CHAPTER 6

POSSIBLE ALLELOPATHIC INTERFERENCE IN SAND FOREST: A PRELIMINARY STUDY

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Possible allelopathic interference in Sand Forest: a preliminary study[*]

Abstract

Sand Forest is a rare, species-rich tropical dry forest type mainly restricted to ancient coastal sand dunes in Maputaland. Forest patches are typically sharply delineated by a narrow (about 2–4 m wide) zone of bare or sparsely vegetated sand, followed by grassland and then woodland, which is the prevailing vegetation type in the region. We propose the hypothesis that Sand Forest may have allelopathic effects on its environment, hence the characteristic zonation of the surrounding vegetation. Data of exploratory germination trials utilising wheat and lettuce as bioassay plants, as well as inorganic and organic soil analyses, are presented to test this hypothesis. Sand Forest soil shows an inhibitory effect on the emergence and growth of wheat and lettuce; wheat being more sensitive than lettuce. Inhibition decreases progressively from Sand Forest through grassland to woodland. The inhibitory principle(s) can be mobilised (leached out) from soil by water. Certain, as yet unidentified, organic compounds present in Sand Forest soil occur in lesser quantity at the edge of the Sand Forest, but are apparently absent in the grassland and woodland soils.

Introduction

Floristically the Forest Biome in southern Africa may be classified into three broad forest types (Low & Rebelo 1996), namely Afromontane Forest, from temperate, mainly high altitude inland regions; Coastal Forest, from the subtropical/tropical eastern seaboard; and Sand Forest, a rare, tropical, dry forest type from the southern parts of the Mozambican Coastal Plain. Of these three forest types, Sand Forest is the least studied and poorest known. It is, however, of considerable biological and conservation interest because of its very restricted occurrence, rich biodiversity and presumed relictual, yet relatively recent, evolutionary status.

Sand Forest (Moll 1977; Moll & White 1978; Moll, 1980), also known as *Licuati* Forest in Mozambique (Myre 1964; Myre 1971), is more or less confined to the broad coastal plain between St Lucia in northern KwaZulu-Natal, South Africa, and Maputo in southern Mozambique—a region known as Maputaland. Forest stands occur as isolated patches mainly associated with

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[*] Findings are preliminary as the experimental design was not statistically robust.

ancient north-south trending inland sand dunes (Matthews *et al*. 2001). Some of these dune cordons, which can be traced for long distances along the inland margin of the coastal zone, mark stillstands during marine regressions (Botha 1997). The oldest ones are probably Pliocene (± 3 Ma BP) whereas the youngest are probably Late Pleistocene (30 000–10 000 BP) (Davis 1976; Hobday 1976; Botha 1997; Wright 1997).

Maputaland is recognised as a globally important region of plant diversity and endemism, referred to as the Maputaland Centre [MC] (Van Wyk 1994; Van Wyk 1996). In the MC high levels of endemism (especially neo-endemics) are spread across virtually the whole taxonomic spectrum, involving both plants and animals. A significant number of these endemics/near-endemics are associated with Sand Forest, making this perhaps the most remarkable plant community in the MC (Van Wyk 1996; Matthews *et al*. 2001).

An outstanding feature of Sand Forest is its very sharp edges, in most cases delineated by narrow (about 2–4 m wide) zones of bare to sparsely vegetated sand (Matthews *et al*. 2001). In Maputaland these zones of white sand are unique to Sand Forest and particularly noticeable from the air, even in satellite images. In most cases the sparsely vegetated zones are followed by grassy areas; these have a general appearance reminiscent of early successional (disturbed) vegetation due to the presence of pioneering plant species such as the grass *Perotis patens* Gand. (Matthews *et al*. 2001). Hitherto the bare to sparsely vegetated zones were generally assumed to have been caused by the trampling effect of game and cattle, with no special ecological significance attached to the phenomenon. This assumption is based on the fact that Sand Forest is a very dense (almost impenetrable) vegetation type, hence larger mammals are forced to walk around the edges.

In this paper we propose, for the first time, the hypothesis that the bare zones around Sand Forest are the result of an inhibitory effect induced by allelochemicals originating from the forest. Allelopathy is any direct or indirect beneficial or harmful effect of one plant species (including microorganisms) on the other through release of chemical compounds (allelochemicals) into the environment (Rice 1984). A plant may interfere with the growth of its neighbours directly through resource competition or chemical inhibition, or indirectly if it harbours or attracts organisms such as herbivores or pathogens that affect neighbours (Harper 1977; Fuerst & Putnam 1983; Weidenhamer 1996). Plant-plant interference (Rice 1984) may involve not only competition for water, light and nutrients, but also allelopathic phenomena that release toxic organic compounds into the environment. Under appropriate conditions, these chemicals are released in sufficient quantities to affect the growth and development of individuals of the same or other species (Seigler

1996). These substances are released into the environment through leaching of living plants, root exudates, volatilisation, residue decomposition and microbial activity (Muller 1969).

Proving that bioactive compounds (or their derivatives) exist in nature (Fuerst & Putnam 1983) and/or enter the environment (rhizosphere) to affect other organisms (Nilsson 1994), is exceedingly difficult, but it is well supported experimentally in studies performed under controlled conditions (Weidenhamer *et al*. 1989; Weston 1996). Such experiments have established that a large number of plants have the potential to inhibit seed germination and the growth of other plants through the action of allelochemicals. Here we present field observations and provisional experimental results carried out to test for potential allelopathic activity of Sand Forest soil. Although inconlusive in several respects, it is hoped that the new ideas raised may stimulate debate and further research.

Material and methods

This study comprises two components, namely various germination trials, and an investigation into the soil chemistry of selected sites. Fieldwork was conducted in the southern portion of the Tembe Elephant Park, northern KwaZulu-Natal. Tembe Elephant Park lies in the southern part of the Mozambican Coastal Plain and contains large representative samples of well-developed Sand Forest. In the study area the sparsely vegetated border zone of a *Drypetes arguta*-*Uvaria lucida* Sand Forest (Myre 1971) community on deep sandy soil is followed by *Andropogon schirensis*-*Tephrosia longipes* grassland (Myre 1971) that intergrade into various woodland communities. Samples of surface soil (not deeper than 200 mm) were collected from four different sites, along a transect from Sand Forest to woodland, as well as an additional site which once carried Sand Forest; these are described in more detail below.

Site 1: Sand Forest, sample taken in the Sand Forest approximately 10 m in from the edge of the sand forest border;

Site 2: Sparsely vegetated border zone directly adjacent to the Sand Forest, sample taken approximately 2 m outside the Sand Forest edge;

Site 3: Grassland directly bordering and associated with Sand Forest, but well away from the sparsely vegetated zone, sample taken about 15 m from the Sand Forest edge;

Site 4: Woodland, sample taken from a representative area of woodland, which is the prevailing vegetation type in the areas between Sand Forest;

Site 5: Sand Forest patch which was totally destroyed by a devastating crown fire approximately one year before. The area was still essentially devoid of vegetation.

All plant species present at Sites 1 to 4 (in a radius of approximately 10 m) were recorded, and an estimate of cover-abundance noted for each species (Table 1). These four soil samples formed the basis for most of the seed germination trials as well as some of the soil analyses. Soils at all the sample sites consist of dystrophic regosols. They are well leached (dystrophic) and relatively acidic [pH (H_2O) approximately 5.5–6].

Germination trials

Germination trials were conducted in pots in a greenhouse at the Department of Botany, University of Pretoria, Pretoria, under prevailing temperature and light conditions and begun on the 11 March 1997. We investigated the emergence and subsequent growth behaviour of lettuce (*Lactuca sativa* cv. Great Lakes) and wheat (*Triticum aestivum* cv. Inia) to test for possible soil-inhibitory effects. Soil samples were collected five days prior to the start of the trials.

In Trial 1 ten seeds were planted per pot, with five replicates for each soil sample, and in Trial 2 one seed was planted per pot, with 20 replicates for each soil sample. This was done for soil samples from Sites 1 to 4 and for both seed cultivars. Rainwater was used to water the pots. Excess water was collected in the base of each pot, and re-used in the watering of the same pot; this ensured that any compounds that could be leached form the soil would be returned to the same pot. Water collected in the base also preventing the soil from drying out. After 12 days the percentage emergence (percentage of total number of seeds planted that emerged above ground) was calculated based on seedlings present per pot. After 20 days the seedlings were carefully removed from the pots, the roots cleaned in water, the above and below ground parts separated and lengths measured. These parts were then dried to a constant dry mass in an oven (for 40 hrs) and weighed to obtain their mass. All these were done separately for the different trials and seed cultivars. Results are shown in Figures 1 & 2.

Table 1 Plant species composition, with cover-abundance percentages for each species, at the four primary soil-sampling sites in Tembe Elephant Park, northern KwaZulu-Natal.

Taxon	**Cover (%)**			
	Sand Forest (Site 1)	**Sand Forest edge (Site 2)**	**Grassland (Site 3)**	**Woodland (Site 4)**
Drypetes arguta	1–5			
Croton pseudopulchellus	1–5	rare		
Psydrax fragrantissima	1–5			
Landolphia kirkii	1–5			<1
Cyperus albostriatus	1–5			
Hymenocardia ulmoides	<1			rare
Manilkara discolor	<1			
Brachylaena huillensis	<1			
Tricalysia capensis	<1			
Pteleopsis myrtifolia	<1			
Cola greenwayi	<1			
Grewia microthyrsa	<1			
Hippocratea delagoensis	<1			
Uvaria lucida subsp. *virens*	<1			
Oplismenus hirtellus	<1			
Panicum deustum	<1.			
Tricalysia junodii	rare			
Phyllanthus sp. nov	rare			
Perotis patens		50	<1	
Indigofera podophylla		<1	<1	
Psydrax locuples		rare		<1
Andropogon schirensis			5–12	
Aristida stipitata subsp. *spicata*			1–5	
Digitaria natalensis			1–5	
Urelytrum agropyroides			<1	
Schizachyrium sanguineum			<1	
Pavonia leptocalyx			<1	
Panicum maximum				25–50
Strychnos spinosa				1–5
Euclea natalensis				1–5
Trichilia emetica				1–5
Tabernaemontana elegans				1–5
Bridelia cathartica				<1
Afzelia quanzensis				<1
Canthium setiflorum				<1
Ochna barbosa				<1
Justica flava				<1
Asparagus sp.				<1
Cleistanthus schlechteri				rare

In Trial 3 freshly prepared rainwater leachate (solution) from the Sand Forest soil sample (Site 1) were used in a series of germination treatments involving woodland soil (Site 4) and burned Sand Forest soil (Site 5). Five seeds of each of the two seed cultivars were planted per pot, with five replicates per treatment. The different treatments were as follows: (a) woodland soil watered with rainwater throughout the trial (control); (b) woodland soil watered with leachate from Sand Forest soil throughout the trial; (c) woodland soil watered with rainwater until the first emergence, thereafter watered with Sand Forest soil leachate; (d) burned Sand Forest soil watered with rainwater throughout the trial. Results are shown in Fig. 3.

In Trial 4 only soil from Sand Forest (Site 1) was used. The soil was first baked at 150°C for two hours. Five seeds were planted per pot, with five replicates for each seed cultivar. Rainwater was used to water the pots.

Soil analyses

A sub-sample of each of the soils from Sites 1 to 4 was subjected to soil analyses. In a first phase study, soil samples were analysed by means of X-ray fluorescent spectroscopy (Table 2). In a second phase study, soil samples from Sites 1 to 4 were supplemented by two additional soil samples representative of each biotype from sites elsewhere in Tembe Elephant Park (Table 3). Three soil samples per biotype were used to gain some understanding of the variation in soil chemistry within types. Soil samples were dried at 110 °C, homogenised, and split using a cone quartering method. One sub-sample from each sample was leached with distilled water using a mechanical shaker with an eccentric motion. Selected elements and physico-chemical characteristics were determined by conventional wet chemical methods and atomic absorption spectroscopy. One sub-sample from each type was leached with methanol, and a trace of the organic compounds present obtained on a gas chromatograph [GC] coupled to a mass spectrometer [MS]. No attempt was made to identify the organic compounds since this was considered essentially an exploratory investigation.

Table 2 Phase one soil analysis of the four principal soil types used in the germination trials

Component (ppm)	**Soil sampling site**			
	Sand Forest (Site 1)	**Sand Forest edge** (Site 2)	**Grassland** (Site 3)	**Woodland** (Site 4)
Density (g/ml)	1.34	1.43	1.43	1.42
Acidity	0.78	1.14	1.12	0.15
Total cations	2.36	1.65	1.64	4.66
pH (KCL)	3.61	3.91	3.88	5.09
Organic carbon (%)	38	0	0	0
C:N ratio	14.1	-	11.2	12.1
NIRS clay (%)	16	13	12	9
P	3	2	6	5
K	143	43	83	164
Ca	109	33	25	583
Mg	82	28	22	144
Acid sat.	33	69	68	3
Zn	0.6	0.3	0.3	1
Mn	12	4	3	5
C total	0.788	0.417	0.369	0.601
C organic	0.733	0.349	0.309	0.515
C/CO_3	0.055	0.068	0.06	0.086
B ppm	81	89	78	122
SiO_2	96.23	96.23	95.4	94.77
TiO_2	0.21	0.21	0.17	0.22
Al_2O_3	2.1	2.1	1.76	2.12
Fe_2O_3	0.8	0.8	0.64	0.98
MnO	*<0.02*	*<0.02*	*<0.02*	0.02
MgO	*<0.02*	*<0.02*	*<0.02*	0.03
CaO	0.02	0.02	0.02	0.12
Na_2O	0.06	0.06	0.06	0.21
K_2O	0.52	0.52	0.58	0.69
P2O5	0.03	*<0.02*	*<0.02*	*<0.02*
Cr_2O_3	*<0.01*	*<0.01*	*<0.01*	0.01
L.O.I.	1.03	1.03	0.95	1.66
TOTAL	100.84	100.84	99.44	100.54
Ba	137	114	124	139
Cr	23	20	18	108
Cu	15	15	15	14
Ga	*<5*	*<5*	*<5*	*<5*
Hf	*<5*	6	5	6
Mo	*<2*	*<2*	*<2*	3
Nb	4	4	4	4
Ni	4	4	5	6
Pb	12	12	12	13
Rb	28	24	24	26
Sc	4	5	3	5
Sr	24	18	19	30
Ta	*<5*	*<5*	*<5*	*<5*
Th	*<5*	*<5*	*<5*	*<5*
U	3	*<2*	3	3
V	16	15	14	17
W	*<5*	*<5*	*<5*	6
Y	*<5*	*<5*	*<5*	*<5*
Zn	5	5	5	7
Zr	150	150	131	176

Results and discussion

Germination trials

The emergence recorded in Trials 1 and 2 is depicted in Fig. 1. In all trials both lettuce and wheat seed showed a very low percentage emergence in Sand Forest soil (as low as 0–5%). Wheat showed a percent emergence lower than lettuce in all trails including those using the Sand Forest leachate. Wheat also showed an increased percentage emergence gradient from Sand Forest to woodland. In the case of lettuce, however, no clear gradient was observed in any of the trials: it only showed low emergence in all the Sand Forest soil trials. It would appear that some attribute of the Sand Forest soil is inhibiting emergence. No plant emergence was recorded in the baked Sand Forest soil, suggesting that the factor contributing to the inhibition of growth (germination) is present even after prolonged exposure to high temperature.

Figures 2 & 3 depict the total dry mass of the belowground and aboveground parts of the seedlings in trials 1 to 3. Because of the extremely small mass of the individual plant parts per pot, these had to be combined to make weighing practical. Hence no statistical analyses could be applied to these data sets of plant mass. We nevertheless did a single factor ANOVA analysis of the length measurements of the plant parts per pot, which gives an indication of the variability of the data (Figs 2B & 3). In nearly all the trials in which seed cultivars were exposed to the Sand Forest soil or leachate, the plants had the lowest mean dry mass (plant growth was inhibited or suppressed by some attribute of these soils). In Trial 2 (Fig. 2A), however, wheat planted in Sand Forest soil did not have the lowest dry mass. This can be explained by the fact that there was only one plant to be weighed; clearly not a sufficient sample. However, in the same trial lettuce planted in Sand Forest soil provided a sufficient sample and yielded the second lowest mean dry mass. In all the trials (except for the one with wheat noted above) there were distinct gradients along the soil sample transect from low to high mean dry mass. Greatest suppression of growth occurred in the Sand Forest soils, with the inhibition gradually decreasing with increasing distance from this biotype. Woodland soil always yielded the highest mean dry biomass.

Results of the trials with soil from the old burnt Sand Forest compared well with those from the woodland trials. It is possible that the inhibiting factor/compound in the old Sand Forest soil had been reduced to approximately the same levels as that found in woodland soil. This may be due to either leaching as a result of greater infiltration of rainwater (these areas were totally denuded of vegetation for about a year) or natural degradation in the soil, or a combination of both.

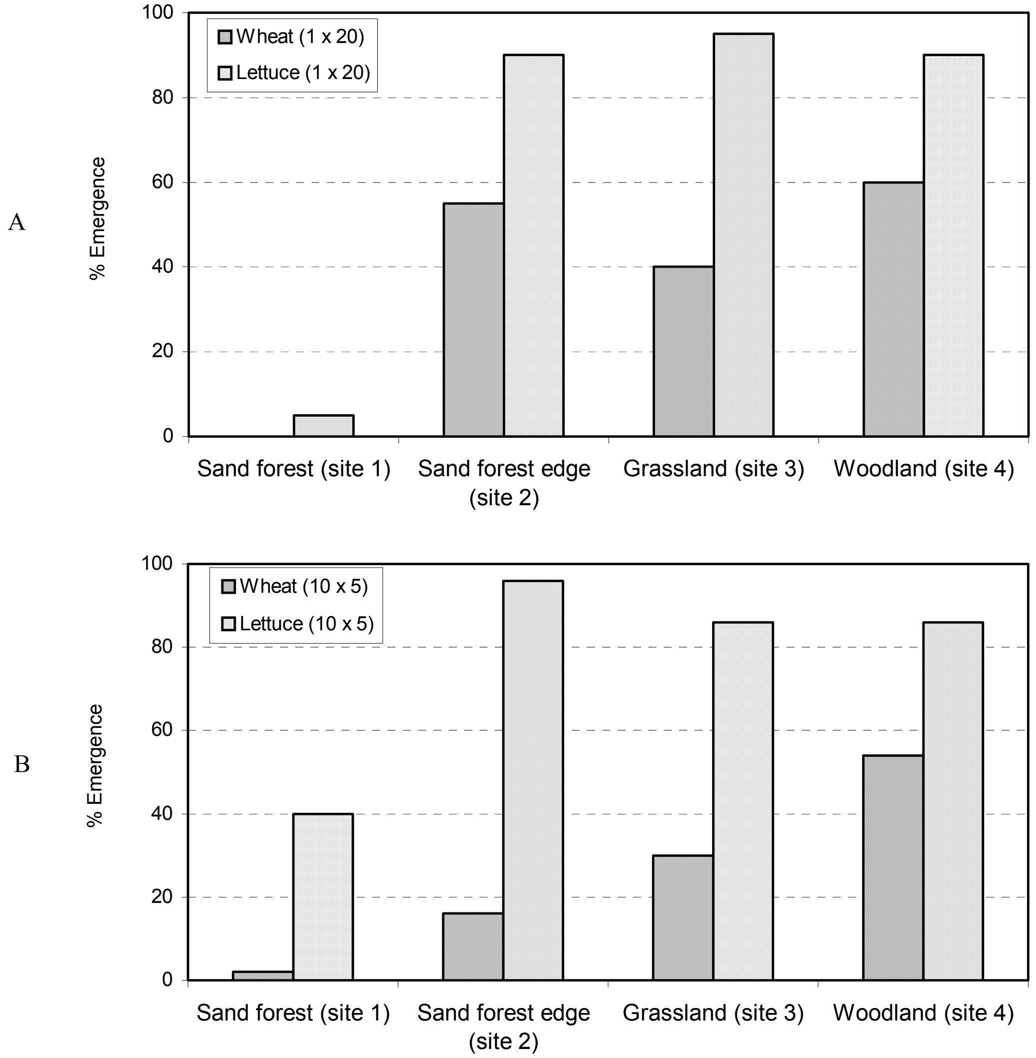


Figure 1 Percentage emergence of wheat and lettuce in soil samples from four different habitats. A: ten seeds per pot; five repetitions per species; watered with rainwater. B: one seed per pot; twenty repetitions per species; watered with rainwater.

The Sand Forest soil leachate trials also showed a distinct gradient. Treatments using Sand Forest leachate throughout the duration of the trial yielded the lowest mean dry mass. These results indicate that the compound/factor that suppresses growth can be mobilised by water moving through the soil, and is thus being leached. Results of the burnt Sand Forest soil trials support this deduction.

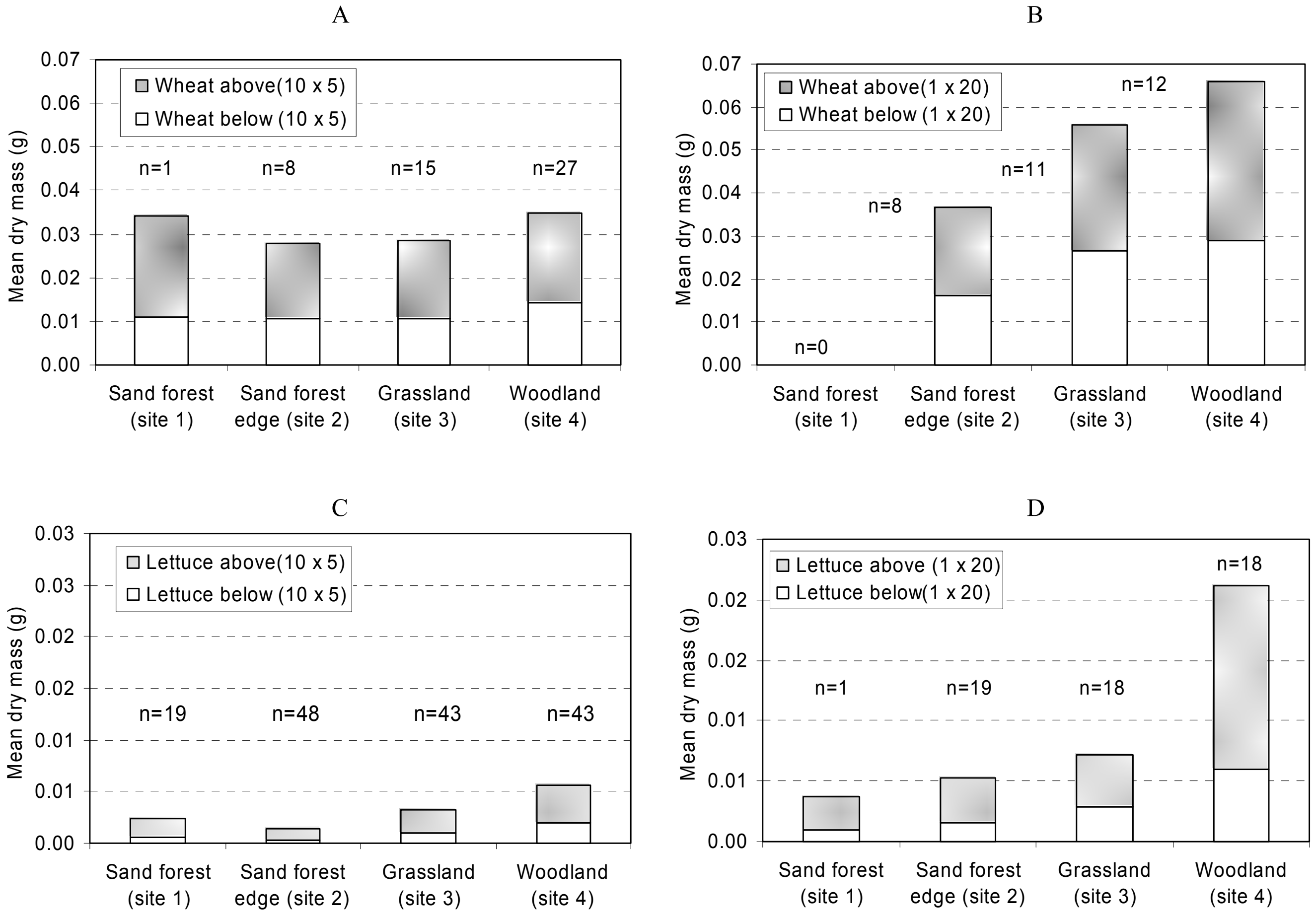


Figure 2 Mean dry mass (g) of the above and below ground parts of wheat and lettuce plants that emerged in soil samples from four different habitats. A&C: ten seeds per pot; five repetitions per species; watered with rainwater. B&D: one seed per pot; 20 repetitions per species; watered with rainwater. Single factor ANOVA analysis of the length measurements of the plant parts per pot (see text) in B indicates significant differences between treatments (Wheat, above: P=0.05, P-value 1.47^{-5}; below: P=0.05, P-value 5.63^{-6}. Lettuce, above: P=0.0, P-value 4.31^{-28}; below: P=0.05, P-value 1.93^{-13}).

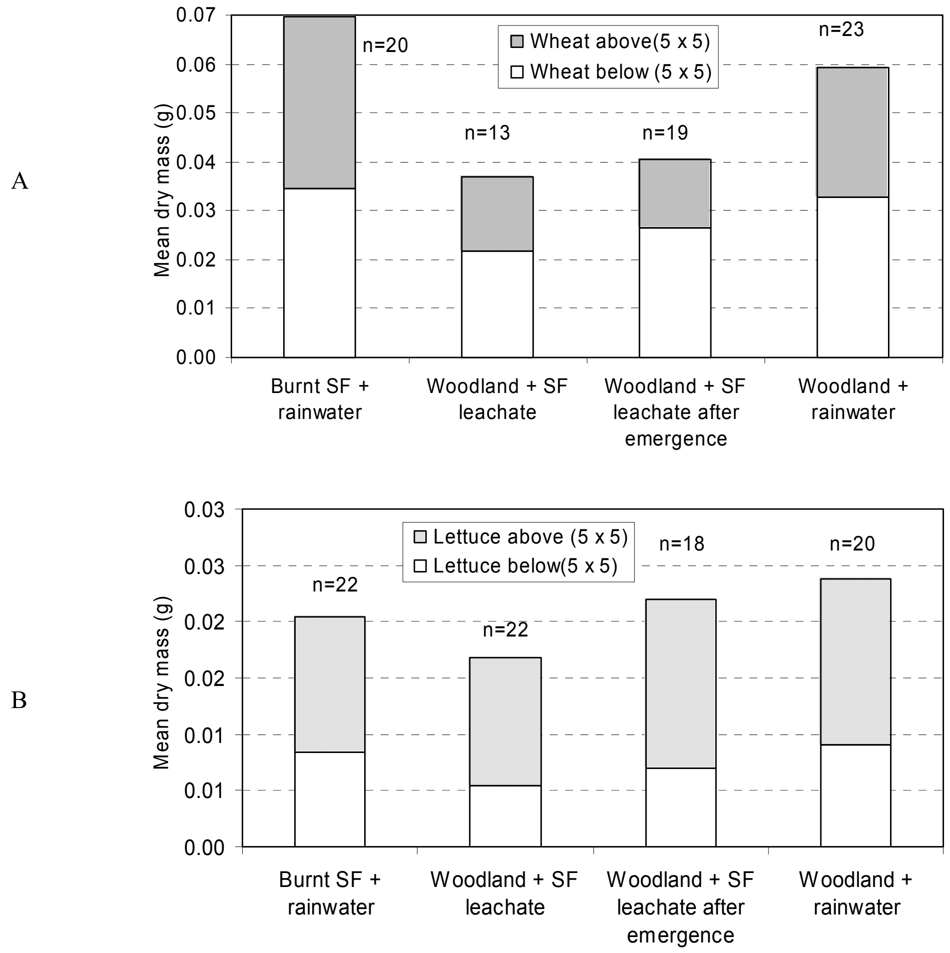


Figure 3 Mean dry mass (g) of the above and below ground parts of wheat (A) and lettuce (B) plants that emerged from soils subjected to different treatments (five seeds per pot; five repetitions per species). Treatments (from left to right): (a) old burned Sand Forest soil, watered with Sand Forest leachate; (b) woodland soil, watered with Sand Forest leachate; (c) woodland soil, watered with rainwater prior to plant emergence, thereafter with Sand Forest leachate; (d) woodland soil, watered with rainwater. Single factor ANOVA analysis of the length measurements of the plant parts per pot (see text) indicates significant differences between treatments (Wheat, above: P=0.05, P-value 0.0034; below: P=0.05, P-value 0.031. Lettuce, above: P=0.05, P-value 0.168; below: P=0.05, P-value 0.0088).

