Classification and dynamics of the forest vegetation of Hluhluwe Nature Reserve, Kwa Zulu-Natal.

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Abstract

The forests of Hluhluwe Nature Reserve, Kwa Zulu-Natal, were examined to determine composition, grain, classification, dynamics and conservation value. Field sampling took the form of recording DBH for all species in twenty-one 0.04 ha circular plots, walking 5-metre wide transects in mature and marginal forest to record size-classes and analysis of twenty gaps. Data were analysed by the multivariate programs, TWINSPAN and CANOCO. The composition of the canopy and subcanopy is distinct. Four canopy and two subcanopy communities can be detected. Community succession in the mature forest takes the form of almost random replacement of canopy trees through two subcanopy communities. Size-class distributions indicate a prevalence of shade-intolerant species. This forest is deemed to be coarse-grained and can be classified as coastal scarp forest. Comparisons with other forests shows Hluhluwe to have slightly above average species richness. A removal of anthropogenic disturbance by the creation of the reserve may have resulted in present forest canopy structure. Management for conservation of species diversity should encourage disturbance. There is potential for harvesting of certain shade-tolerant species by local communities. This forest is a pristine fragment of a rapidly diminishing vegetation type and efforts should be made to conserve its entire expanse, within Hluhluwe Nature Reserve, in order to prevent species loss.

Introduction:

In southern Africa, the study of forest dynamics is an emerging field, as can be seen by the sudden appearance in the literature of several key articles (Everard *et al.* 1995; Midgley *et al.*, 1995a; Midgley *et al.*, 1995b; Midgley *et al.*, 1995c; Midgley *et al.*, 1990; van Wyk *et al.*, 1996). It may be argued that forest dynamics is of little importance in southern Africa due to the relatively small area covered by this growth form (<1%). However, others may feel that understanding the driving forces in our diminishing forest patches is a pressing issue due directly to their small size. In an age of conservation, the emergence of the study of southern African forest dynamics is a timely one.

- **Forest dynamics**

For all practical purposes, forest dynamics is centred around the complex interaction of three factors, namely the disturbance regime, the degree of shade-tolerance of constituent species and factors affecting regeneration (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.*, 1995; van Wyk *et al.*, 1996) and large-scale, allogenic processes such as earthquakes, volcanism and fires (Veblen, 1992; Akashi & Mueller-Dombois, 1995; Okitsu, 1995). 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.*, 1995c). Factors effecting regeneration can include recruitment bottlenecks and the dominance of sprouts (Espelta, 1995), a factor which has not received enough attention in the literature (see Kruger *et al.*, 1996).

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 disturbance occur and the latter enables the regeneration of shade-intolerant species, but not near their adults. All southern African forests can be seen as fitting along a continuum between the two extremes (Everard *et al.*, 1995; van Wyk & Everard, 1995; van Wyk *et al.*, 1996). Grain is a useful classificatory measure especially for conservation, as forests of similar grain have similar dynamics and can be managed as such (see van Wyk & Everard, 1994; Everard *et al.*, 1995).

- **South-eastern African forests**

Forests in south-eastern Africa have been broadly classified into Afromontane forests of the uplands and lowland subtropical forests of the Indian Ocean Coastal Belt (Moll & White, 1978), consisting of coastal scarp, coastal lowland, sand, dune, swamp and riverine forests (see Everard *et al.*, 1995). Everard *et al.* (1995) provided a preliminary examination the dynamics of some of these forest types, and showed that the coastal forests tended from intermediate-grained for the coastal scarp forests, to coarse-grained for the coastal lowland forests (also see van Wyk & Everard, 1995). Other than this study, the dynamics of these forests has been largely unexplored, an exception being the analysis of the Dukuduku coastal lowland forest performed by van Wyk *et al.* (1996).

This aim of this study was to classify and examine the floristics and dynamics of the north-eastern forests of the Hluhluwe-Umfolozi Nature Reserve and by so doing, to contribute to the documentation of the forests in Kwa Zulu-Natal.

Study site

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 Kwa Zulu-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). 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). Forest communities are restricted to the high rainfall hillsides or to riverine belts (Brooks & Macdonald, 1983).

Although most of the Complex is covered by shales and sandstones of the Volksrust, Vryheid and Pietermaritzburg formations (Ecca series), areas of dwyka tillite, table mountain sandstone and granite occur on the southern boundary of Hluhluwe Reserve (Whately & Porter, 1983). The eastern part of Hluhluwe Reserve is covered mainly by shales and sandstones belonging to the Beaufort series and a small part of basalt lava is also present (Whately & Porter, 1983). This climatic, edaphic and topographic heterogeneity allows a wide

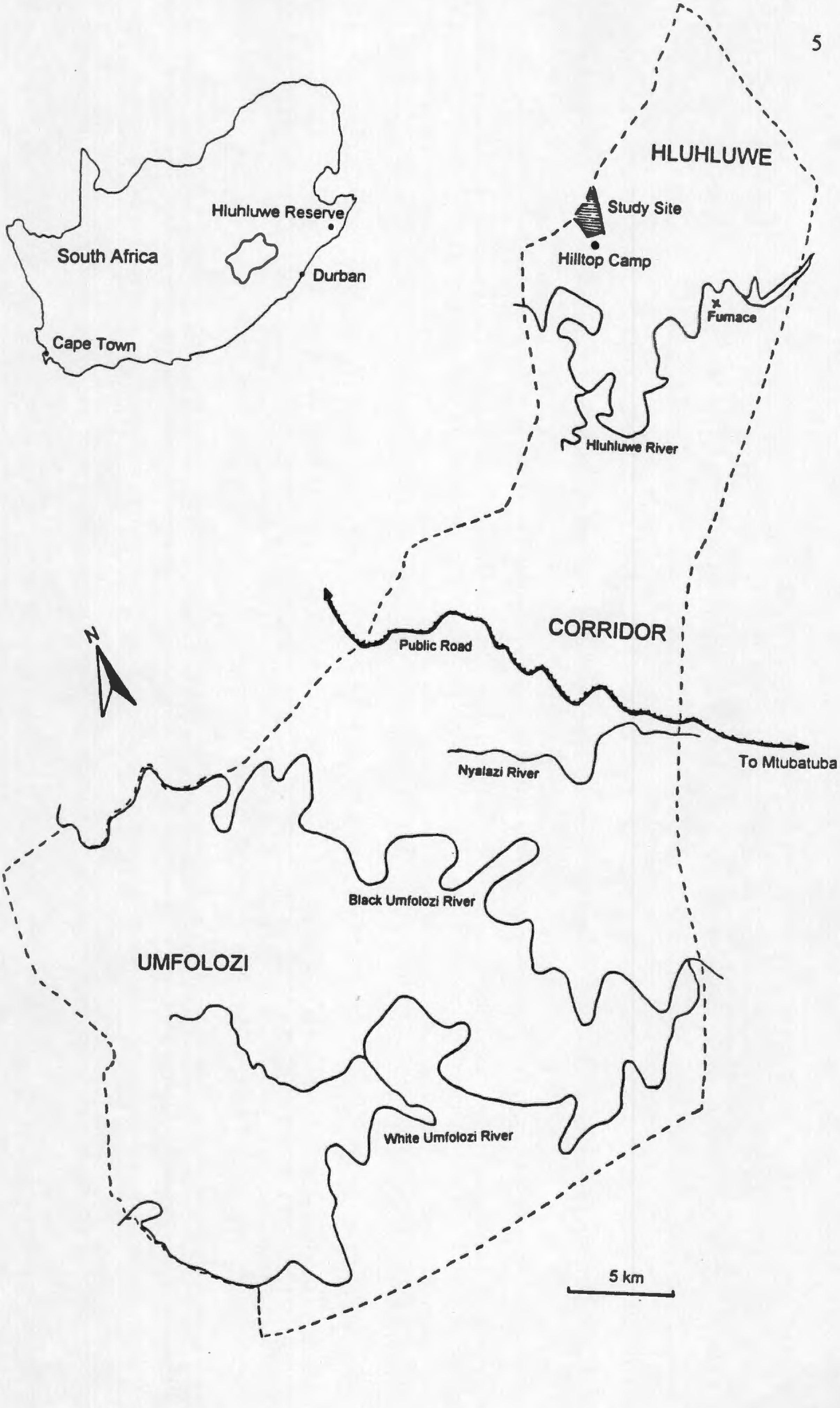


Figure 1: The Hluhluwe-Umfolozi Nature Reserve

variety of vegetation types to exist in Hluhluwe Nature Reserve, from forest to broad-leafed woodlands and grasslands.

