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Floristics and dynamics of Sand Forest,
a subtropical dry forest type in South Africa

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Statement

The conception, planning, execution and writing of this thesis were entirely my own, with the following exceptions:

Chapter 2 is adapted from a published paper co-authored with my supervisor Jeremy Midgley. As with the rest of this thesis, his contribution was limited to discussion and suggestions to improve the manuscript.

Chapter 5 is based on the realisation that soil water-repellency may play a role in Sand Forest seedling dynamics. This idea arose from discussion with Mark Botha, although he did not contribute to the planning, execution or writing of this work.

University of Cape Town

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Thesis summary

Unlike most dry forests, Sand Forest has been largely untransformed by human activity until very recently, and provides a rare opportunity to investigate the dynamics of old-growth dry forests.

Twinspan classification and DCA ordination (Detrended Correspondence Analysis, an indirect gradient analysis) of a wide range of forest samples in north-eastern KwaZulu Natal, South Africa, indicated that Tropical Dry Forest species composition differs substantially from all other forests, and further, that Sand Forest samples, which occur on inland dune sands of Pleistocene origin, form a cohesive group with a characteristic set of species, including *Cleistanthus schlechteri*, *Hymenocardia ulmoides*, *Psydrax obovata*, *Croton pseudopulchellus* and *Drypetes arguta*. The very high dominance of two canopy species, *C. schlechteri* and *Newtonia hildebrandtii*, at the majority of sites, implies that ecological functioning is similar across the geographical range in north-eastern KwaZulu-Natal. However, turnover of subdominant species between two recognisable Sand Forest subtypes (Western and Eastern Sand Forest) emphasises the need to conserve the full range of extant forest. Further sampling for this thesis was generally replicated in at least two sites representing the range of Sand Forest structure and composition.

Sand Forest structure was typical of undisturbed dry forest, with a relatively high stand basal area (24 - 32 m² ha⁻¹), although average canopy height was short (7 - 11 m). Mortality of adult trees (>10 cm DBH) in the canopy dominant, *C. schlechteri*, was estimated at 1.0 % for a 1 year period. Regeneration in undisturbed old-growth forest was almost entirely by seed, rather than sprouting. After large-scale disturbance by fire however, recovery was entirely by sprouting. Since resprouting is dominated by a previously common subset of species, and other seedlings were almost entirely absent more than two years after fire, it seems unlikely that large-scale disturbance is necessary for the maintenance of species diversity at a whole forest scale.

Juveniles of most important species were non-randomly distributed, but were found close to conspecific adults, indicating that continuous *in situ* recruitment, rather than gap-phase regeneration, predominates in these forests. This conclusion was supported by the distribution of Sand Forest trees with regard to canopy openness. Small seedlings (<15 cm) were more common, or occurred in similar densities, in shaded subcanopy environments compared to open gaps in the forest canopy. Species distributions with regard to canopy openness, both in the extremes of gaps and shaded subcanopy areas, and from estimates of canopy openness above the crowns of 2273 individual trees at Mkuzi and 3361 individuals at Phinda, suggest a degree of niche specialisation. The latter data indicate that species were non-randomly arrayed along the continuum of canopy openness, although overlap between species suggests that niche partitioning of this continuum is unlikely to be the only mechanism of species coexistence. This is amongst the first evidence that varying degrees of canopy openness are important in the dynamics of dry forests, although the classic models of gap-phase dynamics developed in moister forests are unlikely to apply.

In old-growth Sand Forest in conserved areas, tree size-class distributions reveal a relative scarcity of seedlings and saplings of most important species, including the two canopy dominants, *C. schlechteri* and *N. hildebrandtii*. All sampled Sand Forest soil exhibited severe and highly persistent water-repellency, resulting in poor wetting of soil surface layers. Experimental evidence indicates that this exacerbates low seedling germination and high seedling mortality in an already dry environment. These data also suggest that seedling distribution in relatively shaded environments is a result of high mortality and lower growth of moderately drought-stressed seedlings in high light environments, rather than differences in germination. Although water-repellent (hydrophobic) soils may contribute to the low numbers of juveniles observed in conserved Sand Forest, for many species the complete absence of saplings (<2 m in height), despite the presence of smaller seedlings (<30 cm), indicates that low survival of large seedlings and saplings is important. Many tree species in conserved old-growth Sand Forest have size-class distributions which suggest that recruitment is greatly impacted by ungulate browsing. Trees shorter than two metres are vulnerable to browsing, and precisely these size classes are underrepresented or absent from tree populations. The causative role of browsing was confirmed in two ways. First, relative density of saplings (0.5 - 2 m) in tree species was strongly correlated with a species-specific index of browsing pressure (i.e. palatability). Second, seedling (<0.5 m) and sapling densities of *C. schlechteri* and *N. hildebrandtii* in two conserved areas with high antelope densities were compared to an undisturbed sacred forest on communal lands with no antelope, cattle or goats. Densities of seedlings were similar and low at all sites, but densities of saplings of both species were at least twenty times higher in the unbrowsed forest. Transplanted two year old seedlings of two Sand Forest tree species (highly palatable *N. hildebrandtii* and moderately palatable *Combretum mkuzense*) exposed to normal levels of browsing at Mkuzi Game Reserve for six months were nearly all browsed, resulting in 77 % lower vertical growth compared to control seedlings protected from browsing. No difference in mortality was detected, but it is likely that continuous removal of foliage from slow-growing species would affect mortality over the long term. The almost complete absence of saplings of many Sand Forest tree species in conserved areas, especially of the canopy dominants, *C. schlechteri* and *N. hildebrandtii*, suggests that continuous browsing pressure could cause negative population growth in affected species, and potentially dramatically alter forest structure and function.

I investigated the possibility of obtaining growth rate estimates from annual growth rings in *C. schlechteri* and *N. hildebrandtii*. Growth rings in *N. hildebrandtii* were difficult to distinguish and appeared not to be annual in nature. A single radiocarbon date from a 23 cm diameter sample suggests a diameter growth increment of 2.2 mm year⁻¹ DBH. In five specimens of *C. schlechteri*, ring anatomy, phenology, cross-dating of recent growth rings and a ring count corroborated by a precise radiocarbon date indicated that visible growth increments were in fact annual rings. Annual growth increments were indistinguishable very close to the pith, and increased from less than 0.5 mm in width within 5 mm of the pith to over 1.0 mm beyond 10 mm from the pith (i.e. stem diameter > 2 cm). Average ring width ($\pm$ S.D.) in adult trees (>10 cm DBH) was 1.33 mm $\pm$ 0.63 mm (i.e. diameter growth of 2.7 mm year⁻¹ DBH) and did not change substantially with increasing diameter. The results suggest that the largest trees in the Tembe area where these samples were harvested (>50 cm DBH) may reach 200

years or more. The extremely low growth rates in juvenile trees confirms that low juvenile densities are not the result of high juvenile growth through these size-classes, and that the impacts of excessive browsing are likely to be important. These results also highlight the possibility of obtaining valuable long-term data on tree growth rates and age from the investigation of growth rings in *C. schlechteri* throughout its range, as well as from other dry species growing in environments with a pronounced dry season, even where rings are not exactly aged by cross-dating.

The evidence presented in this thesis has a number of implications for the management and conservation of Sand Forest, and these are discussed in the individual chapters and the conclusion.



Plate 1. Sand Forest typically consists of north/south aligned strips, patchily distributed in a matrix of open savanna or woodland on the same Pleistocene sands. Note the sharp boundaries between forest and savanna.

Introduction

Tropical dry forests¹ once covered large areas of the tropics and subtropics, particularly in Africa. World-wide however, they are a preferred environment for people, and have been intensively exploited, often for thousands of years. Now, the last remnants of dry forest are being degraded, cut and cleared (Murphy & Lugo 1986). Virtually unnoticed by researchers and conservationists until recently, and without the glamour of wet tropical forests, they are still poorly known and inadequately conserved.

Sand Forest, a dry forest growing on the subtropical Maputaland coastal plain in South Africa and Mozambique, is exceptional for a number of reasons. Globally, Sand Forest is unusual in that human population densities have been very low in and around these forests until very recently. The aeolian sands on which these forests grow are highly infertile and unsuitable for agriculture (Maud 1980; Pooley 1996; Ceruti 1999), unlike most dry forest soils that tend to be fertile (Murphy & Lugo 1986; Bullock *et al.* 1995). In addition, the absence of available water over most of the South African range prevented settlement of large areas until the roads and piped water of the modern world reached this rural backwater in the last few years. In Mozambique, civil war lasting decades depopulated a large portion of Maputaland countryside, reducing modern human impacts dramatically. Although Sand Forest is now being rapidly degraded by overutilisation and clearing for unsustainable subsistence agriculture outside of conserved areas, there are still opportunities to study and conserve dry forests that have probably been largely undisturbed for millennia, an unheard of situation for dry forest. On a more local scale, Sand Forest is perhaps the most interesting and unique vegetation type in the Maputaland Centre of Endemism, and is associated with a large number of Maputaland endemics and near-endemics (van Wyk 1994a; Matthews *et al.* 2001; van Wyk & Smith 2001).

Study site and vegetation

Maputaland forms the narrow southern portion (approx. 5700 km²) of a large coastal plain extending up the east coast into tropical East Africa, and beyond to Somalia (Watkeys *et al.* 1993). Maputaland is both a transition zone, where many plant and animal species reach their southern limit (Moll & White 1978; White 1983), and an important centre of endemism in its own right (van Wyk 1994b; van Wyk & Smith 2001). This biogeographic area is clearly delimited by the narrow Lebombo Mountain range in the west and the Indian Ocean in the East (Moll 1978; Bruton & Cooper 1980; Maud 1980). The northern and southern limits are more arbitrary, but are generally accepted to extend as far as Maputo in the north (25°58' S) and the Mkuzi River (Bruton & Cooper 1980), or more recently, the Lake St. Lucia estuary in the south (28°24' S)(van Wyk & Smith 2001), which also corresponds to the extreme southern limit of Sand Forest (see Chapter 2). Biogeographically, Maputaland has affinities with the

¹ Note that the term tropical dry forest usually includes both tropical and subtropical types.

tropical flora of the Indian Ocean Coastal Belt (Moll & White 1978; White 1983), and is also part of the Maputaland-Pondoland Regional Mosaic extending southward (White 1983).

The vegetation of Maputaland is a complex mosaic of forest, thicket, savannah and grassland with abrupt local changes in response to soils and climate (Moll 1980). Despite the botanical importance of the area, it has only recently been scientifically explored. Bayer, in a 1938 study encompassing the coastal belt and midlands of Zululand, stated: '...there is no doubt that throughout the coastbelt proper, evergreen sub-tropical forest ... is a true climatic climax. However, moist, evergreen forest is certainly not the only forest type in the region. References to dry forest with a unique complement of species first appear in the literature in the mid-1960's (e.g. Myre 1964; Vahrmeijer 1966; Tinley 1967). Although Adamson (1938) first applied the name Sand Forest to the vegetation of the coastal dune cordon (now known as Dune Forest), by the time Moll (1968; 1978; 1980) and Moll & White (1978) described the vegetation of Maputaland, the term Sand Forest was used locally to describe the dry semideciduous forest occurring on sandy soils well inland of the coast. They list a variety of common and widespread tree species, including *Newtonia hildebrandtii*, *Cleistanthus schlechteri*, *Hymenocardia ulmoides*, *Balanites maughamii*, *Ptaeroxylon obliquum* and others. The term Sand Forest has since passed into general (e.g. Goodman 1990; Midgley *et al.* 1997) and popular use (e.g. Pooley 1993; Craib 1995). In South Africa, this name has been used to refer to dense forests with numerous trees and shrubs (De Moor *et al.* 1977; Moll 1978; Moll & White 1978; Moll 1980; Maass 1995) with a relatively short canopy (6 m or higher: De Moor *et al.* 1977. 10–25 m: Moll & White 1978; Moll 1978, 1980. 5–13 m with emergents above 15 m: Ward 1981), occurring in dry conditions (600–1000 mm: Tinley 1967. 700–900 mm: Moll & White 1978) on white to deep red sandy soils (Vahrmeijer 1966; Tinley 1967; De Moor *et al.* 1977; Moll & White 1978; Moll 1978, 1980; Ward 1981). These forests tend to be patchily distributed in characteristic north-south oriented strips (Vahrmeijer 1966; Moll 1978, 1980; Moll & White 1978; Ward 1981, see Plate 1).

Geology and soils

The formation of the modern Maputaland coastal plain started after the resistant volcanic rhyolite lavas that form the Lebombo Range and underlie the coastal plain were steeply tilted eastward during the break up of Gondwanaland about 140 million years ago. At the newly formed coastline, on the seaward sloping rhyolite base, Cretaceous marine sedimentary rock and conglomerates were laid down to form the present day level coastal plain (Maud 1980). From the end of the Cretaceous, through the Tertiary and Quaternary, the coastal plain was repeatedly exposed and submerged as the southern African continental margin flexed and world-wide sea levels rose and fell. The repeated marine transgressions and regressions resulted in cycles of sedimentation and erosion, with marine deposits being laid down, then eroded and redistributed by wind and water.

Thus most of the Maputaland coastal plain is covered in recent infertile wind distributed sands. The result has been the formation of a distinctive series of north-south aligned dune ridges parallel to the present day coastline (Goodman 1990). These dune cordons decrease in age from west to east, and the

oldest, most westerly dune cordon may date from the Plio-Pleistocene (Davies 1976). These oldest palaeo-dunes are not well preserved and are deep red in colour due to advanced mineral diagenesis. The soils on younger, more easterly dunes are generally poorly developed, yellow to orange arenosols. Sand Forest occurs on the full range of the inland dune sands. The tall coastal dune cordon is composed of dystrophic pallid sands, with steep slopes stabilised by Dune Forest (*sensu* MacDevette *et al.* 1989) and scrub. Between the dune ridges, the coastal plain is flat to gently undulating, and often covered with loose dystrophic sands (Watkeys *et al.* 1993). It seems likely that most of the Maputaland landscape is younger than one million years.

Climate

The climate of Maputaland is moist subtropical along the coast where rainfall is over 1000 mm per annum, becoming dry subtropical a short distance inland with less than 600 mm per annum. Rainfall increases to over 800 mm per annum along the crest of the Lebombo Mountains (Maud 1980; Watkeys *et al.* 1993). Summers are hot and humid with the highest monthly precipitation between September and April. Winters are cool and dry. Mean annual temperature varies from 21°C along the Lebombo Mountains to 23°C in the centre of the coastal plain, moderating slightly along the coast to 22°C. The area tends to be humid throughout the year, even in the drier centre of the coastal plain, although evaporation rates are high (Watkeys *et al.* 1993).

The inland areas of the Maputaland coastal plain that support Sand Forest fall into Holdridge's (1967) Tropical Dry Forest bioclimatic zone. Rainfall in this area varies from 620 mm year⁻¹ to 860 mm year⁻¹ and is strongly seasonal (Figure 2). The high variability between sites characteristic of the region is evident in the pronounced difference in rainfall quantity and pattern between False Bay Park and the Mkuzi Game Reserve weather station only 40 km northwest.

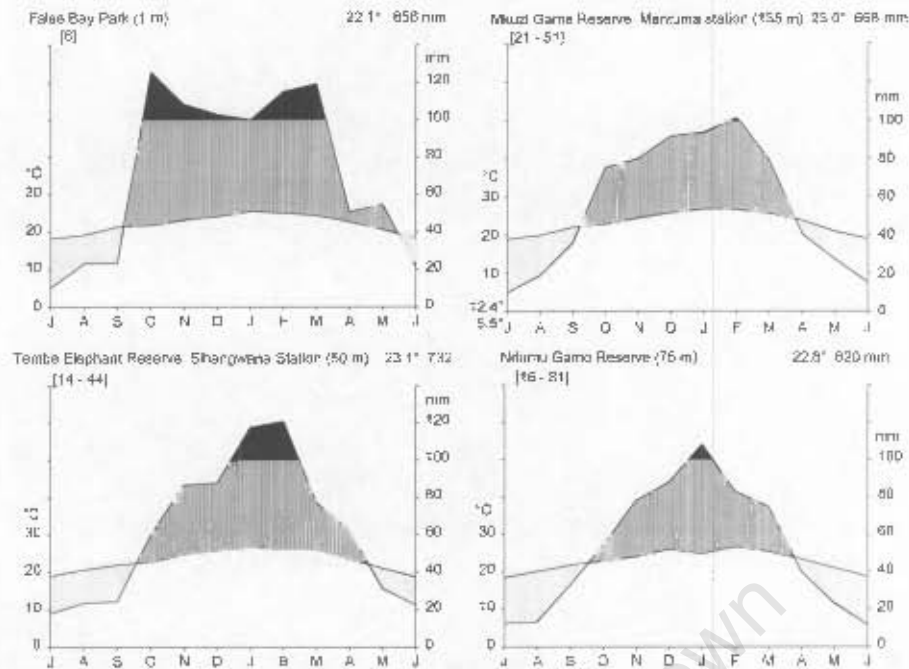


Figure 1. Climate diagrams for a range Sand Forest sites sampled in this study. Data for False Bay Park supplied by ISCW, Agromet Section, data for remaining sites supplied by the KwaZulu-Natal Nature Conservation Service (KZNNS).

Rainfall figures recorded at Sand Forest sites are at the low end of the ranges for dry forest globally (see e.g. Bullock *et al.* 1995), and high potential evaporation (Figure 2) in forests with sandy soils of low water holding capacity indicates that these forests are likely to suffer moisture deficit throughout the year, despite the fact that they occur at the extreme southern limits of the subtropical zone.

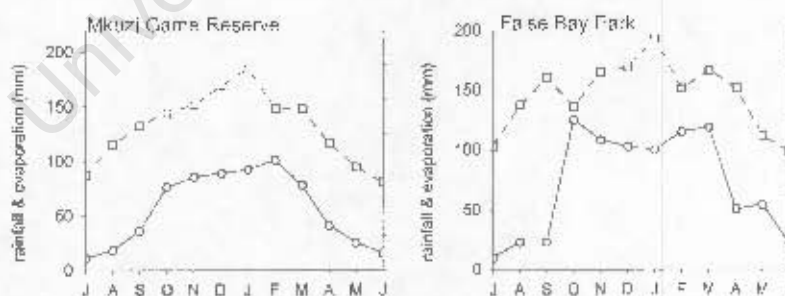


Figure 2. Evaporation data are available for only two Sand Forest sites: Mkuzi Game Reserve (data: KZNNS) and False Bay Park (data: ISCW). The upper line is average monthly evaporation, the lower line is average monthly rainfall. Mkuzi was one of the driest Sand Forest sites, while False Bay Park had the highest recorded rainfall (see Figure 1).

Long-term rainfall patterns from the three oldest weather stations in the Sand Forest zone confirms that rainfall can vary greatly over short distances (ca. 25 km), and from year to year (Figure 3).

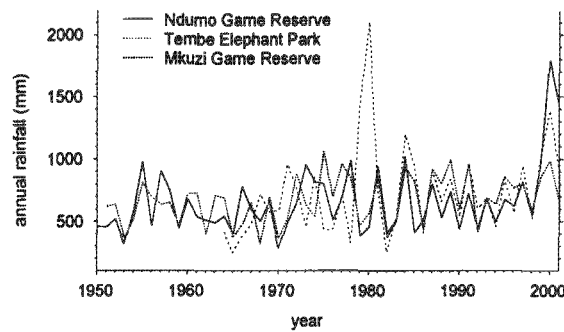


Figure 3. Long term annual rainfall for three sites in the Sand Forest zone of the Maputaland coastal plain. Note the high year to year variability at all sites and the poor correlation between Tembe and Ndumo which are separated by only 25 km with no major differences in relief.

Sand Forest conservation

The conservation of Sand Forest in South Africa is considered important for a number of reasons. Sand Forest covers a small total area (McKenzie 1996) and is heavily impacted outside of conserved areas (Moll 1978; Geldenhuys & MacDevette 1989; McKenzie 1996; pers.obs). It is rich in woody species (Moll & White 1978), and has a number of endemic plant species restricted entirely to this forest type (pers. obs., Matthews *et al.* 2001). Sand Forest is also the habitat of a number of unusual or rare animals, such as the Suni, *Neotragus moschatus* (Lawson 1986), the Samango monkey, *Cercopithecus mitis* (Lawes 1992), the African broadbill, *Smithornis capensis*, and Neergaard's sunbird, *Nectarinia neergaardi*, which is largely confined to the Sand Forest (Harrison *et al.* 1997). It is a drawcard for tourists (Macfarlane 1993; Craib 1995) and an important local resource, providing a range of building materials, traditional medicines and some food plants (Cunningham 1985).

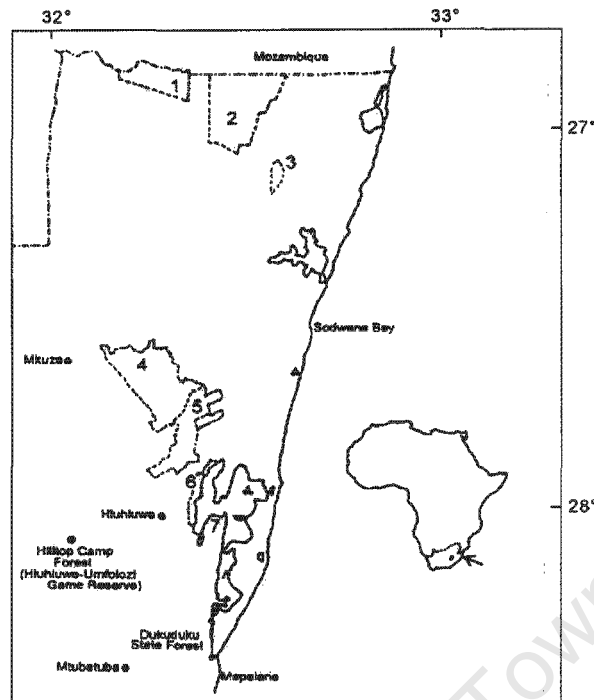


Figure 4. Study area. Reserves containing Sand Forest are numbered as follows: 1, False Bay Park; 2, Phinda Resource Reserve; 3, Mkuzi Game Reserve; 4, Ndumo Game Reserve; 5, Tembe Elephant Park; 6, Sileza Forest Reserve. All except the privately owned and run Phinda are administered by the KwaZulu Nature Conservation Service (KZNNCS). Hell's Gate, sampled during a floristic survey of dry forests in the area (see Chapter 2), is numbered 7.

In South Africa Sand Forest is primarily conserved in formal reserves under the auspices of the KwaZulu-Natal Nature Conservation Service. These reserves are False Bay Park, Mkuzi Game Reserve, Ndumo Game Reserve, Tembe Elephant Park and Sileza Forest Reserve (see Figure 1). Other than the Phinda Resource Reserve, which contains important areas of forest, little Sand Forest is conserved on privately owned and managed land. While this appears to be an extensive list, total area of protected Sand Forest is low (pers. obs., see Chapter 2), and has not been adequately measured. Outside of reserves in South Africa, Sand Forest occurs patchily in a north-south oriented band stretching from False Bay Park in the south and widening to the north to include areas west of Ndumo and east of Tembe. Sileza Forest Reserve is essentially an outlier, occurring on an isolated patch of dune sand in a matrix of flat palm veld and differs floristically from the very characteristic composition of typical Sand Forest in south Africa (see Chapter 2). The recent provision of amenities such as new roads and particularly potable water in Maputaland by the present South African government has done a lot to improve quality of life for many rural villagers. Unfortunately, the result has been the rapid transformation of the largest areas of Sand Forest on rural communal lands as population numbers grow far beyond historical levels.

Only areas of the Lebombos, riverine vegetation and areas of Coastal Grassland against the coastal dune cordon are currently considered underrepresented in the present formal reserve system by the KZNNCS and the establishment of further formal conservation areas containing Sand Forest by this body is unlikely (Goodman 2001, pers. comm.). However the Maputaland-Pondoland region has recently been identified a conservation 'hotspot' by Conservation International (Frazee 2002, pers. comm.). These are areas of exceptional biodiversity that has been highly transformed by human activity (Myers 1990), as such are likely to receive additional attention and more ambitious conservation targets.

In southern Mozambique, which contains extensive areas of Sand Forest, only Maputo Elephant Reserve (900 km²) and the small Licuati Forest Reserve are formally protected. Neither are effectively conserved or managed, and poaching, logging and human settlement are major problems (Botha 1996, pers. comm.; Siebert *et al.* 2002). Also, an ill-conceived harbour scheme on the southern boundary of Maputo Elephant Reserve poses a major threat to that reserve and threatens to derail plans for a large, continuous transfrontier reserve system linking the KZNNCS reserve network and Kruger National Park (South African National Parks) in South Africa to large areas of southern Mozambique (Weaver 2002).

Study background and approach

At the time this study was initiated in 1995, very little was known about Sand Forest species composition, variation or floristic affinities (see Chapter 2). Structural descriptions were based largely on casual observation (this Chapter), and the investigation of forest dynamic processes was limited to two studies relying almost entirely on interpretation of size-class data from a limited range of sites (Chapter 3, Everard *et al.* 1995; Midgley *et al.* 1995).

The first stage of this project was therefore to survey the floristic variation in the South African range of Sand Forest, while attempting to get as much information on important forest dynamic processes as possible at the same time. In the initial sampling, I censused a large number of 400 m² sample plots in a range of forest localities, to obtain not only basal area and density values for floristic analyses, but height and diameter size-class distributions for all tree species at each locality (see Chapters 2 & 3). I was already aware of the apparent absence of regeneration by many species, including the canopy dominants, from casual observation, and documented in preliminary investigations by Everard *et al.* (1995) and Midgley *et al.* (1995). The more obvious impacts of antelope in conserved forests, from the formation of a visible browse line to juvenile plants reduced to neatly clipped balls by continuous browsing, suggested that the role of antelope herbivory in the system was important and warranted investigation. Furthermore, although it is often assumed that light is of little importance in the internal dynamics of dry forests (Mooney *et al.* 1995; Oliveira-Filho *et al.* 1998), which are relatively short and open, I knew that even in the open-canopied environment of savanna, tree succession can be mediated

by shade-tolerance and intolerance (Smith & Goodman 1987; Yeaton 1988), and recent evidence had indicated that the survival and growth of dry forest trees could be influenced by canopy openness (Gerhardt 1993). Thus, as for most forests world-wide, I suspected that varying degrees of canopy openness would be important in the internal dynamics of these forests, although not necessarily in the context of the traditional gap/non-gap dichotomy. I therefore included measures of browsing on juvenile trees and canopy openness for all trees in sampled plots (see Chapters 4 & 6). Interestingly, my approach to forest light environments, based partly on individual trees, rather than traditional samples in extremes of canopy gaps and deep shade, closely paralleled that of Lieberman *et al.* (1989) and Lieberman *et al.* (1995), which I must confess, to my shame, that I was not aware of at the time. In order to obtain the above data, I distributed individual 400 m² plots subjectively at each locality to ensure that the broad range of variation in canopy height and composition was represented, with the actual plot position randomly chosen at a local scale to avoid subjective bias in the actual measures. Thus I consider my data on structural measures, size-distributions, measures of light environment and levels of browsing to be representative at a whole forest scale.

The first phase of the study provided convincing evidence that two Sand Forest subtypes were structurally and compositionally uniform enough to allow generalisations to be made regarding the ecology of these forests. Nonetheless, where possible further investigations have been replicated in at least two to three sites to encompass the range of variation in these forests. The second stage of this study therefore consisted of descriptive and experimental work to complement the data on forest structure and dynamics, light environments and browsing already collected. The apparent absence of regeneration in these forests is clearly a key research and conservation issue in these forests, and I concentrated on potential causes for this, from those inherent in the system (e.g. naturally water-repellent soils in dry forest, Chapter 5) to those that could be affected by different management strategies (e.g. browsing levels altered by controlling antelope densities).

From an academic point of view, this thesis is largely descriptive. I do not apologise for this, and consider it a necessary approach in a virtually unstudied forest type of tremendous conservation importance, particularly given the extremely limited resources available to me. The work in chapter 2 (Kirkwood & Midgley 1999) has already helped inform conservation planning in the subregion (Goodman 2001) and hopefully I have succeeded in identifying key issues for further research.

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The floristics of Sand Forest in northern KwaZulu-Natal, South Africa

Abstract

I use multivariate analyses (ordination and classification) to assess both the floristic uniqueness of the woody vegetation of Sand Forest in relation to a range of other forest types in the region, and the range of variation within Sand Forest. Two broad Sand Forest subtypes and related Ecotonal Forests are described and grouped under the term Tropical Dry Forest, distinct from all moist evergreen forests in South Africa. Sand Forest, a dry semi-deciduous type in north-eastern KwaZulu-Natal is defined by the presence of the canopy dominant *Cleistanthus schlechteri* as well as *Hymenocardia ulmoides*, *Psydrax fragrantissima*, *Croton pseudopulchellus* and *Drypetes arguta*. Sand Forests form a cohesive group in both DCA and TWINSpan analyses, with similar composition of important species (high density and basal area) at sampled sites. This, together with the very high dominance of the canopy species *C. schlechteri* and *Newtonia hildebrandtii* at the majority of sites, implies that ecological functioning is similar across the geographical range in north-eastern KwaZulu-Natal. However, turnover of subdominant species between recognisable Sand Forest types emphasises the need to conserve the full range of extant forests.

Keywords: *Cleistanthus schlechteri*, DCA, endemism, KwaZulu-Natal, Maputaland, *Newtonia hildebrandtii*, Sand Forest, Tropical and Subtropical Dry Forest, TWINSpan

Introduction

Although Sand Forest is a conspicuous feature of the Maputaland coastal plain (Moll & White 1978; Moll 1980), until recently published descriptions were cursory (e.g. Vahrmeijer 1966; Tinley 1967; Moll 1978; Moll & White 1978; Moll 1980) or very local (e.g. De Moor *et al.* 1977; Goodman 1990). Most of the older accounts are based on casual observation, and tend to feature the largest canopy emergents such as *Newtonia hildebrandtii* and *Balanites maughamii* which are often associated with other vegetation types (this chapter; pers. obs.) As a result, there has been, and still is, confusion regarding the definition of Sand Forest and which plant species are representative and characteristic (e.g. Moll & White 1978 *cf.* McKenzie 1996, Kirkwood & Midgley 1999 *cf.* Kirkwood & Midgley 1999 cited by van Wyk & Smith 2001)..

It is also unclear how closely Sand Forest is related to other forests in the region. Moll (1978, 1980) simply treats Sand Forest as one of thirteen or fifteen vegetation types in Maputaland. Moll & White (1978), in a description of the Indian Ocean Coastal Belt (a floristic zone stretching from just south of Somalia to the Cape), include Sand Forest in the Tongaland-Pondoland Regional Mosaic with four

other forest types. Midgley *et al.* (1997) follow this approach and that of White (1983) which emphasises the separation of the South African forest flora into the Afromontane types and the Tongaland-Pondoland Regional Mosaic which includes Sand Forest. MacDevette *et al.* (1989), in a preliminary classification of the KwaZulu-Natal indigenous forests, group an Eastern and Western Sand Forest type under the title Tropical Dry Forest with four other Coastal Forest types. Their main division separates Coastal Forests from Interior Forests in a similar manner to the treatments described above. Tinley (1967; 1977), however, regards Tropical Dry Semideciduous Forest in South Africa as part of a much larger Southern Tropical Sand Forest Domain, completely separate from all moist evergreen forests (including evergreen coastal forests). Moll & White (1978) list a variety of Sand Forest species linking the Pondoland-Tongaland Regional Mosaic with Dry Forests in the Zanzibar-Inhambane Regional Mosaic, which would seem to support Tinley's approach.

Before the publication of this chapter (Kirkwood & Midgley 1999), there was little information available for conservation planning, or for the delimitation of sensible ecological units for management and research into the dynamics of this little known forest type. This description is important in ascertaining the conservation worthiness of the forest type as a whole and how well the range of floristic variation is presently conserved. In addition it serves as a basis for further ecological work.

My aims were: (1) to determine how similar Sand Forest in northern KwaZulu-Natal is to other South African forests, especially the moist evergreen Coastal Forests of KwaZulu-Natal; (2) to define Sand Forest in terms of its woody species composition; and (3) to describe any variation within the Sand Forest type.

Methods

Data collection

Analyses were based on two data sets, a 'Sand Forest' data subset, sampled specifically for this study, was combined with a regional North-eastern KwaZulu-Natal data set, to allow comparisons among a range of forest types. Sampling was confined to woody vegetation for a number of reasons. Non-woody understorey vegetation is temporally and spatially variable in these seasonally dry forests, and a short term sampling program could not adequately assess this component. From a practical point of view, my aim was to delimit ecological units, and it is the trees that most affect the forest environment. In Sand Forest the non-woody component is particularly sparse and contributes little to total biomass. Also, trees, shrubs and lianes are easier to find and identify than grasses and herbs, and I hope this study will be accessible to non-specialists.

'Sand Forest' Data Set

Forests growing on or near sandy soils in Maputaland (excluding dune forests) were sampled to represent all the so-called Sand or Tropical Dry Forest types mentioned by De Moor *et al.* (1977), Moll (1978; 1980), Moll & White (1978), Ward (1981), MacDevette *et al.* (1989) and Goodman (1990). Sampled sites include the KwaZulu-Natal Nature Conservation Services reserves; False Bay Park,

Mkuzi Game Reserve, Tembe Elephant Park, Ndumu Game Reserve and Sileza Forest Reserve, the privately owned Phinda Resource Reserve (hereafter referred to as False Bay, Mkuzi, Sileza, Tembe, Ndumu and Phinda respectively) and relatively undisturbed nearby areas which will be referred to by the same locality names (see Figure 1 in Chapter 1). Protected areas were preferred for this survey as unprotected forests are usually heavily disturbed, complicating the recognition and definition of sand forest types.

At each locality, areas of forest (closed canopy, woody communities, >5 m, MacDevette *et al.* 1989; Midgley *et al.* 1997) were chosen subjectively to represent the range of variation in structure and species composition. Within these areas, quadrats were randomly located, with the proviso that they be at least 50 m from any previous quadrats and the forest edge. The number of quadrats located at each locality was subjectively determined. Sampling was halted when the variation in species composition was adequately represented. Due to the naturally patchy and discontinuous nature of Sand Forest, which is further fragmented outside of protected areas, a more structured approach was considered impractical.

Samples consisted of circular 400 m² quadrats. This is a suitable size for short forest communities (Kent & Coker 1992), represents the approximate point of inflection of a species/area curve within a homogenous area of sand forest (Goodman 1990; D. Kirkwood unpubl. data) and is compatible with samples collected by other workers in the region. Species abundance values in each quadrat are total diameter at breast height (DBH), calculated from the sum of area at breast height of all individuals. DBH of all woody individuals taller than 2 m, rooted within the quadrat was measured. Height of trees shorter than 2 m was measured, and converted to an estimate of diameter from a linear regression of height vs. DBH for all trees between 2 and 3 m high at a site. Shrubs (largest individuals usually <2 m), woody lianes and creepers were assigned an arbitrary total DBH of 2 cm. Tree species names follow Pooley (1993), except where they have been updated by Van Wyk & Van Wyk (1997).

North-eastern KwaZulu-Natal Data Set

I used data from circular 400 m² quadrats sampled in a range of north-eastern KwaZulu-Natal forests (see Chapter 1). Sites were chosen to represent Coastal and Inland Forest types (*sensu* MacDevette *et al.* 1989): Mapelane (35 quadrats) and Sodwana (34 quadrats) from the coastal dune cordon and Dukuduku Forest (20 quadrats) correspond to Undifferentiated Coastal Forest (*sensu* MacDevette *et al.* 1989) (Undifferentiated Lowland Forest *sensu* Moll & White 1978 or Coastal Forest *sensu* Lubke & McKenzie 1996) (R. van Wyk, D.R. MacDevette, D. Everard and I. Gordon, unpubl. data). Coast Scarp Forest (*sensu* MacDevette *et al.* 1989) (Lebombo Forest *sensu* Moll 1978, 1980), sampled in 1996 around Hluhluwe Game Reserve Hilltop Camp (21 quadrats: A. West, D. Kirkwood & J.J. Midgley unpubl. data), represents the Inland Forests.

These quadrats from coastal and inland types were combined with the 135 quadrats sampled for this study from as wide a range as possible of 'Sand Forest' and related types in Maputaland. This includes 16 quadrats sampled in Hell's Gate, just south of False Bay Park (D. Kirkwood unpubl. data), an area

administered by the S. A. National Defence Force. The Hell's Gate quadrats are only included in the regional data set as the forest was substantially different floristically from other Sand Forest/Tropical Dry Forest types.

In this regional data set, abundance values were simplified to presence/absence of species, and small shrub, liane and creeper species were excluded, in order to overcome compatibility problems. While this reduces the information content of the data, it allows the robustness of results from analysis of the 'Sand Forest' data subset to be assessed.

Multivariate analysis

This classification and definition of forest types, as well as the ordinations of samples are derived from indirect gradient analyses, utilising only floristic data. The most meaningful results were obtained using two well known, robust and complementary techniques (Gauch 1982; Kent & Coker 1992): Two-Way Indicator Species Analysis (TWINSpan, Hill 1979), a polythetic, divisive program and the Detrended Correspondence Analysis (DCA) option in the package CANOCO (ter Braak 1991). These quantitative multivariate techniques were used to analyse the two data sets.

For all TWINSpan analyses the following defaults were used: 10 indicator species per division and a minimum group size for division of five quadrats. Three levels of division were adequate to separate the regional data set into groups consisting of quadrats largely from one locality. Four levels of division resulted in meaningful final groups used for the detailed classification of the Sand Forest data subset, which has a higher information content. Pseudospecies cut levels for the Sand Forest analysis were set at 0, 2.5, 10, 20 and 40 cm total DBH.

Analyses of the regional data set utilised all quadrats and only presence/absence abundance values were used. For the Sand Forest Data, two outlier plots significantly changed the relationships amongst the remaining plots. These were found to be quadrats in woodland clumps on the margin of sand forest patches in Tembe and Mkuzi and were thus eliminated from the final analysis. My final classification of Sand Forest and related types is based on TWINSpan analyses of both the regional and Sand Forest data sets. TWINSpan, which is based on a reciprocal averaging algorithm, successively divides groups of samples utilizing the differential presence or absence of species (Gauch 1982; Kent & Coker 1992). The program identifies indicator species for each division; "characteristic species" are those which consistently occur in only one of the two groups of samples under consideration; "preferential species" occur in a greater proportion of samples in one group than in the other.

All quadrats were used in the DCA of the regional data set. Similarly, although the related Hell's Gate Forests were not incorporated, all other Sand Forest/Tropical Dry Forest type quadrats were used in the DCA analyses of the 'Sand Forest' data set. Two separate DCA analyses of the 'Sand Forest' data set were performed. The first uses species abundance values of total DBH. The subsequent analysis uses only presence/absence values to reduce the influence of dominant species.

