, but also for pottery or other artefacts.

Unfortunately, the search for pottery yielded only one find, a small potsherd found near Cape Vidal. This potsherd was identified as being from indeterminate Iron Age, possibly from the Matola Phase (250-300 AD), by the Natal Museum and the specimen was lodged there.

Small charcoal fragments were discovered in low quantities in most sites in Cape Vidal. However, quantities were too small and inconsistent to allow a meaningful analysis of spatial distribution of charcoal. I collected all of the charcoal found in the field and took this for analysis in Dr. Ed February's laboratory in the South African Museum. The fragments proved to be too small for identification and after several unsuccessful attempts at identifying the species of wood burnt, the study was abandoned.

Thus the hope that charcoal and pottery would be useful indicators for identifying human impacted vegetation proved to be false. Pottery proved to be too rare and difficult to discover. Charcoal analysis proved to be unsuccessful in this study. However, in future studies I would not rule out the use of charcoal as an indicator of human impacts. In other areas the type of species burnt and the soil conditions might be more conducive to charcoal formation, longevity and ultimately identification. This technique has been used successfully in studies of Iron Age ecology (Prins 1993) and I feel that it is potentially useful for studies of human impacts.

Apart from the techniques described above, there are other approaches that could be used to detect the presence of humans. For example, heavy metal soil analysis has been recently used to detect low status archaeological sites (Aston *et al* 1998) and soil nutrient analysis can be used to trace areas of human and domestic animal occupation (Kinahan 1999). Techniques such as these might prove successful in identifying areas of human impacts in future studies.

Human disturbance and functional types

Another potential indicator of past human disturbance could be the presence of certain types of plants in areas of historical disturbance. Cape Vidal, on the Zululand coastal dune cordon, was chosen as the study site to test this due to its known anthropogenic disturbance history. Slash-and-burn farming has been occurring in the dune cordon for at least the last 1600 years (Hall 1981). Thus this study site presented the perfect opportunity to test for the existence of a functional group of species associated with human disturbance. If I could distinguish a functional group of species specifically linked to human disturbance, then I could search for similar functional groups in other forests and potentially link these to human disturbance.

In the dune cordon at Cape Vidal, human disturbance was limited to the dune slacks. From aerial photographs I could calculate when slash-and-burn fields had been abandoned to recover to forest vegetation. Sampling these old fields allowed for the comparison of sites of various ages since slash-and-burn agricultural disturbance. Forest on the tops of dune ridges was not seen to be disturbed in the aerial photographs. Thus a comparison between species occurring in the slacks and on the ridges allowed for the analysis of different functional types found in human disturbed areas as opposed to undisturbed areas.

For each forest species recorded I examined characters of specific leaf area, ratio of single to multistemmed plants, fruit size and seed dispersers in order to try and define functional groups. These characters incorporate those proposed by Westoby (1998) in his leaf, height, seed (LHS) scheme. By creating a species-plot table from the Cape Vidal data and weighting each species by the four characters listed above, I hoped to be able to distinguish a dune slack grouping and a ridge grouping. From this I hoped to be able to select characters that were directly or indirectly favoured by human disturbance. Although it was possible to separate out species limited to slacks and species limited to ridges, I was not able to detect any specific combinations of characters that would define and distinguish the functional groups. This could well be due to the fact that characters themselves were not specific enough to account for any differences between species. Grouping species into functional groups is notoriously difficult (Smith *et al* 1997). This facet of the study indicated the difficulties associated with attempting to distinguish common characteristics from a diverse range of species.

