Regeneration failure and the *Acacia karroo* successional pathway in coastal dune forests in KwaZulu-Natal, South Africa

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Submitted in fulfilment of the academic
requirements for the degree of
MASTER OF SCIENCE
in the Discipline Ecology
in the
School of Biological and Conservation Science
University of KwaZulu-Natal

Pietermaritzburg
2007

This project was carried out within the

Forest Biodiversity Research Unit

School of Biological and Conservation Sciences
University of KwaZulu-Natal, Pietermaritzburg

FOREST
BIODIVERSITY
RESEARCH UNIT
UNIVERSITY OF
KWAZULU-NATAL

By never making it to where I wanted to go, I ended up where I wanted to be

Abstract

Monospecific stands of *Acacia karroo* establish naturally on disturbed coastal dunes in KwaZulu-Natal, South Africa. While the *A. karroo* successional pathway is successful in rehabilitating mined dunes at the Richards Bay Minerals mining company (RBM), the same pathway has become arrested in the coastal dune forest at Cape Vidal in the Greater St. Lucia Wetland Park. This study examines the efficacy of the *A. karroo* successional pathway for restoring disturbed coastal dune forests.

Dispersal of seeds and successful recruitment of seedlings are essential for habitat restoration. Seed and seedling banks were compared between previously disturbed *A. karroo* stands and adjacent forest at Cape Vidal. Different seed bank composition and higher seed bank richness in the forest suggest that seed dispersal into *A. karroo* stands is limited. Protected seed banks in *A. karroo* stands had increased seedling richness, indicating that dispersal limitation does not fully explain the lack of seedling establishment. At RBM, the seed bank richness of *A. karroo* stands increased with age since mining. While cumulative species richness of the seed bank of the oldest *A. karroo* stand at RBM was marginally lower than that at Cape Vidal, successful rehabilitation at RBM is associated with low seedling mortality. Consequently, forest tree species richness is high at RBM in the *A. karroo* stands and is converging on natural forest richness and composition. Although seed dispersal is reduced, it does not totally limit establishment of forest tree species in *A. karroo* stands at Cape Vidal, which implicates a post-establishment factor.

Soil fertility potentially reduces seed germination and seedling growth. Soil nutrients in *A. karroo* stands at Cape Vidal were similar to those in the adjacent forest, and total nitrogen levels in *A. karroo* stands at Cape Vidal were higher than at RBM. Thus, soil conditions were unlikely to be limiting tree regeneration in *A. karroo* stands. Total nitrogen accumulated in the oldest stand at RBM at a rate of $10.0\ g.m^2.yr^{-1}$ and a similarly rapid rate occurred at Cape Vidal. Therefore the *A. karroo* stands were not nitrogen limited. Nitrogen supplementation experiments at Cape Vidal demonstrated that a range of forest tree species establish in *A. karroo* stands regardless of nitrogen level, but there is low survival of seedlings. Thus, nitrogen availability is not arresting succession at Cape Vidal.

Herbivory can also inhibit seedling recruitment. Selective feeding may enhance the persistence of species with defences against herbivory, such as *A. karroo*, ultimately altering the tree community composition. Browsing and trampling by large mammalian herbivores in *A. karroo* stands at Cape Vidal decreased survival and growth of forest tree seedlings. Large herbivores such as kudu, waterbuck, bushbuck and red duiker preferentially used the *A. karroo* stands as they offer abundant food and their topography allowed easy movement. This top-down pressure reduced recruitment, growth, and survival of seedlings of undefended species. Few wild herbivores occur at RBM, which allowed succession to proceed unhindered, ultimately restoring coastal dune forest at this site.

Despite successful rehabilitation of coastal dune forest on mined dunes at RBM, limited seed dispersal and high levels of herbivory have arrested succession at Cape Vidal. Thus, the *A. karroo* successional pathway must be implemented only after careful consideration of site-specific factors such as distance to a source of propagules and the intensity of herbivory in the system. In areas where herbivore densities are high, management interventions focusing on reducing herbivory and encouraging visitation by seed dispersers are necessary for the successful use of this successional pathway.

Preface

The experimental work described in this dissertation was conducted in the Forest Biodiversity Research Unit in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, from January 2004 to July 2006, under the supervision of Prof. M.J. Lawes and Dr M.E. Griffiths. The study represents original work by the author and has not been submitted in any form to another university. Where use has been made of the work of others, it is duly acknowledged in the text.

The thesis is compiled as a collection of papers (apart from the Introduction - Chapter 1, and Summary - Chapter 5) and the chapters are formatted in accordance with the journal *Applied Vegetation Science*. The chapters depart from this format in the following areas: (1) tables and figures appear in the text and not separately at the end of each chapter; (2) only one acknowledgements section appears at the beginning of the dissertation; and (3) the study site is outlined in detail only in Chapter 2 to reduce repetition.

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March 2007

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Acknowledgements

This project would not have been possible without the assistance, advice and support of many people and organisations. I have tried to mention you all (in no particular order), but to those I may have omitted, I apologise - you are no less appreciated!

A special thanks to my supervisors, Prof. M.J. Lawes and Dr M.E. Griffiths for their guidance, patience, and for encouraging me to achieve higher standards. Thank you to Prof. Lawes who provided a grantholder NRF (National Research Foundation) bursary and a subsistence bursary. The Gay Langmuir Foundation also provided financial support. I'm very grateful to Megan for her tireless proof-reading and moral support.

Dr A. Manson provided invaluable interpretation and insight to soil fertility data and on soil ecology in general. Thanks to Dr. J. Kotze for his much needed help with discriminant function analysis. I'm grateful to Essack Abib in the Soil Science Dept. at UKZN for his help and patience with me in his lab while analysing countless soil samples.

Alastair Cambell, Stephanie Pollock, Cathrine Perrier, Adam Shuttleworth and many other long-suffering friends provided invaluable, enthusiastic field assistance that made fieldwork entertaining, providing comic relief during many sense-of-humour failures. A very special thank you to Andrew Booth for his moral support and encouragement throughout this and for his sense of reason when mine abandoned me!

Many thanks to the Ezemvelo KZN Wildlife (EKZNW) staff at St. Lucia, particularly Ricky Taylor, Caroline Fox and Leo Frankell who provided support throughout this study. Thanks to EKZNW for allowing me to conduct my fieldwork within the Greater St. Lucia Wetland Park. Thanks to Richards Bay Minerals (RBM) for allowing me to conduct fieldwork in their rehab sites and to Rynhard Kok for facilitating this fieldwork. Also a special thank you to Mr and Mrs Cameron for their kindness and welcoming me into their home for the duration of fieldwork conducted at RBM.

To my family and friends who believed in me when I did not and helped me to believe that I could do this, a huge thank you. I would have given up long ago without your support and faith in me! Last but not least, my parents instilled in me a love of nature and allowed me to follow my interests, which lead me down this road. Mom and Dad, thank you - this is for you.

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Chapter 1

Introduction

Natural and anthropogenic disturbance in coastal dune forests in northern KwaZulu-Natal, South Africa, is resulting in increasingly fragmented patches of undisturbed forest. The Cape Vidal coastal dune forests have been subjected to a long history of anthropogenic disturbance, resulting in the establishment of a number of monospecific *Acacia karroo* stands in previously settled sites. This is the first stage in a successional pathway towards forest. The process appears to be arrested at Cape Vidal as there are no signs of vegetation community convergence between undisturbed forest and *A. karroo* stands after 50 years. Just south of Cape Vidal, the Richards Bay Minerals mining company (RBM) has been strip-mining coastal dunes around Richards Bay since 1976. Mined sites are rehabilitated using *A. karroo*, resulting in monospecific *A. karroo* stands of known age in which the stages of the successional process can be monitored. Unlike at Cape Vidal, the *A. karroo* stands at RBM are showing signs of succession of forest vegetation, and complete restoration of forest is expected to occur within 54 – 70 years (Mentis & Ellery 1998; Wassenaar 2003). This project addresses the reasons for successional failure at Cape Vidal; specifically why the *A. karroo* pathway facilitates succession at RBM but not at Cape Vidal.

Disturbance and succession

Disturbances are events that disrupt an ecosystem, community, or population, and alter the resource availability, substrate, and/or nature of the physical environment (Pickett & White 1985). Natural disturbances such as wind blows, tree-falls and fires affect the composition and structure of communities (Gotelli 2001) by creating heterogeneity and increasing species richness as niches become available for colonization by new species. Following disturbance, natural communities undergo the complex process of species succession, during which the community composition re-assembles (Gotelli 2001). Succession is categorized as primary succession when it occurs on sterile locations, such as volcanic sites and glaciers, where vegetation is establishing for the first time; and as secondary succession when it occurs on disturbed sites where the vegetation community has been disrupted and must re-assemble (Clements 1916). This study deals specifically with secondary succession of forest vegetation following disturbance in coastal dune forests in north-eastern South Africa.

Succession was originally recognised as an ecological process in 1899 (Cowles 1899), and has remained a contentious topic ever since. According to early successional theory (the so-called Clementsian view), all disturbances on a particular site should lead to successional species sequences ultimately resulting in similar community species compositions (Clements 1916; Clements 1936). Although many others proposed alternative approaches to succession that acknowledged the role of immigration of plant propagules and the past and prevailing environmental conditions (Gleason 1926; Tansley 1935), Clementsian successional theory remained popular until the 1950s. Later, Connell & Slayter (1977) argued that very different species compositions could be produced by succession at one site, in which case an ecosystem has multiple stable points. The latter is more consistent with modern thinking where ecosystems are considered as dynamic, and disturbance to an otherwise stable plant community may result in the development and establishment of a different community composition (Seabloom & Richards 2003).

Connell & Slayter (1977) also introduced the facilitation, tolerance and inhibition models of succession. Facilitation occurs when colonisation of later successional species is dependent on the earlier species preparing and improving the growing conditions. Tolerance occurs when species do not compete for the same resources, enabling them to co-exist. The inhibition model suggests that early successional species prevent colonisation by later species by dominating the resources. The model followed by succession will depend on the characteristics of the early colonisers, and the abiotic and biotic environment (Connell & Slayter 1977).

The particular nature of the successional process is determined by factors such as the intensity and frequency of disturbances, and the habitat type in which the disturbance occurs (Pickett & White 1985). The extent and severity in time and space of the disturbance influences the duration of succession, with long-lasting and more severe disturbances theoretically more likely to result in a final species composition different to the pre-disturbance composition (Connell & Slayter 1977). For a disturbed site to return to its original vegetation community structure and function, a number of processes must occur, including seed dispersal, avoidance of seed predation, successful germination, as well as the growth and survival of seedlings (Holl et al. 2000).

Recruitment limitation

Recruitment limitation is the failure of all potentially colonisable sites to receive propagules from all competing species and/or failure for propagules to germinate or establish, resulting in reduced species abundance (Muller-Landau et al. 2002). This can affect either the seed or seedling stage of plant growth and, like Muller-Landau et al. (2002), recruitment limitation will be used in this thesis in the context of limitation of either seed or seedling stages by any abiotic or biotic factor that prevents the plant from arriving and establishing. If any of the requirements for successful community restoration mentioned previously are not met, recruitment will be limited and forest recovery interrupted.

Seed limitation can occur as a result of low fruit production in the source population, limited dispersal by frugivores, or seeds not being dispersed to suitable microsites for establishment (Jordano & Godoy 2002). Disturbed areas have generally had some or all of their vegetation removed and the availability of reproductively mature trees is low (Duncan & Chapman 2002). Under these conditions, regeneration of the plant community is dependent on seeds already present in the seed bank and those dispersed from mature trees in nearby undisturbed habitat. However, seeds of forest trees typically have no dormancy and so viable seeds are not abundantly present in the forest seed bank (Garwood 1989; Khurana & Singh 2001; Fenner & Thompson 2005). Thus, successful regeneration becomes increasingly dependent on wind and animal seed dispersal (Corlett 2002; Duncan & Chapman 2002).

Seed dispersal has important consequences in terms of the fitness of individual trees, but it also has ecological consequences for population and community structure (Willson 1992). The vegetation population structure of a habitat is determined by the gene-flow created by seeds arriving in and leaving the habitat. The community structure is determined by what species are able to colonise the area, therefore dispersal mode influences how a vegetation community develops (Willson 1992). The majority of tropical forest trees produce seeds with adaptations for animal dispersal (Howe 1984; Stiles 1992; Wunderle 1997) and this is the case for the coastal dune forest species in this study (Griffiths & Lawes 2006). This emphasises the vital role played by frugivorous birds, bats and terrestrial mammals as seed dispersers in the regeneration of disturbed areas (Wunderle 1997). Seed dispersal into disturbed habitats is often limited, and is known to reduce the rate of succession (Aide et al. 1995; Holl 1999; Holl et al. 2000). Seed dispersal limitation can arise when disturbed patches are isolated from a seed source (Wunderle 1997), or by low availability of perches for birds acting as seed dispersers (Zanini & Ganade 2005), resulting in few visitations to the disturbed habitat.

For the reason that forest species' seeds seldom show dormancy, forests are often dependent on the seedling bank rather than the seed bank for regeneration (Garwood 1989; Pickett & McDonnell 1989; Wassie & Teketay 2006). Seedlings can remain in the forest understory for a few to over a hundred years, until such time as resources become available to complete their life-cycle (Barden 1979; Canham 1985; Canham 1990). This "advanced regeneration" allows habitats to begin regeneration rapidly following a disturbance.

Successful seed germination and recruitment of seedlings into the seedling bank is dependent on the quality of the microsite (Clark et al. 1999). This is determined by abiotic and biotic factors such as soil fertility, sufficient light availability, and the absence of predation (Holl et al. 2000; Khurana & Singh 2001). When community composition and structure are limited by abiotic factors such as the availability of soil nutrients, it is considered to be a "bottom-up" controlled system (Hunter & Price 1992). The availability of essential soil nutrients such as carbon, nitrogen, phosphorous and water, influences plant growth, and in doing so, can direct the successional process (Tilman 1987). Of these, nitrogen is an important limiting nutrient affecting species composition and richness, and it is often limiting in secondary succession (Tilman 1986; Tilman 1987; Holl et al. 2000). Many early successional species are particularly tolerant of low soil nitrogen conditions (Tilman 1987; van Aarde et al. 1998), allowing them to establish at early stages of succession when conditions are unfavourable for most species. Only once soil nitrogen has accumulated, can secondary successional species begin to establish (Crawley 1997). Thus, large amounts of nitrogen added to the soil by nitrogen-fixing species that establish during primary and secondary succession, facilitate colonization by later successional species (Gerlach et al. 1994). This sequence of events is an example of succession via the facilitation model described by Connell & Slayter (1977).

Microsites may also be unfavourable for recruitment of seedlings into the adult vegetation as a result of biotic interactions such as herbivory (Clark et al. 1999). Restriction of the vegetation community by herbivores is regarded as "top-down" control (Hunter & Price 1992). The direct (herbivory and trampling) and indirect effects (increased light availability) of herbivores selectively feeding on and moving through favoured vegetation types, can inhibit plant growth and increase seedling mortality (Plumptre 1993). Seedling survival increases when herbivores are excluded (Dlott & Turkington 2000; van der Wal et al. 2000) and seedlings may be particularly sensitive to herbivory (Huntly 1991). Many studies demonstrate the negative effects of browsing and trampling by large mammalian herbivores on seedling growth and survival (McInnes et al. 1992; Molofsky & Fisher 1993; Plumptre 1993; Terborgh & Wright 1994; Dlott & Turkington 2000; Liang & Seagle 2002; Lawes & Chapman 2006), which ultimately results in a modified forest canopy composition (Huntly 1991; Augustine & McNaughton 1998). Thus the direct and indirect effects of herbivory may cause arrested succession in disturbed forest habitats.

In addition to herbivory, competition with understory herb species is known to suppress or arrest regeneration of canopy tree species (George & Bazzaz 1999; Griffiths et al. in press). This "ecological filter" affects the composition, diversity and abundance of the seedling bank by limiting establishment of certain species. Thus it is evident that recruitment can be limited at different stages of plant life by a variety of different abiotic and biotic factors and succession does not always successfully restore plant communities.

Disturbance and succession on coastal dunes

Two distinctly different secondary successional trajectories have been described for the recovery of disturbed coastal dunes to fully restored coastal dune forest in northern KwaZulu-Natal: the bush-clump pathway and the *Acacia karroo* pathway (von Maltitz et al. 1996). The bush-clump pathway is initiated beneath individual trees within abandoned grasslands or cleared fields (von Maltitz et al. 1996). These trees are often located on old termite mounds or in other fire-safe sites in the grassland. These facilitator trees, often *Syzygium cordatum*, *Garcinia livingstonei* or *Phoenix reclinata* individuals, have fleshy fruits that are attractive to birds and mammals, are fire tolerant, have rapid growth rates and reach maturity rapidly (von Maltitz et al. 1996). Bird- or mammal-dispersed species establish beneath the tree, facilitated by the shade, increased moisture, and protection from fire provided by the tree. As the bush clumps develop, grasses are excluded, the risk of fire entering the clumps decreases, and fire-sensitive species can establish. With time, these bush clumps expand, eventually merging with other bush clumps to form continuous forest patches.

In contrast, the *A. karroo* pathway is initiated by the establishment of single cohort, even-aged stands of *A. karroo* trees in areas of recent disturbance (Camp & Weisser 1991). *Acacia karroo* has many different growth forms and the coastal variety is often referred to as *A. kosiensis* (Coates Palgrave 2002). In this thesis it will be referred to as *A. karroo*, however, as no concrete genetic evidence has shown it to be a separate species (Mboumba & Ward submitted). These trees typically have a main stem of up to 20 m tall, with a broad, spreading crown (Pooley 2003). *Acacia karroo* reputedly facilitates the establishment of forest tree species by improving the growing conditions (Lubke et al. 1996). Approximately 25 years after establishment, the *A. karroo* trees begin to senesce and die, and are replaced by pioneer forest species, such as *Celtis africana*, *Teclea gerrardii*, *Clausena anisata* and *Ziziphus mucronata* (von Maltitz et al. 1996). Such species become increasingly dominant, resulting in a shift in community composition and an increase in species diversity in the stands as time since disturbance increases. Eventually mature forest tree species replace the pioneer species and the *A. karroo* stands return to mature dune forest condition.

Role of Acacia karroo *in succession*

Acacia karroo woodland is a natural ecotope of coastal dunes in KwaZulu-Natal (Weisser & Marques 1979), but is commonly associated with former human settlements, wind-blows and sites of anthropogenic disturbance (Weisser & Marques 1979; van Aarde et al. 1996; Mentis & Ellery 1998; West et al. 2000; Wassenaar 2003). This species is known for its ability to rapidly colonise areas where coastal forests and grasslands have been disturbed. Using aerial photographs of the area between Richards Bay and the Mfolozi River taken at 37-year intervals, Weisser & Marques (1979) established that disturbed grassland developed into *A. karroo* woodlands within 25 – 60 years, and proceeded to secondary dune forest within an additional 30 – 150 years. However, more recent studies of the convergence of biotic and abiotic communities in these mined sites on a benchmark forest condition (Mentis & Ellery 1998; Wassenaar 2003) suggest that these *A. karroo* stands approach climax dune forest condition within 54 – 80 years. At present, the *A. karroo* pathway is thought to be the easiest secondary successional pathway for dune rehabilitation after mining because of the rapid growth rate and high seed production rate of *A. karroo* (Lubke et al. 1996).

As nitrogen-fixing species, Acacias have an advantage over many other woody plants in the early stages of primary and secondary succession when soil nitrogen levels may be low (Tilman 1986; Tilman 1987). Photosynthesis, growth and reproduction are dependent on the presence of large amounts of nitrogen in the soil (Barbour et al. 1999). Experiments have shown that woody plants cannot invade successional communities until nitrogen pools of 400 – 1200 kg·ha^{-1} have accumulated in the soil (Crawley 1997). Thus, nitrogen may be a limiting nutrient for woody plants in the early stages of succession. Many early colonizing plant species are capable of fixing nitrogen and therefore can exploit soils with low nitrogen levels where other species are excluded. These species also add substantial quantities of nitrogen to the soil pool and, in doing so, modify the soil environment so that it is more favourable for plant growth (Lubke et al. 1996). For this reason, nitrogen-fixing species are successful early successional species, and facilitate invasion and colonization by secondary successional species. *Acacia karroo* is a nitrogen-fixing species with root nodules present (pers. obs.), thus enabling it to facilitate succession by improving soil conditions.