Dominance

In order to evaluate the relative influence of dominant species on the grouping of Sand Forest quadrats by the DCA, dominance diversity curves were constructed for the six sites sampled. Importance values for these curves were calculated as the average of a species' relative dominance value (species total DBH/locality total DBH) and its relative density (no. plants/total no. plants) over all quadrats sampled in an area, excluding those shown to be outliers in the DCA ordinations. Quadrats sampled from the same area are grouped together by all analyses with very few exceptions, indicating that forests are locally uniform, and sites can be used as natural units.

RESULTS

Affinities

The first two ordination axes of the detrended correspondence analysis of the north-eastern KwaZulu-Natal forests (Figure 1) reveal that the majority of 'Sand Forest' quadrats are more widely separated from Coastal Forest types in Maputaland (Mapelane, Sodwana and Dukuduku), than these Coastal Forest types are from an Inland Forest type represented by the Hluhluwe Game Reserve locality. Most of the quadrats sampled to represent 'Sand Forest' types form a tight group. Quadrats sampled at Hell's Gate forest and some 'Sand Forest' quadrats are however not closely allied to the other Sand Forest samples, and although distinct, are not widely separated from the Undifferentiated Coastal Forests of Dukuduku.

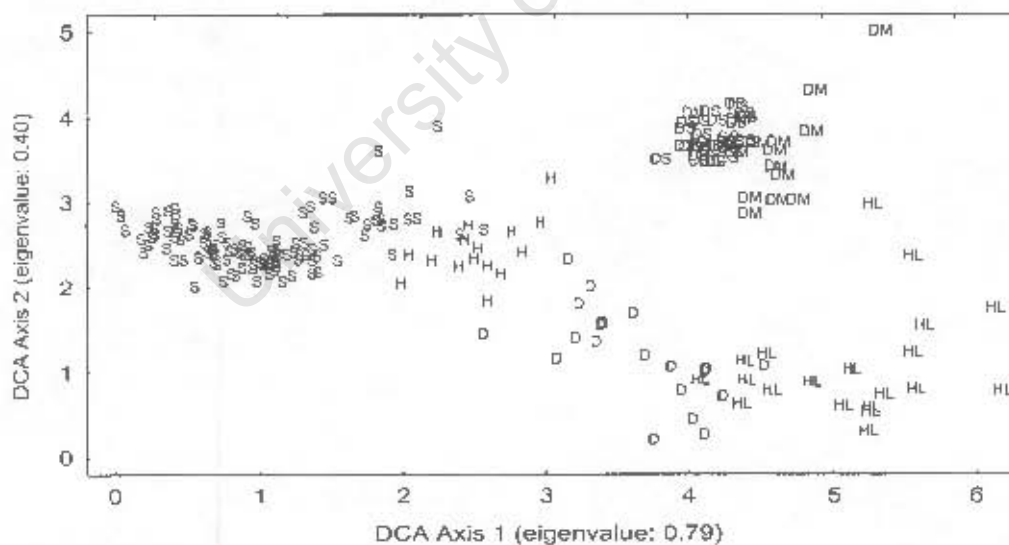


Figure 1. Detrended correspondence analysis ordination of quadrats from a range of north-eastern KwaZulu-Natal forests. S 'Sand Forest' types; HG Hell's Gate; D Dukuduku Forest, DS Sodwana Dune Forest; DM Mapelane Dune Forest; HL forest around Hluhluwe Hilltop Camp.

The TWINSpan classification of the same data set (Figure 2) emphasises the separation of samples of 'Sand Forest' and its allies from those of the moist evergreen Coastal and Interior Forests in the first division (eigenvalue: 0.749).

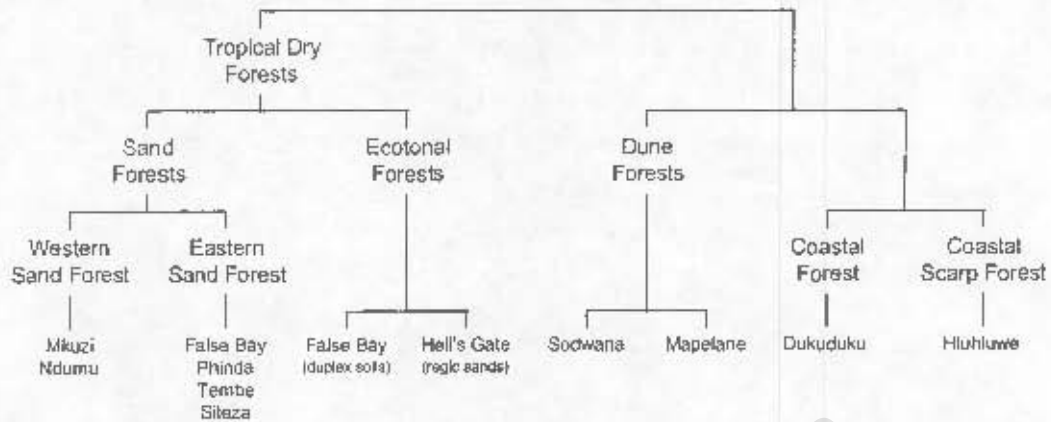


Figure 2. TWINSpan classification of the north-eastern KwaZulu-Natal data set. For clarity, final groups are presented only as locality names, as quadrats from the same locality are consistently grouped together (only 7 exceptions from 234 quadrats).

Classification

In classifying the Sand Forest types I follow the terminology of MacDevette *et al.* (1989), whose group names are sensible and easily remembered. However, it is important to note that the groups are substantially modified and many of my characteristic and representative species differ from theirs. A summary of the groups described below and their species is presented in Appendix 2.

TWINSpan analyses of the regional data set (Figure 2) and the Sand Forest data set (Figure 3) produce congruent classifications. Characteristic and preferential species based on divisions 1 and 2 of the regional analysis and divisions 2, 3 and 4 of the Sand Forest analysis are presented in this classification.

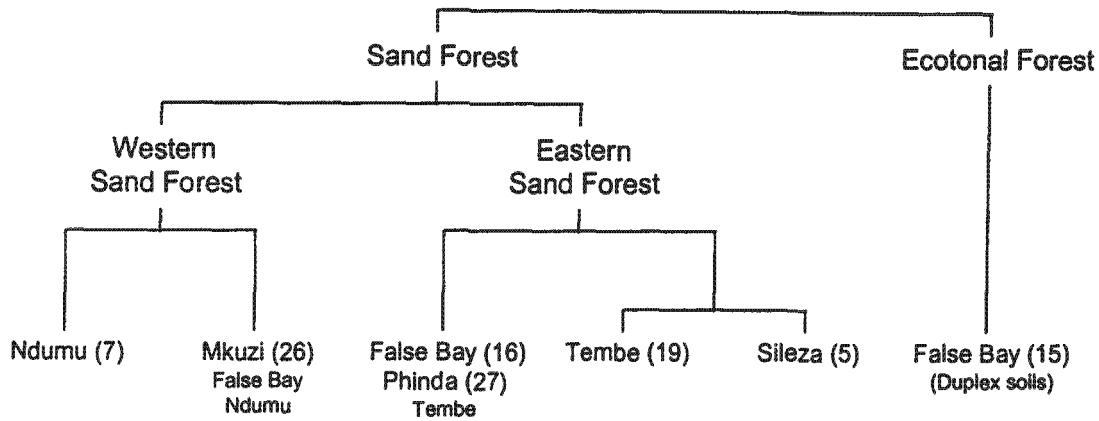


Figure 3. TWINSpan classification of the Sand Forest data set. The number of quadrats from each area occurring in a final group are indicated in parentheses behind locality names. Lowercase place names indicate that one quadrat from that locality occurs in the final group.

I suggest that the term 'Tropical Dry Forest' be used in South Africa to encompass both Sand Forest and allied dry forests. Although these forests are strictly subtropical, it seems likely that they are floristically allied and ecologically similar to other Tropical Dry Forests in Africa.

Tropical Dry Forest

This forest type is defined by the presence of the following tree species:

Characteristic tree species:	Preferential tree species:
<i>Hymenocardia ulmoides</i>	<i>Cola greenwayi</i>
<i>Wrightia natalitia</i>	<i>Hyperacanthus amoenus</i>
<i>Pteleopsis myrtifolia</i>	<i>Boscia foetida</i>
<i>Cleistanthus schlechteri</i>	<i>Brachylaena huillensis</i>
<i>Newtonia hildebrandtii</i>	<i>Combretum mkuzense</i>
<i>Drypetes arguta</i>	<i>Dialium schlechteri</i>
	<i>Grewia microthyrsa</i>
	<i>Haplocoelum gallense</i>
	<i>Monodora junodii</i>
	<i>Psydrax fragrantissima</i>
	<i>Ptaeroxylon obliquum</i>
	<i>Strychnos henningsii</i>
	<i>Toddaliopsis bremekampii</i>
	<i>Tricalysia lanceolata</i>

Although I comprehensively sampled Tropical Dry Forest, only a small range of KwaZulu-Natal forests is used for comparison here. While the tree species characterising Tropical Dry Forest at this

level of classification are representative, they may not be definitive when used in comparison with forests not included in this analysis.

Tropical Dry Forest is divided into two subtypes: Sand Forest and Ecotonal Forest (eigenvalue: 0.326).

ECOTONAL FOREST

These samples, while clearly allied to Sand Forest, are floristically diverse and occur on a variety of soils. Quadrats sampled in False Bay Park on duplex soils and soils with a high clay content fall into this group, as do quadrats on grey regic sands from the Hell's Gate area. Due to the variable species composition of quadrats in this group, I will not define subtypes within this group.

Characteristic tree species:	Preferential tree species:
<i>Strychnos usambarensis</i>	<i>Chaetachme aristata</i>
<i>Catunaregam spinosa</i> subsp. <i>spinosa</i>	<i>Diospyros inhacaensis</i>
	<i>Drypetes natalensis</i>
	<i>Manilkara concolor</i>
	<i>Strychnos gerrardii</i> .

SAND FOREST

This type includes the majority of Tropical Dry Forest samples (103 of 143) and forms a cohesive group in the DCA of the regional data set (Figure 1). These samples occurred on fine grained sands of the stable inland dunes, and soils were typically red to yellowish or grey in colour.

Characteristic tree species:	Preferential tree species:
<i>Cleistanthus schlechteri</i>	<i>Boscia foetida</i>
<i>Hymenocardia ulmoides</i>	<i>Combretum mkuzense</i>
<i>Toddaliopsis bremekampii</i>	<i>Croton gratissimus</i>
<i>Psydrax fragrantissima</i>	<i>Hyperacanthus microphyllus</i>
<i>Pteleopsis myrtifolia</i>	<i>Monodora junodii</i>
<i>Haplocoelum gallense</i>	<i>Vitex ferruginea</i> subsp. <i>amboniensis</i>

For further divisions, the results of the TWINSpan analysis of the Sand Forest data subset are presented. Shrubs and lianes, as well as abundance values for all woody species are recorded in this subset of quadrats. Where a species name is marked with an asterisk or double asterisk, this denotes that a characteristic or preferential species of a group is abundant (total DBH > 20 cm) or very abundant (total DBH > 40 cm). Despite the increased information content of this data set, the TWINSpan classification of Sand Forest samples (Figure 3) corresponds exactly with the divisions produced using the regional data set (Figure 2).

Sand Forest can be subdivided into two broad types, Western and Eastern Sand Forest (eigenvalue: 0.216):

Western Sand Forest

This type is represented by the Sand Forests from Mkuzi and Ndumu Game Reserves.

Characteristic species (trees):	Preferential tree species:
<i>Croton gratissimus</i>	<i>Brachylaena huillensis</i> **
<i>Brachylaena huillensis</i>	<i>Combretum mkuzense</i> *
	<i>Commiphora neglecta</i>
	<i>Craibia zimmermanii</i>
	<i>Croton gratissimus</i> *
	<i>Gardenia cornuta</i>
	<i>Rhus gueinzii</i>
	<i>Strychnos spinosa</i> ¹
	Preferential liane and creeper species:
	<i>Combretum</i> sp. ²
	<i>Grewia caffra</i> .

¹ Forest growth form, known locally as umHlakolotshe.

² *Combretum* cf. *celastroides*, an unidentified but common climber in these forests.

Eastern Sand Forest

Eastern Sand Forest includes the samples from False Bay Park, Phinda, Tembe and Sileza. It is notable that the characteristic species consist entirely of subcanopy trees. Mature stands of Eastern Sand Forest are considerably taller than Western Sand Forest, even where canopy dominants are identical (see structural analysis to follow).

Characteristic species (subcanopy trees):	Preferential species (trees):
<i>Cola greenwayi</i>	<i>Balanites maughamii</i>
<i>Drypetes arguta</i>	<i>Cola greenwayi</i> **
<i>Tricalysia lanceolata</i>	<i>Dialium schlechteri</i>
	<i>Dovyalis zeyheri</i>
	<i>Drypetes arguta</i> *
	<i>Erythrophleum lasianthum</i>
	<i>Grewia microthyrsa</i>
	<i>Haplocoelum gallense</i> *
	<i>Hyperacanthus amoenus</i>
	<i>Leptactina delagoensis</i>
	<i>Manilkara discolor</i>

Ochna arborea

O. natalitia

Oxyanthus latifolius

Psydrax locuples

*P. fragrantissima**

Ptaeroxylon obliquum

Strychnos henningsii

Suregada zanzibariensis

Toddaliopsis bremekampii

Vitex ferruginea subsp.
amboniensis

**Preferential species (llanes
and creepers):**

Acacia kraussiana

Dalbergia obovata

Landolphia kirkii

Monanthotaxis caffra

Synaptolepis kirkii.

The third level of division in the TWINSpan classification of the Sand Forest data set (Figure 4) essentially subdivides both the Western (eigenvalue: 0.207) and the Eastern (eigenvalue: 0.260) Sand Forest types into groups of samples that reflect species turnover between geographically separate sites. Only quadrats from Phinda and those on sandy soil at False Bay are grouped together. In the fourth and final level of division (not illustrated) it is notable that both the Mkuzi quadrats (Western Sand Forest), and the Phinda/False Bay quadrats (Eastern Sand Forest) are subdivided into groups characterised by the presence or absence of *Newtonia hildebrandtii*. Localised stands dominated by this tree, a large, spreading canopy emergent, are a conspicuous feature of these forests (pers. obs., Moll & White 1978).

Species Turnover and Dominance in Sand Forest Samples

In a DCA ordination of the same Sand Forest data subset (Figure 4), with species abundance values of total diameter at breast height (DBH), quadrats are not separated into the groups described above. Samples from False Bay, Mkuzi, Phinda, Tembe and Ndumu are grouped together, with a high degree of overlap within a range of two half changes (each DCA unit or average standard deviation of species turnover is approximately equivalent to a 50% change in species composition of samples, Gauch 1982).

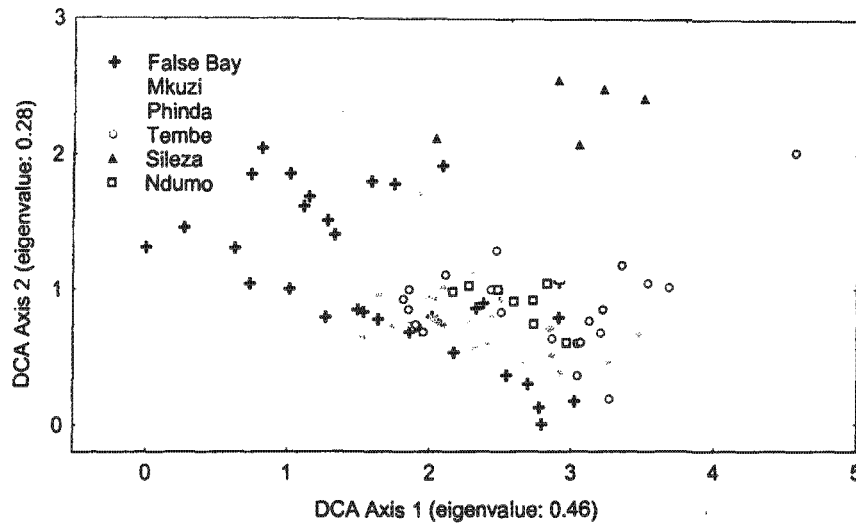


Figure 4. Detrended correspondence analysis ordination of Sand Forest and associated quadrats utilising species abundance values of total diameter at breast height (DBH). Further axes do not reveal identifiable groups.

Only quadrats from Ecotonal Forest on duplex soils at False Bay and the Sileza samples are clearly separated from the main group. However, when species abundance values are reduced to presence/absence values, the resulting DCA ordination plot (Figure 5), groups quadrats in an identical manner to the final level of the TWINSpan classification illustrated in Figure 3. This result confirms the validity of the classification. In addition, ground-truthing using this classification outside of sampled areas indicated that I have adequately covered the range of variation of Sand Forest in Maputaland.

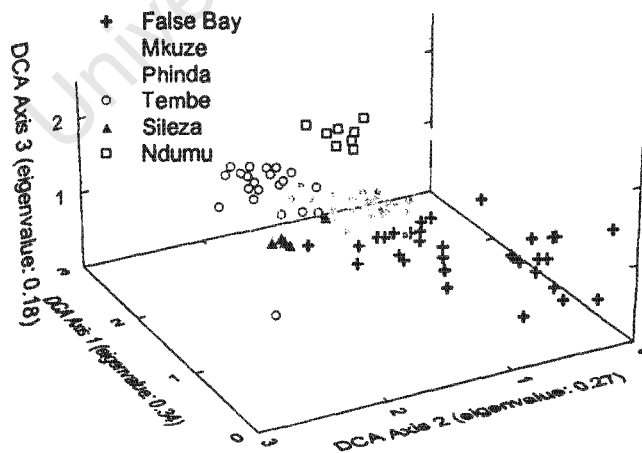


Figure 5. Detrended correspondence analysis ordination of Sand Forest and associated quadrats utilizing only species presence or absence (cf. Figure 4).

Separation of Sand Forest sub-types in the DCA ordination presented in Figure 5 results from reducing the influence of dominant species. This indicates that within the Sand Forest type, forests have similar dominant species, but there is significant turnover of the less common species between groups. Dominance-diversity curves at each locality (Figure 6) confirm that this is the case. *Cleistanthus schlechteri* and *Newtonia hildebrandtii* rank consistently higher than any other species. Note the disparity between the importance values of the one or two most dominant species and the other species at most sites.

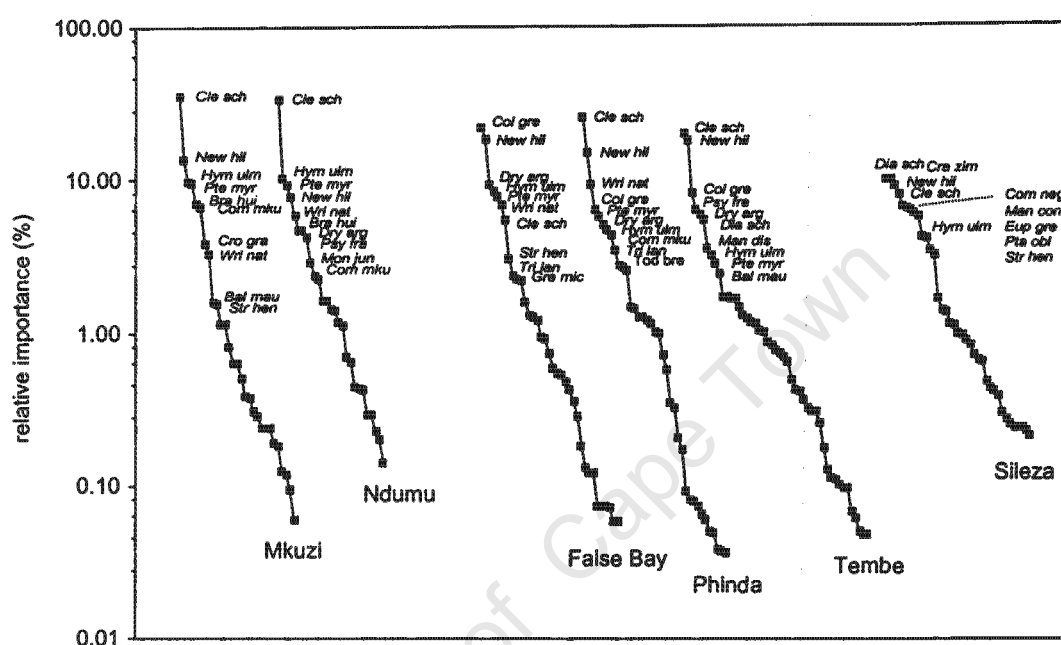


Figure 6. Dominance diversity curves of Sand Forests at sampled sites. Importance values for these curves were calculated as the average of a species' relative dominance (species total DBH/locality total DBH) and its relative density (no. plants/total no. plants) over all quadrats sampled in an area, excluding those shown to be outliers in the DCAs. See appendix 1 for full species names.

Although the division between Western and Eastern Sand Forest is justified and convenient, it seems that the most natural grouping of forests is into three groups: the Mkuzi/Ndumu Group, separated from all other samples on the first and third DCA axes in Figure 5, and the Phinda/False Bay Group separated from the Tembe/Sileza Group on the second axis. These groups may represent a soil gradient, from the oldest red sands of Western Mkuzi/Ndumu Group, through orange to yellow sands of Sand Forests at Phinda and False Bay Park, to the predominantly yellow to white sands of Tembe and Sileza, although the Western Sand Forests do receive slightly lower rainfall than the Eastern Sand Forests. The samples at Sileza, an isolated forest occurring on dystrophic white sands and surrounded by *Hyphaene natalensis* Palm Veld, although included in Eastern Sand Forest, are separated from other Sand Forests by all DCAs and should not be considered typical.

A sample by species table of the Sand Forest data set is presented in Appendix 1 with a complete species list for all the localities sampled. Importance value classes in the table matrix represent total

stem diameter at breast height for a species: 1 = 0–2.5 cm DBH, 2 = 2.5–10 cm DBH, 3 = 10–20 cm DBH, 4 = 20–40 cm DBH, 5 = >40 cm DBH.

Discussion and Conclusions

In KwaZulu-Natal, Tropical Dry Forest, including Sand Forest and Ecotonal types, is clearly distinct from both coastal forests and an interior forest. This supports Tinley's (1967; 1977) approach emphasizing the separation of Tropical Dry Forests from all evergreen forests, rather than the more widely accepted approach, grouping dry Sand Forest and related types with more mesic South African Coastal Forests (*sensu* MacDevette *et al.* 1989). In fact, South African Sand Forest represents the southernmost distribution of a number of East African coastal plain dry forest species, many of which are dominant or common across the entire range (see Table 1).

Table 1. Sand Forest tree species recorded as dominant or common in eastern African Coastal Dry Forest (from Burgess & Clarke 2000).

Dominant species

Azelia quanzensis, *Albizia petersiana*, *Balanites maughamii*, *Cleistanthus schlechteri*, *Craibia zimmermannii*, *Drypetes arguta*, *Hymenocardia ulmoides*, *Manilkara discolor*, *Pteleopsis myrtifolia*, *Strychnos henningsii*, *Suregada zanzibariensis*

Common species

Drypetes arguta, *Erythroxylon emarginatum*, *Ficus tremula*, *Pteleopsis myrtifolia*, *Strychnos henningsii*, *Vitex ferruginea*

In the sampled range of Tropical Dry Forests in KwaZulu-Natal, Sand Forest samples form a natural and cohesive group, with most sites dominated by a similar range of species, primarily *Cleistanthus schlechteri* and *Newtonia hildebrandtii*. Sand Forest is however characterised by the presence of *Cleistanthus schlechteri*, *Hymenocardia ulmoides*, *Toddaliopsis bremekampii*, *Psydrax fragrantissima*, *Pteleopsis myrtifolia* and *Haplocoelum gallense*.

In the most comprehensive floristic study of KwaZulu-Natal forests to date, MacDevette *et al.* (1989) classified the indigenous forests of KwaZulu-Natal using species lists (of varying reliability) from 105 sites. Tropical Dry Forests, characterised by the presence of *Cleistanthus schlechteri*, are classified as a subtype of the Coastal Forests with *Pteleopsis myrtifolia*, *Suregada zanzibariensis*, *Monodora junodii*, *Salacia leptoclada* and *Croton pseudopulchellus* as preferential species. Tropical Dry Forests are further divided into Western and Eastern Sand Forests. Western Sand Forests include forests in Ndumu Game Reserve, Mkuzi Game Reserve, False Bay Park and the area now included in Phinda Resource Reserve and have *Brachylaena huillense*, *Boscia foetida*, *Cadaba natalensis*, *Newtonia hildebrandtii*, *Haplocoelum gallense*, *Wrightia natalensis* and *Strychnos usambarensis* as preferential species. Eastern Sand Forests (Manguzi Forest, Sileza Forest and forests in Tembe Elephant Park and Sodwana

State Forest) are said to occur from Cape Vidal northwards with *Canthium setiflorum*, *Coffea racemosa*, *Tarenna supra-axillaris* subsp. *barbetonensis*, *Inhambanella henriquesii*, *Ephippiocarpa orientalis*, *Cavacoa aurea* and *Apodytes dimidiata* as preferential species. Their study provides a useful framework for comparison, although discrimination at fine scales is probably poor due to the use of whole forests as individual sample units, with only presence/absence of species noted. I support MacDevette *et al.* (1989) in dividing Sand Forest into convenient Western and Eastern types, although my groups do differ.

The similarity in terms of dominant tree species across the range of Sand Forests suggests that these forests can be treated as functionally uniform. This is important, as it allows us to extrapolate the results of ecological research and apply similar management practices throughout. Significant turnover of plant species does occur however, and since many species are confined to these forests (pers. obs., van Wyk 1994; Matthews *et al.* 2001; van Wyk & Smith 2001), conservation of a wide range of variation is crucial. This survey of woody plants indicates that both major Sand Forest types in South Africa are currently represented in conserved areas. Forests in Mkuzi and Ndumu Game Reserves represent the Western Sand Forest, while forests in False Bay Park, Phinda Resource Reserve (privately owned), Tembe Elephant Park and Sileza Forest Reserve represent the more variable Eastern Sand Forest. Although an assessment of the conservation status of Sand Forest is beyond the scope of this study, the suggestion by Low & Rebelo (Low & Rebelo 1996) that Sand Forest is well conserved seems premature. For example Mkuzi and Ndumu Game Reserves together probably contain no more than 10 km² of Western Sand Forest in a few small patches (D. Kirkwood, unpubl. data, De Moor *et al.* 1977). Fortunately, recent attention focused on the Maputaland Centre of Endemism and the importance of Sand Forest (van Wyk & Smith 2001) is likely to result in a reassessment of Sand Forest conservation in the near future.

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Appendix 2. Characteristic and preferential species for Tropical Dry Forest and its subtypes in South Africa. Lianes and creepers are indicated with an arrow, all other species are trees.

Forest type	Characteristic species	Preferential species
Tropical Dry Forest	<i>Hymenocardia ulmoides</i> <i>Wrightia natalitia</i> <i>Pteleopsis myrtifolia</i> <i>Cleistanthus schlechteri</i> <i>Newtonia hildebrandtii</i> <i>Drypetes arguta</i>	<i>Cola greenwayi</i> , <i>Hyperacanthus amoenus</i> , <i>Boscia foetida</i> , <i>Brachylaena huillensis</i> , <i>Combretum mkuzense</i> , <i>Dialium schlechteri</i> , <i>Grewia microthyrsa</i> , <i>Haplocoelum gallense</i> , <i>Monodora junodii</i> , <i>Psydrax fragrantissima</i> , <i>Ptaeroxylon obliquum</i> , <i>Strychnos henningsii</i> , <i>Toddaliopsis bremekampii</i> , <i>Tricalysia lanceolata</i>
Ecotonal Forest	<i>Strychnos usambarensis</i> <i>Catunaregam spinosa</i> subsp. <i>spinosa</i> .	<i>Chaetachme aristata</i> , <i>Diospyros inhacaensis</i> , <i>Drypetes natalensis</i> , <i>Manilkara concolor</i> , <i>Strychnos gerrardii</i>
Sand Forest	<i>Cleistanthus schlechteri</i> <i>Hymenocardia ulmoides</i> <i>Toddaliopsis bremekampii</i> <i>Psydrax fragrantissima</i> <i>Pteleopsis myrtifolia</i> <i>Haplocoelum gallense</i>	<i>Boscia foetida</i> , <i>Combretum mkuzense</i> , <i>Croton gratissimus</i> , <i>Hyperacanthus microphyllus</i> , <i>Monodora junodii</i> , <i>Vitex ferruginea</i> subsp. <i>amboniensis</i>

Appendix 2 continued...

Western Sand Forest	<i>Croton gratissimus</i>	<i>Brachylaena huillensis</i> **, <i>Combretum mkuzense</i> *, <i>Commiphora neglecta</i> , <i>Craibia zimmermanii</i> , <i>Croton gratissimus</i> *, <i>Gardenia cornuta</i> , <i>Rhus gueinzii</i> , <i>Strychnos spinosa</i> l, <i>Combretum celastrides</i> subsp. <i>orientale</i> , <i>Grewia caffra</i>
	<i>Brachylaena huillensis</i>	
Eastern Sand Forest	<i>Cola greenwayi</i>	o <i>Balanites maughamii</i> , <i>Cola greenwayi</i> **, <i>Dialium schlechteri</i> , <i>Dovyalis zeyheri</i> , <i>Drypetes arguta</i> *, <i>Erythrophleum lasianthum</i> , <i>Grewia microthyrsa</i> , <i>Haplocoelum gallense</i> *, <i>Hyperacanthus amoenus</i> , <i>Leptactina delagoensis</i> , <i>Manilkara discolor</i> , <i>Ochna arborea</i> , <i>O. natalitia</i> , <i>Oxyanthus latifolius</i> , <i>Psydrax locuples</i> , <i>Psydrax fragrantissima</i> *, <i>Ptaeroxylon obliquum</i> , <i>Strychnos henningsii</i> , <i>Suregada zanzibariensis</i> , <i>Toddaliopsis bremekampii</i> , <i>Vitex ferruginea</i> subsp. <i>amboniensis</i> , <i>Acacia kraussiana</i> , <i>Dalbergia obovata</i> , <i>Landolphia kirkii</i> , <i>Monanthotaxis caffra</i> , <i>Synaptolepis kirkii</i>
	<i>Drypetes arguta</i>	
	<i>Tricalysia lanceolata</i>	

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Structure and dynamics of Sand Forest

Abstract

I investigated forest structure and dynamics at three sites representative of the range of South African Sand Forest. Forests were short and open, ranging from 7 to 11 m in height, with canopy gaps comprising from 4 % to nearly 21 % of total area. Structural features indicated that these were old-growth forests and had not been subject to large-scale disturbance for a considerable time. Reproduction was predominantly from seed in old-growth forest, and root suckering and adult resprouting were relatively unimportant despite the low canopy height. However, forest recovery 27 months after large-scale disturbance caused by fire was primarily by resprouting and root suckering of a common subset of old-growth species. Recruitment from seed in the post-fire environment was negligible. In old-growth forest, the proportion of adult trees (> 10 cm DBH) of the canopy dominant, *Cleistanthus schlechteri*, estimated to have died in the previous one year period (i.e. a snapshot measure of annual mortality) comprised 1.0 % of a pooled population. This is a normal value for tropical forests. Most trees died standing and canopy gaps were small, with gaps less than 6 m in diameter comprising the majority of gap area. Juveniles of most important species were located near conspecific adults more often than would be expected if they were randomly distributed, indicating that continuous *in situ* recruitment, rather than gap-phase regeneration, predominates in these forests. Conservation management of old-growth Sand Forest should prevent any increase rates of gap formation, such as would be caused by elephant, and exclude fire in order to maintain forest structure and composition. Preliminary evidence from size distributions indicates that conspicuously low densities of seedlings and saplings of many important old-growth species are a result of ungulate herbivory, and may be cause for concern.

Keywords: disturbance, fire, herbivory, mortality, regeneration, size-classes, sprouting, structure

Introduction

Worldwide, dry forest dynamics are poorly understood (Murphy & Lugo 1986a; Mooney *et al.* 1995), although structure is often described in detail (e.g. Bullock *et al.* 1995). In South Africa, Sand Forest is poorly known despite its high local conservation importance (Low & Rebelo 1996 and see Chapter 1) and the global conservation importance of dry forests (Mooney *et al.* 1995). Sand Forest dynamics have been briefly examined in two publications (Everard *et al.* 1995; Midgley *et al.* 1995b), structural description is confined to one published canopy profile diagram (Moll 1968), and until recently the few descriptions of the floristics were cursory and confused (Chapter 2).

An understanding of forest dynamics is essential for effective management and conservation. Anything that affects the regeneration, growth or survival of component species is likely to affect forest composition, structure and function. The nature and frequency of disturbance is a major determinant of forest dynamics. In old-growth forest, the death of a single branch or tree is usually associated with *in situ* regeneration of shade-tolerant species (Midgley *et al.* 1990). Larger disturbances, such as blowdowns of several trees, can allow the establishment of shade-intolerant trees, which in the absence of further disturbance, might eventually be replaced by shade-tolerant species, resulting in a mosaic of different patches (Hubbell & Foster 1986; Brokaw & Scheiner 1989; Lugo & Scatena 1996). Entire forests may even be dominated by mostly single-aged shade-intolerant species that require disturbances of many hectares in extent in order to regenerate (e.g. Stewart & Rose 1989). These large-scale disturbances can be caused by wildfire (Spies & Franklin 1989), wind (Everham & Brokaw 1996), landslides (Garwood *et al.* 1979), vulcanism (Leathwick & Mitchell 1992) or clearing by humans (Johansson & Kaarakka 1992; Donfack *et al.* 1995). In South Africa, the study of forest dynamics is still in its infancy. In the absence of long-term demographic studies, easily aged tree species (Lilly 1977 and see Chapter 7) or knowledge of past disturbance regimes (Midgley *et al.* 1995b), modern understanding of forest dynamic processes is based largely on interpretations of tree size distributions (e.g. Midgley *et al.* 1990; Midgley & Gobetz 1993; Everard *et al.* 1995; Midgley *et al.* 1995b; van Wyk *et al.* 1996). It has been suggested that an abundance of subcanopy juveniles of species dominating the forest canopy indicates that forests are subject to fine-scale autogenic disturbance events, and are dominated by shade-tolerant species capable of continuous recruitment in this environment ('fine-grain pattern' *sensu* Midgley *et al.* 1990; Midgley & Gobetz 1993). This interpretation is bolstered by evidence of proximity of saplings to canopy species (Midgley *et al.* 1990) and the absence of any distinctive gap flora (Midgley *et al.* 1995a). However, many South African forests, including Sand Forest (Everard *et al.* 1995; Midgley *et al.* 1995b) appear to have a relative scarcity of juveniles of canopy species. Explanations for low numbers of juveniles generally invoke reasons for lack of regeneration, from dependence on some unspecified medium- to large-scale disturbance that would allow recruitment by shade-intolerant species (Midgley 1992; Midgley *et al.* 1995b; van Wyk *et al.* 1996) to increased levels of herbivory or perhaps disruption of specialised dispersal mutualisms (Midgley *et al.* 1995b). However, the basic assumption that low numbers of juveniles relative to adults suggests lack of recruitment into the adult population is not supported by recent work. Condit *et al.* (1998) showed that in 216 tree populations in the wet tropics the relative number of juveniles in the subcanopy was more strongly related to juvenile growth rates than survival or changes in population size, and sensibly cautioned against interpreting size distributions in the absence of demographic information.

The important role of sprouting in many forests was also only recently recognised (Midgley & Cowling 1993; Paciorek *et al.* 2000; Bond & Midgley 2001 and references therein). Until now, the vast literature on forest dynamics tended to focus on regeneration from seed, and local studies are no exception (e.g. Midgley *et al.* 1990; Midgley 1992; Midgley & Gobetz 1993; Everard *et al.* 1995; Midgley *et al.* 1995b; Cowling *et al.* 1997). However, root suckers and resprouts can grow faster than

seedlings and may suffer lower mortality (Bond & Midgley 2001). Resprouts can replace fallen or dying stems (e.g. Ramón & Fernández-Palacios 1998), reducing turnover rates, minimising the effects of disturbance and reducing or virtually eliminating dependence on seed (Bond & Midgley 2001). Kruger *et al.* (1997) demonstrated that canopy height was correlated with levels of recruitment from seed and inversely correlated with multistemmedness in a range of old-growth South African forests. Based on this evidence, they proposed a continuum ranging from tall forests dominated by single stemmed reseeders through to short forests entirely dominated by multistemmed sprouters, with low numbers of seedlings relative to root suckers. In terms of this model, structural attributes of Sand Forest, such as low canopy height, and low branching height relative to canopy height, indicate that forest dynamics would be dominated by resprouting and recruitment from seed would be relatively unimportant. Tropical dry forests typically resprout strongly in response to human disturbance or fire (Murphy & Lugo 1986a; Murphy & Lugo 1986b; Sampaio *et al.* 1993; Miller & Kauffman 1998), but in many undisturbed old-growth forests regeneration from seed appears to be more important (Swaine *et al.* 1990; Lieberman & Li 1992; Gerhardt 1993; Gerhardt 1996; Khurana & Singh 2001). However, the relative importance of sprouting and regeneration from seed in old-growth dry forest has received little attention, probably in part because relatively undisturbed dry forests are uncommon (Murphy & Lugo 1986a).

The broad aims of this chapter are twofold: first, to present an overview of Sand Forest structure and dynamics on which to base further research, and second, to identify aspects of dynamics that are likely to be affected by forest management practices. In particular, I address the following questions: How important is vegetative reproduction and resprouting for the recruitment and persistence of important Sand Forest tree species? Do the spatial patterns of conspecific juveniles and adults indicate continuous *in situ* recruitment by important species in forests which only experience small-scale autogenic disturbance events? How do Sand Forest species and particularly the canopy dominant, *Cleistanthus schlechteri*, respond to large-scale disturbance such as fire? Is Sand Forest dominated by species with low numbers of juveniles, and if so, what are possible causes?

Study sites

Sand Forest structure and dynamics were investigated at three sites considered to represent the range of floristic variation in Maputaland (see Chapter 2). The Sand Forest patch at Mkuzi Game Reserve (Mkuzi) represents the short and very dry Western Sand Forest type while the forests at Phinda Resource Reserve (Phinda) and Tembe Elephant Park (Tembe) represent the taller, more mesic and more variable Eastern Sand Forest type. Although *Cleistanthus schlechteri* and *Newtonia hildebrandtii* dominate the Sand Forest canopy layer at all three sites, there is substantial turnover of sub-dominant tree species. Sampling was confined to old-growth (*sensu* Clark 1996) forested areas with very low direct human impact, and thus largely restricted to conserved areas.