Thus despite sampling an area that has undergone possibly the longest Iron Age anthropogenic disturbance in South Africa I was not able to characterise a functional group or suite of species specifically associated with human disturbance. However this approach was not a complete failure. There are very definitely some species that seem to thrive with large-scale disturbance and consequently have an increased abundance in areas of past human disturbance. Species such as *Protorhus longifolia*, *Calodendrum capense*, *Harpephyllum caffrum and Margaritaria discoidea* at Hluhluwe (Chapter 2) and *Acacia karroo*, *Celtis africana*, *Sideroxylon inerme*, *Teclea gerrardii* and *Ziziphus mucronata* at Cape Vidal (Chapter 3) are examples of these. These species are much more common in suspected old lands then they are in the forest in general, indicating that they could be part of a functional group of species appearing after human disturbance. Such species have been classified "long-lived biological nomads" (van Steenis 1958). These species wait until a major disturbance, often human-generated, liberates space for them and then tend to persist for many years once the gap has been filled (Balée & Campbell 1990). However, attempts to define characteristics common to these species can be extremely abstruse. Nevertheless, these positive examples serve to indicate the potential of using particular species as indicators of old human disturbance. This approach has been used to classify liana forests in the Amazon as secondary systems (Balée & Campbell 1990).

I believe that functional group analysis represents potentially the most useful approach to examining human impacts. The identification of species dependent on large-scale disturbance, as mentioned above, indicates that with further refinement this technique has much to offer the study of human impacts on ecosystems.

Identifying large-scale disturbance using isotopic techniques

Central to this thesis is the assumption that human disturbance leads to large-scale disturbance. This disturbance is interpreted as ranging from large forest gaps to extensive cleared areas. The ability to detect easily and conclusively the presence of this large-scale disturbance would obviously aid the study of human impacts. During this thesis, I tested two isotopic techniques to detect large-scale disturbance. The first of these I developed during this study and involved comparing the $\delta^{13}C$ signals at different positions along a tree core

(Chapter 4). The second involved determining the $\delta^{13}C$ of soil organic matter down a soil profile (Chapter 5).

♦ *$\delta^{13}C$ of tree cores reflect recruitment environments*

This study showed that one could distinguish between various recruitment environments of individual trees using $\delta^{13}C$ signals along the tree cores. Adult trees were shown to have recruited either in closed canopy and small gap environments or in open areas and large gap environments. The ability to distinguish between these two recruitment environments allows one to recreate a picture of the forest structure at the time of recruitment of the individuals. By sampling several trees within a patch, one can extend this picture to a larger scale and can start to detect cohort-like recruitment after large-scale disturbances. Thus in a forest with an undocumented disturbance history, a relatively detailed record of events should be obtainable from the application of this technique. This record can be both spatially and temporally explicit. Temporal resolution would depend on the accuracy of dating methods, such as dendrochronology. Spatial resolution depends solely on the number of samples taken and could theoretically be resolved to the extent of every tree in the forest being sampled.

I suggest that this technique has great potential for the analysis of patch-size forest dynamics. It offers the ability of understanding past regeneration conditions and forest structure in areas where there are no other records. In conjunction with other techniques, it offers a novel and robust method of detecting large-scale disturbance.

♦ *Attempts to trace old fields using $\delta^{13}C$ of soil organic matter*

Soil organic matter (SOM) isotopic studies have been conducted in a variety of locations around the world mainly in an attempt to show landscape-scale vegetation change. In this thesis I attempted to detect a much smaller scale change between forest vegetation and C_4 croplands within present forest communities. The disturbances I was trying to trace were old slash-and-burn fields located within forest communities that had been re-vegetated by forest species. The detection of such fields would conclusively show that humans had actively disturbed the forest in question and would provide excellent evidence for the hypothesis central to this thesis. However, attempts to detect such fields failed, probably due to the relatively brief duration of the C_4 crop and the potential dilution of the C_4 signal by surrounding C_3 plants. The SOM isotope technique was not sensitive enough to overcome these factors. This fact suggests that this technique will be of little use for future studies of this nature.

Reviewing human-dependent landscapes

I stated in the beginning of this thesis that I hoped to be able to address the larger issue of "ecosystem virginity" and to what extent landscapes with a lengthy history of human habitation are dependant on human-generated disturbance.