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

Methods

• Sampling methods

Plot data was recorded using nineteen 0.04 ha circular plots (radius 11.28m) randomly located in stands of mature forest. Two plots were sampled on the forest margins. In all the plots, the total height or stem diameter at breast height (DBH) for all woody species were recorded. Categories used were: seedlings (<25 cm in height); understorey (>25 cm but <2 m high); subcanopy (>2 mH but clearly not reaching canopy) and canopy (>2 mH and in the canopy). The criterion for canopy status was 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 one metre squared subsamples were used per hundred metres squared.

At each of these plots a site description was taken, including aspect, slope, mean canopy height and estimated distance from forest margin. Plants were identified from the "Trees of Natal" field guide (Pooley, 1994).

Five metre wide transects were sampled through the mature forest in order to supplement the plot data for 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 size-classes. A similar procedure was used for transects along the forest margins, however here the forest edge served to delimit the course of the transect.

Twenty 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. It was also attempted to ascertain the gap-maker and potential gap-taker or cause of gap closure, however this was not always possible.

- **Community analysis**

The data were initially classified using the hierarchical classification program TWINSPAN (Hill, 1979). The program was run with defaults and number of stems per species per plot were used as the importance values. Only woody plants were used, as data was not complete for other creepers and herbs. The analysis was run for all species and then again with the dominant understorey species removed.

As TWINSPAN is a polythetic divisive method (Kent & Coker, 1992), plots are separated on the basis of total species composition. Thus, the dendrogram produced by TWINSPAN provides 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.

Ordinations were performed as detrended correspondence analyses (DCA) by the computer package CANOCO (ter Braak, 1988a, as cited by Kent & Coker, 1992; 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 was 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 understorey species removed. The output of this analysis was graphed, the similarity between samples being 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 enabling the examination of both grain and succession, as shall be explained later.

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 visually. From these size-class distributions one should be able to tell whether or not the species is recruiting under the canopy and from this one can construe relative shade-tolerance. Species with inverse-J shaped curves are assumed to be shade-tolerant and characteristic of fine-grained forests (Midgley *et al.*, 1990), whereas species with flat, unimodal or bimodal curves are assumed to be shade-intolerant and indicative of coarse-grained forests (Everard *et al.*, 1995).

Results

In total, eighty-seven woody species were recorded during the study, of which 73 were recorded in the sample plots (Table 1). This indicates that the total woody flora of the forest is in excess of this figure. This is supported by the relationship between species and area (Figure 2). Species-area curves should take the form of an increasing slope, decreasing logarythmically. However, Figure 2 shows a curve that has not yet flattened out. In fact, a linear regression returns a R^2=0.89. One would expect this curve to flatten out over a further increase in area, the extent of which cannot be determined by this data.

Table 1: A species list (excluding creepers), based on 21 sample plots of the north-western forest vegetation of Hluhluwe Nature Reserve

	Number of plots		
	Understorey (0.25 - 2 m)	Sub-canopy (>2 m tall)	Canopy (> 2m tall, in canopy)
Alberta sp.	1		
Albizia suluensis			1
Allophylus africanus		1	1
Allophylus dregeanus		4	
Brachylaena uniflora		1	
Bridelia micrantha		1	
Buxus natalensis	2	2	
Calodendrum capense			1
Calpurnia aurea	1	5	3
Canthium inerme	1	7	1
Carissa bispinosa	1	1	
Cassipourea gerrardii	7	7	1
Celtis africana	2	6	13
Celtis durandii		2	2
Chaetacme aristata	3	10	8
Chionanthus foveolatus	1	2	
Chrysophyllum viridifolium		3	2
Cola greenwayi	15	12	
Combretum kraussii	1	5	8
Croton sylvaticus	2	2	7
Cussonia sphaerocephala		1	2
Dichrostachis cineria			1
Diospyros natalensis	2	5	
Dombeya rotundifolia		1	
Dovyalis longispina		2	
Drypetes arguta	6	5	
Drypetes gerrardii	2	9	8
Ekebergia capensis	8	5	4
Englerophytum natalense	21	21	2
Erythrina caffra			1
Erythrina lysistemon		1	
Erythroxylum emarginatum	1	11	
Euclea natalensis	11	3	3
Euclea racemosa subspp. zuluensis	1	1	
Harpephyllum caffrum		3	6
Homalium dentatum		2	1
Hyperacanthus amoenus	6	6	
Kiggelaria africana			2
Maytenus mossambicensis	2	5	
Maytenus nemorosa		14	1
Maytenus peduncularis		2	1
Maytenus undata		1	2
Memecylon natalensis		2	

Mimusops obovata		1	1
Ochna arborea	1	1	
Olea capensis		1	3
Olea woodiana		4	2
Oxyanthus speciosus	1	1	
Pancovia golungensis	16		
Pavetta sp.	1		
Protorhus longifolia		1	6
Psychotria capensis		4	
Rawsonia lucida	20	11	
Rhus chirindensis		2	4
Rothmannia globosa	1	5	
Sapium ellipticum			3
Scolopia mundii		1	2
Scolopia zeyheri		5	2
Scutia myrtina		3	
Sideroxylon inerme		1	
Strychnos henningsii	1	2	
Strychnos mitis		4	2
Strychnos usambarensis	1		
Teclea gerrardii		1	
Teclea natalensis		1	
Tricalysia sonderiana		2	
Trichilia dregeana	1		7
Trimeria grandifolia		5	
Turreae floribunda		3	1
Vangueria randii		13	2
Vepris lanceolata		2	4
Vepris reflexa		1	1
Zanthoxylum capense		1	

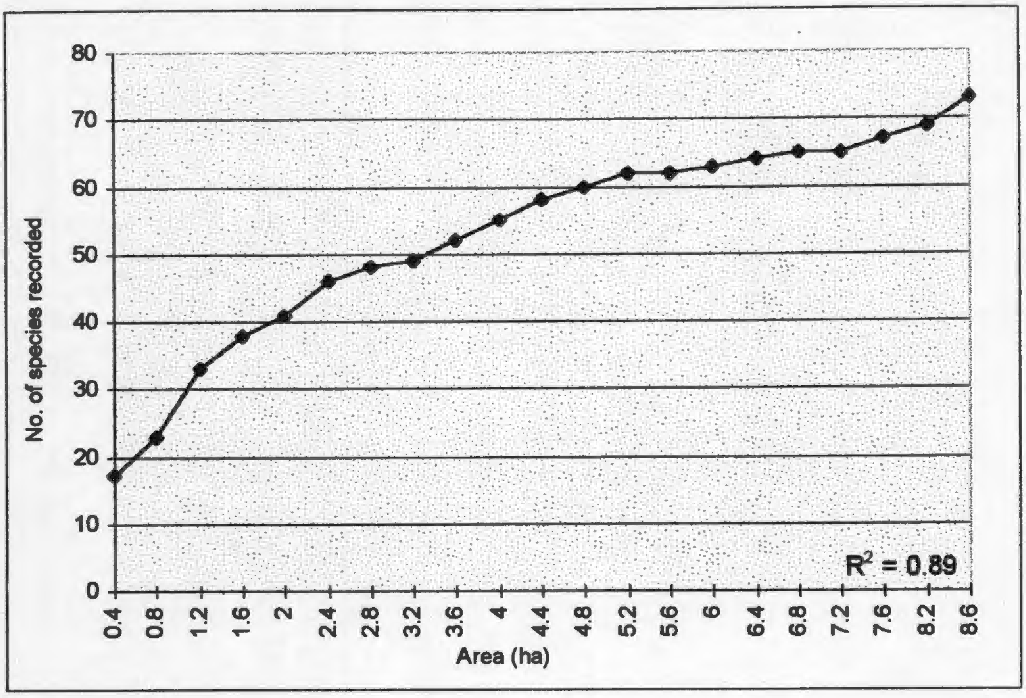


Figure 2: Cumulative woody species total with increasing area sampled.

Table 2: Number of plots found in various aspect and slope categories.

Aspect classes			
1-90°	91-180°	181-270°	271-360°
5	11	2	3
Slope classes			
0-10°	11-20°	21-30°	31-40°
7	8	2	4

Average tree density (>10 cm DBH) was 830 stems per hectare, with the maximum density obtained in a plot being 62 stems. This compares with the average density of 275 stems ha^{-1} for Dukuduku (van Wyk *et al.*, 1996) and maximum density of 74 stems in a plot (0.04 ha) for Umtiza Nature Reserve (Midgley & Gobetz, 1993).

Slope and aspect varied considerably between plots (Table 2). The majority of sites faced between 0-180° and slopes of 0-20° were most common.