Methods

Forest structure

Structural and floristic data were obtained from a single sampling program (see Chapter 2). Stem diameters of trees taller than two metres and height of all tree seedlings, saplings and adults were enumerated in 400 m² circular quadrats sampled inside Sand Forest. Sampling of the three localities was done at different times of the year, which is likely to have influenced the numbers of small seedlings encountered. Sampling was done in December 1994 - January 1995 at Mkuzi, May - June 1995 at Phinda, and June - July 1995 at Tembe. At each locality, areas of forest (closed canopy, woody communities, >5 m, MacDevette *et al.* 1989; Midgley *et al.* 1997) were chosen subjectively to represent the variation in structure and species composition. Within each of these areas, a quadrat was randomly located, with the proviso that it was at least 50 m from any previous quadrat and the forest edge. No restrictions were placed on plot location with regard to local canopy structure or openness. The number of quadrats sampled at each locality was subjectively determined and sampling was halted when the variation in species composition was adequately represented. Due to the naturally patchy and discontinuous nature of Sand Forest, which is further fragmented outside of protected areas, a more structured approach was considered impractical. The 27 quadrats each from Mkuzi and Phinda and the 20 quadrats from Tembe represent a sampled area of 1.08 ha and 0.80 ha respectively. Stem circumference of the main stems on each tree was measured at breast height. Diameter at breast height (DBH) for each tree was calculated from total stem area of all stems, assuming stems were cylindrical. Height from the apex of the crown to the ground was measured for all trees shorter than two metres. Height of taller trees was estimated with the aid of an optical rangefinder: the distance to the highest visible foliage was measured from vertically below with a rangefinder, and any additional height was estimated visually from a position where the tree crown was visible. This departure from the usual methods employing triangulation (Korning & Thomsen 1994) was necessary as most of this work was carried out by a single person in understorey vegetation dense enough to obscure the trunk of the measured tree from a few metres away. In these short forests this method proved to be quick and adequately precise: estimates were within 1 m of measured height below 10 m and within 2 m above 10 m for a subsample of 30 trees at Phinda. The number of main stems at breast height (1.3 m) and the height of branching was noted. Canopy openness above every individual was noted as full sunlight if there was no overhead cover within a cone subtending 45° above the apex of the tree. The numbers of diameter samples of the two canopy dominants, *C. schlechteri* and *N. hildebrandtii*, in the sampled quadrats were augmented with measurements of trees from 100 randomly placed 2 x 50 m transects at Mkuzi and Phinda.

Canopy gap diameters and the proportion of forest area made up of canopy gaps was assessed using randomly sited 100 m line transects (see results for replication) in December of 1997 during the middle of the summer rainfall growth season. Gaps were defined as holes in the forest canopy extending vertically to within 2 m of the ground (Brokaw 1982), with a minimum diameter of 0.2 m. Randomly located gaps of various sizes were surveyed at Phinda and Mkuzi in order to investigate the distribution

of Sand Forest tree species with regard to canopy openness (see Chapter 4 for details). Gap features and causes of gap formation for these samples are presented here.

Sprouting in Sand Forest trees

In order to investigate to what extent dominant tree species produce new individuals (recruits) by vegetative reproduction (root suckering) rather than the establishment of true seedlings, I excavated individuals shorter than 30 cm in height of each species at sites across the South African range of Sand Forest. Since recruits of most of these species are rare and excavation usually results in death, sampling was only done where recruits were relatively abundant, and was not extensive or systematic. No more than one recruit of any species was excavated in any localised patch, with conspecific samples separated by at least 50 m.

The ability of dominant species to resprout was determined from observations of response to natural damage (disease, elephants and mechanical failure of branches) and human damage (particularly harvesting of stems) inside and outside of conserved areas. I present broad classifications compiled from numerous observations of damage of varying ages, types, severity and localities. Response to fire is considered separately.

Tree mortality and resprouting for C. schlechteri

I estimated mortality and resprouting rates for *C. schlechteri*, the canopy dominant (see Chapter 2), from the number of recently dead trees encountered during the sampling program described above. Trees were considered to have died within a one year period if they still retained dead leaves, fruit, or fine terminal twigs (< 2 mm diameter). These criteria were based on observations of the decay of trees cut at a known date at Mkuzi Game Reserve and by woodcarvers south of Tembe Elephant Reserve. The criteria are conservative and probably underestimate population mortality rates. Only dead trees taller than two metres were considered due to the high probability of overlooking or not correctly identifying smaller individuals. Numbers of recently dead trees were low and required the pooling of data from Mkuzi, Phinda, Tembe, False Bay Park and Ndumu Game Reserve. Since diameter-class distributions for *C. schlechteri* were very similar at all these South African Sand Forest sites, it was assumed that demographic parameters for these species do not vary substantially across the range.

Forest recovery after fire

Areas of forest burnt at Tembe in September 1995 were surveyed 27 months later in December 1997 to assess survival, resprouting of burnt trees and the recruitment of new trees. Three 2 x 50 m transects were randomly located in separate patches of burnt forest at least 10 m from the forest edge. All burnt stems with bases inside transects were counted, and where possible, their diameter at breast height or basal diameter measured. The length and position of origin of the longest resprouting stem was noted. In addition, any recruits (new shoots not closely associated with burnt trees) were excavated to determine whether they were seedlings or vegetatively produced root suckers. Resprouting in shrub,

creeper and liana species was noted, but not measured. Seedling densities were assessed separately: the number of seedlings of any woody species were counted in 40 2 x 50 m transects. These transects were randomly located at least 10 m inside the forest edge and separated by at least 50 m. No more than two transects were located in each burnt patch.

In order to assess the response of the canopy dominant, *C. schlechteri* to fire damage (rated light, medium and heavy; see Table 9 for definitions), location of sprouts (crown branches, trunk or base of trunk) and stem circumference at breast height were noted. Trees were considered to have died when no living foliage or shoots were visible and a stem slash revealed dead cambial tissue. Parallel transects 10 m in width and 20 m apart were laid out perpendicular to the longest axis of burnt patches of Sand Forest, starting at 10 m from the forest edge. Sampling was continued across eight separate burnt forest patches until 100 individuals had been sampled. *C. schlechteri* has characteristic bark and is easily identified, even when dead.

Associations between conspecific juvenile and adult trees

I used Chi-Square analyses (χ^2 , Zar 1996) to test whether juvenile trees tended to occur together with, or away from, conspecific adults more often than if they were randomly distributed in the forest environment. The expected proportion of randomly distributed 400 m² samples containing at least one adult tree was derived from the vegetation sampling program described above. A juvenile was considered to co-occur with an adult if any portion of a conspecific adult was inside a circular 400 m² quadrat centred on that juvenile. Randomly oriented and located transects were walked until 50 juveniles of each of the 10 most important trees at Mkuzi Game Reserve, Phinda and Tembe Elephant Park were sampled. Fewer seedlings were sampled for species where low densities would have required impractically high sampling effort. Each juvenile sampled was at least 25 m from the nearest sampled conspecific juvenile and samples were assumed to be independent. I defined juveniles of canopy species as non-reproductive, established (>5 cm height) recruits shorter than 3 m, and adults as reproductive individuals taller than 5 m. For sub-canopy species, juveniles are plants shorter than 1 m, while adults are taller than 2 m.

Results

Forest structure: canopy height and openness, stem area and density

The forests of the three localities chosen as floristically and structurally representative of Sand Forest height were all short, with a medium to high percentage of forest area composed of gaps, from 4 % at Phinda to nearly 21 % at Tembe (Table 1). These estimates include all gaps larger than 0.2 m in diameter, while most published estimates include only gaps large enough to have been caused by disturbances such as falling branches or whole trees (e.g. Barden 1989). If gaps smaller than 2 m in diameter are excluded, the proportion of canopy gap area in the forest is still high: 6.3 % at Mkuzi, 3.2 % at Phinda and 16.9 % at Tembe.

Table 1. Canopy height and percentage of forest area covered by canopy gaps at Mkuzi, Phinda and Tembe. Canopy heights were estimated for 0.04 ha survey plots. Gap percentages are from randomly sited 100 m line transects.

Site	Canopy height			Percentage gap	
	Ave. $\pm$ SD	Range	n	Ave. $\pm$ SD	n
Mkuzi	6.7 $\pm$ 1.6 m	3.5–10 m	27	10.7 $\pm$ 4.6 %	10
Phinda	11.0 $\pm$ 2.7 m	4.5–15 m	27	3.9 $\pm$ 5.1 %	8
Tembe	8.5 $\pm$ 2.0 m	5.0–12 m	20	20.5 $\pm$ 7.8 %	8

Canopy height varied substantially within each 0.04 ha plot. A better representation of the three-dimensional forest structure and distribution of biomass is obtained from canopy profiles constructed using height and stem basal area data from individual trees (Figure 1).

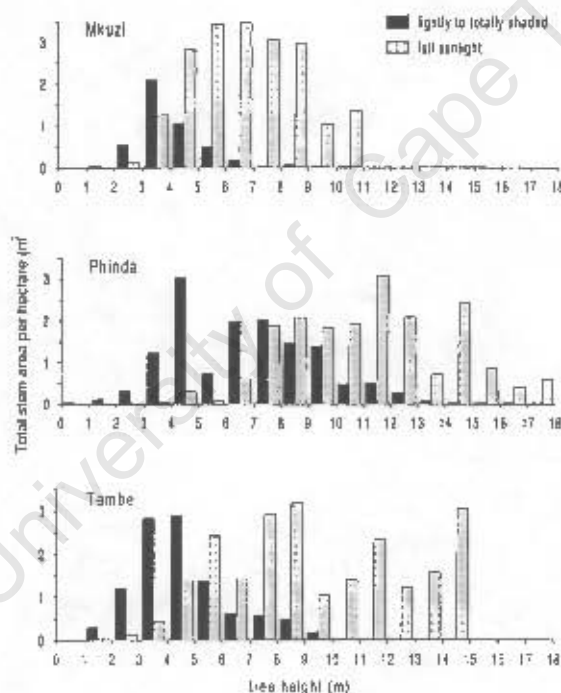


Figure 1. Stem area of trees in each height class. Trees were considered to be shaded if there was any overhead foliage in a cone subtending 45° above the apex of the crown.

Total stem basal area of trees in full sunlight in each height class is likely to be linearly correlated with the actual proportions of upper canopy surface area. While trees close to average canopy height at both sites comprise most of the biomass in full sunlight, and hence most of the upper canopy surface area, a large proportion of stem area is from canopy trees both substantially taller and shorter than average values. These data confirm the visual impression of structural heterogeneity of Sand Forest canopies. At all sites the upper canopy was not a layer of uniform height with an occasional emergent tree, but

rather an irregular surface composed trees of a range of heights, albeit with the highest proportion of canopy tree biomass corresponding to average canopy height (Figure 1). Although the relatively few canopy trees in full sun comprise by far the largest proportion of forest biomass (total stem area), smaller trees that are lightly or totally shaded are far more numerous. The biomass of subcanopy vegetation was highest in the tallest forests at Phinda ($14.08 \text{ m}^2 \text{ ha}^{-1}$ stem area of shaded trees vs. $20.43 \text{ m}^2 \text{ ha}^{-1}$ in full sunlight), intermediate at Tembe ($10.48 \text{ m}^2 \text{ ha}^{-1}$ vs. $22.53 \text{ m}^2 \text{ ha}^{-1}$) and lowest in the short forest at Mkuzi ($4.72 \text{ m}^2 \text{ ha}^{-1}$ vs. $20.26 \text{ m}^2 \text{ ha}^{-1}$).

Table 2. Stem area and tree density of Sand Forest at Mkuzi, Phinda and Tembe (ave. $\pm$ SD).

Site	Stem area at BH ($\text{m}^2 \text{ ha}^{-1}$)		Tree density (trees ha^{-1})	
	All trees	> 10 cm DBH	All > 0.3 m ht.	> 10 cm DBH
Mkuzi	24.1 ± 7.7	22.4 ± 8.4	$2\,757 \pm 1\,789$	569 ± 241
Phinda	33.2 ± 9.6	29.3 ± 9.6	$3\,383 \pm 2\,349$	641 ± 154
Tembe	32.0 ± 12.1	26.8 ± 12.2	$4\,790 \pm 1\,684$	525 ± 179

Forest structure: gap features and size distribution

Although gaps made up a large proportion of forest area, most canopy gaps were small. Nearly half of all gaps were less than one metre in diameter, and gaps less than four metres in diameter contributed more than 60 % of total gap area in a combined sample from Mkuzi, Phinda and Tembe. (Figure 2). Most of the gaps of less than one metre in diameter had no apparent cause, and seemed to be a normal feature of the canopy.

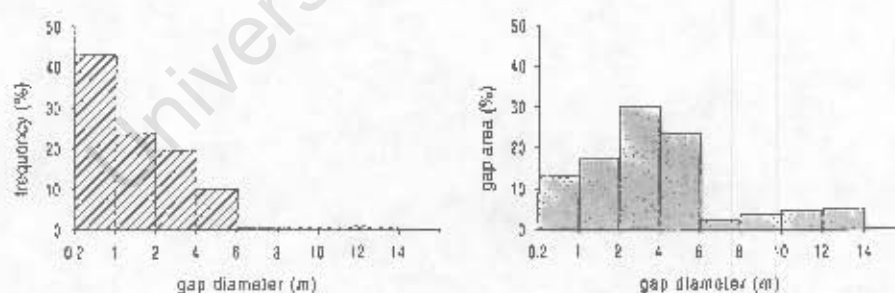


Figure 2 Distribution of gap sizes in a combined sample from Mkuzi, Phinda and Tembe (10, 8 and 8 transects respectively of 100 m). The proportion of total gap area contributed by each size class is illustrated on the right.

Mean area ($\pm$ SD) of randomly sampled canopy gaps large enough to have been caused by the death of branches or trees (i.e. gaps $> 2 \text{ m}^2$) at Mkuzi was 26.0 m^2 , with a range from 2.4 m^2 to 95.0 m^2 . Canopy gaps in the taller forests at Phinda were larger, with mean size of 70.4 m^2 , and a range from 3.2 m^2 to 188.5 m^2 . The intermediate height forests at Tembe had the largest mean gap size of 75.2 m^2 , and a

range from 6.3 m² to 339.3 m² (see Table 3 for replication). Although the remains of dead standing and fallen trees were present in many gaps, nearly half of these larger gaps had no obvious cause (Table 3).

Table 3. Causes of canopy gap formation at Mkuzi, Phinda and Tembe.

Site	n	Dead standing tree	Gap cause		
			Fallen tree	branch fall	Unknown
Mkuzi	21	3	4	0	14
Phinda	18	4	7*	2	5
Tembe	10	3	3	0	4

* 1 tree still living and 1 killed by elephant activity

Only one gap (at Phinda) was obviously caused by elephants pushing over and killing a living tree. Two gaps at Phinda were caused by falling *N. hildebrandtii* branches. Only one fallen tree (at Phinda) was still living. At all sites, it appeared that most fallen trees died standing and subsequently collapsed due to decay. Windthrow appeared to be a negligible cause of mortality in these forests, and an extensive survey after an unusually violent windstorm revealed no toppled trees (I. Rushworth, pers. comm.).

Forest structure: tree structure

Sand Forest canopy trees branch relatively close to the ground, and some are multitemmed from ground level (Table 4). Branching height, the ratio of branching height to tree height, and degree of multitemmedness are all inversely correlated with mean canopy height at each locality (see Table 1). Of the important canopy species, only *Combretum mkuzense* is naturally multitemmed from ground level. Other species such as *Pteleopsis myrtifolia* and *Hymenocardia ulnoides* are often multitemmed, but this is usually a coppice response to stem damage caused by herbivory or fire.

Table 4. Structural characteristics of Sand Forest canopy trees (trees with a total DBH of 10 cm or greater and at least 90 % canopy openness). Multiple stems originate at or below ground level.

Site	Mean branching height (m) $\pm$ SD	Mean and range of branch ht. / tree ht.	Percentage with multiple stems	Mean number of stems
Mkuzi (n = 451)	1.0 $\pm$ 1.0	0.18 (0 - 0.82)	19.1 %	1.59
Phinda (n = 359)	2.2 $\pm$ 1.9	0.22 (0 - 0.75)	9.3 %	1.36
Tembe (n = 261)	1.6 $\pm$ 1.4	0.22 (0 - 0.78)	15.1	1.42

Forest structure: tree size distributions

Sand Forest trees tend to be small, with few individuals (< 1 %) exceeding 50 cm DBH (Figure 3). The largest tree measured at each locality was *N. hildebrandtii*, with stem diameters of 107 cm, 160 cm and 136 cm respectively at Mkuzi, Phinda and Tembe. The only other species that often exceeds 100 cm DBH is the buttressed emergent *Balanites maughamii*. The canopy dominant, *C. schlechteri*, tends to

be considerably smaller, and the largest trees encountered were 50 cm, 91 cm and 51 cm DBH respectively at Mkuzi, Phinda and Tembe.

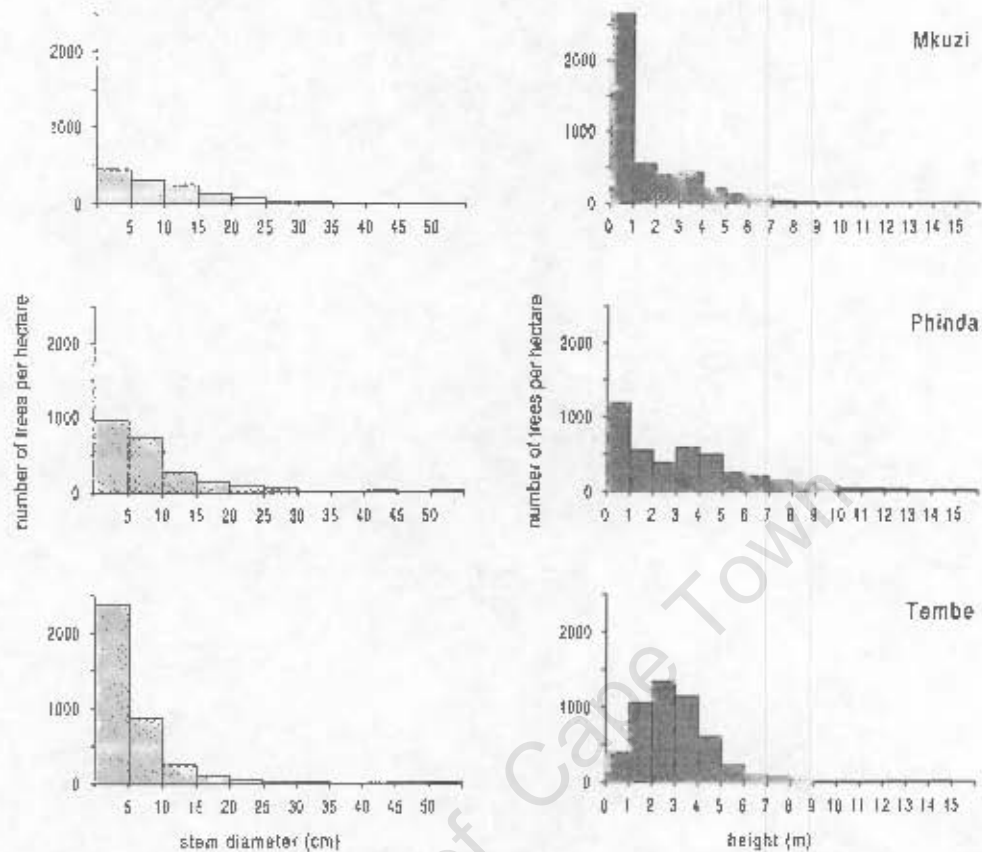


Figure 3 Diameter-class distributions of all trees taller than 2 m, and height-class distributions of all trees at the three sampled localities.

The diameter distributions of combined samples of all trees at the three localities are typically 'reverse J' shaped, although the slope of the distribution varies. There were lower densities of small trees (< 10 cm DBH, but taller than 2 m) at Mkuzi, intermediate densities at Phinda, and highest densities at Tembe.

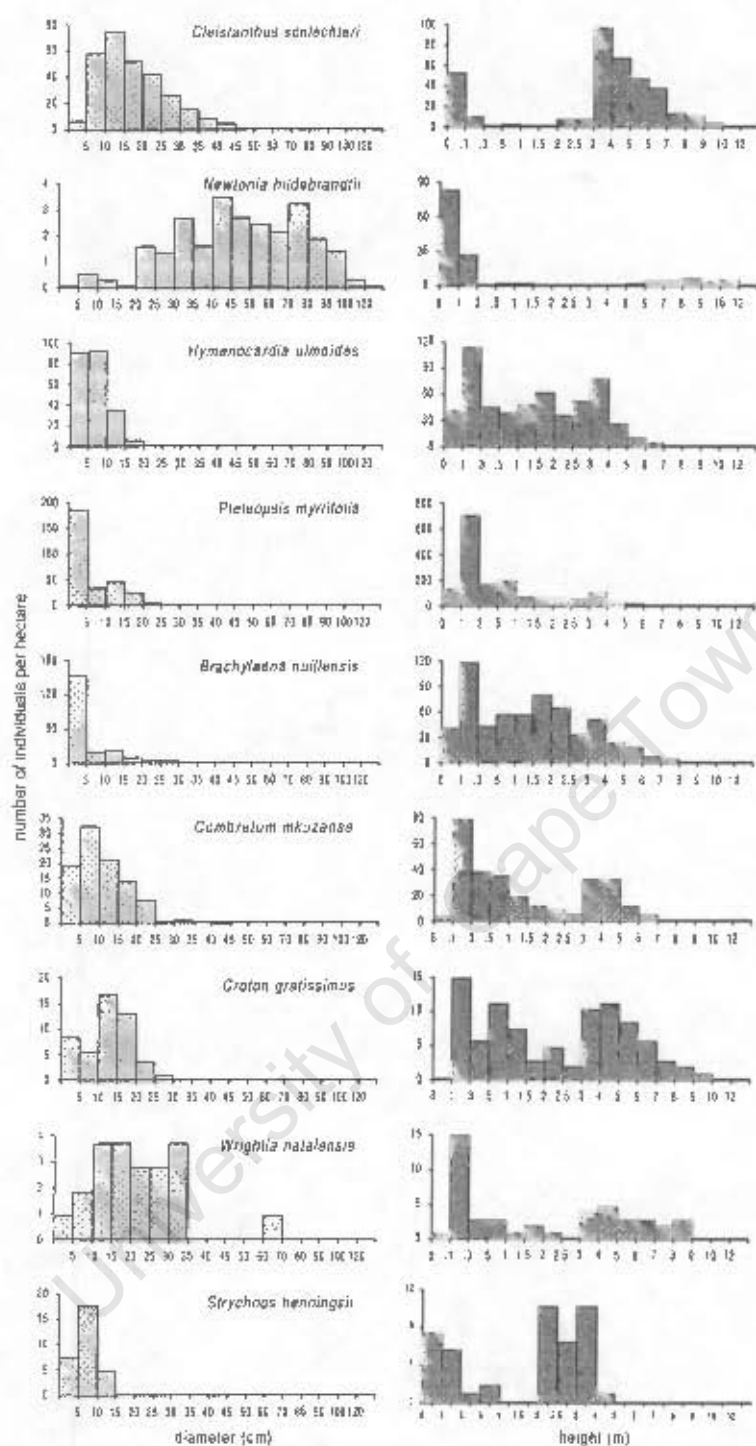


Figure 4 Diameter- and height-class distributions of nine of the most important species (90.6 % of total importance, see Table 6 for details) at Mkuzi Game Reserve. Note that size-classes are not even. *Balanites maughamii*, ranked 9th at this locality was omitted due to the low number of stems sampled.

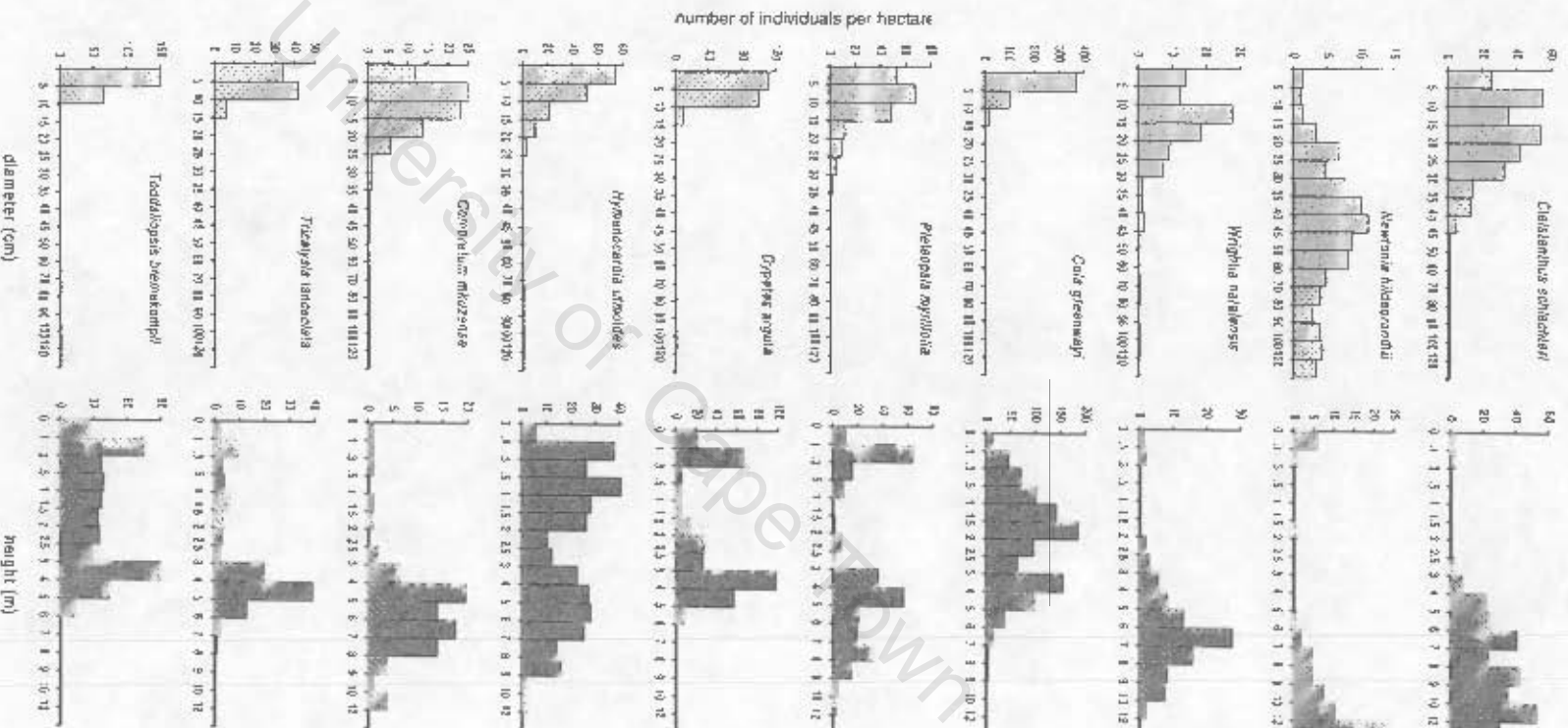


Figure 5 Diameter- and height-class distributions of the ten most important species (81.8 % of total importance, see Table 6 for details) at Phinda Resource Reserve. Note that size-classes are not even.

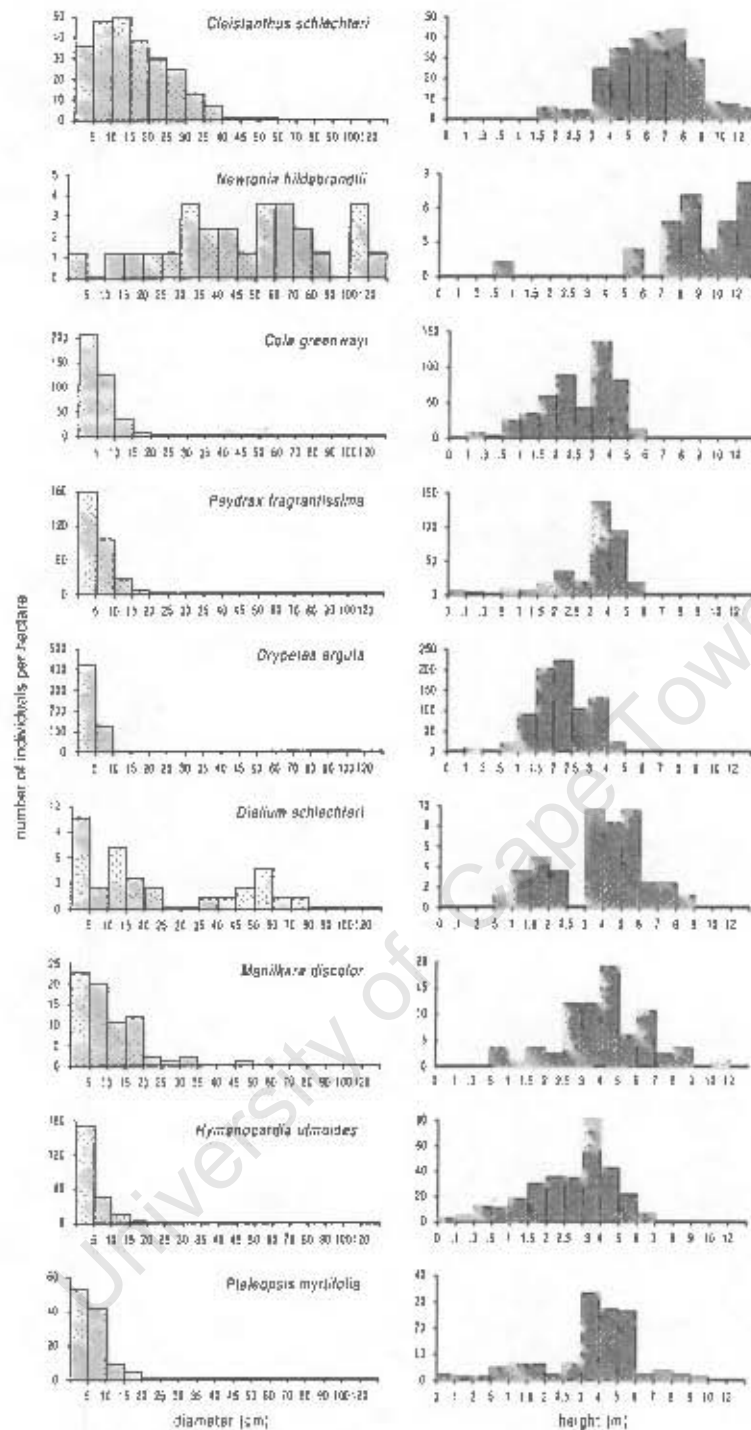


Figure 6 Diameter- and height-class distributions of the nine most important species (73.6 % of total importance, see Table 6 for details) at Tembe Elephant Reserve. Note that size-classes are not even. *Balanites maughanii*, ranked 10th at this locality was omitted due to the low number of stems sampled.

Many of the individual species at each site, including the two most important canopy dominants, *C. schlechteri* and *N. hildebrandtii*, have flat size distributions, or relatively few small individuals (Figures 4, 5 and 6). The relative scarcity of small individuals in many species is more apparent in the height-class distributions, which include individual trees shorter than two metres. Trees shorter than two metres are vulnerable to browsing, and precisely these size classes are underrepresented or absent from tree populations. This effect is particularly conspicuous in the most palatable species such as *C. schlechteri*, *N. hildebrandtii*, *W. natalensis*, *D. arguta*, *S. henningsii* and *T. lanceolata*, but still visible in moderately palatable species such as *P. myrtifolia*, *C. mkuzense* and *P. fragrantissima*. The relative lack of small trees within the range of sizes affected by browsing is even visible in the combined height-class distribution of all sampled trees at each locality (Figure 3). Only *D. schlechteri* at Tembe (Figure 6) and *N. hildebrandtii* at all localities (Figures 4, 5 and 6) have multimodal diameter-class distributions that might indicate episodic recruitment.

Since one year-old seedlings are unlikely to have exceeded 30 cm in height (see Chapters 5 & 6), the densities of seedlings of this size can give some indication of maximum annual recruitment from seed. Densities of seedlings of *C. schlechteri* varied substantially from locality to locality, from 61.9 seedlings per hectare at Mkuzi, to only 4.7 seedlings per hectare at Phinda and no seedlings at Tembe (Table 5). It should be noted that sampling was conducted in the middle of the summer wet season at Mkuzi, when all seedling germination and establishment was likely to have occurred, but near the middle of the winter dry season at Phinda and Tembe, when seedling mortality was likely to have been high. The densities presented here are from all old-growth forest samples and are not biased to represent any particular regeneration environments such as gaps or the forest understorey.

Table 5. Density per hectare of seedlings (≤ 30 cm height) and adult trees (> 10 cm DBH) of *C. schlechteri*. Samples (27 0.04 ha quadrats for Mkuzi and Phinda and 20 quadrats for Tembe) were randomly located with regard to canopy openness.

Site	Seedling density (≤ 10 cm height)	Seedling density (>10 -30 cm height)	Tree density (> 10 cm DBH)	Stem area of trees (> 10 cm DBH)
Mkuzi	51.9	9.3	223.1	8.4 m ²
Phinda	1.9	2.8	198.1	9.8 m ²
Tembe	0	0	175.0	6.9 m ²

Sprouting in Sand Forest tree species

It is extremely difficult to categorise sprouting responses in plants (Bond & Midgley 2001). There are many possible responses to a wide range of disturbance types of varying severity. Even within one species, response may vary with age, size or environment. Here I classified trees' abilities to produce stem (epicormic) and basal sprouts (*sensu* Bond & Midgley 2001) in response to death or loss of large branches and main stems or to burning of aboveground biomass. Nearly all Sand Forest species had some ability to produce new shoots to replace lost or damaged stems (Table 6). However, rates of

resprouting relative to mortality appeared to be fairly low for most species in undisturbed forests (pers.obs.).

Table 6. Proportion of seedlings to root suckers and resprouting ability (production of stem and basal resprouts) in the 10 most important old-growth forest species at Mkuzi Game Reserve, Phinda Resource Reserve and Tembe Elephant Park. Resprouting refers to the species' ability to survive and form new stems after losing stems to disease or physical damage: low—few individuals survive damage (> 0 % but < 25 %); medium—a high proportion of individuals survive damage (25—50 %); vigorous—most individuals survive damage and produce new stems (>50 %). Importance is calculated from the average of each species' relative density and its relative dominance (total stem cross-sectional area) at each site.

Species	number of		resprouting ability	Importance (%)		
	seedlings	suckers		Phinda	Tembe	Mkuzi
<i>Cleistanthus schlechteri</i>	10	0	low - medium	25.1	19.8	35.1
<i>Newtonia hildebrandtii</i>	10	0	low - medium	14.9	18.0	13.7
* <i>Pteleopsis myrtifolia</i>	20	0	vigorous	5.7	2.9	9.5
<i>Hymenocardia ulmoides</i>	16	0	vigorous	4.7	3.2	9.8
<i>Cola greenwayi</i>	15	0	medium	6.3	8.3	
<i>Wrightia natalensis</i>	10	0	vigorous	9.3		3.3
<i>Combretum mkuzense</i>	10	0	vigorous	4.3		6.8
<i>Drypetes arguta</i>	33	0	medium - vigorous	5.1	5.9	
<i>Brachylaena huillensis</i>	15	0	vigorous			7.0
<i>Psydrax fragrantissima</i>	5	12	vigorous		6.4	
<i>Dialium schlechteri</i>	10	0	vigorous		5.5	
<i>Balanites maughamii</i>	6	2	vigorous		2.4	1.6
<i>Croton gratissimus</i>	7	0	low			3.9
<i>Manilkara discolor</i>	-	-	medium (?)		3.6	
<i>Tricalysia lanceolata</i>	-	-	vigorous	3.5		
<i>Toddaliopsis bremekampii</i>	12	0	vigorous	2.8		
<i>Strychnos heningsii</i>	4	1	medium			1.6

* *P. myrtifolia* can produce root suckers after fire: of 10 recruits excavated in a burnt area at Tembe, 7 originated from root suckers and only 3 were seedlings.

While a few Sand Forest tree species, most notably *P. fragrantissima*, were able to produce individuals vegetatively by means of root suckering, the most important species (in terms of stem density and total stem cross-sectional area) appeared to reproduce entirely by means of seed in old-growth forest.

Mortality and resprouting in Cleistanthus schlechteri

In undisturbed old-growth forest, estimates of adult mortality rates derived from numbers of recently dead trees in a standing population were relatively low for the canopy dominant, *C. schlechteri* (Table 7), as would be expected for a slow growing, long-lived tree (see Chapter 7).

Table 7. Estimates of annual mortality and resprouting rates in *Cleistanthus schlechteri* derived from numbers of recently dead trees in 1995. Data are pooled from five Sand Forest localities in South Africa.

Diameter class	No. individuals	No. dead	Mortality	No. resprouts	Resprouting
≤ 10 cm DBH (> 2 m height)	251	2	0.8 %	0	0 %
> 10 cm — 40 cm DBH	702	7	1.0 %	3	0.4 %

There was no evidence that mortality rates were higher for small trees (less than 10 cm DBH, but taller than 2 m) than for trees larger than 10 cm DBH, but this estimate may also be unreliable as a result of small sample size. Less than one-third of adult trees larger than 10 cm DBH in which the aboveground biomass had died back had survived and produced new basal or stem shoots (resprouts).

Sand Forest recovery after fire

The randomly sampled burnt patches at Tembe appear to have been representative of sampled old-growth forests at this locality, with a typical species complement and a stem diameter distribution that closely resembled that of unburnt forests sampled in 1995 (data not presented). Of the 60.7 ± 33.2 trees per 100 m² transect (ave. $\pm$ SD, $n = 3$) before the 1995 fire, 79.2 ± 11.7 % were still standing, but with all aboveground stems killed by fire, 17.7 ± 9.4 % had fallen, and 3.2 ± 3.9 % had burnt completely, leaving only stumps. Despite the death of nearly all aboveground biomass, 53.6 ± 4.2 % of all existing trees had produced new basal stem shoots (resprouts) with a median length of 42 cm (longest shoot on each tree, $n = 97$; range: 2 cm to 158 cm) 27 months after the fire. All burnt trees without resprouts appeared to be dead. Ability to survive and resprout was not related to stem diameter (Logit regression, $n = 180$, $P = 0.12$). In addition to the 32.3 ± 17.2 resprouts per 100 m², there were 5.3 ± 6.8 new individuals produced vegetatively from root suckers. Only one seedling (*P. myrtifolia*) was found in three transects.

A large proportion (66 %) of the living trees in the burnt transects were from only five species (Table 8) which had resprouted vigorously and, in the case of *P. locuples* and *P. myrtifolia*, also produced root suckers. *Cola greenwayi* and *Toddaliopsis bremekampii* were common (average of 5 and 4.5 individuals per 100 m² respectively, ranked 2nd and 3rd after *D. arguta*) and widespread (occurring in 17 out of 20 samples) in unburnt forests in 1995. However, resprouting individuals of these species were absent from burnt transects, and rare elsewhere in the burnt forest areas. Resprouts and root suckers of *Psyrax fragrantissima*, although present in low densities in the sample, were common elsewhere in burnt forest areas. Common liane and creeper species resprouted vigorously and often covered large areas of ground. See Appendix 1 for a list of all species observed to resprout after fire. The cover of grass and forb in burnt forest areas was between 50 % and 90 %, often approaching that of adjacent savannah and grassland areas.

Table 8. Common sprouting species in three 100 m² transects in burnt Sand Forest at Tembe Elephant Park. Resprouts are stem shoots from existing trees burnt in the fire. Suckers are clonal stems arising from belowground roots. Density values for unburnt quadrats are based on 20 400 m² samples.