The RBM mining company has been using *A. karroo* to facilitate dune forest recovery on mined dunes in Richards Bay on the north-eastern coast of KwaZulu-Natal since 1976 (Camp & Weisser 1991; Lubke et al. 1996; van Aarde et al. 1996; von Maltitz et al. 1996). A recent study conducted on these mined dunes of the trajectories of plant, invertebrate and vertebrate species assemblages relative to a benchmark undisturbed forest, indicated that communities do converge with those of undisturbed habitats after a period of recovery (Wassenaar et al. 2005). The average convergence time from a cleared, mined dune was 41 years, with the relative abundance and composition of tree species reaching the benchmark level within 38 – 41 years. In addition, soil nutrient levels, including nitrogen, increased with time since disturbance (van Aarde et al. 1998; Wassenaar et al. 2005). This age-related increase in soil nutrient levels potentially facilitates the establishment of forest tree species as succession progresses and conditions improve. These studies indicate that the *A. karroo* pathway is proceeding to coastal dune forest at the RBM site.

Coastal dune forest succession at Cape Vidal

Human settlements were located in the Cape Vidal coastal dune forests until 1952 (Weisser & Muller 1983). These settlements were relocated from the Greater St. Lucia Wetland Park, leaving disturbed patches in the dune slacks with a history of slash-and-burn agriculture. These patches were naturally colonised by even-aged cohorts of *A. karroo* individuals, which initiated the secondary successional pathway towards re-established coastal dune forest (von Maltitz et al. 1996).

Although the *A. karroo* pathway seems to be successfully restoring mined dunes at RBM (Camp & Weisser 1991; Mentis & Ellery 1994; Lubke et al. 1996; van Aarde et al. 1996; Mentis & Ellery 1998), this successional pathway appears to have broken down at Cape Vidal. Here, the *A. karroo* stands are more than 50 years old and although they are showing signs of senescence, typical coastal dune forest tree species are poorly represented in the stands (West et al. 2000). The *A. karroo* individuals appear to be replacing themselves and there is little evidence of dune forest succession within these *A. karroo* stands. This is despite being surrounded by mature dune forest with easy seed dispersal opportunity via wind- and animal-dispersal. In addition, stands that do progress to secondary dune forest do not regain a large proportion of their original plant species diversity, and so do not progress to fully restored dune forest (West et al. 2000). Due to the *A. karroo* successional pathway resulting in decreased species diversity at sites like Cape Vidal, von Maltitz et al. (1996) prefer the bush-clump pathway for rehabilitation of coastal dune forest that promotes seed dispersal and habitat heterogeneity.

Given these findings, the efficacy of the *A. karroo* successional pathway for rehabilitation of coastal dune forest vegetation has been questioned (West et al. 2000). Regardless of the potentially facilitative role that *A. karroo* plays in secondary succession and rehabilitation of mined dunes, species diversity in the *A. karroo* stands at Cape Vidal is low more than 50 years after disturbance and recovery of dune forests via the *A. karroo* successional pathway is relatively slow.

Summary

Few studies test the complex interactions between abiotic and biotic factors that affect the direction and rate of recovery of disturbed habitats (Holl et al. 2000). This thesis addresses the role of *A. karroo* in forest succession on disturbed coastal dunes with the objective to determine whether it is effective at restoring plant community diversity in disturbed areas. This will increase our knowledge of succession on coastal dunes so that informed management of naturally and anthropogenically disturbed coastal dune forests can be ensured. Specifically, I examine three possible hypotheses proposed to explain the arrested dune forest succession in *A. karroo* stands; namely the potential existence and effects of (1) recruitment limitation, (2) soil nitrogen limitation, and (3) herbivory and trampling of forest seedlings, on the growth and survival of seedlings and the process of forest succession in disturbed dune forest. In addition, I consider the effect that *A. karroo* stands themselves play in constraining dune forest recovery. The relative role of each ecological factor in shaping the vegetation community structure and slowing the rate at which regeneration is occurring at Cape Vidal, is examined in detail. These factors are not mutually exclusive and the slow rate of recovery may be a result of complex interactions between them. A long-standing debate exists as to the importance of top-down or bottom-up forces in controlling ecosystems. This study examines some of these principles and how they affect a natural (Cape Vidal) and managed (RBM) successional system.

Objectives of this Study

1. To compare the relative rates of regeneration of *A. karroo* dominated coastal dune forest at Cape Vidal with previously mined sites at RBM. In particular, to determine the factors limiting the rate of dune forest recovery after disturbance in dune forest in the Greater St. Lucia Wetland Park, compared to the rapid recovery, via the *A. karroo* successional pathway, of mined dune sites near Richards Bay.
2. To examine three possible mechanisms (recruitment limitation, soil nutrients, and herbivory) proposed to explain the low diversity of forest species in *A. karroo* stands and the apparent regeneration failure of the *A. karroo* pathway at Cape Vidal, using a combination of field and greenhouse experiments. The proposition that *A. karroo* facilitates forest tree succession by initially colonising disturbed areas and improving

the soil conditions such that they become more suitable for pioneer, and eventually for mature forest species, will also be examined.

3. In addition, I examine the hypothesis that *A. karroo* seedlings have greater survival and growth in the dune slacks than a typical pioneer forest species (*Celtis africana*) or a climax forest species (*Diospyros natalensis*), and may out-compete these species when other disturbance effects, such as herbivory are controlled for. I also examine the converse that the pioneer and climax forest species survive and grow better in the more shaded dune forest than *A. karroo*.
4. To examine whether the arrested nature of the succession is due to some feature of dune slacks themselves, and is correlated with the presence and effect of *A. karroo* in the dune slacks i.e., that *A. karroo* itself arrests succession.

Thesis Outline

Chapter 1 is a general introduction describing the two successional pathways that are suggested to occur on coastal dunes in KwaZulu-Natal, South Africa. The role played by *A. karroo* in succession towards climax dune forest and the rate of naturally occurring regeneration via the *A. karroo* pathway at Cape Vidal is discussed. Three potential explanations for this relatively slow succession are proposed, and the literature is reviewed.

Chapter 2 examines the possibility that limited seed dispersal and establishment of seedlings is limiting recruitment and interrupting succession at Cape Vidal. Seed dispersal is critical in the regeneration of disturbed habitats and diversity cannot be restored until the full complement of tree species propagules have been returned to the habitat via various dispersal mechanisms. Germination trials and seedling surveys were conducted at Cape Vidal and RBM to compare the seed and seedling banks of the two habitats where succession is proceeding via the *A. karroo* pathway.

Chapter 3 examines the soil fertility and nitrogen levels in the forest and *A. karroo* stands at Cape Vidal and different aged *A. karroo* stands at RBM. As a nitrogen-fixing species, *A. karroo* has a competitive advantage in nitrogen-limited environments, which could explain its dominance in the dune slacks at Cape Vidal. The soil nitrogen levels and rates of nitrogen mineralization are determined for both Cape Vidal habitats (forest and *A. karroo* stands) as well as for the *A. karroo* stands at RBM.

Chapter 4 deals with the possibility that herbivory and trampling may be reducing growth and survival of forest tree species in the *A. karroo* stands at Cape Vidal so that succession cannot proceed towards fully restored dune forest. Exclosure plots are used to compare the effects of herbivory on various tree species seedlings in the *A. karroo* stands and adjacent forests at Cape Vidal, and herbivore density estimates are compared between these two habitats at Cape Vidal, and among the *A. karroo* stands at Cape Vidal and RBM.

Chapter 5 summarises the findings of this thesis relating to three possible explanations for the apparent regeneration failure at Cape Vidal. General results are discussed in the context of previous studies. The potential success of the rehabilitation programme at RBM is re-examined in light of findings from Cape Vidal, as are the general mechanisms of succession on coastal dunes in northern KwaZulu-Natal. Some management guidelines are suggested for regenerating areas such as Cape Vidal.

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Chapter 2

Roles of seed dispersal and seedling recruitment in arrested succession of disturbed coastal dune forest

Abstract

Question: Is seed dispersal into disturbed sites following *Acacia karroo* establishment limited? Is poor microsite quality limiting seed germination and seedling survival in *A. karroo* stands at Cape Vidal?

Location: Cape Vidal and Richards Bay Minerals mining lease areas (RBM), northern KwaZulu-Natal, South Africa.

Methods: I examined the seed and seedling bank of *A. karroo* stands and adjacent forest at Cape Vidal, and those of three *A. karroo* stands of varying age (7 – 27 years old) since rehabilitation at RBM. Experimental treatment plots were used to monitor the establishment and growth of planted and *in situ* seedlings.

Results: The seed bank community in *A. karroo* stands and adjacent forests at Cape Vidal was different 50 years post-disturbance. Seed bank species richness and abundance in *A. karroo* stands at RBM showed an age-related increase. Growth of planted seedlings in both habitats at Cape Vidal were unchanged by nutrient enrichment, but species richness and abundance of *in situ* seedlings increased over time in the absence of herbivory, particularly in the *A. karroo* stands.

Conclusions: Not all propagules of forest tree species reach the *A. karroo* stands at Cape Vidal. However, a range of forest seedling species were able to establish and grow in the *A. karroo* stands in the absence of herbivory. There is a reduced role for seed dispersal limitation as a major cause of regeneration failure at Cape Vidal and it is clear that a post-dispersal factor affecting seedling survival limits recruitment and potentially arrests succession in *A. karroo* stands.

Keywords: *Acacia karroo*; Cape Vidal; microsite quality; Richards Bay Minerals; regeneration; seed bank; seedling bank; seedling emergence.

Nomenclature: Coates Palgrave (2002).

Abbreviations: ANOVA = analysis of variance; LAN = Limestone Ammonium Nitrate; MRPP = multi-response permutation procedure; RBM = Richards Bay Minerals mining lease areas.

Introduction

Recruitment dynamics have a large impact on the manner in which vegetation communities assemble (Clark et al. 1999), and forest regeneration can be affected by the two mechanisms that limit recruitment. First, dispersal limitation may arise where seed supply is disrupted, low or uncertain, for example where the seed production or seed delivery or both is insufficient to saturate microsites (Jordano & Godoy 2002). Second, recruitment limitation can arise where post-dispersal effects prevent seedling establishment. Factors affecting growth and mortality in seed banks and seedling stages are potentially limiting, such as distribution and quality of microsites. Mechanisms of seed dispersal limitation cause reduced seed bank diversity and abundance, whereas light availability, competition, low soil nutrients and seed and seedling predation are all post-dispersal factors affecting the quality of the microsites, restricting growth and survival or the recruitment of seedlings (Holl et al. 2000). Limited seed dispersal and establishment in forests are both known to reduce the rate of forest succession, or even arrest it completely (da Silva et al. 1996; Holl 1999; Holl et al. 2000).

At Cape Vidal, parts of the coastal dune forest were once settled by subsistence farmers (Weisser & Marques 1979; Weisser & Muller 1983). Following relocation of the settlements in the 1950s, *Acacia karroo* stands established naturally, which initiated the *A. karroo* successional pathway (von Maltitz et al. 1996). The *A. karroo* trees senesce and die after approximately 25 years, giving way to pioneer forest species and eventually to mature forest tree species. Despite evidence that this pathway successfully restores mined dunes at Richards Bay (70 km south of Cape Vidal) within 54 – 70 years (Mentis & Ellery 1998; Wassenaar et al. 2005), the disturbed areas in the dune slacks at Cape Vidal remain species-poor more than 50 years post-disturbance (West et al. 2000). *Acacia karroo* trees in the slacks are senescing, but rather than forest pioneer species establishing in their place. The senescing individuals are being replaced by young *A. karroo* individuals. Thus the *A. karroo* successional pathway appears to have been arrested at Cape Vidal and coastal dune forest regeneration has failed.

The low availability of reproductively mature trees in disturbed habitats like the *A. karroo* stands at Cape Vidal can result in low local seed production and seedling communities whose diversity is solely dependent on dispersal (Duncan & Chapman 2002). In addition to this, 40% of the forest trees at Cape Vidal are known to reproduce vegetatively (Nzunda et al. In press) and have relatively small seed crops and depauperate seed banks (Bond & Midgely 2001). Thus seed availability is naturally low at Cape Vidal, and may result in low levels of seedling recruitment. A possible explanation for regeneration failure at Cape Vidal is therefore that seed dispersal into the previously disturbed *A. karroo* stands is limited, slowing recruitment of individuals into the seedling bank. The species diversity of seeds dispersed into disturbed regions is dependent on the size and composition of the species pool from which dispersed seeds originate (da Silva et al. 1996). We might expect the seed and seedling banks of the narrow (50 – 100 m wide) *A. karroo* stands at Cape Vidal, which are surrounded by mature coastal dune forest, to comprise similar forest tree species propagules. The mature vegetation in these stands is dominated by *A. karroo*, which is likely to be reflected in the seed bank species composition.

While seed diversity is determined by the composition of the source population, seed abundance is determined by the efficiency of dispersal vectors. Disruption of the soil seed bank by disturbance means that regeneration is increasingly dependent on dispersal of seeds by vectors such as birds and mammals (Corlett 2002). In addition, succession in dune slacks has been shown to be more reliant on dispersal events than on the seed bank (Bossuyt & Hermy 2004). Dispersal of seed is dependent on visitation by disperser organisms, but regeneration of disturbed sites is often associated with low seed dispersal (da Silva et al. 1996; Holl 1999). This is a direct result of the low visitation rates in disturbed areas associated with few resources available such as food and perches, presenting little incentive for frugivorous birds and mammals to enter them.

Over 90% of the forest tree species at Cape Vidal have animal-dispersed propagules (Griffiths & Lawes 2006), so this system is expected to be largely reliant on regeneration from dispersal events. However, although *Acacia* seeds and seed pods are a popular food source among large mammals (Or & Ward 2003), *A. karroo* does not have fleshy fruits, and so frugivorous birds may overlook them. In addition, birds and mammals may be at greater risk of predation in the open *A. karroo* stands and may enter them less frequently than expected (Corlett 2002; Duncan & Chapman 2002). Consequently, the potential for bird- or mammal-dispersed forest tree species establishing in the *A karroo* stands at Cape Vidal may be lower than expected, and seed banks correspondingly depauperate.

Forest species generally do not produce dormant seeds, however, (Garwood 1989; Fenner & Thompson 2005), so forests are often reliant on the seedling bank rather than the seed bank for regeneration. Under these circumstances, post-dispersal factors such as seed germination and seedling survival may be important factors affecting the diversity and structure of the regeneration community. In this study, I separate post-dispersal effects (recruitment limitation) from those of seed dispersal (dispersal limitation).

Alternatively, seed dispersal may be adequate, but factors affecting microsite quality such as seed and seedling predation (Schnurr et al. 2004), competition (van der Wal et al. 2000; Zanini & Ganade 2005) and low soil fertility (Holl 1999; Holl et al. 2000) may reduce seedling establishment, causing decreased recruitment. Both are plausible explanations for the low numbers of forest tree seedlings germinating in the *A. karroo* stands and may clarify why the vegetation community composition of the stands is not converging on that of mature forest.

In this chapter I examine the hypothesis that the relatively slow rate of forest regeneration at Cape Vidal is due to a seed dispersal limitation which reduces recruitment into the seedling bank. A comparison is made among seed and seedling banks of previously disturbed *A. karroo* stands and neighbouring forest at Cape Vidal and previously mined *A. karroo* stands of various ages since rehabilitation at Richards Bay. In doing so, the following questions are addressed: (1) is seed dispersal into disturbed sites at Cape Vidal and Richards Bay limited; and (2) is poor microsite quality causing low seedling survival and limiting recruitment from the seed bank in *A. karroo* stands at Cape Vidal? This knowledge will provide a more comprehensive understanding of the factors which limit the *A. karroo* successional pathway so that successful restoration of disturbed coastal dune forests can be implemented.

Materials and methods

Study sites

The Cape Vidal coastal dune forests (28°16'S; 32°29'E) are located in the Greater St. Lucia Wetland Park in northern KwaZulu-Natal province, South Africa. The forest is bounded by the Indian Ocean in the east and by Lake St. Lucia in the west. The site has a subtropical, humid and hot climate with a mean annual temperature of 21.5 °C and an average annual rainfall of 1 300 mm (Cape St. Lucia Weather Station; Camp & Weisser 1991; von Maltitz et al. 1996).

The coastal dunes at Cape Vidal mark the southern limit of the Mozambique coastal plain. They have deep and sandy soils of mainly granitic origins, with little clay or organic material. Due to high permeability and rapid leaching, the soil is generally low in natural fertility (Maud 1991), although the dune slacks do accumulate organic matter. The Zululand coastal dunes were vegetated by climax dune forest prior to settlement by humans 1 600 BP (Weisser & Muller 1983) and there has been an almost constant human presence in the dune forests since. However, in 1952 the last of the modern inhabitants of the dunes were relocated (Weisser & Marques 1979) to make way for afforestation. Most of the exotic tree plantations have since been removed, and the current vegetation is a mosaic of mature dune forest, monospecific *A. karroo* stands which have established on previously settled sites (Weisser & Marques 1979; West et al. 2000), secondary dune forest and grassland (von Maltitz et al. 1996). The *A. karroo* stands at Cape Vidal typically form 50 – 100 m wide, longitudinal strips in the dune slacks, and mature forest grows on the coastal dunes between the *A. karroo* stands. The stands thus occur as isolated, longitudinal patches surrounded by mature coastal dune forest vegetation. Three of these stands, at least 500 m apart, were selected for experimentation.

The mined dune sites at the Richards Bay Minerals mining company (RBM) are situated approximately 13 km north-east of Richards Bay (28°40'S; 32°14'E) along the northern coast of KwaZulu-Natal, and approximately 70 km south of Cape Vidal. Richards Bay has a humid and warm to hot subtropical climate with a slightly higher average annual rainfall than at Cape Vidal of 1650 mm (Camp & Weisser 1991).

The coastal dunes at RBM have been mined since 1977 with rehabilitation (initiated in 1978) occurring as mining is completed at each site (Camp & Weisser 1991). A wet-mining procedure is used that involves the removal of existing vegetation and the gravitational extraction of heavy metals such as ilmenite, zircon and rutile (Camp & Weisser 1991) from the dune sand. Following mining the dune sand is returned and reshaped to approximately its original topography, after which the topsoil collected prior to mining is spread on top of the sand and further seeded with a grass and herb cover (Lubke et al. 1996; van Aarde et al. 1996). Because seeds of forest tree species typically have no dormancy (Garwood 1989; Fenner & Thompson 2005), this topsoil is likely to contain only early successional and herbaceous species. Secondary succession has resulted in a series of known aged stands dominated by *A. karroo*, which in time (> 14 years old) begin to senesce and die, creating gaps for colonization by forest species.

The landscape includes a series of longitudinal stands up to 2 km in length at various stages of rehabilitation, varying from immediately post-mining to 27-year-old stands at the time of this study. This provides an opportunity to compare stands of similar vegetation at varying stages in the successional process. Three stands of increasing age since rehabilitation were selected for experimentation: those mined and subsequently rehabilitated in 1978, 1991 and 1998.

Seed bank assessment

Soil seed bank samples were collected to determine what species' propagules were present in the seed banks of the habitats at Cape Vidal and RBM. Soil samples were collected from five sites in each of the three *A. karroo* stands at Cape Vidal and matched with an equivalent number of samples from sites in the adjacent forest. As January is the peak fruit production time for forest trees in this region (Griffiths & Lawes 2006), seed bank samples were collected in January 2004 and repeated at different locations within the sites in January 2005, resulting in 30 samples. At each site two sub-samples were collected comprising the top 5 cm of soil from a surface area of 20 × 20 cm and pooled. Fifteen samples were collected in January 2005 in the same way from each *A. karroo* stand at RBM for comparison.

The soil was removed by sieving according to the methods of ter Heerdt et al. (1996) and remaining seed and organic matter was spread on top of a 3 – 5 cm thick layer of sterilized dune sand. Seedling emergence from these concentrated samples was monitored in the greenhouse at the University of KwaZulu-Natal, Pietermaritzburg, for a period of six weeks until no further germinations occurred. Greenhouse temperatures ranged from 15 to 25°C, humidity from 60 – 80% and seed trays were watered every 2 – 3 days to keep the soil moist. Germinated seedlings were removed from the trays as soon as they were identified to avoid competition among seedlings in the samples. This method has been shown to increase the number of species germinating and germination success of individual seedlings significantly (ter Heerdt et al. 1996; Bossuyt et al. 2000).

Seedling bank assessment

This experiment was conducted to examine the effects of post-dispersal factors on establishment and growth of both planted and naturally occurring seedlings. At Cape Vidal, paired experimental sites were set up in the three *A. karroo* stands and adjacent forest (Fig. 2.1a). Two 1 m^2 plots were cleared of all herbaceous vegetation at each of 15 experimental sites across the three stands (Fig. 2.1b). One of the plots was fenced with weld-mesh fencing and the other left unfenced to monitor establishment and survival of naturally occurring *in situ* seedlings (Fig. 2.1c). Four additional plots were cleared of all existing vegetation and planted with 15 seedlings, five each from three species: an early successional species (*A. karroo*), a forest pioneer species (*Celtis africana*) and a mature forest species (*Diospyros natalensis*). In each plot the seedlings were planted 20 cm apart but their position in the array was randomized. Two of these plots were fenced, and two (one fenced and one unfenced) were enriched with 20 $g.m^{-2}$ of Limestone Ammonium Nitrate (LAN) fertilizer annually and the other served as a control. All plots were freestanding, with a minimum distance of 1.5 m between plots. These experimental plots were matched with 15 replicates in the adjacent forest. The change in species richness and abundance of woody species in the unplanted plots, and the growth and survival of seedlings in the planted plots was monitored over a period of two years (February 2004 – January 2006).