In Trial 1, where ten seeds were used per pot, the influence of competition (Weidenhamer Richaedson & Fisher 1989; Thijs Shann & Weidenhamer 1994; Weidenhamer 1996) for resources by the different emerging plants could come to the fore. However, results from this trial were almost identical to those of the other trials, except that the plants were smaller. This may be a possible indication of competition for resources, compounded by the effect of the hypothesised growth-suppressing compound. In this case intraspecific competition is considered to have complemented the suppression of growth. Water and light were not limiting in this case, with the result that competition may well have involved macro and/or micro-nutrients. The primary objective of an allelopathic species is to eliminate other species (Seigler 1996). This means that allelopathy mainly manifests at the interspecific level, whereas resource competition occurs both at inter- and intraspecific levels.

Soil analyses

Results of the first phase soil study (Table 2) show the dominant oxide in all the samples to be silica, indicating that the coversands in the study area consist mainly of quartz sand. Lesser quantities of aluminium, manganese, calcium, sodium and potassium are indicative of the mineral suite associated with resistates, for instance feldspars. The trace element analyses show that boron, barium, chromium, hafnium, niobium, nickel, lead, rubidium, scandium, titanium, iron, strontium, uranium, vanadium, zinc and zircon are present in noticeable concentrations. The rare earth elements, plus the presence of uranium, zircon and titanium is indicative of a heavy mineral suite similar to that found in the present-day coastal dune cordon along the Maputaland Coast. Typical minerals would include zircon (accounting for the presence of uranium, zirconium and hafnium) and ilmenite (titanium and iron). These minerals are stable oxides and silicates with the result that the metals should not be available for uptake by plants and animals. The high boron concentration evident in all the samples is ascribed to the presence of tourmaline, a boron-containing stable complex silicate mineral. Since the potential for these elements to have toxic effects on plants may be high, it was considered necessary to investigate the bio-availability of some of the elements in a second phase analyses. Boron, molybdenum, calcium, copper, sodium and vanadium in particular were investigated due to their potential positive/negative effects on plant growth.

Inorganic analyses

Inorganic analyses of the soil samples (Table 3) indicate that calcium, copper, molybdenum, sodium and vanadium are present in low concentrations in all the samples. Boron is present in concentrations at approximately the lower detection limit for the instrumentation (0.5 ppm), with the exception of one sub-sample from the Sand Forest where the boron concentration was slightly higher (1.5 ppm). Aluminium values were relatively high, although no marked difference in concentrations can be seen between the different biotypes. Acidity of the distilled water extract as well as the conductivity, however, show marked differences between Sand Forest soils and those from the other three biotypes. Sand Forest soils give rise to a leachate that is more acidic, and contains more dissolved solids. The pH of the Sand Forest edge, grassland and woodland soils ranged from 5.5–6.4, while that of the Sand Forest itself ranged from 3.8–5.8. The conductivity, a measure of the total amount of dissolved solids in solution, ranged from 15.4–22.6 mS/m in the case of the Sand Forest leachate, while the values for all the other sites ranged from 6.6–12.9 mS/m. From these results it is clear that the Sand Forest leachate contains a compound or compounds that render the soil more acidic. Basic inorganic soil chemistry is, however, essentially similar for soils from all four the sites, as indicated in Table 1.

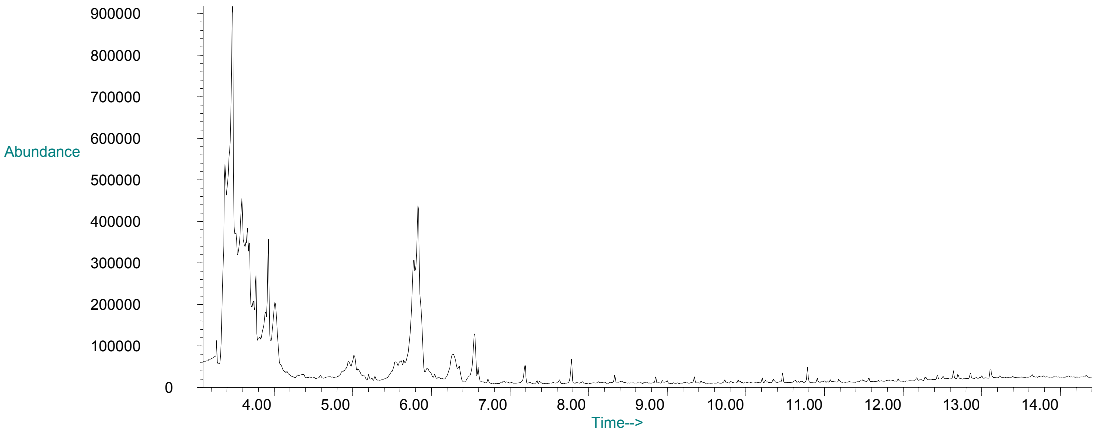
Table 3 Phase two selected inorganic soil analysis of soils from four different biotypes: Sand Forest, Sand Forest edge (border zone), grassland and woodland. In addition to the sample used in the germination trials, two more soil samples for each biotype from different localities (1, 2 & 3) were analysed to gain some understanding of the variation in soil chemistry within the biotypes.

Component (ppm)	**Soil sampling site**											
	Sand Forest			**Sand Forest edge**			**Grassland**			**Woodland**		
	1	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
pH (KCL)	3.8	3.9	5.8	5.7	5.7	5.6	5.5	6	6	6.4	6.3	6.3
Conductivity	15.4	20.2	22.6	5.7	8.2	8	7.4	6.4	5.6	12.9	8.2	8.3
Al	1.18	1.61	0.46	2.01	1.7	1.15	2.42	1	1.97	1.44	0.88	3.29
B	1.5	0.7	0.7	0.5	0.5	0.4	0.5	0.7	0.7	0.6	0.4	0.6
Ca	2	3	23	2	3	3	2	2	2	10	7	8
Cu	0	0.03	0.01	0	0.01	0	0	0	0	0.01	0	0
Mo	0	0	0	0	0	0	0	0	0	0	0	0
Na	6	8	8	6	7	6	7	6	6	6	5	6
V	0	0	0	0	0.01	0.01	0.01	0.01	0.01	0.01	0	0.01

Organic analyses

Methanol leachates produced for analysis were colourless, except for the Sand Forest sample, which had a yellow colour (perhaps indicative of plant phenolics). GC-MS traces of the organic compounds showed compositional differences between the leachates from the different biotypes. The traces for woodland and grassland habitats were virtually identical, both in terms of the compounds present as well as relative abundance. Most of the compounds in the leachates from these biotypes moved very rapidly through the column. In the sample from the edge of the Sand Forest there is a small decrease in the relative abundance of the most prominent compound noted in the first two types, while there are small increases in compounds with slightly retarded rates of movement. The sample from the Sand Forest shows the continuation of the trend, with a major increase in slow-moving compounds and concomitant decrease in fast-moving compounds.

Sample wl



Sample gl

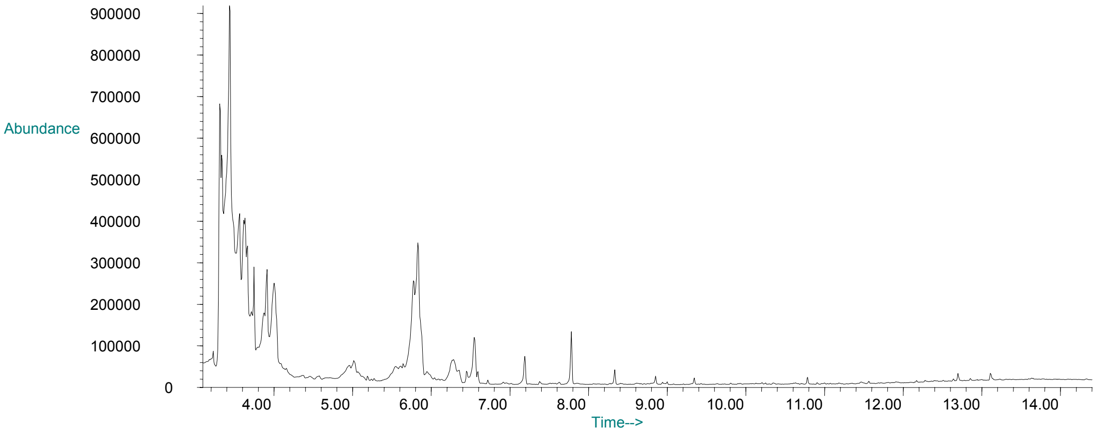
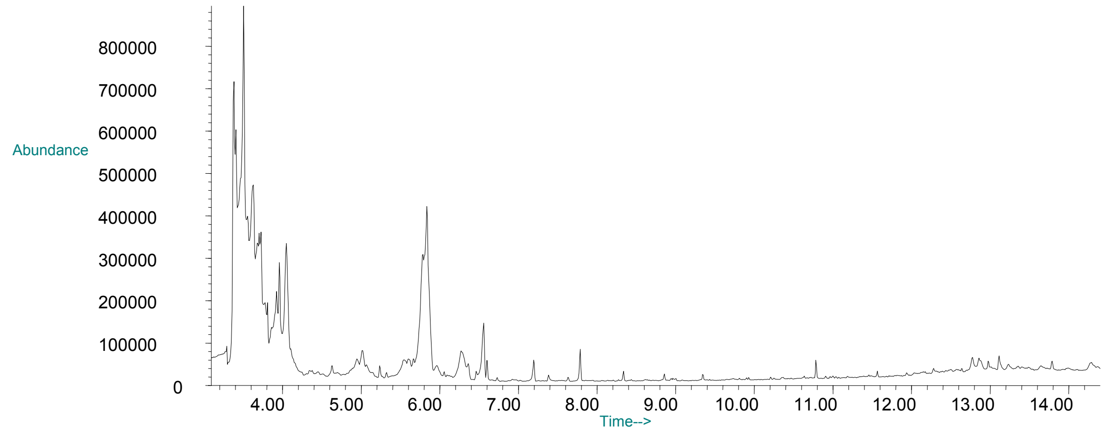


Figure 4 GC-MS traces of organic compounds (methanol leachates) in the four principal soil types used in the germination trials, namely woodland (wl) and grassland (gl). Note increase in slow-moving compounds and concomitant decrease in fast moving ones in soil samples from the Sand Forest edge and Sand Forest.

Sample sfe



Sample sf

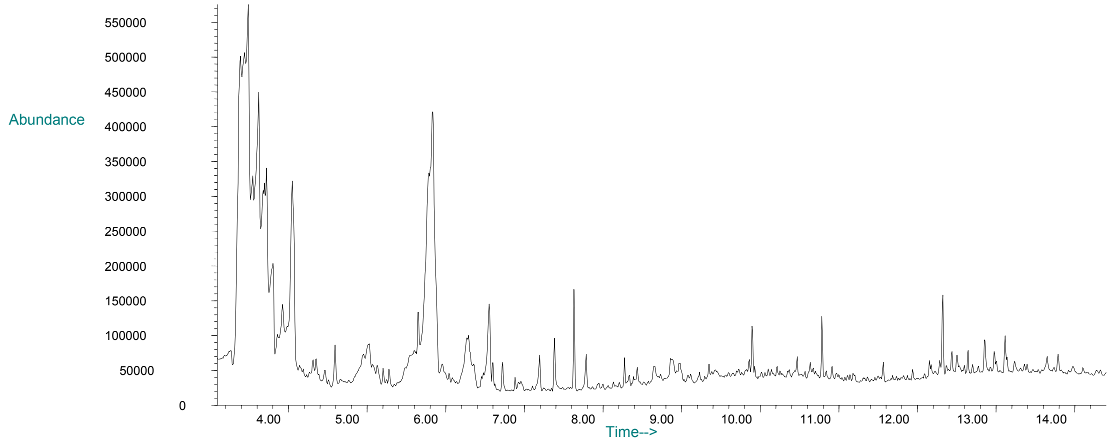


Figure 4 (Continued.) GC-MS traces of organic compounds (methanol leachates) in the four principal soil types used in the germination trials, namely Sand Forest edge (sfe) and Sand Forest (sf). Note increase in slow-moving compounds and concomitant decrease in fast moving ones in soil samples from the Sand Forest edge and Sand Forest.

Potential benefits of allelopathy to Sand Forest

Assuming that the inhibitory effects displayed by Sand Forest soils in the germination trials also operate under natural conditions, what is the potential benefit of allelopathic properties to Sand Forest? Which would be the target species inhibited by the allelochemicals? It is speculated that in the case of Sand Forest the target species are likely to be found among non-Sand Forest specialist, although there may well be Sand Forest species that are also affected. However, as Sand Forest is floristically so distinctive, the bulk of the species of this community, at least in the recruiting phase, must somehow cope with this inhibition. That woodland species are particularly sensitive to the inhibitory compound(s) are perhaps suggested by the nearly total lack of transition of woodland to Sand Forest. Whereas Sand Forest species are to be found in woodland (as isolated outliers), woodland species (again as outliers) are very rarely seen in typical stands of Sand Forest, especially in the drier inland parts of Maputaland. In the wetter more coastal forms of Sand Forest (for example *Artabotrys monteiroae-Dialium schlechteri* Forest (Matthews, Van Wyk & Van Rooyen 1999), some woodland species have been recorded—again very few, but nevertheless more than what is present in the drier Sand Forest patches. This difference could be due to the higher rainfall which would manifest in higher infiltration, leaching and microbial decomposition, thus resulting in more rapid removal of the active inhibitory compounds.

Sand Forest is an unusual forest type in the sense that it is found under relatively low rainfall (average ~600 mm/annum)—conditions not normally associated with major forest development. In the drier inland parts of Maputaland, such as in Tembe Elephant Park, no development of new Sand Forest patches is evident, nor is there any evidence of regeneration following the occasional complete destruction by fire of existing patches. Hence, at least in the latter parts, Sand Forest appears to be a relict vegetation type, having probably evolved in response to aridification over a considerable period of time from perhaps a Coastal Forest type that covered the dune cordons during former wetter climatic conditions. Sand Forest therefore has to directly compete with woodland species and communities well adapted to arid and fire conditions. By evolving allelopathic properties, Sand Forest may well have attained an advantage in a habitat/biozone that it would otherwise not be able to compete in.

Furthermore, Sand Forest is extremely sensitive to fire; it does not regenerate after being burned. Yet, natural woodland and grassland fires are of frequent occurrence throughout Maputaland. The bare or sparsely vegetated zones surrounding Sand Forest undoubtedly also serve as an effective natural fire break. In this regard striking parallelisms seem to exist between the pattern of Sand Forest distribution in Maputaland and that of Florida Scrub in the United States of America, a dense, fire-sensitive vegetation type that occurs as isolated islands throughout the more common fire-adapted Florida Sandhill vegetation (Williamson, Richardson & Fisher 1992; Fischer *et al*. 1994; Weidenhamer 1996).

Is Sand Forest allelopathic?

For proof of an allelopathic interference, the following criteria, modelled after Koch's postulates in microbiology, should ideally be met (Fuerst & Putnam 1983): (a) identify and quantify specific symptoms of interference; (b) isolate, identify, and synthesize the toxin, characterising its biological activity through bioassays; (c) simulate the interference by providing the toxin as it would be provided in nature; and (d) quantify the amount of toxin released to the environment and taken up by the target plant.

As the present study was exploratory in purpose and approach, these criteria are far from being satisfied. On the other hand, owing to the complexities of allelopathic interations, apparently no cases of unambiguous proof of allelopathy in the field, according to the criteria proposed above, has yet been reported. However, while conclusive proof of chemical interference may not be attainable, the challenge of obtaining strong supportive evidence for chemical interference remains (Weidenhamer 1996). Our field observations and the results of germination trials and soil analyses strongly suggest that some type of allelopathic interference is taking place in and around Sand Forest. Furthermore, in the case of Sand Forest, we suspect that plant phenolics (reviewed by Inderjit 1996) may well be implicated as allelochemicals.

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CHAPTER 7

VEGETATION-ELEPHANT INTERACTION IN TEMBE ELEPHANT PARK

MANUSCRIPT

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The comparative use of woody species in different habitats by elephants in Tembe Elephant Park, Maputaland, northern KwaZulu-Natal

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Abstract

The use of woody species by elephants in different vegetation types in Tembe Elephant Park was investigated using a modified Point-Centred-Quarter sampling design. Samples were located in seven different vegetation types and the intensity of utilization of individuals of different plant species was measured by estimating the proportion of the canopy volume that had been removed by elephants. A classification of species into utilization categories was produced which enabled assessment of the importance of different species to elephants, and also of the potential impact of elephants on different tree species. Ninety of the 137 plant species encountered in the study were utilized. Thirteen species were selected for, 32 were used at random, 35 were avoided and at least 9 were rejected totally. Selection at the plant family level also occurred. Seventy five percent of the diet was made up by seven plant species and 90% by 13 species. Because the staple diet was made up by relatively abundant species, rarer species which are highly preferred may be threatened. Species were utilized with different intensities in different habitats. Those that were selected for in one type were also usually heavily utilized in other types but with different intensities. The number of species that were utilized in any habitat was proportional to the number found in that vegetation type. The results suggest that elephants could have serious negative impact on the diversity of Sand Forest. The need for monitoring and further study in this regard is indicated.

Introduction

Management of elephant populations requires a thorough understanding of their impact on plant populations. The first step in developing this understanding is to establish the intensity of utilisation of individuals of different plant species. To date no data on the use of plants by elephants have been collected for Tembe Elephant Park [TEP]. The studies available on food selection by elephants in other localities are not helpful in enabling prediction of the use of plants in Tembe Elephant Park as no general principles emerge from these studies. A sampling strategy, that provided relatively comprehensive data quickly and effectively, was used. An adaptation of the Point-Centred-Quarter (PCQ) technique (Cottam & Curtis 1956) that reduced the number of measurements required was used to establish utilization of woody species in different plant communities (vegetation types). These data were used to construct a classification of woody species in terms of their abundance, importance in the elephant diet, and the potential effect of feeding on the demographics of the species. Results are compared to those from other localities. The primary aim of this paper is to detail the vegetation types and species selected for by elephant based on utilization levels and to make predictions about which vegetation communities and woody species are most vulnerable to extirpation and/or transformation, in Tembe Elephant Park.

Study area

Tembe Elephant Park is 30 013 ha in extent and located in Maputaland, northern KwaZulu-Natal (Figure 1). The stratigraphy consists of a multi-layered sequence of aeolian sand deposits of marine origin, which forms north-south trending dune ridges (SACS 1980). Elevation ranges from about 50 m to 129 m above sea level. The soils of the study area developed from the relative homogeneous, grey, silicaceous, aeolian sands and are highly leached (dystrophic) and relatively acidic (Watkeys *et al*. 1993). In the depressions between the ridges, duplex soils consisting of a clay layer occurring in depressions in the sands, that in the wet season, form pans. The only permanent surface water in the reserve for most years is the Muzi swamp, in the east of the reserve. This flows north into Mozambique. The region has a warm to hot, humid sub-tropical climate with hot summers and cool to warm winters (Schultze 1982). Temperatures range from 4° C to 45° C with a mean of 23.6° C. Rain is received throughout the year with a summer peak. Total annual rainfall at Sihangwana varies from 245 mm to 2 105 mm with a mean of 716 mm. Average humidity’s are relatively high even in the drier inland parts of the region.

For Figure 1; Vegetation map of Tembe Elephant Park showing place names and road network see Chapter 5.

Tembe Elephant Park is located within the Maputaland Centre of Endemism. More than 2 500 plant species occur in the centre, which includes 230 endemics and near-endemic plant species and/or infraspecific taxa (Van Wyk 1994). Eighty-four Maputaland Centre endemic plant taxa have been recorded for the study area (Matthews *et al.* 2003). According to the revised vegetation map of South Africa, Tembe Elephant Park falls into the *Subhumid Lowveld Bushveld* (Granger 1996) of the Savanna Biome. Moll & White (1978) distinguish four vegetation zones in Tembe Elephant Park i.e. Pallid-sand Bushveld, Sand Forest, the Muzi Swamp and Palmveld. Matthews *et al.* (2004) recognises eight physionomic units with different species composition (Fig 1). Based on these the following types were differentiated in this study:

1. *Sand Forest.* This type occurs as a forest – grassland mosaic with many small open grassland patches scattered in the forest matrix. Prominent species are *Drypetes arguta, Cola greenwayi, Uvaria lucida* and large specimens of *Newtonia hildebrandtii*. Sand Forest is rich in plant species with many endemics. (Sand Forest covers about 15% of Tembe Elephant Park).

2. *Thicket on sand*. Prominent species are *Acacia burkei, Grewia caffra, Zanthoxylum capense* and *Vepris lanceolata*. In places, this habitat can become very dense. (This thicket covers about 10% of Tembe Elephant Park).

3. *Closed Woodland/Thicket on clays*. Prominent species are *Spirostachys africana, Coddia rudis, Ziziphus mucronata, Schotia brachypetala* and the geophyte *Sansevieria hyacinthoides*. This habitat is characterised by large termiteria on which bushclumps occur. (This type covers about 5% of Tembe Elephant Park).

4. *Closed woodland on Sand.* This type is a slightly more open form of Thicket. (This type covers about 10% of Tembe Elephant Park).

5. *Open Woodland*. Prominent species are *Strychnos madagascariensis*, *Albizia adianthifolia*, *Albizia versicolor*, *Acacia burkei, Terminalia sericea, Combretum molle*, and the grasses *Panicum maximum* and *Andropogon gayanus*. Two forms can be recognised; one in which *Albizia adianthifolia* is abundant (OW/A), and one where it is less abundant (OW). (This type covers about 35% of Tembe Elephant Park: OW - 20%, OW/*A - 15%*).

6. *Sparse Woodland*. Prominent species are the grasses *Themeda triandra, Pogonarthria squarrosa, Trachypogon spicatus.* The shrubs and trees are represented by *Strychnos madagascariensis, Terminalia sericea* and many geoxylic suffrutices such as *Dichapetalum*

cymosum, Parinari capensis subsp. *incohata*. (This type covers about 10% of Tembe Elephant Park)

7. Different *Grassland / Wooded Grassland* types. (This type covers about 10% of Tembe Elephant Park).

8. *Wetlands*. The most important of the wetlands is the Muzi swamp, in the east of the reserve It is covered by reeds through most of its length with only a few places having open water. The other wetlands are perennial pans on duplex soils where depressions have formed and been filled by rainwater. (Wetlands covers about 5% of Tembe Elephant Park).

The area was proclaimed a reserve in 1983 and the south, west and eastern borders were fenced with a game proof and electric fence. In 1989 the northern border with Mozambique was fenced. When Tembe Elephant Park was proclaimed many of the large types of mammal were absent or at very low numbers. Nine types of animal, White Rhinoceros (35), Black Rhinoceros (21), Burchell's Zebra (100), Impala (800), Eland (80), Waterbuck (100), Kudu (unknown), Blue Wildebeest (50) and Giraffe (50) were re-established, and the existing populations of Buffalo (50), Nyala (200), Bushbuck (unknown) Reedbuck (250), Warthog (unknown), was boosted by reintroduction. Numbers in brackets are the population estimates during the study (Matthews 1994).

Elephants have been recorded in the region more or less continuously since 1840 (Harris 1852; Baldwin 1895; Bulpin 1966). No accurate estimate of numbers has been obtained to date because accurate counts are not possible in the Closed Woodlands and Sand Forests. In 1940 around 40 elephants were thought to be resident in the region. Since then the estimate has ranged between 30 and 85. The current estimate is around 155-185 individuals (Matthews 2004). The sex ratio is biased towards bachelor bulls. Ostrosky (1989) estimated a male to female ratio of 1.5: 1.

Local opinion maintains that a more or less stable breeding group has probably been resident in the region of Tembe Elephant Park for a long time. The limits to their home range are thought to have been the Muzi swamps in the south-east and the Rio Maputo floodplains some 28 km to the north-west in Mozambique. This area would have included all of the northern and most of the central sections of the current Tembe Elephant Park area. Crude densities are therefore probably higher than prior to fencing.

Methods

Data Collection

Food selection has been studied in elephants using a wide range of techniques. The direct methods include observation of feeding (Napier-Bax & Sheldrick 1963; Jarman 1971; Guy 1976; Kalermera 1989; Paley & Kerley 1998), gut content analysis (Buss 1961), and faecal analysis (Ward 1982). Indirect methods include counting of the frequencies of use on individuals of different plant species (Coetzee *et al.* 1979) and estimates of the intensity of use on individuals of different plant species sampled in transects and quadrats (Van Wyk & Fairall 1969; Anderson & Walker 1974; Penzhorn *et al.* 1974; Jachmann & Bell 1985; Okula & Sise 1986; Viljoen 1989; Stuart-Hill 1992).

The objectives of this study were to determine the intensity of use of different species in different vegetation / habitat types. A secondary objective (not reported on in this paper) was to determine the spatial distribution of utilisation. Because plotless sampling methods are usually less time consuming than plot-based techniques (Walker 1970), the Point-Centre-Quarter (PCQ) Method (Cottam & Curtis 1956) was selected as an appropriate strategy, but this was modified so that the sample sizes required for accurate estimates of density of each species and the intensity of utilisation could be reduced by reducing the sampling bias towards individuals in the smaller height classes. This was achieved by recording distances to the nearest individual in five different height categories (<0.5 m, 0.5–3 m, >3–5 m, >5–8 m, >8 m) in each quarter.

Sample sites were distributed in a stratified random manner throughout the study area, in the seven vegetation/habitat types (i) Sand Forest, (ii) Thicket on sand, (iii) Thicket on clay, (iv) Closed Woodland on sand. The Open Woodland on sand was subdivided into two strata on the basis of the density of *Albizia adianthifolia* giving (v) Open Woodland with low densities of *A. adianthifolia* and (vi) Open Woodland with high densities of *A. adianthifolia,* and (vii) Sparse Woodland on sand. Sampling sites were more or less equally distributed in the seven vegetation types based on the Tembe Elephant Park road network (a pilot survey revealed no association of utilisation of trees by elephant with the roads). Forty-five sampling sites were consequently distributed at random distances along the road network. At each site, six PCQ points were located along a line that ran at an approximately right angle to the road. Three points were located on each side of the road, with the first suitably away in from the road to ensure that individuals were included in each quarter without having to cross the road. At each point distances to the nearest individual in the five height categories were measured in each quarter. Five to nine sites were sampled in each vegetation type, giving from 30 to 54 PCQ points at which five sets of distances were measured (five height classes) in each habitat type. This gave a sample of 150 to 270 PCQ points and 600 to 1080 distance measurements in each stratum. The PCQ method usually requires samples larger than 250 PCQ recordings for estimating the densities of species in a particular vegetation type (Heyting 1968). Because both the variation in distance measurements and the variation in relative abundance were decreased by subsampling in the five height categories in different vegetation types, the sample size was considered adequate to obtain the estimates of density required. The number of individuals utilised by elephants at each PCQ point ranged from one to 16 individuals, with a mean of seven. This was considered adequate to obtain estimates of the frequency of utilisation of the different species.

For each individual plant, the species was identified and the height estimated. Canopy reduction by elephant (or other cause) was estimated using Walker's (1976) method for estimating the percentage of the canopy volume removed using eight classes, 0, from 1–10% of the canopy removed, >10–25%, >25–50%, >50–75%, >75–90%, >90–99% and 100%. Where no individual occurred in a particular height category in a particular quarter, a cut-off distance or the next nearest individual in one of the other quarters was used. If no fourth individual could be found nearby, a pseudo-species with a cut-off distance of half the distance between the sample points (10–100 m) was introduced. Sampling was carried out from January to October 1995.