Species	Burnt transects		Unburnt quadrats	
	No. resprouts per 100 m ² (ave. $\pm$ SD)	No. suckers per 100 m ² (ave. $\pm$ SD)	No. of individuals per 100 m ² (ave.)	Rank (stem no.)
<i>Hymenocardia ulmoides</i>	6.0 $\pm$ 2.6	—	2.9	5
<i>Psyrax locuples</i>	3.0 $\pm$ 3.5	3.3 $\pm$ 5.8	0.9	15
<i>Pteleopsis myrtifolia</i>	5.0 $\pm$ 5.2	1 $\pm$ 1.7	1.2	9
<i>Drypetes arguta</i>	3.3 $\pm$ 1.5	—	8.2	1
<i>Brachylaena huillensis</i>	2.7 $\pm$ 4.6	—	2.7	6

The low seedling densities in the initial sample were consistent with densities over a wider area: although sampling was conducted at the height of the summer rainfall growth season only two seedlings (one *P. myrtifolia* and one *Erythrophleum lasianthum*) were found in 40 100 m² transects in burnt Sand Forest. This is considerably lower than the average density of 1.2 seedlings ($\leq$ 30 cm tall) per 100 m² in unburnt Sand Forest at Tembe in dry season of June/July 1995, or the densities of 14.7 seedlings per 100 m² at Mkuzi in Dec./Jan 1994/1995 and 6.8 seedlings per 100 m² at Phinda in May/June 1995.

Table 9. Response of *Cleistanthus schlechteri* to fire damage in Tembe Elephant Park.

Tree damage	n	mode of resprouting in survivors			dead
		base of stem	stem	branches	
light	19	1	1	16	2
medium	69	24	3	0	42
heavy	12	2	0	0	10
Total	100	27	4	16	54

light—some foliage survived fire or no substantial blackening of bark; medium—no living foliage, bark lightly to heavily blackened by fire, but still intact on main stem and most branches; heavy—bark heavily blackened over much of tree or burnt through bark on main stem or many of branches.

Total mortality in a sample of 100 burnt *C. schlechteri* was 54 % (Table 9). Mortality was strongly related to the degree of damage by fire (Chi-Square test, $P < 0.001$), but unrelated to tree size (Logit regression, $P = 0.86$), which ranged from 3 cm to 56 cm DBH in this sample. However, the diameters of trees in this sample are approximately normally distributed, unlike more extensive samples from unburnt areas in 1995, which have a higher proportion of stems smaller than 10 cm DBH. This may indicate that more small stems did not resprout but were too burnt to identify. Resprouting from crown branches was common in lightly damaged trees (occurring in all 13 individuals which retained some

living foliage from before the fire), but did not occur in severely scorched or burnt trees. When these more heavily damaged individuals did resprout, it was only from the base of the stem or occasionally from cambial tissue on the trunk. Only two trees in the sample had fallen, both apparently because of removal of aerial support rather than damage to roots or trunks.

Regeneration patterns and forest grain

At the scale of 400 m² samples, juveniles of most Sand Forest species were significantly associated with conspecific adults at all three Sand Forest sites (Table 10).

Table 10. Association between juvenile and adult trees of dominant Sand Forest species (ranked by importance at each site). A + indicates that juveniles are found together with adults more often than would be expected if they were randomly distributed, while a – indicates that juveniles are found away from adults more often than would be expected. Juveniles of canopy species are established plants shorter than 3 m, adults are taller than 5 m. For sub-canopy species (denoted by *), juveniles are shorter than 1 m and adults are taller than 2 m. Juveniles were considered to co-occur with adults where any portion of a conspecific adult was inside a circular 400 m² quadrat centred on that juvenile. Associations were tested with a Chi-Square (χ^2) test: n.s. $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

/ Species	Site	Juveniles with adults	Juveniles without adults	n	Expected proportion with adults	Assoc.	χ^2
Mkuzi G.R.							
<i>Cleistanthus schlechteri</i>		49	1	50	0.83	+	8.1**
<i>Newtonia hildebrandtii</i>		31	19	50	0.48	+	4.9*
<i>Hymenocardia ulmoides</i>		32	18	50	0.41	+	10.5**
<i>Pteleopsis myrtifolia</i>		43	7	50	0.72	+	4.6*
<i>Brachylaena huillensis</i>		27	23	50	0.38	+	5.5*
<i>Combretum mkuzense</i>		15	35	50	0.52	–	9.5**
<i>Croton gratissimus</i>		36	14	50	0.48	+	11.3***
<i>Wrightia natalensis</i>		16	34	50	0.41	–	1.8 n.s.
<i>Strychnos henningsii</i> *		44	6	50	0.48	+	31.6***
<i>Balanites maughamii</i>		5	26	31	0.14	+	0.1 n.s.
Phinda							
<i>Cleistanthus schlechteri</i>		31	0	31	0.74	+	10.9**
<i>Newtonia hildebrandtii</i>		26	1	27	0.74	+	6.9**
<i>Wrightia natalensis</i>		44	6	50	0.85	+	0.3 n.s.
<i>Cola greenwayi</i> *		48	2	50	0.63	+	23.4***
<i>Pteleopsis myrtifolia</i>		48	2	50	0.56	+	33.1***
<i>Drypetes arguta</i> *		48	2	50	0.81	+	7.0**
<i>Hymenocardia ulmoides</i>		47	3	50	0.63	+	20.7***
<i>Combretum mkuzense</i>		8	27	35	0.30	–	0.8 n.s.
<i>Tricalysia lanceolata</i> *		47	3	50	0.81	+	5.2*
<i>Toddaliopsis bremekampii</i> *		35	15	50	0.85	–	9.1**
Tembe							
<i>Cleistanthus schlechteri</i>		37	1	38	0.81	+	6.6**

<i>Newtonia hildebrandtii</i>	4	0	4	0.57	+	—
<i>Cola greenwayi</i>	50	0	50	0.76	+	15.6***
<i>Psydrax obovata</i>	41	9	50	0.57	+	12.6***
<i>Drypetes arguta</i> ♀	50	0	50	0.90	+	5.3*
<i>Dialium schlechteri</i>	14	2	16	0.38	+	16.6***
<i>Manilkara discolor</i>	34	16	50	0.52	+	4.9*
<i>Hymenocardia ulmoides</i>	44	6	50	0.62	+	14.4***
<i>Pteleopsis myrtifolia</i>	47	3	50	0.71	+	12.5***
<i>Balanites maughamii</i>	0	7	7	0.24	—	—

Only *C. mkuzense*, a wind dispersed, light demanding species which tends to be associated with gaps (see Chapter 4) and *T. bremekampii*, a shade tolerant, bird dispersed understorey species have juveniles which are non-randomly distributed away from conspecific adults. Seedlings of *W. natalensis* were consistently randomly distributed with regard to conspecific adults. Although this species tended to be distributed in slightly lower than average light environments (Chapter 4), its small, light seeds with dandelion-like parachutes are very widely and evenly dispersed.

Discussion

Structure and past disturbance

Sand Forest is amongst the driest forests worldwide, with a strongly seasonal rainfall pattern and occurs on free-draining, nutrient poor sands (see Chapter 1). Not surprisingly, I found that sampled forests were short, often multistemmed, and structurally simple, particularly at the driest locality described here, Mkuzi. Although dry forests seldom reach more than 40 m in height, the average canopy heights of approximately 7 to 11 m (with very few emergents taller than 18 m) also place these forests amongst the shortest worldwide (see e.g. Murphy & Lugo 1986a; Menaut *et al.* 1995; Murphy & Lugo 1995; Rundel & Boonpragob 1995; Sampaio 1995). Nonetheless, tree density was intermediate (Table 2) and stem area of the woody vegetation was moderately high, ranging from 24.1 m² ha⁻¹ to 33.2 m² ha⁻¹ (excluding lianes and shrubs not capable of exceeding 2 m height).

Dry forest structure can be greatly modified by disturbance ranging from stem harvesting to forest clearing and fire (Sampaio 1995; Lowe & Clarke 2000), and these effects persist for almost a century (e.g. Murphy & Lugo 1986b; Lowe & Clarke 2000) and probably longer (Swaine *et al.* 1990 and see Chapter 7). Despite very low rainfall, stem area in sampled Sand Forest is typical of undisturbed dry forests (Murphy & Lugo 1986a; Lowe & Clarke 2000), and higher than in East African dry forests with a known history of disturbance (Lowe & Clarke 2000). Nearly all stem area is contributed by few large trees, unlike forests where large-scale stem harvesting has occurred (e.g. Murphy & Lugo 1986b; Gonzalez & Zak 1996). Although the study sites described here are all conserved areas, there has been some harvesting, mostly stems of pole size. However, only forests where direct human impact was low were sampled, and the presence of epiphytes, large lianas, very large trees, and a range of tree sizes,

are further indicators that these should be considered old-growth forests (*sensu* Clark 1996). Note that extensive short thickets (< 4 m) with many species in common with Sand Forest and occurring in a matrix with Sand Forest in and around Tembe Elephant Park were not sampled. It seems likely that sampled forests have not been subject to large-scale natural or human disturbance for centuries and perhaps millennia, and certainly not since the advent of aerial photography in the region in the 1930's (pers. obs.).

Sprouting in undisturbed old-growth forest

Kruger *et al.* (1997) suggest that the apparent lack of recruitment in many South African forests is simply a function of high levels of sprouting and therefore not necessarily cause for concern. Worldwide, the high incidence of sprouting in tropical dry forests in response to clearing or burning (Murphy & Lugo 1986a; Murphy & Lugo 1986b; Sampaio *et al.* 1993; Miller & Kauffman 1998) implies that persistence and regeneration by sprouting may be important even in largely undisturbed dry forests. In Sand Forest this does not appear to be the case. In some ways Sand Forests conform to the model of Kruger *et al.* (1997), which proposes that short forests have low branching height, high multistemmedness, low recruitment from seed, and presumably high dependence on adult resprouting. Structural indices thought to be related to sprouting vary in the predicted direction across the range of canopy heights. Most, if not all, species have some ability to resprout following damage, and numbers of seedlings relative to adults is low. However, mean number of stems per tree is relatively low and very few species appear to be able to maintain their position in the forest by resprouting. The canopy dominant and most important species at all localities, *C. schlechteri* (see Table 6 and Chapter 2), had resprouting rates of only 0.4 % per annum in undisturbed forest compared to mortality rates of 1.0 % (trees > 10 cm DBH). While resprouting may contribute to adult persistence, these values seem to indicate that recruitment from seed is more important than resprouting for populations of *C. schlechteri*. Although there is little information on resprouting in undisturbed old-growth forests, tall moist tropical forests in Panama had much higher resprouting rates of 1.7 %, vs. mortality rates of 1.5 % per annum (Paciorek *et al.* 2000). In undisturbed Sand Forest, trees primarily died standing as a result of senescence, disease or shading, which would reduce the incidence of sprouting relative to taller forests where physical damage from treefalls is frequent (Paciorek *et al.* 2000). Vegetative reproduction by sprouting also appeared to be relatively unimportant in Sand Forest. Kruger *et al.* (1997) found seeding indices (no. seedlings/no. all recruits) of approximately 0.5 or less for forests with canopy heights similar to Sand Forest (ca. 7 to 11 m). Seeding indexes for Sand Forest, based on the 10 most important species at each locality, ranged from 0.89 to 1 (0.93 to 1 if weighted by species' importance) and were not correlated with canopy height. Although data from Sand Forests support the broad conclusions of Kruger *et al.* (1997) regarding relationships between canopy height and inherent ability of forest trees to resprout, the tight relationship between these characteristics, background rates of resprouting and the importance of recruitment from seed in old-growth forests does not appear to hold. It is unlikely that a simple structural characteristic such as canopy height could provide a framework for predicting and interpreting forest dynamics, or inform management and conservation decisions as the authors suggest.

1995; Midgley *et al.* 1995b). Leaf characteristics appear to support these conclusions (Midgley *et al.* 1995c, but see Chapter 4). In the more detailed of these studies, Everard *et al.* (1995) classified Sand Forest as 'mixed [fine and coarse grained?] with an intermediate grain'. This implies that canopy trees require medium- to large-scale disturbance for regeneration. The conclusion is partly based on the high ordination distance between subcanopy and canopy samples of 400 m² quadrats, with the incorrect assumption that continuous *in situ* replacement ('fine grain') would necessarily result in similar frequencies of species in both samples (see e.g. Condit *et al.* 1998). Ordination distance is interpreted in the light of diameter distributions, the graphics of which contain serious errors, with identical distributions presented for the same species in different forest types and even for different species within the same forest type. The authors do not identify the locality of the Sand Forest sampled, which has an atypical species composition, referring only to an unpublished report. It seems that the conclusions of this study should be regarded with caution. The data presented in this chapter indicate that old-growth Sand Forest experienced primarily small-scale autogenic disturbance events. Although canopy gaps comprised a large proportion of Sand Forest area, most gaps were small. Nearly all trees died standing and gaps smaller than six metres in diameter contributed the bulk of gap area. Windthrow has not been observed. Like Midgley *et al.* (1995b) and Everard *et al.* (1995), I found a relative scarcity of seedlings and saplings of Sand Forest species, particularly of the two canopy dominants, *C. schlechteri* and *N. hildebrandtii*. However, juvenile trees of these and most other important species occurred together with conspecific adults in small (400 m²) samples significantly more often than would be expected if they were randomly distributed, or if recruitment was limited to canopy gaps. This indicates that these forests should be considered fine grained despite the low densities of juvenile trees, with most important species able to recruit in subcanopy environments close to conspecific adults. Results from Chapter 4, where I examine how Sand Forest tree species are distributed with regard to the available range of canopy openness, support this conclusion. Small seedlings of most species were actually distributed away from the most open gap environments. Although larger seedlings and especially saplings tended to occur in higher densities below canopy gaps, indicating that these environments increase growth and/or survival in established trees, no species appeared to be completely dependent on gap-phase regeneration in Sand Forest.

Canopy gap turnover

Canopy gaps occupied between 4 and 21 % of sampled Sand Forest area. This is substantially higher than most temperate or tropical old-growth forests, which typically have approximately 1% of total area under newly formed gaps (Lorimer 1989 and references therein; Schupp *et al.* 1989). Although identifiable gap-makers were absent in many cases, particularly at Mkuzi, there appeared to be no edaphic cause for gaps in the forest canopy. Since decomposition rates of dead trees are slow as a result of the dry climate and resistant wood of most species, it seems likely that gap turnover rates are extremely slow.

Large-scale disturbance in Sand Forest: fire

In managed conservation areas, fire is common in the savanna vegetation surrounding Sand Forest, even occurring annually when there is adequate grass biomass. Despite this, Sand Forest very seldom burns. The short (< 4 m), multistemmed *Pteleopsis myrtifolia* and *Hymenocardia ulmoides* stands on the forest margin may burn (and resprout vigorously), but fire does not penetrate the abrupt margins between the savanna and the forest (pers. obs.). There are no records or memory of fire burning forest patches at Mkuzi Game Reserve (proclaimed 1903) or Phinda Resource Reserve (managed as private game reserve for at least several decades). During several months spent working inside Sand Forests from a variety of localities across the region I did not see charred trunks, fire scarred stems or other obvious signs of fire inside closed forest. Despite the apparent absence of fire from Sand Forest, it is possible that very infrequent, large-scale disturbance caused by fire may be an important part of normal Sand Forest dynamics, allowing the regeneration of certain species and perhaps contributing to the maintenance of species diversity. Evidence of fire has been found in all tropical forests where it has been sought, and is likely to be more frequent in dry forests than in moister types (Swaine 1992).

Some Sand Forest did burn in an unusually severe fire that burnt approximately 40 % of Tembe Elephant Park on the 10th September 1995. The fire was largely confined to savanna vegetation between forest patches, but crown fires burnt through perhaps 5 to 10 % of Sand Forest in that area. The burnt portions of forest patches amounted to several hectares in extent (pers. obs., Matthews 1997). I investigated forest recovery in burnt patches 27 months after this serendipitous natural experiment. More than two years, and well into the third growth season after burning, forest recovery at Tembe consisted almost entirely of resprouting. Despite the death of almost all aboveground biomass, just over half of all trees had survived and produced new shoots. Species able to resprout vigorously were a common subset of the typical old-growth species complement. Recruitment of new juvenile trees into burnt patches was primarily by the production of root suckers by some of these common resprouting species. Recruitment from seed after the fire was negligible. Fire thus appeared to cause a shift toward lower tree density, development of multiple stems and dominance by resprouting and suckering trees and lianes. These patches would probably be of lower stature for many years, and may be vulnerable to repeated burning in the short term due to much higher grass cover than in unburnt forest. Sample sizes were too small to attempt to detect whether burning lowered species diversity or richness, but there was no evidence of substantial resprouting or any recruitment from seed by species with low numbers of juveniles in mature forest, such as the canopy dominant *C. schlechteri*. Instead, species composition in burnt areas was dominated by resprouts from previously existing populations of *H. ulmoides*, *P. locuples*, *P. fragrantissima*, *P. myrtifolia*, *D. arguta*, *B. huillehsis* and lianes. All of these species, even the most shade-intolerant such as *P. myrtifolia*, can maintain adult populations and recruit continuously in undisturbed old-growth forest.

There is therefore no evidence that large-scale disturbance by fire acts to facilitate recruitment of any forest species with low levels of recruitment in undisturbed old-growth forest, including the canopy dominants. The negligible levels of recruitment by seed in the post-fire environment and potentially slow growth rates in Sand Forest trees (Chapter 7) imply that recovery of non-resprouting species would be slow. It is therefore unlikely that fire would act to maintain or increase woody species richness. Unless further research contradicts these conclusions, conservation management should strive to prevent any burning of Sand Forest.

Demography of Sand Forest species: where are all the small trees?

Adult mortality (individuals > 10 cm DBH) of the canopy dominant, *C. schlechteri*, was 1.0 % within a one year period, at the low end of the normal range of background mortality in tropical forests (Swaine *et al.* 1987; Lugo & Scatena 1996). If the composition of these forests has been stable for a long period of time, as appears to be the case, we would expect that recruitment would balance mortality. However, a striking feature in all conserved Sand Forests was the relative scarcity of large seedlings and saplings of *C. schlechteri* and other important Sand Forest canopy and subcanopy species. Theory predicts that three demographic parameters can influence the steepness of a typical negative exponential ('reverse J') size distribution (i.e. the relative abundance of juveniles vs. adults): population growth, survival and growth. All other things being equal, high population growth results in a more steeply negative size distribution, and this is usually the only factor taken into account when interpreting size distributions (Condit *et al.* 1998). However, high survival, particularly adult survival, results in a flatter size distribution, with few juveniles relative to adult trees. Less intuitively, high growth rates, especially in the juvenile stages, would also result in flatter size distributions. In forest tree populations, Condit *et al.* (1998) actually found that the shape of the size distribution was more strongly correlated with growth rates than population growth. They cautioned against interpreting low juvenile density relative to adult density as indicative of population decline without an understanding of other demographic parameters (but see Lykke 1998). In Sand Forest, neither growth nor survival are likely to contribute to flat size-distributions or low juvenile density. Adult growth of *C. schlechteri* and *N. hildebrandtii* is slow, with average diameter increments of less than 3 mm per year. Juvenile growth of *C. schlechteri* is lower than adult growth (Chapter 7). Given the harsh environment (Chapters 1, 4 & 5), this is likely to be the case for most species. This would tend to result in a more steeply negative exponential size distribution. At least for *C. schlechteri*, survival appears to be in the normal range for forest trees and probably not high enough to result in a flat size distribution. In light of this demographic information, it seems that the absence of juveniles in certain Sand Forest species may well indicate that recruitment from seed was too low to replace adult mortality. Since these species maintain populations by *in situ* regeneration, and recruitment is not linked to large-scale disturbance, this is cause for concern.

A number of features of the Sand Forest environment appear to contribute to low seedling establishment. Seed banks seem to be virtually non-existent for tree species despite copious production of seed (D. Kirkwood, unpubl. data). Low rainfall and water-repellent (non-wetting) sandy soil act in

tandem to reduce seed germination and increase mortality of small (< 30 cm) seedlings (Chapter 5). These factors are likely to have been a normal part of this ecosystem for millennia and would act to reduce the densities of seedlings in the smallest size classes. However, relative densities of small seedlings were relatively high in some species with very few larger seedling and saplings. If we assume that recruitment, survival and growth are approximately constant from year to year, this suggests that some other factor is acting to reduce survival and/or growth in the larger seedlings and saplings. In most cases, height classes with particularly low numbers of individuals corresponded closely with the range of tree heights accessible to ungulate herbivores, particularly Nyala, *Tregalaphus angasii*, and the effect is most noticeable in palatable species, including the canopy dominants, *C. schlechteri* and *N. hildebrandtii*. Thus size distributions suggest that ungulate browsers in conserved areas are dramatically reducing regeneration of many Sand Forest species, and perhaps even be causing the decline of certain species. Despite regular culling, it is quite possible that in the absence of significant numbers of large predators, modern densities of Nyala in conserved areas are substantially higher than they ever would have been (see Chapter 6). Given the limited distribution and small area of Sand Forest actually conserved (see Chapter 1), this preliminary evidence that selective browsing by ungulates could alter Sand Forest dynamics and composition warrants further investigation.

Although the scarcity of juveniles in conserved areas could be an indication that periodic recruitment events are important (e.g. years with unusually high rainfall), data presented in Chapter 6 indicates that under similar conditions only a few kilometres away, numbers of juveniles are far higher in the absence of browsing. Thus, as in most tropical forests (Condit *et al.* 1998), it seems likely that recruitment in Sand Forest is continuous rather than episodic.

Conclusions

Structural characteristics in sampled Sand Forest were consistent with the long-term absence of large-scale disturbance. Disturbance in old-growth Sand Forest consisted almost entirely of small-scale autogenic events. Despite its low stature, recruitment by important tree species in old-growth Sand Forest was almost entirely by seed rather than vegetative reproduction by root suckers. Similarly, resprouting after death of aboveground biomass was low in the canopy dominant, *C. schlechteri*. Low numbers of seedlings and saplings are therefore not a function of dominance by sprouting species with inherently low ability to recruit from seed. The distribution of juveniles with regard to adults suggests that most species were capable of continuous *in situ* recruitment in the relatively open subcanopy environments, and canopy gaps were relatively unimportant. Recovery after large-scale disturbance caused by fire is limited almost entirely to resprouting, with a shift in dominance toward a few vigorously resprouting and suckering species. The relative absence of juveniles of many important species in undisturbed old-growth Sand Forest therefore does not seem to be caused by a requirement for medium- or large-scale disturbance as suggested by earlier workers (Everard *et al.* 1995; Midgley *et al.* 1995b). This implies that management strategies should attempt to avoid larger-scale or more frequent disturbance, such as would be caused by high densities of African elephant, *Loxodonta*

africana, harvesting of trees or forest fires. Increased disturbance is likely to change forest structure and composition, opening the forest canopy even further and favouring short, light demanding and vigorously resprouting species such as *P. myrtifolia*, *H. ulmoides* and *P. fragrantissima*. These species were already a common component of sampled old-growth forest, with moderate to high densities of juveniles despite the predominance of small-scale disturbance. Increased disturbance would be unlikely to increase recruitment of the taller canopy dominants, *C. schlechteri* and *N. hildebrandtii*, and other important species which had low relative densities of juvenile trees. Although the harsh environment probably contributes to the low densities of juveniles of many important tree species, browsing by ungulates, particularly Nyala, *T. angasii*, may be the primary cause. The effect of ungulate browsing is an important management issue, and is investigated in more depth later in this thesis. Preliminary evidence suggests that numbers of ungulates may be too high and could negatively impact populations of palatable species such as *C. schlechteri* and *N. hildebrandtii*, changing forest composition and structure over time.

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Appendix 1. List of species observed to resprout or produce root suckers in response to fire at Tembe Elephant Park. Vigorously resprouting species (> 50% of burnt individuals) are marked with a *, species capable of vegetative reproduction by means of roots suckers are marked with †.

Tree species†*Albizia adianthifolia***Balanites maughamii**Boscia foetida* ssp. *rehmanniana***Brachylaena huillensis**Cleistanthus schlechteri***Combretum mkuzense**Dialium schlechteri**Drypetes arguta***Erythrophleum lasianthum**Haplocoelum gallense*†**Hymenocardia ulmoides**Hyperacanthus microphyllus***Lagynias lasiantha**Leptactina delagoensis**Manilkara discolor***Monodora junodii**Pavetta* cf. *schumanniana*†**Psydrax fragrantissima*†**Psydrax locuples*†**Ptaeroxylon obliquum*†**Pteleopsis myrtifolia***Suregada zanzibariensis**Tarennia supra-axillaris**Toddaliopsis bremekampii***Tricalysia lanceolata**Tricalysia* sp.**Vitex ferruginea* subsp. *amboniensis***Wrightia natalensis***Zanthoxylum leprieuri***Scrambling shrubs or trees**†**Salacia leptoclada**Grewia microthyrsa**Grewia monticola***Shrubs****Croton pseudopulchellus**Croton steenkampianus**Erythroxylum emarginatum***Creepers and lianes****Acacia kraussiana***Combretum celastroides* subsp. *orientale***Hippocratea delagoensis***Landolphia kirkii***Monanthotaxis caffra***Rhoicissus digitata***Synaptolepis kirkii***Uvaria* sp.

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Canopy gaps, light environments and the distribution of Sand Forest trees

"Yew pados and joint-firs rejoice exceedingly in shade.

Others, one may say in general, prefer a sunny position."

Theophrastus (b. 370 b.c.), quoted by Horn (1971)

Abstract

The distribution of tree species with regard to canopy openness was evaluated at two sites representing the range of Sand Forest structure in South Africa: the relatively short (ave. 7 m), open (11 % gap) forest at Mkuzi Game Reserve; and the taller (11 m) and more closed (4 % gap) forest at Phinda Resource Reserve. Floristic composition in gaps and fully shaded areas were compared. Canopy openness (gap vs. non-gap) was a highly significant explanatory variable of the variation in composition revealed by two multivariate techniques (CCA and DCA). The density of small seedlings (<15 cm height) was lower in canopy gaps than in shaded areas, particularly at Mkuzi. Percentage canopy openness was estimated above the crowns of 2273 individuals at Mkuzi and 3361 individuals at Phinda of all heights ≥ 20 cm. For each individual, the residual from the average canopy openness of all trees in the same height class was used to correct for the effects of height on canopy openness. The residuals of species with at least 8 individuals (24 species at Mkuzi and 25 species at Phinda) were compared to the residuals of all individuals sampled. Two species at Mkuzi and six species at Phinda were distributed in significantly more open conditions than average ($P < 0.05$), while six species at Mkuzi and seven species at Phinda were distributed in significantly more shaded conditions. Species' residuals were also compared to one another, and no species was found to be distributed at random with regard to light environments, with species arrayed along the continuum of canopy openness. This distribution of species along the continuum of canopy openness supports recent questioning of classic gap-phase dynamics. Although these relatively species poor dry forests appear to be composed of specialists, the substantial overlap between species indicates that niche partitioning of the continuum of canopy openness is unlikely to be the only mechanism of species coexistence. Nonetheless, this study is one of the first to show that canopy openness has a large effect on the distribution and dynamics of dry forest tree species.

Keywords: coexistence, niche partitioning, relative illumination

Introduction

The three-dimensional structure of mature forest is highly variable in both space and time, resulting in a wide range of internal light environments (Brokaw 1982; Richards 1983; Lieberman *et al.* 1995). The response by tree species to varying degrees of canopy openness, usually framed in terms of a gap/non-gap dichotomy, has been demonstrated to be important in the internal dynamics of a broad variety of forest types world-wide, from tropical (e.g. Brokaw 1985; Denslow & Hartshorn 1994), through temperate (e.g. Veblen *et al.* 1992; Rebertus & Veblen 1993) and boreal forests (Dai 1996; Kneeshaw & Bergeron 1998). Little research has focused on the dynamics, or even the general ecology of dry tropical and subtropical forests. Primarily because dry forests are lower in stature, with lower biomass and simpler vertical structure than moist forests (Murphy & Lugo 1986; Gerhardt & Hytteborn 1992), it has been assumed that light is of little importance in their internal dynamics (Mooney *et al.* 1995; Oliveira-Filho *et al.* 1998). Although the gap theories formulated for wetter forests may not apply (Mooney *et al.* 1995), there is recent evidence that the survival, growth and distribution of dry forest trees may be influenced by canopy openness (Gerhardt 1993; Gerhardt 1996; Oliveira-Filho *et al.* 1998). This is not surprising, as even in the open-canopied environment of savanna, tree succession can be mediated by shade-tolerance and intolerance (Smith & Goodman 1987; Yeaton 1988). Furthermore, although the quantity of light is the factor that varies most in response to canopy openness (Scholes *et al.* 1997), and is perhaps the most important (Denslow 1987), temperature and humidity are also affected (Scholes *et al.* 1997) and an increase in soil nutrients and decrease in root competition may be associated with canopy gaps (Gerhardt 1996; Coomes & Grubb 1998). The Sand Forest of our study area is a very dry, short, semideciduous subtropical forest type with strongly seasonal rainfall pattern. Total annual rainfall ranges from about 620 to 860 mm (Chapter 1). Occurring on deep, uniform, sandy soils with no substantial relief, canopy openness appears to represent the only major environmental gradient within these forests. Sand Forests are thus ideal for investigation of the importance of light environments in dry forest dynamics.

Investigation of forest trees' light environments has both theoretical and practical implications. Niche partitioning of forest gap microenvironments has been touted as a mechanism for tree species coexistence, particularly in the tropics (see e.g. Denslow 1980; Denslow 1987). A substantial body of work has shown that species' germination, establishment, growth and mortality differ in response to varying light levels (e.g. Welden *et al.* 1991; Holmes & Cowling 1993; Ashton 1995; Gray & Spies 1996; Lee *et al.* 1996; Zipperlen & Press 1996; Scholes *et al.* 1997; Dalling *et al.* 1998; Davies *et al.* 1998; Huante & Rincón 1998). However, research to date has not revealed substantial niche partitioning. Instead, there is evidence of considerable overlap of species along gradients of canopy openness (Brokaw & Busing 2000, but see Pacala *et al.* 1996). This may be because few studies have sampled the distribution of species along the entire continuum of available light environments (Lieberman *et al.* 1989; Lieberman *et al.* 1995), and many have considered too small a range of species or size classes (Brokaw & Busing 2000). Theory aside, an understanding of species' distributions along a gradient of canopy openness allows us to predict how ecosystem process and forest

composition might respond to various scales of disturbance, from the creation of small gaps to large-scale clearing.

This chapter reports on the spatial distribution of tree species in relation to the range of canopy openness present in Sand Forest. I have taken two approaches: The extremes of the canopy openness continuum, gaps and shaded subcanopy areas (non-gaps), were surveyed so that floristic composition and the densities of stems in four height categories could be compared. However, because the subcanopy environment of dry forests is relatively well lit compared to taller moist forests (see e.g. Barradas 1991 *cf.* Chazdon & Fetcher 1984), providing a wider range of sites for establishment and growth, I also examined species distributions along the entire continuum of canopy openness. I have taken a similar approach to Lieberman *et al.* (1995), and estimated canopy openness above individual trees from the full range of species and size classes present. This allows me to test whether species are distributed non-randomly along the gradient of canopy openness and assess the degree of species overlap. In addition, the average canopy openness in each height class is presented for the most common species to illustrate how species' distributions with regard to canopy openness change as they grow. As Sand Forest varies in stature across its range, all work was replicated in two areas; the forest at Mkuzi Game Reserve represents the short and very dry (ca. 670 mm year⁻¹) Western Sand Forest type, while the forests at Phinda Resource Reserve are the tallest of the Eastern Sand Forest type and receive more rainfall (ca. 860 mm year⁻¹, see Chapters 1 & 2).

Methods

Gap sampling and analyses

Canopy gaps were identified along randomly oriented linear transects at least 50 m from the forest edge during December 1997. Gaps were defined as holes in the forest canopy extending to within two metres of the ground (Brokaw 1982), with a minimum diameter of 0.2 m. Within each gap the number of stems of every tree species in each of four height classes (0-15 cm, 15-60 cm, 0.6-2 m; > 2 m but shorter than the canopy) were counted. The same was done in the nearest possible area of the same size and shape below continuous canopy (non-gap; > 95 % cover). The proximity was necessary to minimise any differences in seed density as a result of variation in adult plant densities (see e.g. Reader *et al.* 1995). The number of stems in gap and non-gap pairs were compared using the nonparametric Wilcoxon's signed ranks test for matched pairs. For each gap, the presence or absence, and if possible the mode of death of the gap maker (alive or dead, standing or fallen) was noted. Gap size was recorded as the length of the longest axis, and the width perpendicular to that, with area calculated using the formula for an ellipsoid ($\pi \times \frac{1}{2} \text{length} \times \frac{1}{2} \text{width}$). Stem densities in gaps and non-gaps are standardised to 50 m² for data presentation, an approximation of average gap sizes at Phinda and Mkuzi. The multivariate technique, Canonical Correspondence Analysis (CCA, ter Braak 1986; computer program Canoco, ter Braak & Smilauer 1999) was used to evaluate the effect of canopy openness on sample composition and to provide a distribution-free Monte Carlo test of significance. Detrended Correspondence Analysis

(DCA), which does not constrain ordination axes, was used to assess the degree of separation between gap and non-gap samples. For all multivariate analyses, each of the four size classes of each species was treated as separate species, with number of individuals per sample as importance values. The only environmental variable included was coded as either 'gap' or 'non-gap'.

Tree heights and light environments

Most of the data collected for this paper were obtained during a comprehensive floristic survey of Sand Forest patches including Mkuzi Game Reserve and Phinda Resource Reserve, henceforth referred to simply as Mkuzi and Phinda (see Chapter 2). At each site, 27 circular 400 m² quadrats were randomly located in areas of forests chosen to represent the range of variation in structure and species composition. In every quadrat, canopy height was estimated, and the circumference at breast height of every tree was measured. In addition, tree height and percentage cover above trees 20 cm high and taller were estimated for trees in three-quarters of each quadrat. Height of trees taller than 2 m was estimated visually with the aid of a rangefinder, shorter trees were measured. The light environment of each individual tree was assessed simply as the percentage cover above the apex of the crown of that tree for a cone subtending 45°. All cover estimates were made visually by the author. While this method is clearly not ideal in terms of accuracy, a vast number of individuals were surveyed with little preconception, and any subjective bias is unlikely. It seems likely that visual assessment of cover is at least as accurate as the approach of Lieberman *et al.* (1995), who estimated light environment at any point as a function of the diameters (correlated with height) and distances of all taller trees in a given radius. Any estimate of cover is actually a poor measure of light environment, since the total of direct and diffuse light received over a period of time varies greatly with orientation of canopy gaps (Anderson 1964). The considerable practical difficulties involved in taking accurate measurements of total light received by a shaded area, whether instantaneous or continuous (see e.g. Anderson 1964; Salminen *et al.* 1983; Chazdon & Field 1987; Barrie *et al.* 1990) have largely precluded the use of such measurements in studies of forest dynamics. Given the stochasticity involved in dispersal, germination, mortality and growth, and thus distribution of trees, my estimate of light environment was considered adequate, with the need to sample a large number of individuals taking precedence over precision.

Analysis of species distribution along canopy openness gradient

Since smaller individuals tend to be in conditions of low light, and large individuals tend to be in the open, the effect of tree height on the light environment of each individual needs to be corrected before different species can be ranked and their distribution compared. Individuals smaller than 20 cm in height, which might not have experienced a dry season, or may have been dependant on seed reserves, were excluded from the data set. All individuals were allocated to one metre height classes (0.2 - 1 m; >1 - 2 m; >2 - 3 m; etc.). For each individual, the residual of canopy openness from the average of all individuals of the same height class provides a relative measure of its light environment free from the effect of height. Those individuals with positive residuals occur in more open conditions than the average for that height class, while those with negative residuals occur in shadier conditions than

would be expected on average for that height. Lieberman et al. (1995) use t-tests to compare the residuals of each species with the residuals of all individuals sampled, to determine whether species occur in shadier or higher light levels than would be expected by chance. Species which do not differ significantly from the average of all individuals are assumed to occupy all available light conditions indiscriminately. However, this statistical method cannot discriminate between species which are really distributed randomly with regard to light environments from those species which occupy a narrow and specific range of light environments close to, or overlapping the average of all individuals sampled. I followed the method of Lieberman et al. (1995) to allow comparison, but also compared the residuals of all species to one another using multiple range tests (LSD) of a standard one-way ANOVA. These are effectively multiple pair-wise comparisons using a t-test for independent samples (StatSoft 1996) and thus result in an alpha-type error rate of 5%. Since all canopy openness estimates are percentages, original data were arcsine transformed ($P' = \arcsin \sqrt{P}$) to normalise the underlying distributions for statistical analysis (Zar 1996). Only species with at least eight individuals were included in statistical comparisons. Since species' response relative to the average of all species also varies with height, actual canopy openness preferences of all size classes of species with more than 80 individuals are presented. Average values for height classes with fewer than five individuals are excluded.

Results

Species and size distribution in gaps and non-gaps

In ordination diagrams of the first two axes of a Detrended Correspondence Analysis (DCA), gap and non-gap samples form separate groups, although there is some overlap (Fig. 1). The difference is larger for samples from the taller forests of Phinda, with a separation of gap and non-gap centroids of 1.3 DCA units, compared to only 0.8 for Mkuzi. Each DCA unit (or average standard deviation of species turnover) is equivalent to a 50 % turnover in sample species composition (Gauch 1982).

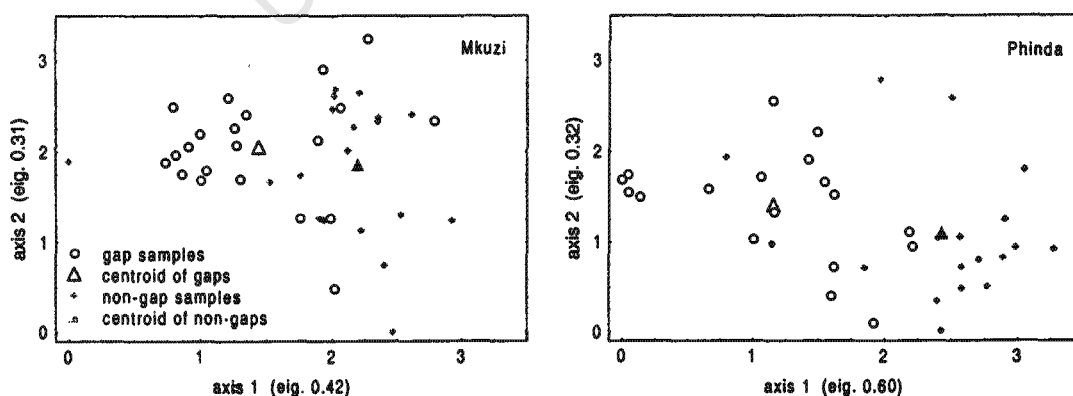


Figure 1. Detrended Correspondence Analysis ordination of gap and non-gap samples at Mkuzi and Phinda. Abundance values are number of individuals per sample. Each species was separated into four size classes or pseudospecies for analysis (<15 cm; 15–60 cm; 0.6–2 m; >2 m).