Worldwide, forest systems are heavily impacted by humans (Noble & Dirzo 1997). My work during this thesis indicated that humans have potentially impacted all of the forest ecosystems in KwaZulu-Natal to some extent. In addition to the sites where I collected my data, during my fieldwork I managed to examine several other forests in KwaZulu-Natal. I spent a month as a research assistant in the sand forests at Tembe Elephant Park and surrounding community areas. I managed to visit the sand forest at False Bay Park and Mkuze, the riparian and floodplain forests of Ndumu and Mkuze, the coastal dune forests at Kosi Bay, Lake Sibaya, Sodwana Bay and Mapelana, the coastal lowland forest at Dukuduku and Futululu and the coastal scarp forest at Ngoya. From these observations it became clear to me that past or present human impacts in these forests are ubiquitous. One can see a lack of regeneration of certain species in the sand forests. The coastal dune forest has a lengthy anthropogenic disturbance history. People are currently living a slash-and-burn lifestyle in the vicinity of Tembe Elephant Park and in the Dukuduku State Forest. Ngoya Forest has unrestricted access, and cattle can be seen to graze on the forest margins indicating that this forest is utilised by the local people. Even the riparian and floodplain forests that historically operated on a climate-dependant disturbance cycle independent of human influences are impacted by humans today with the construction of dams and the regulation of water flow. Thus, none of these systems, including reserves proclaimed a hundred years ago, can be regarded as having been free from human influence. There is a lengthy history of human disturbance across the whole of KwaZulu-Natal and these forests have certainly been impacted by it.

The question that this thesis then asks is whether KwaZulu-Natal forests that have previously been regarded as primary forests are in fact secondary systems reflecting regeneration after human disturbance and if so, how can one detect this?

There are threads of evidence that indicate that the compositions of these forests are dependent on human disturbance. This "human-dependence" has been shown for deciduous forests in Sweden (Lindbladh & Bradshaw 1998) and tropical forest in the Amazon (Balée 1989, Balée & Campbell 1990). The evidence of large-scale disturbance (Chapters 2 and 4) and the presence of large gap specialists (Chapters 2 and 3) in forests with no such natural disturbance regime is seen as evidence of potential human disturbance. In addition, preliminary comparative work between forests inside reserves and in surrounding community areas has indicated startling increases in the regeneration of some canopy species in areas utilised, disturbed and subsequently abandoned by people. This was discovered for *Newtonia hildebrandii* at Tembe (Brereton-Stiles, thesis in prep.) and subsequently for *Celtis africana*, *Harpephyllum caffrum* and *Croton sylvaticus* at Hluhluwe (West, unpublished data). Unfortunately this encouraging line of study was not able to be completed during the course of this thesis and is mentioned here solely as an indication of exciting future work to be done.

Thus there is preliminary evidence in KwaZulu-Natal that forests can recover from human-generated disturbance and consequently species composition may be dependent on this disturbance. In fact forests, such as Hluhluwe, previously thought to be primary ecosystems could well be secondary forests, strongly influenced by humans. These findings are similar to those described in other parts of the world. In fact in the Amazon Basin it has been stated that shifting agriculture was once so widespread in Guyana that it is hazardous to regard any forests there as being primary (Fanshawe 1954). This is taken a step further by recent work done in West Africa (Fairhead & Leach 1996). In Guinée, it was previously accepted that humans were responsible for extensive deforestation (see Fairhead & Leach 1996). However, recent work suggests that people not only protect these forest patches, but may in fact create them through gardening practices such as the suppression of fire, the altering of soil conditions and even active planting of forest trees (Leach & Fairhead 1993, Fairhead & Leach 1996). People seem to assist and accelerate the transition from savanna to forest, rather than the reverse (Fairhead & Leach 1996). Thus, it seems as if we are getting closer to realising the importance of potentially positive interactions between people and forest communities (Posey 1989). Obviously this has major implications for conservation, especially in Southern Africa where nature reserves are under increasing pressure to be of benefit to the local communities. Realising that, under controlled densities, utilisation by local people could benefit the reserve's forest management policy would be a popular discovery and one that needs to be examined closely.

Finally, this thesis has pointed out the difficulties in examining historical human impacts in forest ecosystems. I hope however that it has also indicated where future work can be directed. The history and extent of human influence on current landscapes is a fascinating and important topic and one that certainly deserves more attention world-wide. I am certain that significant advances are still to be made in this demanding field.

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