Calculations

Several methods have been used to assess the intensity of use of various plant species by elephant. The simplest index used is the percentage of individual’s utilized (Coetzee *et al.* 1979). The proportion of the canopy removed from various species was used by Anderson & Walker (1974). The relative proportion of mouthfuls ingested was used by Guy (1976). Preference indices of various forms that express the proportion that a species makes up in the diet, as a fraction of the proportion that it makes up in the habitat, have been used in several studies on feeding in elephants (Petrides 1975, Guy 1976, Ishwaran 1983, Viljoen 1989). Similarly they have been used in studies on food selection in a wide range of types of animals (Manly *et al.* 1993). The use of preference indices of this form has also been widely criticized by many authors e.g. Lechowicz 1982, Owen-Smith & Cooper 1987, Manly *et al.* 1993 and Schooley 1994. For these reasons three different types of indices were calculated in this study (i) The Forage Ratio, (ii) Manly’s Alpha and (iii) Ivlev’s Electivity Index (Krebs 1989). The three different indices produced almost identical results. In only a very few instances where the value of the index lay on the threshold separating neutral use and slight avoidance, the electivity index indicated slight avoidance whilst the other two indicated neutral use.

The purpose of using preference ratios in this study is twofold: (i) to establish which species might be impacted by elephant feeding, (ii) to establish how both the absolute and relative abundance of a particular species in different habitats influenced the degree of selection. An index was therefore required which would allow comparisons between vegetation types.

Direct comparison of the value of Manly's Alpha index in different habitats is cumbersome because the threshold value between preference and avoidance is different for each habitat. The Electivity Index and Forage Ratio are much more easily compared, but the biological meaning of the Electivity Index is not easily interpretable. Manly's Alpha index allows test of significance for differences in preference in the different habitats (Manly 1974). The form of the ratios result in the value of all three indices, but particularly the Forage Ratio being influenced by the relative abundance of the different species. However, relative abundance also influences preference in real terms because a preferred species may be utilized more heavily where there is less interference from other food sources. The fact that there was agreement between the Forage Ratio and Manly's Alpha index suggests that the differences in the absolute value were more likely a consequence of real changes in selection rather than an artifact of the way that the forage ratio is calculated. Because preference is influenced by relative abundance, in environments where the relative abundance is changing, (such as in environments where elephants have been recently confined) the preference shown for different species can also be expected to change. For this reason any classification of trees in terms of their preference in Tembe Elephant Park at this time should be regarded as preliminary.

This logic resulted in our selection of the Forage Ratio as the index used to construct the classification and determine the influence of composition on use, with the following considerations taken into account. In theory, when the proportion that a species makes up in the diet is the same as its relative abundance, the Forage (Preference) Ratio is equal to 1. However, when utilisation rates are low (number of all species utilised / number of all species available < about 0.3), and where diversity is high, and the number of any one species in the sample low, small (about 10%) changes in the proportion of a particular species utilised, result in large changes to the preference ratio (Fig 2). Because of the effort required to obtain adequate samples in diverse vegetation, sample sizes are almost always low (number of any particular species

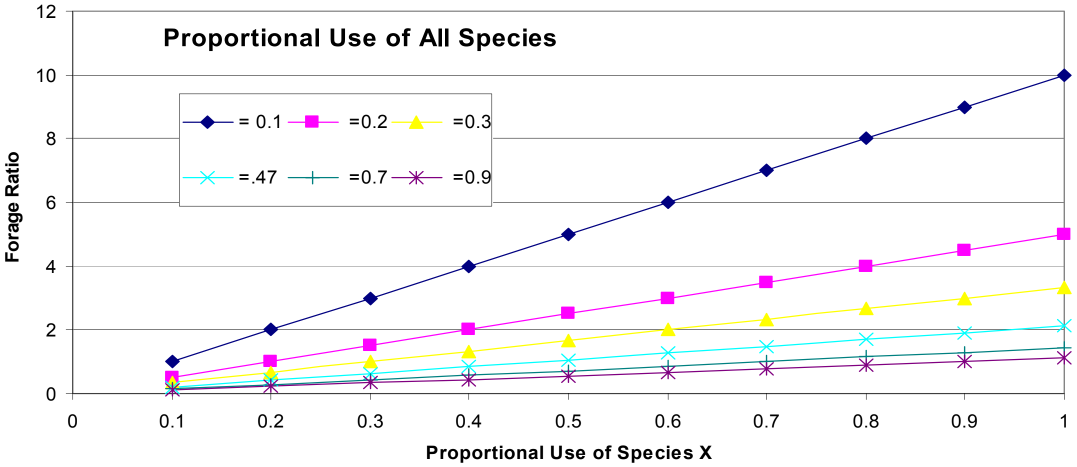

Figure 2. The relationship between the proportion of a particular species utilized and the forage ratio at different proportions of all species utilized.

(species X) available is low), so random, slight changes in the number of utilized individuals in the sample for any particular species result in large changes to the value of the Forage Ratio. The proportion of individuals utilised in this study was 47% (of individuals > 0.5 m height). Fig 2 shows that for the curve where the ratio of the number of all species utilised / the number of all species available is equal to 0.47, a 5% change in the ratio of the number of the particular species (Spp. X) utilised / number of the particular species (Spp X) available, changes the Forage Ratio value by 0.1. In this study the proportions utilized in different habitats varied between 24% and 62%. For the curve where the ratio is 0.24, a 5% change in the ratio results in a change in the Forage Ratio of 0.3 and at 0.62 a change of 0.1. A 10% leeway seems acceptable in deciding on whether the species is selected for or not. This effectively gives 90% confidence intervals. Boundaries for the worst case were used and the following range was applied. Neutral or random use was assumed where the Forage Ratio fell in the range 0.7–1.3, selection where the ratio was greater than 1.3, and rejection in the range >0 <0.7, and total rejection where no use was observed. Samples of less than three individuals, although listed, were treated with caution in the analysis.

To determine the importance of any species to elephant and at the same time establish what impact elephants might have on any particular species, the values for three parameters were used. These are the volume utilized from each species, the degree of selection (preference) shown for different species (assumed to be a reflection of the nutritional status), and the density of each species. If one examines the combinations of selection and density that together result in a particular intensity of use (in terms of the volumes of material removed) only certain combinations are logically possible. For example, if the volumes removed are categorized as high, moderate, low, or trace, the preference ratios as selected for, neutral use, rejection, and total rejection, and the densities as high, moderate, low, rare, 52 combinations which result in either high, moderate, low or trace volumes removed are possible. However of these only twelve are logical. For example, high volumes removed cannot be obtained from a combination of strong rejection and low densities. Thus species which make up a high proportion of the diet (high volumes removed) may (i) have high to low abundance and be lightly to strongly selected for, or (ii) have high abundance and be used at random (neutral selection). Species, which make up a moderate proportion of the diet may (iii) have low abundance and be selected for, (iv) have moderate abundance and be randomly utilized. Species, which make up a low proportion of the diet may (v) have low to rare abundance and be selected for, (vi) have low densities and be neutrally used*,* (vii) have low to moderate densities and be rejected. Species, which have trace volumes in the diet, may (viii) be rare and selected for, (ix) be rare and neutrally used, (x) have moderate to low densities and be rejected. Totally rejected species add two further categories, depending on whether they have moderate to high, or low to rare abundance.

The species which are the principle food sources which comprise the elephant's staple diet, and which supports them, come from categories (i) to (v). In terms of the impact on the populations of any particular species, those that are most likely to decline in both relative and absolute abundance are those species that are relatively rare and strongly selected for. Those species which are totally rejected or which have moderate to high abundance and are rejected will increase in relative abundance and are likely to increase in absolute abundance as well if any competitive advantages of the selected for species are removed. Thus species that fall into categories (i) to (vi) and in (viii) are those most likely to decline. Those in categories (vii), (ix), (xi), and (xii) are those most likely to increase in abundance. In evaluating the classification it is important to bear in mind that it is a loose classification, since any particular species may be allocated to a different group in different communities and could be allocated to a different group entirely as relative abundances change over time. The purpose of the classification is to indicate (i) which woody species elephants depend on as their staple diet, and (ii) which species might be threatened in terms of extirpation and therefore of concern to conservation managers at this particular point in time.

Densities were calculated for individuals in each height category separately following the method outlined by Mueller-Dombois & Ellenberg (1974).

Results and discussion

Selection for and intensity of utilisation of different woody species

Overall use

In this study 4 913 individual woody plants were sampled. No utilization was recorded in the <0.5 m height class. Of the 3 773 individuals over 0.5 m in height, 1 766 or 47% were utilised.

Of the 200 tree and shrub species occurring in Tembe Elephant Park (Tembe Herbarium Collection Records) 137 were encountered in this study. Of these 90 (66%) were utilised, and 61 (45%) had more than 10% of the canopy removed.

Douglas-Hamilton (1972) reports 134 out of 650 plant species utilized in Lake Manyara National Park, Uganda (21%); Jachmann & Bell (1985) report 35 out of 41 tree species (85%) used in *Brachystegia* Woodland in Kasungu National Park, Malawi.

The AHC (all habitats combined) column of Table 1 gives the Preference Ratios for each species in all vegetation types combined. It is immediately apparent that some species are utilized much more intensively than others. There are 13 species (10%) that are selected for (17 species {14%} if samples with <3 individuals are included). Thirty-two species (24%) (or 38 {30%} including species with <3 individuals), are neutrally utilized. Thirty five species (28%) are rejected, and nine (7%) (or 35 {28%} including species of <3 individuals) are totally rejected. There are undoubtedly some species amongst the 24 species which have samples of less than three and for which no utilization was recorded which are neutrally used or rejected.

Jachmann & Bell (1985) report 13 out of 35 species (37%) as being selected for and 22 out of 35 (63%) non-selected for. (The proportions in this study for PR values >1 are 34 out of 91 utilized species, which is also 37%).

There are relatively few species that have large volumes removed. Fifty percent of the total canopy volume removed, is made up by three species: *Albizia adianthifolia* (22.25%), *Terminalia sericea* (16.21%) and *Albizia versicolor* (10.83%). The next 25% of the total canopy volume removed, is made up by four species: *Acacia burkei* (8.95%), *Sclerocarya birrea* subsp.

caffra (7.43%), *Dialium schlechteri* (4.97%) and *Strychnos madagascariensis* (3.75%). The next 15 % is made up by six species; *Combretum molle* (3.6%), *Afzelia quanzensis* (3.17%), *Acacia robusta* subsp. *clavigera* (2.97%), *Trichilia emetica* (2.36%), *Spirostachys africana* (2.0%), *Hymenocardia ulmoides* (1.45%).

A comparison of Anderson & Walker's (1974) utilisation data measured as the proportion of the canopy volume removed, and Guy's (1976) data measured as the number of mouthfuls ingested, both from the Sengwa Wildlife Research Area, Zimbabwe, indicates that the two indices (Forage (and total canopy volume removed) are related. For those species common to the two studies, mouthfuls = 0.25 $*$ canopy volume; $r^2 = 0.85$. It may therefore be assumed that the volume removed can be used as a measure of the importance of a species in the diet. Thus 90% of the contribution to the diet by trees is made up by 13 species. The other 75 species make up the remaining 10%.

Mohosho (1997) calculated that 10 % of the winter diet was made up by monocotyledons (grass and unidentified monocotyledons). Bowland & Yeaton (1997) in the Natal Lion Park, South Africa, recorded an average 45% of the diet consisted of grass. This amount however ranged between 12% and 74% depending on the season, with the highest amount used in autumn and the lowest in late winter. The summer utilization of grasses in Tembe Elephant Park is slightly higher than the winter values (Mohosho 1997), so it is likely that the proportion of the diet made up by monocotyledons over the year is higher, probably around 15–20%.

De Boer *et al.* (2000), working in the Maputo Elephant Reserve (MER) some 70 km NE of Tembe Elephant Park recorded 31.1% of the diet is made up by grass and unidentified monocotyledons. The Maputo Elephant Reserve has much more open grassland than Tembe Elephant Park, so the proportion is probably a lot less in Tembe Elephant Park. From this can be seen that the Tembe Elephant Park and Maputo Elephant Reserve elephant diet is bias towards dicotyledons.

Trends in which a few species make up the bulk of the diet have been reported from other areas. In Murchison Falls National Park, Buss (1961) reports that, ± 90% of the diet is made up by grass. The data Table 1, presented by Buss (1961) shows that three species make up 72% of the contribution to the diet by woody plants. The next four woody species contribute 7%. From Guy's (1976) data a rough estimate of the percentage contribution can be calculated, which yields about a 50% contribution by three species, an additional 14% by the next four woody species, and the next ten species add a further 18%. Paley & Kerley's (1998) data show that grass and forbs made up 45% of the winter diet of elephants in Addo. Of the trees (succulents and shrubs) six species made up 53% of the diet. Of the woody species encountered in Bowland & Yeaton's (1997) study in the Natal Lion Park, five woody species made up 75% of the diet and 19 species made up 90%.

In the study by De Boer *et al.* (2000) in the Maputo Elephant Reserve, five species only make up 25% of the diet of woody plants. Ten species make up 46% of the diet, 20 species make up 68%, and 30 species 83% of the diet. The biases inherent in determining dietary composition from faecal analysis are thought to account for this disparity.

The only study on food selection in elephants where species composition is sufficiently similar to make comparisons with Tembe Elephant Park is the study by De Boer *et al.* (2000). There was a 15% overlap in the species recorded for this study and that by De Boer *et al.* (2000), [23 species in common]. Of the 17 preferred species in this study, two (*Sclerocarya birrea* and *Terminalia sericea*) were recorded as preferred in Maputo Elephant Reserve. Of the remaining species in common, which are preferred in Tembe Elephant Park, three (*Afzelia quanzensis, Albizia adianthifolia, Euphorbia tirrucalli*) are used at random, and four (*Albizia versicolor, Phyllanthus reticulatus, Strychnos madagascariensis, Syzygium cordatum)* are rejected in Maputo Elephant Reserve. Of the species that are neutrally used in Tembe Elephant Park, four (*Acacia karroo, Balanites maughamii, Commiphora neglecta, Dialium schlechteri*) are also used at random in Maputo Elephant Reserve. One (*Ziziphus mucronata*) is preferred in Maputo Elephant Reserve and two (*Acacia burkei, Mimusops caffra*) avoided. Of the species avoided in Tembe Elephant Park, three (*Phyllanthus reticulatus, Xylotheca kraussiana, Zanthoxylum capense*) were also avoided in Maputo Elephant Reserve, four (*Dichrostachys cinerea, Euclea natalensis*, *Grewia caffra, Vangueria infausta*) were neutrally used. None that were avoided in Tembe Elephant Park were preferred in Maputo Elephant Reserve. Similarly none of the species preferred in Maputo Elephant Reserve were rejected in Tembe Elephant Park.

Selection appears to occur at the family level as well as the species level. Based on selectivity indices calculated as the proportion of individuals in a family that are utilized, as a ratio of the proportion of individuals in a family available, of the 40 families recorded, ten are selected for, eight neutrally used, nineteen rejected, and three totally rejected. The families Anacardiaceae (1.7; 3/4; where the figures are the Preference Ratio, the Number of Species Used in the Family / Number of Species in the Family recorded in TEP), Combretaceae (1.7; 4/5), Mimosaceae (1.4;

8/11), Myrtaceae (1.8; 1/2), Meliaceae (2.4; 2/3), Bignoniaceae (2.8; 1/1), Clusiaceae (1.6; 1/1), Lythraceae (1.9; 1/1), and Vitaceae (2.8; 1/1) are selected for (Tables 2 and 3). The Euphorbiaceae (0.8;; 14/19), Caesalpiniaceae (1.1; 3/5), Loganiaceae (1.0; 3/4), Rhamnaceae (1.2; 2/2), Sapotaceae (1.1; 3/4), Balanitaceae (0.7;1/1), Capparaceae (1.1; 1/2) and Meastomataceae (0.9; 1/1), are neutrally selected for. The Annonaceae (0.2; 3/3), Asteraceae (0.2; 1/2), Ebenaceae (0.2; 2/5), Rutaceae (0.2; 4/6), Malvaceae (0; 1/1), Rhizophoraceae (0; 1/1), are moderately to strongly ejected. The Ochnaceae (0; 0/3), Sapindaceae (0; 0/3) and Verbenaceae (0; 0/3) are totally rejected.

Within and between habitat differences in species use

In each of the habitats some species are selected for (7–32 species; 10–38% of the species present, excluding those less than 0.5m in height), some neutrally used (5–17 species; 6–26% of the species present), some rejected (1–11 species; 3–17% of the species present), and some are not used at all (13–38 species; 37–49% of the species present) (Tables 1 & 2).

Of the list of the forage species (those that were utilized in any vegetation type), a relatively small proportion of the individuals of any particular species (between 25% and 67%, excluding samples with less than three individuals) were utilized in a particular vegetation type. In general, the more species in the vegetation type, the more species were used (a linear regression of number of species utilized (y) against number of species in the vegetation type (x) yields $y = 0.617 x - 2.451$; $r^2 = 0.93$). The proportion of species utilized in the different vegetation types, distinguished for this study, however, appears to be relatively constant, with mostly just over a half the available species being utilized, (with a range between 50% and 65%), and around a third being relatively well utilized (>10% canopy volume removed). Thus Sand Forest has the most species used followed by Thicket on clay, Closed Woodland, Open Woodland (with high *Albizia adianthifolia* densities), Thicket on sand, Open Woodland and Sparse Woodland. About two thirds of the plant families present in any one vegetation type were utilized, again with the number of families utilized being higher where the number of families was higher, and lower in the types with fewer Families. Sand Forest and Thicket have the greatest number of families utilized, followed by Open Woodland, Open Woodland (with high *Albizia adianthifolia* densities), Thicket, Closed Woodland and Sparse Woodland (Table 2).

Unlike the number of species utilised the volume removed from each vegetation type is not related to any of the number of species, the number of species utilised or the density in the vegetation type (Table 2). Rather it is related to the abundance of large preferred trees which are used in proportion to their abundance or which are selected for. Thus those vegetation types with high abundance of species from Utilisation Classes (i)–(vi) and (viii), are most heavily utilised in terms of the volumes removed. Open Woodland (with high *Albizia adianthifolia* densities) and Open Woodland are most heavily utilised. Thicket on Clay, Thicket and Closed Woodland are utilised with moderate intensity, and Sand Forest and Sparse Woodland, least intensively (Tables 2 and 3). The only comparable data from the literature appears to be Anderson & Walker's (1974) statement that in the Sengwa Wildlife Research Area, Zimbabwe, those types with the highest abundance of favoured species were most heavily utilised. The implication of this for the management of elephants is that the staple diet species (Utilization classes (i), (ii) and (iii)) comes from these habitats. Much of the diversity of interest to conservation occurs in a single vegetation type such as Sand Forest. The rare selected for species in Utilization classes (viii) play no part in influencing the survival or fecundity of elephants, and are therefore likely to be impacted on negatively

There are 32 species selected for (PR>1.3) in Sand Forest, 15 in Thicket on sand, 22 in Thicket on Clay, 20 in Closed Woodland, 11 in Open Woodland, seven in Open Woodland (with high *Albizia adianthifolia* densities), and ten in Sparse Woodland (Table 1). The numbers of species selected for in any one habitat, as with the total number of species utilized, follows the trend in numbers of species present in each habitat type ($y=0.37x-6.1$; $r^2 = 0.5$, where y is the number of species selected for in the habitat type and x is the number present).

It is apparent in Table 1 (preference indices) that many of the forage species are selected for with more or less equal intensity in each of the vegetation types, whilst some species are selected for more intensively, and others less intensively in a particular vegetation type compared to others. In general where a species is strongly selected for, it is selected for in all types, though with varying intensities, which range from neutral use to strong selection. These species all occur in Utilization classes (ii), (iii), (v) – *Albizia adianthifolia, Albizia versicolor, Sclerocarya birrea, Terminalia sericea, Acacia robusta, Afzelia quanzensis, Trichilia emetica, Galpinia transvaalica, Garcinia livingstonei, Antidesma venosum, Manilkara discolor* and *Syzygium cordatum*. Again in general the preference ratio is higher in those types where the relative abundance of the species is lower; indicating that if a species is preferred it is actively sought after even when a large number of other species may be present. The relationship is however not apparent for all species, as some species show a wide variation in use in the different vegetation types, with the species being selected for in some types and rejected in others. These species come from a wide range of Utilization classes and include *Acacia burkei, Balanites maughamii, Psydrax locuples* and *Dichrostachys cinerea*. Many of the rare species that occur in only one habitat type are moderately to strongly selected for. These include all of the species from Utilization class (viii) and *Newtonia hildebrantii* and *Wrightia natalensis* in Sand Forest. A large proportion of the species which occur only in Thicket on Clay or in Thicket on Clay and only one or two other habitat types are selected for. These include *Manilkara discolor, Boscia foetida, Euclea divinorum, Cordia caffra, Elaeodendron transvaalensis, Euphorbia tirucalli.* On the other hand many of the species confined to Sand Forest are not, examples are *Manilkara discolor, Erythrophleum lasianthum, Cleistanthus schlechteri, Drypetes arguta, Tricalysia delagoense*. This suggests that perhaps the better nutritional status of clays soils may be a factor influencing selection. Only three widely dispersed species are rejected entirely. These are all from Utilization class (xi).

It has been relatively well established that species composition influences selection so it would be surprising if different habitats were not in fact utilized with different intensities. However the wide variation in the degree of selection for forage species in the different habitats suggests that there is no single factor that explains the differences in the intensity of use for many of the species discussed above. Rather different combinations of factors may be important in different situations.

Conclusions

1. The bulk of the elephants diet is made up by species which are relatively common, and which are strongly, moderately, lightly or neutrally selected for i.e. those belong to Utilisation Classes (i)–(iv). These are *Acacia burkei, Acacia robusta, Afzelia quanzensis, Albizia adianthifolia, Albizia versicolor, Combretum molle, Dialium schlechteri, Sclerocarya birrea, Strychnos madagascariensis, Terminalia sericea and Trichilia emetica.*

2. It appears that the suite of species, including both relatively common and rare species, that are strongly selected for are being utilised to the extent that they may be reduced to very low levels, or possibly local extinction. The threat to each of these species depends on the demographic responses of each one to environmental conditions, including utilisation by elephants. These species which include those from Utilisation Classes (i), (iii), (v), and (viii) are *Acacia robusta, Afzelia quanzensis, Albizia adianthifolia, Albizia versicolor, Antidesma venosum, Elaeodendron transvaalensis, Euphorbia tirucalli, Ficus stuhlmannii, Galpinia*

transvaalica, Garcinia livingstonei, Hyperacanthus microphyllus, Kigelia africana, Manilkara discolor, Newtonia hildebrandtii, Phyllanthus reticulatus, Syzygium cordatum, Sclerocarya birrea, Terminalia sericea, Tricalysia junodii, Trichilia emetica, Warneckea sousae and *Wrightia natalensis.*

3. More species are utilised in diverse habitats than in less diverse habitats. The proportion selected appears to be more or less constant at around 60% of the species available.

4. Those species most highly selected for are used in all habitats in which they occur, but the degree of selection (the relative preference) is different in the different habitats, and appears to be influenced, for example, by the relative abundance of other forage species.

5. Several species which are Maputaland Centre endemics with a limited distribution, and which have very little conservation status outside of Tembe Elephant Park may be threatened by elephant impact. These are *Combretum mkuzense, Dialium schlechteri Hyperacanthus microphyllus, Warneckea sousae, Tricalysia junodii* var. *junodii* and *Wrightia natalensis*.

6. Because utilization is influenced by relative abundance, the classification presented here should be expected to change. For this reason only potential impact of elephants on any particular species can be predicted from this single survey. The accurate prediction required for the successful management of biodiversity requires that all of the factors influencing demographics be established first and thereafter monitored continuously.

Although the elephants prefer plant species from woodland habitats, evidence suggest that they are increasingly utilising Sand Forest species. Sand Forest is a unique vegetation type of limited distribution and contains many Maputaland Centre endemics species. Currently indications are that Sand Forest integrity may be threatened as a vegetation type within Tembe Elephant Park, as a result of elephant forage patterns. This is as a result of general thinning of intact forest, as well as extirpation of plant species which are a) highly selected for, b) recruits infrequently and usually in small numbers and c) species that grow slowly so that adults are not easily recruited.

Management implications: concluding remarks

The primary reasons for the proclamation of TEP was the protection of the natural elephant population of Maputaland AND the protection of Sand Forest (TEP has the greatest area of protected Sand Forest in South Africa). This has lead to a conflict of interests between Sand Forest and elephant.

Issues that need to be considered in the management around Sand Forest and elephant within TEP are:

- Expand the range of the elephant (increase surface of protected area) so as to reduce time spent in the Sand Forest zones.
- Reduce return rates of elephant to the Sand Forest areas in the western portion of the Park where most of the Sand Forest in the Park is to be found, this could potentially be done through water point management.
- Reduce direct foraging impacts on Sand Forest, which are thinning the forest as well as removing Sand Forest recruitment possibilities. Elephant and other wildlife numbers should be curtailed within TEP, especially if the range expansion possibilities cannot be achieved in the near future.
- Elephant exclusion areas, electric fencing of Sand Forest such as in done in Phinda Game Reserve.

As a rapid survey technique the approach taken in the present study appears to have worked well. Useful information on the relative use of different species and the likelihood of negative impact on their abundance from elephant feeding activity has been provided.

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Table 1.

Table showing the preference index for each species in each habitat type. The species are grouped (thick dashed line) in terms of the volume utilized and the volume available, and then in terms of selection in all habitats combined (see text). Abbreviations are: SF – Sand Forest, Th – Thicket, ThC – Thicket on Clay, CW – Closed Woodland, OW- Open Woodland, OWA – Open Woodland with high *A. adianthifolia* densities, SW – Sparse Woodland
AHC – All Habitats Combined, VPD – Volume removed/Preference/Density, CLS – Utilization Class.
For the volumes removed H – High, M – Moderate, L – Low, T – Trace.
For the Preferences S – Selected (>1.3), N – Neutral Use (0.7-1.3), R – Rejected (>0 <0.7).
For the Densities Available H – High Densities, M – Moderate, L – Low, R – Rare.
* indicates samples of less than 3 individuals. # indicates those species where the All Habitats Combined data result in a classification which is different to that for most of the separate habitats.
The figures surrounded by a light dotted line indicate where the utilisation of a particular species in a particular habitat type differs substantially from the intensity of use in other habitats types.