Comparison of the eigenvalues of constrained ordination (CCA) with Detrended Correspondence Analysis, and comparison of constrained and unconstrained CCA axes reveal that the bivariate environmental variable used (gap vs. non-gap) accounts for a substantial portion of the variation in the species data, particularly for Phinda (Table 1).

Table 1. Summary of eigenvalues corresponding to the first three ordination axes of DCA and CCA analyses. A bivariate environmental variable (gap/non-gap) was used to constrain the first CCA axes (eigenvalues marked by a '!').

	Analysis	Eig. 1	Eig. 2	Eig. 3	Sum unconstrained axes
Mkuzi	DCA	0.42	0.31	0.22	5.13
	CCA	0.25!	0.40	0.39	5.13
Phinda	DCA	0.60	0.32	0.21	4.67
	CCA	0.43!	0.41	0.41	4.67

The correlation of the gap/non-gap variable with the first DCA axis is relatively high ($r = 0.58$ and $r = 0.78$ respectively for Mkuzi and Phinda), and this simple measure of canopy openness is highly significant in both CCA analyses ($P = 0.005$ for Mkuzi and Phinda, Monte Carlo permutation test). It is clear that the species composition in four height classes (all shorter than the surrounding canopy height) differed substantially in canopy gap samples compared to shaded subcanopy sites. The densities of stems of various height classes differed greatly in gaps and adjacent shaded subcanopy areas (Table 2).

Table 2. Average number of individuals of all species in gap and closed canopy samples (standardised to 50 m²). Differences between paired samples were tested with the Wilcoxon matched pair test using unstandardised data; n.s. $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Site	Height class	Average no. individuals per 50 m ² ($\pm$ SE)		Wilcoxon matched pair test Z- value (Gap vs. closed canopy)
		Gaps	Closed canopy	
Mkuzi G.R. (n = 21)	0-15 cm	13.9 $\pm$ 4.0	35.9 $\pm$ 11.8	2.154 *
	15-60 cm	69.5 $\pm$ 29.6	68.3 $\pm$ 30.2	0.744 n.s.
	0.6-2 m	29.6 $\pm$ 5.4	15.3 $\pm$ 5.3	2.893 **
	>2 m	10.7 $\pm$ 2.1	15.7 $\pm$ 6.8	2.146 *
Phinda (n = 18)	0-15 cm	15.0 $\pm$ 5.2	16.3 $\pm$ 6.4	0.213 n.s.
	15-60 cm	47.1 $\pm$ 20.2	7.3 $\pm$ 3.3	3.621 ***
	0.6-2 m	9.6 $\pm$ 2.6	3.7 $\pm$ 2.1	2.225 *
	>2 m	14.5 $\pm$ 6.7	27.5 $\pm$ 9.7	3.337 ***

At Mkuzi, the average density of small seedlings (less than 15 cm high) in gaps was less than half the density in shaded subcanopy areas, while the density of large seedlings (15–60 cm) was approximately the same. At Phinda, the density of small seedlings was similar in gaps and non-gaps,

but there were more than six times as many large seedlings in gaps than non-gaps. At both Mkuzi and Phinda the distribution of larger individuals was very similar; saplings (0.6–2 m in height) were more dense in gaps, while small trees (>2 m, but shorter than the top canopy stratum) were more dense below the canopy.

Table 3. Average number of individuals in of *Pteleopsis myrtifolia* in gap and closed canopy samples (standardised to 50 m²). Differences between paired samples were tested with the Wilcoxon matched pair test using unstandardised data; n.s. $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Site	Height class	Average no. individuals per 50 m ² ($\pm$ SE)		Wilcoxon matched pair test Z- value (Gap vs. closed canopy)
		Gaps	Closed canopy	
Mkuzi G.R. (n = 21)	0-15 cm	8.1 $\pm$ 2.8	10.8 $\pm$ 3.3	1.221 n.s.
	15-60 cm	44.3 $\pm$ 23.5	39.3 $\pm$ 17.2	1.500 n.s.
	0.6-2 m	12.3 $\pm$ 4.6	2.0 $\pm$ 1.1	2.794 **
	>2 m	1.0 $\pm$ 0.4	0 $\pm$ 0	2.521 *
Phinda (n = 18)	0-15 cm	1.6 $\pm$ 0.7	0.2 $\pm$ 0.2	2.201 *
	15-60 cm	19.6 $\pm$ 10.3	2.1 $\pm$ 1.9	3.296 ***
	0.6-2 m	3.1 $\pm$ 1.3	0.1 $\pm$ 0.1	2.521 *
	>2 m	0.3 $\pm$ 0.1	0 $\pm$ 0	2.023 *

The number of individuals of particular species in each sample tended to be too low for adequate comparison between gaps and non-gaps. However, it is useful to note that the most shade-intolerant species at both sites, *Pteleopsis myrtifolia*, tended to be concentrated in gaps at all size classes (Table 3), but seedlings (0–60 cm) were common in shaded subcanopy areas, particularly in the shorter and more open forests at Mkuzi. Thus juveniles of even the most light demanding species in these forests are capable of survival and growth in shaded environments.

Distribution of trees in relation to entire range of sand forest light environments

As expected, small trees tended to be in relatively low light environments, while larger trees tended to occur in the open (Fig. 2). Trees were distributed in more open condition for their size at Mkuzi than in the taller forests at Phinda. At both sites, small trees greatly outnumbered larger trees, and most individuals had less than 10 % open sky overhead.

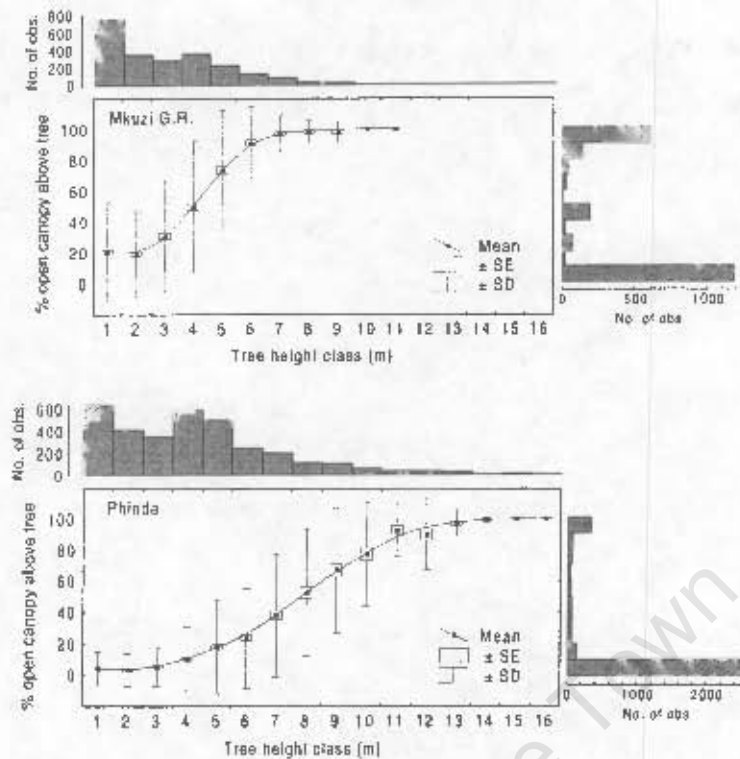


Figure 2. Relationship between tree height and the percentage of open canopy (i.e. inverse of cover) overhead. Low values are in the shade, while 100 % indicates full sunlight with no overhead cover. All individuals 20 cm and taller are included.

For each tree, the difference between the percentage canopy openness above that individual and the average canopy openness above all individuals in the same one metre height class (i.e. the residual from the height vs. canopy openness relationship for all individuals) provides a measure of the light environment free from the effects of height. Trees with positive residuals are distributed in more open conditions than average while trees with negative residuals are in shadier conditions than average.

Residuals of the percentage canopy openness form slightly right-skewed distributions, centred close to zero (Fig. 3), indicating that most individuals were situated in conditions of canopy openness close to average for their height.

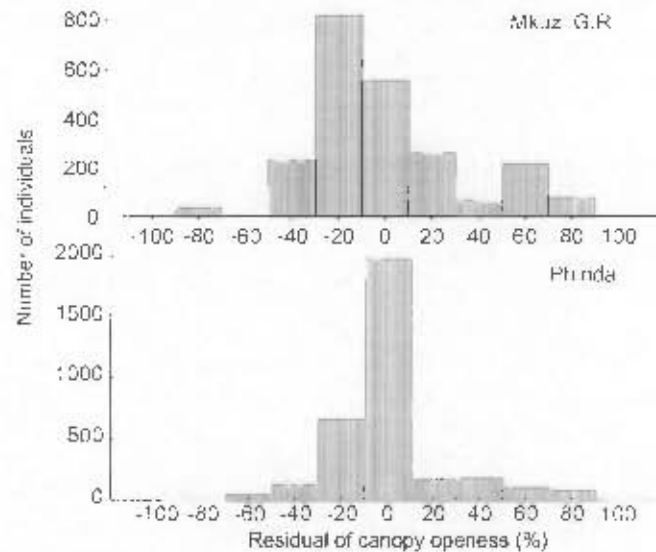


Figure 3. Frequency distribution of the residual of canopy openness for all trees ≥ 20 cm in height.

All residuals (Mkuzi, $n = 2273$; Phinda, $n = 3361$) were sorted according to species. Statistical comparison of species' mean residuals was limited to species with eight or more individuals (Mkuzi, 24 spp.; Phinda 25 spp.). One method to assessing species' distribution with regard to canopy openness is to compare the residuals of each species with the residuals of all trees sampled using a Student's *t*-test (Lieberman *et al.* 1995). As original data are proportions, this was done using residuals from arcsine transformed data. The results of this analysis are presented in Table 4, with species ranked by the Student's *t*-value. Of the 24 species from Mkuzi, two were distributed in significantly higher light levels than average, and six in significantly lower light levels than average ($P < 0.05$). Of the 25 species tested from Phinda six were in significantly higher light conditions than average, and seven in significantly lower light conditions than average. Thus the null hypothesis was rejected for eight species from Mkuzi and thirteen from Phinda, or 33.3 % and 52 % of the species respectively. In multiple comparisons of this kind we would expect 1.2 and 1.25 rejections respectively as a result of type 1 error at the five percent level of probability.

Table 4. Mean residuals of canopy openness of tree species from short (Mkuzi) and tall (Phinda) Sand Forest sites. Residuals are the difference between percentage openness above individual trees and the average openness for all individuals of the same height. Positive residuals are distributed in lighter conditions than average, negative residuals are in shadier conditions than average. Species with at least 8 individuals were included. Species are ranked according to Student's *t* comparing species' residuals to those of all sampled trees (arcsine transformed data); ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$. Species in bold font occur in both data sets.

Mkuzi species	Mean residual	N	t	Phinda species	Mean residual	N	t
<i>Pteleopsis myrtifolia</i>	16.1	278	-8.00***	<i>Pteleopsis myrtifolia</i>	29.5	220	-18.11***
<i>Croton gratissimus</i>	10.0	90	-2.57**	<i>Combretum mkuzense</i>	17.2	90	-6.59***
<i>Combretum mkuzense</i>	4.3	238	-1.35	<i>Psydrax fragrantissima</i>	5.9	148	-4.30***
<i>Ocotea arborea</i>	13.7	10	-1.28	<i>Hymenocardia ulmoides</i>	3.8	272	-3.54***
<i>Psydrax fragrantissima</i>	5.9	25	-1.12	<i>Grewia microthyrsa</i>	7.2	72	-3.05**
<i>Cleistanthus schlechteri</i>	-0.6	316	0.12	<i>Ptaeroxylon obliquum</i>	17.6	18	-2.71**
<i>Hymenocardia ulmoides</i>	0.2	325	0.18	<i>Monodora junodii</i>	4.1	32	-0.82
<i>Grewia microthyrsa</i>	-3.3	54	0.23	<i>Ocotea arborea</i>	1.4	30	-0.76
<i>Newtonia hildebrandtii</i>	-3.4	41	0.35	<i>Dialium schlechteri</i>	2.3	37	-0.73
<i>Craibia zimmermannii</i>	-0.5	135	0.40	<i>Newtonia hildebrandtii</i>	1.0	57	-0.66
<i>Vitex ferruginea</i>	-4.4	28	0.41	<i>Vitex ferruginea</i>	0.8	39	-0.48
<i>Wrightia natalensis</i>	-1.7	31	0.41	<i>Suregada zanzibariensis</i>	-4.2	20	0.81
<i>Balanites maughanii</i>	-4.7	14	0.55	<i>Dovyalis zeyheri</i>	-3.5	8	0.81
<i>Canthium setiflorum</i>	-8.1	33	0.65	<i>Lagynias lasiantha</i>	-7.8	8	0.83
<i>Haplocoelum gallense</i>	-5.4	9	0.67	<i>Balanites maughanii</i>	-4.6	13	0.96
<i>Monodora junodii</i>	-8.1	53	0.80	<i>Tricalysia lanceolata</i>	-3.3	102	1.08
<i>Boscia albitrunca</i>	-15.9	10	1.49	<i>Hyperacanthus amoensis</i>	-3.9	93	1.11
<i>Commiphora neglecta</i>	-13.0	18	1.83	<i>Cleistanthus schlechteri</i>	-2.4	304	1.65
<i>Brachylaena huillensis</i>	-4.6	391	2.42*	<i>Strychnos decussata</i>	-9.4	27	2.11*
<i>Gardenia cornuta</i>	-11.8	56	2.69**	<i>Haplocoelum gallense</i>	-10.5	25	2.55*
<i>Strychnos decussata</i>	-21.7	15	2.91**	<i>Wrightia natalensis</i>	-6.9	97	2.93**
<i>Hyperacanthus microphyllus</i>	-33.7	9	3.45***	<i>Strychnos henningsii</i>	-8.5	80	3.19**
<i>Rhus gweinzii</i>	-23.3	26	4.29***	<i>Drypetes arguta</i>	-5.3	287	3.37***
<i>Strychnos henningsii</i>	-30.2	33	5.86***	<i>Toddaliopsis bremekampii</i>	-3.9	409	3.50***
				<i>Cola greenwayi</i>	-6.5	762	9.38***

Species' residuals not significantly different from those of all individuals sampled have been interpreted to mean that those species are distributed at random with regard to light environments (Lieberman *et al.* 1989; Lieberman *et al.* 1995). In the forests sampled for this study this is not the case. No species appeared to occupy the full range of available light environments indiscriminately (Fig. 4), and species with their distribution in light environments not significantly different from average did not occupy a wider range of light environments than other species; at both sites the variances of these species' residuals were not significantly larger than the variances of species occurring in significantly more open or shady conditions than average (one-tailed *t*-test for unpaired samples, Mkuzi: $P = 0.14$; d.f. = 22, Phinda: $P = 0.16$; d.f. = 23).

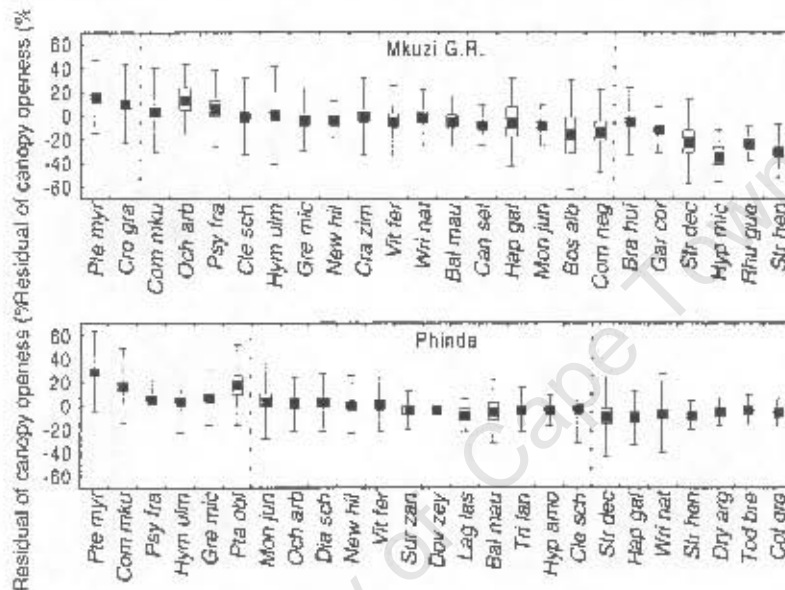


Figure 4. Mean residuals of percentage canopy closure of tree species from short (Mkuzi) and tall (Phinda) Sand Forest sites. Error columns are SE, error bars are SD. Species are ranked according to Student's *t* comparing species' residuals to those of all sampled trees (arcsine transformed data). Species to the left and right of the dashed line are distributed in significantly lighter, and significantly shadier conditions, respectively than average ($P < 0.05$).

Since comparison of species' residuals with the residuals of all individuals cannot discriminate between species which are really distributed randomly with regard to light environments from those species which occupy a narrow and specific range of light environments close to the average of all individuals sampled, I compared the residuals of each species to the residuals of every other species. A one-way analysis of variance (ANOVA) of species' residuals revealed that at both sites, residuals varied highly significantly between species (Mkuzi, $P = 4 \times 10^{-27}$; Phinda, $P = 0$; see Table 4 for replication), confirming that the distributions of individual tree species with regard to canopy openness do differ from one another. *Post hoc* comparison of species with an LSD test, equivalent to multiple pair-wise comparisons with the *t*-test for independent samples (StatSoft 1996), provided a better idea of the degree of niche separation between species (Tables 5 and 6).

Table 5. *P* values from multiple pair-wise comparisons of species' residuals of canopy openness from Mkuzi. Residuals are the degree of canopy openness above trees corrected for the effect of height. All significant ($P < 0.05$) interactions are included.

Species	Pm	Cg	Cm	Oa	Pf	Cs	Hu	Gm	Nh	Cz	Vl	Wn	Bm	Ca	Hg	Mj	Ba	Cn	Bh	Gc	Sd	Hm	Rg	Sh
<i>Pteleopsis mytilifolia</i>			.000			.000	.000	.000	.001	.000	.002	.002	.014	.001	.025	.000	.002	.000	.000	.000	.000	.000	.000	.000
<i>Croton griffithii</i>						.014	.013			.018				.047		.021	.020	.004	.000	.000	.000	.000	.000	.000
<i>Combretum mkuzense</i>	.000																	.025	.005	.002	.001	.000	.000	.000
<i>Ochna arborea</i>																	.042	.027		.021	.003	.000	.001	.000
<i>Psychotria fragrantissima</i>																		.027		.012	.002	.000	.000	.000
<i>Cleistanthus schlechteri</i>	.000	.014																		.011	.003	.000	.000	.000
<i>Hymenocardia ulmoides</i>	.000	.013																		.012	.004	.000	.000	.000
<i>Grewia microthyrsa</i>	.000																				.010	.001	.000	.000
<i>Newtonia hildebrandtii</i>	.001																				.017	.002	.001	.000
<i>Cratogeomys zimmermannii</i>	.000	.018																			.034	.006	.001	.000
<i>Vitex ferruginea</i>	.002																				.029	.004	.004	.000
<i>Wrightia natalensis</i>	.002																				.025	.003	.003	.000
<i>Balanites naughanii</i>	.014																					.015	.030	.004
<i>Canthium setiferum</i>	.001	.047																				.033	.004	.004
<i>Haplocosmium gailense</i>	.026																						.042	.029
<i>Monodora junodii</i>	.000	.021																				.023	.003	.002
<i>Boscia albitrunca</i>	.002	.020	.042																					
<i>Commiphora neglecta</i>	.000	.004	.025	.027	.027																			.037
<i>Brachylaena huillensis</i>	.000	.000	.005																				.014	.002
<i>Gardenia comuta</i>	.000	.000	.002	.021	.012	.011	.012			.034													.023	.036
<i>Strychnos decussata</i>	.000	.000	.001	.003	.002	.003	.004	.010	.017	.006	.029	.025		.033	.023			.014						
<i>Hyperacanthus microphyllus</i>	.000	.000	.000	.000	.000	.000	.000	.001	.002	.001	.004	.003	.015	.004	.042	.003		.002	.023					
<i>Rhus greslinii</i>	.000	.000	.000	.001	.000	.000	.000	.000	.001	.000	.004	.003	.030	.004		.002		.000	.036					
<i>Strychnos henningsii</i>	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.004	.000	.026	.000		.037	.000	.002				

Each species differed significantly from at least 13.0 % of species tested at Mkuzi and 16.7 % at Phinda. Many species which were not significantly different from the mean of all individuals sampled differed significantly from species with both higher and lower residuals of canopy openness. One example of a species with a non-random distribution centred near the average of all species sampled is *Cleistanthus schlechteri*, the canopy dominant at both sites. It appears that no species occupied all available conditions of canopy openness indiscriminately, although there is considerable overlap between species. Again, one would expect false rejections of the null hypothesis as a result of type I error in multiple comparisons like this. At Mkuzi 105 (i.e. 38.0 %) of 276 possible comparisons of 24 species were significant, of which 5.25 were likely to be spurious rejections of the null hypothesis. At Phinda 139 (i.e. 46.3 %) of 300 possible combinations of 25 species were significant, of which 6.95 were likely to be spurious.

Table 6. *P* values from multiple pair-wise comparisons of species' residuals of canopy openness from Phinda. Residuals are the degree of canopy openness above trees corrected for the effect of height. All significant ($P < 0.05$) interactions are included.

Species	Pm	Cri	Pl	Hu	Gm	Fu	Mj	Da	Ds	Nh	Vf	Sz	Dz	Li	Bm	Ti	Ha	Cr	Sa	Hg	Wv	Sh	Ca	Tb	Cg
<i>Pteleopsis myrtifolia</i>		.000	.000	.000	.000	.003	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
<i>Combretum mkuzense</i>	.000		.004	.005	.015		.002	.003	.001	.000	.000	.000	.003	.003	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
<i>Psychotria fragrantissima</i>	.000	.004										.012	.048	.046	.016	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
<i>Hymenocardia ulmoides</i>	.000	.000														.001	.002	.000	.000	.000	.000	.000	.000	.000	.000
<i>Grewia microthyrsa</i>	.000	.015										.017		.050	.022	.021	.001	.000	.000	.000	.000	.000	.000	.000	.000
<i>Phaenoxylon obliquum</i>	.003								.043	.023	.027	.055	.015	.014	.005	.001	.001	.001	.000	.000	.000	.000	.000	.000	.000
<i>Monodora junodii</i>	.000	.002																	.018	.006	.014	.006	.035		.003
<i>Ocotea arborea</i>	.000	.003																	.021	.007	.018	.010	.048		.003
<i>Dialium schlechteri</i>	.000	.001				.043													.020	.007	.014	.007	.040		.002
<i>Newtonia hildebrandii</i>	.000	.000				.023													.018	.005	.009	.004	.025	.037	.003
<i>Vitex ferruginea</i>	.000	.000				.027													.031	.011	.025	.013			.004
<i>Suregada ruziziensis</i>	.000	.000	.012		.017	.005																			
<i>Davallia zeyheri</i>	.000	.003	.046		.015																				
<i>Lagynis lasiantha</i>	.000	.003	.046		.050	.014																			
<i>Balanites mughamii</i>	.000	.000	.016		.020	.005																			
<i>Tincazia lanceolata</i>	.000	.000	.000	.001	.001	.001														.044					.011
<i>Hyperacanthus amoenus</i>	.000	.000	.000	.002	.001	.001														.050					.018
<i>Cleistanthus schlechteri</i>	.000	.000	.000	.000	.000	.001														.026		.023			.000
<i>Strychnos decussata</i>	.000	.000	.000	.000	.000	.000	.018	.021	.020	.016	.031														
<i>Haplocaelum gillense</i>	.000	.000	.000	.000	.000	.000	.008	.007	.007	.005	.011				.041	.050	.028								
<i>Wrightia natalensis</i>	.000	.000	.000	.000	.000	.000	.014	.018	.014	.005	.025														
<i>Strychnos henningsii</i>	.000	.000	.000	.000	.000	.000	.008	.010	.007	.004	.013						.023								
<i>Drypetes arguta</i>	.000	.000	.000	.000	.000	.000	.009	.046	.040	.025															.017
<i>Toddalopsis bremekampii</i>	.000	.000	.000	.000	.000	.000				.037															.002
<i>Cola greenwayi</i>	.000	.000	.000	.000	.000	.000	.002	.003	.002	.000	.004				.011	.018	.000						.017	.002	

Ranking and comparing average residuals of canopy openness of species is a useful technique, but represents a gross oversimplification of species' actual strategies. Not only do species occur below a particular range of canopy openness, but their relative distribution with regard to canopy openness may change as they grow taller (Figures 5 & 6), so rank may change with height. In the short forests at Mkuzi (Figure 5), the light demanding species *Pteleopsis myrtifolia*, *Croton gratissimus* and *Combretum mkuzense* occurred in higher light conditions than average at all heights, and were distributed in conditions of full sunlight (close to 100 % canopy openness) at lower heights than other species. *Hymenocardia ulmoides* occupied higher than average light conditions while shorter than four metres in height, but lower than average conditions from four metres to its maximum height of about eight metres. *H. ulmoides* appeared to be capable of recruiting in extremely open conditions relative to other species, and to be tolerant of higher levels of shading than other species when adult. *Craibia zimmermannii* and *Brachylaena hillebrandii* had a contrasting strategy, occurring in lower than average light environments while small, yet higher than average light environments near full adult size. The canopy dominant species at Mkuzi, *Cleistanthus schlechteri*, appeared to be capable of recruiting and

growing in relatively shaded light environments when small, approaching average conditions at four metres in height and above. A broader range of strategies occurred in the taller forests at Phinda (Figure 6). As at Mkuzi, the most light demanding species, *P. myrtifolia* and *C. mkuzense*, occurred in higher than average light environments at nearly all heights. *Psydrax fragrantissima*, the only species of those examined here that recruits largely vegetatively by means of root suckers, had a highly variable distribution. *Hymenocardia ulmoides*, although in a lower range of light environments than at Mkuzi, is moderately light demanding at Phinda, occurring in slightly higher than average light environments until it tends to be overtopped close to its maximum size. Both *Tricalysia lanceolata* and *Hyperacanthus amoenus* are small trees which occurred in slightly higher than average light environments when shorter than three metres. However, both species occupied a similar range of absolute light environments at all heights, with the result that individuals taller than three metres tended to be in lower than average light environments. *Cleistanthus schlechteri*, also the canopy dominant at Phinda, occurred in lower than average light environments below eight metres in height, but close to average light environments above that height. *Wrightia natalensis* occurs in shadier conditions than average at most heights. *Toddaliopsis bremekampii*, *Drypetes arguta* and *Cola greenwayi* represent classic shade tolerant understorey species, and only occur in taller Sand Forests. All three species occupied shadier than average conditions at all heights, with larger individuals tending to occur in similar absolute light environments (>90 % cover) to small individuals.

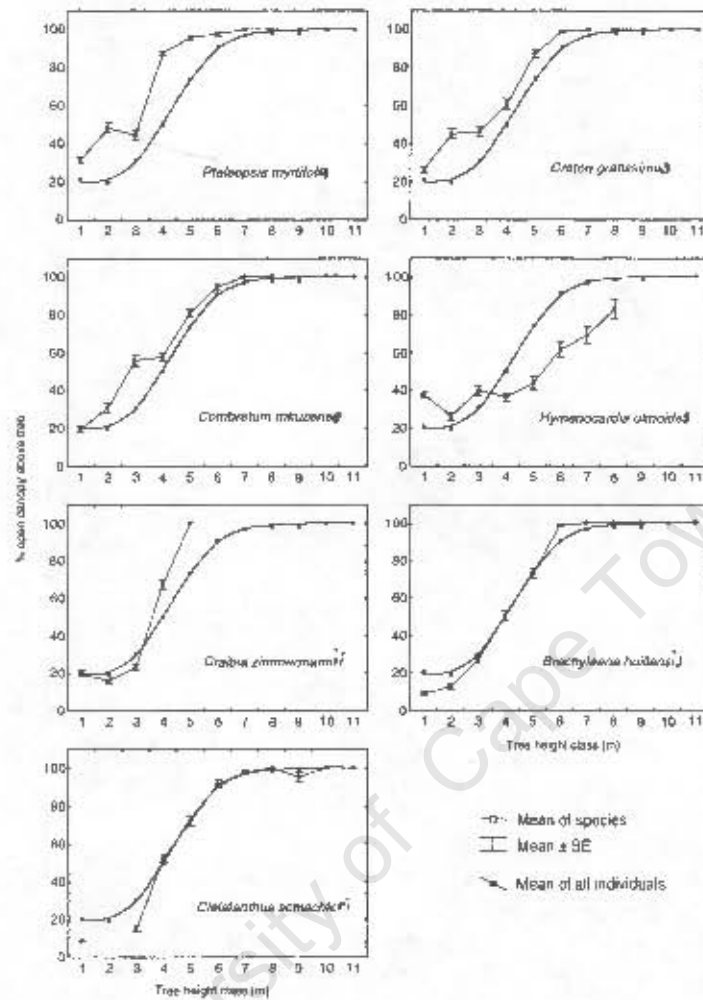


Figure 5. Relationship between height and average canopy openness for the most common species at Mkuzi. The open circles connected by a dotted line represent the mean canopy openness in each height class for one species. Only height classes with at least five measurements were included. Error bars are standard error. The solid squares fitted with a smooth curve represent the mean canopy openness of all individuals sampled.

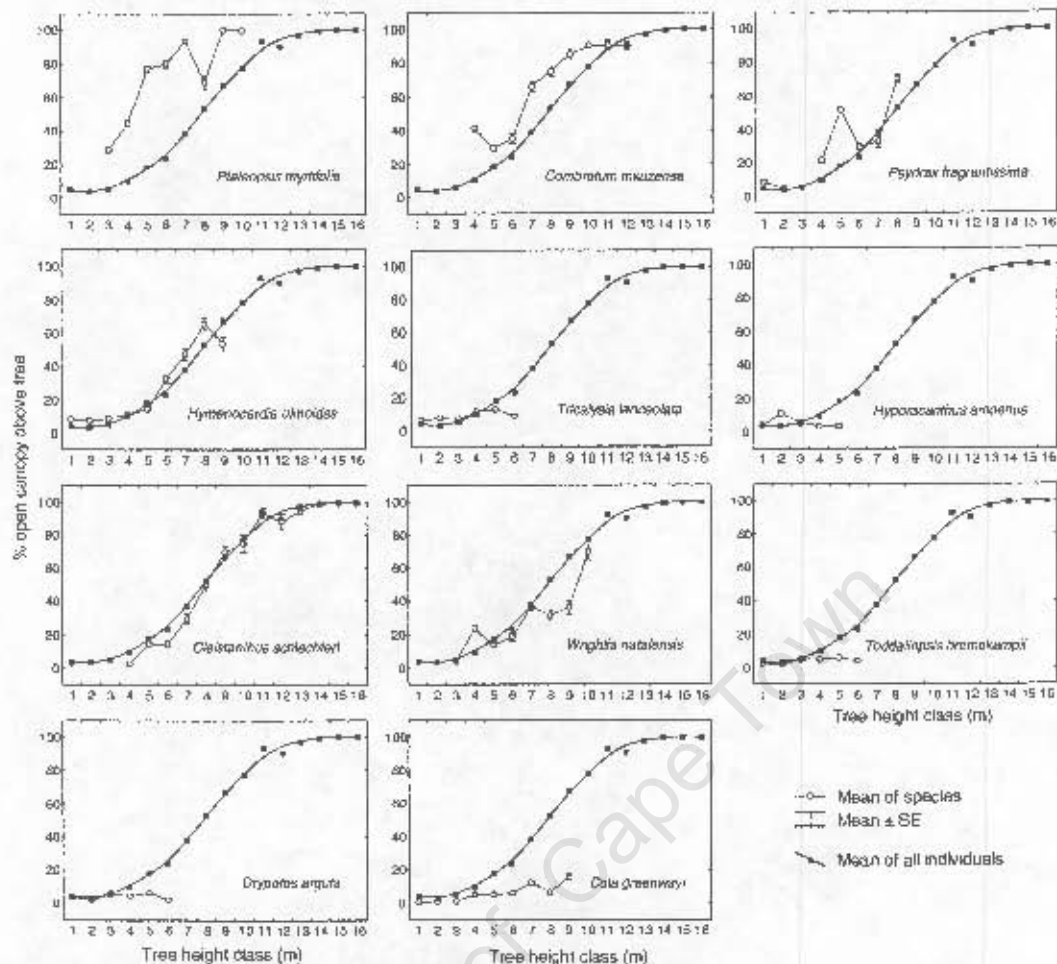


Figure 6. Relationship between height and average canopy openness for the most common species at Phinda. The open circles connected by a dotted line represent the mean canopy openness in each height class for one species. Only height classes with at least five measurements were included. Error bars are standard error. The solid squares fitted with a smooth curve represent the mean canopy openness of all individuals sampled.

Discussion

As Sand Forest is extremely dry, with a strongly seasonal rainfall pattern, the canopy is short and relatively open. Average canopy heights of approximately 7 to 11 m (with few emergents taller than 18 m, see chapter 2) place these dry forests amongst the shortest world-wide (see e.g. Murphy & Lugo 1986; Menaut *et al.* 1995; Murphy & Lugo 1995; Rundel & Boonpragob 1995; Sampaio 1995). Nonetheless, the distributions of sand forest species respond strongly to varying degrees of canopy openness.

In moist tropical, temperate and boreal forests, germination, growth and survival tend to be highest below gaps in the canopy (see e.g. Canham 1989; Poulson & Platt 1989; Spies & Franklin 1989; Denslow & Hartshorn 1994). In Sand Forest, the density of small seedlings (<15 cm) in gaps was either the same, or in the drier forests at Mkuzi, far lower than in adjacent shaded areas (Table 2). On the dry, water-repellent sands of these forests, high insolation can result in increased rates of mortality and

decreased growth in this size class (see Chapter 5). Similar observations have been made in dry forests elsewhere, with higher seedling survival in more shady environments during dry periods (Gerhardt 1996), and higher densities of seedlings away from gaps (Lieberman & Li 1992). Densities of larger Sand Forest seedlings (15–60 cm) were the same in gaps and non-gaps at Mkuzi, but more dense in gaps at Phinda (Table 2), a pattern typical of moister forests. Sand Forest seedlings are unusually deep rooted and once established may not be as susceptible to increased mortality due to higher insolation (pers. obs.). Saplings (0.6–2 m) were more dense in gaps, while small trees (>2 m, but shorter than the canopy) were more dense in shaded subcanopy areas. Apart from seedlings, which are highly susceptible to drought-induced mortality, patterns of regeneration in gaps appear to resemble those observed in most forests, albeit at low stem densities. Although certain species were distributed preferentially in canopy gaps, no species was completely dependant on gap-phase regeneration. There are a large number of gaps without any obvious cause of gap creation (see Chapter 2), particularly at Mkuzi. Since there appears to be no edaphic cause for gaps in the forest canopy, and decomposition rates of dead trees are slow as a result of the dry climate and extremely resistant wood of most species, it seems likely that gap turnover rates are extremely slow.

Relatively large canopy gaps and completely shaded areas are only two extremes of the continuum of canopy openness. Most canopy gaps are much smaller than one metre in diameter, and most gap area is made up of gaps less than four metres in diameter. Even in short Sand Forest, canopy density and height vary greatly. The centres of distribution of Sand Forest tree species were arranged along the wide range of available light environments at both short (ave. 7 m) and taller (ave. 11 m) forest sites. No species appeared to be distributed at random with regard to canopy openness. Even those species that did not differ significantly from the average canopy openness of all individuals did not occupy all available light environments indiscriminately. Relative changes in light environment with height varied widely between species, indicating further specialisation. Although there is no evidence of a clear distinction between shade-intolerant pioneer species and shade-tolerant climax species (as defined by Whitmore 1989), my results indicate that the dynamics of these dry forests are strongly influenced by canopy openness. We can expect that regeneration and forest composition would be affected by changes in disturbance regimes and canopy openness. This is not simply a theoretical consideration. Elephant populations at both Phinda and Mkuzi are likely to increase following recent re-introductions into both reserves, and data from Tembe Elephant Park indicate that these large herbivores have a dramatic impact on Sand Forest structure (W. Matthews, pers. comm.). The opening up of the forest canopy that is likely to result could cause a long-term increase in the proportions of short, multistemmed species such as *Pteleopsis myrtifolia*, *Hymenocardia ulmoides*, *Croton gratissimus* and *Combretum mkuzense* that seem to be competitively superior in more open environments.

Although tree species were distributed in different degrees of canopy openness, the range of light environments occupied by most species was relatively wide. Even *Pteleopsis myrtifolia*, which was consistently distributed in the most open environments, was capable of regeneration and growth in the most shaded environments recorded. Similarly, all size classes of the most shade-tolerant species in the taller forests at Phinda, *Cola greenwayi*, did occur in gaps. However, the truly shade tolerant

species, *Drypetes arguta*, *Toddaliopsis bremekampii* and *C. greenwayi*, occur only at the taller sites like Phinda. Multivariate analysis confirms that while gap and non-gap floristic composition does differ, there is substantial overlap (Fig. 1). While niche partitioning of light environments in Sand Forest may contribute to species coexistence, particularly in light of the individualistic responses of species throughout their life span, the degree of overlap indicates that chance events play an important role. Uneven dispersal (see e.g. Reader *et al.* 1995) may help to prevent competitive exclusion. In order to demonstrate coexistence solely through niche partitioning, it would be necessary to show not only that tree species perform differently along the gradient of canopy openness, but that the niches are narrow and exclusive (Lieberman *et al.* 1995; Brokaw & Busing 2000). This is clearly not the case in Sand Forest, although it also does not seem that these forests could be considered assemblages of diffusely co-evolved, generalist species (Hubbell & Foster 1986). As seems to be the case in most forests, tree communities are determined by both niche and chance (Brokaw & Busing 2000).

Given the inherent mistrust of most scientists of subjective visual estimates, it is important that the light environments in which plants are distributed be measured using more objective and accurate methods. These measurements need to be compared to the actual light environments of the forest as a whole, rather than just the average light environments of all individuals sampled. Estimation of light environments using hemispherical canopy photographs has major advantages; both quantity and type (direct or diffuse) of light over any period chosen can be estimated from algorithms utilising superimposed solar tracks and average weather conditions at any location (Horn 1971; Chazdon & Field 1987). With conventional cameras and film, such surveys have been expensive, impractical and time-consuming. The advent of cheap digital cameras (with 180° fisheye lens attachments) and powerful portable computers able to store and process these images in the field with easily available software (see e.g. Barrie *et al.* 1990) should make the collection of such data relatively easy. Despite this, I know of no study that has used hemispherical canopy photographs to measure the average light environments at all heights on whole forest scales and the individual light environments of large numbers of trees. Getting a camera into the canopy is less of a problem in short forests. Rigorous measurement of light environments should give a better estimate of species absolute distributions and niche partitioning, and allow comparison of species' actual light environments under different circumstances (see e.g. Veblen 1989).