Altogether this design resulted in: (1) 15 experimental sites in each of two habitats (*A. karroo* stands and adjacent forest); (2) at each site, a pair of planted, fenced (P+ F+) and unfenced (P+ F–) plots with no fertilizer (N–) added; (3) at each site, a pair of planted, fenced (P+ F+) and unfenced (P+ F–) plots to which fertilizer was added (N+); and (4) two unplanted plots per site, one fenced (P– F+) and one unfenced (P– F–).

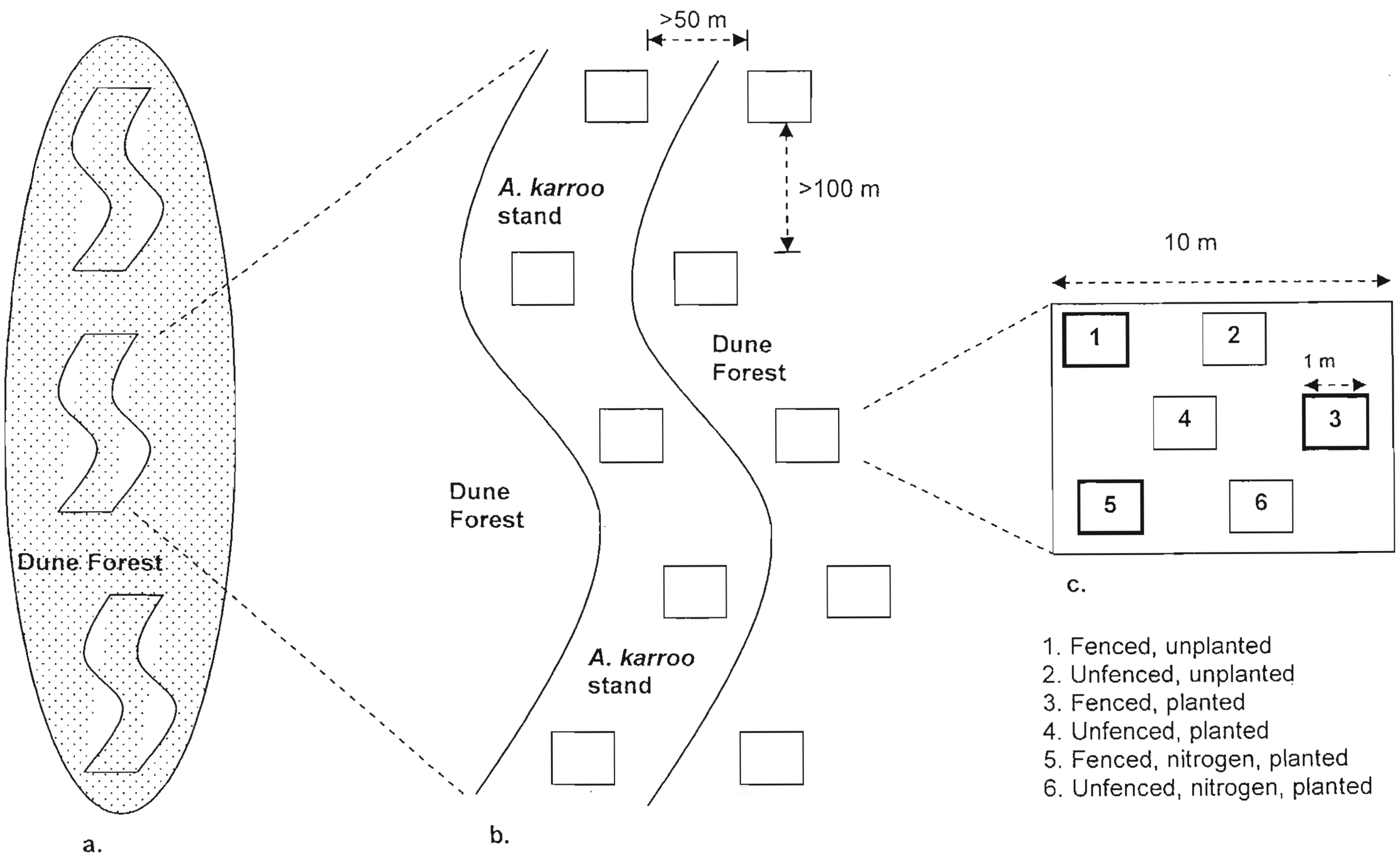

Fig. 2.1. Map of the experimental design in a) the three *A. karroo* stands within the coastal dune forest at Cape Vidal, and b) the layout of the 5 paired experimental sites in the stands and adjacent forest. c) The treatment plots were arranged randomly at each site, and the plots were no less than 1.5 m apart. Bold lines in Fig. 2.1c indicate fenced plots.

The natural seedling bank was surveyed in all three rehabilitation stands of known age at RBM. Richness and abundance of woody species seedlings greater than 10 cm in height and with DBH < 5 cm were recorded in 12 × 5 m unfenced, unplanted plots (P– F–) in each stand. Fourteen randomly placed replicates were conducted in each *A. karroo* stand.

Data analyses

Green's Index of Dispersion (GI) was used to examine the spatial pattern of numbers of seeds, seedlings, and numbers of species (Ludwig & Reynolds 1988). This index is a useful measure of the degree of clumping of individuals as it is independent of the total number of individuals in a sample. When individuals are randomly distributed across the samples GI = 0; when individuals are clumped in the samples GI = 1; and GI = -1 when individuals are randomly distributed across the samples. Species richness and the abundance of the seed and seedling banks from forest and *A. karroo* stand habitats at Cape Vidal and the known-aged stands at RBM were compared using univariate analysis of variance (ANOVA). The change in seedling bank richness and seedling abundance in the fenced and unfenced plots in the forest and *A. karroo* habitats at Cape Vidal from 2004 to 2006 were compared using repeated measures ANOVA. Seedling growth in nitrogen-enriched and control plots at Cape Vidal was compared using a nested, hierarchical ANOVA. There was no significant effect of the stands and these were grouped in further analyses. These analyses were conducted using SPSS Version 13.0 (SPSS 2004).

The composition of the seed and seedling banks among the habitats was compared using multi-response permutation procedures (MRPP). A Euclidean distance measure was used for this analysis, and groups were defined by stand age at RBM and habitat type and at Cape Vidal. The Cape Vidal plots were further defined by their fencing treatment. These analyses were conducted using PC-ORD for Windows Version 4 (McCune & Mefford 1999). The test statistic, T, describes the separation between the groups. The more negative T is, the stronger the separation. The A statistic describes the within-group homogeneity, compared to the random expectation. When all items are identical within groups, $A = 1$. $A = 0$ when heterogeneity within groups equals the expectation by chance, and $A < 0$ if there is more heterogeneity than expected by chance. The P-values were adjusted using a Bonferroni correction to avoid type I errors.

Results

Seed bank assessment

i. Richness and abundance

At Cape Vidal, both the seed bank richness and seed abundance were significantly higher in the forest habitat than in the *A. karroo* stands ($F_{1,58} = 14.78$, $P < 0.001$; and $F_{1,58} = 19.61$, $P < 0.001$, respectively; Table 2.1). At RBM, the mean and cumulative species richness increased with age since rehabilitation (Table 2.1), however mean species richness was only significantly different between the oldest (1978) and youngest (1998) stands (Tukey's post-hoc test; $P = 0.001$). The abundance of seed in the soil also increased significantly with age at RBM ($F_{2,42} = 35.26$, $P < 0.001$; Table 2.1). The seed bank of the oldest stand (1978) had more than twice the abundance of stand 1991, and more than 12 times that of the most recently rehabilitated stand (1998). Of all the *A. karroo* stands examined, the seed bank of the stands at Cape Vidal had the highest cumulative species richness (Table 2.1), but this was only slightly higher than that of the oldest stand (1978) at RBM. Stand 1978 at RBM had a much higher seed bank density that that of the Cape Vidal stands, however.

Table 2.1. Mean (± 1 SE) seed bank species richness and seed abundance per m^2 of the forest and *A. karroo* stands at Cape Vidal and the three rehabilitated *A. karroo* stands (1978, 1991 and 1998) at RBM.

Study site	**Habitat**	**Mean number of seeds**	**Mean species richness**	**Cumulative species richness**	**n**
Cape Vidal	Forest	242.9 ± 57.26	29.6 ± 4.22	10	30
	A. karroo stand	28.3 ± 8.85	10.8 ± 2.45	6	30
RBM	**1978**	160.8 ± 23.56	18.3 ± 2.07	5	15
	1991	53.3 ± 13.61	13.3 ± 1.48	3	15
	1998	8.3 ± 3.59	6.7 ± 2.40	2	15

ii. Composition

The species composition of the seed bank was significantly different between the forest and *A. karroo* stands at Cape Vidal (Table 2.2). The following species were absent from the seed bank of the A. *karroo* stands: *Cordia caffra*, *Diospyros natalensis*, *Mimusops caffra*, *Sideroxylon inerme* and *Teclea gerrardii*, all of which are common forest species at Cape Vidal. *Adenopodia spicata,* a forest margin species (Coates Palgrave 2002), was unique to the *A. karroo* stand seed bank, which was dominated by *A. karroo,* an early successional species. *Acacia karroo* seeds were present in the forest seed bank only in very small numbers, and *Celtis africana*, a typical forest pioneer or early succession species at Cape Vidal, was present in large numbers in the forest seed bank, but was rare in the seed bank in *A. karroo* stands. The seed bank community composition of all the stands at RBM were significantly different from one another (Table 2.2), but stands 1978 and 1998 showed the most dissimilarity (T = -14.0).

Table 2.2. Results of the Multi-Response Permutation Procedure analysis of the natural seed bank species compositions between the forest and *A. karroo* stands at Cape Vidal, and the three rehabilitating *A. karroo* stands at RBM. *T*-values are reported, followed by *A*-values in parentheses. * represents significance using a Bonferroni correction to avoid type I errors.

		Cape Vidal	RBM	
Study site		*A. karroo* **stand**	**1991**	**1998**
Cape Vidal	**Forest**	-10.11(0.11)*	–	–
RBM	**1978**	–	-6.12(0.17)*	-14.01(0.41)*
	1991	–	–	-7.09(0.19)*

Although the seed bank composition in the two habitats at Cape Vidal were different, in both habitats the number of seeds and species were randomly distributed across the soil samples (Table 2.3). This indicates that dispersal of seeds from forest species into the *A. karroo* stands was random. At RBM, the number of seeds was also randomly distributed across the soil samples, but seed species distribution tended to be more uniform in the two older stands (1978 and 1991; Table 2.3). An age-related increase in seed bank species richness and seed abundance is evident in the RBM stands. The *A. karroo* stand seed bank at Cape Vidal is predominantly composed of *A. karroo* seeds and a small number of *Adenopodia spicata*, *Apodytes dimidiata*, *Celtis africana*, *Grewia caffra* and *Ziziphus mucronata* individuals, of which, *A. dimidiata*, *Grewia* spp. and *Z. mucronata* are known to have dormant seeds (Geldenhuys 1996). This enables them to persist in the seed bank until microsite conditions are suitable for germination.

Seedling bank assessment

i. Richness and abundance

Under natural levels of herbivory (unfenced plots) the *A. karroo* stands had significantly lower seedling species richness than the adjacent forest (Table 2.4; $F_{1,8} = 7.85$, $P = 0.009$) and there was no significant difference in seedling abundance between the two habitats ($F_{1,28} = 0.54$, $P = 0.468$). In the absence of herbivory, seedling species richness in the forest was significantly higher than in the *A. karroo* stands (Table 2.4; $F_{1,28} = 5.92$, $P < 0.022$). However, the seedling species richness of fenced plots in the *A. karroo* stands was double that of the unfenced plots. In addition, seedling abundance in fenced plots in the *A. karroo* stands was double that in the forest ($F_{1,28} = 4.50$, $P = 0.043$). These results indicated a strong negative effect of herbivory on seedling abundance and diversity, particularly in the *A. karroo* stands.

Table 2.3. Green's Index of Dispersion of the distribution of seeds and species among the seed bank samples in the forest and *A. karroo* stand habitats at Cape Vidal, and the three *A. karroo* stands at RBM.

		Green's Index	
Study site	**Treatment**	**Number of seeds**	**Species. richness**
Cape Vidal	**Forest**	0.054	0.049
	***A. karroo* stand**	0.084	0.066
RBM	**1978**	0.016	-0.180
	1991	0.050	-0.402
	1998	0.095	0.036

Forest and *A. karroo* stand seed bank: n = 30 samples per habitat; 1978, 1991 and 1998 seed bank: n = 15 samples per stand.

At RBM, both the seedling species richness and seedling abundance were significantly different among the *A. karroo* stands ($F_{2,39} = 14.08$, $P < 0.001$; and $F_{2,39} = 26.03$, $P < 0.001$, respectively). Although the mean species richness was higher in stand 1991 than in stand 1978 and the seedling abundance higher in stand 1978 (Table 2.4), neither of these differences were significant (Tukey's post-hoc test; $P = 0.562$ and $P = 0.812$, respectively). The youngest stand (1998) had a significantly higher seedling species richness than both stand 1978 and 1991 (Tukey's post-hoc test; Table 2.4; $P < 0.001$ and $P = 0.001$, respectively). This stand also had a significantly higher seedling abundance than both older stands (Tukey's post-hoc test; $P < 0.001$ in both cases). The RBM stands had considerably lower seedling abundance and species richness than all the treatment plots at Cape Vidal (Table 2.4).

Table 2.4. Mean (± 1 SE) seedling species richness and seedling abundance per m^2 among the fenced (F+) and unfenced (F–) plots in the forest and *A. karroo* stand habitats at Cape Vidal, and the three *A. karroo* stands at RBM. All plots were unplanted.

Study site	Treatment	n	Mean number of Seedlings (m^{-2})	Mean species Richness (m^{-2})
Cape Vidal	F- Forest	15	4.9 ± 0.86	2.70 ± 0.39
	F+ Forest	15	8.3 ± 1.75	4.10 ± 0.54
	F- *A. karroo* stand	15	6.9 ± 1.30	1.40 ± 0.24
	F+ *A. karroo* stand	15	15.3 ± 3.26	2.60 ± 0.35
RBM	1978	14	0.2 ± 0.06	0.06 ± 0.01
	1991	14	0.1 ± 0.02	0.07 ± 0.01
	1998	14	0.7 ± 0.05	0.13 ± 0.01

ii. Composition

The composition of the fenced seedling bank represents seedlings recruited from seeds stored in the seed bank as well as those without dormancy which germinate immediately following dispersal. At Cape Vidal, the seedling bank community composition is similar in the fenced and unfenced plots in both habitats (Table 2.5). Although not significant, fenced and unfenced plots in the *A. karroo* stands are more dissimilar than the forest plots ($T = -1.68$ and $T = 0.60$, respectively). The fenced and unfenced plots have significantly different seedling compositions when compared between the habitats (Table 2.5). *Acacia karroo* is the dominant species in the *A. karroo* stands but is rare in the forest, and low numbers of *Celtis africana* were noticeable in the *A. karroo* stands. At RBM, the seedling bank community composition was similar between the two older stands (1978 and 1991; Table 2.5), but the seedling bank composition of the youngest stand (1998), was significantly different to those of both stand 1978 and stand 1991. Stand 1998 had high numbers of germinating *A. karroo* individuals, but species such as *Cordia caffra*, *Dovyalis longispina*, *Grewia caffra*, *Mimusops. caffra*, and *Zanthoxylum davyi* were present in this stand but absent from the older two stands.

At Cape Vidal, the dispersion of seedling species across the plots in all treatments was random (Table 2.6). The abundance of seedlings was randomly distributed in all treatments except the unfenced plots in the *A. karroo* habitat (Table 2.6). Here seedling abundance was clumped in a few of the plots, indicating that unprotected microsites have lower seedling survival in the *A. karroo* stands. At RBM, both species and number of seedlings were randomly distributed across the plots (Table 2.6).

Table 2.5. Results of the Multi-Response Permutation Procedure analysis of the *in situ* (P–) seedling bank species compositions between the fenced (F+) and unfenced (F–) treatments in the forest and *A. karroo* stands at Cape Vidal and the three regenerating *A. karroo* stands at RBM. All plots were unsupplemented. *T*-values are reported, followed by *A*-values in parentheses. * represents significance using a Bonferroni correction to avoid type I errors.

		Cape Vidal			RBM	
		F-	F+	F-		
Study site		**Forest**	***A. karroo* stand**	***A. karroo* stand**	**1991**	**1998**
Cape Vidal	**F+ Forest**	0.60(-0.01)	-9.35(0.17)*	-	–	–
	F- Forest	–	–	-9.73(0.18)*	–	–
	F+ *A. karroo* stand	–	–	-1.68(0.04)	–	–
RBM	**1978**	–	–	–	-2.21(0.04)	-13.59(0.32)*
	1991	–	–	–	–	-14.84(0.44)*

iii. Impact of supplementary nitrogen on seedling establishment and growth

The effect of supplementary nitrogen on seedling survival and growth was examined in the forest and *A. karroo* habitats at Cape Vidal. Seedling growth in both habitats was unaffected by increasing soil nitrogen levels ($F_{3,814} = 1.11$, $P = 0.342$). Seedlings planted in both supplemented and unsupplemented plots showed a similar increase in height in the *A. karroo* habitat, regardless of nitrogen enrichment (Fig. 2.2). Although *A. karroo* seedlings showed the greatest increase in growth in the *A. karroo* stands in both treatments, vertical growth of all species was improved when planted in this habitat. This indicates that pioneer and mature forest species seedlings can survive and grow well in the *A. karroo* stands in natural soils.

Table 2.6. Green's Index of Dispersion of the distribution of seedling individuals and species among the seedling bank samples in the fenced (F+) and unfenced (F–) plots in the forest and *A. karroo* stand habitats at Cape Vidal, and the three *A. karroo* stands at RBM.

			Green's Index	
Study Site	**Treatment**	**n**	**Number of seedlings**	**Species richness**
Cape Vidal	**F- Forest**	15	0.018	-0.150
	F+ Forest	15	0.036	0.039
	F- *A. karroo* stands	15	0.670	-0.102
	F+ *A. karroo* stands	15	0.041	-0.051
RBM	**1978**	15	0.106	0.000
	1991	15	0.012	0.001
	1998	15	0.007	0.000

iv. Change in seedling bank over time

Seedling bank species richness increased over time in both *A. karroo* and forest habitat when protected (Fig. 2.3; Wilks' $\lambda = 0.78$, $F_{1,56} = 15.97$, $P < 0.001$). The species composition was similar between the fenced and unfenced plots in the *A. karroo* stands (Table 2.5), but interestingly, in the *A. karroo* stands the unfenced plots showed a marginal decrease in seedling bank species richness. Both fenced and unfenced plots in the forest showed an increase in seedling bank species richness over time, although the observed increase was much greater in the fenced plots. Seedling abundance increased significantly in both habitats in fenced plots (Fig. 2.4; Wilks' $\lambda = 0.87$, $F_{1,56} = 8.10$, $P = 0.006$). The increase in seedling abundance was greater in the *A. karroo* stands than the forest (Fig. 2.4a & b), indicating a stronger effect of fencing or protection in this habitat. There was little or no change in seedling abundance over time in unfenced plots in both habitats.

Discussion

Disturbed areas have generally had some or all of their vegetation removed and the local availability and diversity of reproductively mature trees is low. Under these circumstances, regeneration of the plant community is dependent on germination of seeds already present in the seed bank and those recently dispersed from mature trees in source populations within dispersal range (Duncan & Chapman 2002). Density and species richness of short-lived propagules in the seed bank are known to follow the changes in the mature vegetation

(Bossuyt & Hermy 2004). The dominant species present in the seed bank in *A. karroo* stands at Cape Vidal were early successional and forest margin species that are common in the mature vegetation. That *C. africana*, a forest pioneer species common in the forest canopy, is rare in the seed bank and mature vegetation of these old *A. karroo* stands (> 45 years) indicates that natural forest regeneration has become arrested.