- **Classification and ordination**

For both the TWINSPAN and the CANOCO analyses, understorey species *Buxus natalensis*, *Cola greenwayi*, *Englerophytum natalense* and *Rawsonia lucida* were excluded. The abundance and ubiquity of these species, especially *E. 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 (Appendix 1), a dendrogram of plot relationships was created (Figure 3). In this figure, one can see selected indicators species and the eigenvalues of the individual divisions. The plots have been separated into canopy and subcanopy components, the letter after the plot number designating to which level the sample belongs. The groupings marked represent what are interpreted as distinct communities. One can see that these divisions are not uniform, nor completely continuous with the TWINSPAN classification. This is due to the fact that these communities have been classified from the combined analysis of the TWINSPAN classification and DCA-ordination (Figure 4). These groupings have been superimposed on the DCA ordination space.

Figure 4 shows the DCA-ordination produced from CANOCO. The eigenvalues of both Axis 1 (0.870) and Axis 2 (0.560) are reasonably high, suggesting a degree of robustness. However, no strong linear arrangement is obvious from this ordination. In general, communities do not seen to be sharply defined, rather groups are linked loosely together across both axes. There also seems to be no close grouping between the canopy and subcanopy components of

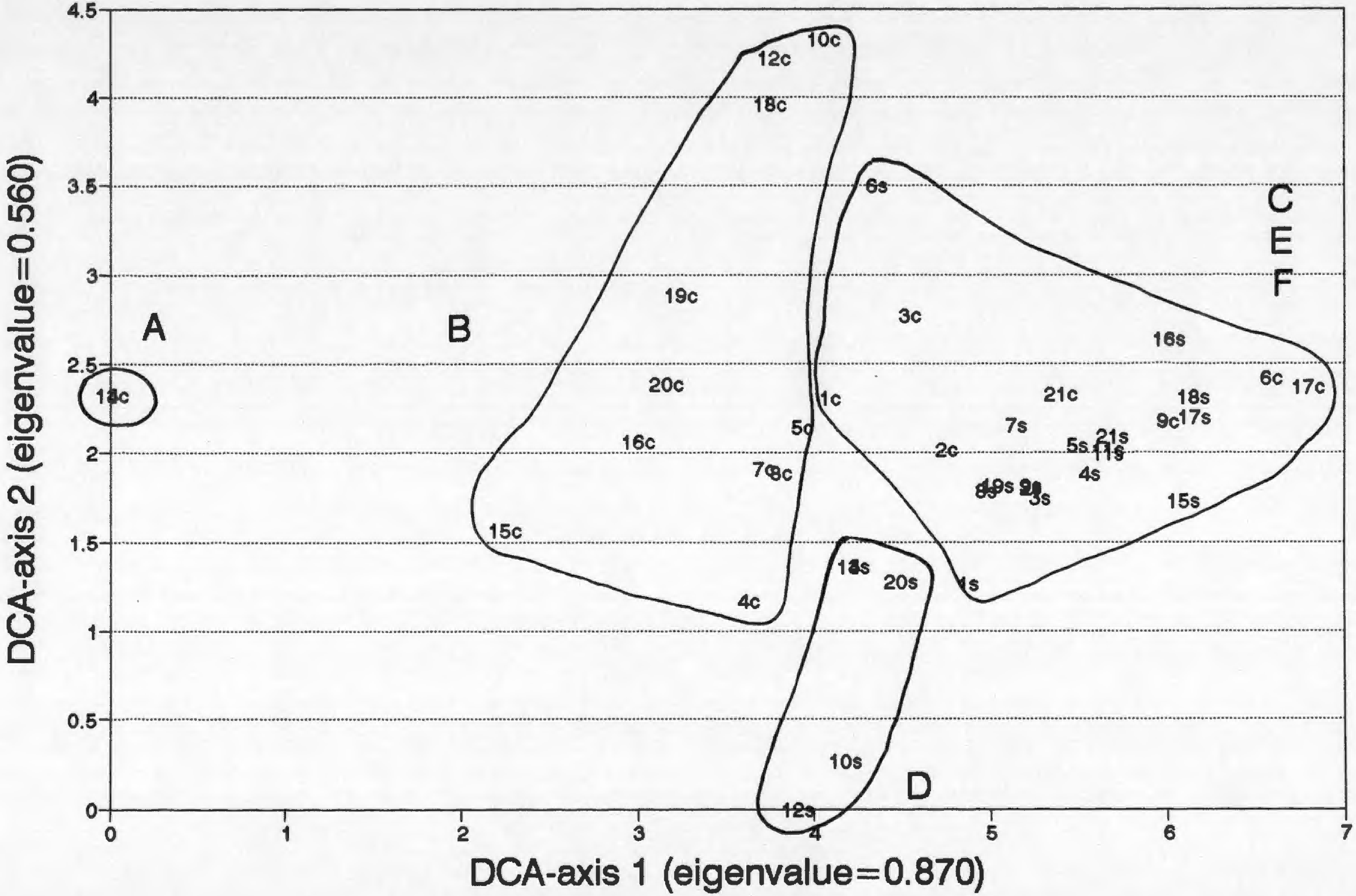
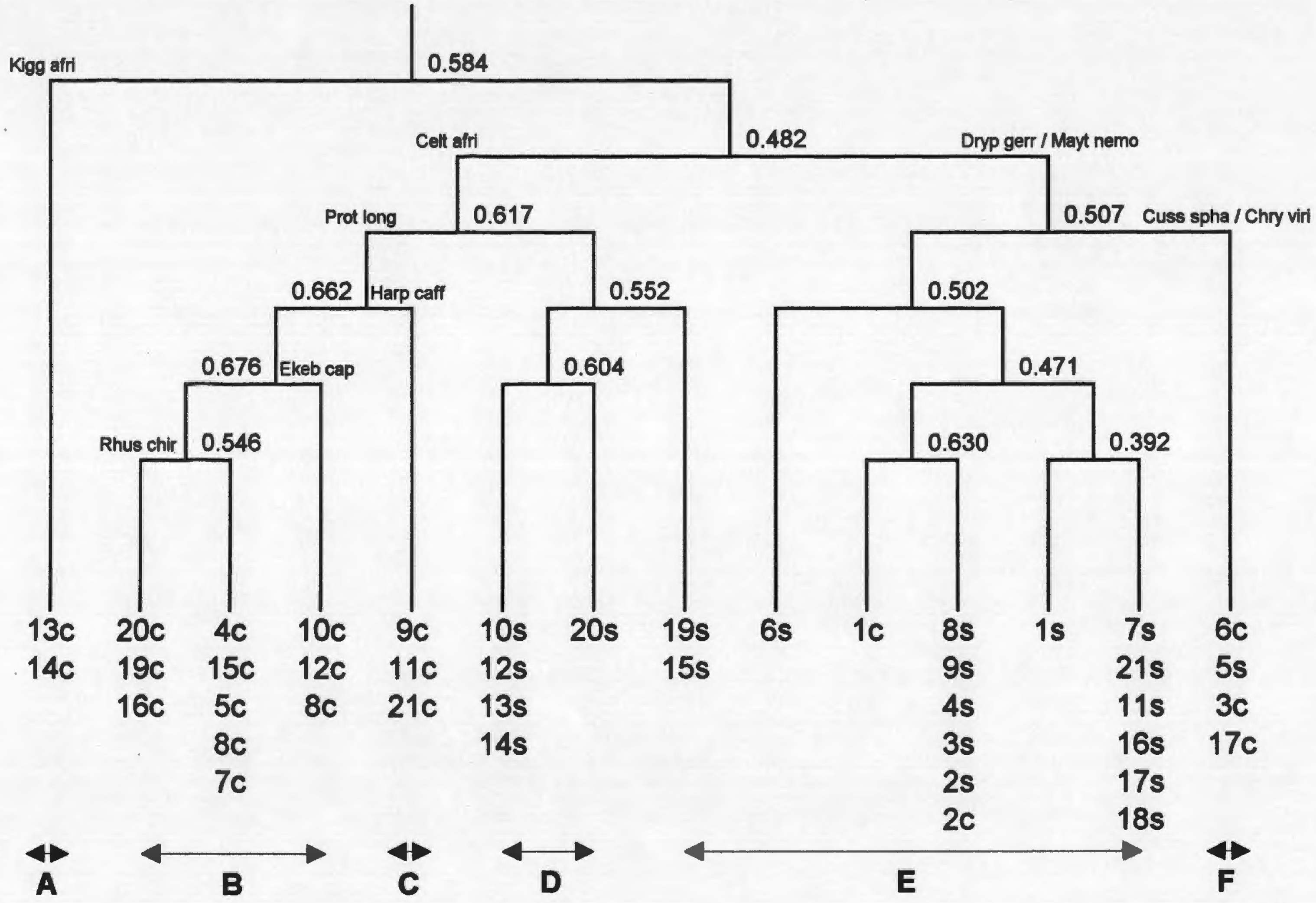


Figure 4: DCA ordination of plots, seperated into canopy and subcanopy subplots No. of stems as importance values. Groupings represent communities.