Conclusion

Until very recently, light or canopy openness was assumed to have little effect on dry forest dynamics. Although classic gap-phase regeneration seems to be relatively unimportant and niche differentiation does not appear to be solely responsible for Sand Forest species coexistence, varying degrees of canopy openness influence the density and distribution of all species differently. Thus any change in forest structure is likely to influence species composition in the long term. This evidence of the importance of light environments in Sand Forest supports the small body of recent evidence that light is an important determinant in the dynamics of even relatively short and open dry forest systems.

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The effect of naturally water-repellent soil on the germination, survival and growth of two Sand Forest canopy tree species

Abstract

Sand Forest is a South African dry subtropical forest type with a notable lack of natural regeneration of canopy tree species. The existence of severe and highly persistent water-repellency in Sand Forest soils is described. Variable degrees of water-repellency also occur below individual and clumped savanna trees. Two Sand Forest canopy species, *Wrightia natalensis* and *Newtonia hildebrandtii* were used to evaluate the effects of water-repellent soil and differing light environments on seedling germination, survival and growth in a greenhouse experiment. Under experimental conditions of moderate drought stress, survival of both species was substantially reduced on water-repellent forest sands compared to the same sands treated with a wetting-agent to eliminate repellency. Both reduced germination and increased seedling mortality on water-repellent forest soil contributed to reduced survival. Growth appeared to be unaffected by water-repellency. *W. natalensis* did however have lower growth on savanna soils with low organic matter content. Seedling survival of both species, and growth of *N. hildebrandtii* was also lower in full sun compared to a shaded treatment equivalent to 30% of ambient PAR. Lower survival in high light was largely a result of increased mortality, with little difference in germination. Increased survival in shade is consistent with observations that densities of Sand Forest tree seedlings are higher in shaded environments than in canopy gaps. It seems likely that low germination and increased mortality as a result of soil water-repellency could contribute substantially to the low number of established seedlings and saplings in Sand Forests.

Keywords: allelopathy, forest dynamics, germination, hydrophobic soils, light environments, non-wetting soils, seedling growth, seedling survival, shading

Introduction

The occurrence of water-repellent soils has been widely reported: in economically important systems such as catchments, plantations, lawns and agricultural systems; as well as in a variety of natural systems ranging from open grassland to closed forests (Osborne *et al.* 1967; DeBano 1981; King 1981; Giovannini & Lucchesi 1984; Wallis & Horne 1992; Dekker & Ritsema 1994; Scott 1994). In southern Africa, although the phenomenon is not well known, water-repellency has been observed below thicket and scrub vegetation on coastal dunes (Tinley 1985), on the sandy Cape Flats of the Fynbos Biome (Scott 1994, pers. obs.), in a range of indigenous forests, timber plantations and particularly Eucalyptus plantations (Scott 1994). It appears that water-repellent soils are actually widespread, and far more common than is generally realised (Giovannini & Lucchesi 1984; Wallis & Horne 1992; Ritsema *et al.*

1997; Bauters *et al.* 1998). Worldwide, water-repellency appears not to have been observed in dry forests, although it seems likely to occur in these habitats.

Water-repellency in soil is caused by the presence of hydrophobic plant and fungal derived organic and humic compounds, usually adhering to or coating mineral soil surfaces (DeBano 1981; Wallis & Horne 1992). The non-polar organic substances responsible for the effect are complex and variable, and are seldom identified, although they may be characterised by method of extraction (DeBano 1981; Giovannini & Lucchesi 1984; Wallis & Horne 1992). The hydrophobic properties that prevent or slow water infiltration into water-repellent soils are generally most pronounced in dry, or near-dry soils, and are reduced or eliminated as water contents approach field capacity (DeBano 1981; King 1981; Ritsema *et al.* 1997; de Jonge *et al.* 1999). Repellency can result from the long term breakdown of plant litter, and has been particularly associated with the presence of fungal mycelia (DeBano 1981; King 1981; Bauters *et al.* 1998). Heating of soil can increase water-repellency (DeBano 1981; de Jonge *et al.* 1999), but very high temperatures, generally more than 288° C, destroy the substances responsible for water-repellency (DeBano 1981). Thus fires may cause or intensify water-repellency in soil by heating organic particles sufficiently to coat and chemically bond with mineral soil particles or, if hot enough, reduce repellency by destroying these substances. In addition, the steep temperature gradients in the upper soil profile may redistribute hydrophobic organic compounds, which are volatilised at or near the soil surface by fire and distributed down though the soil where they condense on cooler mineral soil particles (DeBano 1981). Although water-repellency affects many soil types (DeBano 1981; Dekker & Ritsema 1994; de Jonge *et al.* 1999), sandy soils are more likely to be severely affected. Coarse textured soil, with relatively low specific surface area, is easily coated if hydrophobic substances are present (DeBano 1981; Scott 1994). Ultimately, the presence of particular plants or vegetation types, and history are largely responsible for the development of water-repellency in susceptible soils (DeBano 1981; King 1981; Wallis & Horne 1992; Dekker & Ritsema 1994; Scott 1994; de Jonge *et al.* 1999).

It is accepted that water-repellency can significantly affect seed germination, plant survival and growth (King 1981; Wallis & Horne 1992; Bauters *et al.* 1998), although there are very few explicit tests of this assumption. Osborne *et al.* (1967) and Wallis *et al.* (1990) showed that naturally occurring water-repellent soils reduced germination and establishment of a variety of grass species. Wallis and Horne (1992) cites two instances of delayed and reduced germination resulting in reduced crop yields. Water-repellent soils strongly resist surface water infiltration, and can be air dry a few millimetres below the surface even after heavy rain (DeBano 1981, pers. obs.). This results in increased run-off and uneven distribution of water. Water movement through the soil is also limited, and water-repellency has been associated with preferential flow, where water penetrates repellent sandy soils in a fingered pattern, instead of the more usual uniform wetting front (Ritsema & Dekker 1994). This effect is likely to be more pronounced in heterogeneous forest soil, where root channels, hollows, animal burrows and points of lower repellence would provide favoured pathways for the movement of water (Ritsema & Dekker 1994). Preferential flow can leave a water-repellent layer relatively dry, with water penetrating in places to allow wetting of deeper soils (Ritsema & Dekker 1994). While this could actually make

more water available to deep rooted trees and shrubs, seedlings and shallow rooted plants are likely to suffer from reduced germination, increased mortality and reduced growth, at least until water-repellency is completely overcome by thorough wetting of the soil. These effects are likely to be particularly important in dry forests, where forest dynamics are controlled primarily by water (Murphy & Lugo 1986), and seedling mortality varies largely in response to seasonal rainfall periods (Lieberman & Li 1992; Gerhardt 1993; Gerhardt 1996).

In forests, varying light environments are likely to interact with the effects of water-repellent soil. Unlike the situation in moist tropical, temperate and boreal forests, where germination, growth and survival are generally highest in gaps (see e.g. Canham 1989; Poulson & Platt 1989; Spies & Franklin 1989; Denslow & Hartshorn 1994), many dry forest species may have higher growth and survival in lower light environments during dry periods (e.g. Gerhardt 1996), resulting in seedlings being concentrated away from gaps (Lieberman & Li 1992). Although species responses to light are known to vary widely (Denslow & Hartshorn 1994), there may be a general shift toward regeneration and growth in lower light environments in dry systems, particularly those where water-repellency occurs, extending (King 1981) and intensifying dry periods experienced by plants with root systems near the soil surface.

Sand Forest is a dry subtropical forest type on the South African Maputaland coastal plain, with low and strongly seasonal rainfall (see Chapter 1). Most Sand Forest occurs as small irregular patches and strips in a matrix of open savanna, all growing on inland sands of Quaternary origin (Goodman 1990). Although the sands are of identical origin, savanna soils with a medium cover of bunch grasses are completely freely wetting, whereas adjacent forest soils, with a higher organic content, are severely water-repellent. A distinct lack of regeneration by canopy trees is apparent throughout the range, particularly inside reserves, and seedlings of most tree species are distributed in sites of intermediate to low canopy closure, with very little regeneration in gaps (Chapter 4). Since the vast majority of Sand Forest canopy species regenerate primarily by means of seed, rather than ramets, suckers or sprouts, processes that affect seedling germination, survival and growth are vital determinants of forest dynamics (Chapter 2).

This paper describes the occurrence of water-repellent soil in unburnt and burnt Sand Forest and other nearby vegetation, measured using a modified water drop penetration time test (WDPT, DeBano 1981). I used a glasshouse based experimental study to investigate whether germination, survival and growth of two sand forest species (1) would be reduced by water-repellency in Sand Forest soils, (2) would differ between forest soils and adjacent savanna soils, and (3) would differ at two different light levels (full ambient light, and 70% shade). The two species used for this study were *Wrightia natalensis*, a small-seeded, deciduous, fast growing tree and *Newtonia hildebrandtii*, an evergreen, larger seeded tree with extremely slow growth.

Methods

Measurement of water-repellency in Sand Forest soils

Water penetration into the soil surface was studied in the field at Mkuzi Game Reserve and Tembe Elephant Park, with three transects across unburnt forest margins at each site, and 5 transects across burnt forest margins at Tembe. Transects were randomly located in areas where the Sand Forest boundary was clearly defined and adjacent to open savanna, with little tree cover and soils of the same origin. Along each transect, penetration time was measured at 20 m and 2 m beyond the forest margin in the savanna, and 2 m and 10 m inside the forest margin, below established canopy trees. In addition, water penetration was assessed in a variety of potential regeneration environments outside the forest, ranging from soil below isolated dwarf trees to closed canopy woodland. A standard quantity (15 ml) of rainwater was poured onto undisturbed, bare, level soil. This method results in similar penetration times to the water droplet (King 1981) or water drop penetration time (WDPT, DeBano 1981) test, and effectively measures the persistence of water-repellency (King 1981; Carrillo *et al.* 1999). Below the forest canopy it was usually necessary to carefully clear coarse litter from the soil surface. The time taken for all water to be completely absorbed by the soil was recorded with the aid of a stopwatch. Timing was stopped at 10 minutes where penetration had not yet occurred. This simple method was considered adequate to demonstrate the large huge disparity in soil water-repellency across the forest margin. All water penetration measurements were conducted during the dry season of 1998, during the first week of June. The fire that swept through areas of savanna and forest at Tembe occurred 3 years previously, during September 1995. The molarity of an ethanol droplet (MED test) required for an aqueous solution to penetrate soil in less than 5 seconds was determined using a range of ethanol solutions in 0.2 M steps for three soil samples from Mkuzi. This test is suitable for determining initial water-repellence of soils with a high degree of repellency, and allows comparison with other studies (King 1981; Wallis *et al.* 1990). Soil samples were taken from the top 15 cm of soil, excluding as much litter as possible, from 10 m within the forest. These were brought back to Cape Town and air-dried for one month before testing at a room temperature of 25° C.

Effect of water-repellent soil on seedling germination, survival and growth

Seeds of Sand Forest canopy trees were planted in pots in a greenhouse in a factorial experiment with seed germination, seedling survival and vertical growth as response variables. Three replicate pots per factor combination were used to evaluate the effect of :

1. soil treatment: water-repellent sand from below the forest canopy; the same forest soil with the addition of a wetting agent to eliminate water-repellency; easily wetting soil from adjacent open savanna; savanna soil with wetting agent
2. site: soils collected from Tembe Elephant Park vs. Mkuzi Game Reserve
3. light: full sun vs. 70% shade
4. Species: *N. hildebrandtii* vs. *W. natalensis*

One forest soil replicate (forest soil, Tembe, shade, both species) was eliminated at the start of the experiment as it was easily wettable. Factor effects on seedling height were tested using individual seedlings as replicates, rather than pots (see results for actual number of replicates).

Soil sample replicates were collected from randomly located transects across the Sand Forest margin where there was adjacent open savanna on soils of the same origin. Samples were taken from 10 m inside and outside the forest margin to a depth of 150 mm. Course litter was cleared from the soil surface and no attempt was made to preserve the intact profile. In Cape Town soils were transferred to 125 mm deep, 150 mm diameter plastic pots. A circle of 1 mm plastic mesh was placed in the bottom of the pots, and covered with a 10 mm layer of course, washed river sand in order to prevent the fine-textured sands from running through drainage holes and to ensure thorough drainage. The pots were filled with collected soils to within 10 mm of the brim. In the treatments with wetting agent, water-repellency in forest soils was completely overcome by treating the soil in each pot with 180 ml of 0.25 % solution of a blended non-ionic soil wetting agent (Aqua-GRO[®], produced in South Africa by Fleuron Universal Selected Services, P.O. Box 31245, Braamfontein 2017, distributed by EFEKTO). This treatment remained effective for the entire duration of the experiment, with water penetrating the soil surface evenly and generally soaking into the soil completely in less than 5 seconds. No change in water penetration times on treated savanna soils was apparent.

Half the pots were situated in an unshaded area of the greenhouse while the other half were situated in an adjacent area shaded by overhanging vegetation, resulting in a 70% reduction in light (unshaded vs. shaded: $p < 0.04 \times 10^{-17}$). Average PAR ($\pm$ SE) measured above the unshaded replicates was $1\,581 \pm 51 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($n = 20$). PAR immediately above the shaded replicates was $474 \pm 43 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($n = 20$). PAR outside the greenhouse at the time was $2\,232 \pm 2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($n = 10$). All measurements were taken at midday on a cloudless Summer day (30 November 1999) using a Skye Instruments Ltd. SKP200 light meter coupled to the 'PAR Quantum' sensor. Position of treatments was reordered in each row, so that no treatment could receive a consistently different amount of light than any other.

Four seeds of *W. natalensis*, and five seeds of *N. hildebrandtii* were planted in each pot. *Wrightia* seed was collected from Ndumu Game Reserve, while *Newtonia* seed was collected from Phinda Resource Reserve. Previous trials with plump, healthy seed of both species had resulted in 100% germination. *Wrightia* seeds are small, wind dispersed parachutes (average weight $\pm$ SD: 0.022 ± 0.003 g; $n = 20$) and were buried at 5 mm depth. *Newtonia* are relatively larger and flattened (average weight $\pm$ SD: 0.081 ± 0.013 g; $n = 20$) and were buried to a depth of approximately 10 mm, leaving some of the seed protruding.

The experiment was started on the 18th January 1999 with an initial watering of 360 ml, sufficient to completely saturate wettable soils. Throughout the experiment only de-ionised water was used. After initial watering, the Summer watering regime consisted of 90 ml per pot every 2 days for the first 8 weeks, then 90 ml every 2–4 days, whenever more than 20% of either species seedlings showed signs of drought stress. This was always seedlings of *N. hildebrandtii*, which exhibit folded pinnae when

drought stressed. During the cooler Winter period (1/5/1999 to 30/8/1999), watering was reduced to imitate the natural cycle of Winter drought. During this period 50% of seedlings were allowed to show signs of water stress, and in practice the watering period was increased to 90 ml per pot every 7 – 12 days. *W. natalensis* responded by shedding all leaves near the start of this period. From the start of September (1/9/1999), the Summer watering regime was resumed until the experiment was terminated on 18/10/1999, 36 weeks later. My intention was to initiate germination, then maintain seedlings in a reasonably water stressed state, so that the effects of naturally dry conditions on germination, growth and mortality in all treatments could be examined. Given that temperature and humidity in the Cape Town greenhouse were not controlled, and that soil drainage was artificial, so that conditions may have differed from those encountered by the plants in their natural habitat, no attempt was made to closely mimic rainfall patterns and quantities in the field. For comparison, 90 ml per pot every 2 days and every 7 days would closely approximate the quantity of rainfall in Summer (October – March) and Winter (April – September) respectively at Mkuzi Game Reserve (KwaZulu Natal Conservation Services rainfall records).

Throughout the experiment weeds were continuously removed with scissors to minimise soil disturbance.

Survival refers to the number of living seedlings in each pot after 36 weeks, germination is the number of germinated seeds in each pot. Because of the small seed size of *W. natalensis*, it was impossible to distinguish seedlings which had germinated and died from those that had not germinated. Thus measurement and analysis of germination and mortality for the initial 36 week period were confined to *N. hildebrandtii*, where the persistent dried radicle made it easy to determine which seeds had germinated. Mortality of *N. hildebrandtii* is the number of dead individuals as a proportion of germinated seedlings at the end of the 36 week study period. Mortality of both species after an additional 6 weeks of severe drought stress is the number of dead individuals as a proportion of the number of living seedlings at the start.

All except two *N. hildebrandtii* seedlings and one *W. natalensis* seedling germinated within the first two weeks. Thus height measurements after 36 weeks are considered to be growth over the entire period.

Analysis and Data Presentation

All statistical analyses were one- or multi-factor analysis of variance (anova) using the computer program Statistica (StatSoft 1996). Where necessary data were transformed to meet the assumptions of normality and homoscedasticity: penetration times in the field were log transformed ($X' = \log(X + 1)$) to eliminate heteroscedasticity; number of surviving seedlings were square root transformed ($X' = \sqrt{X + 3/8}$) where variances were proportional to the means; all mortality data are proportions and were arcsine transformed ($P' = \arcsin \sqrt{P}$) to normalise the underlying distribution (Zar 1996). All other data were untransformed for analysis. Differences between individual factor groups were analysed by LSD test for post hoc planned comparisons.

Due to loss of replicates as a result of mortality before the 6 week period of severe water stress, the effect of the four soil treatments on mortality could not be included in the ANOVA design. Similarly, the effects of site on seedling height after 36 weeks could not be analysed.

All survival and mortality data are graphically presented as percentages for ease of comparison.

Results

Water-repellency in Sand Forest soils

Differences in penetration times across forest margins at both Mkuzi Game Reserve and Tembe Elephant Park (Figure 1) were highly significant (Table 1), and this effect was modified by fire at Tembe Elephant Park.

Table 1. *F* -values and *P* - levels from an analysis of variance of the effects of position on a 20 m transect across forest margin and burning on the time required for 15 ml water to be absorbed by soil (seconds, log transformed data) at Mkuzi Game Reserve and Tembe Elephant Park.

Source of variation	Mkuzi G. R.		Tembe E. P.	
	<i>F</i>	<i>P</i> - level	<i>F</i>	<i>P</i> - level
<u>Main effects</u>				
Position on transect (10 m out, 2 m out, 2 m in, 10 m in)	137.4	0.0000**	125.4	0.0000**
Burning treatment (burnt, unburnt)	—	—	25.7	0.0000**
<u>2-way interactions</u>				
position on transect x burning	—	—	10.7	0.0001**

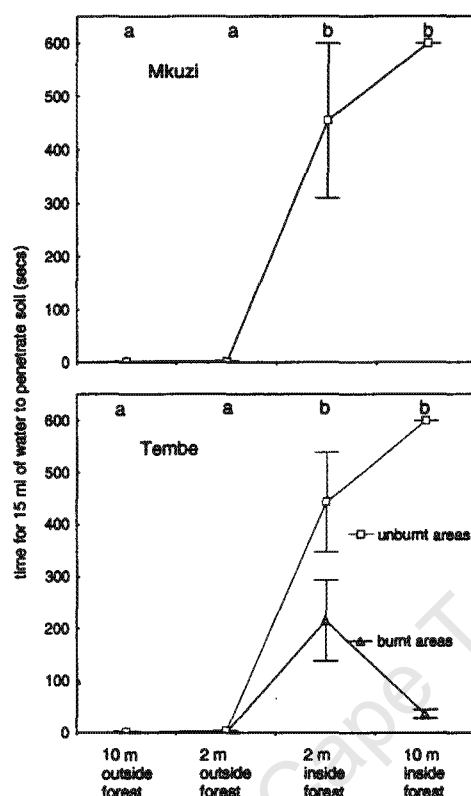


Figure 1. Time required for 15 ml water to be absorbed by soils on a 20 m transect across the forest margin at Mkuzi Game Reserve (above) and Tembe Elephant Park (below). Data from Tembe include a burnt treatment. Different lowercase letters indicate highly significant ($P = 0.0000$) differences between samples (LSD test, log transformed data). $n = 3$ for all unburnt sites, and $n = 5$ for burnt sites.

Savanna soils 2 m and 10 m beyond the forest margin were not at all water-repellent, with penetration times of less than 6 seconds. Inside the forest margin at unburnt sites, water-repellency was pronounced, although more variable at 2 m inside. At 10 m inside the margin at all unburnt sites, no penetration of water had occurred after 600 seconds. Water penetration time in forest soils 3 years after fire at Tembe was greatly reduced compared to unburnt soils, and this effect varied along the transect across the forest margin (interaction, Table 1). Reduction in water-repellency was more pronounced at 10 m than at 2 m inside the forest margin (Figure 1). Water penetration times outside the margin in burnt savanna were not different to those in unburnt savanna at Tembe.

A two-way anova of penetration times on unburnt sites at both localities revealed no significant difference ($F_{1,16} = 0.29$, $P = 0.60$) between mean penetration times at Tembe Elephant Park and Mkuzi Game Reserve.

Tests on 3 air-dry soil samples from 10 m inside the Mkuzi forests indicate that the effect is extremely persistent, with penetration times exceeding 1 hour, measured at 25° C. The average molarity of ethanol solutions ($\pm$ SD) required to give a penetration time of less than 5 seconds was 2.9 ± 0.1 M ($n = 3$), equivalent to a 17.1 ± 0.7 % v/v solution.

Survival

The effects of both soil treatment and light on seedling survival after 36 weeks were highly significant (Table 2), while there was no significant difference in survival on soils from the two different localities or between *W. natalensis* and *N. hildebrandtii*.

Table 2. *F* - values and *P* - levels from an analysis of variance of the effects soil treatment, light treatment, site and species on seedling survival (seedlings/pot, square root transformed). No interactions were significant (*P* > 0.05, all *p* were in fact > 0.18).

Source of variation	<i>F</i>	<i>P</i> - level
Main effects		
Soil treatment (in, out, in + wet, out + wet)	6.7	0.00052**
Light (unshaded vs. shaded)	8.6	0.0046**
Locality (Mkuzi C.R. vs. Tembe E.P.)	1.0	0.33
Species: <i>Wrightia</i> vs. <i>Newtonia</i>	0.3	0.59

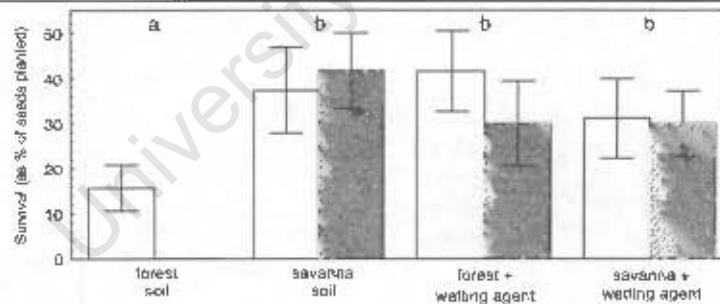


Figure 2. Seedling survival after 36 weeks for *W. natalensis* (□) and *N. hildebrandtii* (▨) on different soil treatments. Survival is expressed as an average percentage ($\pm$ SE) of the number of seeds planted. Seedlings were grown on 4 soil treatments: forest soil — soil taken from below established forest canopy ($n = 11$ for each sp.); savanna soil — soil from nearby open savanna area ($n = 12$ for each sp.); forest + wetting agent — forest soil with the addition of a wetting agent to eliminate hydrophoby ($n=12$ for each sp.); savanna + wetting agent — savanna soil with wetting agent ($n=12$ for each sp.). Different lowercase letters indicate highly significant ($p < 0.005$) differences between soil types, with data from both species analysed together (seedlings/pot, square root transformed).

The number of living seedlings on the water-repellent forest soil after 36 weeks was significantly lower than on any of the other soil treatments (Figure 2). Of the *N. hildebrandtii* seedlings, 0% were alive on water-repellent forest sands, compared to between 30% and 42% on the freely wetting forest and savanna soil treatments. Although *W. natalensis* had approximately 16% survival on water-repellent forest soils, this was significantly lower than survival on the easily wetting treatments. Different light treatments also had a large effect on survival (Figure 3). Seedling survival was highly significantly reduced in full sun compared to the shaded treatment, and the effect did not vary across soil treatments. Although survival of *W. natalensis* was slightly higher than that of *N. hildebrandtii* in most factor treatments, this difference was not significant.

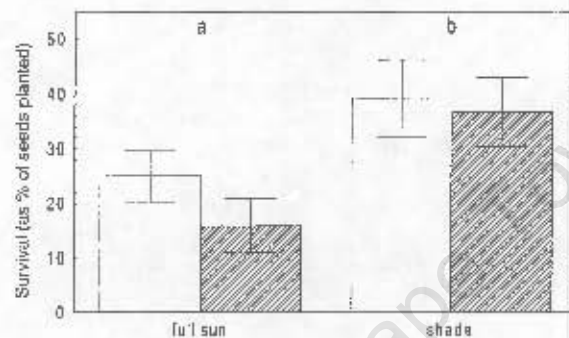


Figure 3. Seedling survival after 36 weeks for *W. natalensis* (□) and *N. hildebrandtii* (▨) subjected to two different light treatments. Survival is expressed as an average percentage ($\pm$ SE) of the number of seeds planted. The light treatments are: full sun — pots in open greenhouse exposed to full ambient sunlight ($n = 24$); shade — pots in shaded area exposed to approximately 30% of ambient PAR ($n = 23$). Different lowercase letters indicate highly significant ($P < 0.005$) differences between light treatments, with data from both species analysed together (seedlings/pot, square root transformed).

Germination and Mortality

Survival, the number of living seedlings, results from two processes: seed germination and seedling mortality. Both germination and mortality in *N. hildebrandtii* were highly significantly affected by soil treatment (Table 3). Light had no effect on germination, but did have a significant effect on seedling mortality. The locality from which the soil was collected had no effect on either germination or mortality. There was no significant interaction between factors for germination or mortality.

Table 3. *F* - values and *P* - levels from an analysis of variance of the effects of soil treatment, light treatment and site on *N. hildebrandtii* seed germination (no. seeds/pot, untransformed) and seedling mortality (proportion of germinated seedlings/pot, arcsine transformed) after a period of 36 weeks. No interactions were significant ($P > 0.05$).

Source of variation	Germination		Mortality	
	<i>F</i>	<i>P</i> - level	<i>F</i>	<i>P</i> - level
<u>Main effects</u>				
Soil treatment (in, out, in + wet, out + wet)	4.5	0.0096 ^{***}	6.5	0.0017 ^{***}
Light (unshaded vs. shaded)	0.41	0.52	6.7	0.015 ^{**}
Locality (Mkuzi G.R. vs. Tembe E.P.)	2.8	0.11	0.40	0.53

Reduced germination and increased mortality both contribute to low seedling survival on water-repellent forest soils (Figure 4).

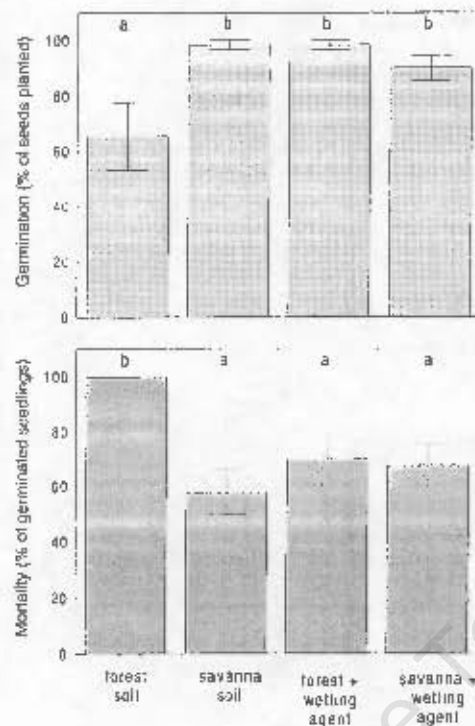


Figure 4. Germination (above) and mortality (below) of *N. hildebrandtii* on four different soil treatments. Germination is expressed as an average percentage ($\pm$ SE) of the number of seeds planted. Mortality is expressed as an average percentage ($\pm$ SE) of germinated seedlings. Soil treatments are: forest soil — soil taken from below established forest canopy ($n = 11$ for each sp.); savanna soil — soil from nearby open savanna area ($n = 12$ for each sp.); forest + wetting agent — forest soil with the addition of a wetting agent to eliminate water-repellency ($n=12$ for each sp.); savanna + wetting agent — savanna soil with wetting agent ($n=12$ for each sp.). Different lowercase letters indicate significant ($p < 0.05$) differences between soil types.

Although germination was slightly higher in the shade compared to the full sun treatment (Figure 5), this effect is not significant (Table 3). Mortality is significantly higher in full sun compared to treatments receiving approximately 30% of ambient PAR.

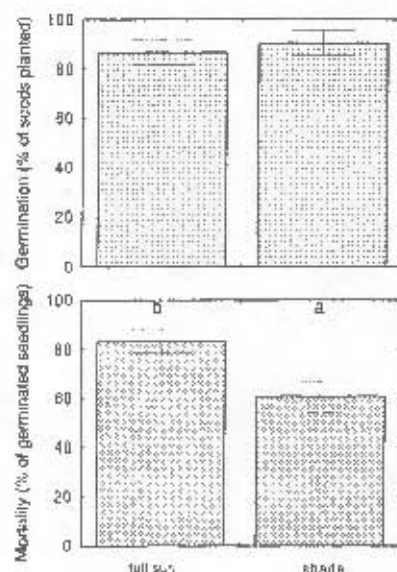


Figure 5. Germination (above) and mortality (below) of *N. hildebrandtii* subjected to two different light treatments. Germination is expressed as an average percentage ($\pm$ SE) of seeds planted. Mortality is expressed as an average percentage ($\pm$ SE) of germinated seedlings. The light treatments are: full sun — pots in open greenhouse exposed to full ambient sunlight ($n = 24$); shade — pots in shaded area exposed to approximately 30% of ambient PAR ($n = 23$). Different lowercase letters indicate significant ($p < 0.05$) differences between light treatments.

Seedling growth

Seedling heights were measured after 36 weeks of growth. The response of seedling height to both soil and light treatments showed significant interactions with species ($P = 0.0065$ and $P = 0.023$ respectively, log transformed data), indicating that *N. hildebrandtii* and *W. natalensis* responded differently to these factors. Each species' response was therefore analysed separately. Loss of replication as a result of mortality precluded the testing of soil locality effect in either anova design. Heights of *W. natalensis* varied significantly on different soil treatments (Table 4), with significantly taller seedlings on wetting and non-wetting forest soil compared to savanna soils (Figure 6).

Table 4. *F* - values and *P* - levels from analysis of variance of the effects of soil treatment and light on seedling heights (mm, untransformed data) of *N. hildebrandtii* and *W. natalensis* after 36 weeks. No interactions were significant ($P > 0.05$).

Source of variation	<i>N. hildebrandtii</i>		<i>W. natalensis</i>	
	<i>F</i>	<i>P</i> - level	<i>F</i>	<i>P</i> - level
Main effects				
Soil treatment (in, out, in + wet, out + wet)	0.72	0.55	8.1	0.00016
Light (unshaded vs. shaded)	10.2	0.0022	0.24	0.63

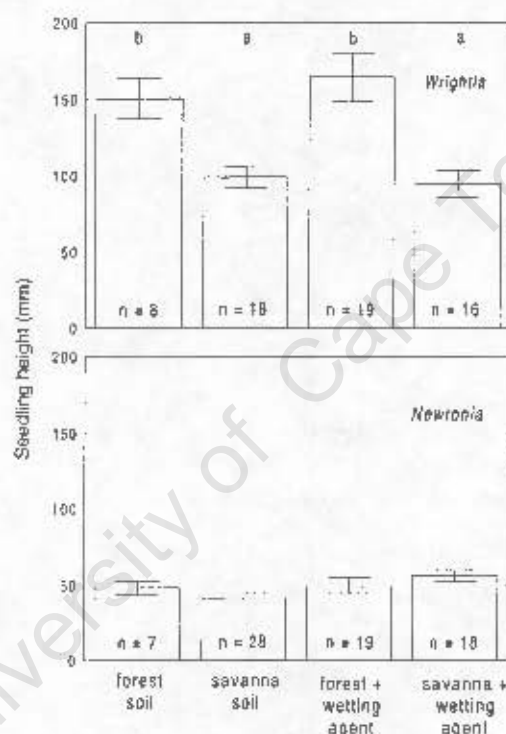


Figure 6. Heights of *N. hildebrandtii* (top) and *W. natalensis* (bottom) seedlings after 36 weeks on four different soil treatments. Soil treatments are: forest soil — soil taken from below established forest canopy; savanna soil — soil from nearby open savanna area; forest + wetting agent — forest soil with the addition of a wetting agent to eliminate water-repellency; savanna + wetting agent — savanna soil with wetting agent. Different lowercase letters indicate significant ($P < 0.05$) differences between soil types. Error bars are standard error.

W. natalensis seedlings on savanna soils were stunted and chlorotic in appearance, while those on both forest soil treatments looked healthy and normal, and were 65.8 % taller. In contrast, *N. hildebrandtii*

heights did not vary significantly in response to soil treatment (Table 4), and little difference between plants on forest and savanna soils was apparent (3.4 %, Figure 6).

Conversely, there was almost no difference ($< 1\%$) between *W. natalensis* seedling heights in full sun and shade (n.s., Table 4), while *N. hildebrandtii* seedlings were significantly taller (42 %) in shaded treatments (Figure 7).

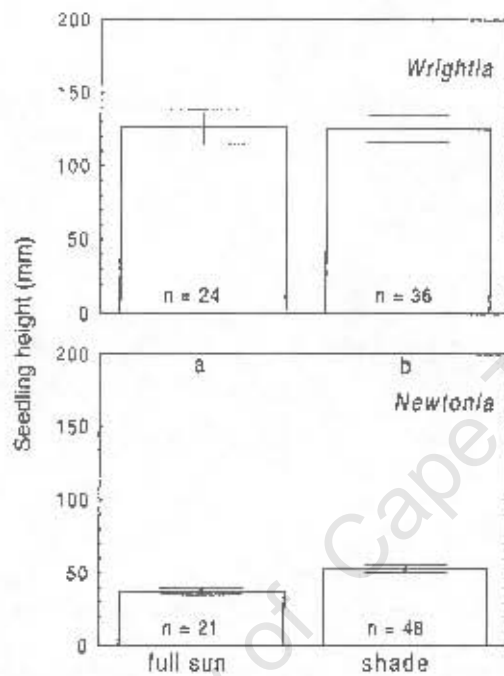


Figure 7. Heights of *N. hildebrandtii* (top) and *W. natalensis* (bottom) seedlings after 36 weeks below two different light treatments. The light treatments are: full sun — pots in open greenhouse exposed to full ambient sunlight; shade — pots in shaded area exposed to approximately 30% of ambient PAR. Different lowercase letters indicate significant ($p < 0.05$) differences between light treatments.

Discussion

Water-repellent soils in Sand Forest and surrounding vegetation

Although water-repellent soils appear to be widespread world-wide, there seem to have been no published observations of water-repellence in dry forests. Sand Forest soils exhibit severe and extremely persistent water-repellency. At 10 m inside the forest margin, water penetration times consistently exceeded an arbitrary measurement period of 600 seconds in the dry season, compared to penetration times of a few seconds or less in adjacent savanna sands. On air-dry soil from the Mkuzi forests tested in the laboratory, penetration times varied between approximately 80 minutes and 170

minutes. Ethanol solutions of 2.8 M to 3.0 M were required to reduce penetration times below 5 seconds on the same soils, equivalent to a 96° to 97° solid/water contact angle, and indicative of severe repellency (King 1981). The field penetration tests indicate that water-repellency in these dry forests is widespread, occurring in two separate areas representing different Sand Forest subtypes, Mkuzi Game Reserve (Western Sand Forest), and Tembe Elephant Park (Eastern Sand Forest). Sand Forests at Mkuzi Game Reserve grow on the oldest palaeo-dunes on the Maputaland Plain, with deep orange and red sands, while the Tembe site has some of the youngest dunes supporting Sand Forest on orange to pale yellow and grey sands (see Chapters 1 & 2). Similar levels of water-repellency occur in other Sand Forests in the region (pers. obs.).

A wildfire at Tembe Elephant Park substantially reduced water penetration times on burnt forest soils, but had no effect on freely wetting savanna soils. Fires that burn into these forest patches are extremely unusual, and although the high temperatures involved have reduced water-repellency at the soil surface, hydrophobic substances may have been transported down the soil profile and severe repellency could persist or even be intensified in deeper soil layers. It is noteworthy that three years after the Tembe fire, there was virtually no recruitment by tree seedlings into burnt forest patches (see Chapter 2). This may be the result of lack of seed, lack of shade, competition with weedy grasses, or the persistence or even increase of water-repellence in deeper soil layers. However, it seems unlikely that fire is a mechanism for forest regeneration through reduction in cover and soil water-repellence, or that fire plays any role in the development of severe water-repellency in forest soils.

Effect of water-repellent soils on survival, germination, mortality and growth

The striking lack of seedlings and saplings of canopy trees in Sand Forest is noticeable throughout the range, but is hard to account for. During the wet Summer growth season, numbers of small seedlings can be high, but these do not survive (see Chapter 2). There is a complete spectrum of regeneration environments available, from closed canopy forest to a range of gap sizes. Even large scale openings caused by fire result in negligible regeneration. While heavy browsing pressure by antelope in conserved areas are likely to reduce densities of larger seedlings and saplings (see Chapter 2), the experimental evidence presented here indicates that severely water-repellent soils play an important role in reducing seed germination and increasing seedling mortality, thus reducing overall survival. After nearly 9 months of growth under conditions of moderate water stress, survival of both *W. natalensis* and *N. hildebrandtii* was substantially lower on water-repellent forest soil than on the same soil treated with a wetting agent to eliminate water-repellency. Survival of *W. natalensis* was reduced by approximately 60 %, while no seedlings of *N. hildebrandtii* survived on the water-repellent soil, although differences between the two species were not significant. The reduction in survival in *N. hildebrandtii* resulted from both low germination and increased mortality on water-repellent forest soil.

I expected that seedling growth would also be reduced by lower water availability in water-repellent soils. In the field, this would decrease the likelihood of seedlings becoming established during favourable periods, and lengthen the time period that small plants are exposed to herbivores. I found no evidence of this however. Although vertical heights of both study species were slightly lower on non-

wetting forest soils than on forest soil treated to eliminate water-repellency, differences were not significant. *W. natalensis* seedlings growing on savanna sand with low organic matter were substantially shorter than those on non-wetting and wetting forest soils with higher organic matter content and appeared chlorotic and nutrient deficient. The heights of *N. hildebrandtii* seedlings, with much lower growth rates, were very similar on all four soil treatments, with growth apparently unaffected by soil organic content or wettability. This species (Family: Mimosaceae) is a nitrogen fixer, and thus may not respond to differences in nitrogen levels.

Effect of soil origin

Experimental soils were taken from both Mkuzi and Tembe in order to evaluate differences due to soil origin. There was no difference in survival, germination or mortality on experimental soils from either site, nor interaction with any other treatment factors. It seems that the effect of water-repellency in Sand Forest soils is similar within these two forests representing the major Sand Forest subtypes (chapter 2).