Species	SF	Th	ThC	CW	OW	OWA	SW	AHC	VPD	CLS
Albizia adianthifolia	4.2	2.5*	2.4*	2*	2.1	1.5		2.1	HSL	i
Albizia versicolor		2.5*	2	2	1.9	1.5	1.7	1.9	HSL	i
Sclerocarya birrea sub. caffra	2.4	1.9	2	1.8	1.9	1.2	1.5	1.8	HSM	i
Terminalia sericea	4.2*	2.1	1.5	1.6	1.6	1.2	1.4	1.6	HSH	i
Acacia burkei	1.4	1.4	1	0.9	0.6	0.7	0.7	0.8	HNH	ii
Acacia robusta sub. clavigera	2.8	2.5*	2.1	2		0.8		1.7	MSL	iii
Afzelia quanzensis	1.4	1.9	1.9	0.9	1.8	1.3	2*	1.4	MSL#	iii
Trichilia emetica	4.2*		1.2*	1.4	2.1		2*	2	MSL	iii
Combretum molle	0*	1.3	1.7	1.1	1	1	1.2	1.2	MNM	iv
Dialium schlechteri	1.7	1.3	1.6	0.5	0.9	1	0	0.9	MNM	iv
Strychnos madagascariensis	2.1*	2.1	1.4	1.3	0.9	1.1	1.2	1.3	MNH#	iv
Galpinia transvaalica	4.2*		2.4*					2.1	LSL	v
Garcinia livingstonei			2.4*	2	1.3	1	2*	1.5	LSL	v
Antidesma venosum			0.8	1.2	1.8	1.3		1.6	LSL	v
Manilkara discolor	1.8		2.4*					1	LSL*	v
Newtonia hildebrandtii	2.6							1.3	LSL	v
Wrightia natalensis	1.4							0.7	LSL	v
Ficus stuhlmannii					2.1*			2	LSR	v
Syzygium cordatum			0.8	1.2	1.8	1.6*	2*	1.4	LSR	v
Erythrophleum lasianthum	0.7					1.6		0.9	LNL	vi
Sapium integerrimum	2.1*	0*		1.1	0.9	0.9		1.1	LNL	vi
Ziziphus mucronata		0*	1.3	2*	0.7	0.7	0*	0.9	LNL	vi
Balanites maughamii	0	2	0*	0*	2.1*	0.5		0.7	LNL	vi
Commiphora neglecta	0*	1.4	1.8	0	1.1*			0.8	LNM#	vi
Psydrax fragrantissima	1.7							0.9	LNM	vi
Pteleopsis myrtifolia	2.4	0.8				0*		1.1	LNM#	vi
Spirostachys africana	2.8	1.7	0.9	0.8	1.2	0.3	0.7	0.9	LNM#	vi
Strychnos spinosa	2.1*	1.2	0.5	0.6	0.9	0.8	1	0.9	LNM#	vi
Cordia caffra			2.4*	0*				1.1	LNR	vi
Cleistanthus schlechteri v. schlecteri	0.3					1.1		0.6	LRL	vii
Acacia senegal v. rostrata			0.7					0.6	LRM	vii
Psydrax locuples	2.8	0.7	0.2	1.8	1.1*	0.8		0.8	LRM#	vii

Tabernaemontana elegans	0.8	0.5	0	1.5	0.6	0.5		0.7	LRM$^{\#}$	vii
Dichrostachys cinerea	2.8	1.5	0.3	2	0.6	0.6	0	0.5	LRM$^{\#}$	vii
Euclea natalensis	0	0.6	0.5	0	0.1	0	0*	0.2	LRM	vii
Hymenocardia ulmoides	1	1				0.2	0	0.5	LRM	vii
Vepris lanceolata	0.7	0.3	0	0.7		0*		0.3	LRM	vii
Drypetes arguta	0.3	0						0.1	LRH	vii

Hyperacanthus microphyllus		2.5*						2	TSL*	viii
Warneckea sousae	1.4*							0.7	TSL*	viii
Tricalysia junodii var. junodii	2.1*							1.1	TSL*	viii
Elaeodendron transvaalensis			2.4*					2.1	TSR*	viii
Euphorbia tirucalli			2*					2.1	TSR*	viii
Kigelia africana				2*	2.1*			2.1	TSR*	viii
Phyllanthus reticulatus				2*				2.1	TSR*	viii

Boscia foetida sub. rehmanniana		1	2.4*					1.1	TNL*	ix
Canthium setiflorum sub. setiflorum		0*		1			0*	0.7	TNL*	ix
Euclea divinorum		0.8	1.6					1.1	TNL$^{\#}$	ix
Mimusops caffra	2.4			0				0.7	TNL$^{\#}$	ix
Rothmannia fisheri sub. moramballae	1.4							0.7	TNL	ix
Sideroxylon inerme			1					0.9	TNL	ix
Tricalysia delagoensis	0*			2*				1.1	TNL*	ix
Drypetes natalensis	1.7							0.9	TNL	ix
Bridelia cathcartica	1.4	0*	0.8	0.9	0.9	0.5		0.8	TNM	ix
Lagynias lasiantha	1.4							0.7	TNM	ix
Rhus gueinzii	2.8	0*	0.6	1.5	0.8	0		0.8	TNM$^{\#}$	ix
Acacia nilotica sub. kraussiana	0*		0.9	1*		1.6		1.2	TNR	ix
Berchemia zeyheri			1.2*					1.1	TNR	ix
Combretum mkuzense						1		1.3	TNR	ix
Ekebergia capensis			2.4*	0*				1.1	TNR*	ix
Schotia brachypetala			1.2*	2*		0*		1.1	TNR	ix

Canthium inerme	0		0*	2	0*			0.7	TRL$^{\#}$	x
Monodora junodii	0	2.5*						0.4	TRL	x
Acalypha glabrata	2.1*	0*						0.5	TRL	x
Acridocarpus natalitius v. linearifolius	0*				0	0.5		0.3	TRL	x
Ancylanthos monteiroi		0			1.1*			0.4	TRL	x
Dovyalis longispina	0*		0*	1*				0.5	TRL	x
Erythroxylum delagoense	2.1*			0	0*	1.6*		0.6	TRL	x
Grewia microthyrsa		0	2.4*		0.5	0		0.5	TRL	x
Margaritaria discoidea		0*		1*	0*			0.4	TRL	x
Maytenus senegalensis		2.5*	0	0*	0.5	0*		0.3	TRL	x
Ozoroa engleri				0*	0.2	0.3	0	0.2	TRL	x
Pavetta catophylla		0*	1.2*			0*		0.4	TRL	x
Phoenix reclinata	0*		0.4	2*				0.5	TRL	x
Ptaeroxylon obliquum	0	0*	0.6	2*		0*		0.3	TRL	x
Vangueria esculenta	0*		0*		0	0*	2*	0.4	TRL	x
Xylotheca kraussiana	0*	0*	0*	2*		0*		0.3	TRL	x
Zanthoxylum capense	0*	1.7	2.4*	0.7	0	0*		0.6	TRL	x
Acacia borleae			0					0	TRL	x
Grewia caffra	2.1	0.5	0*		0*	0		0.4	TRM$^{\#}$	x
Hyphaene coriacea	0.6		0	0.5	0	1.6	0.7	0.3	TRM$^{\#}$	x
Salacia leptoclada	0.4							0.2	TRM	x
Strychnos decussata	1.4	0.5	0.8		0*			0.5	TRM$^{\#}$	x
Teclea gerrardii	0.4	0	0*	0		0		0.1	TRM	x
Todalliopsis bremekampii	0.6							0.3	TRM	x
Tricalysia capensis	0	1	1.2*	0*		0*		0.5	TRM	x
Vangueria infausta sub. infausta	0*	0.6	1.9	1	0.4	0.2	0.5	0.5	TRM$^{\#}$	x
Catunaregam spinosa sub. spinosa	1.2	0	0*	0.3	0	0	0	0.2	TRH$^{\#}$	x

Cola greenwayi	0.3	0*						0.1	TRH$^{\#}$	x
Brachylaena huillensis	0.4	0.4	0*	0	0	0.5	0	0.1	TRH$^{\#}$	x
Croton pseudopulchellus	0.4	0*	0*					0.2	TRH$^{\#}$	x
Clausena anisata	0*	0*	0*	0	0	0		0	CM	xi
Coddia rudis	0*	0	0	0*	0*	0*		0	CM	xi
Plectroniella armata	0*		0	0		0*		0	CM	xi
Coffea racemosa			0*					0	CL*	xii
Diospyros inhacaensis	0*			0*				0	CL*	xii
Ehretia rigida		0*	0*					0	CL*	xii
Euphorbia ingens		0	0*	0*	0*	0*		0	CL	xii
Gardenia volkensii			0*				0	0	CL*	xii
Haplocoelum gallense	0	0*						0	CL*	xii
Hyperacanthus amoenus	0							0	CL*	xii
Mundulia sericea				0	0	0	0*	0	CL	xii
Ochna arborea var. arborea	0*	0*						0	CL*	xii
Ochna barbosae	0*					0*		0	CL	xii
Ochna natalitia		0*	0	0*	0*	0		0	CL	xii
Oxyanthus latifolius	0*							0	CL*	xii
Strychnos henningsii	0				0*			0	CL	xii
Suregada zanzibariensis	0*							0	CL*	xii
Tarenna junodii	0*							0	CL*	xii
Vitex amboniensis	0				0*	0*		0	CL	xii
Acacia karroo			0*					0	CR*	xii
Albizia forbesii		0						0	CR*	xii
Casearia gladiiformis				0*				0	CR*	xii
Cassipourea mossambicensis	0*							0	CR*	xii
Combretum celastroides sub. orientale	0*							0	CR*	xii
Erythroxylum emarginatum			0*					0	CR*	xii
Euclea schimperi						0*		0	CR*	xii
Eugenia natalitia		0*						0	CR*	xii
Euphorbia grandidens				0*				0	CR*	xii
Lannea antiscorbutica	0*							0	CR*	xii
Manilkara concolor				0*				0	CR*	xii
Maytenus undata				0*		0*		0	CR*	xii
Premna mooiensis						0*		0	CR*	xii
Pseudobersama mossambicensis	0*							0	CR*	xii
Thespesia acutiloba			0*					0	CR*	xii

Table 2. Numbers and ratios of species and families in the sample and the proportions utilized. Ht = height; Util. = Utilized.

Vegetation Type	Sand Forest	Thicket on sand	Thicket on clay	Closed woodland	Open Woodland	Open Woodland (*Albizia*)	Sparse Woodland
Number of Species in Sample	86	64	79	71	61	71	35
Number of Species in Sample >0.5 Ht	84	61	71	67	54	66	30
Number of Species Utilised	47	34	46	40	33	35	15
Number of Species Utilised Index >1	27	22	30	21	25	26	11
Percent of Species Utilised	54.7	53.1	58.2	56.3	54.1	49.3	42.9
Percent Species Utilised Index >1	31.4	34.4	38.0	29.6	41.0	36.6	31.4
Percent Species > 0.5 Ht. Utilised	56.0	55.7	64.8	59.7	61.1	53.0	50.0
Number Families	31	27	31	29	30	29	20
Number Families Utilised	20	18	23	18	20	18	11
Percent of Families Utilised	64.5	66.7	74.2	62.1	66.7	62.1	55.0
Densities	4726.4	2325.6	1012.6	1392.5	396.1	451.1	461.3
Volumes Utilised	5501	8095	8477	7231	18786	37347	3012

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CHAPTER 8

SAND FOREST: CHARACTERISTICS, ECOLOGY AND HYPOTHESES ON ORIGIN

8.1 Introduction

The earth is not a static place—it has always been characterized by change and it will always be so. Change is one of the most important realities in a plant community, especially on an ecological time scale**.** In interpreting vegetation change, a diverse set of factors is often operative (Niering 1987). Long-term vegetation changes operate at a rate which is comparable to a managers working life and on a large spatial scale which makes them difficult to observe, measure or comprehend. Consequently, slow processes are poorly understood (Stafford Smith & Pickup 1993). Traditional succession/climax concepts can often hinder rather than aid in sound vegetation management. Community development (Odum 1997) over the short to medium term (1000 years or less) is widely known as ecological succession (the ecological time scale)—an active process involving changes in both the organisms and physical environment. Changes over geological time scales (millions of years) fall under the heading of organic evolution.

Forests are difficult systems to study because the demographics that govern their long-term behaviours occur on disparate spatial and temporal scales, from square meters and weeks for germination and seedling establishment, to hectares and millennia for mortality events. Also many different processes control the structure of forest plant communities. From a variety of observations it is clear that the species richness, species composition and species dominance of plant communities are greatly affected by the availability of limiting resources (Brokaw 1985).

The modern view of forests is of a dynamic system of ever-changing mature, gap and building phases, and gap-phase species replacement/regeneration (Lawes *et al*. 2004). Thus, 'gap dynamics' has been a pervasive theme of the study of forests. An added complication is that gaps need not be canopy gaps. When a tree falls in the forest, the canopy hole or 'light gap' it creates sets in motion a chain of events known as 'gap dynamics (gap-phase regeneration)' which culminates in the replacement of the previous canopy tree by a new one (Hubbell & Foster 1986a). Canopy gap fill in with regrowth from three sources: seed, plants established prior to gap formation, and lateral in-growth of branches from trees on the gap periphery. In large gaps, pioneers and late secondary species, germinate from seed arriving before and after gap formation, grow rapidly and overtop the slower-growing established juveniles of primary species which survived the tree fall (Hartshorn 1978). Gap disturbances provide the principal or only means by which most forest tree species can maintain their representation in closed canopy forests. Such seemingly simple events such as tree replacement and gap-phase regeneration are actually complex processes that are still poorly understood. Biology, chance, and history all play a role in the replacement process (Hubbell & Foster 1986b).

Three basic gap-phase regeneration guilds can be distinguished based on life history, namely mature forest trees, early pioneers and late secondary species (Hartshorn 1978; Brokaw 1985). a) Primary tree species germinate in the shade or in both sun and shade, and can persist as suppressed juveniles for some time until a gap opens. b) Early pioneers species have a different strategy for waiting for gaps to open; they frequently persist for long periods as dormant seeds in the soil. These seeds require specific gap disturbances cues to germinate. c) Late secondary species are typically shade intolerant, sun loving plants with growth (life history) similar to early pioneer species, however they often grow to much larger sizes and persist for longer periods in the canopy.

The ‘grain’ of a forest type can be categorized based on its spatial scale of forest dynamics (Everard *et al.* 1994, 1995). The spatial scale of regeneration of a species, fine grained species regenerate over a small scale (area) and seedlings and saplings of a species are found beneath or close to mature individuals, course grained species regenerate over a large area and seedlings and saplings are often rare and seldom found beneath mature individuals.

The ecology, floristics and distribution of Sand Forest in the landscape are influenced by a complex combination of biotic and abiotic factors. These would include the evolutionary history of plant species, their biology, adaptive flexibility and dispersal potential, the geology, geomorphology, soil properties, climate and its changes, and finally interaction with other plant species and animals (including man), presently and in the past (Van Wyk & Smith 2001). Under each of these, a complex of interactions and relationships exist, for example the establishment and growth of vegetation at a point in the landscape occur in response to the availability of seed (propagules) and three main resources: water, nutrients and energy (solar radiation). These resources can vary as follows: Seed may be available from local sources, or by redistribution from elsewhere, and their survival may be affected by climatic conditions and predation. Water availability depends on the soil texture, balance between infiltration and storage in the soil, and evapotranspiration. Water may be supplied directly from rainfall, but that supply can be greatly reduced or increased by the redistribution process of run-on and run-off. Nutrient availability depends on the balance between the rates of turnover in relation to the total amount of nutrients stored in the soil and vegetation, and the competitive use of these resources by other plants.

Nutrients can also be redistributed across the landscape by wind, water or animals. Solar radiation input is largely pre-determined by latitude, but it can vary locally with topographic factors such as slope, aspect, and shading.

The aim of this chapter is to consider the functioning and development, albeit largely hypothetical, of Sand Forest by taking as many of the above-mentioned biophysical factors into consideration so as to formulate some ideas on the origin and definition of Sand Forest as a community. The first part of the chapter will define Sand Forest diagnostic characters based on current information. Differences between the Afromontane, Dune Forest and Sand Forest will also be included as a means of highlighting differences. Dune Forest is important as it relates to the second part of the chapter, in which hypothesises will be proposed on Sand Forest development in which Dune Forest occupies a key position.

8.2 Sand Forest characteristics

8.2.1 What is Sand Forest?

A community is a collection of species populations that occur in the same area at the same time. The definitions are, however, different for zoologists and botanists. The largest component of an ecosystem is the plant growth and is known as the plant community. A plant community is a combination of plants that are dependent on their environment and influence one another and modify their own environment (Mueller-Dombois & Ellenberg 1974). Put simply a plant community is an assemblage of different plant species within a specific habitat and with a specific physiognomy and structure that forms an organised ecological unit in a specific area. The "climax" is a buffered and stable community, with high resilience and strong resistance to change, so it can withstand a disturbance. The climax is heterogeneous and not fixed but can change according to prevailing environmental conditions (Krebs 1985). The climax stage is self-sustainable and in equilibrium with the physical and biotic environment. Climate varies on a geological as well as an ecological time scale (~1 000 years or less) and it is therefore difficult to grasp that equilibrium can be achieved. Therefore climax is an abstract concept and the term "steady-state" (Park 1970) has been suggested to replace the term "climax communities". Sand Forest will be characterize in light of the above explanations and definitions.

White (1983) associated southern Africa forests with two phytochoria, namely the Afromontane Archipelago-like Regional Centre of Endemism (which extends to the northeastern African uplands); and the Tongaland-Pondoland Regional Mosaic (which is largely restricted to the eastern coastal belt of South Africa). Sand Forest is classified under the Tongaland-Pondoland Regional Mosaic. Sand Forest (Licuáti Forest) is also an unique inland feature of Maputaland and has been variously referred to as:- Licuáti forest (Myre 1964); Tongaland Sand Forest, Msinga bush (Moll 1968); Sand forest (Moll 1978; Moll & White 1978; Moll 1980; Taylor 1980; Ward 1981; Brooks *et al.* 1982; Cooper 1985; Felton 1999; Smith 2001; Matthews *et al*. 2003; Van Rooyen 2003); *Artabotrys monteiroae-Dialium schlechteri* Forest (Matthews *et al*. 1999); Sand Thicket and Forest (Smith 2001); Eastern Sand Forest, Western Sand Forest (Kirkwood & Midgley 1999); and Licuati Sand Forest (Mucina & Geldenhuys 2004). White's (1983) mapping was not at a scale fine enough to separate the "Sand Forests" of northern KwaZulu-Natal from other Tongaland-Pondoland forest types.

The first description of Sand Forest, under the name Licuáti Forest, was by Myre (1964). He described it from southern Mozambique as dense forest of low to average height (~5-12m). Characteristic woody species are *Balanites maughamii, Dialium schlechteri, Newtonia hildebrandtii, Afzelia quanzensis* and *Pteleopsis myrtifolia.* Moll (1978) also describes the forest patches as very dense with numerous woody, subcanopy shrub and small tree species, with relatively few herbs. The forest patches being quite distinct. Moll (1978) lists *Balanites maughamii, Cleistanthus schlechteri, Cola greenwayi, Dialium schlechteri, Erythrophleum lasianthum, Hymenocardia ulmoides, Newtonia hildebrandtii* and *Ptaeroxylon obliquum* as the common and widespread tree species of the Sand Forest.

From phytosociological and other vegetation studies (Lubbe 1996; Kirkwood & Midgley 1999; Matthews *et al*. 1999, 2003) carried out in northern Maputaland, the following species are considered characteristic of Sand Forest: *Balanites maughamii, Cola greenwayi, Croton pseudopulchellus, Dialium schlechteri, Drypetes arguta, Hymenocardia ulmoides, Hyperacanthus microphyllus, Monodora junodii, Ochna barbosa, Ptaeroxylon obliquum, Pteleopsis myrtifolia, Strychnos henningsii, Todalliopsis bremekampii, Uvaria lucida* and the sedge *Cyperus albostriatus.* Some species are distinctive to Sand Forest while being not that constant in their presence. Examples include *Newtonia hildebrandtii, Croton steenkampianus, Cleistanthus schlechteri, Erythrophleum lasianthum* and *Combretum celastroides.* All the preceding species can be referred to as "floristic elements" of Sand Forest.

Sand Forest are dense with a lack of forbs and small shrubs in the understory, and has distinct boundaries. Canopies in this forest type can be low (approximately 5m) to high (approximately

15m). Sand Forest has a conspicuous compliment of semi-deciduous to deciduous species, a feature unique for southern African forests. Sand Forest is associated with sandy soils, which in many cases are old dunes systems. Moisture levels in these sandy soils are lower than that of the neighbouring grassland and woodlands (Unpublished neutron probe data). Rainfall in areas with Sand Forest varies from 600 to 800 mm per annum and the occurrence of mist is not uncommon. Leaf attributes are generally fairly similar to all forests, for example, Sand Forest leaves are generally evergreen (although many species in Sand Forest tend to be drought-deciduous), mesophyllous; lacking in spines; with entire margins; and non-compound (Midgley *et al*. 1995).

Moll & White (1978) considered many typical Sand Forest species (e.g. *Balanites maughamii*, *Cleistanthus schlechteri* and *Newtonia hildebrandtii*) to be Zanzibar-Inhambane linking species (the Zanzibar-Inhambane Region is the coastal phytochorion extending from southern Mozambique to East Africa). This phytochorion, together with the Tongaland-Pondoland Region, form White's (1983) Indian Ocean Belt. There are also some outlier areas where plant species which can be referred to as Sand Forest floristic elements can be found outside typical Sand Forest. Other types of dry forest under fairly similar environmental conditions as in Sand Forest, include the sandveld communities of the Pafuri area, Kruger National Park (Van Rooyen *et al.* 1981) and in the Gonarezhou National Park, Zimbabwe (P. Goodman pers. comm.).

Midgley *et al*. (1997) recognised two major forest complexes: Afromontane types associated with temperate environments, and Indian Ocean types associated with subtropical climates. The Indian Ocean forest types include Sand Forest and Dune Forests.

8.2.1.1 Distribution

Sand Forest is limited to the drier inland areas in northern KwaZulu-Natal and southern Mozambique (Maputaland). The currently known distribution of Sand Forest is from False Bay in the Greater St Lucia Wetland Park to Maputo Bay. From work done by Tinley (1971) in southern Mozambique, he referred to semi-deciduous forest with characteristic species as listed for Sand Forest, although in the northern areas (north of Maputo Bay) he noted a slight floristic change. He mapped the distribution of this dry forest type as a narrow zone up to Quissico (± 100 km south of Inhambane) Mozambique. Thus this forest type is confined to a narrow zone on the coastal plains of northern KwaZulu-Natal and southern Mozambique, from approximately False Bay up to Quissico. A narrow zone covering the approximately distance of 500 km makes this quite a limited area for this forest, especially in South Africa (zone of approximately 150 km). Cooper (1985) estimated the total area covered by Sand Forest in South Africa at approximately 5 986 ha. Woody species similar to those that occur in Sand Forest do occur in forests north of Maputo Bay, but the species composition of these forests is different (Tinley 1971), and they are therefore not classified as Sand Forest. The increasing narrowness of the Mozambique plain to its southern end acts as a biotic filter to plant and animal dispersion and distribution.

Unlike Afromontane Forest, both Dune Forest and Sand Forest are tropical/subtropical vegetation types. Dune Forest is a relatively widespread vegetation type found along the east coast of Africa on recent (young) sand dunes. Sand Forest occurs only in Maputaland (between False Bay and Maputo Bay), and is hemmed in by the Lebombo Mountains to the west, Maputo Bay in the north, the temperate climatic conditions to the south, and the Indian Ocean to the east.

In Maputaland, where both Dune and Sand Forest occur, Dune Forest tends to inhabit the wetter habitats and younger sand dunes closer to the ocean, while Sand Forest inhabit the drier plains and ancient sand dunes further inland. Dune and Sand Forest mosaics can occur in places where Sand Forest is located closer to the coastline. At the southern most point of distribution, namely False Bay, Sand Forest and Dune Forest both occur, and seem to intermingle in places. To distinguish between the two forest types one has to look at the floristic composition. It is worth noting that one does find a few Dune Forest species in some of the driest of the Sand Forest communities, e.g. *Mimusops caffra* (form), *Acacia kraussiana* and *Isoglossa woodii.* In these dry Sand Forest communities the growth form and vegetative characteristics of the tree *Mimusops caffra* are atypical of what is to be seen in the coastal Dune Forest—perhaps an incipient species?

Afromontane Forest is a temperate vegetation type found mainly on high mountain plateaus and in protected kloofs and gullies throughout most of sub-Saharan Africa. It is mostly associated with Afromontane grassland, but in the Cape Floristic Region it is associated with Fynbos.

8.2.1.2 Species richness and endemicity

Species diversity, or species richness, is a community attribute that reflects the combined influence of such processes as immigration, speciation, competition, predation and extinction (Glenn-Lewin *et al.* 1992). A frequently reported pattern has been for diversity to peak in late succession after most of the climax species have entered, and then to decrease as successional species are lost (Glenn-Lewin *et al.* 1992) but many conflicting observations have also been made. Part of the explanation can be that change in diversity during succession depends on the environmental contribution, where more than one factor is involved. The creation of a general model of successional change in diversity is much more difficult and perhaps impossible (Glenn-Lewin 1977, 1980; Whittaker 1977).

In Sand Forest the β-diversity (the turnover of species between the different forest patches) is very high for both dominant and rare species (Van Rensburg *et al.* 2000). Therefore conserving one patch of Sand Forest will not nearly conserve all of the genetic complement of Sand Forest. Dune Forest shows a low β-diversity. The α-diversity of Sand Forest is rather similar to that of the southern African Afromontane forests (Geldenhuys 1992; Mucina & Geldenhuys 2004). Floristic richness (α-diversity) and β-diversity are probably relatively low in Afromontane forest. The southern African Afromontane plant species are noticeably very wide-ranging, with relatively very little local and regional endemicity (Geldenhuys 1992). Patches of Afromontane forests throughout Africa tend to have very similar species compositions (White 1978). This perhaps explains the ability of Afromontane forest to return (re-establish itself) after destruction in the relatively short period of approximately 50–200 years, if it is adequately protected from further destruction. Also during the last glacial period, many areas that are today forest were denuded of forest. Thus in approximately 10 000 years, forest has been able to re-establish on these denuded areas (Moore *et al.* 1996).

Sand Forest does not have many fern and moss species, and those few species present, are able to withstand severe desiccation. Many epiphytes that occur in Sand Forest are lichen-like, and can withstand repeated desiccation, while the epiphytic orchids are often xerophytic with, for example, bulb-like basal thickenings. There is no well-developed herbaceous or ground layer in Sand Forest. Contrary to what Kirkwood & Midgley (1996) has claimed, the absence or shortage of a conspicuous ground layer and the lower understory in Sand Forest is not due to herbivory, but could rather be ascribed to aridity compounded by allelopathic characteristics. In contrast, Afromontane Forests with its relatively high rainfall regime, and with soil moisture further supplemented by the capturing of mist, supports a rich herbaceous layer with a relatively large and diverse fern and moss flora (Mucina & Geldenhuys 2004). Epiphytes and orchids are also of frequent occurrence. Macro-fungi, associated with the thick organic layer covering the soil in Afromontane Forest, and the higher rainfall and soil moisture content, are very prolific in these forests. In comparison to Sand Forest, Dune Forest also has a relatively large diversity of ferns and mosses and a well-developed herbaceous layer (Mucina & Geldenhuys 2004).

Southern African Forests at a local and regional scale show low levels of tree endemism (White 1983; Midgley *et al*. 1997; Matthews *et al*. 2003). Similarly for the southern African forests, few tree species are rare (MacDevette *et al*. 1989), and uncommon species are generally those in ecosystems such as Sand Forests that just penetrate southern Africa from the northeast, as in the Maputaland Centre of Plant Endemism (Van Wyk 1994). Sand Forest is a rare habitat (Van Wyk 1994), which is rich in woody species (Moll & White 1978). The species composition of Sand Forest is unique and includes several rare and Maputaland Centre endemic species (Van Wyk 1994). A significant number of endemic species, which may be plants and animals, are associated with Sand Forest, and Van Wyk (1994) and Van Wyk & Smith (2001) consider this perhaps the most remarkable plant community in the Maputaland Centre. Matthews *et al.* (2003) found that of the 225 endemic plant species recorded for Maputaland (including Lebombo Mountain endemics), 33 are found in Sand Forest with 20 largely restricted to this vegetation type. This makes this one of the communities with the highest restricted plant endemic species in Maputaland. Van Rensburg (1998) also found that certain bird species were closely associated with Sand Forest and of these species, three are endemic to the Maputaland Centre. Knowing that the distribution of Sand Forest in adjacent Mozambique covers larger areas than in KwaZulu-Natal, genuine rarity of trees must still be confirmed.