Figure 3: 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.



individual plots. This is indicative of a coarse-grained forest, as in a fine-grained forest, canopy and subcanopy should be extremely similar (Midgley *et al.*, 1990).

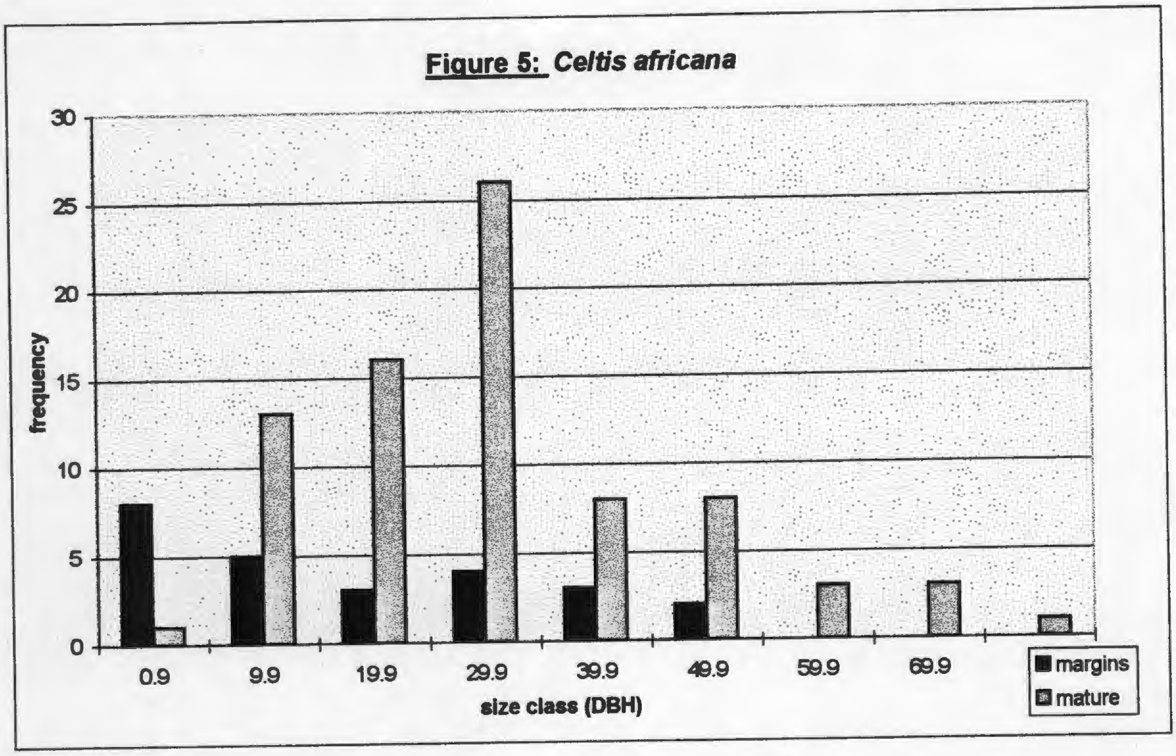
Neither of the environmental variables tested account for the distribution seen. Aspect has an extremely weak relation to both axis. Slope fits slightly better with negative correlations with both axes. The regression coefficient is -0.503 with Axis 1 and -0.114 with Axis 2. However, these are not particularly strong correlations and it would seem that slope cannot be construed to have a too meaningful impact on the definition of communities.

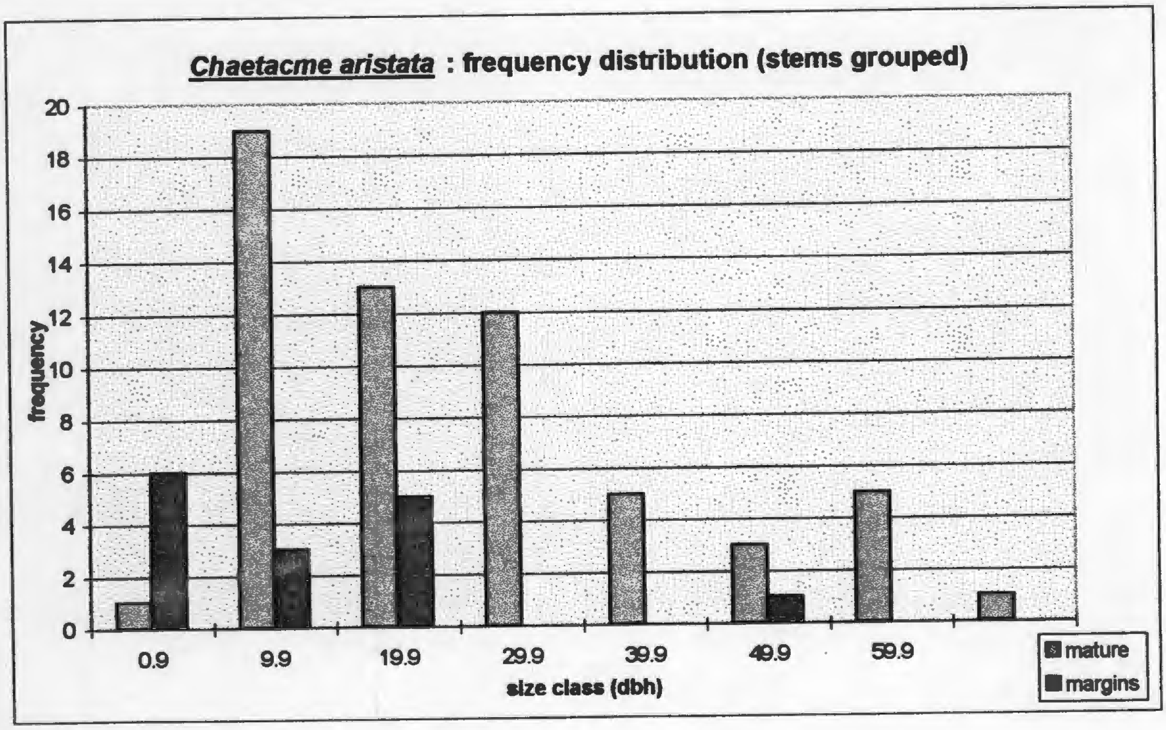
- **Size-class distributions**

The size-class distributions of the eight most common canopy species are shown in Figures 5-12. As for Everard *et al.* (1995), only eight size-classes are shown here as the rarity of other species prevented the accumulation of sufficient data to create meaningful size-class distributions. Only one species, *Ekebergia capensis*, shows the true inverse J-shaped curve. All the other species examined here exhibit unimodal or bimodal shaped curves, with very low levels of recruitment. This indicates a course-grained forest.

Table 3 shows the range and the average of the number of stems per individual for selected species. From this, one can see that *Chaetacme aristata* and *Combretum kraussii* are relatively strong sprouters, *Croton sylvaticus* and *Ekebergia capensis* are weak sprouters. *Celtis africana*, *Chrysophyllum viridifolium*, *Harpephyllum caffrum*, *Protorhus longifolia* and *Vepris lanceolata* are, for all intents and purposes, non-sprouters.