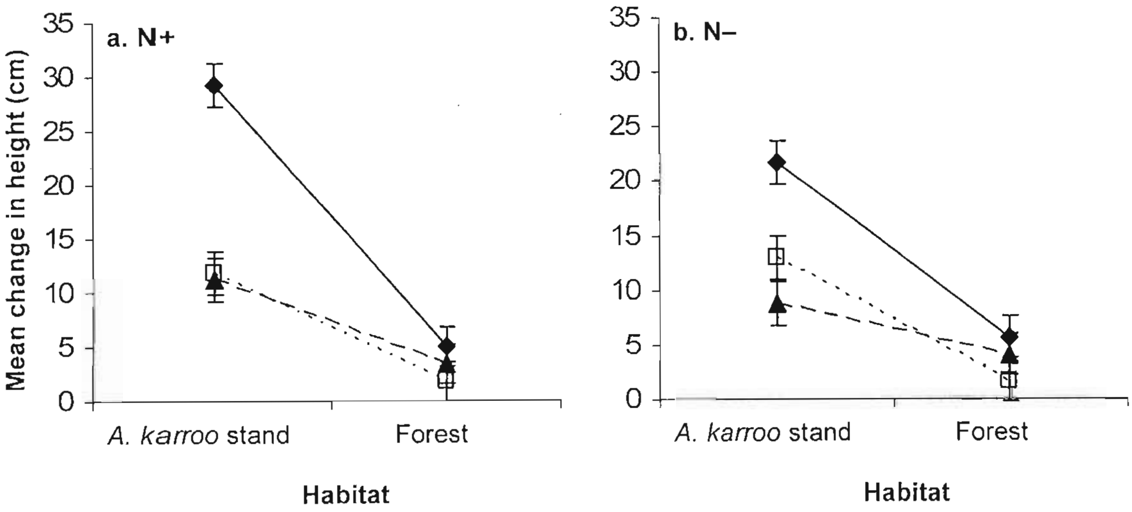

Fig. 2.2. Mean increase in growth (± 1 SE, n = 20 per species in each habitat) of seedlings from three planted species. Growth in the forest and *A. karroo* habitats at Cape Vidal are compared under the following treatments: **(a)** soil enriched (N+) and **(b)** soil not enriched (N-). All plots were protected by fencing. *Acacia karroo* seedlings are indicated by a solid diamond (◆) with a solid line, *C. africana* seedlings by an open square (□) with a dotted line, and *D. natalensis* seedlings by a solid triangle (▲) with dashed line.

Forest tree species commonly do not have dormant seeds (Garwood 1989; Fenner & Thompson 2005); rather dispersal events and the seedling bank are of greater importance to successful regeneration in these habitats (Pickett & McDonnell 1989). The low species diversity of the seed bank in *A. karroo* stands suggests that like most tropical forests, the Cape Vidal coastal dune forests do not rely on a persistent soil seed bank for regeneration. Instead, seed dispersal and the seedling bank are more influential to the vegetation community composition.

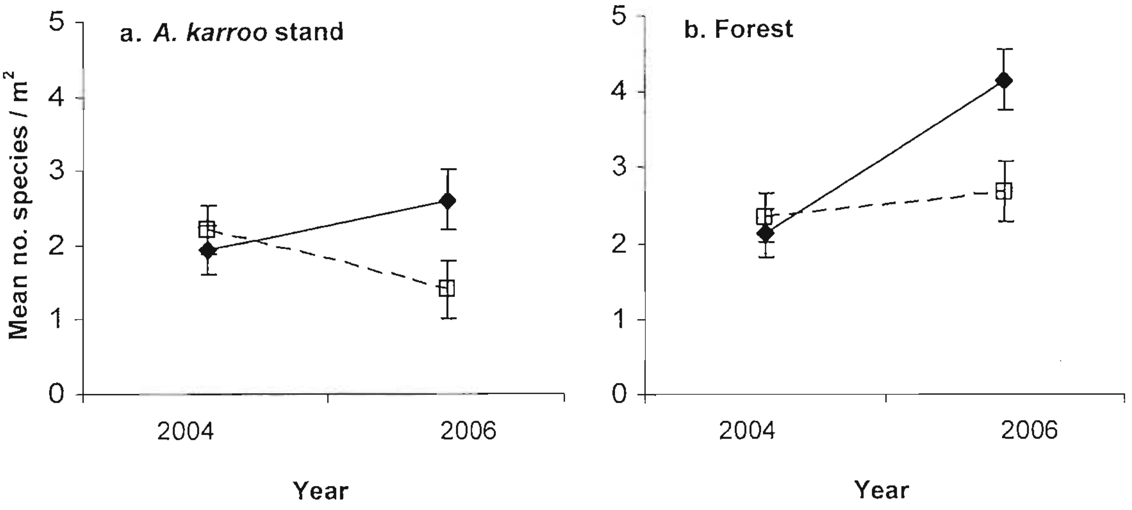

Fig. 2.3. Change in mean seedling species richness (± 1 SE; n = 15 samples per habitat) over two years in unplanted plots in **(a)** the *A. karroo* stands and **(b)** forest at Cape Vidal. Fenced (F+) plots are indicated by a solid diamond (◆) with a solid line and unfenced (F–) plots are indicated by an open square (□) with a dashed line.

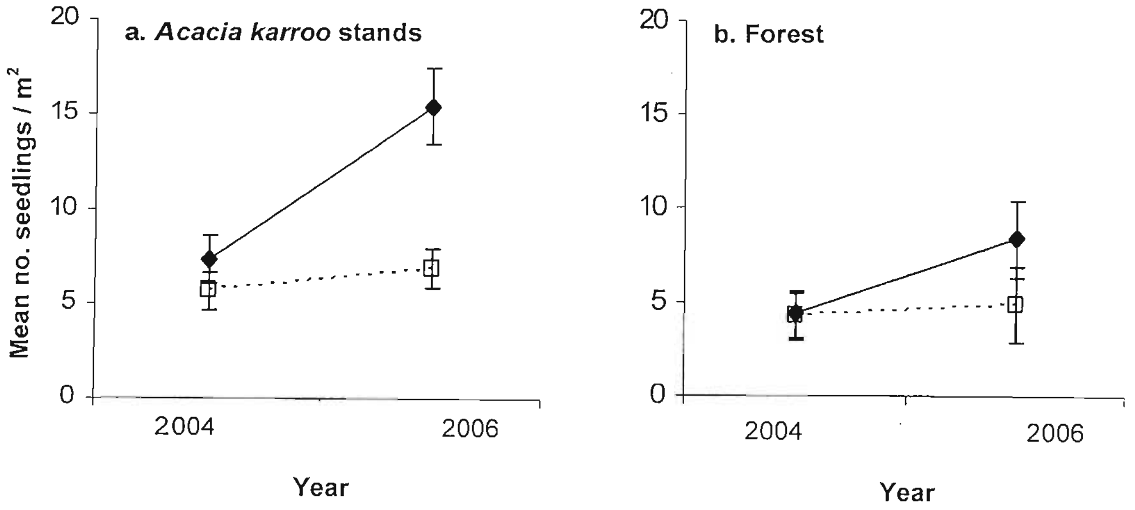

Fig. 2.4. Change in mean seedling abundance (± 1 SE; n = 15 samples per habitat) over two years in unplanted plots in **(a)** *A. karroo* stands and **(b)** forest at Cape Vidal. Fenced (F+) plots are indicated by a solid diamond (◆) with a solid line and unfenced (F–) plots are indicated by an open square (□) with a dotted line.

The 20 most common tree species at Cape Vidal all show some degree of multi-stemming, and 40% of all trees, reproduce vegetatively and thus produce few seeds (Nzunda et al. In press). This is consistent with the implication that the role of the seed bank in regeneration is negligible. At RBM however, an age-related increase in seed bank diversity and abundance is evident. This is a reflection of the greater abundance and species richness of mature reproducing trees present in the older regenerating stands at RBM (Bossuyt & Hermy 2004). Despite lower total seed abundance in the seed bank of the *A. karroo* stands at Cape Vidal than in the stands at RBM, the Cape Vidal stands had a higher species richness. This indicates that a variety of seed species do reach the naturally regenerating *A. karroo* stands from the surrounding forest at Cape Vidal.

In many regions, seed dispersal by animals, which has the potential to facilitate or inhibit recolonization, is the principal form of dissemination of seeds (Wunderle 1997). The arrested succession in the dune slacks at Cape Vidal can be partly attributed to limited seed dispersal. The forest seed bank was significantly different from that of the *A. karroo* stands in terms of seed abundance, species richness and thus species composition. Few forest species were present in the *A. karroo* stand seed bank at Cape Vidal, despite the close proximity of the seed source in the adjacent forest. The limited dispersal of forest species propagules into the *A. karroo* stands is potentially a result of low visitation rates by frugivorous birds (Jordano & Godoy 2002; Muller-Landau et al. 2002). The difference may be emphasised by the higher abundance and diversity of reproductively mature trees in the forest habitat, from which seeds are dispersed by gravity and wind (Bossuyt & Hermy 2004).

Although seed influx into the *A. karroo* stands is limited, that seed which did arrive was randomly distributed among sampled sites. Yet seedling diversity and distribution was clumped among unprotected sampled sites compared to protected sample sites. Together these findings suggest that the dispersal of forest tree species into the *A. karroo* stands is limited, but also that a post-dispersal factor decreases recruitment of seeds and seedlings in the *A. karroo* stands at Cape Vidal. The dispersion of seedlings was random in all stands at RBM, in contrast to the *A. karroo* stands at Cape Vidal, demonstrating that natural, relatively undisturbed recruitment occurs at RBM.

A possible explanation for the low levels of recruitment in the previously disturbed *A. karroo* stands at Cape Vidal is that a post-dispersal factor affecting microsites may be limiting seed germination and seedling growth (Clark et al. 1999; Holl et al. 2000). One such factor known to decrease plant growth, and thereby reduce the rate of succession, is soil fertility (Holl 1999; Jordano & Godoy 2002). In this study, however, seedling survival and growth were unaffected by improved microsite quality (soil fertility) in the forest or *A. karroo* stands at Cape Vidal and a range of forest species were able to establish and grow well here. Restoration of *Araucaria* forest in Brazil was similarly unaffected by soil enrichment (Zanini & Ganade 2005). As demonstrated here, soil fertility does not limit establishment and growth of forest species seedlings in the *A. karroo* stands and so reduced microsite quality is not inhibiting regeneration in previously disturbed sites at Cape Vidal.

The vegetation community composition of disturbed coastal dune sites undergoes age-related changes as succession proceeds (Weisser & Marques 1979; West et al. 2000). There is a switch from early to late successional species at an intermediate stage, which are finally replaced with mature-community species. The composition of the youngest stand at RBM differed from those of the older two, which contained a large degree of species over-lap. This demonstrated vegetation convergence occurs over time here and that natural successional processes are operating at RBM. Although *A. karroo* was still dominant in the seedling bank of the youngest stand, it also had the highest seedling bank species richness and seedling abundance. Thus, despite a large number of early successional species still present in young seedling banks, a high rate of recruitment of forest species from recently dispersed seed in the youngest stand at RBM ensures that successional regeneration occurs here. This enables the convergence of mature vegetation with benchmark levels demonstrated by Wassenaar et al. (2005).

At Cape Vidal, however, the forest and *A. karroo* stand seedling bank community compositions do differ. The seedling bank compositions of the respective habitats at Cape Vidal were unaffected by protecting the natural seedling bank, but the influx of forest tree seeds into the *A. karroo* stands is low. Thus the species composition of the seedling bank community is potentially affected by reduced dispersal events by frugivores. Consequently, the disturbed vegetation community in the *A. karroo* stands does not converge with the undisturbed forest at Cape Vidal, as occurs at RBM.

At RBM, natural seedling abundance and richness per unit area of all *A. karroo* stands was considerably lower than that in the Cape Vidal *A. karroo* stands, but greater survival of the seedlings present at RBM appears to account for the successful rehabilitation via the *A. karroo* successional pathway at this site. Although community composition was unaffected by protecting the seedling bank at Cape Vidal, this had a considerable positive influence effect on the seedling bank species richness and seedling abundance over time in both habitats. The forest seedling bank species richness remained relatively constant when unprotected, however in the *A. karroo* stands a marginal decrease was noted. Additionally, although only slight, the fenced and unfenced seedling communities were more dissimilar in the *A. karroo* stands than the forest. Thus protecting microsites enhances seedling species richness in the *A. karroo* habitat. Recruitment is clearly increased in both habitats when microsites are protected, although to a larger degree in the *A. karroo* stands.

Conclusions

Regeneration failure appears to be related in the first instance to limited dispersal of forest species into the *A. karroo* stands, and secondly, to the poor survival of those seedlings that do establish in the *A. karroo* stands. Thus, a post-seed-dispersal factor associated with seedling survival, possibly herbivory, and not the quality of microsites *per se* appears to be reducing seedling species richness and recruitment in *A. karroo* stands at Cape Vidal, causing arrested succession. This will be examined more closely in later chapters of this thesis. Although the seed bank may play a greater role in vegetation succession in the managed, previously mined RBM system, successful regeneration here is also strongly linked to recruitment from the seedling bank and greater survival of seedlings. At Cape Vidal, however, the role of the seed bank in the natural regeneration and succession appears to be much reduced. Rather, recruitment from the seedling bank and vegetative regeneration are more important in recolonization here. This regeneration strategy promotes recruitment and rapid regeneration during periods when conditions are favourable.

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Chapter 3

Soil nitrogen does not limit recovery of disturbed sites dominated by *Acacia karroo* in coastal dune forest

Abstract

Question: Does nitrogen availability in previously disturbed *A. karroo* stand soils limit forest tree species growth at Cape Vidal where regeneration of coastal dune forest is following the *A. karroo* successional pathway? Have soil nitrogen levels continued to accumulate in previously mined *A. karroo* stands at Richards Bay Minerals (RBM)?

Location: Cape Vidal and RBM, in northern KwaZulu-Natal, South Africa.

Methods: Soil fertility of *A. karroo* stands and neighbouring forest at Cape Vidal, and that of previously mined *A. karroo* stands at four stages of succession at RBM (early, early-mid, mid-late and late successional) were compared. Experimental treatment plots were used to monitor the establishment and growth of planted and *in situ* seedlings. The effects of nitrogen supplementation on growth of three tree species (a typical pioneer species, a forest species, and *A. karroo*) were examined in experimental plots in the *A. karroo* stands and adjacent forest at Cape Vidal.

Results: Soil fertility in the *A. karroo* stands and adjacent forest at Cape Vidal was similar and total and mineralized nitrogen were not limiting in the *A. karroo*. At RBM, total nitrogen accumulated rapidly over time. The oldest rehabilitating stand at RBM, had similar total nitrogen levels to those at Cape Vidal that were twice the age. Seedling growth was unaffected by nitrogen supplementation in both habitats at Cape Vidal. All species grew fastest in the *A. karroo* stands, but *A. karroo* individuals were better nitrogen competitors than *Celtis africana* and *Diospyros natalensis*.

Conclusions: Together, these results indicate that *A. karroo* stands, and specifically their soil nutrient levels, are suitable for forest species growth. Soil fertility and particularly available nitrogen, are not limiting secondary succession at Cape Vidal. Alternative post-emergence factors must be responsible for the lack of coastal dune forest recovery in *A. karroo*-dominated stands.

Keywords: *Acacia karroo* successional pathway; accumulation; bottom-up forces; Cape Vidal; mining; nutrient addition; Richards Bay; soil fertility.

Nomenclature: Coates Palgrave (2002).

Abbreviations: ANOVA = analysis of variance; DFA = discriminant function analysis; LAN = Limestone Ammonium Nitrate; MANOVA = multivariate analysis of variance; MRPP = multi-response permutation procedure; RBM = Richards Bay Minerals.

Introduction

Anthropogenic disturbances such as burning, ploughing and logging alter soil nutrient balance and fertility (Chen & Li 2003). Complete recovery of plant communities and habitats only occur once soil nutrient levels re-accumulate to pre-disturbance levels through facilitation by early successional plant species and deposition of organic matter (Barbour et al. 1999). For this reason, soil nutrients, a so-called "bottom-up" force (Hunter & Price 1992), are considered a key factor influencing vegetation establishment and subsequent habitat recovery (Barbour et al. 1999). Low soil fertility is known to reduce the rate of vegetation recovery following disturbance (Holl 1999; Jordano & Godoy 2002). The availability of essential soil nutrients such as carbon, nitrogen, phosphorous, and water influences plant growth (Öpik & Rolfe 2005), and in doing so can direct the successional process (Tilman 1987). Of these, nitrogen has an important influence on plant species composition and richness, and is often limiting in secondary succession (Tilman 1986; Tilman 1987; Holl et al. 2000).

Nitrogen levels require a lengthy period to recover following disturbance. Models show that 95% of soil nitrogen depleted by extensive cultivation in northern USA required 180 years to re-accumulate at a rate of 1.23g $N.m^{-2}.yr^{-1}$ (Knops & Tilman 2000). Recovery of soil nitrogen following disturbance in temperate coastal dunes proceeds more slowly, however, at a rate of 0.403g $N.m^{-2}.yr^{-1}$ (Gerlach et al. 1994), and nitrogen levels only begin to stabilize after 250 years. Thus recovery following disturbance in this habitat type is potentially a very long process.

Since 1952, when subsistence farmers left the dune forests at Cape Vidal, natural succession processes have occurred in the dune forests. Following the departure of these settlers, even-aged stands of *Acacia karroo* individuals established naturally in the disturbed areas (von Maltitz et al. 1996). The *A. karroo* successional pathway is being used successfully to rehabilitate mined dunes 70 km south of Cape Vidal at Richards Bay (Mentis & Ellery 1998; Wassenaar 2003) and is thought to be the easiest method of restoring disturbed coastal dunes in this area (Lubke et al. 1996).

Where the *A. karroo* successional pathway has been used to facilitate dune forest recovery, soil nutrients including nitrogen accumulate with increasing age since mining (van Aarde et al. 1998). As nitrogen-fixing species, *Acacias* have an advantage over many other woody plants in the early stages of primary and secondary succession when nitrogen levels have been depleted and limit the growth of most species (Tilman 1986; Tilman 1987). As an early-successional, nitrogen-fixing species, *A. karroo* can establish in nutrient-poor soils, and the nitrogen added to the soil through nitrogen fixation may facilitate recovery and invasion by later successional species (Lubke et al. 1996). A study conducted by van Aarde et al. (1998) in the Richards Bay Minerals mining lease areas (RBM), on stands of coastal dune forests that are regeneratig in response to a RBM-initiated rehabilitation program, showed that although nitrogen levels do increase over time with vegetation succession, levels recorded in the rehabilitating areas were low compared to nearby unmined habitats. The oldest disturbed area sampled by van Aarde et al. (1998) was only 18 years post-mining and the low nitrogen levels were likely a reflection of their relatively early successional state (Gerlach et al. 1994).

Despite the apparent success of the *A. karroo* successional pathway in restoring coastal forest on mined dunes at Richards Bay, succession is arrested in previously disturbed sites at Cape Vidal. Here, *A. karroo* stands are more than 50 years old but forest tree species diversity remains low and the vegetation community is not converging with that of adjacent, undisturbed forest (West et al. 2000). Instead, young *A. karroo* individuals, rather than pioneer forest species, are replacing the initial cohort of *A. karroo* trees that is now senescing. If post-disturbance soils in the dune slacks at Cape Vidal have particularly low nitrogen level and succession at Cape Vidal is controlled by soil nutrient levels (bottom-up forces; Hunter & Price 1992; Gerlach et al. 1994), this may explain *A.*

karroo dominance and the low diversity of forest tree species in the dune slacks. The dominance of *A. karroo* in the dune slacks at Cape Vidal may thus be a result of its superior competitive ability for available nutrients, particularly nitrogen, over other forest species in a nitrogen-poor environment.

This study examines the hypothesis that soil nitrogen is low in the dune slacks, allowing *A. karroo* individuals to thrive, but exclude typical dune forest tree species. At Richards Bay, soil nutrient levels in *A. karroo* stands at different stages of succession are examined and compared with the findings of previous studies conducted there. The following specific questions are addressed: (1) does nitrogen availability in *A. karroo* stand soils at Cape Vidal limit forest tree species growth; (2) do dune slacks in general have specific soil conditions that exclude forest tree species growth; and (3) have nitrogen levels continued to accumulate in rehabilitating *A. karroo* stands at Richards Bay, as initially demonstrated by van Aarde et al. (1998)? By answering these questions this study will provide a better understanding of the mechanisms driving the *A. karroo* successional pathway and allow for informed management of naturally and anthropogenically disturbed coastal dune forests in South Africa.