Evidence for allelopathic effects

Matthew *et al.* (2001) and van Wyk & Smith (2001) have suggested that allelopathy in Sand Forest species may affect plant germination, survival and growth in Sand Forest soils, and is likely to play a role in the formation of the distinctive rings of bare sand on the margin of Sand Forest patches in the Tembe region and southern Mozambique. Matthews (pers. comm.) has even suggested that allelopathy may affect Sand Forest tree regeneration, contributing to the conspicuously low densities of seedlings and saplings observed in conserved Sand Forests (see Chapter 3). If allelopathy were widespread in these forests, germination, survival and growth would be reduced on both forest soil treatments compared to savanna soils. I find no evidence of this. Germination, mortality and overall survival of both study species is not significantly different on the savanna soils compared to the forest soil treated with wetting agent, and growth of *W. natalensis* is actually higher on forest soils.

Effect of wetting agent

Although soil wetting agents are potentially phytotoxic and can reduce germination and seedling growth, this may be reduced when these substances are adsorbed to soil (Osborne *et al.* 1967; Miyamoto & Bird 1978). Throughout this experiment, there were no significant differences in germination, survival or growth between the easily wettable savanna sands and the same soil treated with a non-ionic wetting agent. Thus any effect, apart from a reduction in the non-wetting properties of water-repellent soils, can be ignored.

Effect of shading on survival, germination, mortality and growth

The widely varying light levels in moist forests are known to result in differential growth, survival and thus distribution of many species. In contrast, dry forests are assumed to be too short and simple in structure for light to be an important determinant of ecosystem processes (Oliveira-Filho *et al.* 1998),

and the importance of canopy gaps in the internal dynamics of dry forests is unknown (Mooney *et al.* 1995).

The two Sand Forest tree species studied in this experiment both responded to different light levels. Seedling survival of both *W. natalensis* and *N. hildebrandtii* was substantially higher in shade (approx. 30% of ambient PAR) compared to full sun after 36 weeks of growth under conditions of moderate drought stress. Low survival of *N. hildebrandtii* in full sun was almost entirely a result of high mortality, rather than any differential germination, indicating that plant stress due to increased heat loading and evapotranspiration, rather than direct water loss from the soil surface is probably largely responsible for the effect. The response to light treatment did not vary significantly across soil treatments, possibly as a result of the very low number of seedlings surviving on water-repellent forest soils.

Different light levels also affected the growth of *N. hildebrandtii*. Seedlings grown in shade were taller than those in full sun, although there was no similar effect for *W. natalensis*.

Although both species would be expected to be fairly shade intolerant from their leaf characteristics (Midgley *et al.* 1995), the results presented here suggest that in the relatively dry Sand Forest environment, moderate shading could reduce mortality and increase growth in small seedlings compared to completely open environments.

Conclusion

Within the forest itself, it seems likely that regeneration of all but the most drought-tolerant seedlings would be severely reduced by the water-repellent properties of Sand Forest soils. The few seedlings that do manage to germinate and survive in these soils are likely to be vulnerable to any factors that further increase stress, such as excessive browsing. Lower survival in high light environments under conditions of moderate to severe drought, may also explain the observed absence of regeneration in canopy gaps (Chapter 4). With a naturally low annual rainfall and a lengthy seasonal dry period, the decrease in available water near the soil surface caused by water-repellency appears to be a major contributing factor to the extremely low levels of regeneration observed in Sand Forest.

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Plate 1. Browsing by Nyala, *Tragelaphus angasii*, and its impact on Sand Forest. Clockwise from top left. (1), (2) & (3): Nyala browse on foliage from ground level to a height of approximately 1.5 m. Note the 'topiary' effect on the shrub in the middle image caused by repeated browsing. (4): Clear browse line on a low branch of the extremely palatable *Newtonia hildebrandtii*. (5): Where browsing pressure is extremely high, as in this site at False Bay Park, both the ground and understorey layers are dramatically affected and no regeneration by canopy trees is possible. (6) In the absence of browsing, understorey vegetation is typically more dense than is usually observed in any conserved area with high densities of ungulate browsers. This photograph was taken in a protected area with low antelope densities, immediately adjacent to False Bay Park, and not more than 1 km from the site pictured in image (5).

University of Cape Town

The impact of browsing by antelope on tree species recruitment in Sand Forest

When I asked if I should be sure to see some, they replied, “ The imbala-intendi (the local name in this part of Amatongaland for the inyala) is very cunning; he lives in the very densest jungle, and never comes into the open except at night; he is very cunning; he is a witch is the imbala-intendi.”

from: F.C. Selous (1908) ‘African Nature Notes and Reminiscences’
quoted by Anderson (1978)

Abstract

Nyala *Tragelaphus angasii* are the largest and most common antelope in Sand Forest, but impala *Aepyceros melampus* subsp. *melampus*, red duiker *Cephalophus natalensis* and suni *Neotragus moschatus* may also be important browsers. I found that in two conserved areas where these animals are common, saplings (0.5 to 2 m height) of the Sand Forest canopy dominant tree species, *Cleistanthus schlechteri* and *Newtonia hildebrandtii*, were absent or scarce (densities lower than 0.07 per 100 m²). In contrast sapling densities in a defaunated but otherwise undisturbed Sand Forest site were significantly higher (approx. 2 saplings per 100 m², $p < 0.0001$ for both species). Seedlings of both species were present in conserved areas indicating that differences in sapling densities are not a result of processes prior to seedling establishment. In two conserved areas, recruitment of woody species was strongly negatively correlated with a species-specific index of browsing pressure, with the lowest proportions of juveniles in populations of the most palatable species, such as the canopy dominant *C. schlechteri* (Phinda: $R^2 = 0.44$, $p = 0.005$; Mkuzi: $R^2 = 0.62$, $p = 0.002$). After six months uncaged planted two year old seedlings of two common Sand Forest tree species in a conserved forest had grown significantly less than caged seedlings ($p = 0.0018$). No differences in mortality were detected over this time period. I argue that the evidence presented in this paper/chapter indicates that current levels of browsing pressure in Sand Forest will cause undesirable long-term changes in forest species composition and structure and recommend localised reduction of antelope populations in currently conserved areas.

Keywords: browsing, herbivory, recruitment, seedling growth, seedling mortality

Introduction

The importance of ungulate browsers in dry tropical and subtropical forests has received little attention (Dirzo & Domínguez 1995). However, browser biomass in dry tropical forests can exceed 2000 kg km⁻² (Karanth & Sunquist 1992), substantially higher than average values of 300 kg km⁻² in lowland rain forest (Coley & Barone 1996). Even when total leaf damage caused by ground-living browsers is only a fraction of the damage caused by folivorous insects and arboreal vertebrates (Janzen 1981; Coley & Barone 1996), browsing can affect recruitment, changing forest structure and composition over time (Coley & Barone 1996). Reduction in seedling growth and survival caused by terrestrial mammalian herbivores has been observed in a few African tropical dry forests (Tsingalia 1989; Swaine *et al.* 1990), but appears not to have been noted in dry forests elsewhere (e.g. Gerhardt 1993; Dirzo & Domínguez 1995; Gerhardt 1996).

Many tree species in conserved old-growth Sand Forest, including the canopy dominants, *Cleistanthus schlechteri* and *Newtonia hildebrandtii*, have size-class distributions that suggest that recruitment is greatly reduced by ungulate browsing (see chapter 3). Trees shorter than two metres are vulnerable to browsing, and precisely these size classes are underrepresented or absent from tree populations. The great majority of dominant Sand Forest tree species recruit entirely from seed, and often the presence of seedlings indicates that neither seed supply nor establishment is limiting. Similarly all species appear to be capable of continuous regeneration and growth in the range of environments available, from closed understorey to small canopy gaps created by tree death. Other circumstantial evidence, from the visible pruning of palatable species, to the presence of a distinct browse line at 1.6 m, indicates that ungulate browsing may be responsible for the low recruitment of many species (pers. obs.).

In temperate coniferous and broad-leaved forests, primarily in Europe and North America, the effects of ungulate herbivory have been well documented. Much of this research reveals the potentially negative effects resulting from high ungulate densities. Intensive browsing by various species of deer has been shown to suppress the regeneration of palatable tree species (Shimoda *et al.* 1994; Putman 1996; Van Hees *et al.* 1996; Cornett *et al.* 2000; Zamora *et al.* 2001; Kuiters & Slim 2002; but see Mladenoff & Stearns 1993) and reduce seedling diversity (Liang & Seagle 2002). Long-term effects can include undesirable changes to forest structure and composition (Anderson & Katz 1993), such as reduction in abundance or loss of tree species (Ammer 1996; González Hernández & Javier Silva-Pando 1996), loss of species from the ground-layer (Rooney & Dress 1997), and reduced songbird abundance and diversity (deCalesta 1994). However, ungulate browsing is a natural feature of many forests, and moderate browsing may also act to increase diversity by reducing competitive dominance, or opening up the forest understorey (Putman 1996).

In this chapter I investigate how browsing impacts recruitment dynamics in Sand Forest, and whether this could have an effect on forest composition, structure and function. Specifically I test the following predictions: (1) that browsing by ungulates is primarily responsible for the very low levels of

recruitment observed in the two most dominant Sand Forest tree species in conserved areas; (2) that the proportion of juveniles in tree species' populations is negatively correlated with browsing pressure on those species; and (3) that levels of browsing experienced by unprotected palatable seedlings in a conserved forest would increase mortality and reduce vertical growth compared to seedlings protected from browsing.

Ungulate browsers in Sand Forest

All four antelope occurring in conserved Sand Forests in northern KwaZulu rely on browse for a portion of their diet (Table 1.). Nyala are the largest and most common of these, and likely to have the greatest impact on Sand Forest. Forests form an essential component of their stable home ranges (Anderson 1978) and, except when fresh grass is available after rain, browse in the form of leaves and twigs forms the bulk of their diet (Anderson 1978; Skinner & Smithers 1990). Even when nyala graze in grasslands or open woodlands (Anderson 1978), they shelter and browse in Sand Forest during the day (pers. obs.). Male nyala can reach vegetation as high as two metres above the ground by standing on their hind legs, but most browsing seems to be concentrated from ground level to 1.5 m (pers. obs.). Impala are smaller and favour more open environments than nyala (Skinner & Smithers 1990), but do shelter and feed in Sand Forest (pers. obs.). Browse in the form of leaves and fine twigs can form up to 49 % of their diet and like nyala, browse is a more important component of their diet during in the dry season (Skinner & Smithers 1990).

Browsing by smaller antelope may also affect forest seedling and sapling growth and survival (e.g. Tsingalia 1989). The diminutive red duiker and suni are both associated predominantly with closed canopy environments (Skinner & Smithers 1990), and spoor, dung middens and sightings can be relatively common in conserved Sand Forest (pers. obs.). Red duiker eat leaves and fine stems in addition to fruit and flowers (Skinner & Smithers 1990). Although the tiny suni antelope feed predominantly on fallen leaves, they will eat growing shoot tips (Lawson 1986) and could therefore impact seedling growth and survival.

Table 1. Summary of mean mass and diet of common antelope in Sand Forest (from Skinner & Smithers 1990).

Nyala, <i>Tragelaphus angasii</i> , males 108 kg, females 62 kg, predominantly browsers, fresh grass when available
Impala, <i>Aepyceros melampus</i> subsp. <i>melampus</i> , males 55 kg, females 41 kg, mixed grazers and browsers
Red duiker, <i>Cephalophus natalensis</i> , males 11.7 kg, females 11.9 kg, selective browsers
Suni, <i>Neotragus moschatus</i> , males 5.1 kg, females 5.5 kg, highly selective feeders, fallen leaves, flowers, fruit, growing shoot tips

Although adult Hook-lipped Rhinoceros *Diceros bicornis* weigh 800 to 1100 kg and subsist almost entirely on browse (Skinner & Smithers 1990), I have seldom seen their distinctive spoor inside Sand Forest except on well-defined trails traversing forest patches. This implies that although they favour dense thickets associated with Sand Forest patches, they seldom feed in true forest.

Table 2. Nyala and impala densities at Mkuzi Game Reserve, 1996 and 1997. Surveys did not differentiate between Sand Forest and the *Acacia burkei-Terminalia sericia* open woodland on Pleistocene sands (2 273 ha.). Data for all other vegetation types in the reserve are pooled; these include various types of mixed savanna, thicket, riparian forest and woodland, and dry mountain bushveld (26 306 ha.). The controlled hunting area of the reserve was omitted. Estimates are based on counts and distance from permanent line transects (KwaZulu Nature Conservation Service data).

Sample unit	Nyala density (animals ha ⁻¹)		Impala density (animals ha ⁻¹)	
	1996	1997	1996	1997
Sand forest/savanna matrix	0.21	0.18	0.32	0.27
Other (pooled)	0.10	0.11	0.20	0.21
Other (range)	0.06 — 0.16	0.04 — 0.15	0.13 — 0.27	0.18 — 0.23

The only census data for nyala and impala from reserves with Sand Forest at the time of this study was from Mkuzi Game Reserve. For 1996 and 1997 these data indicate that densities of both antelope are higher on the Pleistocene sands that support a matrix of Sand Forest and savanna than on any other habitat in the reserve (Table 2). If sex ratios are 1:1, an average density of 0.2 animals per hectare implies that nyala biomass alone amounts to 1700 kg km⁻² in and around Sand Forest, and is probably at least three times as high inside Sand Forest (pers. obs.).

Methods

Comparison of seedling and sapling densities of canopy dominant species from heavily browsed conserved areas and a nearby sacred forest with very little browsing

In order to investigate whether high ungulate browsing pressure in conserved Sand Forests is responsible for the very low levels of recruitment observed in canopy dominant species, I compared seedling and sapling densities of the two most dominant canopy species from two formally conserved forests with an unconserved forest with little or no browsing. Sand Forests outside conserved areas are usually heavily disturbed by human activity, and this disturbance could also be responsible for any differences in recruitment. However, I found one site where harvesting of trees or poles was taboo, with Sand Forest largely undisturbed by people, although hunting was allowed. Ungulates appeared to have been absent from the site for some time, and I saw no droppings or tracks of wild antelope or domestic stock, nor evidence of browsing on foliage inside the forest. This site (27° 37.253' S, 32° 23.111' E), a sacred burial ground for local kings and chiefs (Inkosi), was in the KwaJobe district north-east of Mkuzi Game Reserve (Mkuzi). The local chief granted permission for one morning's sampling (10 December 1997). I counted numbers of seedlings (≤ 0.3 m height) and saplings (0.3 m to

3 m height) of the two Sand Forest canopy dominant species, *Cleistanthus schlechteri* and *Newtonia hildebrandtii*, in ten randomly located 10 x 10 m quadrats in areas with no evidence of woodcutting by people. These samples were compared to 100 m² subsamples of randomly located quadrats in Sand Forest at Phinda Resource Reserve and Mkuzi Game Reserve (see below). Nonparametric Mann-Whitney U tests were used as counts of seedlings and saplings at Phinda and Mkuzi were not normally distributed.

The woody component of the KwaJobe forest was floristically and structurally similar to the privately conserved Sand Forests at Phinda 15 km due south and occurs on the same dune series. Samples were also compared to forests in Mkuzi Game Reserve 20 km due west on older dune series. Although there is some turnover of species between the eastern Sand Forest type represented by KwaJobe and Phinda and the Western Sand Forest type represented by Mkuzi, the basal area and density of the canopy dominants, *C. schlechteri* and *N. hildebrandtii*, is very similar (see Chapters 2 & 3), and the use of KwaJobe as an unbrowsed control for both conserved sites seems reasonable.

Correlation between browsing pressure and regeneration levels in tree species from conserved forests

The effect of browsing pressure on regeneration levels of tree species was evaluated by means of a simple linear regression model, with two variables: a species-specific index of browsing pressure; and the proportion of juveniles in a sampled population for each species (i.e. species' regeneration level).

Data were sampled at the same time as forest structural and floristic data from 27 locally randomly located circular 400 m² quadrats at both Mkuzi and Phinda (see Chapters 2 & 3).

Antelope browsing on seedling and sapling foliage leaves characteristic evidence, from chewed leaves to cleanly cut twigs. This makes it possible to construct a simple species-specific index of browsing pressure based on the proportion of individuals in a population showing obvious signs of browsing. I only considered individuals shorter than 2 m, as foliage on taller trees could be beyond the reach of antelope. Since heavy browsing pressure is likely to have a larger effect on plant growth and survival than light browsing pressure, I weighted each individual according to how heavily it was browsed: class 0, plants with less than 5 % of shoot-tips browsed were weighted 0; class 1, with 5 % to 10 % browsed were weighted by 1, class 2, with 10 % to 20 % browsed were weighted by 2; and the final class 3, with > 20 % of foliage showed evidence of browsing or canopy structure obviously modified by browsing were weighted by 3. The calculated index, with a possible range from 0 to 3, was then divided by three to give a maximum value of 1 (i.e. all individuals in the population in class 3). Only species in which more than five individuals shorter than 2 m were encountered were included in the regression.

Recruitment for each species was described by the proportion of juveniles in a sampled population of juveniles and adults and is also scaled from 0 to 1. Established plants within the range of sizes where all foliage is vulnerable to browsing, from 0.5 m to 2 m tall, were considered to be juveniles. Adults were considered to be individuals from 3 m to 5 m in height. The low maximum height limit for adults was chosen to allow comparison of trees of different sizes, including subcanopy species. Only species

with at least 10 juveniles and adults sampled were included in the regression analysis. *Psydrax fragrantissima*, the only species which regenerates predominantly by resprouting (Chapter 3), was also omitted from analyses.

The best fit for the regression analysis was obtained with log transformed data ($X' = \log_e X$). Although both variables are proportions, arcsine transformation (Zar 1996) was not necessary as neither variable had a strongly binomial distribution.

Effects of browsing on two Sand Forest species in a conserved area

Two year old seedlings of moderately palatable *Combretum mkuzense* and highly palatable *Newtonia hildebrandtii* were planted out at Mkuzi Game Reserve in order to assess herbivore impact on seedling mortality and growth. At the time, Mkuzi was the only reserve with Sand Forest where herbivore densities had been accurately censused (see Table 2).

Seedlings of each species were planted in pairs 5 m apart, every 10 m along three line transects running roughly parallel to the long axis of the Mkuzi Sand Forest patch. One seedling in each species pair was enclosed in a 40 x 40 x 50 cm cage of fine wire netting with a mesh size of 58 mm. The two species were alternated along the transects. Seedlings were planted in the middle of the wet season on 5 December 1997 and watered the following day. Care was taken not to disturb the root mass at transplanting. After allowing the seedlings to settle for one week, the height, and canopy width were measured to the nearest 0.5 cm and the seedlings watered again. All seedlings were still healthy, appeared unaffected by the transplanting process and some had produced new growth 17 days after planting. The seedlings were measured again and any mortality noted six months after planting on 8 June 1998. The volume of initial foliage removed by browsing over the 6 month period was estimated from detailed sketches of each seedling.

Seedlings for this experiment were grown at the KwaZulu Nature Conservation Services nursery in Pietermaritzburg under 40 % shade cloth from seed collected at Mkuzi Game Reserve. Seedlings were planted and germinated in September 1995, and by the time of planting out 27 months later had reached mean vertical heights of 18.7 ± 4.0 cm for *N. hildebrandtii*, and 34.9 ± 4.2 cm for *C. mkuzense*. Seedlings were grown in a potting soil mix and kept moist, and were likely to have grown larger than would be likely in the dystrophic, dry sands of the Sand Forest. Seed of the canopy dominant, *Cleistanthus schlechteri*, failed to germinate and the common, unpalatable *Hymenocardia ulmoides* also chosen as a study species had negligible germination, both apparently as a result of insect damage to seed.

Results

Comparison of seedling and sapling densities of canopy dominant species from heavily browsed conserved areas and a nearby sacred forest with very little browsing

For both Sand Forest canopy dominant species, *C. schlechteri* and *N. hildebrandtii*, saplings (>0.3 to 3 m) were either entirely absent or occurred at extremely low densities at both conserved sites (Phinda and Mkuzi) with high ungulate densities. In contrast, saplings of both species were common at KwaJobe, an unconserved site with few ungulate browsers, and this difference was highly significant (Figure 1, Table 3). Densities of seedlings (<0.3 m) of both species were slightly higher at KwaJobe than either conserved site, but this difference was only significant for *N. hildebrandtii* (Table 3). High sapling densities of *C. schlechteri* at KwaJobe, despite seedling densities similar to the low values observed at the two conserved sites, implies that factors influencing seedling establishment are not primarily responsible for low levels of regeneration observed in conserved areas.

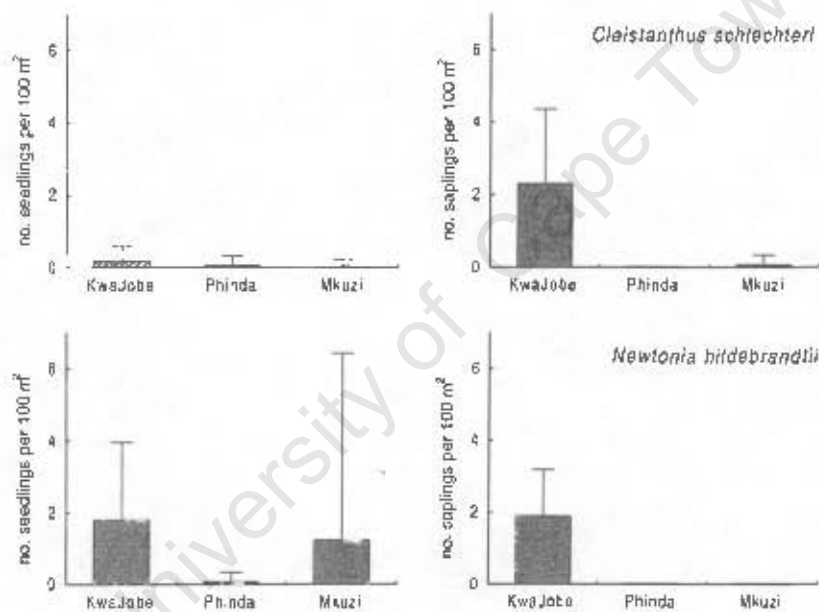


Figure 1. Mean density of seedlings and saplings of the dominant tree species in old-growth Sand Forest at three sites; a sacred forest at KwaJobe which has few or no ungulate browsers, and Phinda and Mkuzi which have large numbers of ungulate browsers typical of formally conserved areas. Whiskers are standard deviation. See Table 3 for sample sizes.

Table 3. *p*-values for Mann-Whitney U tests comparing numbers of seedlings and saplings in 100 m² Sand Forest samples from unbrowsed forest at KwaJobe (*n* = 10) with samples from two nearby reserves, Phinda (*n* = 27) and Mkuzi (*n* = 27).

	KwaJobe vs. Phinda		KwaJobe vs. Mkuzi	
	seedlings	saplings	seedlings	saplings
<i>C. schlechteri</i>	<i>p</i> = 0.6	<i>p</i> < 0.0001	<i>p</i> = 0.5	<i>p</i> < 0.0001
<i>N. hildebrandtii</i>	<i>p</i> = 0.0025	<i>p</i> < 0.0001	<i>p</i> = 0.014	<i>p</i> < 0.0001

Correlation of recruitment with browsing pressure

The proportion of juveniles in tree species' populations was strongly negatively correlated with a species-specific index of browsing pressure for both Sand Forests in conserved areas (Phinda: $R^2 = 0.44$, $p = 0.005$, $n = 16$; Mkuzi: $R^2 = 0.62$, $p = 0.002$, $n = 12$).

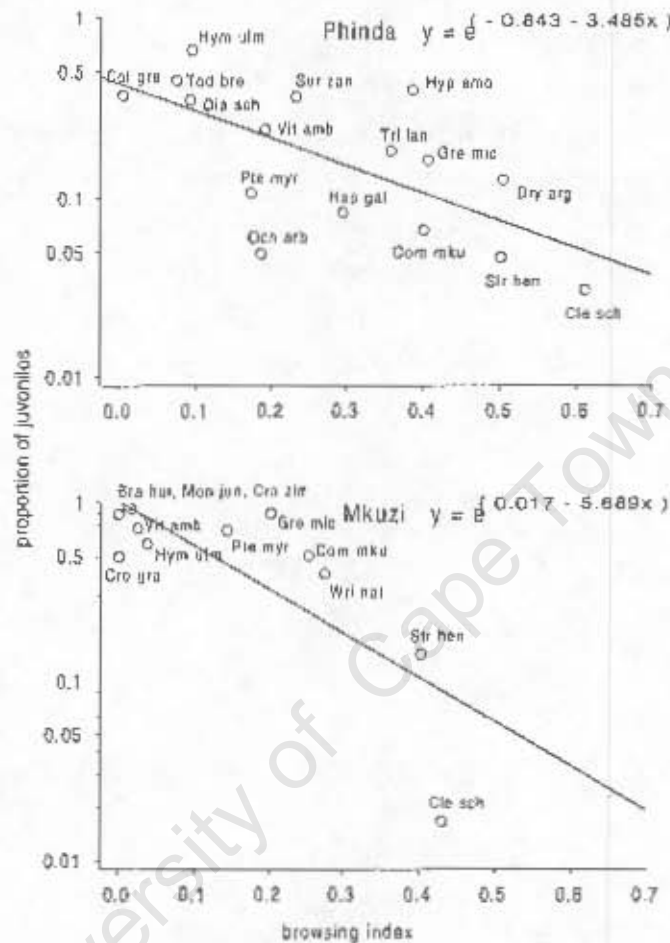


Figure 2. Proportion of juveniles (height 0.5–2 m) in species populations in response to level of browsing pressure. A high browsing index (close to 1) indicates heavy browsing pressure on that species.

Palatable species (i.e. with a high proportion of foliage on juvenile trees showing evidence of browsing) tended to have a lower proportion of juvenile trees in the population (Figure 2). This effect is apparent despite the exclusion of species with the lowest proportion of juveniles from the analysis due to the inability to calculate a browsing index when very few juveniles were encountered. The most notable example of this is one of the two important canopy dominants, *N. hildebrandtii*, which appears to be the most palatable Sand Forest tree species, with all foliage in reach of antelope heavily browsed (pers. obs., Plate 1).

Effects of browsing on two Sand Forest species in Mkuzi Game Reserve

Mortality of planted two year old seedlings unprotected from browsing was not significantly higher than for caged seedlings for either study species over a six month period from the middle of the wet season to the middle of the dry season. For *N. hildebrandtii*, 3 of 20 uncaged seedlings died vs. 1 of 20 seedlings protected from browsing. No seedlings of *C. mkuzense* died.

However, uncaged seedlings of both species were negatively impacted by browsing. For *N. hildebrandtii*, 2 of 20 uncaged seedlings had been browsed after only the first week and after six months 19 of 20 uncaged seedlings showed evidence of ungulate browsing. For *C. mkuzense*, 7 of 20 uncaged seedlings had been browsed after the first week and all 20 were browsed after six months. A larger proportion of seedling foliage had been removed for *N. hildebrandtii* than for *C. mkuzense* (mean $\pm$ SD: $37 \pm 26\%$ vs. $9 \pm 11\%$, Mann-Whitney U test: $p = 0.011$). No seedling had more than minimal insect damage.

Table 4. Change in height of *N. hildebrandtii* and *C. mkuzense* seedlings exposed to browsing for six months compared to seedlings protected from browsing by wire netting.

Treatment	Mean growth $\pm$ SD	n	Range	negative/0	positive
<i>Newtonia hildebrandtii</i>					
open to browsing	0.8 ± 4.4 cm	17	-5.5 — 9 cm	10	7
caged	3.1 ± 2.8 cm	19	-1.5 — 8 cm	4	15
<i>Combretum mkuzense</i>					
open to browsing	1.0 ± 4.4 cm	20	-6 — 11 cm	11	9
caged	4.8 ± 3.4 cm	20	-2 — 11 cm	3	17

After six months, uncaged seedlings had grown only 23 % as much as caged seedlings protected from browsing (Table 4, Two-level Anova, browsing treatment: $F = 10.55$, $p = 0.0018$) and a higher proportion of uncaged seedlings were the same size or shorter than at the start of the experiment. Although growth in caged seedlings was higher for *C. mkuzense* than for *N. hildebrandtii*, as would be expected from the relative sizes of two year old seedlings at the start of the experiment (mean of 34.9 cm vs. 18.7 cm), and a higher proportion of foliage was removed from *N. hildebrandtii* seedlings, these differences did not result in a significant difference in vertical growth between species (Two-level Anova, species effect: $F = 0.76$, $p = 0.39$), nor significant interaction between species effect and browsing treatment (Two-level Anova, interaction: $F = 0.33$, $p = 0.57$).

Discussion and conclusions

Ungulate browsing appears to suppress regeneration of the two canopy dominant species in conserved Sand Forests. In forests with high ungulate densities small saplings of *C. schlechteri* and *N. hildebrandtii* (0.5 m to 2 m height) were either entirely absent, or occurred at very low densities

(< 0.07 per 100m²). In contrast, saplings of both species were common (2 per 100m²) in an undisturbed old-growth forest with negligible browsing pressure. Given the very low densities of trees between 0.5 m and 2 m in height in the conserved areas, it seems unlikely that sufficient individuals could recruit through these size classes to balance adult mortality, which appears to be at least 1 % per annum for *C. schlechteri* (Chapter 3).

Similarly, in conserved areas recruitment of woody species was strongly negatively correlated with species-specific browsing pressure, with the lowest proportions of juveniles in populations of the most palatable species, such as the canopy dominant *C. schlechteri* (Figure 2) This not only confirms that browsing pressure is responsible for the suppression of recruitment in palatable species, but implies that long term heavy browsing pressure could change forest species composition, perhaps even eliminating the most vulnerable species.

Nearly all unprotected planted two year old seedlings of two species were browsed over a six month period. Although this did not significantly increase mortality compared to protected seedlings, average vertical growth of unprotected seedlings was reduced by 74 % for *N. hildebrandtii* and 79 % for *C. mkuzense*. This effect alone would reduce the sapling densities, and it seems likely that continued removal of an average of 37 % of foliage in *N. hildebrandtii* and 9 % in *C. mkuzense* would increase mortality over a longer time period.

The data presented in this paper/chapter suggest that browsing by high densities of ungulates is having a large effect on regeneration in conserved old-growth Sand Forests, and particularly on recruitment by the two most dominant tree species. The effects of browsing are not always undesirable, and need to be evaluated in terms of conservation goals (see discussions in Putman 1996; Reimoser *et al.* 1999). For example, browsed tropical forests may be substantially more diverse than defaunated forests, presumably because browsing suppresses competitive dominance (Coley & Barone 1996). However, a number of factors indicate that browsing pressure in conserved Sand Forests is too high. In unbrowsed forests the ground layer vegetation is dense and diverse, with high cover of *Zamioculcas zamiifolia* which is completely absent in conserved forests. In conserved forests, trampled areas, tracks and dung of antelope are common, the ground layer is generally sparse or absent, there is a distinct browse line at approximately 1.6 m, many palatable shrubs show a 'topiary' effect, and seedlings of palatable seedlings are browsed level with the ground layer. At some sites these effects are more pronounced and in places the shrub layer is entirely absent (Plate 1). These factors would indicate 'heavy' or 'very heavy' browsing pressure in temperate forests (Reimoser *et al.* 1999), sufficient to prevent recruitment by palatable species.

We do not know how common nyala and other ungulates were before the early 1900's (see e.g. Anderson 1978), but it is probable that in the absence of significant numbers of large predators, modern densities of antelope in conserved areas are substantially higher than they ever would have been. In areas of Europe and North America growth of wild ungulate populations in recent decades has often had a large and usually undesirable impact on forest regeneration and composition (e.g. Jones *et al.* 1993; Motta 1996; Zamora *et al.* 2001). The most severe negative effects of browsing are seen at

densities of approximately 8 whitetail deer per km² and above in American temperate hardwood forests (Jones *et al.* 1993), and densities of more than 5 to 15 deer per km² are considered too high in European temperate forests (Putman 1996). In the savanna/Sand Forest matrix at Mkuzi game reserve in 1996/1997, line transect surveys recorded approximately 30 impala and 20 nyala per km², despite regular culling of both species (KwaZulu-Natal Nature Conservation Services data). Due to their preference for savanna and forest habitats respectively, densities of impala are likely to be much lower, and densities of nyala much higher in Mkuzi Sand Forest. Browsing damage suggests that numbers are even higher at the privately conserved Phinda Resource Reserve. These figures indicate that ungulate densities in conserved Sand Forest are far higher than would be considered acceptable in managed temperate forests. Given the slow growth rates of dry forest trees compared to moist tropical forests (see Chapter 7), the use of temperate forest models for comparison seems sensible.

C. schlechteri is by far the most dominant species at most South African Sand Forest sites, and together *C. schlechteri* and *N. hildebrandtii* contribute between 40 % and 49 % of total importance at these sites (average of relative basal area and relative density, Chapter 2). The consistency of composition and structure of many discrete dry forest patches distributed over a wide area, from the western shore of Lake St. Lucia in the south to beyond the Mozambique border 130 km to the north (Chapters 2 & 3), implies these forests have been stable for a considerable period of time. Further, the high dominance by two very palatable species with slow growth rates indicates that browsing pressure was low in the past. I suggest that current levels of browsing in conserved areas are sufficient to change forest composition over the long-term, reducing or even eliminating populations of the most palatable species. Given the strong dominance by two species, both of which appear to be amongst the most vulnerable to recruitment failure caused by browsing, the impact of ungulate browsers is of enormous concern. Rather than simply causing a shift in species composition, continued heavy browsing pressure in Sand Forest could ultimately completely change the structure, and thus the entire biotic environment, potentially leading to dramatic species loss. It is essential that any degradation of Sand Forest is prevented. Dry forest globally is highly threatened (Murphy & Lugo 1986; Mooney *et al.* 1995) and Sand Forest has a unique and characteristic flora and fauna, including a number of endemics entirely restricted to this forest type (Kirkwood & Midgley 1999; Matthews *et al.* 2001).

Further research is urgently required. Most easily achieved, game counts in both the dry and wet season need to differentiate Sand Forest from other vegetation to accurately measure ungulate browser numbers throughout the year, and estimate relative browsing damage by different species. Comparison of species richness and composition of both tree and herbaceous ground flora in conserved and undisturbed areas with little browsing pressure would be useful. Long-term selective exclosure plots in conserved areas would provide a real control for browsed forests and if carefully designed could differentiate between the impact of large ungulate browsers, particularly nyala, and small browsers such as red duiker and suni.

A reasonable conservation goal for Sand Forest would be the regeneration of all species currently present and 'maintenance of dominant, representative vegetation' (Williams *et al.* 2000). It seems likely that in order to meet this goal in conserved areas, densities of ungulate browsers, particularly

nyala, in Sand Forest will have to be greatly reduced. Nyala have fairly stable home ranges (Anderson 1978) and localised culling may create persistent low density areas without greatly reducing conserved population sizes (McNulty *et al.* 1997). Since conflicting conservation goals for animals and plants in currently conserved areas may never be resolved, the establishment of further Sand Forest reserves is highly desirable in order to properly conserve this unique and important dry forest type.

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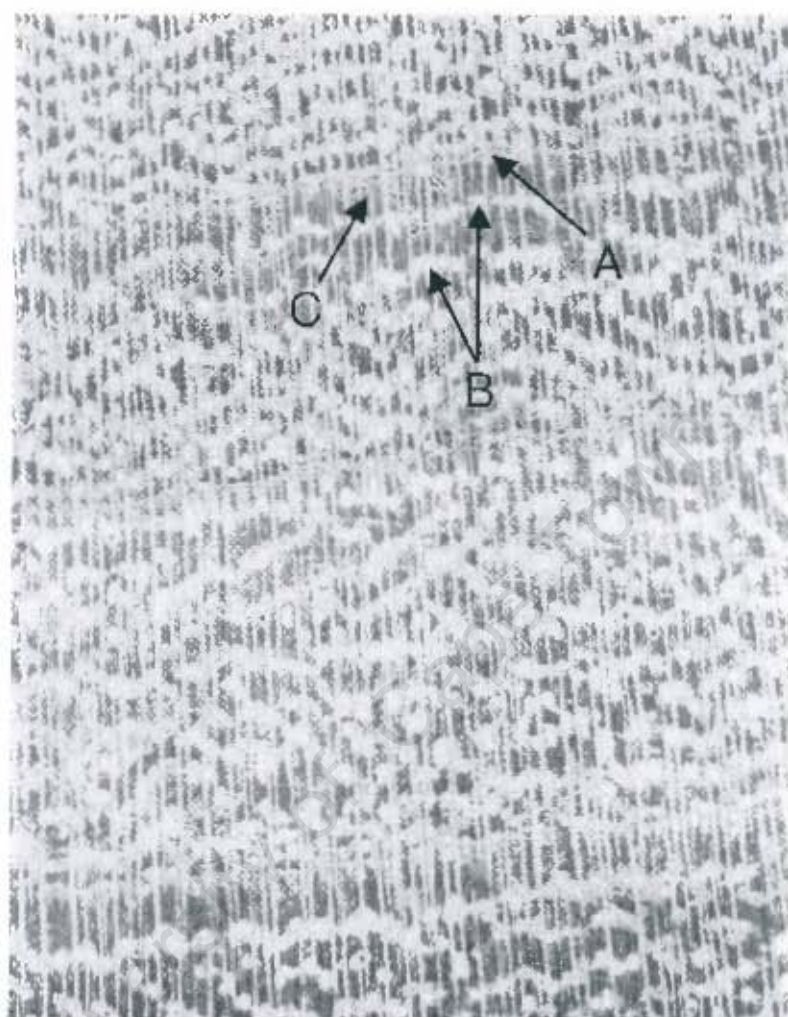


Plate 1. Wood anatomy of *C. schlechteri*. Note the ring boundaries demarcated by a fine continuous band of apotracheal marginal parenchyma (A), scattered groups of paratracheal parenchyma forming irregular concentric bands decreasing in frequency from the start to the end of each growth ring (B), and the latewood zone devoid of vessels and paratracheal parenchyma (C). Latewood typically appears darker than earlywood as a result of decreasing vessel density across the ring. There is no change in vessel diameter from earlywood to latewood.

**Annual rings and growth in the sand forest canopy dominants,
Cleistanthus schlechteri and *Newtonia hildebrandtii***

Abstract

My aim was to determine if the two most dominant Sand Forest canopy species formed annual rings, and to use annual ring widths in conjunction with radiocarbon dating to estimate growth rates in these species. In the single 23 cm diameter *Newtonia hildebrandtii* disk sampled, visible growth increments appeared not to be annual in nature. A radiocarbon age of 33 years for wood 37 mm from the cambial layer gives a low average radial growth rate of 1.12 mm per year, implying that the largest trees in the area, 150 cm DBH and more, may be well over 700 years old. In *Cleistanthus schlechteri*, ring anatomy, phenology, cross-dating of recent growth rings and a ring count corroborated by a precise radiocarbon date indicated that visible growth increments were in fact annual rings. Most rings in *C. schlechteri* had two features typical of tropical semi ring porous annual rings: a fine band of apotracheal marginal parenchyma delimiting the ring boundary and a decrease in density of vessels and paratracheal parenchyma bands from earlywood to latewood. In many rings the final latewood zone was clear of paratracheal parenchyma bands. In all five tree samples harvested at the height of the dry season, the outermost ring appeared complete, and patterns of growth in the 10 most recent rings were highly synchronised between trees (average multiple $r = 0.91$, all $p < 0.05$). Annual growth increments were indistinguishable very close to the pith, and increased from less than 0.5 mm in width within 5 mm of the pith to over 1.0 mm beyond 10 mm from of the pith (i.e. stem diameter > 2 cm). Average ring width ($\pm$ S.D.) in adult trees (> 10 cm DBH) was 1.33 mm (± 0.63 mm) and did not change substantially with increasing diameter. Age of the largest 39 cm diameter specimen was estimated at 150 years from pith formation, and growth rates suggest that the largest trees in the Tembe area where these samples were harvested (> 50 cm DBH) may reach 200 years or more. Although I did not attempt to exactly age long ring chronologies by cross-dating specimens, these first accurate estimates of growth rate in any Sand Forest species are important for the management and study of Sand Forest dynamics. The results suggest that investigation of growth rings in a wider range of species from these and other dry forests would be worthwhile.