Figures 5-12: Size-class distributions of various species in mature forest





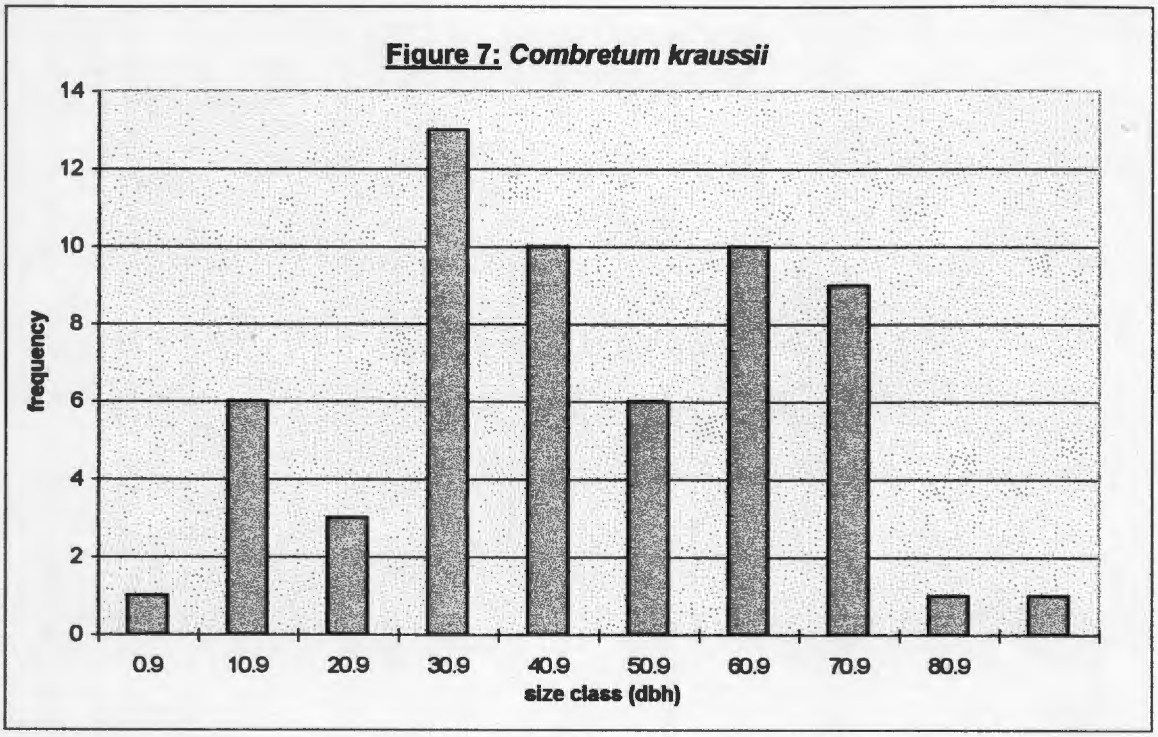


Figure 7: *Combretum kraussii*
frequency
14
12
10
8
6
4
2
0
0.9
10.9
20.9
30.9
40.9
50.9
60.9
70.9
80.9
size class (dbh)

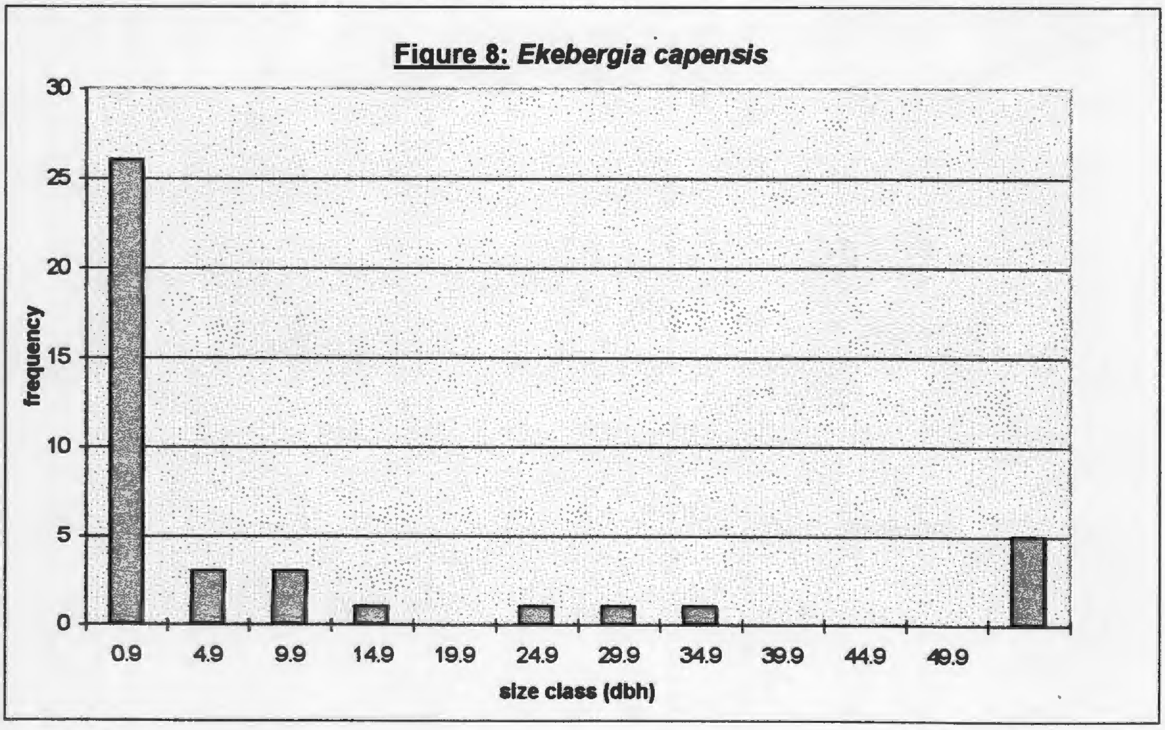


Figure 8: *Ekebergia capensis*
frequency
30
25
20
15
10
5
0
0.9
4.9
9.9
14.9
19.9
24.9
29.9
34.9
39.9
44.9
49.9
size class (dbh)