Materials and methods

Study sites

Two sites were used in this study: Cape Vidal and Richards Bay Minerals (RBM; see Chapter 2 for a full description of sites). At Cape Vidal, experimental sites were located in three previously disturbed dune slacks (valleys between dunes) that have been colonised by *A. karroo*, and in the adjacent undisturbed forest. Soil samples were also collected from undisturbed, forested dune slacks at Cape Vidal. At RBM, previously mined dunes comprising *A. karroo* stands at different successional stages were selected for sampling: early successional (10 – 13 years since mining), early-mid successional (16 – 19 years since mining), mid-late successional (20 – 22 years since mining), and late successional (23 – 25 years since mining) stands were examined. These same stands were sampled by van Aarde et al. (1998) 11 years ago, which allowed changes in particular stands at different successional stages to be followed through the course of secondary succession.

Soil fertility

Soil fertility was analysed to examine the difference in microsite conditions that influence vegetation growth and survival at the various habitats at Cape Vidal and at different successional stages at RBM. Soil samples were collected from the forest and *A. karroo* stands at Cape Vidal to examine soil fertility and nutrient content in January – February 2004 when most seedlings establish. Soil was collected from top soil (0 – 5 cm) and deep soil (5 – 20 cm) horizons using a beta-auger. Ten to fifteen sub-samples were taken from a 10 m × 10 m area within each experimental site in the *A. karroo* stands and forest. These samples were then pooled, following standard soil sampling methods (Carter 1993). Two such samples were collected at each site, resulting in four samples (two per soil horizon) per sample site and 40 per stand. Three soil samples were collected from each of five forested, undisturbed dune slacks at Cape Vidal to measure natural soil conditions. Twenty samples were collected in June 2005 from previously mined *A. karroo* stands at each of four different successional stages (early, early-mid, mid-late and late successional stages) at RBM using the same protocol (n = 80).

Most of the nitrogen used by plants comes from continuous recycling of nitrogen from decaying biomass to inorganic nutrients and CO_2 through the process of mineralization. Mineralization is the decomposition of organic matter in soil by micro-organisms (Barbour et al. 1999). Mineralized nitrogen was measured in the disturbed *A. karroo* stands and adjacent forest soils at Cape Vidal. The amount of nitrogen mineralization occurring in the soil at any particular time indicates the amount of inorganic nitrogen (nitrate and ammonium) available for uptake by plants. All analyses of Cape Vidal soils were conducted by the Soil Science Department at Cedara Agricultural College, KwaZulu-Natal. The same protocol was used to analyze the RBM soils, but was conducted in the Soil Science Department, University of KwaZulu-Natal, Pietermaritzburg. All samples were tested for general fertility, including acidity, acid saturation, ammonium, calcium, cations, clay, copper, magnesium, manganese, nitrate, pH, phosphorus, potassium, total nitrogen, and zinc.

Seedling growth response to nitrogen addition

This experiment was designed to primarily examine the effect of two variables on seedling growth at Cape Vidal: supplementary nitrogen addition and habitat (*A. karroo* stand vs. undisturbed forest). Plots were set up in 15 paired experimental sites – five in each of three *A. karroo* stands and adjacent forest, as described in Chapter 2. All plots were freestanding, with a minimum distance of 1.5 m between plots. At each sample site four 1 m^2 plots were cleared of all vegetation and planted with five seedlings each of an early successional species (*A. karroo*), a typical forest pioneer species (*Celtis africana*) and a typical mature forest species (*Diospyros natalensis*). In each plot the seedlings were planted 20 cm apart but their position in the array was randomized. Seedlings that died within two weeks from transplant shock were replaced, but those that were browsed or trampled were left. Two plots were enclosed in a weld-mesh fence, and two (one fenced and one unfenced) plots were treated with 20 $g.m^{-2}$ of Limestone Ammonium Nitrate (LAN), a granulated 28% nitrogen-based fertilizer, while the other served as a control. The frequency of LAN application was based on standard agricultural practices and timed to coincide with the summer rain (John & Turkington 1997; Turkington et al. 2002). Seedling height and stem diameter were monitored every 6 – 7 weeks for a period of one year (February 2004 – January 2005), and every three months for a second year (February 2005 – January 2006). Changes in seedling diameter were slight and height was selected as the more useful measure of plant growth. The relative change in seedling height over two years (final height - initial height) was used for analysis.

Altogether, this design resulted in: (1) 15 experimental sites in each of two habitats (*A. karroo* stands and adjacent forest); (2) at each site, a pair of fenced (F+) and unfenced (F–) plots with no nitrogen (N–) added; and (3) at each site, a pair of fenced (F+) and unfenced (F–) plots to which supplementary nitrogen was added (N+).

Data analyses

To avoid incurring type I errors by testing the same hypothesis several times over, multivariate analysis of variance (MANOVA) was used to simultaneously test for differences in multiple soil nutrients between the three habitats at Cape Vidal and among stands at all successional stages at RBM. The Wilks' λ (likelihood ratio criterion) varies between 0 and 1, and tests the overall significance of the treatments on the variables. If this test is significant, the univariate F-tests are then checked to determine which of the factors causes the overall significant effects.

The difference in amount of mineralized nitrogen present in the *A. karroo* stand and adjacent forest soils at Cape Vidal were analysed using univariate analysis of variance (ANOVA). A nested hierarchical ANOVA was used to compare the growth of seedlings of three tree species between nitrogen supplementation and control plots in the *A. karroo* stands and adjacent forest. There was no significant effect of stand location and the data from all three *A. karroo* stands were pooled. These analyses were conducted using SPSS 13.0 (SPSS 2004).

The composition of the soil nutrients in both soil horizons was compared among the habitats at Cape Vidal and RBM using multi-response permutation procedures (MRPP) run in PC-ORD for Windows Version 4 (McCune & Mefford 1999). A Euclidean distance measure was used, and groups were defined by successional stage at RBM and habitat type at Cape Vidal. The test statistic, T, describes the separation between groups. The more negative T is, the stronger the separation. The A statistic describes within-group homogeneity compared to the random expectation. When all items are identical within groups, $A = 1$. $A = 0$ when heterogeneity within groups equals the expectation by chance, and $A < 0$ if there is more heterogeneity than expected by chance.

Discriminant function analysis (DFA; canonical variates analysis) was used to detect whether the soil characteristics predicted habitat membership, i.e. whether habitat types could be predicted from soil variables. This generates a linear combination of discriminant functions based on combinations of predictor variables (soil nutrients) that provide the best discriminants or mean differences between predetermined habitat groups (Quinn & Keough 2002). The assumptions of this method are: (1) predictors are not highly correlated with each other; (2) the mean and variance of a given predictor are not correlated; (3) the correlation between two predictors is constant across groups; and (4) values of each predictor have a normal distribution.

Fifteen soil nutrient variables were surveyed from the top (0 – 5 cm depth) and deep soil (5 cm – 20 cm). Seven habitat groups were defined (see above, Table 3.6). Standardized canonical discriminant function coefficients were examined to determine the power or weighting of each variable to discriminate between habitat groups. Group centroids were also examined to interpret discriminant analysis results. This analysis was conducted using SPSS 13.0 (SPSS 2004).

Results

Soil fertility

i. General Fertility

Soil nutrient levels at Cape Vidal differed significantly among *A. karroo* stands, forest and undisturbed, forested dune slacks in both soil horizons (MANOVA; top soil: Wilks' $\lambda = 0.08$, $F_{22,64} = 7.23$, $P < 0.001$; deep soil: Wilks' $\lambda = 0.03$, $F_{20,66} = 16.92$, $P < 0.001$). Differences in soils nutrient levels among the habitats were similar in both soil horizons. Most soil nutrients were significantly higher in the dune slack soil (Tukey's post-hoc test; Table 3.1); total nitrogen, phosphorus, potassium and pH were the exceptions. Phosphorous was significantly higher in the *A. karroo* stands and dune slacks than in the forest habitat, while pH levels were similar among all habitats. Potassium was consistently lowest in the *A. karroo* stands and highest in the forested dune slacks, with intermediate levels in the neighbouring forest. Importantly, total nitrogen levels were similar in all habitats in both soil horizons (Tukey's post-hoc test; top soil: $P = 0.090$; deep soil: $P = 0.349$).

At Cape Vidal, inorganic nitrogen (ammonium and nitrate) in the top soil was significantly different between all habitats (MANOVA; Wilks' $\lambda = 0.49$, $F_{4,62} = 6.65$, $P < 0.001$). In the top soil the undisturbed dune slacks had significantly higher levels of ammonium than the *A. karroo* stands (Tukey's post-hoc test; $P = 0.023$; Table 3.2), and the forest ammonium levels were intermediate between these. Nitrate was significantly lower in the dune slack top soil than both the *A. karroo* stands and forest soils (Tukey's post-hoc test; $P = 0.001$ and $P = 0.072$, respectively; Table 3.2) and levels were highest in the *A. karroo* stands. Similar trends in both nutrients occurred in the deep soil horizon (Table 3.2).

Table 3.1. Mean (± 1 SE; n = 30 samples per soil horizon in each habitat) soil nutrients in both soil horizons in the *A. karroo* stands, forest and undisturbed dune slack habitats at Cape Vidal.

	Top soil			**Deep soil**		
Nutrient	***A. karroo* stand**	**Forest**	**Dune slack**	***A. karroo* stand**	**Forest**	**Dune slack**
Ca (mg/L)	1347.3 ± 152.50^{a}	1380.9 ± 152.50^{a}	2711.4 ± 152.50^{b}	1154.3 ± 119.30^{a}	1177.7 ± 119.30^{a}	2133.9 ± 119.31^{b}
Cations (cmol$_c$/L)	8.2 ± 0.84^{a}	8.5 ± 0.84^{a}	15.7 ± 0.84^{b}	6.8 ± 0.64^{a}	7.1 ± 0.64^{a}	12.1 ± 0.60^{b}
Clay (%)	9.1 ± 0.73^{a}	9.8 ± 0.73^{a}	14.4 ± 0.73^{b}	–	–	–
Cu (mg/L)	0.4 ± 0.05^{a}	0.4 ± 0.05^{a}	0.6 ± 0.05^{b}	0.4 ± 0.06^{a}	0.4 ± 0.06^{a}	0.67 ± 0.06^{b}
K (mg/L)	62.6 ± 7.36^{a}	75.5 ± 7.36^{a}	103.0 ± 7.36^{b}	47.3 ± 4.17^{a}	$60.7 \pm 4.17^{a,b}$	64.3 ± 4.17^{b}
Mg (mg/L)	146.3 ± 15.55^{a}	$166.1 \pm 5.55^{a,b}$	216.9 ± 15.55^{b}	105.5 ± 10.57^{a}	$118.7 \pm 10.57^{a,b}$	152.5 ± 10.57^{b}
Mn (mg/L)	4.7 ± 0.73^{a}	2.8 ± 0.73^{a}	7.3 ± 0.73^{b}	3.7 ± 0.60^{a}	2.4 ± 0.60^{b}	8.7 ± 0.60^{c}
Total N (%)	0.2 ± 0.02^{a}	0.2 ± 0.02^{a}	0.2 ± 0.02^{a}	0.1 ± 0.01^{a}	0.1 ± 0.01^{a}	0.2 ± 0.01^{a}
P (mg/L)	28.7 ± 3.06^{a}	16.3 ± 3.06^{b}	$21.9 \pm 3.06^{a,b}$	27.7 ± 3.43^{a}	12.3 ± 3.43^{b}	29.8 ± 3.43^{a}
pH (KCl)	6.7 ± 0.22^{a}	6.8 ± 0.22^{a}	7.2 ± 0.22^{a}	6.7 ± 0.24^{a}	6.7 ± 0.24^{a}	7.3 ± 0.24^{a}
Zn (mg/L)	1.7 ± 0.21^{a}	1.8 ± 0.21^{a}	2.7 ± 0.20^{b}	$1.3 \pm 0.19^{a,b}$	1.1 ± 0.19^{a}	2.0 ± 0.19^{b}

$^{a, b}$ and ^{c} represent homogenous groups. Groups with different letters represent significant differences ($P < 0.05$) in a nutrient level according to Tukey's post-hoc test.

Mean mineralized nitrogen available for plant uptake was slightly higher in the *A. karroo* stands than in the forest in both soil horizons (Table 3.2), however, this difference was not significant in both the top ($F_{1,28} = 2.24$, $P = 0.146$) and deep ($F_{1,28} = 1.03$, $P = 0.319$) soil horizons at Cape Vidal.

Soil nutrient composition in the *A. karroo* stands at Cape Vidal was similar to soil in the adjacent forest in both soil horizons (Table 3.3), but the undisturbed dune slack soil had significantly different soil nutrient composition to both the *A. karroo* stands and the forest ($P < 0.001$ in both cases). The *A. karroo* stands and adjacent forest soil had the smallest difference in nutrient compositions of all the habitats (Table 3.3).

Table 3.2. Mean (± 1 SE; n = 30 samples per soil horizon in each habitat) ammonium (NH_4N), nitrate (NO_3N) and mineralized nitrogen (mg/L) in the top and deep soil horizons in the three habitats at Cape Vidal.

		Habitat		
Soil horizon	**Nutrient**	***A. karroo* stand**	**Forest**	**Dune slack**
Top soil	**NH_4N**	5.4 ± 0.95^{a}	$7.4 \pm 0.95^{a,b}$	11.4 ± 1.64^{b}
	NO_3N	32.9 ± 3.67^{a}	21.1 ± 3.67^{a}	11.4 ± 6.35^{b}
	Mineralized N	31.9 ± 2.83	25.9 ± 2.83	–
Deep soil	**NH_4N**	5.9 ± 1.16^{a}	6.0 ± 1.16^{a}	11.4 ± 2.01^{a}
	NO_3N	26.0 ± 4.37^{a}	26.0 ± 4.38^{a}	7.4 ± 7.58^{b}
	Mineralized N	29.6 ± 2.54	26.0 ± 2.54	–

$^{a, b}$ and ^{c} represent homogenous groups. Groups with different letters represent significant differences ($P < 0.05$) in a nutrient level according to Tukey's post-hoc test.

At RBM, soil nutrient levels differed significantly among the stands in both soil horizons (MANOVA; top soil: Wilks' $\lambda = 0.04$, $F_{39,\,190} = 9.28$, $P < 0.001$; deep soil: Wilks' $\lambda = 0.06$, $F_{39,\,187} = 7.35$, $P < 0.001$). Most soil nutrient levels were higher in the top soil than in the deep soil (Table 3.4) due to accumulated organic matter in the top soil. Mean clay, copper, potassium, magnesium and total nitrogen increased with advancing successional stage in the top soil (Table 3.4), but soil nutrient levels were independent of successional stage in the deep soil. Total nitrogen levels were slightly lower in the early-mid and mid-late successional stands, but highest in the late successional stands in the deep soil. Interestingly, potassium levels increase with age in the top soil as a result of accumulation of organic matter, but the opposite trend is evident in the deep soil.

Table 3.3. Results of the Multi-Response Permutation Procedure analysis of soil nutrient composition among the forest, *A. karroo* stands and undisturbed dune slacks at Cape Vidal, and the *A. karroo* stands at four successional stages at R Mean (± 1 SE; n = 30 samples per soil horizon in each habitat) ammonium (NH_4N), nitrate (NO_3N) and mineralized nitrogen (mg/L) in the top and deep soil horizons in the three habitats at Cape Vidal BM. *T*-values are reported, followed by *A*-values in parentheses. * represents significance results ($P < 0.5$).

Study site	Groups	Top soil	Deep soil
Cape Vidal	***A. karroo* stands vs. Forest**	0.81(-0.02)	0.79(-0.02)
	***A. karroo* stands vs. Dune slack**	-12.38(0.34)*	-12.42(0.36)*
	Forest vs. Dune slack	-11.84(0.34)*	-10.40(0.31)*
RBM	**Late vs. Mid-late**	-5.87(0.08)*	-8.64(0.08)*
	Late vs. Early-mid	-15.13(0.24)*	-5.69(0.08)*
	Late vs. Early	-16.02(0.26)*	-12.03(0.16)*
	Mid-late vs. Early-mid	-14.58(0.22)*	-9.14(0.10)*
	Mid-late vs. Early	-6.30(0.12)*	-0.39(0.00)
	Early-mid vs. Early	-1.96(0.03)	-12.97(0.20)*

Inorganic nitrogen levels (ammonium and nitrate) were similar among all successional stages at RBM in both soil horizons (MANOVA; top soil: Wilks' $\lambda = 0.70$, $F_{6, 22} = 0.70$, $P = 0.648$; deep soil: Wilks' $\lambda = 0.88$, $F_{6, 22} = 0.25$, $P = 0.956$). Ammonium showed no particular pattern of accumulation, but nitrate was consistently lowest in the early successional stands (Table 3.5).

The soil nutrient composition in the top soil was similar only between the youngest two successional stages (early and early-mid successional stands). The separation in soil nutrient composition of the *A. karroo* stands increased with age since mining (Table 3.3) and nutrient composition of the early and late successional stands were the most dissimilar in the top soil. In the deep soil, only early and mid-late successional stands had similar soil nutrient compositions, while all other successional stages differed significantly (Table 3.3).

Table 3.4. Mean (± 1 SE; n = 10 samples per soil horizon in each *A. karroo* stand) soil nutrients in both soil horizons in the *A. karroo* stands at four stages of succession at RBM. Bold text indicates mean increase in soil nutrient level with stand age.

	Top soil				**Deep soils**			
Nutrient	**Early**	**Early-mid**	**Mid-late**	**Late**	**Early**	**Early-mid**	**Mid-late**	**Late**
Acidity (cmol$_c$/L)	0.1 ± 0.01^{a}	0.1 ± 0.01^{b}	$0.1 \pm 0.01^{a,\ b}$	$0.1 \pm 0.01^{a,\ b}$	$0.1 \pm 0.01^{a,\ b}$	0.1 ± 0.01^{c}	0.1 ± 0.01^{b}	0.1 ± 0.01^{a}
Acid saturation (%)	0.9 ± 0.17^{a}	1.9 ± 0.17^{b}	0.8 ± 0.17^{a}	0.8 ± 0.17^{a}	0.9 ± 0.31^{a}	4.1 ± 0.31^{b}	1.4 ± 0.31^{a}	1.2 ± 0.31^{a}
Ca (mg/kg)	$1100.8 \pm 115.10^{a,\ b}$	892.4 ± 115.10^{a}	1779.2 ± 115.01^{c}	1270.7 ± 115.10^{b}	769.1 ± 99.40^{a}	377.2 ± 99.40^{b}	808.9 ± 99.40^{a}	403.4 ± 102.40^{b}
Cations (cmol$_c$/L)	9.2 ± 0.76^{a}	7.4 ± 0.76^{a}	13.1 ± 0.76^{b}	10.0 ± 0.76^{a}	6.7 ± 0.88^{a}	3.6 ± 0.88^{b}	7.1 ± 0.88^{a}	3.9 ± 0.88^{b}
Clay (%)	**12.1 ± 2.74^{a}**	**31.5 ± 2.74^{b}**	**34.8 ± 2.74^{b}**	**38.0 ± 2.74^{b}**	**14.4 ± 2.52^{a}**	**$21.8 \pm 2.52^{a,\ b}$**	**$23.2 \pm 2.52^{a,\ b}$**	**25.6 ± 2.59^{b}**
Cu (mg/L)	**0.5 ± 0.22^{a}**	**$0.6 \pm 0.22^{a,\ b}$**	**$0.6 \pm 0.22^{a,\ b}$**	**1.2 ± 0.22^{b}**	0.5 ± 0.03^{a}	05 ± 0.03^{a}	0.4 ± 0.03^{a}	0.4 ± 0.03^{a}
K (mg/kg)	**50.7 ± 6.48^{a}**	**72.1 ± 6.48^{b}**	**74.0 ± 6.48^{b}**	**80.1 ± 6.48^{b}**	36.0 ± 2.91^{a}	34.9 ± 2.91^{a}	30.8 ± 2.91^{a}	30.7 ± 2.98^{a}
Mg (mg/kg)	**94.5 ± 10.21^{a}**	**$123.6 \pm 10.21^{a,\ b}$**	**160.7 ± 10.21^{b}**	**157.7 ± 10.21^{b}**	58.8 ± 3.95^{a}	50.9 ± 3.95^{a}	51.1 ± 3.95^{a}	50.1 ± 4.05^{a}
Mn (mg/L)	7.2 ± 1.55^{a}	27.4 ± 1.55^{b}	10.8 ± 1.55^{c}	21.7 ± 1.55^{b}	6.1 ± 1.50^{a}	22.9 ± 1.50^{b}	6.3 ± 1.50^{a}	12.5 ± 1.50^{c}
Total N (mg/kg)	**722.4 ± 106.68^{a}**	**916.9 ± 106.68^{a}**	**1597.1 ± 106.68^{b}**	**1898.6 ± 106.68^{b}**	$471.1 \pm 48.46^{a,\ b}$	344.0 ± 48.46^{c}	$404.0 \pm 48.46^{b,\ c}$	622.2 ± 49.72^{a}
Total N (%)	**0.1 ± 0.01**	**0.1 ± 0.01**	**0.2 ± 0.01**	**0.2 ± 0.01**	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.01
P (mg/kg)	18.6 ± 1.27^{a}	15.2 ± 1.27^{a}	18.9 ± 1.27^{a}	17.3 ± 1.27^{a}	15.2 ± 0.98^{a}	8.7 ± 0.98^{b}	9.2 ± 0.98^{b}	7.2 ± 1.01^{b}
pH (KCl)	7.2 ± 0.11^{a}	4.8 ± 0.11^{b}	5.9 ± 0.11^{c}	5.3 ± 0.11^{d}	7.5 ± 0.17^{b}	5.0 ± 0.17^{a}	6.5 ± 0.17^{c}	5.4 ± 0.17^{a}
Zn (mg/L)	4.0 ± 0.71^{a}	2.2 ± 0.71^{a}	$3.7 \pm 0.71^{a\ b}$	5.3 ± 0.71^{b}	2.2 ± 0.44^{a}	0.9 ± 0.44^{a}	1.2 ± 0.44^{a}	1.2 ± 0.44^{a}

$^{a,\ b,\ c}$ and ^{d} represent homogenous groups. Groups with different letters represent significant differences ($P < 0.05$) in a nutrient level according to Tukey's post-hoc test. *Acacia karroo* stand soil samples:.