Keywords: tropical and subtropical dry forest, annual growth rings, growth rate, tree age

Introduction

Growth rates in trees can be measured by four methods: first, repeat measurements of girth; second, girth measurement in trees of known age; third, the identification, ageing and measurement of annual rings; and fourth, radiocarbon dating of wood samples (Mariaux 1981; Worbes & Junk 1989). Although repeated measurements are simple, they require large numbers of trees of a range of diameters, are extremely time-consuming to perform, and require measurement over many years to account for year to year variation (Mariaux 1981). This method is likely to be particularly impractical in dry forests where tree growth rates can be extremely low (e.g. Kigomo 1994), seasonal shrinkage and expansion as a result of water availability can exceed annual growth increments (e.g. Lieberman 1982; Swaine 1992), and year to year variability in growth rates can be high (e.g. Swaine 1992). As for most forest species in southern Africa, there appear to be no trees of known age, such as might be found in plantations, for any Sand Forest species (pers. obs.). Fortunately the study of tree rings has considerable promise in seasonally dry tropical forests, particularly when supported by data from precisely dated wood, either from experimental cambial wounding or radiocarbon dates (Worbes 1995). Radiocarbon dating alone is too expensive for general application, and wood laid down after 1650 and prior to 1955 cannot be dated with precision, limiting the usefulness of this method (Stuiver *et al.* 1981; Worbes & Junk 1989).

Analysis of tree rings is a vital tool in the study of forest dynamics in temperate regions where low winter temperatures and short day length induce annual cambial dormancy, resulting in clear growth rings in stem cross-sections (Fahn *et al.* 1981). It has long been assumed that annual rings are rarely present in tropical and subtropical tree species (Lieberman *et al.* 1985; Kigomo 1994; Worbes 1995). However, many regions in the tropics and subtropics have one or sometimes two distinct dry seasons per annum, and annual tree rings resulting from drought induced cambial dormancy have been found where dry periods have less than 60 mm of rainfall per month for two to three months (Worbes 1995). In dry forests, where drought stress during the dry season can be considerable (Olivares & Medina 1992; Holbrook *et al.* 1995), and phenology is typically strongly related to seasonal rainfall patterns (e.g. Lieberman 1982; Holbrook *et al.* 1995; but see also Borchert 1994), it is likely that annual rings are actually fairly widespread. Although studies investigating ring formation and age determination in tropical and subtropical trees are relatively rare (Bormann & Berlyn 1981), annual rings have been recorded Asia, tropical Australia, Africa and Latin America (see citations in Eckstein *et al.* 1981; Fahn *et al.* 1981; Worbes 1999, but see also Lieberman *et al.* 1985). In southern and east Africa, annual growth rings have been recorded in a variety of *Acacia* species (Gourlay 1995) and in *Pterocarpus angolensis* (Bryant 1968 cited by Mariaux 1981; Stahle *et al.* 1999). Five tree species in southern Africa, including *Albizia forbesii*, which is associated with Sand Forest, appear to have annual rings suitable for dendrochronological analysis (Lilly 1977).

Although exactly datable annual growth rings have a variety of uses, from the investigation of past climates to the dating of forest disturbance events (Fritts 1976; Dynesius & Jonsson 1991), even when occasional missing rings, false rings or uneven growth typical of tropical woods prevent precise dating,

accurate estimates of radial growth can still be obtained (Bormann & Berlyn 1981). Knowledge of tree growth rates is necessary in order to understand forest dynamics and effectively manage any forests.

In this chapter I concentrate on the two species which overwhelmingly dominate the Sand Forest canopy, *Cleistanthus schlechteri* and *Newtonia hildebrandtii* (see Chapter 2). *C. schlechteri* is particularly important as it is associated with dry forest and woodland through Mozambique as far north as Kenya, and west into Zimbabwe and Malawi (pers. obs., Burgess & Clarke 2000). I describe the occurrence and nature of annual growth rings in *C. schlechteri* and describe the relationship between diameter, growth rate and age in this species. Although annual rings were not identified in *N. hildebrandtii*, a measurement of growth rate from one radiocarbon date in one specimen is presented. Both these species are harvested outside of formally conserved areas. *C. schlechteri* is heavily utilised to provide wood for carving (pers. obs.), while *N. hildebrandtii* is often killed by ringbarking to provide high quality firewood (pers. obs., C. Hanekom, pers. comm.). As for any situation where timber is harvested from natural stands (e.g. Bussman 1999), it is impossible to determine at what level these activities are sustainable without a knowledge of growth rates. An understanding of the population dynamics of these species is particularly important in conserved forests, where both appear to be experiencing recruitment failure, probably as a result of high browsing ungulate densities (see Chapters 3, 6 & 8).

Methods

I obtained entire stem cross sections from five *C. schlechteri* trees and one *N. hildebrandtii* tree felled for carving by local craftsmen in Sand Forest west of Tembe Elephant Park (23°03'S, 32°27'E) in July 1995. The specimens were cut between 45 cm and 95 cm above ground level and were separated by at least 500 m from one another. At the time of sampling, no further specimens were available from this or any other Sand Forest site. The disks were sanded with progressively finer grades of sandpaper once air-dry, finishing with 1000 grit waterpaper to achieve the fine polish necessary see ring features.

Radiocarbon dating of Cleistanthus schlechteri and Newtonia hildebrandtii

Samples of wood were cut from the centre of the largest (42 cm diameter) *C. schlechteri* specimen and the single (23 cm diameter) *N. hildebrandtii* specimen, taking care to extract the samples from as close to the core as possible, and not extending more than 1.5 cm radially. These samples (Pta-7569 and Pta-7560 respectively) were analysed by the Quaternary Dating Research Unit (QuaDRU) of the South African CSIR. Ages were corrected for variations in isotope fluctuations and calibrated for the southern hemisphere. Due to fluctuations in the radiocarbon levels in the environment between 1650 and 1955, it could only be ascertained that both samples were older than 60 years and younger than 350 years. Further samples were therefore cut from younger wood, two-thirds of the distance from the core to the outside of the stem. These samples did not extend more than 0.4 cm radially and were cut along the same few growth rings. In the *C. schlechteri* specimen, this sample corresponded to three annual growth rings. These samples of younger wood (QuaDRU analysis numbers Pta-7681 and Pta-7679 respectively) were both laid down subsequent to 1955, a period in which nuclear bomb testing

artificially raised atmospheric ^{14}C levels (Stuiver *et al.* 1981), with the result that radiocarbon dates are accurate to within one year.

Estimating growth rates in C. schlechteri from annual ring widths

The main purpose of identifying and measuring growth rings was to estimate radial growth rates and relate these to stem diameter. Entire stem cross sections are necessary in order to properly identify and measure growth increments in *C. schlechteri* due to indistinct ring boundaries in portions of cross section and considerable lobing which resulted in the formation of very narrow rings in places (Worbes 1995). In order to reduce the variation in ring width around the stem resulting from uneven growth, I used the following procedure. Individual rings were measured along radii where rings were relatively wide and well defined (Eckstein *et al.* 1981), with the restriction that every ten consecutive rings were measured along the same radius. Each of the ring widths in these ten-ring bands were then proportionately adjusted so that the width of all ten rings was equal to the average width of the ten-ring band at ten evenly spaced radii around the stem. The boundary of every tenth ring was marked with a fine fibre-tip pen around the entire stem to facilitate ring identification and avoid confusion. Measurements were made using a binocular microscope fitted with an eyepiece micrometer, at magnifications of $\times 40$, and are precise to 0.05 mm.

I did not attempt to cross-date stems, since uneven growth resulting in lobing would make this a difficult and time-consuming task (see Stahle *et al.* 1999 for a concise description of methods). Therefore false or missing rings, a common feature of trees in the tropics and subtropics (Détienne 1989; Worbes 1995), could only be identified by means of wood anatomy. Wherever ring boundaries were unclear, data were omitted from the ring width analysis (see results).

Results

Semi-ring-porous growth rings were visible on polished cross sections of *C. schlechteri*, and ring anatomy, phenology, the correlation of ring widths in different trees, and radiocarbon dating all indicate that these rings are exactly annual growth increments.

Annual growth rings in C. schlechteri - wood anatomy

Growth ring boundaries in *C. schlechteri* were fairly distinct, demarcated by a fine continuous band of apotracheal marginal parenchyma which was seldom obscured by paratracheal parenchyma (A in Plate 1). Scattered groups of paratracheal parenchyma associated with one to four vessels formed irregular concentric bands decreasing in frequency from the start to the end of each growth ring (B in Plate 1). Many rings featured a latewood zone completely devoid of vessels and paratracheal parenchyma (C in Plate 1), although such zones were occasionally associated with earlywood. Latewood typically appeared darker than earlywood as a result of decreasing vessel density across the ring. There appeared to be no change in vessel diameter from earlywood and latewood.

Identification of some annual rings was difficult. Often paratracheal parenchyma bands obscured marginal parenchyma, although abrupt changes in density of these bands usually allowed ring boundaries to be distinguished clearly. More problematic were situations where growth features changed little across the ring and ring boundaries were faint or absent around the entire stem circumference. Where zones devoid of paratracheal parenchyma bands were associated with gradual changes in density of these bands on either side and no evidence of marginal parenchyma was present, this feature was not considered to demarcate a ring boundary.

Annual growth rings in C. schlechteri - phenology

All five specimens of *C. schlechteri* were felled in July 1995 at the height of the dry season and had typical and complete outermost growth rings, with the latewood zone adjacent to the cambial layer free of vessels and paratracheal parenchyma bands.

Annual growth rings in C. schlechteri - correlation between growth ring width in different trees

Although I did not attempt to cross-date the five tree samples, variation in ring width over the outermost 10 rings was highly synchronised between the different trees (Figure 1), providing further evidence that growth rings are annual.

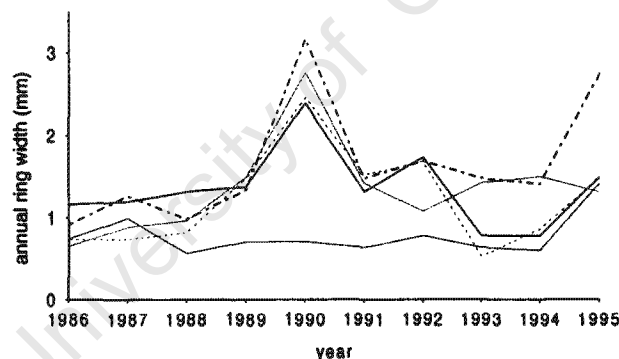


Figure 1. Width of same-aged annual rings in five samples of *C. schlechteri* felled in July 1995 approximately 5 km west of Tembe Elephant Reserve. Individual ring widths and radial distance were adjusted to reduce the effect of lobing (see methods).

Correlation of same-aged ring widths between samples was high, with multiple correlation coefficients (r) for each sample contrasted with all other samples ranging from 0.82 to 0.94 (all $p < 0.05$), and an average multiple r of 0.91.

Annual growth rings in C. schlechteri - radiocarbon dating

In a 42 cm diameter specimen of *C. schlechteri* felled in 1995, a radiocarbon date of 1956 (39 years prior to felling, precise to within one year, $\delta^{13}\text{C}$: -26.4 ‰ PDB) was obtained for a three ring band

sampled 1/3 of the radial distance from the tree exterior to the core. This corresponds exactly to the ring count of 38 through 40 years for the sampled rings, completed before the radiocarbon date was obtained, and confirms that growth rings are in fact annual rings.

Growth rates in C. schlechteri

Growth rates in *C. schlechteri* were low, and in five trees, annual ring width ranged from less than 0.2 mm to a maximum of 4.5 mm. In the largest sample, the very dark heartwood within 57 mm of the centre of the stem prevented reliable identification of rings or ring boundaries. In all remaining samples ring boundaries became indistinguishable within a few millimetres of the pith as rings became extremely narrow.

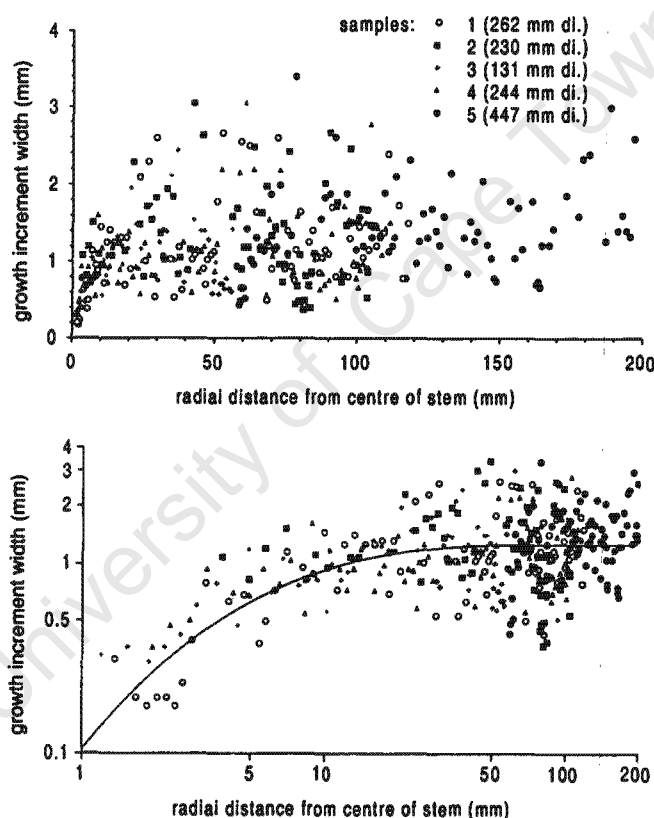


Figure 2. Radial growth in *C. schlechteri* as a function of stem diameter. The top scatter represents untransformed data, while the lower curve is a quadratic equation fitted to $\log_e$ transformed data. Individual ring widths and radial distance were adjusted to reduce the effect of lobing (see methods). Ambiguous rings were excluded.

Radial growth as a function of stem diameter in *C. schlechteri* was similar in all five samples (Figure 2). Annual rings laid down when the trees were young were substantially narrower than for adult growth. In the four samples in which growth increments could be identified close to the pith, ring

widths increased rapidly from less than 0.5 mm in width within 5 mm of the pith, to approximately 1.0 mm with 10 mm of the pith. Beyond this, ring width increased more slowly before levelling off approximately 50 mm from the pith. Average ring width ($\pm$ S.D.) for rings laid down more than 50 mm from the pith was 1.33 mm ($\pm$ 0.63 mm).

The best fit for radial growth as a function of stem diameter was provided by a curve described by the quadratic equation:

$$y = -2.226 + 1.617x - 0.349x^2 + 0.025x^3 \quad R^2 = 0.30 \quad (1)$$

for $\log_e$ transformed data (figure 2, bottom graphic), where y is the $\log_e$ of the radial distance from the pith (mm) and x is the $\log_e$ of the ring width (mm). A linear model fitted to untransformed data provided a poor fit ($R^2 = 0.07$).

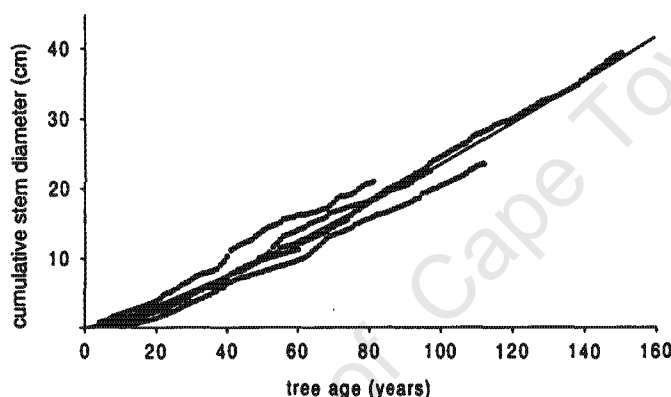


Figure 3. The relationship between age, from annual ring counts, and stem diameter for five sample *C. schlechteri* trees. Ring widths were doubled, then accumulated from the pith to the outermost ring. Individual ring widths were adjusted to reduce the effect of lobing (see methods). Estimates of the number of years taken to grow from the pith to the first distinguishable annual ring are based on average width of the 10 youngest visible rings and are probably underestimates given the rapid decrease in ring width close to the pith. For the largest sample the age of the youngest visible ring was taken as the average of the other four samples at the same diameter.

On average across the five trees sampled, 11.1 % of rings identified were ambiguous. However, uncertainties as to whether identified single rings should be separated into more than one ring, or whether separation of rings was in fact spurious, were similar in frequency. It is therefore reasonable to plot cumulative stem diameter as a function of tree age in years from the actual ring count (Figure 3). In this analysis, as before, the calendar date of each growth ring is not important. I estimate that at most, true age could be 6.3 % higher or 5.6 % lower than the values presented due to misidentification of annual rings. The diameter growth curve is described by the power function:

$$y = 0.814 x^{1.230} \quad R^2 = 0.97 \quad (2)$$

where y is the cumulative stump diameter (mm) and x is the tree age in years (excluding the time taken for the seedling to start lateral growth at the measured height).

Growth and rings in N. hildebrandtii

Although growth increments resembling annual rings were visible at places on the single 23 cm diameter *N. hildebrandtii* disk, with a layer of marginal parenchyma forming a clear boundary and changes in vessel density across the rings, these features were often not continuous around the stem and wide bands without discernible rings or ring boundaries were common. The outermost and latest formed ring appeared incomplete at the time of felling during the height of the dry season, suggesting that visible growth rings were not closely synchronised with an annual environmental cycle.

A 4 mm wide concentric band of wood sampled 1/3 of the radial distance from the exterior of the stem to the core yielded a radiocarbon date of 1962, 33 years prior to felling (precise to within one year, $\delta^{13}\text{C}$: -28.7 ‰ PDB). The centre of this sample was 37 mm from the cambium, indicating a low average growth rate over the 33 years of 1.12 mm per year.

Discussion

Annual growth rings in C. schlechteri and N. hildebrandtii

The anatomical structure of growth rings in *C. schlechteri* included several features typical of annual growth rings in tropical and subtropical tree species from areas with a marked single dry season (see e.g. Lilly 1977; Fahn *et al.* 1981; Détienne 1989; Stahle *et al.* 1999). Together with evidence that outermost rings were complete at the height of the dry season and patterns of growth in recent rings were highly synchronised between five tree samples, this provides strong support for the conclusion that visible rings are exactly annual growth increments and ring boundaries correspond to the cessation of cambial wood production during the cooler dry season. This is corroborated by a radiocarbon date in one specimen which corresponded exactly to a count of rings.

Although *C. schlechteri* is not dry-season deciduous, the presence of annual rings is not surprising given the strongly seasonal nature of the Sand Forest environment (see Chapter 1). Across the South African range of Sand Forest, average rainfall per month during the six month winter dry season (April to September) does not exceed 60 mm and drops to approximately 10 mm for July, the driest month. Despite this pronounced seasonality, it is unlikely that all species would have annual rings (Bormann & Berlyn 1981). Indeed, it appeared that visible growth rings in the other important canopy dominant, *N. hildebrandtii*, were not annual rings, or at least could not be identified easily enough to be useful (but see Worbes 1995). Nonetheless, investigation of rings in a variety of Sand Forest species is likely to reveal further species with visible annual rings, including species suitable for more complex dendrochronological analyses than were possible for *C. schlechteri*. For example, disks cut from branches of *Pteleopsis myrtifolia* and *Croton gratissimus* have clear and regularly spaced growth rings (pers. obs.), and *Wrightia natalensis* is strongly dry season deciduous, a feature associated with

cambial dormancy and the formation of annual rings (Tomlinson & Longman 1981). Lilly (1977) described annual rings with a diffuse porous ring structure and boundary parenchyma in *Albizia forbesii*.

Growth rates in C. schlechteri and N. hildebrandtii

Annual ring widths in *C. schlechteri* were small, and correspond to an average diameter increment ($\pm$ S.D.) of $2.66 \text{ mm year}^{-1}$ ($\pm 0.63 \text{ mm year}^{-1}$) for trees larger than 10 cm DBH. *C. schlechteri* is unusual in that growth is much slower in juvenile trees than in adults, with growth rings becoming progressively narrower, and eventually almost non-existent close to the pith (but see Tshinkel 1966 cited by Mariaux, 1981). Also, there was no evidence that ring width decreased substantially with increasing diameter as in most trees (Fritts 1976; Schweingruber 1996). Although year to year variability in growth was high, average growth was very similar in the five trees sampled. At age 80 there was less than 5 cm difference in diameter between the largest and smallest diameter trees sampled. Age of the largest 39 cm diameter specimen was estimated at 150 years from the start of diameter growth, and a simple power function relating age in years to total diameter suggests that the largest trees in the Tembe area where these samples were harvested ($>50 \text{ cm DBH}$) may reach 200 years or more.

Although I did not identify annual rings in *Newtonia hildebrandtii*, one radiocarbon date of 33 years for wood 37 mm from the cambial layer gives an average radial growth rate of $1.12 \text{ mm year}^{-1}$, slightly lower than for adult *C. schlechteri*. The extremely slow growth of *N. hildebrandtii* seedlings (see Chapters 5 & 6) suggests that juvenile growth is slower than adult growth, as for *C. schlechteri*. Even if radial growth is constant and the above value is typical for *N. hildebrandtii*, this implies that the largest trees in the area, 150 cm DBH and more, may be over 700 years old, and exceptional specimens of over 200 cm DBH may exceed 1000 years in age. If diameter growth rates decrease with size and age, as is likely (Fritts 1976; Schweingruber 1996), large trees may be much older than these estimates.

Adult diameter increments in *C. schlechteri* and *N. hildebrandtii* are almost double those reported for canopy trees in a Ghanaian dry forest (0.7 to 1.4 mm year^{-1} , Swaine *et al.* 1990) and slightly lower than has been found for *Brachylaena huillensis* growing in Kenyan dry forest (3.2 mm year^{-1} , Kigomo 1994). Growth rates in African dry forest canopy species, including *C. schlechteri*, are substantially lower than in a variety of southern and East African dry savanna species (6.5 to $38.4 \text{ mm year}^{-1}$, Gourlay 1995), and at the low end of a range of values for canopy species in a neotropical wet forest (1.0 to 9.1 mm year^{-1} , Lieberman *et al.* 1985) and an East African montane forest (2.5 to $15.0 \text{ mm year}^{-1}$, Bussman 1999).

It should be noted that samples were only harvested near Tembe Elephant Park, and growth rates may be slightly higher at sites such as Phinda where this species attains larger sizes, and lower at sites such as Ndumu where trees are typically smaller (see Chapter 3).

Implications for research, management and conservation

In the five specimens of *C. schlechteri*, annual growth increments correlated well with tree diameter, and growth rates for all trees measured were very similar. Although the sample size is admittedly small, this suggests that tree diameter is a good substitute for age, and that diameter-class distributions (see Chapter 3) provide an indication of real population age structure in this species (c.f. White 1980; Condit *et al.* 1998). Further samples from a range of sites are necessary to confirm this.

Knowledge of average growth rates is vital for the study of population dynamics (Bormann & Berlyn 1981), and the data presented in this chapter are incorporated in a simple population model for *C. schlechteri* in the following chapter (Chapter 8). The ability to approximately age *C. schlechteri* rings and whole specimens may also have wider application. The presence of fire scars in growth rings of old trees could reveal the occurrence and frequency of forest fires over the last 200 years. If, as seems likely, species with exactly datable rings are found, there is the possibility of precisely dating growth release from small-scale disturbance events (e.g. Dynesius & Jonsson 1991).

Although growth rate is just one factor influencing population growth and structure, diameter growth data can contribute to management and conservation decisions. With the slow growth rates demonstrated for *C. schlechteri* and suggested for *N. hildebrandtii*, it is unlikely that continuous harvesting of these species is sustainable. Although resprouting in harvested *C. schlechteri* may prevent the extinction of this species outside of formally conserved areas (pers. obs., R. Brereton-Stiles, pers. comm.), current levels of harvesting will probably eliminate this species as a resource in only a few years. However, it may be hard to convince local craftsmen of this, given the widespread assumption that large *C. schlechteri* specimens are at most one to two decades old (pers. obs.).

In formally conserved areas, there are very few *C. schlechteri* saplings, and particularly at Mkuzi Game Reserve, few individuals smaller than 5 cm DBH. Since juvenile growth rates in this species are even lower than for the slow growing adults, we would expect a reverse-J shaped size distribution, with a relative abundance of juveniles in a continuously recruiting population (Condit *et al.* 1998; Lykke 1998). This situation exists in undisturbed sites outside of conserved areas (see Chapter 6), excluding the possibility that recruitment in this species is dependant on periodic large-scale disturbance or unusual climatic events (e.g. Midgley *et al.* 1995). I have suggested that heavy browsing pressure by antelope is responsible for the absence of juveniles, and if growth rates presented in this chapter are applied at Mkuzi Game Reserve, the virtual absence of trees less than 5 cm in diameter indicates that there has been little recruitment through smaller size classes for approximately 28 years. This should be considered a minimum estimate as growth rates are likely to be slightly lower in the drier forests at Mkuzi Game Reserve. Given the long time taken to reach maximum size in this species, populations could survive for many years without recruitment. Nonetheless, the use of growth rates to predict population structure and estimate time since continuous recruitment bolsters the argument that high browsing levels are likely to cause a reduction in the population size of this critically important species, a problem that at very least requires immediate research attention.

Conclusion

Growth ring analysis corroborated by radiocarbon dating indicates that *C. schlechteri* forms annual rings, and although it was not feasible to exactly date individual annual rings, the derivation of growth curves for this species is of considerable value, and should be pursued at other Sand Forest sites, and elsewhere throughout its extensive southern and East African range. The presence of annual rings in *C. schlechteri* suggests that tree ring analysis would be worthwhile in a variety of Sand Forest species, and at other southern and East African dry forests sites with a strongly seasonal rainfall pattern.

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Conclusions

Sand Forest in a global context

Sand Forest in South Africa is relatively unique among tropical and subtropical dry forests worldwide in that the soils are highly infertile sands (*c.f.* Högborg 1992; references in Bullock *et al.* 1995; Gerhardt 1996; Gonzalez & Zak 1996; Oliveira-Filho *et al.* 1998), a large proportion of forest area has not been greatly disturbed by humans until relatively recently (see Chapter 1), and although very dry, these forests occur at the extreme southern limit of the subtropical zone. However, results presented in this thesis suggest that many aspects of Sand Forest ecology are similar to those recorded for other tropical dry forests globally.

Forest structure

Sand Forest has extremely low, seasonal rainfall and occurs on free-draining, nutrient poor sands (see Chapter 1). It is therefore not surprising that sampled Sand Forests were short and structurally simple, particularly at the driest locality, Mkuzi. Although dry forests seldom reach more than 40 m in height, the average canopy heights of approximately 7 to 11 m (with very few emergents taller than 18 m) place these forests amongst the shortest worldwide (see e.g. Murphy & Lugo 1986a; Menaut *et al.* 1995; Murphy & Lugo 1995; Rundel & Boonpragob 1995; Sampaio 1995). Despite its low stature, stem area was moderately high, ranging from 24.1 m² ha⁻¹ to 33.2 m² ha⁻¹. These values are normal for dry forests, but they do suggest that sampled Sand Forests had not been disturbed for at least a century or more (e.g. Murphy & Lugo 1986b; Swaine *et al.* 1990; Lowe & Clarke 2000 and see Chapter 7).

Forest dynamics - regeneration from seed

The study of regeneration in wet tropical forests has largely focused on classic gap-phase dynamics in which both pioneer and climax species (*sensu* Whitmore 1989) require or are assisted by treefall gaps to reach the canopy (e.g. Brokaw 1985; Hartshorn 1989; Whitmore 1989; Mabberly 1992; Denslow & Hartshorn 1994; Lieberman *et al.* 1995; but see Lieberman *et al.* 1989).

Until very recently, the role of canopy openness in the internal dynamics of dry forest systems had not been considered (Mooney *et al.* 1995; Oliveira-Filho *et al.* 1998), mostly it appears, because it was not thought to be important in these short and relatively open systems. However, in the 1990's, a few studies found that the survival, growth and distribution of dry forest trees may be influenced by canopy openness (Gerhardt 1993; Gerhardt 1996; Oliveira-Filho *et al.* 1998). Interestingly, seedling survival was typically highest in shaded environments (Gerhardt 1993; Gerhardt 1996), and seedlings occurred in higher densities than in canopy gaps (Lieberman & Li 1992). I found a similar pattern in Sand Forest, with higher (or similar) densities of small seedlings in completely shaded subcanopy environments than in canopy gaps. Similarly, under experimental conditions of moderate drought stress, seedling survival and growth in two Sand Forest species was lower in full sun than in the shade.

Further, species composition for all size-classes differed in gaps and non-gaps, and individual species were arrayed along a continuum of canopy openness (Chapters 4 & 5). This work contributes to the early evidence that canopy openness influences survival and growth in dry forest seedlings, and as a result affects species composition. It appears that unlike most mesic and wet forests, where seedling regeneration dynamics are driven largely by light availability, patterns of seedling regeneration in dry forests are also strongly influenced by drought tolerance.

These results suggest that seedling regeneration in Sand Forest, and probably most dry forests, is unlikely to be limited by the availability of canopy openings caused by small, autogenic, or large-scale catastrophic disturbance events (*c.f.* Everard *et al.* 1995; Midgley *et al.* 1995), and that most species are likely to have continuous *in situ* regeneration.

Forest dynamics - regeneration by sprouting

Of course, patterns of seedling regeneration are largely unimportant where the primary mode of regeneration is by sprouting (Midgley & Cowling 1993; Kruger *et al.* 1997; Ramón & Fernández-Palacios 1998; Paciorek *et al.* 2000; Bond & Midgley 2001 and references therein). Tropical dry forests typically resprout strongly in response to cutting or fire (Murphy & Lugo 1986a; Murphy & Lugo 1986b; Sampaio *et al.* 1993; Miller & Kauffman 1998), an expected trait, given their low canopy height (Kruger *et al.* 1997). This suggests that in many dry forests, and particularly in relatively short Sand Forest, sprouting may even dominate tree regeneration in undisturbed forests. However, regeneration of important Sand Forest species was almost entirely by seed in undisturbed old growth forests (Chapter 3), as appears to be the case in the few studies of largely undisturbed old-growth dry forests (Swaine *et al.* 1990; Lieberman & Li 1992; Gerhardt 1993; Gerhardt 1996; Khurana & Singh 2001).

Nearly all Sand Forest trees do have the ability to sprout however, and as for other dry forests, resprouting was the primary mode of recovery after large-scale disturbance caused by fire.

Naturally water-repellent soil in Sand Forest

To the best of my knowledge, the existence of naturally water-repellent soil has not been recorded in dry forests before. While sandy soils are particularly likely to develop soil water repellency (DeBano 1981; Scott 1994), this phenomenon is widespread (Giovannini & Lucchesi 1984; Wallis & Horne 1992; Ritsema *et al.* 1997; Bauters *et al.* 1998) and is likely to be found in other dry forests. Pot based experiments indicated that water repellent Sand Forest soil exacerbates low seedling germination and survival, particularly in high light environments such as would be found in canopy gaps, and is important in dry forest regeneration dynamics (Chapter 5).

The impact of browsing in forest

In temperate coniferous and broad-leaved forests, primarily in Europe and North America, the often negative effects of high levels of ungulate herbivory have been well documented. Intensive browsing by various ungulates has been shown to suppress the regeneration of palatable tree species (Shimoda *et*

al. 1994; Putman 1996; Van Hees *et al.* 1996; Cornett *et al.* 2000; Zamora *et al.* 2001; Kuiters & Slim 2002; but see Mladenoff & Stearns 1993) and reduce seedling diversity (Liang & Seagle 2002). Long-term effects can include undesirable changes to forest structure and composition (Anderson & Katz 1993), such as reduction in abundance or loss of tree species (Ammer 1996; González Hernández & Javier Silva-Pando 1996), loss of species from the ground-layer (Rooney & Dress 1997), and reduced songbird abundance and diversity (deCalesta 1994).

Many tree species in conserved old-growth Sand Forest, including the canopy dominants, *C. schlechteri* and *N. hildebrandtii*, have size-class distributions which suggest that recruitment is greatly reduced by ungulate browsing. Trees shorter than two metres are vulnerable to browsing, and precisely these size classes are underrepresented or absent from tree populations. In old-growth Sand Forest, important tree species recruit entirely from seed, and often the presence of seedlings indicates that neither seed supply nor establishment is limiting. Similarly species with apparent regeneration failure do not appear to be dependant on some form of disturbance for recruitment and are capable of continuous *in situ* regeneration and growth in the range of environments. Inside conserved areas, the visible pruning of palatable species and the presence of a distinct browse line at 1.6 m, indicates that ungulate browsing may be responsible for the low recruitment of many species. This is confirmed by data indicating that regeneration of both canopy dominants is high in nearby undisturbed forests with no browsers, also eliminating the possibility that these forests might depend on unusual climatic conditions for episodic recruitment. Even inside conserved areas, various species' regeneration was strongly negatively correlated with browsing pressure (i.e. palatability). Finally, nearly all planted seedlings were browsed in a six month period, indicating unusually high browsing levels. It seems likely that in conserved Sand Forest, similarly high densities of antelope over the long term are likely to cause the decline and loss of the most palatable species, probably considerably degrading the conservation value of these forests.

The importance of ungulate browsers in dry tropical and subtropical forests has received little attention (Dirzo & Domínguez 1995). However, browser biomass in dry tropical forests can exceed 2000 kg km⁻² (Karanth & Sunquist 1992), substantially higher than average values of 300 kg km⁻² recorded in lowland rain forest (Coley & Barone 1996). Even when total leaf damage caused by ground-living browsers is only a fraction of the damage caused by folivorous insects and arboreal vertebrates (Janzen 1981; Coley & Barone 1996), browsing can affect recruitment, changing forest structure and composition over time (Coley & Barone 1996). Reduction in seedling growth and survival caused by terrestrial mammalian herbivores has been observed in a few African tropical dry forests (Tsingalia 1989; Swaine *et al.* 1990), but appears not to have been noted in dry forests elsewhere (e.g. Gerhardt 1993; Dirzo & Domínguez 1995; Gerhardt 1996). Given the already low seedling recruitment as a result of harsh dry forest environments (e.g. Lieberman & Li 1992; Gerhardt 1993; Gerhardt 1996, and this thesis) it seems likely that in many conserved dry forests, even moderate browser biomass could have large impacts, and the negative impacts of high browsing pressure may be widespread.

Sand Forest in a local context

Floristic uniqueness and affinities

Although the Sand Forests of north-eastern KwaZulu and southern Mozambique are allied to dry forests of the coastal plain stretching through Mozambique, Tanzania and into Kenya (Tinley 1967; Tinley 1977; Moll & White 1978; Burgess & Clarke 2000, see Chapter 2), southern African Sand Forest does not simply represent the depauperate southernmost distribution of tropical dry forest on the east coast of Africa. Sand Forest in South Africa has a unique and distinctive species composition (Chapter 2), is one of the most important vegetation types in the Maputaland Centre of Endemism, and contains a large number of endemics and near endemics (van Wyk 1994a; van Wyk 1994b; van Wyk & Smith 2001). Nonetheless, we currently know virtually nothing about the southern Mozambican dry forest flora.

Evidence for the existence of allelopathy in Sand Forest

Matthew *et al.* (2001) and van Wyk & Smith (2001) have suggested that allelopathy in Sand Forest species may affect plant germination, survival and growth in Sand Forest soils, and is likely to play a role in the formation of the distinctive rings of bare sand on the margin of Sand Forest patches in the Tembe region and southern Mozambique. Matthews' *et al.* (2001) implies that it may even be an adaptive response to reduce grass cover at forest boundaries and hence exclude fire. This group selectionist argument, which implies a coordinated evolutionary response by a group of species, is unsubstantiated by the authors. The strips with low grass density at the edge of many Sand Forest patches may simply correspond to the root zone of forest trees, with the typically high fine root density of dry forest trees near the soil surface (e.g. Gerhardt 1996) outcompeting grasses. Certainly, I found no evidence of allelopathic effects, and in a pot-based greenhouse experiment, lower germination and survival on Sand Forest soils compared to adjacent savanna soils could be attributed entirely to soil water-repellency, an affect which was entirely eliminated by treatment with wetting agent.

Sand Forest conservation and research

Dry forests in general, and Sand Forest in particular, are extremely poorly known. A list of interesting ecological questions would fill dozens of pages. However, I feel that the evidence presented in this thesis has a few immediate implications for research, conservation and management in Sand Forest:

1. In order to properly conserve the full range of Sand Forest in South Africa, it is likely that a higher proportion of the drier, shorter Western Sand Forest subtype will need to be conserved. A thorough survey of the Mozambican range of Sand Forest is urgently required in order to properly set conservation targets across the region.
2. Large scale disturbance by fire does not appear be necessary to maintain forest diversity at a patch or whole forest scale, and should be avoided.

3. Differential response by tree species to varying degrees of canopy openness means that even changes in the small-scale disturbance regime, such as would be caused by elephant, are likely to alter forest species composition, structure and function, and should be minimised if possible. More canopy openings are likely to favour common light-demanding species at the expense of more shade-tolerant canopy species, such as *C. schlechteri*.
4. The impact of continuous browsing pressure by antelope in conserved areas in a system with naturally low seedling establishment and growth appears to be responsible for the absence of regeneration in a range of Sand Forest species, including the most important dominant species, and is likely to result in negative population growth over the long-term. This could cause dramatic changes in what appears to have been a very stable ecosystem until recently. Perhaps the most immediate way to confirm the negative impacts of high browsing pressure would be a comparison of the composition and species richness of the herbaceous ground layer and woody flora in undisturbed but unbrowsed forests outside of formally conserved areas with those inside conserved areas. However, I feel the evidence presented in this thesis is convincing enough to recommend localised culling to reduce antelope numbers inside Sand Forest. In the longer term, a research program to obtain a full range of demographic parameters under different management scenarios for important species is necessary.
5. Low juvenile and adult growth rates suggest that even moderate continuous harvesting of adult trees on communal lands outside of conserved areas is likely to be unsustainable, leading to loss of a valuable resource even if resprouting prevents the extinction of harvested species. Again, a more thorough knowledge of population dynamics is vital in order to properly manage harvested species.

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