8.2.1.3 Forest structure and deciduousness

Afromontane Forest is by far the tallest of the three forest types, with trees up to 50 m in height. Dune Forest is shorter than Afromontane forest, but can be higher than Sand Forest. In Sand Forest individual specimens may reach heights of 20 m, which in most cases are old individuals of *Newtonia hildebrandtii.*

Two physiognomic or structural types of Sand Forest occur (Matthews *et al.* 2003). One fits the basic physiognomic definition of forest, while the other can be better described as a thicket (short 5–6 m high dense vegetation). These structural differences are also reflected in the floristics of the two types. Thus, what is usually described as Sand Forest actually comprises (includes) two vegetation types, namely Tall Sand Forest and Short Sand Forest (thicket), which differ in terms of both floristic and structural attributes (Matthews *et al.* 2003). As the single name ‘Sand Forest’ cannot be used at two different levels of classification, it is proposed that the term ‘Licuáti’ (the original name used by Myre 1964) be used in the future to refer to all types of Sand Forest, with ‘Tall Licuáti Forest’ or ‘Tall Sand Forest’ and ‘Licuáti Thicket’ or ‘Sand Thicket’ the two components (Izidine 2004).

Most plant species in the three main southern Africa forest types are evergreen, although some deciduous species do occur in each type of forest, with Sand Forest having the largest proportion of deciduous species. Some of the dominant species in Sand Forest are sometimes semi-deciduous, resulting in the forest appearing deciduous at times, although this is for a very short period, e.g. a month or two (Matthews, unpublished phenological data). Species playing a role here are *Combretum celastroides, Pteleopsis myrtifolia, Croton steenkampianus* and *Dialium schlechteri.* Many Sand Forest trees sometimes, drop their leaves and become dormant when it is very dry. So-called, drought-deciduous trees furthermore exacerbate this effect of deciduousness e.g. *Hymenocardia ulmoides.* Drought-deciduousness is much better developed in Sand Forest than in either Dune or Afromontane forest. The proportion of deciduous species increases where the mean annual precipitation is lower (Meadows 1985). It is mainly the presence of drought-deciduous species that has lead to Sand Forest being referred to as deciduous vegetation.

In comparison with associated woodland matrix (Matthews *et al.* 2003), species of the Sand Forest are definitely the more evergreen of the two vegetation types. In winter, the woodland communities become more open, while Sand Forest remains closed and green. This suggests that Sand Forest is closer to being evergreen than totally deciduous.

Wood decomposition tends to be much slower in Sand Forest than in either of the other two forest types (Afromontane and Dune Forest). The abundance of such long-lasting hardwood in Sand Forest is probably conducive to the high insect diversity found there. It may also increase the risk of fire penetrating the forests resulting in relatively hot fires. The soils of the woodlands surrounding Sand Forest are indistinguishable from that underlying Sand Forest itself.

8.2.1.4 Dispersal and fruit types

Establishment from seed is a two-step process: dispersal and germination. Effectiveness of seed dispersal is dependent on five main factors: seed production, vector of seed transport, timing of seed release or removal and fate of dispersed seeds (Glenn-Lewin *et al.*1992). Experimental or observational studies of dispersal are concerned usually with primary dispersal, the movement of seed from the parent plant to the ground. These studies reveal that the bulk of the seed of most plant species are deposited only a short distance from the parent plant (Levin & Kerster 1974). Seed that are dispersed by birds, however, may be carried quite far, with few seed deposited near parent plants (Murray 1988). Variability in seed dispersal is enormous and is influenced by vegetation structure and density, wind patterns, and presences of animals including bird communities and bird behaviour.

Seed germination is also a complex physiological process that, as a result of natural selection, has been modified in a variety of ways to ensure that seeds germinate when there is a high probability of seedling survival. Soil conditions also play a major role, e.g. soil moisture, light levels, temperature fluctuations, and chemicals released by plants and plant litter that can inhibit germination (Glenn-Lewin *et al.* 1992).

Life history properties of secondary plant species in tropical lowland forest include a short life cycle, high growth rate, high reproductive resource allocation, continuous and early seed production, small seed size, long seed viability and chemical protection against herbivory (Whitmore 1990) [Compare Table 2.].

There is a large bias towards edible fruit and animal dispersed propagules in all three forest types. Wind seems to become more important as a dispersal agent in coastal regions. Midgley (1993) states that Sand Forest is dominated by species with wind-dispersed seeds, whereas other Indian Ocean forests types (Midgley *et al*. 1997) are dominated by fleshy-fruited species. However, Matthews *et al.* 2003 and unpublished data by Matthews, found that plant species with fleshy fruits were the most common within Sand Forest, even when considering cover-abundance. In Sand Forest, for example, 74 out of 103 investigated taxa (70%) had fleshy fruit. Genuine wind-dispersed seeds, not just fruits with wings that in most cases would come to rest nearby parent plants (e.g. *Combretum* spp. with their winged fruits), were quite rare. The same can be said for the MC endemic plant species in Sand Forest, only two out of the thirty-three endemic species recorded had winged fruit and these were both species of the genus *Combretum*.

8.2.1.5 Rooting

Deep tap root systems have generally been associated with deep sands and arid conditions, as, for example, in the case of the species *Acacia erioloba* found on Kalahari sands. Timberlake (1980) recorded roots at a depth of 46 m. This is not the case, however, in Sand Forest, where the root systems are very shallow, with most of the roots occurring in the upper 1–1.8 m of the soil, and no records of deep tap root systems (Matthews pers. obs.). The trees in the woodlands surrounding Sand Forest also have fairly shallow root systems, as do the trees of the Dune Forest

(Matthews pers. obs.). Afromontane forest trees have deeper root systems, with the roots growing where the resources are.

8.2.1.6 Fauna

Faunal species richness and diversity is more-or-less similar in all three forest types. However, based on current knowledge, faunal species composition seems to differ. Sand Forest, for example, is rich in insect species such as butterflies and in bird species, while the mammal component is rather low (in diversity and numbers). However, the high β-diversity in the flora of Sand Forest seems to be reflected in the fauna. There seems to be no peak in any particular animal-group in Afromontane Forest and in Dune Forest. The unique faunal elements in all three of the forests are more tropical related.

Maputaland as a region has one of the highest butterfly diversities in South Africa (E. Pringle pers. comm.). Twenty five percent of the about 852 species of butterflies that occur in South Africa may be found in northern Maputaland. This is probably due to the large variety of habitats and abundance of larval food plant taxa, varying from high canopy Sand Forests to low-lying coastal areas, palmveld grasslands, as well as the area being the transition zone between tropical and more temperate regions, and thus has representatives of both.

8.2.1.7 Environment

Climate influences soil properties, nutrient recycling and vegetation growth in numerous ways but these effects are dominated in arid regions by the availability of soil water. From a biological perspective, rainfall records may be treated as events and sequences of events. An event is one or more closely spaced rainfall incidents (or soil moisture impulses), which are large enough to produce a significant vegetation response. The sequences consist of a run of events (and periods with or without rainfall) of sufficient length and magnitude that short term changes in the biological system are progressively reinforced until a new state is reached (Stafford Smith & Pickup 1993).

Rainfall and moisture

Sand Forest occurs under relatively drier conditions compared to other forest types (less than 700 mm of rain per year) and is thus classified by National Forest Classification as tropical dry forest (Von Maltitz *et al.* 2002), and where it does occur in areas of higher rainfall (greater than 700 mm), it retreats to the higher sand dunes where the sands are well-drained. This implies that if the habitat of Sand Forest stays wetter for longer (in terms of soil moisture content) than present, Sand Forest could cease to exist in those areas.

Relatively high air humidity levels can prevail in the areas where Sand Forest occurs, especially in summer. Sand Forest does experience mist, and it would seem to retain and possibly add to the soil moisture content. The high frequencies of epiphytes in Sand Forest would infer that they also benefit substantially from the mist. Marker & Russel (1984) have stated that the presence of mixed forest in low rainfall areas of the Eastern Cape can partly be ascribed to the fog and water holding capacity of deep sand to sustain forest growth. Sand Forest in Maputaland is also found on deep sand, and with the occurrence of heavy dews and low-level mist that are not uncommon, especially in winter, this could help maintain the water content of the soils. Sand Forest (specifically on the high lying areas) does appear to experience more mist than its associated vegetation type, woodland. This implies that mist may play a role in the survival and/or persistence of Sand Forest in the midst of the woodland dominated landscape. The reason may be that the mist, which is mostly of winter-occurrence, together with low soil moisture levels, may keep the transpiration rate down. In other words, mist would play the same role in winter that high air humidity plays in summer.

Dune Forest along the coast receives 1000 mm or more rain per annum (highest rainfall in the Maputaland region), and the ground water added to the soil moisture in these forests leads, in some instances, to the formation of swamp forests such as those in the Sihadla drainage of the Kosi Bay system. Being low-lying and coastal, Dune Forest experience very humid conditions and strong winds, with the seaward side being affected by salt spray. Little wind is experienced inside Dune Forest, and when wind does occur, its effect would be in the top canopy. Dune Forest is regularly exposed to salt and sand laden wind which can be very strong at times.

Temperature

Both Dune and Sand Forest lie in tropical/subtropical areas, but while Dune Forest (being part of a coastal system) experiences equitable/even temperatures throughout the year, the environment in Sand Forest can be relatively cool in winter and very hot in summer.

Afromontane Forest experiences temperate conditions in summer and temperate to cool conditions in winter. The occurrence of frost varies greatly, with some lower lying forests not experiencing any frost, while frost can be a nightly occurrence in winter in some high-altitude localities (White 1983). Rainfall is generally 1000 mm and more per annum in Afromontane forests. Exceptions do occur, however, such as in parts of the Soutpansberg and Lebombo Mountains (Hlatikulu [Gwalaweni] Forest) where the rainfall is lower. Some Soutpansberg Forests exist, at present, also in a state of 'suspended animation' like Sand Forest, relying for survival on supplementation of the rain by the capturing of mist. By "suspended animation" is meant the maintenance of the existing state (vegetation community) till circumstances change to more favourable for normal dynamics or functioning to return. Unlike the situation in most Afromontane Forests, conditions in parts of the Soutpansberg are currently too dry to allow the Afromontane forests to actively establish or expand into new habitats. Many Afromontane Forests supplements their soil moisture by the capturing of mist, which is aided by the presence of mild and moisture-laden winds that improves conditions for the condensation of mist droplets. Most Afromontane Forest occurs in areas with relatively low humidity to times of high humidity (Mucina & Geldenhuys 2004).

Table 1. Approximate mean annual rainfall limits and approximate mean annual maximum, minimum temperatures and mean relative air humidity levels for the environment in which the three main forest types occur.

	Sand Forest	***Dune Forest***	***Afromontane Forest***
Mean annual rainfall variation	600–800 mm	1000–1300 mm	1000–2000 mm
Mean maximum temperature	~30–35 ˚C	~28˚C	~23–25˚C
Mean minimum temperature	~7–10 ˚C	~10–14 ˚C	~3˚C
Mean relative air humidity	Sub humid to humid ~60–85 %	Humid ~75–90%	Sub humid – dry ~50–80%

Historic

On the Maputaland plains there would probably always have been a gradient of rainfall decreasing westwards from the ocean for some distance before increasing towards the Lebombo Mountains. The effect of the transgression and regression of the ocean in the past would therefore have been that the zones on the coastal plain suitable for Sand Forest would have shifted. Near the coast, the ground water table is currently shallow and not favourable for Sand Forest. If the sea level drops, the water table would also drop and this would result in a more favourable environment for Sand Forest, as a relatively deep water table (drier sands) are exactly the conditions that Sand Forest currently prefers.

It can be generalised that the coastal areas of Maputaland have had a reasonably stable environment compared to much of the African hinterland during the Quaternary (Tyson 1999, Adams & Faure 2000). In the last 23–5 million years BP, since the deposition of "Berea type red sands" (Pliocene Dune cordon, the remnant of the oldest ancient dune cordon deposited at the base of the Lebombo Mountains), there were probably no major changes in the climate of the region although their would have been fluctuations related to glacial periods, the near-by Indian Ocean had a considerable impact on stabilizing the overall temperatures been experienced by the region.

8.2.1.8 Substrate: soil and soil moisture

Origin and age of the Sand Forest sands and sand dunes

For at least 23 million years the Maputaland coastal areas (eastern sea board) has been exposed to a constant cycle of sea transgressions and regressions (Davis 1976; Hobday 1976; Partridge & Maud 2000). One can assume that the processes that has been operating during the past 125 000 years may well have been operating for at least the past 25 million years. The one effect that these cycles of transgressions and regressions would have had on Sand Forest and other sand-based communities is that it would have resulted in an increase or decrease in the terrestrial sand substrate available to these communities. The position of these communities is also related to climate conditions, which is directly related to distance from the coast, so these transgressions and regressions would play an important role in determining the positions of the climatically suitable zones for the different communities, and therefore the positions would have shifted during the different cycles.

Currently there are three main distinguishable dune cordons with a fourth more of a dune field (Botha *et al.* 2003), on the Maputaland coastal plains. Each of these cordons relates to a past relatively stable ocean still-stand and as such would have formed the coastline at that stage. These were not the only dune cordons formed, but they were big and stable for long enough to persist. “Dune Cordon 1”, skirts the present-day coastline. The sea-level stabilised at its present level approximately 6 500 years BP (Ramsay 1997) therefore this cordon dates back to about 10 000 years to the present (as dune formation processes are still continuing today). “Dune Cordon 2”, which is more of a dune field, is not distinct and in many ways is a complex of hummock dunes and ridges just back of the current coastline. This dune field has a range of ages of which the oldest dates back to the last glacial maximum (18 000 years ago), at which time the coastal dune cordon would have been out to sea based on the current coastal dune cordon. “Dune Cordon 3” is a reasonable prominent cordon which is distinct throughout most of Maputaland. It is very prominent around Tembe Elephant Park where it is locally known as the Sihangwana Ridge. This dune cordon dates back to 3 million to 125 000 years BP (Pliocene) and is approximately 30–40 km inland from the coast. “Dune Cordon 4”, which is the oldest, lies at the foothills of the Lebombo Mountains along the course of the Pongola and west of the Mkuze Rivers. This is not a distinct cordon, but remnant patches of sand dunes, which in most cases are a distinct red colour and also referred to as "Berea type red sands". This cordon dates back to the Miocene / Pliocene (~25 million) and is 50–70 km inland from the coast.

Sea levels have also fluctuated which in all cases would have resulted in dune cordon formation and removal. During the 25 to 3 million year BP period there were possibly a multitude of sea transgressions and regressions. During this period the coastline would have fluctuated between the base of the Lebombo mountain to further out to sea than the current coastline. During the 3 million to 125 000 years BP period the coastline would have been to the east of the current position of the Pongola River, not withstanding the usual sea transgressions and regressions. Around 800 000–125 000 years BP the coastline was in approximate position between the current Muzi Swamps and inland points of the Kosi Bay system and Lake Sibaya. At approximately 117 000 years BP (Glacial Maximum) the sea level dropped to 45 meters below current ocean levels. During this period the coastal dune cordon would have been out at sea (as seen today). From around 125 000 years BP to the present day the sea has not been further inland than the current position of the Muzi Swamps. At around 18 000 years BP another Glacial Maximum was recorded and resulted in a sea level drop of ~130 m below current levels. During this period the coastal dune cordon would have been far out at sea (as seen today). The sea-level stabilised at its present level at approximately 6 500 years BP and thus the age of the current coastal dune cordon can be said to be 10 000 years to the present (Botha 1997; Maud & Botha 2000).

The sands underlying Dune and Sand Forest are of marine origin, highly leached and very poor in plant nutrients. Most of the sands of the coastal plains (inland) are wind-reworked and referred to as aeolian sand and includes the sand on which Sand Forest is found. Very little stratification takes place, with the sand generally forming an amorphous mass under relatively thin organic layers. There are inconsistencies between surface and deeper soils established ages, these discrepancies between the ages (estimated for the sand dunes by deep soil dating and by near surface soil dating) is the result of this reworking of the sands by wind. The soil top layer of the dune is much younger than the dunes themselves. The topmost layer of soil in Sand Forest is probably not much older than the soils under Dune Forest. The dune systems of Sand Forest are older than those of Dune Forest, thus following a gradient from the youngest to the oldest from the coast inland.

Soil chemistry

There are very little major differences in soil chemistry of the sands over most of the coastal flats of Maputaland (Watkeys *et al*. 1993), except in the deeper layers and between the very old Dune Cordon 4, "Berea type red sands" (Pliocene Dune cordon near the Pongola River) and the more recent cordons (3 million and younger closer to the sea). This brick red colour of the oldest cordon is apparently only obtained after ~ 1 million years (Gardner 1983). There are no differences in those parts of the soil that matters to the plants. Some of the deeper layers of the ancient sand dunes are red because of oxidation that took place. However, Sand Forest occurs on both reddish and white soils. Walker *et al.* (1981) found a similar pattern and described a chronosequence sand mass site along the coast of Queensland, Australia. Soil surfaces there vary in age from a few thousand too perhaps half a million years. Soils are sandy and are subject to relatively rapid nutrient loss through leaching, with the nutrients content of the oldest soils relatively poorer than the younger soils.

Unlike Afromontane Forest, Dune and Sand Forest are almost exclusively found on sand, in most cases in the form of sand dunes. Soils underlying Afromontane Forest tend to be clayey or limey, and may be leached and poor in nutrients, though the water holding capacity of these soils are generally much higher than in the cases of Dune and Sand Forest. The soils are secondarily leached and poor in nutrients due to the high rainfall. Stratification of the soil into definitive horizons does occur under Afromontane forest, and a thick organic layer, almost a mat, develops on top of the soil. Wood decomposition (humification) is relatively fast.

There is a tendency for Sand Forest to occupy the drier habitats in Maputaland, e.g. on the high, ancient sand dunes. This begs the question whether Woodland out competes Sand Forest in moisture areas, and whether Woodland would invade and take over the areas currently occupied by Sand Forest if it should become wetter.

Indications are that the present-day climate regime is not suitable for the establishment of Sand Forest. Sand Forest soils show hydrophobic characteristics under dry conditions, but when they get wet, have a better water-holding capacity than the surrounding Woodland soils (Fourie *et al.* 2002). Plant communities such as Sand Forest therefore seem to be able to generate their own soil moisture regime within the constraints imposed by the climate and, initially, by the physical properties of the soil. In the longer term, even soil properties can be changed because both erosion and deposition rates are closely related to the amount of plant-cover present (Stafford Smith & Pickup 1993). Sand Forest seems to 'manipulate' its soils thereby creating its own habitat, not only by making the soil more suitable for itself, but also by making it less suitable for the surrounding Woodland vegetation. Low soil moisture content in Sand Forest could also have a negative effect on Sand Forest recruitment, which can be very low, effectively keeping Sand Forest from actively expanding and establishing itself. However, Sand Forest is very efficient in capturing all or most of the rainfall that penetrates the first metre of ground; so efficiently, in fact, that the soil below the root zone can be bone-dry (Matthews, unpublished neutron probe data). The 'habit' of Sand Forest to 'create' and 'maintain' its own habitat therefore comes with a trade-off. Although the hydrophobic character of the soils can inhibit the establishment of species from the Woodland-matrix, it also limits Sand Forest from recruiting young forest growth, thus keeping it in a state of 'suspended animation' instead of in a state of 'dynamic change and growth'. This suggests that if the current climatic conditions continue indefinitely, Sand Forest will become extinct in the drier areas because it cannot recruit to any significant degree under the current environmental conditions. That Sand Forest is apparently incapable of recruiting under the current dry climatic and soil conditions seems to indicate that Sand Forest was originally established under relatively moister climatic conditions, and that the current distribution is a self-inflicted refuge.

As soil moisture plays an important role in determining whether a site is more suitable for Sand Forest or for Woodland, there are two processes that could determine which vegetation occurs on a site. Sand Forest on the higher sand dunes will probably expand under wetter climatic conditions, as more moisture in general would mean that Sand Forest could start recruiting again. The higher soil moisture (specifically) on the lower dunes, would, on the other hand, probably cause Woodland to take over and replace Sand Forest in these areas. This will happen because the dryness of the Sand Forest habitat is partly self-inflicted, something that can be demonstrated by what happens when Sand Forest is removed from a site. Prior to Sand Forest being removed, the soil moisture levels recorded for the sand forest site, are on average lower than the average levels of the surrounding vegetation-matrix (be it woodland or grassland). After the removal, the soil moisture level under the site is raised above the average for that of a Sand Forest site. (See Figure 1).

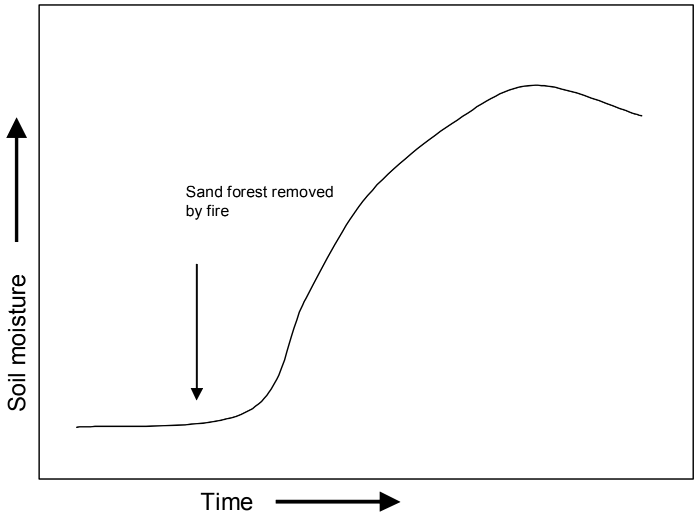

Figure 1. Schematical diagram to show the change over time of mean soil moisture content at a site before and after Sand Forest has been removed by fire (assuming mean rainfall levels). (Inferred from Matthews, unpublished neutron probe data; Fourie *et al.* 2002).

8.2.1.9 Fire

Fire is associated with all three forest types, but specifically with the vegetation which forms the matrix within which the forest are found (Bond 1997; Mucina & Geldenhuys 2004). Fire does not generally penetrate the forests deeply, but stops at the edge (Midgley *et al*. 1997). This is called an ‘edge effect’, and is especially prevalent in two of the forest types, namely Afromontane Forest and Sand Forest. The fringe flora in Afromontane Forest is especially diverse, and appears to differ considerably, in terms of floristic composition, from the core forest. The fringes of Sand Forest are less floristically diverse but also differ from the core forest. Dune Forest does not have a fringe that differs floristically much from the inner forest, but fire usually also stops at the edge (Weisser & Cooper 1993).

When fire does penetrate the core forest, the three forest types respond differently to the resulting impact. Dune Forest, which is a resilient forest type and adapted to respond relatively rapidly to severe damage or even total destruction, recovers and re-establishes itself the quickest (Matthews pers. obs.; Weisser 1979). Afromontane Forest also re-establishes itself rather quickly, but is slightly less resilient than Dune Forest. Sand Forest, on the other hand, has a very low resilience, and *does not appear* to be able to re-establish itself after severe damage by fire (Matthews *et al.* 2003).

Table 2. Summary of main distinguishing characteristics among the three principle forest types in southern Africa.

Attribute	**Forest type**		
	Sand Forest	**Dune Forest**	**Afromontane Forest**
1. Distribution range	x	xx	xxx
2. Species richness/area	xxx	xx	xx
3. Endemicity/area	xxx	xx	xx
4. Deciduousness	xx	x	x
5. Canopy height	xx–x	xx	xxx
6. Rooting depth	x	x	xx–xxx
7. Mean annual rainfall	x–xx	xx–xxx	xxx
8. Average temperatures	xxx–xx	xx–x	x–xx
9. Substrate–sand proportion	xxx	xxx	x–xx
10. Relative substrate age	xx	x	xx–xxx
11. Exposure to fire	xxx	xx	xx-xxx
12. Resilience	x	xxx	xx

xxx – Highest/widest/oldest/deepest; xx – moderate/average/medium; x – lowest/limited/youngest/shallow

8.2.2 Sand Forest dynamics

8.2.2.1 Succession and resilience

Preamble

The six steps of classical Clementsian succession are: nudation (creation of areas bare of plants), migration (arrival on site), ecesis (invasion of plants into new habitat, establishment on site), competition (interaction of organisms on site), re-action (modification of site) and stabilisation. A community can be viewed as a changing mosaic of patches of different sizes, ages, structures and composition. Therefore the spatial patterns are important for the understanding of community change (Glenn-Lewin *et al.* 1992). Climate is one of the most important factors determining how far succession will proceed and what type of plant growth will establish under field conditions. A community seldom reaches the ideal, equilibrium or climax stage, as it is always exposed to changes (Krebs 1985). Succession is influenced by three dimensions of disturbance: space, time and magnitude (Glenn-Lewin *et al.* 1992). A disturbance is an event that causes a significant change from the normal pattern (steady state) in an ecological system (Forman & Godron 1986).

Vegetation dynamics can be divided into seven types (Van der Maarel 1988): fluctuation, gap dynamics, patch dynamics, cyclic succession, secondary succession, primary succession and secular or long-term succession. Miles (1987) states that regardless of plant strategies, an important determinant of the course of any succession, and the prime determinant of secondary succession, is the range of species present at the outset and migrating to the site early in succession. Gleason (1927) states, more definitely: "Succession is an extraordinary mobile phenomenon, whose processes are not to be stated as fixed laws, but only as general principles of exceedingly broad nature, and whose results need not and frequently do not ensue in any definite predictable way' and different models have been put forward to help understand the successional process".

Secular succession concerns long-term changes (greater than 1000 years to geological time scales) in a landscape because of long-term environmental changes, often climate. This also includes the change in the geographic distribution of species. Long-term soil changes accompany secular succession, probably as an integral process rather than as a cause or effect (Glenn-Lewin *et al.* 1992). One aspect of secular succession is the gradual change in the composition and even the structure of the climax community as a result of changes in soil conditions (Beard 1974).

Species diversity increases with time towards the mid-successional stage, where it reaches a peak because of colonisation of the available environment (Mueller-Dombois & Ellenberg 1974).

Table 3. Some general tendencies in early and late succession as it relates to Sand Forest based on Barbour *et al.* 1987.

Traits	**Early stage of succession**	**Late stage of succession**	**Sand Forest traits**
Biomass	Small	Large	Large
Physiognomy	Simple	Complex	Intermediate to complex
Nutrient storage	Soil	Biomass	Biomass
Role of detritus	Minor	Important	Relatively important
Mineral cycles + mineralization rate	Open (leaky), rapid rate of mineralization transfer	Closed slow rate of mineralization transfer	Closed, slow rate of mineralization transfer
Net primary production	High	Low	Low
Site quality	Extreme / xeric	Mesic / moderate	Xeric to mesic / moderate
Importance of microenvironment	Great	Moderate /dampened	moderate
Stability	Low	High	Low to high
Plant diversity	Low	High	Moderate to high
Species life histories	r (pioneer species)	K (climax species)	K (climax species)
Propogule dispersal vector	Wind	Animals	Animals / fleshy fruits
Propogule longevity	Long	Short	Short
Humification	Slow	Fast	Fast

The Initial Floristic Composition Model of Egler (1954) states that succession is determined by the species that first colonise the area and could be pioneer and climax species. This is very similar to the inhibition model of Connell & Slatyer (1977). According to Miles (1987) many studies have shown that the initial floristic composition of a site is an important factor in determining the successional development of a site.

According to the Inhibition Model (Niering 1987), the first colonizers modify the environment so that it becomes less suitable for subsequent recruitment's of both pioneer and secondary species (allelochemicals given off which inhibits germination and growth of other plants). In the inhibition model replacement occurs only when resources are released by the damage or death of previous occupants, the species composition shifts gradually and inevitably (given no further major disturbances) towards species that live longer. Simply by their life-history characteristics, long-lived species eventually dominate the ecological scene.

It seems clear that no succession, primary or secondary, ever occurs in which any single one of these models operates alone (Miles 1987). According to Odum (1997) it is generally accepted today that the ecological succession concept is a two-phased process. Early or pioneer stages tend to be random (i.e. stochastic) opportunistic species colonisation, but later stages tend to be more self-organised (i.e. deterministic).