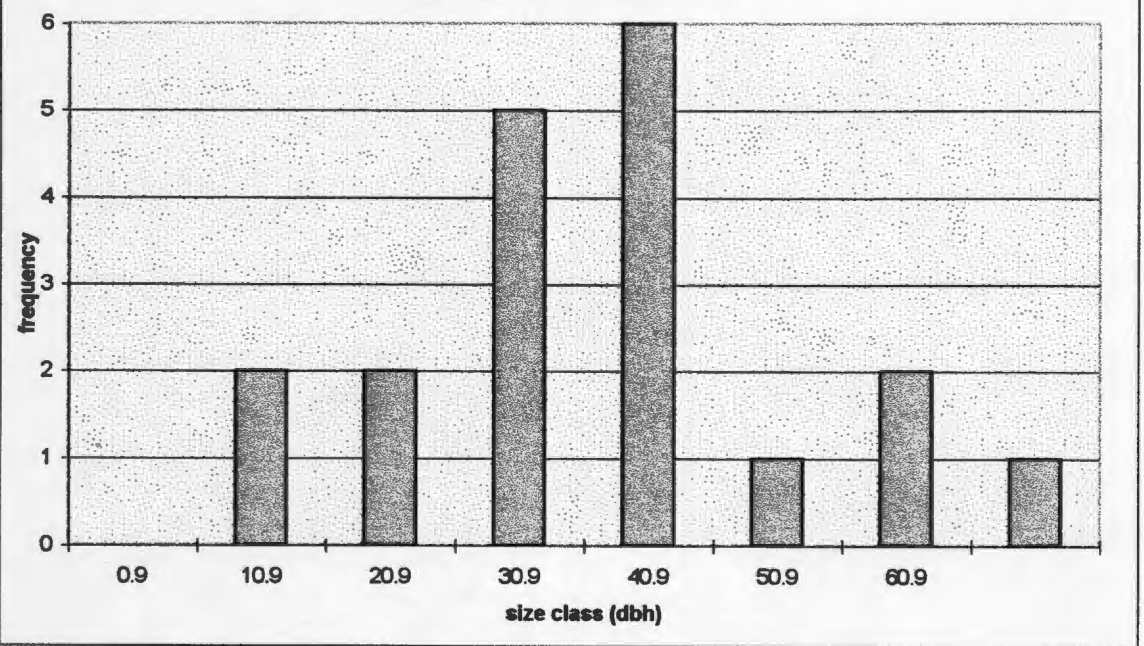


Figure 9: *Vepris lanceolata*

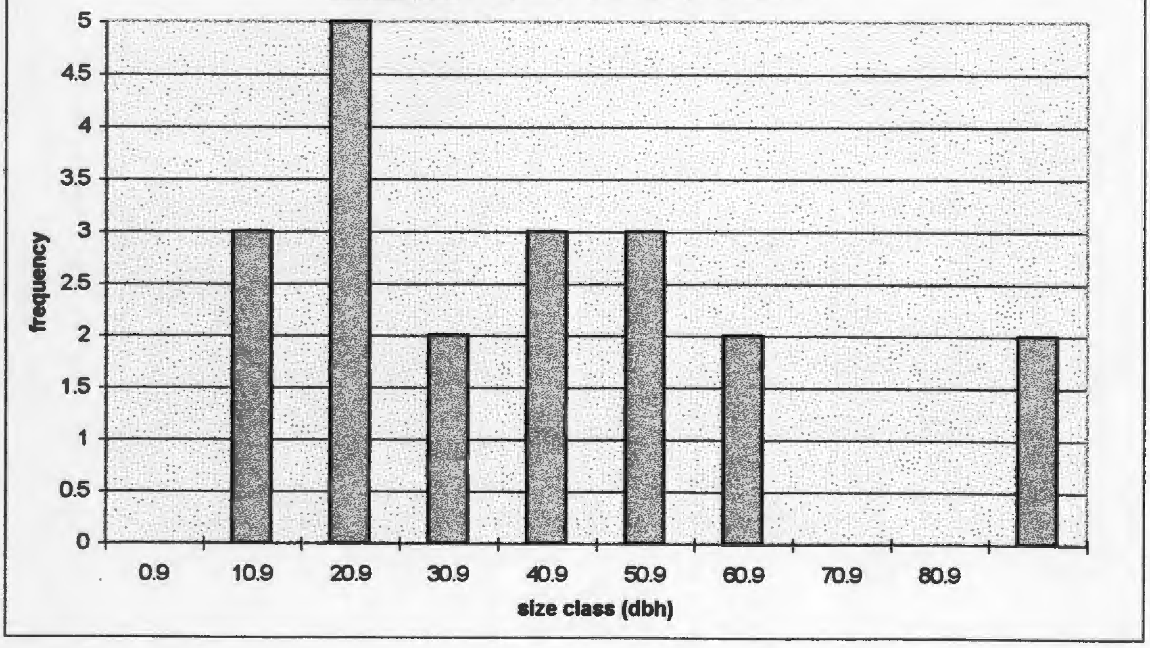


Figure 10: *Chrysophyllum viridifolium*

Figure 11: *Protorhus longifolia*

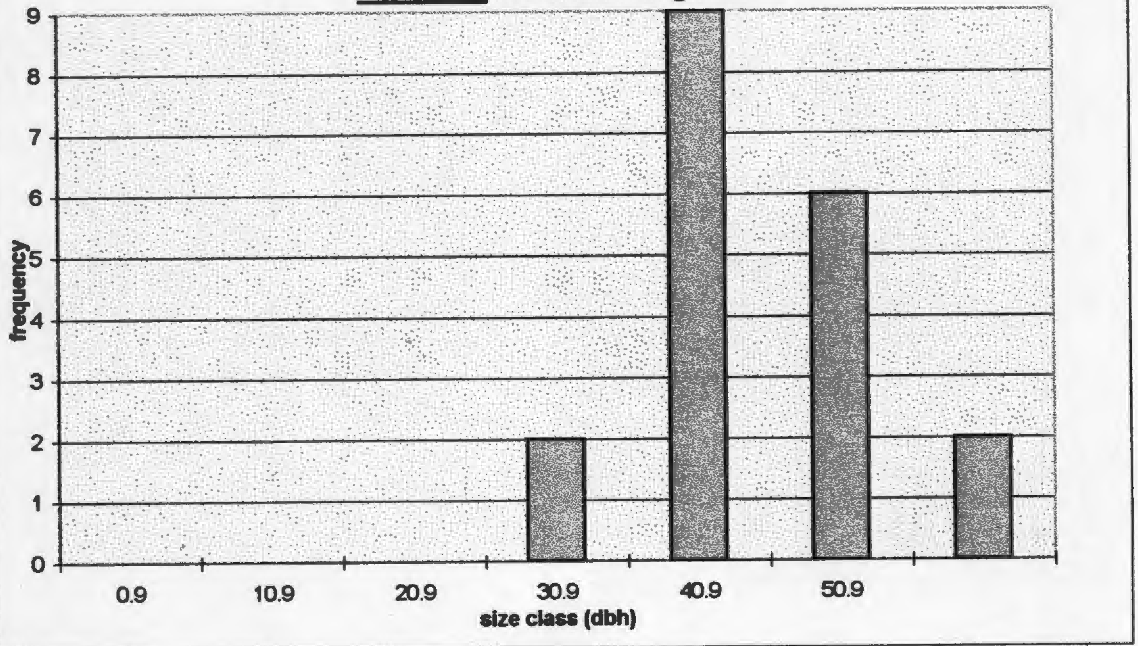


Figure 12: *Drypetes gerrardii*

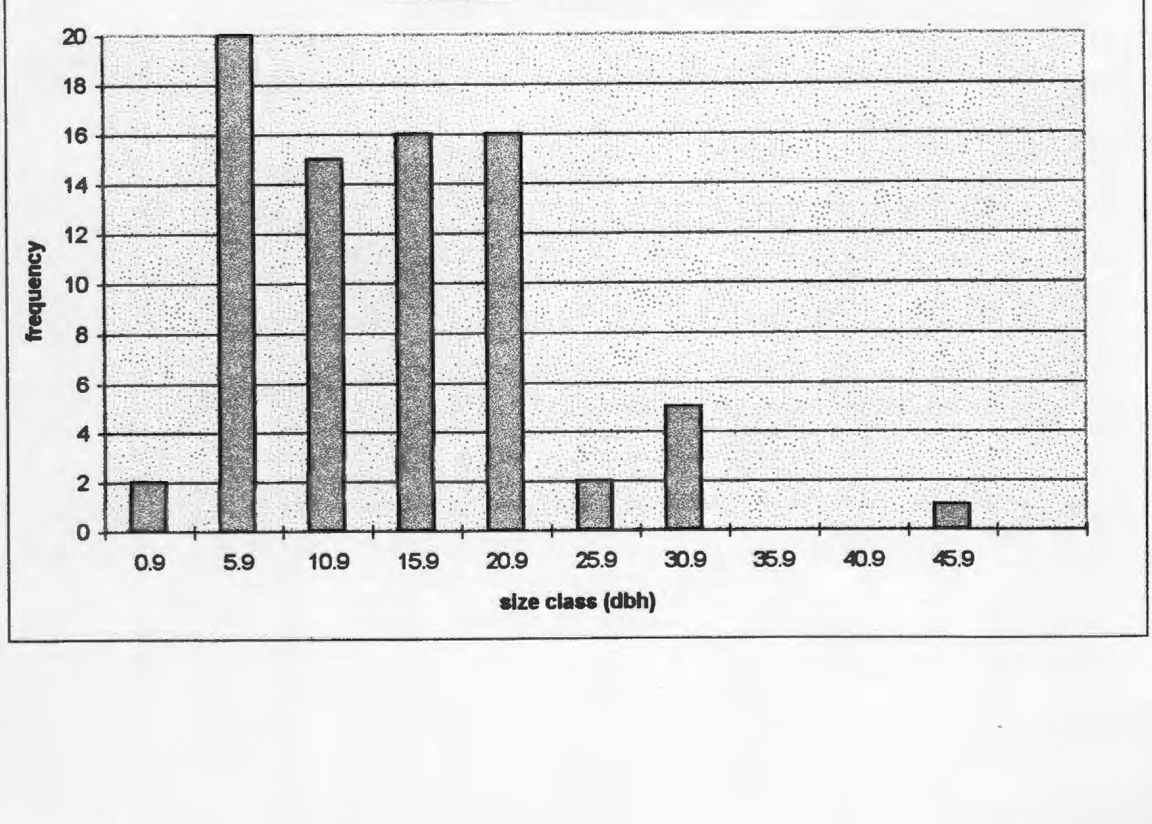


Table 3: Maximum, minimum and average number of stems, at breast height, in mature forest, for selected species. The ratio between trees (over two metres tall) and recruits (between 25 cm and 2 metres) is also shown for these species.

spp code	stems in mature forest max	min	average	trees : recruits >2m : 0.25-2m
Celtis africana	3	1	1.05	1 : 0.06
Chaetacme aristata	8	1	1.76	1 : 0.09
Chrysophyllum viridifolium	2	1	1.05	1 : 0.00
Combretum krausii	9	1	2.07	1 : 0.05
Croton sylvaticus	3	1	1.18	1 : 0.36
Ekebergia capensis	6	1	1.17	1 : 1.67
Harpephyllum caffrum	2	1	1.06	1 : 0.00
Protorhus longifolia	1	1	1	1 : 0.00
Vepris lanceolata	2	1	1.05	1 : 0.00

Table 3 also shows the ratio between plants over 2 m tall and those between 25 cm and 2 m tall for selected species. These values can be compared to those obtained by Whately and Porter (1983) for the same forest. Whately and Porter (1983) interpreted the ratio between plants over 2 m tall and those between 0.10 cm and 2 m tall as indicative of the reproductive status of that species. They reasoned that for those species that had a ratio greater than 1 : 0.20 (i.e. more than 20% of the population as understorey) continued existence was guaranteed. However, from personal observation in the field, it is apparent that the continued existence of plants under 25 cm tall is extremely tenuous, as many are produced and yet very few seem to survive. In shade-intolerant species the reason for this is obvious, as most seedlings are produced under the canopy, where there is insufficient light for them to survive. For shade-tolerant species, a combination of competition and their desirability as fodder must account for seedling mortality. For this reason, the lower category of Whately and Porter (1983) has been changed to between 25 cm and 2 m tall for this study. This should reflect a more realistic situation in terms of continued existence of these species.