Total nitrogen has accumulated in the early, early-mid, mid-late and late successional *A. karroo* stands at RBM at rates of 0.035 $g.kg^{-1}.yr^{-1}$, 0.054 $g.kg^{-1}.yr^{-1}$, 0.128 $g.kg^{-1}.yr^{-1}$ and 0.133 $g.kg^{-1}.yr^{-1}$ respectively. Assuming a bulk density of 1.5 $kg.L^{-1}$ (75 $kg.m^2.yr^{-1}$ in the top 5cm), these rates are equivalent to total nitrogen accumulation rates of 2.6, 4.1, 9.6 and 10.0 $g.m^2.yr^{-1}$ in the top 5 cm alone.

Table 3.5. Mean (± 1 SE; n = 10 samples per soil horizon in each *A. karroo* stand) ammonium (NH_4N) and nitrate (NO_3N; in mg/L) in both soil horizons in the *A. karroo* stands at four successional stages at RBM.

		Successional stage			
Soil horizon	**Nutrient**	**Early**	**Early-mid**	**Mid-late**	**Late**
Top Soil	**NH_4N**	6.0 ± 2.67^a	10.0 ± 2.67^a	4.7 ± 2.67^a	6.5 ± 2.67^a
	NO_3N	38.4 ± 20.50^a	58.0 ± 20.50^a	58.2 ± 20.50^a	58.2 ± 20.60^a
Deep Soil	**NH_4N**	7.0 ± 2.21^a	8.5 ± 2.21^a	5.5 ± 2.21^a	6.7 ± 2.21^a
	NO_3N	40.1 ± 18.96^a	50.4 ± 18.96^a	59.6 ± 18.96^a	48.1 ± 18.96^a

$^{a, b}$ and ^{c} represent homogenous groups. Groups with different letters represent significant differences ($P < 0.05$) in a nutrient level accord to Tukey's post-hoc test.

ii. Habitat classification

Using DFA the soil variables predicted habitat groups with a high degree of accuracy (top soil: 79.8%; deep soil: 80.5%; Table 3.6) and is a useful predictive model of habitat type. The first two discriminant functions accounted for 78.8% of variance among habitats in the top soil and 76.4% of variance among habitats in the deep soil and these two functions were used for interpretation. Of the 15 predictor soil variables, five had important predictive power in the first two functions (Table 3.7).

The first function in the top soil (Fig. 3.1) represents a gradient primarily associated with increasing soil manganese and nitrate, while the second function represents a weaker gradient associated with increasing soil calcium and ammonium (Table 3.7). The first function in the deep soil (Fig. 3.2) represents a gradient primarily associated with increasing soil calcium and total nitrogen, while the second function represents a weaker gradient associated with increasing soil manganese and ammonium (Table 3.7). In both soil horizons the habitats were best separated by gradients of nitrogen content (total nitrogen, ammonium or nitrate).

Table 3.6. Percent classification success of samples into each habitat at Cape Vidal and RBM based on the soil predictor variables using DFA.

	Habitat							
Soil horizon	***A. karroo* stand**	**Forest**	**Early**	**Early-mid**	**Mid-late**	**Late**	**Dune slack**	**Average**
Top soil	73.3	60.0	85.0	90.0	80.0	73.7	93.3	79.8
Deep soil	66.7	66.7	84.2	78.9	70.0	100.0	100.0	80.5

Table 3.7. Standardized discriminant function coefficients for significant predictor variables in the final discriminant models for both top and deep soil at Cape Vidal and RBM. Bold values indicate the primary contribution of a soil nutrient to a function.

	Top soil		Deep soil	
Soil nutrients	**Function 1**	**Function 2**	**Function 1**	**Function 2**
acidity	0.070	-0.220	-0.215	-0.298
acid saturation	-0.103	-0.019	0.146	0.359
Ca	0.009	**0.799**	**0.511**	0.419
clay	0.359	0.111	0.053	-0.053
Cu	0.005	0.057	0.330	0.453
K	0.085	0.051	0.204	-0.180
Mg	-0.105	-0.384	-0.159	-0.288
Mn	**0.458**	0.318	-0.291	**0.571**
P	-0.040	-0.300	0.255	-0.071
pH	-0.355	-0.098	0.189	0.385
NH_4	-0.085	**0.833**	0.383	**0.737**
NO_3	**0.654**	-0.548	-0.268	-0.438
Total N	-0.275	0.107	**0.588**	-0.453
Zn	0.066	-0.169	0.168	-0.100

In the top soil (Fig. 3.1) the soil nutrients with the greatest discriminatory power between habitats were manganese, nitrate, calcium and ammonium. Based on these soil nutrients, the Cape Vidal *A. karroo* stands and adjacent forest soils were grouped as most similar and were closely aligned with early successional *A. karroo* stands at RBM. The three older successional *A. karroo* stands (early-mid, mid-late and late) were grouped together, while the forested dune slacks at Cape Vidal were dissimilar to all other habitats. Similar trends were found in the deep soil (Fig. 3.2), where the soil nutrients with the greatest power of discrimination between habitats again were calcium, manganese and ammonium, together with total nitrogen. It is clear that, although not limiting to species establishment and growth at Cape Vidal, the various forms of soil nitrogen are important soil classifiers in the different coastal dune forest habitats and successional stages in the *A. karroo* successional pathway at RBM.

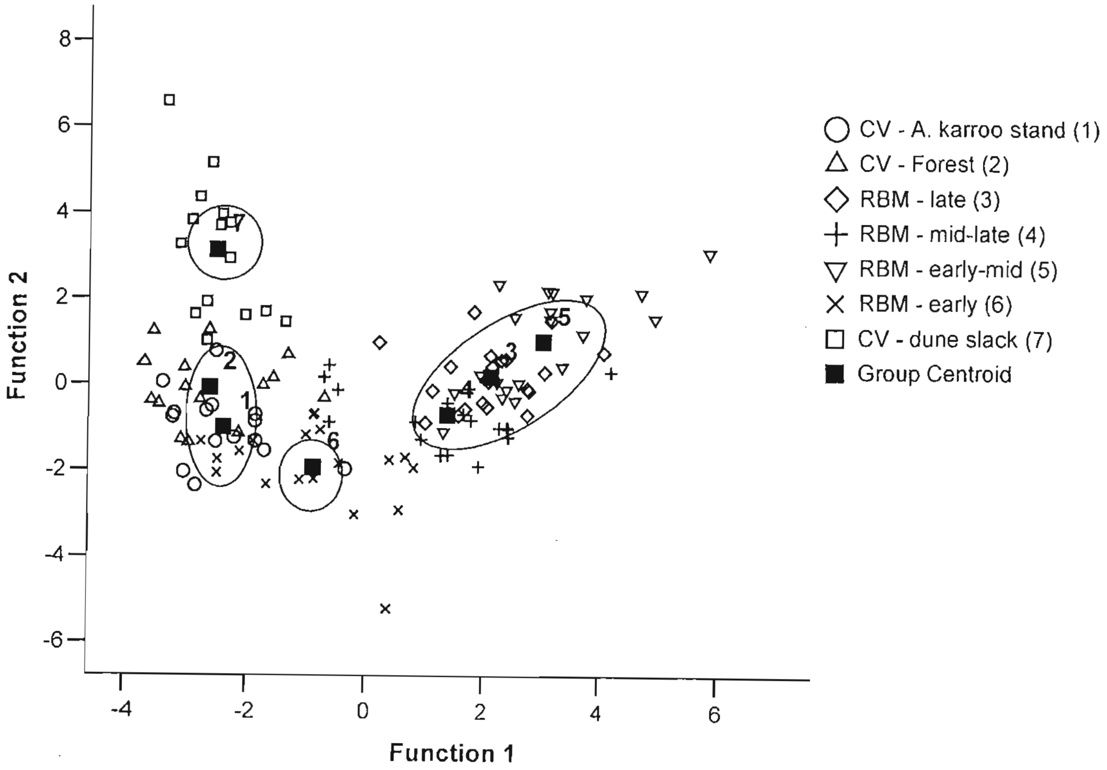

Fig. 3.1. Position of habitats along discriminant functions 1 and 2 from the DFA among soil nutrient characteristics in the top soil horizon of habitats at Cape Vidal (CV) and RBM. The group centroids (■) represent mean discriminant function values for each habitat. Function 1 is associated with soil manganese and nitrate, while function 2 is associated with calcium and ammonium.

Seedling growth response to nitrogen addition

The effect of nitrogen-rich fertilizer on seedling growth of three different tree species was examined in the forest and previously disturbed *A. karroo* stands at Cape Vidal. Seedling growth in both habitats was unaffected by nitrogen supplementation ($F_{3,81}$ =1.11, P = 0.342).

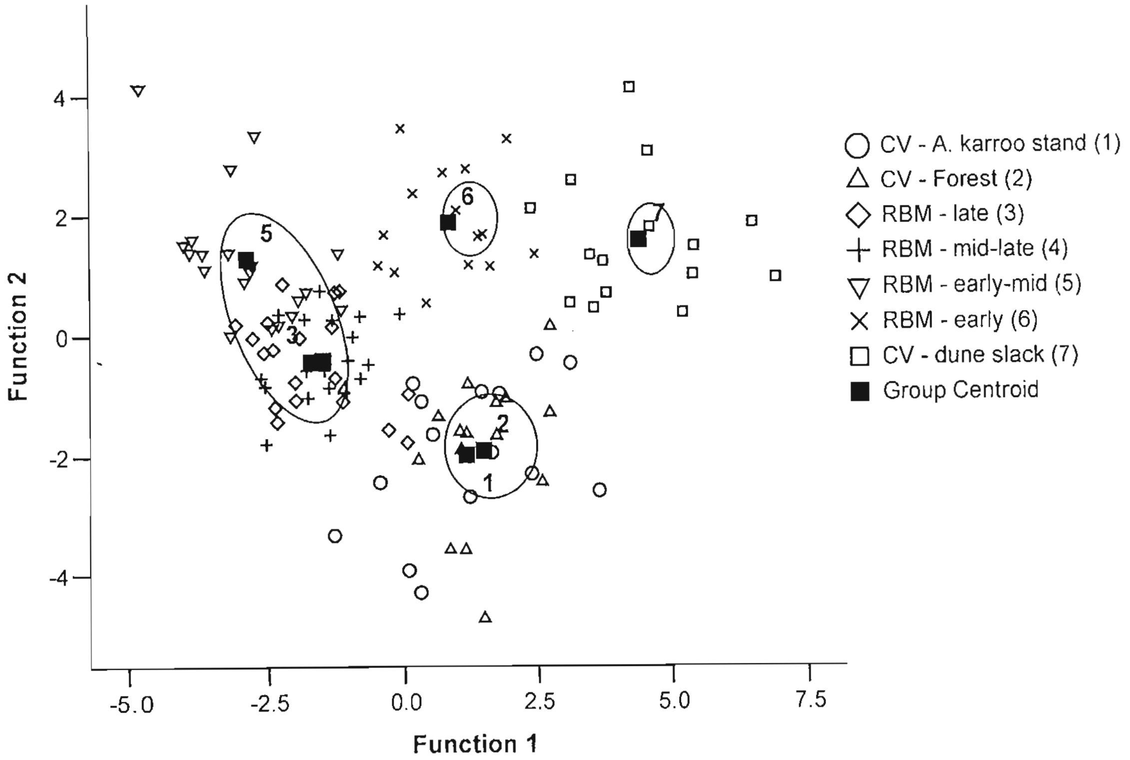

Fig. 3.2. Position of habitats along discriminant functions 1 and 2 from the DFA among soil nutrient characteristics in the deep soil horizon of habitats at Cape Vidal (CV) and RBM. The group centroids (■) represent mean discriminant function values for each habitat. Function 1 is associated with soil calcium and total nitrogen, while function 2 is associated with manganese and ammonium.

However, all species grew faster in both treatment and control plots when planted in the *A. karroo* habitat when compared to those in the forest (Fig. 3.3). Of the three species, *A. karroo* seedlings grew the fastest when planted in the *A. karroo* stands in both treatment and control plots and also showed the greatest increase in height when supplementary nitrogen was applied. Neither *C. africana* nor *D. natalensis* seedlings responded to supplementary nitrogen addition and habitat caused the greatest difference in seedling growth.

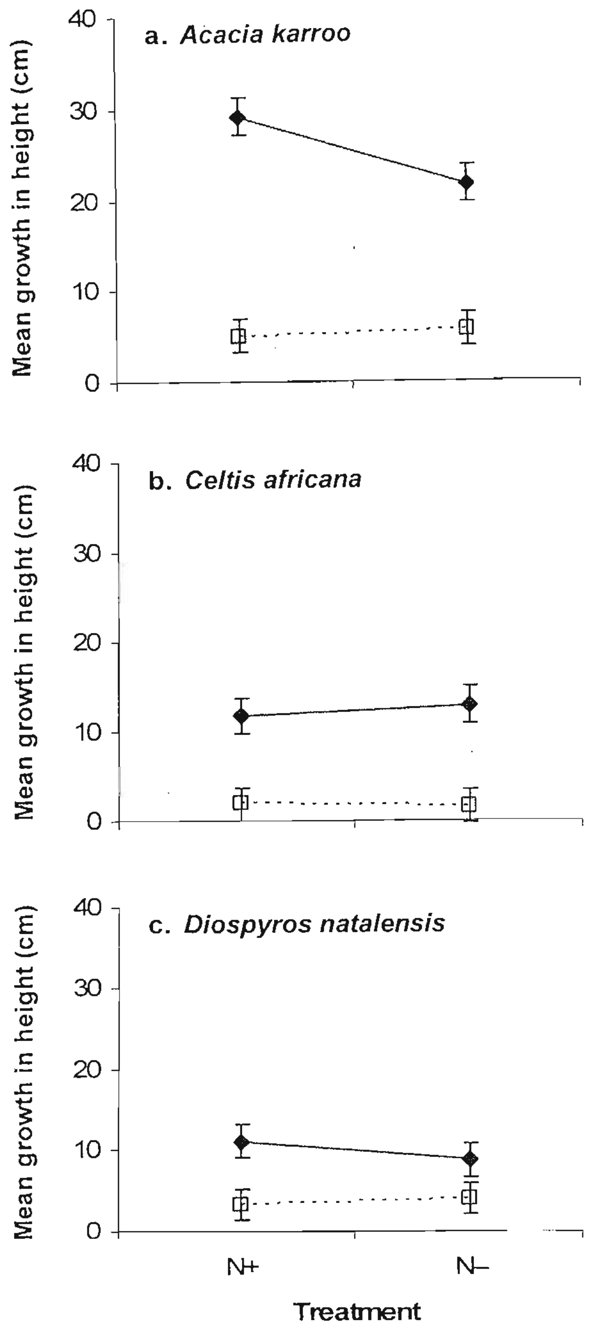

Fig. 3.3. Comparative mean growth in height (± 1 SE; n = 15 samples per habitat) of planted seedlings in the forest and *A. karroo* stand habitats at Cape Vidal in nitrogen-supplemented (N+) and control (N–) plots of **(a)** *Acacia karroo*, **(b)** *Celtis africana*, and **(c)** *Diospyros natalensis* seedlings. All plots were protected by caging. *Acacia karroo* stand plots are

indicated by a solid diamond (◆) with a solid line and the forest plots by an open square (□) with a dashed line.

Discussion

Vegetation recovery following disturbance is associated with soil fertility so that regions with similar soil nutrient levels have been shown to display comparable rates of vegetation regrowth (Moran et al. 2000). Nitrogen is an essential macronutrient needed in large amounts by plants for survival (Öpik & Rolfe 2005) and low available nitrogen can be limiting to plant growth and species diversity (Tilman 1986; Tilman 1987). Although the level of soil nitrogen was expected to be critically low in previously disturbed sites at Cape Vidal, this was not the case. In fact, soil nutrient levels in *A. karroo* stands at Cape Vidal were similar to those of the neighbouring coastal dune forest in both the top and deep soil horizons. In particular, total and mineralized nitrogen available for plant uptake were similar among habitats at Cape Vidal and can be excluded as a factor limiting establishment and growth of coastal dune forest species in the previously disturbed *A. karroo* stands. Thus, the arrested succession of forest tree species in the *A. karroo* stands cannot be attributed to low soil fertility in these previously disturbed areas. These results suggest that the vegetation dynamics at Cape Vidal are not entirely controlled by abiotic, bottom-up forces (Hunter & Price 1992).

Major soil forming processes which are influenced by soil type are accumulation of organic matter and leaching (Sevink 1991). Soils of the Zululand Coastal Plain are characteristically relatively deep and sandy with low clay content (Maud 1991). Rapid decomposition of organic matter and leaching of soluble nutrients released is characteristic of these soil types (Sevink 1991), resulting in low to very low soil fertility in this region (Maud 1991). Soils with higher clay content experience slower organic matter decomposition, resulting in nutrient accumulation in this layer (Sevink 1991) In addition, soil nutrient levels stabilize at a lower level than soils with higher clay content. Total nitrogen levels at Cape Vidal are relatively low with respect to those of other tropical forests (Feeley & Terborgh 2005; Powers et al. 2005), however total nitrogen content of typical white sands (total nitrogen = 0.1%; Richards 1996) is lower than that of the soils at Cape Vidal (total nitrogen = 0.2%). Thus, the total nitrogen content of soils at Cape Vidal is not unusually low. Furthermore, because the Cape Vidal forest has established in sandy soils with typically low nutrient status when compared to other soil types (Richards 1996), the vegetation may be less susceptible to limited nutrient availability than forest types which have established in richer soils (Chapin et al. 1986).

In forest ecosystems, nutrient addition experiments have demonstrated the importance of abiotic, bottom-up forces in determining plant community composition, structure and vegetation growth rates (Dlott & Turkington 2000; Khurana & Singh 2001; Lawrence 2003). A synthesis of the literature on tropical tree seedling responses to nutrient availability demonstrated that a large proportion of light- and shade-adapted tropical seedlings had a positive growth response to nutrient supplementation (Lawrence 2003). At Cape Vidal, however, the growth of seedlings of forest species in the *A. karroo* stands and the adjacent forest was unaffected by supplementary soil nitrogen and increased general fertility. Considering the similar soil conditions between the *A. karroo* stands and neighbouring forest at Cape Vidal, in retrospect this was not a surprising finding. Clearly, naturally available soil nitrogen in the *A. karroo* stands is sufficient for the growth of forest species seedlings, rendering the supplementary nitrogen superfluous.

Dominant species in infertile soils such as coastal dunes are known to be more responsive to nutrient addition than are individuals in more fertile sites (Chapin et al. 1986). While all tree species in both treatment and control plots grew faster in the *A. karroo* stands than in the forest habitat, *A. karroo* seedlings grew the fastest in the *A. karroo* stands when soil nitrogen was supplemented. This species is clearly able to use available nitrogen more efficiently than *C. africana* and *D. natalensis*, making it a better competitor and successful early successional species in this environment (Tilman 1986). Only habitat type affected the growth of *C. africana* and *D. natalensis* seedlings; both species survived better and grew fastest when planted in the *A. karroo* stands. I conclude that seedlings of pioneer and mature forest species can survive and grow well in the *A. karroo* stands regardless of soil nitrogen enrichment.