Colonisation/secondary sites

Secondary sites are usually re-vegetated very quickly because of rapid recruitment from their seed or seedling banks, and/or clonal growth from extant plants on their peripheries (Glenn-Lewin *et al.* 1992). The order of arrival of species on a site can influence both the composition and physiognomy of the vegetation. Colonisation on primary sites is an extremely variable phenomenum, which depends greatly on seed dispersal from adjacent areas, local environmental conditions, and year to year variation in climatic conditions (Glenn-Lewin *et al.* 1992).

Vegetation acting as units or per chance groupings of species.

The different succession models relate to the succession of a particular species in particular situations, and not to vegetation types (Miles 1987). This is an unsurprising conclusion, because in succession it is the individuals and populations that change. For a vegetation to act in successional terms as a unit, and thus to permit useful generalisations about succession at a vegetation level, it would need a tightly integrated network of species, probably co-evolved and co-adapted, possessing hypothetical 'emergent' properties, and thus behaving as a vegetation gestalt. No properties of vegetation have ever been demonstrated that cannot be explained as the effects of species and of interactions of species. To quote West (1964): '…we may conclude that our present plant communities have no long history in the Quaternary, but are merely temporary aggregations under given conditions of climate, other environmental factors and historical factors'.

Lags

Studies by Vaartaja (1962) and Grime & Jeffery (1965) have shown that late-succession species maintain themselves in the presence of dominating early-succession species by having a lower metabolic rate, by repairing damages, and by fending off attacks of herbivores and soil pathogens. The late-successional species simply survive in a state of "suspended animation" until more resources are made available by the damage or death of an adjacent dominating individual. By "suspended animation" is meant the maintenance of the existing state (vegetation community) till circumstances change to more favourable for normal dynamics or functioning to return. Most geomorphic and topographic spatial patterns change very slowly and can be regarded as fixed in time (present themselves as static). Many current landscapes are the product of past climates and the processes which created these landscapes, but now many of these process are no longer active (Stafford Smith & Pickup 1993).

Indications are that the size and number of Sand Forest patches which correlate with Dune Cordon 3 (Tembe zone), approximately 50–60 km from the coast and with a mean annual rainfall of 650–700 mm, have not increased when comparing the most recent aerial photographs with the oldest available aerial photographs dating back to 1942. The Sand Forest mosaic of this zone appears to be in a state of "suspended animation". What is apparent is that there has been a reduction in the distribution and sizes of patches in this zone. This can be attributed to harsh fires that periodically occur in the region. Sand Forest which has been impacted upon by such fires has not been able to recover back to "pristine" Sand Forest (Ostrosky pers. comm. & Matthews pers. obs.) and in most cases are reverting to woodland type communities. However, these patches still do have Sand Forest elements present, for example the more hardy species that can re-sprout and are normally large specimens such as *Cleistanthus schlechteri. Cleistanthus schlechteri* and skeletons of other dead hard wood species can also be seen on these sites. *Cleistanthus schlechteri* has a very hard and resistant wood that lasts for quite long after the tree has died. The possibility exists that many of the large specimens of Sand Forest elements that occur outside Sand Forest in woodlands are remnant survivors of past Sand Forest patches that are not present anymore, and therefore these species did not recruit into these woodlands.

Based on the aerial photograph comparisons, it can be seen though, that the Sand Forest patches closer to the coast, e.g. those in the areas around Sileza Nature Reserve (± 30 km from coast) are recruiting. Comparing the latest aerial-photos with those from 1942 do show that patches of Sand Forest are enlarging (even though just slightly) as well as the establishment of smaller Sand Forest like patches. Environmental conditions here are wetter (rainfall gradient related to distance from coast and higher water table levels) than at the Tembe zone, soils, are very similar. This moister environment and coastal vegetation community influence does show itself in the species composition of these Sand Forest patches in that coastal elements are present which are not recorded for the Sand Forests in Tembe Elephant Park (Tembe zone).

Episodic

Sand Forest appears to be strongly episodic, recruiting only when conducive environmental conditions prevail. These periods will enhance the survival and growth of seedlings and the understory recruited plants. These episodic periods need though to be longer than one or two years for Sand Forest species to recruit.

Semi-arid woodland only rarely, perhaps every 30–50 years, experience the combination of favourable environmental conditions needed for tree regeneration (Peet 1981; Peet unpublished data; White 1985). Therefore, seedling recruitment in these areas is low and often episodic. In addition the final phase is not really a steady state phase, but rather exhibits pulses of establishment alternating with periods of declining tree seedling and sapling densities. Savannas do not represent a stable mixture of trees and grasses, but is an inherently unstable mixture which persists owing to disturbances such as fire, herbivory and fluctuating rainfall (Scholes & Walker 1993).

Time aspect

Succession is a compositional change, usually evident over a few decades to a few centuries. The change is directional, either uni- or multidirectional. Long-term change occurs over many centuries or millennia and results from equally long-term changes such as climatic change or soil development. The distinction between fluctuation and succession is arbitrary, in that a large enough fluctuation over a long enough period of time becomes succession (Bornkamm 1988). It can be said that succession involves changes in dominant or diagnostic species and new species enter the community and become diagnostic whereas fluctuations, the dominant or diagnostic species do not change and new species do not enter the community, or if they do they do not become diagnostic (Miles 1979).

If a community does exhibit some directional, cumulative, non-random change over a period of 1–500 years, it is said to be a successional community (Barbour *et al.* 1987). The time scale in primary succession may involve centuries or even thousands of years. On such a long time-scale, evolutionary changes in species adaptation and speciation cannot be ignored. Vegetation changes are relatively fast in secondary succession as it proceeds from an already established ecosystem.

The time-scale from pioneer stage to a stage of relatively equilibrium or stability can be measured in years or decades (Mueller-Dombois & Ellenberg 1974). The rate of change will be linked to the longevity of the dominant plants (Glenn-Lewin *et al.* 1992.). Secondary succession on favourable sites with ample migration can be expected to require little more than one episode of compositional sorting. In contrast, classical primary succession starting with a bare rock surface can be expected to have a long trajectory with many species coming and going during the process (Walker 1970).

Dune Forest is a dynamic and resilient vegetation type that is characterised by its proximity to the ocean and its ability to re-establish itself relatively quickly following destruction. Dune Forest associates with scrubland or grassland, and, like Afromontane Forest, exist in a state of 'mutual replacement' with its associated vegetation (Midgley *et al.* 1997). Succession in Dune Forest is primary (as well as secondary in cases of disturbance), with Dune Forest and its associated vegetation able to establish on bare, newly formed sand dunes, the latter process which is still active along parts of the Maputaland coast, especially in the south towards the Tugela River Mouth (Tinley 1985).

Sand Forest is less dynamic, and exists in a state of 'suspended animation' in which it is maintaining itself in certain habitats, and to a large extent is not actively establishing itself in new localities. It also tends not to recover after destruction, especially when severely damaged, for example, by fire. These severely damaged Sand Forest sites are usually replaced by woodland vegetation.

Afromontane Forest is a dynamic vegetation type, and exists in a state of 'mutual replacement' with its associated vegetation—forest can replace associated vegetation and *vice versa*. When damaged, Afromontane Forest will return to its prior state through successional processes, as discussed (Mucina & Geldenhuys 2004).

Stability and persistence

After a population is established, the ability of the population to replace individuals, as they are lost, determines whether or not it will persist. Stability can be shortly defined as the lack of change (Barbour *et al.* 1987). However, "stability" is a complex term that includes several distinct qualities (Connell & Slatyer 1977) such as resistance, resilience and persistence. Resistance is the ability of a community to remain unchanged during a period of stress. Resilience is the ability of a community to return to "normal" following a period of stress or disturbance. Persistence is the ability to remain unchanged over time. Some persistent communities are neither resistant nor resilient, but owe their continued existence to a protected, buffered environment.

Stability will increase with succession (higher in so-called “climax communities”). Climax communities have inertia, changing slowly in the face of environmental changes and therefore are more resistant. Stability (resilience) is the ability to return to it balance point (homeostasis) following a major disturbance (fire, etc.) in this case the pre-climax communities are more resilient and climax communities are less resilient, this means that climax communities could be more fragile (the possibility of them recovering to their former state after a disturbance is not guaranteed). There is a difference to resistance to change compared to resilience to change in the face of pressures. In the case of Sand Forest it could have a low resilience to disturbance, e.g. fire, or any other impact, but be resistant to specific impacts such as fire and also be persistent as it has a buffered environment.

8.2.2.2 Allelopathy

Dissolved organic matter (DOM), which leaks out of decomposing plant material as well as from living cells, accumulates in increasing amounts and varieties in the soil. These “extrametabolites” not only power microbial food chains, but some products also act as inhibitors (antibiotics) or growth promoters (vitamins, hormones etc.) that would affect growth and species composition. Creating an increasingly biotic environment is one of the main ways the community facilitates a succession of species (Odum 1997).

A plant may interfere with the growth of its neighbours directly through resource competition or chemical inhibition, or indirectly if it harbours or attracts organisms such as herbivores or pathogens that affect neighbours (Muller 1969; Harper 1977; Fuerst & Putnam 1983; Weidenhamer 1996). Plant-plant interference (Rice 1984) may involve not only competition for water, light and nutrients, but also allelopathic phenomena that release toxic organic compounds into the environment. Under appropriate conditions, these chemicals are released in sufficient quantities to affect the growth and development of individuals of the same or other species (Seigler 1996). These substances are released into the environment through leaching from living plants, root exudates, volatilisation, residue decomposition and microbial activity (Muller 1969). The primary objective of allelopathic species, is to eliminate other species (Muller 1969). This means that allelopathy mainly occurs on an interspecific level, whereas resource competition occurs both at inter- and intraspecific levels.

In addition to the hydrophobic soils, Sand Forest also seems to produce compounds that produce an allelopathic effect. This is probably what produces the bare zone surrounding Sand Forest, an assumption that seems to be substantiated by the fact that the bare zone appears much more distinct in the driest areas—allelopathic effects being more pronounced in these poorly leached areas. Weidenhamer (1996) noted that environmental stress such as water and nutrient limitations, salinity and high plant densities enhances the production of allelochemicals in plants. Whereas the hydrophobic soils benefit neither Sand Forest nor Woodland, the allelopathic substances benefit Sand Forest because it can actively exclude competitors from the habitat, and the bare allelopathic zone can also act as a fire barrier. This allelopathic effect could give Sand Forest an advantage in an environment that is not quite optimal.

It is here proposed that in Sand Forest it is not one plant against its neighbour plant or other Sand Forest plants, but all seem to play a role in some way in producing the allopathic property, which keeps out other competing plant communities such as the woodlands that dominate the area. In many communities, organisms interact for some time and undergo genetic modifications. This close association between species is called co-adaptation (or co-evolution) (Seigler 1996). Selection for organisms that can tolerate, detoxify, or utilise the compounds produced by other community members appears to occur widely and frequently. In natural plant communities, many of the organisms in a community will co-adapt to the release of allelopathic substances (Seigler 1996). This pulls all species together, working as a unit to produce an enhanced allelopathic effect.

Density-dependence

In natural communities the effect of toxins in the soil are intensified by factors such as low plant densities, harsh environmental conditions and nutrient stress (Weidenhamer *et al.* 1989). Thus high densities of plants would effectively result in reduced allelopathic effects and Sand Forest is an example of a vegetation type with high densities of plants. Adult plants at high densities can cope with these concentration levels of allelochemicals, but new recruiting plants must be able to deal directly with the allelochemicals which at these levels could act as toxins.

Rice (1984) has stated that quantitative and qualitative changes in allelochemicals may occur during succession. In natural communities, succession occurs with time. This allelopathic effect in Sand Forest may also be a successional attribute that changes over time, with certain species able to cope with the high concentration at maturity and other species at earlier stages of succession. This could give rise to a state when the juvenile plants of many of the larger species (e.g. *Newtonia hildebrandtii*) in the forest are absent or scarce. The mature species established possibly when conditions were different and the allopathic attributes were not that inhibitive to that specific species. It is recognized that pioneer species exhibit different co-adaptations and interactions than those of most climax species (Seigler 1996).

If vegetation is virtually totally removed, such as in the case of a devastating fire, the allelopathic effect can be amplified. As stated by Inderjit (1996) environmental processes, such as fire, indirectly enhance the allelochemical levels in the soil, by reducing the concentrations of the soil chelators responsible for allelochemical breakdown. It may also increase the hydrophobicity of the soil. If the density of plants has been reduced drastically and the high concentrations present are not metabolised, this could result in these allelochemicals levels being even toxic to the dominant mature species, which normally would have coped with these allelochemicals, such has been the case of Sand Forest. Only after leaching of the inhibiting agent from the soils, will species establish. In the case of Tembe Sand Forest is seems to be between 1–2 years, pending on rainfall before Woodland or Sand Forest species recruit into these major disturbed areas (Matthews pers. obs.). The chance is then that these could also be woodland elements which now can cope with these lower concentrations of the allelochemicals as well as been better adapted to the harsher environment.

8.2.2.3 Gap replacements

Vegetative propagation is an important mechanism for the persistence of species in sites subjected to periodic disturbances, such as fire and tree falls. Gap replacements is where recruitment is restricted to sites where the vegetation is totally, or partially, destroyed as a result of factors such as fire, tree fall and animal activities. It occurs not only in forest, but also in grassland, wetlands and shrublands (Glenn-Lewin *et al.* 1992). Gap dynamics provide new possibilities for establishment and re-establishment of new and/or mature species.

For species whose seeds cannot germinate under a plant canopy, recruitment of new populations is restricted to gaps or openings in the vegetation. Conditions within established vegetation prevent the germination of seeds of most species. This has been shown by studies in which seed has been sown into different types of plant communities (Cavers & Harper 1967; Peart & Foin 1985; Bakker *et al.* 1985; Peart 1989 a, b). Possible reasons for the existence of conditions not conducive for germination include: spectral composition of light, thickness of litter layer, day and night temperatures and soil-moisture levels. For lowland tropical forest in Panama, (Brokaw 1982) estimated a turnover time of 113 years to 126 years depending on the minimum gap size that one assumed.

Gap dynamics is important and very active in Afromontane Forest, where seed banks and already established understory plants ("seedling bank") initiates regeneration after disturbance. There is abundant evidence that many Afromontane forests are still actively establishing themselves and that the distribution of Afromontane Forest has fluctuated considerably over thousands of years (Adams & Faure 2000). During the last glaciation period (18 000–10 000 years BP), large areas were cleared of all forest types including Afromontane Forest, but what we see today, was subsequently re-colonised by the different forest types including Afromontane Forest. It is marked that many Afromontane forest species are very wide ranging, with very little regional endemism. Afromontane forest seems to be able to re-establish itself in places where it was destroyed or did not occur. In case of destruction of forest but where parts of the forest still persist, recovery of the forest can occur in a relatively short period of time, if adequately protected from subsequent disturbance. Tree-fall gaps Mean Return Intervals range between 50–200 years for most forest types, though scattered individuals trees can have much greater longevities (Runkle 1985). Disturbance regimes themselves are subject to change during succession.

Though gap replacements do occur in Dune Forest, it is of less importance than in Afromontane Forest, here the seed banks playing an important role. Dune Forest is very resilient and dynamic, explaining the ability of Dune Forest to re-establish itself very quickly after destruction or disturbance. Weisser (1979) established from aerial photos that it might take a mature *Acacia kosiensis* woodland about 25–60 years to become established on grassland and about 30–150 years to be replaced by secondary Dune Forest. A fire that occurred in a Dune Forest just north of Rocktail Bay in 1994, virtually destroyed extensive parts of the dune forest. After ten years the damaged forest has recovered and is very hard to distinguish from the surrounding un-burnt Dune Forest. Dune Forest forms part of primary succession on the bare sand of a dune that has been denuded of vegetation, or newly laid down through oceanic processes. Dune Forest therefore can be referred to as a type of 'pioneer forest' able to initiate and forms part of primary succession.

Gap dynamics does not appear to play a significant role in Sand Forest; indeed, it seems that gap dynamics may not nearly operate at the scale at which it operates in the other two forest types. Therefore because of this and other aspects as discussed before, Sand Forest can be regarded as not a resilient vegetation type. There are good indications that Sand Forest does not easily recover/re-establish itself after a major impact that has damaged or destroyed the forest (Ostrosky pers. comm., Matthews pers. obs.). There is also no evidence that Sand Forest in the drier inland areas is actively expanding its boundaries and colonising new sites, this under the current climate and environmental conditions. Comparison of aerial photos of 1942 (Matthews *et al.* 2003; Izidine 2004) and the latest aerial photos (2000; a period of 58 years) show no increase in the size or number of patches. Even to the north in Mozambique, the old cut lines (roads) through the Sand Forest (in the Reserva Florestal do Licuáti) are still visible today after about 60 years. Sand Forest seems as if it exists in a state of 'suspended animation'—maintaining itself in areas where it still exists in a pristine state. In this respect, Sand Forest differs significantly from Afromontane and Dune Forest.

Although sometimes recruitment in gaps must have taken place in Sand Forest when environmental conditions are favourable, i.e. when soil moisture and rainfall is above what we currently consider as the mean or norm. These gaps though, should not be open too neighbouring woodland/grassland communities. These gaps should also not be too large as leaching of the allelopathic soils could give woodland species a greater ability to recruit into these gaps. If these gaps are large to medium and open to neighbouring woodland communities (seed source/progule) then these woodland communities would be given a favourable chance to invade as soon as allelopathic conditions have reduced enough to allow woodland species to germinate and establish. Allelopathic conditions directly after gap creation could also be negative to many Sand Forest species recruitment (Weidenhamer *et al.* 1989; Rice 1984), because some leaching could be needed before even Sand Forest species will germinate and recruit. Only those Sand Forest species able to cope with the allelopathic conditions would survive the process that created the gap in the first place. The long term survival of the Sand Forest species could also be temporary if woodland and grassland species took hold in these disturbed areas (substantial higher grass biomass), as the woodland communities would increase the probability of fires occurring, especially if in direct contact with neighbouring woodland. This continued exposure to fire would in effect slowly remove the Sand Forest species from such sites.

Most managerial decisions are made based on short-term evidence. In southern Africa, forest types are often lumped together as 'does not recover from severe disturbance or destruction'. The reality is, however, that Afromontane forest and Dune Forest will probably, given enough time, proper management and adequate protection from further disruptions, recover completely from severe disturbance and even total destruction. The floristic composition of these forests in some cases would probably not be exactly or even nearly the same as it was prior to the disturbance or destruction, but the fully functional forest *system* and *dynamics* will return. The same cannot be said of Sand Forest, however. If destroyed, the Sand Forest system will probably never recover, unless the conditions, which are in favour of Sand Forest formation and/or succession, return, which is linked to climate conditions and possibly even to distance from the coast.

How is gap-fall-succession influenced by allelopathy?

Gap falls in most forest and dense vegetation has a stimulatory effect on surrounding and nearby species, largely because of increased availability of resources. According to Glenn-Lewin *et al.* (1992) the following three mechanisms increase availability of resources. Firstly, the decrease in rate of uptake and use of resources. Secondly, the increased decay and mineralization of nutrients previously held in organic matter. Thirdly, exposure of bare soil where a thick litter layer previously may have impeded seedling establishment. The specific canopy trees may also have had an influence on the species composition of the understory vegetation through their effects on the establishment, growth and mortality of herbs and seedlings of woody plants (Woods & Whittaker 1981; MaGuire & Forman 1983; Beatty 1984). Microsite differences beneath canopy species may result from variations in the quality and quantity of litter, which in turn, may affect availability of soil nutrients or result in allelopathic interactions (e.g. Gauch & Stone 1979; Beatty & Scoles 1988; Boettcher & Kalisz 1990). Therefore, depending where the gap is, its size and rainfall at the time, the recruitment taking place would depend on the recruit's ability to cope with the allelopathic effect. Under favourable conditions, Sand Forest elements could recruit under present Sand Forest canopy as well as at smallish gap-falls inside the forest. However, with large gap-falls and resulted enhanced leaching, the opposite could occur, with grassland and woodland species taking hold, especially since they are able to cope with, what for forest would be more harsher environmental conditions.

8.3. Sand Forest evolution: speculations and hypotheses

"The presence of the same form in distant places is no evidence that it was created twice, but that it can move." Steve Jones – Almost like a whale (1999).

8.3.1 Evolution/speciation preamble

As species composition changes during succession and becomes more predictable with increased competitive sorting, we should expect genetic variation within species to become restricted and the distribution of the remaining genetic variation to be more predictable. Unfortunately, scant information currently exists on changes in genetic variation within species during succession (Gray 1987) but the data that is available is consistent with this prediction. Therefore, Sand Forest species as they occur today should be evolving very slowly, as they are long-lived species that have succeeded in becoming established. Figuratively, to change now genetically is like playing with fire, as it could mean no survival for propagules. It's got a lifetime of a big tree to replace itself, this when conditions are right; it has no need to test for new abilities to survive under current non-suitable conditions. Therefore it has time to change—slowly.

Stress (adverse environmental conditions–evolution)

Energy and other resources necessary for growth, maintenance, survival, and reproduction are usually limited. When sub-optimal conditions exist this produces stress. Stress, as defined by Parsons (1991), arises from any factor causing a potentially lasting injurious change to a biological system. Stress is a common state affecting free-living organisms and it thereby not only imposes important selection pressures on individual organisms, but also affects the development of phenotypes upon which selection acts. After Møller & Swaddle (1997), a host of potentially evolutionary important processors can be affected by sub-optimal conditions experienced by individuals. Adverse environmental conditions have been suggested to affect the level of recombination, mutation, and transposition, the additive genetic and phenotypic variation, the intensity of selection, and hence the speed of micro-evolutionary change. These include phenomena associated with the genetic variation that may give rise to evolutionary change: increased rates of recombination, mutation, and transposition, and increased additive genetic variance.

Organisms have to allocate a very large fraction of their metabolism to cope with extreme environments, and little excess energy will be available for the stable developments of phenotypes and for reproduction. Availability of excess energy for development of stable phenotypes and reproduction will, particularly, be found under moderate sub-optimal habitats, and these may be the conditions most conducive to an evolutionary response to selection. Therefore, moderately sub-optimal environmental conditions are assumed to be permissive for gradual evolutionary change.

Distributional limits of species are important in that they reveal the conditions that prevent further range expansion (Møller & Swaddle 1997). Furthermore, peripheral populations play an important role in several theories of peripatric speciation.

Two evolutionary phenomena may be facilitated by extremely adverse environmental conditions, the destabilisation of the developmental process, and the resultant novel major deviations in phenotypes: speciation and major evolutionary innovations (Møller & Swaddle 1997). Evolutionary novelties have been shown to arise relatively rapidly (on a palaeontological time-scale) during adverse environmental conditions (Gould & Eldredge 1977; Mayr 1982).

Two modes of evolutionary change can be unified if the phenotypic response to adverse environmental conditions depends on the adversity of such conditions.

a) Long-term changes in response to adverse environmental conditions that are gradual and energetically relatively inexpensive in terms of maintenance and repair.
b) Short-term changes in response to severe environmental conditions that will be sudden and energetically expensive to the individual in terms of maintenance and repair. It will rely on environmentally induced unmasking of genetic variability and loss of canalisation (Hofmann 1983; Kieser 1987, 1993). [Canalisation is defined as the stabilised flow of a developmental trajectory of a genotype under different environmental conditions (Schmalhausen 1940; Waddington 1940)].

Moderate sub-optimal conditions results in moderate phenotypic changes that facilitate gradual evolutionary change, while extreme environmental conditions tend to reveal major phenotypic deviants that may give rise to major phenotypic changes as seen in connection with speciation and the evolution of major innovations.

8.3.2 Hypotheses on origin of Sand Forest

Three possible hypotheses are proposed to explain the establishment and foundation for Sand Forest.

- **H_1 : The primary hypotheses is that Sand Forest is (long term successional outcome) transformed Dune Forest.**

- **H_{1a} : A variation of the primary hypotheses is that Dune Forest is the precursor of Sand Forest, but that Sand Forest has subsequently become a separate functioning plant community on its own.**

- **H_2 : The alternative one is that Sand Forest is a self-generating forest community that is independent of Dune Forest precursors.**

Guiding principles and assumptions:

i. The regression of the ocean stimulates the establishment of new plant communities on the Maputaland coastal plain, while transgression can wipe out plant communities on the Maputaland coastal plain.

ii. Regressions and transgressions have been taking place since the break-up of Gondwana, at least 65 million years ago, although the last approximate 5 million years are relevant to the current coastal plains oldest dune formation (Dune Cordon 3), namely the Sihangwana Ridge.

iii. There has been a constant transgression of the coastline for the last 125 000 years. The coast has not been further inland than the Sihangwana Ridge for the past 125 000 years.

iv. No matter where the coastline was at any particular time, there would have been sand and coastal sand dunes, and there would have been Dune Forest like plant assemblages. These Dune Forest communities would not necessarily have had the same floristic composition that Dune Forest has today, but would have had similar functional properties.

v. Dune Forest is strictly associated with the coastline, and as the coastline regressed, the composition of the remaining "dune" forest changed or disappeared, while the true Dune Forest moved with the coastline. If there is bare sand close to the ocean, Dune Forest could establish itself there.

vi. Dune Forest has a relatively quick succession (Weisser 1979). The dynamics of Dune Forest are founded upon primary succession.

vii. Sand Forest communities are "persistent" in a buffered environment.

Primary hypothesis* (H$_1$)*: Sand Forest is transformed Dune Forest.

As the ocean regressed, sand dunes with their assemblages of Dune Forest elements remained behind. These "Dune" forest communities gradually changed their floristic compositions as the ocean moved away and the local climate changed. Those species that were totally dependent on the proximity of the ocean gradually disappeared from the community, while those species that could survive the drier conditions persisted. This differential extinction or elimination would have been the main niche opener in the community. These niches could now be filled in three different ways:

i. Immigration from pre-existing, similarly dry inland habitats could have taken place;
ii. Species that were 'sub-ordinate', 'low-key' or 'rare' in the primary Dune Forest assemblage, could have assumed more prominent positions where tolerances allowed; and
iii. Speciation of species that previously occurred in the primary Dune Forest or surrounding vegetation could have taken place, making those taxa better adapted to the changed environments. This last was probably especially related to Sand Forest, as there still exists a large number of 'aberrant' forms of more widespread taxa in Sand Forest.

This mixture of species that would have resulted is still in existence today, and can be seen in the inland forests of Maputaland, which consist mainly of Dune Forest elements, supplemented by Sand Forest and other forest (tropical and temperate) elements. The arid elements in these 'mixed forests' could have moved in from the north (northern Mozambique), where the coastal plain would always have been much broader and tropical than in the south.

As the ocean pulled back further, the changed Dune Forest would have had to become increasingly drought adapted, as the resulting plains between the Lebombo Mountains in the west and the ocean in the east, would have been drier than the original Dune Forest habitat in terms of both rainfall and soil moisture (water table depth). It had to change in terms of floristic composition, but the original forest structure remained in place. It is speculated that eventually these patches of 'left-behind' Dune or 'mixed' forest, had changed enough from the primary Dune Forest (especially in terms of floristic composition and functioning) that it could be recognised as another community type, what today is called Sand Forest. It is therefore suggested that Sand Forest originated by a process of "evolutionary vegetation change" associated with environmental change in the manner described, over a very long period of time (geological time scales).

Pointers in support of hypothesis

Once Sand Forest has established itself on a sand dune, it can maintain itself in that habitat, but indications are that it cannot colonise primary or exposed dunes. Considering present-day evidence, and behaviour, it would seem that Sand Forest is not capable of colonising an isolated, (non-Sand Forest) sand dune. It also cannot very easily establish itself in woodland or grassland; and where Sand Forest does occur today, neither does it easily re-establish itself after severe destruction. This would support the view that Sand Forest is transformed Dune Forest.

The only opportunities for the establishment of forest on open dunes would always have been along the coast, and these forests would always have been Dune Forest, not Sand Forest. The current inland Sand Forest (as on the Sihangwana Ridge) one can see today must therefore have been maintaining itself for the last 125 000 years (since the last major transgression of the ocean). It is speculated therefore, that when Sand Forest is destroyed, it cannot replace itself, as Dune Forest is necessary as a precursor, and that these dunes are now too far away from the ocean for Dune Forest to establish there.