Whately and Porter (1983) identified *Celtis africana* (1 : 1.17) and *Combretum kraussii* (1 : 0.02) as species with a ratio lower than this and therefore endangered in this forest. The data obtained in this study clearly show that all but two of the major canopy species fall in to this category.

- **Gap dynamics**

The gaps sampled in this study had an extremely heterogeneous and variable nature. The sample size was too small to detect any statistically significant patterns. Nevertheless, the gap data still has worth in illustrating potential trends and processes.

Of the twenty 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. The most frequently occurring gap takers, *Chrysophyllum viridifolium*, *Combretum kraussii* and *Chaetacme aristata*, appeared three times each. One gap was creeper choked and three were closed by lateral infill. The largest gap sampled was 800 m^2, with the average size being 265 m^2. All of the gaps either choked by creeper or closed by lateral infill were small, indicating the importance of larger disturbances in allowing recruitment in this forest.

A comparison of density between understorey plants (<2 mH, >25 cmH) of *Celtis africana* and *Chaetacme aristata* in gaps and non-gaps yields some interesting patterns. For both *Celtis africana* and *Chaetacme aristata*, the density of understorey recruits was much higher in gaps than in non-gaps (Table 4). Although the sample sizes are small, this indicates that these two species are predominantly shade-intolerant and must recruit in gaps. For *Celtis africana*, the density of seedlings (<25 cm) is much lower in the gaps than in the non-gaps (Table 5). Due to the fact that the gap data consisted of several plants in only one or two gaps, no inferential statistics could be used to test for significance.

Table 4: Differences between numbers and densities of *Celtis africana* and *Chaetacme aristata* recruits (> 25 cm but < 2 m tall) in plots (non-gaps) and gaps.

	sample	area (m^2)	no. of stems	density
Celtis africana	plots	8400	4	0.0005
	gaps	4838	15	0.0031
Chaetacme aristata	plots	8400	3	0.0004
	gaps	4838	6	0.0012

Table 5: Difference between the number and density of Celtis africana seedlings (< 25 cm tall) in plots (non-gaps) and gaps.

	sample	area (m^2)	no. of stems	density
Celtis africana	plots	8400	5060	0.6024
	gaps	4838	100	0.0207

Discussion

- **Diversity**

Of all southern African forests, it is clear that the Natal forests have the highest species richness and diversity (Geldenhuys and MacDevette, 1989). Within the Natal forests, the lowland, coastal and dune forests seem to be more speciose than the montane forest type (Geldenhuys and MacDevette, 1989).

The forest in Hluhluwe yielded 86 species, with the potential of more existing being highly probable (see Figure 2). One can compare this with other Kwa Zulu-Natal forests. Moll (1978) cites total species numbers for Sodwana dune forests (115 species), Hawaan forest (63 species) and Hlogweni forest (60 species). MacDevette (unpub. as cited by Geldenhuys and MacDevette, 1989) cite species richness for the forests of Krantzkloof (86 species) and Karkloof (74). van Wyk *et al.* (1996) list 113 woody species as present in the Dukuduku forest. Thus, Hluhluwe seems to have an average species richness for coastal forests in Kwa Zulu-Natal.

- **Size-class distributions**

As Everard *et al.* (1995) explain, shade-tolerant species should exhibit inverse J-shaped curves. This reflects the situation of many small individuals and few large individuals. A species with this type of frequency distribution would appear to be regenerating under the canopy. In shade-intolerant species, recruits cannot develop under the canopy and regeneration is limited to sprouting and gaps. This type of species would typically have more large than small individuals, and would thus exhibit a much flatter, or even bell-shaped curve (Everard *et al.*, 1995).

The size-class distributions shown in Figures 5-12 are typical of a coarse-grained forest. Only *Ekebergia capensis* (Figure 8) shows the inverse J-shaped curve typical of shade-tolerant species regenerating under the canopy. The relatively high frequency of over 50 cm DBH trees is probably due to some favourable recruitment event, such as the lack of large scale disturbance, in the past. Given the same disturbance regime as at present, one would predict that *E. capensis* will become more common with time.

By examining the other size-class distributions, one can interpret the status of individual species in the forest. *Celtis africana* (Figure 5) shows a distinctly unimodal curve. This reflects the low production of recruits in mature forest. In the more disturbed and open margins, relatively more recruits are being produced. This indicates that shading has a negative effect on the recruitment of *C. africana*. The peak in the 20-29.9 cm DBH size-class probably translates to the height required to reach the canopy. A further increase in DBH would only occur relatively slowly after this as energy would be channelled into foliage and canopy spread.

Chaetacme aristata (Figure 6) seems to have the same pattern of recruitment, in mature forest and margins, as *Celtis africana*. However, *C. aristata* has a far greater frequency of small size-classes than does *C. africana*, reflecting its success in recruiting in gaps (see results). It seems as if *C. aristata* is able to tolerate a greater degree of shade than *C. africana*, as *C. aristata* is found in the subcanopy far more often than *C. Africana*. *C. aristata* seems to be a species capable of living in the shade, but incapable of regenerating under the canopy. It may need several gaps events to enable it to reach the canopy. Part of this lack of recruits may be due to its ability to sprout. This is more obvious in *Combretum kraussii*.

Combretum kraussii (Figure 7) displays the bell-shaped curve typical of a shade-intolerant species. There seems to be very little recruitment occurring, however this is probably due to the fact that *C. kraussii* is a strong sprouter and sprouters tend to channel minimum resources into seeds (Kruger *et al.*, 1996). It seems likely that established individuals will just persist, resulting in a preponderance of large size-classes, indicating several large stems belonging to one individual rather than one immensely tall canopy stem. Kruger *et al.* (1996) 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 *C. kraussii*.

Vepris lanceolata and *Chrysophyllum viridifolium* (Figures 9 and 10 respectively) both exhibit curves indicative of shade-intolerant species. The complete lack of recruits in the >1 cm DBH class shows its inability to recruit under the canopy. Recruitment for these species is limited to disturbed patches and gaps. The higher proportion of smaller size-classes seen in *C. viridifolium* reflects its superior gap taking abilities (see results).

Protorhus longifolia (Figure 11) is a classic example of an early forest species that is unable to recruit in mature forest. This species is simply persisting in the form of a few large individuals until large scale disturbance enables it to recruit once again. This species is likely to be lost if the required disturbance does not occur in the future.

Drypetes gerrardii (Figure 12) has a similar distribution to that of *Chaetacme aristata* (Figure 6). It would seem that *D. gerrardii*, although persisting in the subcanopy, is unable to regenerate there. It too would seem to need a break in the canopy, in order to regenerate. This distribution is different from that obtained for *D. gerrardii* by Everard *et al.*, (1995), where the species had an inverse J-shaped curve. It seems as though *D. gerrardii* and *C. aristata*, could well be shade-tolerant species that are suffering a recruitment failure in this forest. This could be due to browsing of seedlings by herbivores such as Nyala, or Red Duiker, in this forest. Tilghman (1989) cites the example of a regeneration failure due to the grazing impacts of white-tailed deer. Certainly, the effects of browsing are visible in the Hluhluwe forests.

Thus, one can see that this forest is certainly coarse-grained. From the size-class distributions of dominant species presented by Everard *et al.* (1995) one can see that the Hluhluwe forests are extremely similar to both the coastal scarp and the coastal lowlands forest type. Hluhluwe has species common to both coastal scarp and coastal lowlands forest types and the shapes of the dominant species curves of Hluhluwe also seem intermediate to these two types. Nevertheless, Hluhluwe is certainly more similar to the coastal scarp forest type and may be classified as an example of this type.

- **Community analysis**

In this forest, one can distinguish four canopy communities and two subcanopy communities.

The first subcanopy community (Group D) is typified by *Celtis africana*, *Canthium inerme*, *Calpurnia aurea* and *Erythroxylum emarginatum*. This community is generally found on north-east to south-east facing slopes, however this is not a defining characteristic. The second subcanopy community (Group E) is dominated by *Drypetes gerrardii*, *Maytenus nemorosa*, *Cassipourea gerrardii*, *Hyperacanthus amoenus* and *Chaetacme aristata*. This community was found in the bulk of the sample plots and is the most common subcanopy community in these forests.

The first canopy community (Group A) is typified by the presence of *Kiggelaria africana*, *Trichilia dregeana* and *Sapium ellipticum*. This community was found on a north-east facing slope, on the opposite side of a ridge from where the majority of sample plots were taken. Due to the aspect, this slope may be drier than South-facing slopes, from where the majority of the data were taken. Certainly, this community is the most distinct.