At Cape Vidal, the undisturbed, forested dune slacks and the *A. karroo*-dominated dune slacks are topographically similar, both occurring in the valleys between the dunes where organic matter may accumulate and increase the soil nutrient content (Sevink 1991). As mature forest species do occur in some dune slacks which have more fertile soils than the *A. karroo* stands (due to slightly higher clay content in these dune slacks causing slower organic matter decomposition), dune slacks in general do not have specific soil conditions that prevent forest species establishment. The soil from the forest adjacent to the *A. karroo* stands was similarly less fertile than the undisturbed, forested dune slacks, yet both are vegetated with mature dune forest. These dune slacks clearly have suitable soil nutrient conditions for forest tree species growth. The higher nutrient levels observed in the forested dune slacks compared to adjacent forest may be a result of habitat topography (Sevink 1991) with slacks accumulating nutrient-rich organic matter more easily. This suggests that the more fertile soil conditions in the forested dune slacks compared to the adjacent forest and *A. karroo* stands is probably a result of their slightly higher clay content rather than of the disturbance histories of the habitats.

Nitrogen fixation plays an important role in secondary forest regrowth (Gehring et al. 2005), and the nitrogen-fixing capabilities of *A. karroo* potentially facilitate the recovery of the mined dunes at RBM. Soil nutrients have accumulated in these mined dunes over time (van Aarde et al. 1998), particularly in the top soil. Calcium, potassium, phosphorus, magnesium and total nitrogen levels recorded by van Aarde et al. (1998) have increased since they were last measured. In particular, there has been a two-fold increase in total nitrogen levels of both the early and late successional stands over the past 11 years. Accumulation of total nitrogen in the oldest stand at RBM occurred at a rate of 10.0 $g.m^{-2}.yr^{-1}$, and assuming a similar rate at Cape Vidal, previously disturbed *A. karroo* stands should not be nitrogen limited. The rates reported in this study are considerably higher than those for temperate coastal dunes and old fields (Gerlach et al. 1994; Knops & Tilman 2000) and are probably a result of very efficient nitrogen-fixation and cycling by the legume, *A. karroo*. Also noteworthy is the soil nutrient levels in the oldest recovering stand at RBM, which have increased over the last 11 years to a level similar to nearby unmined forest (van Aarde et al. 1998). Thus, rehabilitating *A. karroo* stands do accumulate soil nutrients with age, eventually approaching that of unmined habitats within 27 years. *Acacia karroo* clearly facilitates recovery of the abiotic environment on these coastal dunes following mining, which in turn allows succession towards coastal dune forest to proceed (Wassenaar et al. 2005).

Nitrogen is made available for uptake by plants by the process of mineralization (Barbour et al. 1999). Mineralization is known to be high below nitrogen-fixing shrubs (Gerlach et al. 1994). The high levels of soil nitrate, the main nitrogen source for plants (Öpik & Rolfe 2005), present in the soils of *A. karroo* stands at Cape Vidal and RBM are a result of higher levels of nitrogen mineralized from the nitrogen-rich litter and decaying roots of *A. karroo*; the majority of this nitrogen having probably been fixed by nitrogen-fixing bacteria in root nodules (Dilz & Mulder 1962). Nitrate is extremely soluble, so leaches easily from soil in rainwater and needs rapid replenishment as it is absorbed by plants in large quantities (Öpik & Rolfe 2005). The *A. karroo* stands at Cape Vidal are located in the dune slacks, so in addition to the nitrate added to these soils through nitrogen-mineralization, nitrate possibly leaches from the dune slopes and accumulates in the slacks where drainage is poor (Sevink 1991).

Nitrification is controlled by the availability of ammonium (Skiba & Wainwright 1984). When nitrogen availability is low, plants will take up all mineralized ammonium and the nitrification process which converts ammonium to nitrate will be interrupted. In high-nitrogen environments, however, there is sufficient nitrogen available for nitrification to occur, and the system becomes dominated by nitrate (Schimel & Bennett 2004). Thus, the presence of nitrate in all soils tested at Cape Vidal, and in larger amounts in the previously disturbed *A. karroo* stands further suggests that soil nitrogen available for plant use is not limiting.

Although not limiting to tree seedling growth, the DFA demonstrates that the various forms of soil nitrogen are important classifiers of soils in the different coastal dune forest habitats and successional stages in the *A. karroo* successional pathway. This is possibly due to soil nitrogen conditions and changes in the dominant nitrogen form as succession proceeds. Total nitrogen in a system is a function of many factors, an important one being soil texture; sandy soils such as those at Cape Vidal allow for rapid decomposition of organic matter and soil nutrient levels are much lower than on more clayey soils (Sevink 1991). Although total nitrogen is similar between the habitats, this has little bearing on nitrogen availability to plants; inorganic and mineralized nitrogen are available for uptake and so are more important in ecosystems. Soil calcium and manganese are also important factors classifying these habitats. Soil calcium is affected by available lime (calcium carbonate) and pH, where calcium availability decreases as soil acidity increases (McLaughlin & Wimmer 1999). The pH of these study sites is not high however (ranges between 4.8 and 7.5), and plants can tolerate very low calcium levels, so calcium is unlikely to be limiting at these sites. Manganese is also influenced by soil pH and can be toxic at $\text{pH} < 5.5$ or in waterlogged soils, but the relatively high pHs of these study sites and dry, sandy nature of the soils, manganese toxicity is unlikely to occur at these sites. According to the DFA, the *A. karroo* stand and adjacent forest habitats at Cape

Vidal have relatively similar soil nutrient conditions to the early successional *A. karroo* stand at RBM, particularly in the top soil horizon. The three older *A. karroo* successional seres at RBM were grouped together in both the top and deep soil, indicating that their soils are similar. It appears that there is a clear difference between early and late successional soils in rehabilitating coastal dune forests and that nitrogen is an important distinguishing factor between these, although not limiting to plant establishment and growth in these systems.

Soil nutrient status is strongly influenced by soil type, climate and past land-use (Holl 1999; Compton & Boone 2000; Goodale & Aber 2001; Latty et al. 2004; Pérez et al. 2004). Although the soil nutrient status in the *A. karroo* stands directly post-disturbance are not known, areas that have supported human settlements are likely to have left highly variable soil fertility: burning typically causes low soil fertility (Goodale & Aber 2001; Latty et al. 2004), as does cultivation (Compton & Boone 2000). However, soils that have been fertilized with animal manure or had livestock grazing tend to have raised soil nutrient levels, particularly carbon and nitrogen (Compton & Boone 2000). The disturbance undergone in the coastal dune forests at Cape Vidal and the mining at RBM may have had different effects on soil nitrogen and general fertility. Nevertheless, the efficient nitrogen-fixing properties of *A. karroo* have probably facilitated the rapid accumulation of soil nitrogen at RBM and it is possible that soil nitrogen and general fertility have been increasing over time at Cape Vidal as was shown to occur at RBM (van Aarde et al. 1998).

Conclusions

The vegetation regeneration dynamics in *A. karroo* stands at Cape Vidal do not appear to be driven by bottom-up forces and abiotic factors like low available nitrogen are not limiting to succession. This study clearly indicates that naturally occurring nitrogen in previously disturbed *A. karroo* stands is sufficient for forest species seedlings to establish and grow well. Soil nutrient levels are currently favourable for growth of a range of forest species in the previously disturbed *A. karroo* stands. Despite suitable nutrient levels at disturbed sites and evidence of the facilitative role played by *A. karroo* in the recovery of soil fertility and resulting vegetation succession on the mined dunes at RBM, the successional pathway is not proceeding at Cape Vidal. This points to an alternative post-emergence factor limiting seedling establishment and survival respectively, and the lack of convergence of the vegetation community of previously disturbed areas at Cape Vidal with that of pristine forest, which will be further investigated in the next chapter of this thesis.

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Chapter 4

Herbivory by large mammals arrests succession in a previously disturbed coastal dune forest

Abstract

Question: Is the survival and growth of forest seedlings in regenerating *A. karroo* stands at Cape Vidal negatively affected by mammalian herbivory? Do herbivores selectively use *A. karroo* stands rather than the surrounding forest at Cape Vidal? Is herbivory arresting dune forest succession?

Location: Cape Vidal and the Richards Bay Minerals mining lease areas (RBM), in northern KwaZulu-Natal, South Africa.

Methods: Growth and survival of seedlings of *A. karroo*, *Celtis africana* and *Diospyros natalensis* were monitored over two years in *A. karroo* stands and neighbouring forest at Cape Vidal in experimental plots where herbivores were excluded and supplementary nitrogen was added. Natural establishment of woody species was also monitored in fenced and unfenced plots. Densities of large mammalian herbivores were estimated in the two habitats at Cape Vidal and the mined *A. karroo* stands at RBM.

Results: In the absence of herbivory both the survival and growth of planted seedlings increased significantly at Cape Vidal, particularly in the *A. karroo* stands. Higher light availability in the *A. karroo* stands at Cape Vidal explained the increased growth of *A. karroo* and *D. natalensis* relative to that in the forest. Higher densities of herbivores occurred in the *A. karroo* stands at Cape Vidal, while no indigenous herbivores were observed at RBM.

Conclusions: These results suggest that succession at Cape Vidal is limited by seedling mortality caused by selective herbivory. This top-down control of seedling recruitment in the *A. karroo* stands prevents forest tree species from establishing, resulting in arrested succession. The suitability of the *A. karroo* successional pathway for restoration of disturbed coastal dune forests must be evaluated for each site, but appears to be most affected by the levels of herbivory at a site.

Keywords: *Acacia karroo* successional pathway; browsing; Cape Vidal; herbivore exclusion; light availability; seedling survival; top-down forces; trampling.

Nomenclature: Coates Palgrave (2002) for trees; Skinner & Smithers (1990) for mammals.

Abbreviations: ANOVA = analysis of variance; LAN = Limestone Ammonium Nitrate; MANOVA = multivariate analysis of variance; MRPP = multi-response permutation procedure; PAR = photosynthetically active radiation; RBM = Richards Bay Minerals mining lease areas; R:FR = red:far-red light ratio.

Introduction

Herbivory by mammals acts as a disturbance in plant communities (Connell & Slayter 1977; Huntly 1991) and has direct (e.g., removal of biomass) and indirect (e.g., alteration of resource availability) effects on vegetation (Coley et al. 1985; McInnes et al. 1992; Dlott & Turkington 2000; van der Wal et al. 2000). Herbivory is a "top-down" force acting on vegetation (Hunter & Price 1992), and has been associated with both the increase (Rietkerk et al. 2000; Palmer et al. 2003) and decrease of community species diversity (McInnes et al. 1992; Augustine & McNaughton 1998; Liang & Seagle 2002). By altering resource availability, herbivores can create opportunities for new species to invade, causing increased structural and species heterogeneity, and reducing the abundance of dominant species (Allcock & Hik 2003). Alternatively, through selectively feeding on the more palatable species, herbivores can cause dominance by unpalatable plant species (Augustine & McNaughton 1998; Liang & Seagle 2002). Augustine & McNaughton (1998) reviewed studies conducted in a range of forest ecosystems, all of which indicated that selective removal of tree seedlings by browsers acts as an ecological filter, ultimately determining the canopy composition, and potentially many other forest characteristics such as density and average diameter of canopy trees.

The negative effects of browsing on seedling growth and survival in tropical forests are well documented. They have been shown to modify relative species abundance and decrease seedling recruitment into larger size classes (Molofsky & Fisher 1993; Terborgh & Wright 1994; Lawes & Chapman 2006). Few studies have quantified the impact of trampling of vegetation by herbivores. However, Plumptre (1993) and Cole (1987) found that vegetation cover, species, and the organic soil horizons can be reduced as a result of trampling. Thus herbivores can affect plant communities in many ways and have the potential to reduce the rate of succession, potentially arresting it completely (Côté et al. 2004).

The Cape Vidal coastal dune forests are located within the Greater St. Lucia Wetland Park in northern KwaZulu-Natal, where naturally occurring populations of large mammalian herbivores still occur. Natural succession initiated by the establishment of even-aged stands of *Acacia karroo* (von Maltitz et al. 1996), an early successional species, has been occurring in these coastal dune forests since 1952 when subsistence farmers were relocated to allow for commercial afforestation in the area (Weisser & Marques 1979; Weisser & Muller 1983). In 1978 rehabilitation via the *A. karroo* successional pathway was initiated on the mined dunes at Richards Bay, approximately 70 km south of Cape Vidal (Camp & Weisser 1991; Lubke et al. 1996; van Aarde et al. 1996) and the pathway is projected to lead to complete restoration of coastal dune forest within 54 – 70 years (Mentis & Ellery 1998; Wassenaar 2003). At Cape Vidal, however, the *A. karroo* stands are more than 50 years old, yet the diversity of forest tree species in these stands is still low (West et al. 2000). The *A. karroo* trees that initially established in previously disturbed areas at Cape Vidal are now senescing, but they are being replaced by a new cohort of young *A. karroo* trees instead of by pioneer forest species, and succession is arrested.

African *Acacias* are typical savanna species that have co-evolved with large mammalian herbivores (Rohner & Ward 1997), so have evolved paired spines or thorns in response to predation by herbivores. These thorns are particularly pronounced in the seedling and sapling stages of *A. karroo* individuals until they reach a height at which they escape predation by most herbivores (Midgely & Ward 1996).

Although seed dispersal into the *A. karroo* stands was shown in Chapter 2 to be marginally limited, a post-dispersal factor appeared to be the dominant cause of low seedling recruitment. In Chapter 3 I established that availability of common soil nutrients, and particularly that of soil nitrogen were not critically low and thus not limiting to survival and growth of seedlings of three tree species that are common at Cape Vidal. The influence of light availability can also affect seedling composition as particular species germinate under closed canopies, while others, considered pioneer species, usually germinate in gaps (Swaine & Whitmore 1988).

Studies show that long-term selective browsing on specific palatable, undefended species of tree seedlings prevents them from reaching and contributing to the canopy community (McInnes et al. 1992; Augustine & McNaughton 1998; Liang & Seagle 2002). When this occurs, the canopy can become dominated by unpalatable or well defended species that do reach maturity. In light of this and previous findings in this thesis, I examine the premise that the apparent arrested succession in *A. karroo* stands at Cape Vidal, and the dominance of thorny *A. karroo* individuals, is a result of top-down pressure caused by selective herbivory.

The *A. karroo* stands at Cape Vidal are situated in the dune slacks (valleys between dunes) where the topography allows for easy movement and abundant grazing and browsing material is available. As a result, dune slacks may be used more frequently by herbivores than the dune forest. Seedlings of undefended, palatable forest species that establish in the *A. karroo* stands potentially experience higher levels of predation or trampling by animals, thereby reducing growth and survival and ultimately plant diversity. The degree of impact that herbivory has on vegetation depends on the density of herbivores that use the vegetation as a food source, and on the number of animals that pass through an area on a daily basis (Augustine & McNaughton 1998). Considering the large mammalian herbivores that inhabit the Cape Vidal coastal dune forest, including hippopotamus (*Hippopotamus amphibious*), black and white rhinoceros (*Diceros bicornis* and *Ceratotherium simum*, respectively), kudu (*Tragelaphus strepsiceros)*, bushbuck (*Tragelaphus scriptus*), red duiker (*Cephalophus natalensis*) and bush pig (*Potamochoerus porcus*), herbivory and trampling could have a major influence on the vegetation.

This chapter examines the hypothesis that the arrested succession at Cape Vidal is a result of high levels of herbivory in the *A. karroo* stands that reduces growth and survival of seedlings of forest tree species. In doing so, the following specific questions are addressed: (1) does survival and growth of forest seedlings in *A. karroo* stands increase when seedlings are protected from herbivores; (2) do herbivores use *A. karroo* stands at Cape Vidal more intensely than the surrounding forest; and (3) what is the indigenous herbivore density in rehabilitating *A. karroo* stands at Richards Bay? This study will provide a more comprehensive understanding of the role played by top-down forces in the *A. karroo* successional pathway and allow for informed management of regenerating coastal dune forests in both the presence and absence of natural herbivore populations.

Materials and methods

Study sites

Two sites were used in this study: Cape Vidal and the Richards Bay Minerals mining lease areas (RBM; see Chapter 2 for a full description of sites). At Cape Vidal, 15 paired experimental sites were used, 5 in each of three previously disturbed *A. karroo* stands and the adjacent undisturbed forest. At RBM, sites selected for sampling were previously mined dunes now vegetated with *A. karroo* stands at different successional stages (ranging from immediately post-mining to late successional).

Exclosure plots

The experiment was designed to examine primarily the effects of two variables on seedling growth at Cape Vidal: protection from large mammalian herbivores and habitat type (forest vs. *A. karroo* stand). Plots were set up in the paired experimental sites in *A. karroo* stands and adjacent forest. All plots were freestanding, with a minimum distance of 1.5 m between plots. At each experimental site four 1 m^2 plots were cleared of all vegetation and planted with five seedlings each of an aggressive coloniser of disturbed habitats (*A. karroo*), a typical forest pioneer species, the seeds of which can germinate in gaps (*Celtis africana*), and a typical mature forest species, the seeds of which usually germinate under canopies (Swaine & Whitmore 1998) such as *Diospyros natalensis* at Cape Vidal. Seedlings that died from transplant shock were replaced, but those that were browsed or trampled were left. In each plot the seedlings were planted 20 cm apart but their position in the array was randomized. Two treatment plots were enclosed in weld-mesh fencing to exclude large mammalian herbivores and two were left unfenced. Two of these plots (one fenced and one unfenced) were treated with 20 g.m^{-2} of Limestone Ammonium Nitrate (LAN), a granulated 28% nitrogen-based fertilizer. The other unfenced plot served as a control. The LAN was applied to the treatment plots annually in January of each year during the summer rainy season (John & Turkington 1997; Turkington et al. 2002).

Seedling height and stem diameter were measured every 6 – 7 weeks for a period of one year (February 2004 – January 2005) and every three months for a second year (February 2005 – January 2006). The measure of seedling growth used for analysis was the height at each time interval relative to the original seedling size to avoid an effect of the starting seedling size on growth.

At each paired experimental site in the forest and the *A. karroo* stands two additional 1 m^2 plots were cleared of all herbaceous vegetation and the change in richness and abundance of naturally occurring *in situ* woody species in these unplanted plots monitored over two years (February 2004 – January 2006). One of these plots was fenced to exclude large mammalian herbivores and the other left unfenced as a control.

Altogether this design resulted in: (1) 15 experimental sites in each of two habitats (*A. karroo* stands and adjacent forest); (2) at each site, a pair of planted, fenced (P+ F+) and unfenced (P+ F–) plots with no nitrogen (N–) added; (3) at each site, a pair of planted, fenced (P+ F+) and unfenced (P+ F–) plots to which supplementary nitrogen was added (N+); and (4) two unplanted plots per site, one fenced (P– F+) and one unfenced (P– F–).

Light conditions

Light quantity, measured as photosynthetically active radiation (PAR; μmol.m^{-2}.s^{-1}) was included as a covariate of seedling growth (Endler 1993). PAR was estimated from measurement of the red:far-red light ratio (R:FR) in the field and derived as percent transmittance from the exponential regression (Levenberg-Marquardt estimation method; (SPSS 2004) of PAR on R:FR in the field after the method of Capers & Chazdon (2004). All light measurements were conducted using Apogee quantum and red or far-red sensors.

Herbivore density

Herbivore density surveys were conducted to estimate the abundance of large mammalian herbivores using the *A. karroo* stands and forest habitats at Cape Vidal and in the previously mined *A. karroo* stands at RBM. This allowed for a comparison of the absolute densities of herbivores among the habitats. King's strip transect method (Burnham et al. 1980) was used to conduct surveys. This method made the assumptions that: (1) animals in the transect were always sighted; (2) animals were not flushed and do not move before being sighted; (3) individuals were counted only once; and (4) all sightings were independent. In each of the habitats at Cape Vidal a 500 – 600 m transect was measured and walked slowly (approximately 1 – 2 km /hr) twice daily, once in the early mornings (before 1000 h) and once in the late afternoon (after 1500 h) when animals were most active. All herbivores that were sighted, the habitats they were sighted in and their distances from the observer were recorded. Forty transects were conducted spread evenly over a calendar year. The direction and order in which transects were walked were alternated to reduce the potential bias resulting from differential habitat use by herbivores, and from the direction of movement by the observer (Lawes 1992). The density of common herbivore species sighted in each habitat was calculated using the software Distance (Thomas et al. 2006).

At RBM, small numbers of red duiker and bushbuck are present in the rehabilitating *A. karroo* stands (A. Haagner, pers. comm.), and wild herbivores are very rare due to local hunting pressures. For this reason, driven transects were conducted through the stands and herbivore sightings in the different aged stands recorded. The distance travelled was recorded so number of individuals per km could be calculated.