As part of soil carbon studies (Catapano 2004), charcoal layers were consistently found in more sample pits under woodland and grassland, than under Sand Forest. It follows from this that fire is very much a feature of woodland and Woody Grassland (both of these vegetation types are adapted to deal with regular fires), but not so much for Sand Forest. Woodland must have been woodland for a very long time and consistently exposed to fire. However, in the case of Sand Forest, the frequency of occurrence of charcoal and charcoal ^{14}C dating (Catapano 2004) supports the idea that sites with Sand Forest have been in existence for a very long time.

Catapano (2004) concludes that geochronology coupled with carbon isotope data from SOM as well as the abundance of charcoal and the apparent conservation of C:N ratios collectively indicate stable vegetation regimes since approximately 1800 BP.

Sand Forest is surrounded by fire-prone vegetation types, namely the woodland and Woody Grassland mosaic. Occasionally, when fire does penetrate Sand Forest, it is very destructive. If Sand Forest is derived from Dune Forest, all that subsequently happened was that it shrunk due to damage caused by fire. Eventually Sand Forest will become smaller and smaller due to fire impacts. It is a relict vegetation type even though it is relatively recent in geological terms (neo-endemic), because it seems to be "out of sync" with its environment. Sand Forest in the past would have covered larger areas of the Maputaland coastal plains as is the case today. In a protected sand dune island in southern Mozambique there is still a contiguous intact Sand Forest (thicket) of about 25 km long by 15 km wide covering 140 km^2 found in the Licuáti Forest Reserve (Izidine 2004).

Further support for the hypothesis would be to find a gradient of forest types between the ocean and the relict shoreline furthest from the ocean, with pristine Dune Forest occurring closest to the ocean, and pure Sand Forest occurring closest to the mountains on the deepest sand or highest inland dunes, as is the situation currently.

Sand Forest floristic elements are sometimes found in woodland (Matthews *et al*. 2003). One explanation for this occurrence is that these elements are relicts (and not precursors) of Sand Forest that was left behind after severe destruction by fire left the habitat open for woodland to invade. These relicts are mostly the very large hardwood trees that persist as remnants for a relatively short period of time. However, Maputaland is a dynamic region, and speciation and evolutionary processes appear to be very much active and in place. It is therefore quite feasible that some Sand Forest elements are becoming adapted to woodland conditions. Woodland elements, on the other hand, are not able to enter pristine Sand Forest, because Sand Forest is very exclusive. It competitively excludes (competitive exclusion) other vegetation types by chemical (allelopathy) and physical (hydrophobic soils) means—a buffered environment.

Origin of the woodland and other communities

The question that now arises is how the woodland matrix developed. When the ocean retreated, it left behind Dune Forest and associated vegetation. Therefore, just as in some areas Sand Forest replaced Dune Forest, in others woodland could have replaced the Dune Forest. The same may be true for the Woody grasslands of Maputaland, which is basically woodland but occurs in areas with a high water table. As aridity increased, woodland and Woody Grassland would have been more adapted to replace the coastal dune vegetation. It appears that woodland was mainly established by immigration, as there is little evidence of local speciation and most of the woodland species have wide distribution ranges through most of the subtropical savannas of southern Africa.

Arguments for/against the hypothesis as well as alternative hypotheses (based on preceding discussion)

For the alternative hypothesis (**H_2**) [Sand Forest is a self-regenerating forest community that is independent of Dune Forest precursors] to be true, one would expect the following to be true:

- That Sand Forest consists of a mosaic of colonisation and of obviously different plant age classes, *typical* of most forest structures. [False]
- That there would be a uniform diversity throughout its distribution as is the case with Afromontane Forest, which has a low β-diversity. [True & False]
- There should be a good replicate of recruitment stages with a normal growth curve in Sand Forest. Gaps would be filled, and Sand Forest would recover after impacts. At least, the recovery rate should be in harmony with that of the neighbouring vegetation types. One would see both destruction and re-colonisation. Also what is destroyed in one place could be replaced in another. There should be a mutual replacement balance as would be expected of any typical forest. Woodland and Sand Forest should not out-compete each other in the long-term. [False]
- Either Sand Forest would have links to similar forest types in other parts of southern Africa, or it would be more widespread in southern Africa, not as local as it is, or it would develop from scratch from pre-existing species in the area. [False]
- Sand Forest should have dynamics similar to other forest types. [False]
- Chance should play a role in the distribution pattern of Sand Forest. It should have a random distribution where suitable habitat exists. There should be signs of Sand Forest everywhere, just as there are signs of woodland everywhere. Patches of Sand Forest should not always be Sand Forest, and patches of woodland should not always be woodland; especially as the substrate is the same for both vegetation types. [False]

- The evolutionary rate and the pressure to evolve would be low. Sand Forest taxa would have changed little from their ancestors, to keep the competitive advantage that these taxa had over the woodland ancestors. [?]
- There should be little evidence of stress in the vegetation, and many long-lived taxa should occur. [?]

The probability to form a forest *de novo* in a woodland area is lower than the probability that a drought adapted woodland develops. Mesic woodland, when it becomes dry, would become arid woodland, not arid forest. The alternative hypothesis (**H_2**) is therefore very unlikely.

For the primary hypothesis (**H_1**) [Sand Forest is transformed Dune Forest] to be true, one would expect Sand Forest to have the following characteristics:

- Sand Forest would have closer taxa links with Dune Forest than with any other vegetation types. [True & False]
- Floristic relationships would exist between Sand and Dune Forest. [True]
- Sand Forest would show very little ecological interaction with woodland. [True]
- There would be neo-endemics present in Sand Forest, because it would be a relatively stressful environment conducive of speciation. [True]
- There would be no new establishment of Sand Forest where there were no Dune Forest precursors. [?]
- One would expect Sand Forest to occur on sites where well-developed Dune Forest would have been present in the past. If the ocean regressed relatively fast, only the oldest, better-developed dunes would have supported well-developed Dune Forest. The best-developed Sand Forest would occur where the best-developed Dune Forest had occurred, and that would be where the largest and most stable dune cordons were or still currently are. [True / False]
- One would expect to find relatively less amounts of charcoal layers under Sand Forest; one would expect that in the past there should not have been woodland present on those sites. If charcoal does occur, it should be charcoal from Sand or Dune Forest species. [?]
- The break-up of Sand Forest patches would have occurred very early on, because fire is hypothesized as always been a factor on the coastal plains. [True]
- Since the establishment of Sand Forest, on the large scale, only receding (shrinkage) has taken place. It is hypnotized that if intact Sand Forest is present it can slightly expand or retract depending on the water regime, but it cannot establish a new core. It can only expand

from existing cores of Sand Forest. This slight expansion is event-driven. When it is wetter for longer periods of time, it will expand slightly, when it is drier, it will recede; when it is exposed to fire it can be removed from areas. [True - ?]

- If Sand Forest were exterminated completely, one would expect it not to return; instead the site would be taken over by the surrounding matrix vegetation (Woodland). [True]
- There would be a large β-diversity turnover. Some patches would be very diverse. Other would be less so, depending on chance events that influenced it in the past. [True]
- The endemics would be mostly related to Dune Forest taxa. [True & False]

The variation of the primary hypothesis (**H_{1a}**) [Dune Forest is the precursor of Sand Forest, but that Sand Forest has subsequently become a separate functioning plant community on its own] would have most of the characters described for the first hypothesis (**H_1**). Exceptions are that:

- There could be new establishment of Sand Forest where there were no Dune Forest precursors. [True & False]
- There would be a bias towards Dune Forest relatives, but other more tropical taxa could also be present. [True]

The strongest difference between the first (**H_1**) and the variation of the first hypotheses (**H_{1a}**) lies with floristics and the response to changing environments.

Before accepting any of the hypotheses as superior to the others, one must make provisions for climatic change and variance. The lack of recruitment one currently observes in Sand Forest may only be because it is currently a dry period (a dry cycle of ~10 years or more). Thus the lack of recruitment and successional processes could be directly linked to this. Although this would only really influence the first two hypotheses (**H_1** & **H_{1a}**), effectively confirming which of the two is closer to the truth. If climate conditions do become more favourable and Sand Forest does start recruiting independent of Dune Forest precursors, this would definitely support the variation of the primary hypothesis (**H_{1a}**).

Effectively if the environment were to change in the following ways for a long enough period of time what would we expect to happen to "Sand Forest" (or what effectively was the basis for the Sand Forest vegetation community) based on the three hypotheses? :

Wetter

H_1. “Sand Forest” would diminish—prefers drier dunes but needs to be established via Dune Forest dynamics. [Stable to Negative Impact].

H_{1a}. “Sand Forest” would recruit and expand in areas where already present and further from coast and retreat from the moister zones closer to the coast. [Stable to Positive impact].

H_2. “Sand Forest” would recruit and expand in areas where already present as well as in other suitable areas. [Positive impact].

Drier

H_1. “Sand Forest” would diminish—has preference for drier sand dunes but needs to be established via Dune Forest dynamics. [Negative Impact].

H_{1a}. “Sand Forest” would recruit but not expand in areas where already present and retreat from the relative drier zones. [Stable to Negative Impact].

H_2. “Sand Forest” would retreat from unsuitable areas and expand in other suitable areas. [Stable].

Coast transgression/regression.

Transgression or regression would have differing impacts:

H_1. Regression: Sand Forest would recruit and expand in relation to the establishment of Dune Forest precursors. [Stable to Positive impact].

Transgression: would result in the retreat or removal of Sand Forest from unsuitable zones. [Negative Impact].

H_{1a}. Regression: Sand Forest would recruit, but not expand in areas where already present as well as retreating from the drier zones that would develop deeper inland. [Stable to Negative Impact].

Transgression: Sand Forest would recruit and expand in the suitable zones (to a point – only as far as the base of the Lebombo Mountains) and where already present. Sand Forest would retreat from the moister zones close to coast. [Positive impact and then stable to negative].

H_2. Regression: Sand Forest would recruit into suitable areas and retreat from unsuitable zones. [Stable].

Transgression: Sand Forest would recruit into suitable zones and retreat or be removed from unsuitable zones. [Stable to Negative Impact].

Conclusion

The bulk of the evidence supports the variation of the primary hypothesis (**H_{1a}**) [Dune Forest is the precursor of Sand Forest, but that Sand Forest has subsequently become a separate functioning plant community on its own].

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CHAPTER 9

GENERAL DISCUSSION

9.1 General discussion

The *principle hypothesis* of this thesis is that the Maputaland Centre of Plant Endemism is characterised by plant communities each being specific to a particular set of environmental variables, including a rich biodiversity with endemic and rare taxa, and exhibits a relationship with the geomorphological history of the region. The information assembled supports these hypotheses and Figure 1, presents a flow diagram of these hypothesized developmental / succession paths of Sand Forest over time. The Maputaland Centre of Plant Endemism proved to have a diversity of plant communities that are specifically related to certain environmental variables (Chapters 4 to 6). The study did not aim to determine the endemic and threatened taxa, but merely to establish how these species were linked to specific plant communities. Endemic taxa were already determined by the work of Van Wyk (1994) and Van Wyk & Smith (2001). The results of the vegetation studies highlighted two plant communities as playing an important role in the regions biodiversity namely Sand Forest and Woody Grassland. Knowledge of the vegetation and flora of the Maputaland Centre of Plant Endemism and the role that large herbivores (specifically elephant) and fire may play in the dynamics of the different vegetation communities, can help facilitate the formulation of management strategies, specifically for those habitats in the region which play an important role in conserving the regions biodiversity. Following on this is the possibility of also evaluating existing management directives for the region, be it for the conservation of important biodiversity areas, or for sustainable utilisation of the region's natural resources or for ecotourism.

The present study adopted a broad approach to the floristic classification of vegetation to address the need for sound information on the floristics patterns and diversity of the unique and rare plants and communities of the Maputaland Centre of Plant Endemism. It is aimed to provide useful botanical information that was lacking for the region. Apart from the identification of plant communities, analyses of plant-soil associations and plant-herbivore interactions were also explored. Ideas on the phytogeography, possible origins of the habitats, specifically Sand Forest of Maputaland, were presented in an attempt to explain some of the patterns of diversity, vegetation anomalies and dynamics. Various ideas are presented born from speculations on the origin and evolution of Sand Forest (Chapter 8). These ideas on Sand Forest origin and evolution were evaluated with respect to the geological and geomorphological evolution of the region.

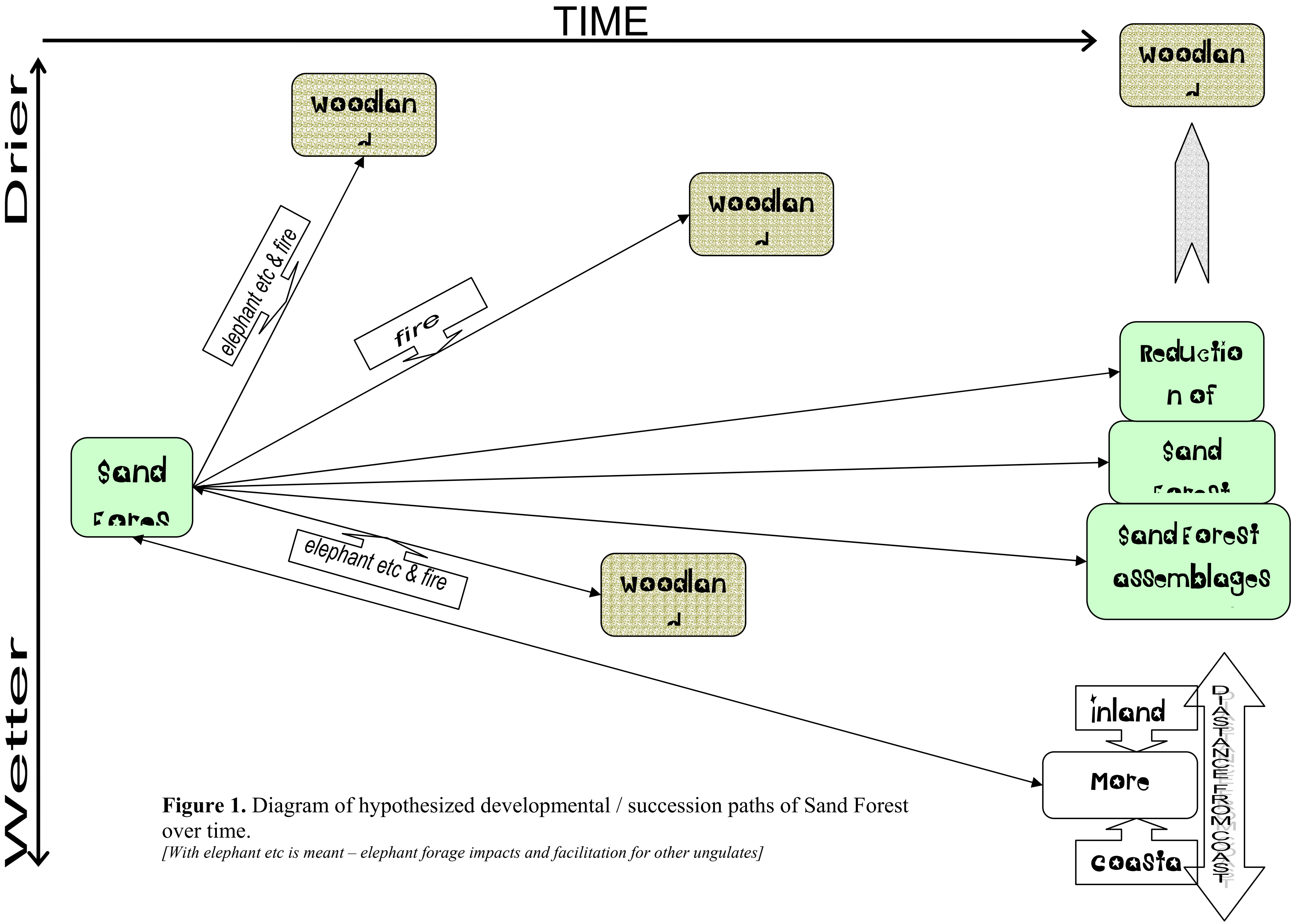

Figure 1. Diagram of hypothesized developmental / succession paths of Sand Forest over time.
[With elephant etc is meant – elephant forage impacts and facilitation for other ungulates]

Research opportunities were addressed (see section 9.3) to focus future work on gaps in knowledge, which could help in interpreting many of the outstanding issues regarding Sand Forest.

9.2 Reflecting on outcome of study

When one does a study like this, most of us would like to bring new information to the fore, this new knowledge to change current beliefs and understanding, and in so doing make science work for man in whatever small way. In a sense, this study has done that, although in future these ideas and understanding of what was thought to be might also be interrogated. Through this cross-examination, new perspectives come into being. These are the building blocks of science and future knowledge. In the following points, I would like to highlight, what for me, is new evidence and information that changes and/or challenges past beliefs or is simply new viewpoints of what possibly is.

> *Scientific inquiry requires investigators to challenge the validity and interpretation of evidence; hence the name research.*
>
> —Wayne G. Watson

- Two main habitats were highlighted as being very important to Maputaland's biodiversity, namely Sand Forest and Woody Grassland. Most of the emphasis of this work was placed on Sand Forest and in the case of this habitat much new information on its composition, dynamics and possible evolution has been brought to light. New insights highlight the role that the habitat type plays in the overall biodiversity to the region. The work also highlights the sensitivity of this habitat in light of the effective management of biological resources and these attributes.

- Two physiognomic or structural types of Sand Forest were distinguished (Matthews *et al.* 2003). One fits the basic physiognomic definition of forest, while the other can be better described as a thicket. These structural differences are also reflected in the floristics.

- Sand Forest seems to "manipulate" its soils thereby creating its own habitat, not only by making the soil more suitable for itself, but also by making it less suitable for the surrounding woodland vegetation (possible allelopathic characteristics). Sand Forest soils show hydrophobic characteristics under dry conditions, but when they get sufficiently wet, have a better water-holding capacity than the surrounding woodland soils (Fourie *et al.* 2002).

- The Sand Forest mosaic of most of Maputaland appears to be in a state of "suspended animation". By "suspended animation" is meant the maintenance of the existing state (vegetation community) till circumstances change to more favourable for normal dynamics or functioning to return. Catapano (2004) concludes that the Sand Forest assemblages must have remained stable since at least ~ 1800 BP years ago.

- In the past the coastal grasslands of Maputaland were seen as secondary in the sense of being "unnaturally" degraded forest or savanna. We contend rather that these grasslands are essentially primary in nature and the association between fire and these grasslands must be as old as the grasslands themselves.

- Some of the coastal grasslands of Maputaland also feature an abundance of geoxylic suffrutices (resulting in the woody nature of these areas) and in many cases these plants in the past were seen as indicative of overgrazed and burnt grasslands conditions. But in actual fact this is a unique feature of a specific habitat. These dwarf woody plants can be compared with extremely stunted trees, a fact which led White (1976) to refer to them as the "underground forests of Africa".

- Kirkwood & Midgley (1996) have argued, the absence or shortage of a conspicuous ground layer and the lower understory in Sand Forest is due to herbivory. However, this study and unpublished data point towards aridity, shade, compounded by possible allelopathic characteristics. Absence of a conspicuous ground layer is the natural state in this forest type.

- Midgley (1993) states that Sand Forest is dominated by species with wind-dispersed seeds. However, Matthews *et al.* (2001) and unpublished data indicate that plant species with fleshy fruits were the most common type in Sand Forest, even when considering cover-abundance.

- We have developed a rapid survey technique for elephant impact, by using a modified Point Centre Quarter (PCQ) technique, which appears to have worked well. Useful information on the relative use of different species and the likelihood of negative impact on their abundance from elephant feeding activity was produced.

9.3 Future research

In all studies there are gaps that become prevalent as one starts trying to interpret the results. These are important to record as it can help direct further research into the subject and related topics. From this study the following gaps and issues would help in interpreting some of the hypotheses presented. The pointers and questions put forward are in no particular order.

- Establish and compare the fauna and faunal diversity of the three principle forest types in southern Africa. More detailed studies are needed on:
    - The unique faunal element in all three of the forest types are all tropical related, but is Sand Forest's complement of tropical related animals the most pronounced?
    - Are Sand Forests and Dune Forest more closely related, faunistically?
    - What are the faunal communities and based on what resources in the three forest types?
- Sand Forest provides considerable opportunity for further research into the validity of its alleged allelopathic effects.
- Trees in Sand Forest seem to reach older ages than in woodland. Is this true and could this also be due to fire or the absence of fire?
- Research the evidence underneath Sand Forest that can reflect on the succession of that site, for example, the charcoal found in the soils underneath Sand Forest. If the hypothesis that Dune Forest is the precursor of Sand Forest, but that Sand Forest has subsequently become a separate functioning community on its own, is correct, then the charcoal under Sand Forest must be either Dune Forest or Sand Forest, but not grassland or woodland. It would, however, be reasonable to find charcoal of woodland or grassland species underlying Dune Forest, which in turn underlies Sand Forest, but if woodland or grassland charcoal were to be found under Sand Forest with no indication of Dune Forest, it could disprove the hypothesis.
- Currently Sand Forest shows a high turnover of species between the different forests patches (Van Rensburg *et al*. 2000), this applies to both dominant and rare species. More work on species turnover between patches on all taxonomic levels would be instructive.
- Does Sand Forest indeed occupy habitats more exposed to mist than woodland, and if this is the case, how does Sand Forest benefit from the exposure to mist?

- How much (i.e. what percentage of) rainfall reaches the ground following interception by the above ground parts of plants—compare between the different habitats of Maputaland.
- To what extent do the fauna collaborate floristic patterns in Maputaland?
- At what elephant population level could Sand Forest and elephant co-exist in a closed system such as Tembe Elephant Park?
- Maputaland combines a number of different and unique habitat types, from woodland to dense Sand Forest to wet coastal dune Forest. Each of these habitats contains species of invertebrates that are unique to it, perhaps one of the best researched examples being the butterflies. Based on the work of E. Pringle (pers. comm.), no less than 25% of the about 852 species of butterflies that occur in South Africa may be found in the KwaZulu-Natal part of Maputaland. Maputaland as a region has the highest biodiversity of butterflies in South Africa, and its species number is much higher than that of the Kruger National Park. Most invertebrates are very poorly known and therefore provides considerable opportunity for inventory research.
- It was considered premature to formally describe most of the syntaxa recognized during the present study. More phytosociological studies in other areas of the Maputaland Coastal plain are needed to correlate results.
- Detailed comparative studies on the ecology of the unusual Woody Grassland, in relation to conventional grassland and savanna, would be most instructive. There is a need to investigate in more detail the possible determinants and evolution of the suffruticose habit in the Woody Grassland of Maputaland.
- The taxonomic status of a *Podocarpus* species in Maputaland requires clarification.
    - Claims that pollen evidence suggests that Afromontane Forest once occurred on the coast of Maputaland (Scott *et al.*1992) need further testing. The *Podocarpus*-pollen that people assume is indicative of temperate conditions may be misleading. *Podocarpus* species are not necessarily Afromontane Forest elements; there exist, for example, what appears to be a form of *Podocarpus falcatus* in the swamp forests of Maputaland. The presence of this *Podocarpus* is indicative of tropical conditions, as it is usually associated with the palm *Raphia australis*. The climatic history of Maputaland furthermore argues against Afromontane Forest ever occurring there.
    - Why is *Raphia australis* pollen not recorded together with *Podocarpus* pollen, currently the two species are both associated with swamp like conditions?
- Palynological analyses of boreholes and peat lands are used in inferring past environmental conditions. It would be very informative to compare the relevant existing

taxa's pollen, with pollen that is currently used in the environmental condition predictions, crucial for correct predictions.

- It is desirable to carry out a much larger number of *in situ* permeability tests, soil wet ability tests and water retention tests to confirm on a broader scale the findings presented in this study.
- Repeat the bioassays for possible allelopathic interference in Sand Forest with a more refined experimental design which is statistically robust.
- This study produced many hypothesis on the dynamics, historic development and the environmental driving forces for Sand Forest development, creating a bases for an intensive modelling exercise which could produce informative results, especially if the current climate change scenarios are applied.
- A quantitative, floristic comparison of Sand Forest on dune ridges along an east–west gradient could assist in interpreting the long term dynamics and evolution of Sand Forest.

CHAPTER 10

MANAGEMENT IMPLICATIONS

Preamble

Park management is big business, getting bigger and more complex everyday, especially with the international expectation that it will be the prime mechanism for maintaining global biological diversity Child (2004) and an integral part of the socio-economic environment in which it is embedded. Today, successful park management requires a much wider perspective than provided by conservation biology alone. If ecological reserves are to survive, each must be an example of sustainable management for all parties concerned. They cannot continue as state-managed areas of poorly executed nature conservation, but should become bridgeheads for better landuse (Child 2002). This highlights the difficult position in which park mangers are placed, in most cases the absence of a clear, socially relevant and legitimate conservation philosophy.

If Conservation management agencies are to understand and manage the challenges they face, Child 2004 suggests that possible solutions lie in the way society sets about conserving and using parks and reserves. The key appears to lie not in making management more *efficient*, but in defining exactly what it aims to accomplish. Help towards achieving this effectiveness is likely to come from disciplines that are largely foreign to conservationists. This could include balancing economic issues, politics, modern business management, institutional strategies, and stakeholders' needs with the ecological and biodiversity purpose of the park. ***Thus to have a clear vision (based on stakeholder participation) and be responsible and accountable to it, this is critical to deliver on a park's mandate.***

Conservation management agencies had and have so many demands that they do not know what to focus on and as Drucker (1973) pointed out, nothing is ever accomplished unless scarce resources are concentrated on a few priorities. Because we cannot manage for something we cannot describe, we therefore need to define what exactly a park's conservation mandate should be, so that we can define the performance and accountability of public conservation management agencies.

The current vehicle that is used to develop a unified, clear vision so as to achieve a park's mandate is the Integrated Management Plan (IMP). The IMP forms the framework within which the reserve will be managed, aligned and developed in an endeavour to achieve the biodiversity conservation, ecotourism and partnership objectives as envisaged and set by the various stakeholders during a consultative planning process.

It is important that today's research findings inform the decision-making process based on a park's clearly defined objectives (*parks mandate - IMP*). As researchers we are not to prescribe our ideas and findings as we are not party to all aspects of the conservation management decision-making—aligned to the IMP. We as researchers therefore need to state outcomes in ways which are inductive, understood and applyable by the management decision forms that are working to meet the broader goals (IMP alignment). We are to *inform the process* so that the management team who is responsible for the park mandate can be accountable to the stakeholders as per the park's vision and overall objectives. With the recommendations that follow, an effort has been made to inform the process and not to prescribe to it.

Efficient biological surveys are a fundamental requirement for the effective management of biological resources and constitute the most basic activity in the field of conservation biology (Margules & Austin 1991). Conservation priorities in Maputaland were identified after a series of reports, including definitive surveys by Bruton & Cooper (1980) and Tinley & Van Riet (1981). Both reports discuss the natural biotic riches of the region and indicate the need to safeguard these attributes. Although many surveys have been carried out, these authors have not defined or identified critical sites for biodiversity protection/conservation management. Much of the work carried out in the present study deals with this last point, although the focus was not specifically on sites but more on the habitats to which many of the biodiversity elements are closely associated. By mapping these habitats and/or being able to recognize these habitats in the field, critical and important sites for biodiversity protection/conservation can be identified and appropriate management procedures put in place.

Two main habitats were highlighted as being particular important to Maputaland's biodiversity, namely Sand Forest and Woody Grassland (the Maputaland Centre's endemic vegetation types). Conservation of these two habitats would have the greatest impact on conservation of Maputaland's unique biodiversity. By understanding the structure and distribution of Sand Forest, Woody Grassland and related habitats, appropriate management guidelines can be put in place, both in and outside conservation areas. The very restricted occurrence of a strong tropical fauna in Maputaland provides another reason why these habitats, which the animals are associated with, should be soundly managed and conserved. Maputaland provides South Africa with a glimpse of the tropics and as such is a national asset.