The second canopy community (Group B) is characterised by *Celtis africana*, *Protorhus longifolia*, *Rhus chirindensis*, *Vepris lanceolata* and *Ekebergia capensis*. This community made up the bulk of the plots sampled and generally lay along southerly facing slopes. However, there is substantial variation in the location and aspect of this community. To give the impression that this community is represented by a homogenous South-facing slope would be an over simplification.

The third canopy community (Group C) is not as distinct as the others. This community has semblance to both Group B and Group E. However, that which distinguishes this community from these groups is the presence of *Combretum kraussii*, *Harpephyllum caffrum* and *Scolopia zeyheri*.

The fourth canopy community (Group F) is nested within the subcanopy community Group E. One can see Group F as the result of the maturation of portions of Group E. This community is similar to Group E, but has in addition the canopy species of *Olea woodiana*, *Olea capensis*, *Cussonia sphaerocephala* and *Chrysophyllum viridifolium*.

It is apparent that the composition of the canopy and subcanopy differ substantially from one another. In addition to this, the canopy and subcanopy components of each plot are distinct. This is as one would expect for a coarse-grained forest. It would seem that the forest is made up of two subcanopy communities, with distinct canopy communities layered on top of these. In general, there does not seem to be consistent connection between the canopy community and the subcanopy community below it.

The differences between the two subcanopy communities identified are in part related to the appearance of young canopy species amongst the obligative subcanopy species. Due to the fact that the canopy and subcanopy components of each plot are not similar, one can assume that the appearance of potential canopy species in the subcanopy layer is a lottery process. Factors that influence the appearance of particular species, and thus communities, must include disturbance regime and environmental conditions.

From the above, one would predict that communities may well be relatively elastic and may fluctuate with time and disturbance regime.

- **Succession**

Due to the fact that mainly mature forest was sampled, a complete successional sequence into forest cannot be shown. Forest margins revealed mostly similar species and size-classes to the mature forest. This indicates that the forest margins sampled are not expanding and could in fact be being encroached upon. It is possible that the adjoining grasslands are burnt too frequently for the establishment or maintenance of forest.

One could interpret the sampled forests of Hluhluwe as being in "stable oscillation". This term refers to the fact that the growth form will remain constant in its climax state of tall forest, but the communities within this growth form will change with time. Periodic disturbance is interpreted as part of this process, and not as a reversion to an earlier successional stage. Thus, without the existence of any significant environmental variables, succession in these forests can only be interpreted in terms of the next upcoming canopy cohort. One could not predict that the subsequent canopy cohort would follow the same pattern.

In its present situation, Group E can be seen as the precursor of possibly three canopy communities. It can lead to closely related Group F. The elevation from subcanopy to canopy status of *Olea woodiana*, *O. capensis* and *Chrysophyllum viridifolium* would herald this succession. Group E could also lead to the establishment of Group B. The dominance of *Chaetacme aristata*, *Drypetes gerrardii* and *Ekebergia capensis* would mark this. The third possibility would be the advancement into Group C, with the maturation of *Scolopia zeyheri* and *Combretum kraussii*.

The second subcanopy community, Group D, is the potential precursor of two canopy communities. An increase in number and size of *Celtis africana* together with *Vepris lanceolata* would lead towards Group B, whereas the maturation of *Harpephyllum caffrum* could lead to Group C. All of the above hypothesised relationships are shown in Figure 4.

Group A is interpreted as a relict from a previous successional stage. Certainly the dominant species of this community are not regenerating in the forest. Under the present disturbance regime, one would expect this community to disappear eventually.

Thus, one can see that there is no real succession from community to community in this forest. Rather, shade-intolerant elements, that appear in different subcanopy communities, combine under varying conditions to provide a composite canopy community for that area. One can almost interpret succession in these forests as a process of random replacement and for confirmation of this, one must look at gap dynamics.

- **Gap dynamics**

From the analysis of the gap data one can see that there do not seem to be any fixed patterns in replacement. 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 inter-specific facilitation, where one species is commonly succeeded by another. Instead, there seems to be much variability in gaps sampled. This leads one to suspect that there may well be relatively random selection for establishment in gaps.

It is apparent that unless the disturbance has created a gap sufficiently large, the canopy will be plugged 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.

Gaps unquestionably influence the reproductive success of certain species. For both *Celtis africana* and *Chaetacme aristata*, there is an increase in understorey sized plants in gaps compared with non-gaps (Table 4). There is also far lower density of seedlings in these gaps (Table 5). This implies that survival and growth to the following size-class of the seedlings is greatly enhanced in gaps. The numerous seedlings produced in non-gap forest, 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 hold for numerous other species in this forest.

Despite this apparent success, gaps seem to be relatively unimportant in the Hluhluwe forests. Most of the dominant canopy trees of this forest are shade-intolerant species incapable of advanced regeneration and many species, especially *Sapium ellipticum*, *Trichilia dregeana*, *Protorhus longifolia* and

Harpephyllum caffrum, do not seem to be recruiting at all. These species will never be 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.

- **Management implications**

The ratio of trees to recruits (Table 3) indicates that of all the species shown, only *E. capensis* and *Croton sylvaticus* have more than twenty percent of their numbers as recruits in the understorey. Whately and Porter (1983) deemed this to be the figure that would ensure the species continued existence. Species with less than the requisite twenty percent were assumed to be endangered. According to this measure, most of the dominant canopy species are endangered in this forest. Although this measure is a little simplistic, and may overlook the effects of gaps and disturbance on shade-intolerant species, it does point out that several species are not recruiting *in situ*. This raises two issues that must be borne in mind when deciding on the management of this forest, namely disturbance regime and the extent of the area to be conserved.

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).

It is apparent from this study that an attempt to conserve anything less than the area presently occupied by this forest would result in species loss. The relationship between species and area (Figure 2) shows that any reduction in area would result in a reduction in species number. In fact, the forest may be losing species and area at present. The analysis of forest margins indicated that the forest may have been, or is being, encroached upon by grassland at this border. Management efforts could be directed at preventing the burning of the grassland in the immediate vicinity of the forest margins.

No effort should be made to curtail natural disturbances in this forest. Natural disturbance and heterogeneous conditions are what maintain species diversity in forests (Yamamoto *et al.*, 1995). In fact, the occasional made-made clearing of a patch may promote the regeneration of some presently non-recruiting shade-intolerant species. This active clearing could well be an important tool, if the maintenance of species diversity is a management goal.

At present, human utilisation of this forest is prohibited, although some evidence of harvesting was visible near the periphery of the reserve. It seems inevitable that South African nature reserves shall, at some point in the future, be forced to be of 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 understorey 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 understorey species, that is targeted for its bark at present (pers. obs.).

- **Hypotheses 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. 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 this coarse-grained forest originated, and still exists, 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. One can only assume 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 and Macdonald, 1983). Before that, one can assume that the area was utilised by indigenous peoples for swidden agriculture and iron-smelting, dating to roughly two thousand years ago (Hall, 1983; Deacon, 1992; Scoles and Walker, 1993). This iron-age lifestyle required a large timber supply, and has been identified as a potentially landscape transforming epoch (Feeley, 1980; Hall, 1983). 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. As one can imagine, 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 Figure 1) supports this assumption.

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 fastgrowing, 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 such as *Ekebergia capensis* are able to establish and increase in dominance. Thus, with time, these coarse-grained forests may become finer.

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, such evidence could be obtained by ethnological studies of habitation patterns, densities and practices of indigenous peoples pre-1895. This date spans back only two generations and thus the location and questioning of descendants should not prove impossible to achieve. Thus, research to test this model shifts from the biological to the social realm.

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 (multiple tree fall or fire) in order to become established. At present these species are mainly represented by large individuals. Very few saplings of these species are regenerating. However, this does not represent an immediate crisis as disturbance is a natural part of a forest and as long as the adults remain, these species may eventually find the opportunity to recruit.

Community succession in this forest seems to take the form of a random replacement of canopy species through two main subcanopy communities. This is similar to the finding of Quigley and Platt (1996), who in their analysis of temperate seasonal forests, found the canopy species randomly distributed but the understorey species uniformly distributed relative to the canopy. In Hluhluwe, one can recognise four canopy communities. There are most likely environmental and edaphic features that delimit these communities, however these could not be ascertained in this study. One can predict that in undisturbed areas, shade-tolerant species, such as *Ekebergia capensis*, will become more prevalent.

Gaps play a role in allowing shade-intolerant species to recruit, as can be seen for *Celtis africana* and *Chaetacme aristata.* The larger the gap the better, for these shade-intolerant species, as creeper choking and lateral infill often closes the smaller gaps.

Management for conservation of this speciose forest involves two aspects. Firstly, the forest does not seem to be expanding and regular burning of the forest margins should not be encouraged as any reduction in area of the forest will 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 invaluable asset is of paramount 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.

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