The people of Maputaland have traditionally harvested natural resources, and for keeping these practices sustainable some type of quota for the harvesting of the remaining resources need to be put in place. However, the only way that this can be achieved is through mitigating impacts and this can only be done based on information gathered on biodiversity and its driving forces in the region. Results presented here would go a long way to address this last need, the information been used in reserve and area management, land-use planning, and extrapolation to other parts of Maputaland, as well as in further ecological studies. Sand Forest areas should also be promoted as a premier ecotourism destination, as it is rich in rare plants, many scarce mammals, reptiles and birds including many unknown invertebrates.

10.1 Maputaland

- As the location of the region's principal habitats is related to climate conditions, which is directly related to distance from the coast, past ocean transgressions and regressions play an important role in determining the positions of the climatically suitable zones for the different habitats. This means that in the long term (100 years and more) management of these areas will need the full range of the current habitats so as to deal with these climate changes.
- The grasslands in the region are relatively poorly conserved and managed.
- Outside the conservation areas in Maputaland, the main threats to the Sand Forest habitat are uncontrolled, such as random fires that are used in clearing areas for agriculture, uncontrolled cattle grazing, as well as selective species utilisation for traditional medicines and timber.
- Uncontrolled cattle grazing and random, uncontrolled fire affects species composition and diversity, but probably do not change the structure of the grasslands (Potgieter per com.).
- The continued afforestation of the Woody Grassland with pines, eucalypts, cashew nuts and other alien trees could, bring about a drop in the level of the water table. This could result in a dramatic increase in the woody component of the vegetation of the region.
- The planting of alien trees species over large tracts of grassland, on the other hand, not only destroys the grassland habitat but is also expected to affect the hydrology of the region negatively.

Recommendations

In the region as a whole, to achieve the maximum conservation of biodiversity of the endemic-rich flora and fauna of the Maputaland Centre (MC), specifically of the two endemic habitats of the MC, the following issues are highlighted.

- The full range of the MC habitats need to be available to deal with climate change, this through corridors or compatible landuse.
- Uncontrolled heavy cattle grazing combined with fire regimes not compatible with current ecology, need to be managed if the full spectrum of the grassland biodiversity is to be conserved and sustainably utilised.
- Continued afforestation of the coastal grasslands needs to be restricted. Afforestation effectively transforms the grasslands into commercial timber plantations, consequently changing water table levels. This will probably result in the grassland communities changing into more woodland type vegetation communities.
- These land transformations are also a major source of alien plant infestations, such as the problem plant *Chromolaena odorata.* Currently millions of Rands are spent on the eradication of this species in infested areas.
- Areas outside formal conservation areas, that have near pristine Sand Forest and coastal grasslands containing Woody Grassland, need to receive conservation attention.

10.2 Sileza Nature Reserve [SNR]

- With relatively little Woody Grassland formally conserved, the SNR, despite its small size, fulfils a crucial role in ensuring the preservation of the endemic-rich flora and fauna of the MC.
- Regular seasonal fire is an important factor in maintaining the Woody Grassland of coastal Maputaland.
- These grasslands are essentially primary in nature and not secondary in the sense of being "unnaturally" degraded forest or savanna.

Recommendations

There currently does not seem to be many pressing management issues in the Sileza Nature Reserve as the ecosystem is maintaining itself quite well under current environmental scenarios.

Sileza Nature Reserve does though fulfil a crucial role in ensuring the preservation of the endemic-rich flora and fauna of the coastal grassland and Sand Forest ecosystems.

The coastal grasslands in and around Sileza Nature Reserve have been receiving annual to bi-annual burns for quite some time already, be it natural or anthropogenic. These grasslands have a component that is unique to the MC, namely a large number of geoxylic suffrutices. The existence of these Woody Grasslands is based on water table levels and regular fires. From the vegetation work done in these grasslands, the current fire regimes, where not combined with high numbers of cattle, seems to have no detrimental effect on the biodiversity of the grasslands but is essential for their maintenance. Therefore, in the case of the management of the Sileza Nature Reserve, it is felt that annual random mosaic burns (as is currently the case) is a sound strategy if the current habitats are to be maintained in a reasonable natural state, although stocking rates of game and cattle should be kept at the lower levels. These regular fires would prevent accumulation of biomass and thus keep to minimum destructive runaway fires, which could penetrate the Sand Forest patches in Sileza Nature Reserve.

10.3 Tembe Elephant Park

- Tembe Elephant Park has the greatest area of protected Sand Forest in South Africa and thus fulfils a crucial role in ensuring the preservation of the endemic-rich flora and fauna of the MC.
- Sand Forest seems to exist in a state of 'suspended animation'—maintaining itself in areas where it exists in a pristine state. In the management of these forest patches, any disturbance should be kept to a minimum, as disturbance would slowly erode these Sand Forest patches.
- The inclusion of Sand Forest in conservation areas, where there is an abundance of large ungulates, is no guarantee of the future persistence of this vegetation type.
- In Sand Forest, β-diversity (defined as the turnover of species between the different forest patches) is very high for both dominant and rare species (Van Rensburg *et al.* 2000). Therefore conserving one patch of Sand Forest will not nearly be adequate to conserve all of the genetic complement of Sand Forest.
- The effects of large herbivores, regular fires and the Sand Forest dynamics itself can lead to the disappearance of this vegetation type. One such threat to Sand Forest within a conservation area is highlighted in Tembe Elephant Park, where the over abundance of elephant is combined with the current fire regime.

- Under the time scale that Sands Forest dynamics seem to operate, any destructive impacts could negatively affect Sand Forest conservation within Tembe Elephant Park.
- The primary reasons for the proclamation of Tembe Elephant Park was the protection of the natural elephant population of Maputaland and the protection of Sand Forest. This has lead to a conflict of interests between Sand Forest and elephant. Although these elephants prefer plant species from woodland habitats, they are increasingly utilising Sand Forest species.
- Presently, it appears that a suite of plant species, including both relatively common and rare species, that are strongly selected for, are being utilised by the elephants to the extent that they may be reduced to very low densities, or possibly local extinction.

In Tembe Elephant Park we have a complex situation with many conflicting scenarios as well as the Park objectives at odds with the long term conservation of the current biodiversity and systems in the Park (TEP has the greatest area of protected Sand Forest in South Africa). To get a good overall balance for the future, well-focused visions for the Park and application of these visions within set time frames is going to be crucial. To paint a picture of the complex nature of the conflicting scenarios facing the managers of this park, here are some of the issues that need to be taken into consideration by management when formulating very specific management policies and practices (not the aim of the present study – IMP process):

- The long-term vision for Tembe Elephant Park is as follows (Extract from Draft Integrated Development Plan based on Proclamation agreements for Tembe Elephant Park): “The ecological integrity and cultural values of Tembe Elephant Park, in conserving the Tembe elephants, Sand Forest and associated biodiversity, is maintained and enhanced in realising sustained benefits to the people of the Tembe community through land partnerships and sustainable tourism”.
- The reserves’ conservation objectives and reason for establishment are to:
  - Protect the lives and property of the local people from damage and injury by free roaming elephant.
  - Preserve the last naturally occurring population of African elephant in KwaZulu-Natal.
  - Conserve and protect the unique Sand Forest.
  - Protect one of the largest populations of suni antelope (*Neotragus moschatus*) in southern Africa.

- Regular seasonal fires are an important part of the woodland/savanna systems in Tembe Elephant Park, yet negative impacts on Sand Forest are of concern (reserve objectives).
- The elephant population of Tembe Elephant Park is expanding and with it comes impacts on the habitat and in this case impact on Sand Forest is of concern (reserve objectives).
- Natural resource use (sustained benefits to the people of the Tembe community) from reed cutting to ad hoc access to registered inyanga's to collect medicinal plants in the Park.
- Sustainable tourism and the need for game numbers to be at a level that regular sightings of specifically "big five" animals (of which elephant is one) are at levels good for tourism.

In trying to balance the issues highlighted it will need to be done through integrated development plans in consultation with *all stakeholders*, which will need to be focused upon *agreed visions*. These agreed visions would dictate the more practical steps to be implemented to balance the issues raised. This will involve different expertise on conservation, tourism, local people needs and political. Recommendations that follow are issues that need to be considered from the point of view of balancing the biodiversity conservation objectives of the park.

In the case of Sand Forest, because it is such a sensitive habitat, any impacts need to be kept to a minimum if the long-term preservation of such forest and its associated fauna is to be achieved, thus all destructive impacts to Sand Forest need to be kept to a minimum. Issues that need to be addressed or put in place that would enhance the viability of the long-term conservation/preservation of the Sand Forest habitat are:

- It is important that the integrity of the Sand Forest edges remains intact to provide some protection against fire, so that the natural mosaic fires of Tembe can continue, as these fires are an essential part of the Tembe Elephant Park ecosystem as a whole.
- The current resource use in the Park is mainly reed harvesting, which has the least impact on the reserves biodiversity objectives, but harvesting of medicinal or any plants in the Sand Forest needs to be monitored closely and kept at sufficiently low levels.
- The most central issue is the one involving the elephant. Specifically in that the elephant of Tembe Elephant Park are a conservation objective for the Park (also KwaZulu-Natal), a tourism draw card as well as a critical part of the proposed Transfrontier initiative with Mozambique. The elephant population is growing and with it comes increased impacts on Tembe Elephant Park's different habitats of which the impacts on Sand Forest is of the most concern (Sand Forest is one of the Parks conservation objectives and part of the

reason for establishment). This is made more complex by the low recovery potential after disturbance of Sand Forest, compounded by the effects of fires penetrating the forest at these disturbed sites. Issues that need to be considered in the management around Sand Forest and elephant are:

- Expand the range of the elephant so as to reduce time spent in the Sand Forest zones. There are two ways this could be addressed, one locally and the other internationally. The local one is the Mbangweni Corridor, which would effectively link Tembe Elephant Park to the more nutritious areas of the Pongola River floodplain in Ndumo Game Reserve. The other, more long term international option, would be to reinstitute the old movement patterns of the elephant through the proposed Transfrontier initiative with Mozambique. This would be by the removal of the northern border fence with Mozambique.
- Reduce return rates of elephant to the Sand Forest areas in the western portion of the Park where most of the Sand Forest in the Park is to be found, this could potentially be done through water point management. There should be no water points kept artificially filled in the western part of the Park, especially during dry periods.
- Reduce direct foraging impacts on Sand Forest, which are thinning the forest as well as removing Sand Forest recruitment possibilities. Elephant numbers and other wildlife numbers should be curtailed within the limited area of Tembe Elephant Park, especially if the range expansion possibilities cannot be achieved in the near future. In the future it might even be necessary to create elephant exclusion areas (fencing or by other effective methods) around Sand Forest patches if pristine intact forest and its associated fauna, (the suni antelope is a conservation objective for the Park) are to be conserved.

CHAPTER 11

CONCLUSIONS

11.1 Maputaland environment and general ecology

- The geological history of Maputaland suggests that the current ecosystems in the region are most probably of recent derivation. The region was last inundated by the ocean approximately 3–1.8 million years BP ago. In fact, many endemic plant taxa comply with the concept of neo-endemics (young taxa). The MC comprises a unique environment in Africa in that it is geologically young with biological evolution, notably speciation, being actively driven.

11.2 Plant-soil characteristics

- The dominant oxide in the soil samples is silica, indicating that the cover sands in the study area consist mainly of quartz sand.
- The trace element analyses show that boron, barium, chromium, hafnium, niobium, nickel, lead, rubidium, scandium, titanium, iron, strontium, uranium, vanadium, zinc and zircon are present in noticeable concentrations.
- Inorganic analyses of soil samples indicate that calcium, copper, molybdenum, sodium and vanadium are present in low concentrations in all the samples.
- The high boron concentration evident in soil samples is ascribed to the presence of tourmaline, a boron-containing stable complex silicate mineral.
- Aluminium values are relatively high, although no marked difference in concentrations can be seen between the different biotypes studied.
- The traces of the organic compounds obtained by gas chromatography for woodland and grassland habitats were virtually identical, both in terms of the compounds present as well as relative abundance. The Sand Forest leachate, however, contains a compound or compounds that render the soil more acidic and contains more dissolved solids.
- From preliminary germination trials in soils of different vegetation types, it would appear that some attribute of the Sand Forest soil is inhibiting emergence and growth. The greatest suppression of growth occurred in the Sand Forest soils.
- Preliminary results indicate that the compound/factor that possibly suppresses growth can be mobilised by water moving through the soil, and is thus being leached.
- Changes in field-saturated permeability of the soils, were found to differ by an order of

magnitude and are likely that differences in unsaturated hydraulic conductivity, which would be closely linked to the water retention characteristics of the soil, might be even more pronounced.

- In Tembe Elephant Park, Sand Forest, and the burning of this vegetation which may occur frequently, does appear to have significant impacts on the hydraulic characteristics of the near-surface soil.

11.3 Phytosociology

- A straightforward situation exists in the phytosociology of the MC, with the important determinants for the vegetation communities in the region as a whole being the interconnected effects of water table (moisture), soil type and topography, upon which fire and vegetation dynamics have been superimposed.
- Dynamics of water in the landscape tend to show a strong relationship with the structure of the plant community at the first physiognomic level.
- Casual observations and comparison with other studies (notably Myre 1964, 1971; Lubbe 1996; Matthews *et al*. 1999: Gaugris 2004) have shown that the plant communities (and thus associated environmental factors) of the present study extend over most of the Maputaland coastal plain.
- The results of the ordination not only confirm the vegetation classification, but also give an indication of floristic and associated habitat gradients.

11.4 Tembe Elephant Park [TEP]

11.4.1 Plant communities

- In the case of Tembe Elephant Park, which lies in a drier and topographically higher part of the Maputaland coastal plain, the water table level is not a leading factor, although soil moisture plays an important role in plant communities’ delineation.
- Eight ecological-interpretable plant communities have been distinguished and described for Tembe Elephant Park.
- All the proposed communities are distinguishable in the field based on structure, growth form, general species composition and character species. This is despite the gradual environmental gradients that cause communities to merge into one another, particularly so in the case of the woodlands.

- The different woodland sub-communities often can be difficult to distinguish based on floristics alone, but structure and density help to distinguish between them.
- In the case of Sand Forest associated with the ancient dune cordons and driest soils, it is suggested that historic plant dynamics, in relation to the coastal plain geomorphology development, could be a major determinant of the present day Sand Forest patches.
- Sand Forest was found to occur in a mosaic with dry woodland and thicket.
- Fire is seen as an important natural ecological factor in the most of the plant communities except in Sand Forest.
- From casual observations and comparison with other areas it was noted that many of the "negatively" fire-impacted Sand Forest patches and margins do not regenerate at all. This leads to the assumption that the extent of Sand Forest is decreasing as a result of fire.
- Indications are that the impacts of large herbivores, such as elephant, which in the past were not closely associated with Sand Forest, in combination with fire, could speed up the changes taking place in Sand Forest and other communities. Under the time scales, that Sand Forest dynamics seems to operate, these added impacts could negatively effect Sand Forest conservation within Tembe Elephant Park.

11.4.2 Floristics

- Eighty-four endemic/near-endemic vascular plant taxa of the Maputaland Centre were recorded in Tembe Elephant Park, but the actual number present is expected to be slightly higher due to incomplete sampling.
- Most endemics plant taxa were associated with only two of the seven major plant communities. Forty-two taxa are associated (27 restricted) with *Drypetes arguta-Uvaria lucida* subsp. *virens* Forest (Sand Forest) and 37 (13 restricted) to the *Strychnos madagascariensis-Combretum molle* Woodland.
- Another community relatively rich in number of endemic plant taxa is the *Spirostachys africana-Berchemia zeyheri* Closed Woodland on clay, where 20 endemic plant taxa have been recorded. This is a restricted community, in terms of size and distribution, in Tembe Elephant Park but many of the endemics have a wider distribution outside the park on similar clay-based substrates.
- In the study area, by far the majority of plant endemics are confined to non-hygrophilous communities.

11.4.3 Large herbivore (elephant) impacts

- The modified Point Centred Quarter (PCQ) approach used as a rapid survey technique worked well. Useful information on the relative use of different plant species and the likelihood of negative impacts on their abundance from elephant feeding activity, has been provided.
- It was found that the bulk of the elephant diet is made up by species which are relatively common, and which are strongly, moderately, lightly or neutrally selected for. These are *Acacia burkei, Acacia robusta, Afzelia quanzensis, Albizia adianthifolia, Albizia versicolor, Combretum molle, Dialium schlechteri, Sclerocarya birrea, Strychnos madagascariensis, Terminalia sericea* and *Trichilia emetica.*
- It appears that the suite of species, including both relatively common and rare species, that are strongly selected for are being utilised to the extent that they may be reduced to very low levels, or possibly local extinction. These species include *Acacia robusta, Afzelia quanzensis, Albizia adianthifolia, Albizia versicolor, Antidesma venosum*, *Elaeodendron transvaalense, Euphorbia tirucalli, Ficus stuhlmannii*, *Galpinia transvaalica, Garcinia livingstonei*, *Hyperacanthus microphyllus, Kigelia africana, Manilkara discolor*, *Newtonia hildebrandtii*, *Phyllanthus reticulatus, Syzygium cordatum, Sclerocarya birrea, Terminalia sericea, Tricalysia junodii, Trichilia emetica, Warneckea sousae* and *Wrightia natalensis*.
- Several plant species which are Maputaland endemics or near-endemics with a limited distribution, may be threatened by elephant impact within Tembe Elephant park. These include *Combretum mkuzense, Dialium schlechteri, Hyperacanthus microphyllus, Warneckea sousae, Tricalysia junodii* var. *junodii* and *Wrightia natalensis.*
- It was found that more plant species are utilised in floristically diverse habitats than in less diverse habitats.
- The proportion of selected for plant species appears to be more or less constant at around 60% of the species available.
- The study showed that those plant species most highly selected for are used in all habitats in which they occur, but the degree of selection is different in the different habitats, and appears to be influenced by the relative abundance of other forage species and other unknown factors.
- Indications are that Sand Forest, a unique vegetation type, of limited distribution and area conserved, may be threatened as a type because of general thinning, as well as direct impacts on particular plant species.

- Because utilization is influenced by relative abundance, the plant species utilization classification presented here should be expected to change. For this reason only potential impacts by elephants on any particular species can be predicted from this survey.
- Tembe Elephant Park currently does not embody prime elephant habitat – owing to limited nutritional resilient habitats and surface water being limited within Park.

11.5 Sileza Nature Reserve and surrounds

11.5.1 Plant communities

- Dynamics of water in the landscape, in this case the water table, show a strong relationship with structure and composition of the major communities.
- Twelve ecologically interpretable plant communities were distinguished and described in Sileza Nature Reserve.
- All the proposed communities are easily distinguishable in the field on the basis of growth form, general species composition and diagnostic species.
- Evidence suggests that fire is an essential factor in maintaining the Woody Grasslands of coastal Maputaland. In fact, the association between fire and these grasslands must be as old as the grasslands themselves.
- It is hypothesised that a drop in water table over the long term would be conducive towards the creation of habitats more suitable for the development of woodland, thicket and even forest.
- From aerial photo comparison it was found that the forests and woodlands of the study area turned out to be stable features—all being strictly confined to the same sites over at least the past 50 years, although size and floristic composition might have changed.

11.5.2 Floristics

- Thirty-five endemic/near-endemic plant taxa of the Maputaland Centre were recorded in Sileza Nature Reserve, but the actual number present is expected to be slightly higher due to incomplete sampling.
- Most endemics were associated with only two of the five major plant communities, with 14 taxa associated with *Artabotrys monteiroae-Dialium schlechteri* Forest (Sand Forest) and 21 with the *Themedeto-Salacietum* Woody Grassland.
- The observed low species diversity and paucity of regional endemics in hygrophilous grassland communities is a common phenomenon throughout southern Africa.

- Maputaland Centre endemics recorded in the study area (and even more so for the centre as a whole) represent a wide spectrum of growth forms, including trees, shrubs, suffrutices, lianas, forbs, geophytes and annual herbs (Van Wyk 1996).
- It was found that the Maputaland Centre endemics are well represented in both grassland and Sand Forest, with the latter, on a regional basis, being perhaps the single richest community in MC in terms of plant taxa endemics.

11.6 Woody Grassland

- Despite White's (1976) statement that relatively few suffruticose species are confined to the Tongaland-Pondoland Regional Mosaic, this study found that plants species with this growth-form are abundant in the study area where they are almost exclusively confined to the *Themedeto-Salacietum* Woody Grassland.
- The present study confirms the observation that geoxylic suffrutices are prevalent in areas of sandy soil and relatively low relief. However, doubt is cast on the validity of White's claim that seasonally waterlogged soil is the primary determinant for the presence of this growth-form. In the study area the distribution of geoxylic suffrutices rather reflects the depth of the water-table, being most abundant in sites where it is high, yet still below 1.8 m. These sites comprise mainly those relatively high-lying, well-drained areas such as dune crests and slopes, the surface soils of which are never waterlogged.
- Geoxylic suffrutices are noticeably absent from inter-dune depressions, the only areas that are clearly seasonally waterlogged.
- Many plant species are endemic to these Woody grasslands, but also several appear to have developed an obligate geoxylic suffruticose habit. It is hypothesised that this signifies a long evolutionary history for this particular vegetation type in the region.
- It is hypothesised that these grasslands are essentially primary in nature and not secondary in the sense of being "unnaturally" degraded forest or savanna.

11.7 Sand Forest ("Licuáti" Forest)

- This study highlighted that Sand Forest is a unique forest type and differs from all other forest types recognised for southern Africa.
- Sand Forest was found confined to a narrow zone on the coastal plains of northern KwaZulu-Natal and southern Mozambique, from approximately False Bay up to

Quissico. This makes Sand Forest quite a limited distributed forest type, especially in South Africa.

- Plant species with fleshy fruits are the most common to be found within Sand Forest, even when considering cover-abundance, and seeds/fruit are therefore chiefly animal dispersed.
- Wind-dispersed seeds, not just fruits with wings, were found to be rare in Sand Forest.
- Evidence suggests that Sand Forest has very shallow root systems, with most of the roots occurring in the upper 1–1.8 m of the soil. There are no records of deep tap root systems.

11.8 Sand Forest structure

- Sand Forests were found to be dense with no well-developed herbaceous or ground layer, with distinct boundaries.
- Indications are that drought-deciduousness is much better developed in Sand Forest than in either Dune or Afromontane Forest.
- Two physiognomic and structural types of Sand Forest were found to occur. One fits the basic physiognomic definition of forest (tall Sand Forest), while the other can be described as a thicket (short Sand Forest).
- Tall Sand Forest and Short Sand Forest (structurally more correctly referred to as thicket) differ in terms of both floristic and structural attributes.

11.9 Environment

- Sand Forest is associated with the relatively drier sandy soils, which in many cases are old dunes systems further inland in the drier northern KwaZulu-Natal and southern Mozambique areas of the greater Maputaland.
- Evidence suggest that Sand Forest occurs under relatively drier conditions compared to other forest types (less than 700 mm of rain per year) and is thus referred to as tropical dry forest, and where it does occur in areas of higher rainfall (greater than 700 mm), it retreats to the higher sand dunes where the sands are well-drained.
- Indications are that Sand Forest is very efficient in capturing all or most of the rainfall that penetrates the first metre of ground.
- Sand Forests in Maputaland are found in areas periodically experiencing heavy dews and low-level mists, especially in winter. This could effectively increase the precipitation and

play a role in the survival and/or persistence of Sand Forest in the midst of the woodland dominated landscape.

- Sand Forest soils were found to show hydrophobic characteristics under dry conditions, but when they get sufficiently wet, have a better water-holding capacity than the surrounding woodland soils.

11.10 Dynamics

- Field observations and the results of germination trials and soil analyses strongly suggest that some type of allelopathic interference is taking place in and around Sand Forest.
- Preliminary findings suggest that Sand Forest competitively excludes other vegetation types via chemical (allelopathy) and physical (hydrophobic soils) means — a buffered environment.
- It is hypothesised that in Sand Forest all plants seem to play a role in some way in producing the allopathic property, keeping out other competing plant communities (e.g. woodlands).
- Evidence suggest that the absence or shortage of a ground layer and the lower understory in Sand Forest is not due to herbivory, but could rather be ascribed to aridity compounded by allelopathic characteristics.
- Evidence suggests that Sand Forest seems as if it exists in a state of 'suspended animation'—maintaining itself in areas where it exists in a pristine state. This characteristic is one in which Sand Forest differs significantly from Afromontane and Dune Forest. Indications are that the present-day climate regime is not suitable for the establishment and expansion of Sand Forest. Indications are that the size and number of Sand Forest patches which correlate with Dune cordon 3 approximately 50–60 km from the coast and with a mean annual rainfall of 650–700 mm, have not increased. Catapano (2004) concludes that in these areas there have been stable vegetation regimes since at least ~ 1800 years BP ago.
- It is suggested that Sand Forest was originally established under relatively moister climatic conditions.
- It is put forward that if the current climatic conditions continue indefinitely, Sand Forest will become extinct in the drier areas because it cannot recruit to any significant degree under the current environmental conditions.
- It is suggested that Sand Forest in the past would have covered larger areas of the Maputaland coastal plains as what is the case today.

- It is hypothesised that the effect of the transgression and regression of the ocean in the past would therefore have been that the zones on the coastal plain suitable for Sand Forest would have shifted plus possibly been more wide-ranging (depending on climate conditions).
- Gap dynamics does not appear to play a significant role in Sand Forest; indeed, it seems that gap dynamics may not nearly operate at the scale at which it operates in the other two forest types. Under favourable conditions, Sand Forest elements could recruit under present Sand Forest canopy as well as in smallish gap-falls inside the forest. However, with large gap-falls the opposite could occur, with grassland and woodland species taking hold.
- Evidence was found that indicate that severely damaged Sand Forest sites (for example by fire or mammals such as elephant and man) are usually replaced by woodland vegetation.
- Indications are that many of the large specimens of Sand Forest elements that occur outside Sand Forest in woodlands are remnants or survivors of past Sand Forest patches that are not present anymore.
- Information suggests that Sand Forest is not a resilient vegetation type.

11.11 Endemicity and floristics

- Sand Forest is a forest type rich in endemic plant taxa (neo-endemics). These Sand forests rich in neo-endemic species are centred in an area south of Maputo–Quissico (Mozambique) to just north of St Lucia.
- Of the 230 endemic or near-endemic plant species recorded for Maputaland, 33 are found in Sand Forest with 20 largely confined to this vegetation type. This makes Sand Forest one of the communities with the highest number of restricted-range plant endemics in Maputaland.
- It was found that Sand Forest does not have many fern and moss species, and those few species present, are able to withstand severe desiccation.
- Informal observations showed that a large proportion of epiphytes that occur in Sand Forest are lichens (not sampled), and can withstand repeated desiccation, while the epiphytic orchids are often xerophytic.

11.12 Fire

- Sand Forest occurs in the midst of fire-prone habitats, namely the woodland and a Woody Grassland mosaic.
- It is suggested that the bare or sparsely vegetated zones (low fuel load) surrounding Sand Forest contribute to lower fire frequencies and intensities thus serve as effective natural firebreaks.
- Indications are that destructive fires which occur periodically are slowly reducing the extent of Sand Forest.

11.13 Sand Forest evolutionary history

- The bulk of the evidence supports the variation of the primary hypothesis that *Dune Forest is the precursor of Sand Forest, but that Sand Forest has subsequently become a separate functioning plant community on its own.*

11.14 Management

- Management recommendations are made for Maputaland in general, as well as more specific ones for Tembe Elephant Park and Sileza Nature Reserve.
- It is highlighted that the some of the more important outcomes of this study to be considered in management plans should be:
    - Biodiversity value of Sand Forest and Woody Grassland
    - Regional connectivity (ecological and geomorphological) of the different vegetation communities
    - Sand Forest sensitivity to impact
    - Fire
        - Woody Grassland require regular seasonal fires
    - Elephant and other large herbivore forage effects
    - Human resource use in sensitive habitats and this on the limited distributed plant species
    - Effect of alien invasive plants in sensitive habitats