Data analyses

To avoid repeatedly testing the same hypothesis and incurring type I errors, multivariate analysis of variance (MANOVA) was used to analyze differences in survival of planted seedlings. Treatment, habitat and species were included as fixed factors in the MANOVA. The Wilks' λ (likelihood ratio criterion) was consulted to assess the reliability of the univariate tests. It varies between 0 and 1, and tests the overall significance of the treatments on the variables. If this test is significant, the univariate F-tests are then checked to determine which of the factors causes the overall significant effects. Repeated measures analysis of variance (ANOVA) was used in a nested hierarchical model to compare growth of the three species of planted seedlings over two years in the herbivore exclusion and nitrogen addition plots in the two habitats. Change in seedling height relative to its original size was used as a measure of plant growth. The percent transmittance was included as a covariate in the ANOVA. In the unplanted plots, the change in seedling richness and abundance were compared between the fenced and unfenced plots in the forest and *A. karroo* habitats at Cape Vidal from 2004 to 2006 using repeated measures ANOVA. There was no effect of *A. karroo* stand and data from all three stands were pooled. These analyses were all conducted using SPSS (SPSS 13.0).

The composition of the seedling banks in the unplanted plots was compared between the habitats using multi-response permutation procedures (MRPP). A Euclidean distance measure was used for this analysis, and groups were defined by stand age and habitat type. This analysis was conducted using PC-ORD for Windows Version 4 (McCune & Mefford 1999). The test statistic, T, describes the separation between the groups. The more negative T is, the stronger the separation. The A statistic describes the within-group homogeneity, compared to the random expectation. When all items are identical within groups, $A = 1$. $A = 0$ when heterogeneity within groups equals the expectation by chance, and $A < 0$ if there is more heterogeneity than expected by chance. The P-values were adjusted using a Bonferroni correction to avoid type I errors.

Results

Exclosure plots

i. Seedling survival

Survival of planted *A. karroo*, *D. natalensis* and *C. africana* seedlings differed significantly in the two habitats at Cape Vidal ($F_{2,336} = 16.84$, $P < 0.001$). Survival of *C. africana* seedlings was lower than both *A. karroo* and *D. natalensis* in both habitats (Fig. 4.1a & b). In all treatments in the *A. karroo* stands, *A. karroo* seedlings survived better than *D. natalensis* (Tukey's post-hoc test; $P = 0.471$; Fig. 4.1a), but *D. natalensis* seedlings had the highest survival in the forest habitat (Fig. 4.1b). Planted seedlings survival was significantly different across the treatments in the *A. karroo* stands and forest ($F_{3,336} = 9.29$, $P < 0.001$).

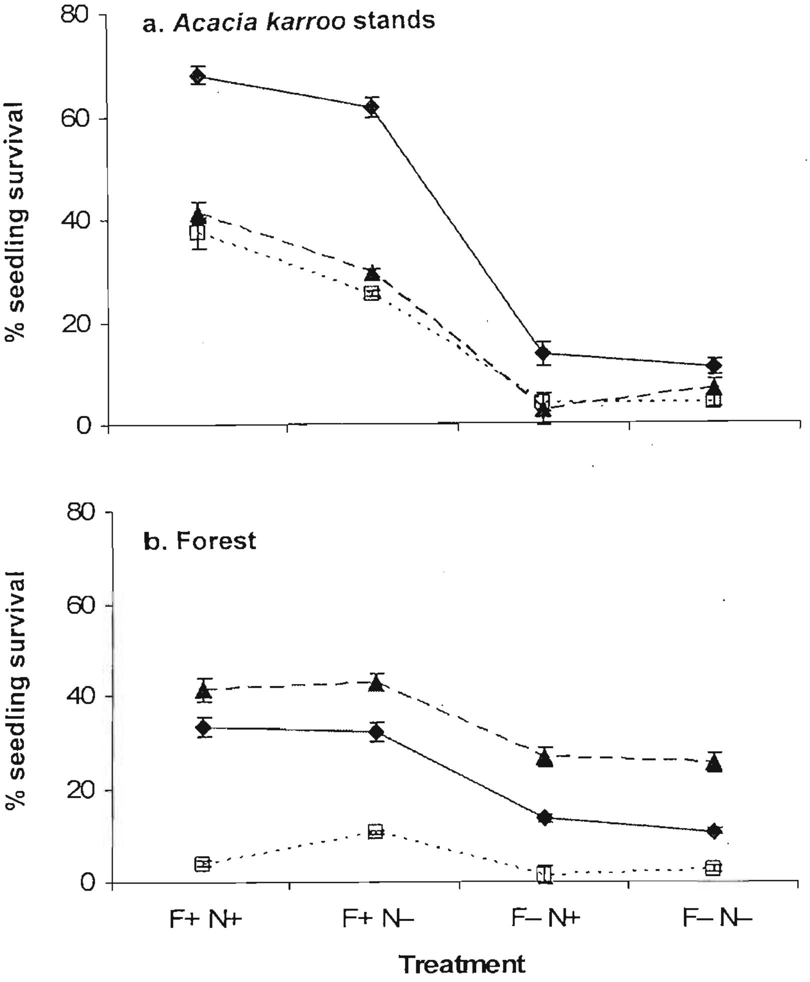

Fig. 4.1. Percentage survival of three seedling species planted (P+) in plots in the **(a)** *A. karroo* stands and **(b)** forest habitat at Cape Vidal under four different treatments: (1) fenced, nitrogen (F+ N+); (2) fenced, no nitrogen (F+ N–); (3) unfenced, nitrogen (F– N+); and (4) unfenced, no nitrogen (F– N–). *Acacia karroo* seedlings are indicated by a solid diamond (◆) with a solid line, *C. africana* seedlings by an open square (□) with a dotted line, and *D. natalensis* seedlings by a solid diamond (▲) with dashed line. Forest and *A. karroo* stands: n = 300 individuals of each species per habitat.

Seedling survival was significantly higher in the fenced treatment plots (Tukey's post-hoc test; $P < 0.001$), and was independent of nitrogen supplementation. The difference in seedling survival between fenced and unfenced plots was most pronounced in the *A. karroo* stands where a greater than two-fold increase in survival occurred across all species when herbivores were excluded (Fig. 4.1a & b).

ii. Seedling growth

At Cape Vidal, habitat type had a significant effect on growth of planted *A. karroo* and *D. natalensis* seedlings ($F_{1,47} = 24.73$, $P < 0.001$; and $F_{1,41} = 29.74$, $P = 0.001$, respectively; Figs. 4.2a & b), with both species growing faster in the *A. karroo* stands. *Celtis africana* seedlings also tended to grow faster in the *A. karroo* stand habitat than in the forest ($F_{1,25} = 4.07$, $P = 0.055$; Fig. 4.2c). Supplementary nitrogen had no affect on planted seedling growth across all species. *Diospyros natalensis* seedlings grew the least in both habitats (Fig. 4.2b), while growth of both *A. karroo* and *C. africana* seedlings increased, particularly in the *A. karroo* stands.

When percent transmittance was included in the analysis as a covariate, it explained a significant amount of the variation in growth of *A. karroo* seedlings between the habitats at Cape Vidal ($F_{1,46} = 1.98$, $P = 0.003$), indicating that the higher light availability in the *A. karroo* stands resulted in increased growth of seedlings of this species. The increased growth of planted *D. natalensis* seedlings in the *A. karroo* stands was also caused by higher percent light transmittance in this habitat ($F_{1,40} = 3.79$, $P = 0.059$). Light availability did not affect the growth of planted *C. africana* seedlings at Cape Vidal ($F_{1,24} = 0.58$, $P = 0.455$).

iii. Seedling species richness and abundance

Seedling abundance was similar in unplanted, unfenced plots in the *A. karroo* stands and the forest at Cape Vidal (Table 4.1; $F_{1,28} = 0.54$, $P = 0.468$), but significantly fewer species occurred in the *A. karroo* stands ($F_{1,28} = 7.85$, $P = 0.009$). While a relatively large number of individuals occurred in the *A. karroo* stands, these were predominantly *A. karroo* seedlings. In the forest habitat, however, fewer individuals of a large diversity of species were present. A positive effect of herbivore exclusion was evident unplanted plots in both the forest and *A. karroo* stands given that both seedling species richness and seedling abundance increased by two-fold compared to unfenced plots. The mean species richness of the fenced plots was also significantly greater in the forest than in the *A. karroo* stands at Cape Vidal (Table 4.1; $F_{1,28} = 5.92$, $P = 0.022$), and seedling abundance was twice as high in the *A. karroo* stands than in the forest ($F_{1,28} = 4.50$, $P = 0.043$). Interestingly, while cumulative seedling species richness increased only marginally in the forest when herbivores were excluded, in the *A. karroo* stands a two-fold increase was evident when protected by caging. This indicates a larger impact of herbivore exclusion on *in situ* seedlings in the A. karroo stand habitat than in the forest.

Table 4.1. Mean (± 1 SE) seedling species richness and abundance per m^2 among the fenced (F+) and unfenced (F–) plots in the forest and *A. karroo* stand habitats at Cape Vidal. All plots were unplanted. Cumulative species richness in the treatments is total number of species recorded over an area of 15 m^2.

Habitat	**Treatment**	**n**	**Mean number of seedlings**	**Mean species richness**	**Cumulative species richness**
Forest	F–	15	4.9 ± 0.86	2.7 ± 0.39	16
	F+	15	8.3 ± 1.75	4.1 ± 0.54	19
A. karroo stand	F–	15	6.9 ± 1.3	1.4 ± 0.24	5
	F+	15	15.3 ± 3.26	2.6 ± 0.35	12

iv. Seedling species composition

At Cape Vidal, the *in situ* seedling community composition was similar in the fenced and unfenced plots in the forest (Table 4.2), indicating that herbivore exclusion had little effect on forest seedling community composition. Seedling composition in the fenced and unfenced plots in the *A. karroo* stands were more dissimilar than the forest plots (T = -1.68 and T = 0.60, respectively), demonstrating that herbivory had a larger effect on seedling composition in the *A. karroo* stands than in the forest. Seedling composition was significantly different in the fenced and unfenced plots when compared between the habitats (Table 4.2). The dominant seedling species in the *A. karroo* stands was *A. karroo* but this species was rare in the forest. In addition, there were noticeably fewer *C. africana* seedlings in the *A. karroo* stands.

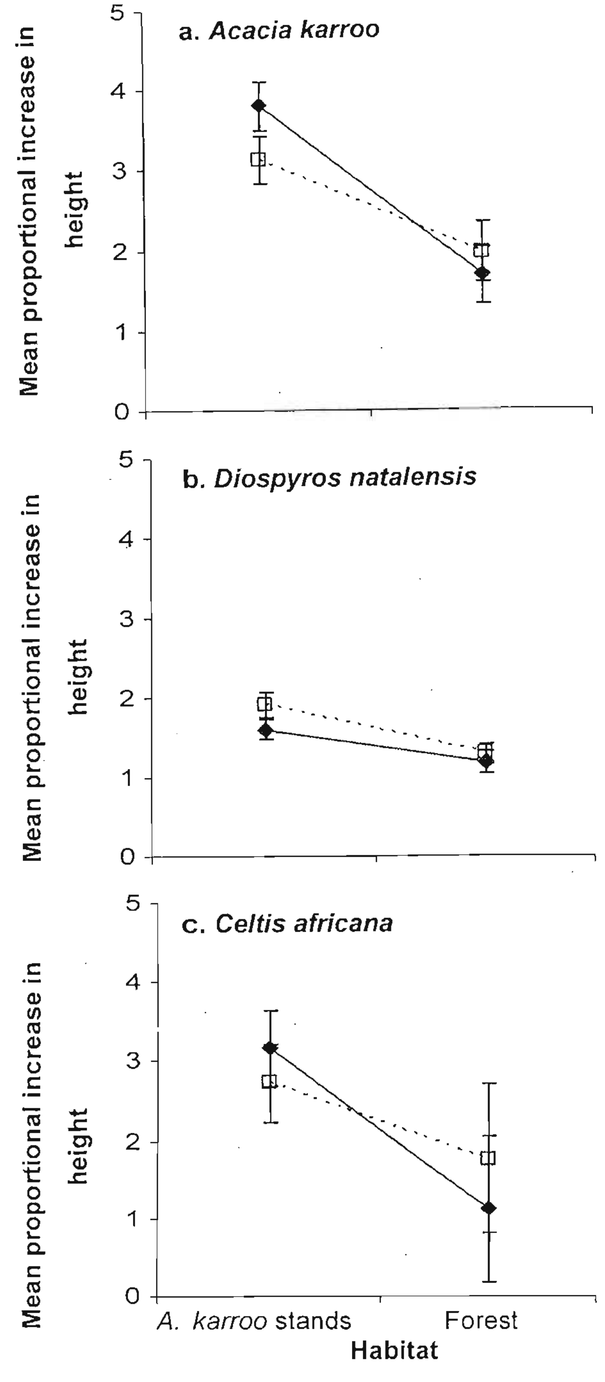

Fig. 4.2. Change in proportional growth (± 1 SE; n = 300 individuals of each species per habitat) of planted seedlings over two years in the forest and *A. karroo* stands at Cape Vidal of **(a)** *Acacia karroo*, **(b)** *Diospyros natalensis*, and **(c)** *Celtis africana* seedlings. All plots were protected by caging (F+). Nitrogen-supplemented plots (N+) are indicated

by a solid diamond (◆) with a solid line and control plots (N–) by an open square (□) with a dashed line.

Herbivore density

The density of bushbuck was higher in the *A. karroo* stands than in the forest (Table 4.3), and species such as kudu (*Tragelaphus strepsiceros*) and waterbuck (*Kobus ellipsiprymnus*) occurred in the *A. karroo* stands but not in the forest. Samango monkey densities were significantly higher, and red duiker densities were slightly higher in the forest. Although hippopotamus were not sighted as they are nocturnal, tracks and fresh faeces were regularly encountered in the morning on the transect in the *A. karroo* stands, but not in the forest. At RBM, 27.3 km were driven over 10 transects through the rehabilitating *A. karroo* stands aged from directly post-mining to 27 years since mining, but no herbivores were sighted.

Table 4.2. Results of the Multi-Response Permutation Procedure analysis of the *in situ* seedling species compositions between the fenced (F+) and unfenced (F–) treatment plots in the *A. karroo* stands and adjacent forest at Cape Vidal. All plots were unsupplemented. *T*-values are reported, followed by *A*-values in parentheses. * represents significance using a Bonferroni correction to avoid type I errors.

	F- Forest	**F+ *A. karroo* stand**	**F- *A. karroo* stand**
F+ Forest	0.60(-0.01)	-9.35(0.17)*	–
F- Forest	–	–	-9.73(0.17)*
F+ *A. karroo* stand	–	–	-1.68(0.04)

Discussion

In forest ecosystems, studies of herbivore feeding preferences combined with long-term exclosure experiments demonstrate that selective seedling removal by herbivores often drives changes in the relative abundance of palatable species (Molofsky & Fisher 1993; Augustine & McNaughton 1998), which is supported by this study. When fenced to exclude large mammalian herbivores in the *A. karroo* stands at Cape Vidal, survival of seedlings of three planted species and natural seedling species richness increased. Thus, in the absence of the negative effects of herbivory, typical pioneer and mature forest species such as *C. africana* and *D. natalensis* would naturally establish and survive in the *A. karroo* stands at Cape Vidal.

Table. 4.3. Comparison of mean density (± 1 C V; n = 40 transects per habitat) of common herbivores in the *A. karroo* stands and adjacent dune forest at Cape Vidal.

Species	Scientific name	*A. karroo* stand	Forest
Bushbuck	*Tragelaphus scriptus*	0.420 ± 0.256	0.202 ± 0.000
Kudu	*Tragelaphus strepsiceros*	0.261 ± 0.500	0.000 ± 0.000
Red duiker	*Cephalophus natalensis*	0.309 ± 0.208	0.449 ± 0.21
Samango monkey	*Cercopithecus mitis*	0.674 ± 0.174	1.216 ± 0.247
Waterbuck	*Kobus ellipsiprymnus*	0.224 ± 0.000	0.000 ± 0.000

Acacia karroo individuals are known to express chemical and physical defences more strongly in the juvenile stages, when they are still within reach of browsing herbivores (Midgely & Ward 1996). It is possibly a result of such anti-herbivore defences that *A. karroo* seedlings survived better than other undefended species in the *A. karroo* stands, where browsing pressures are noticeably high. The high rate of survival of *D. natalensis* seedlings across all treatments in the forest habitat demonstrates shade-tolerance typical of mature forest species (Osunkoya et al. 1993). The high mortality of *C. africana* seedlings (a forest pioneer species common in the mature dune forest vegetation at Cape Vidal) in the *A. karroo* stands was a result of herbivory. Seedling survival was unaffected by nitrogen supplementation in both habitats, particularly in the unfenced plots. Thus herbivory appears to be the dominant factor reducing survival of forest tree species in the *A. karroo* stands.

Growth of all three species of planted seedlings increased in fenced plots in the *A. karroo* stands irrespective of nitrogen supplementation. This increase in growth was greater than in fenced plots in the forest, indicating a larger positive effect of herbivore exclusion in the *A. karroo* stands. The slow growth of *D. natalensis* seedlings across all treatments is also characteristic of mature forest species (Osunkoya et al. 1993).

Seedling growth is positively related to light availability in the understorey (Montgomery & Chazdon 2002), where even small differences in the light environment can affect plant growth (Osunkoya et al. 1993). Similarly, at Cape Vidal, higher light availability in the *A. karroo* stands was partially responsible for the increased growth of *A. karroo* and *D. natalensis* seedlings in this habitat relative to that in the forest. Although the effect of light on *C. africana* growth was not significant, this species also grew fastest in the *A. karroo* stands. Early and pioneer successional species like *A. karroo* and *C. africana* are expected to thrive in high light conditions like those found in the *A. karroo* stands at Cape Vidal. The successful growth of a mature forest species in this habitat as a result of the increased light availability, however, is further indication of the suitability of conditions in the *A. karroo* stands for seedling growth. Forest species were unable to establish naturally in the *A. karroo* stands at Cape Vidal, despite fertile soil conditions described in Chapter 3, and more favourable light conditions. Like Sork (1987) who found that although light conditions affected the performance of *Gustavia superba* seedlings in Panama, herbivory was also the dominant factor controlling seedling establishment at Cape Vidal.

While seedling abundance in the unfenced plots was higher in the *A. karroo* stands than in the forest habitat, the seedling community was dominated by *A. karroo* seedlings, while the forest habitat had a higher species richness. A greater than two-fold increase in species richness was observed when herbivores were excluded compared to unfenced plots in the *A. karroo* stands, and a similar increase in seedling abundance occurred. The seedling species community compositions were significantly different in the fenced and unfenced plots between the habitats, and herbivory had a greater affect on the seedling species richness in the *A. karroo* stands than in the forest. These results further indicate that herbivory prevents recruitment of forest species in the *A. karroo* stands.

Differences in the abundance of mammalian seed and seedling predators may result in a change in the species composition of forests (Molofsky & Fisher 1993). The density of certain herbivores was higher in the *A. karroo* stands than in the forest. In particular, larger numbers of bushbuck were present in the *A. karroo* stands, and species such as kudu and waterbuck were only sighted in the *A. karroo* stands. Higher levels of utilization of the *A. karroo* stands by browsing antelope is responsible for the low seedling survival and diversity observed in the unprotected vegetation in the *A. karroo* stands. Additionally, hippopotamus regularly use the *A. karroo* stands as grazing lawns, or to move between feeding sites. The trampling damage that these and other smaller herbivores can cause (Cole 1987; Plumptre 1993) likely explains the greater influence of fencing on survival and growth of seedlings in this habitat. At RBM, however, i herbivore populations were so small that no sightings were made. The absence of high indigenous herbivore densities at RBM, which remove and trample emerging seedlings is likely the reason why species composition of mined *A. karroo* stands progresses from an *A. karroo*-dominated community towards mature forest. Thus, successful restoration via the *A. karroo* successional pathway occurs at RBM (van Aarde et al. 1996; Mentis & Ellery 1998; Wassenaar 2003).

Conclusions

This study indicates that the vegetation regeneration dynamics in *A. karroo* stands at Cape Vidal are driven by biotic, top-down forces, and that herbivory by large mammalian herbivores is limiting succession. It suggests that browsing and trampling of seedlings by herbivores excluded from some plots in the *A. karroo* stands at Cape Vidal have reduced growth and survival of seedlings of preferred species other than *A. karroo*, thereby potentially limiting recruitment of forest tree species and altering the composition of the mature canopy. Densities of certain herbivore species were higher in the *A. karroo* stands than in the forest at Cape Vidal, and the positive effect of herbivore exclusion on seedling growth, survival, and species richness in this habitat demonstrates that top-down forces play a more dominant role in the *A. karroo* stands than in the forest. At RBM, where the vegetation community of previously mined *A. karroo* stands is converging with that of undisturbed forest, populations of wild herbivores are very small and have a negligible impact on the vegetation. The post-emergence recruitment limitation by herbivores at Cape Vidal is preventing community convergence with that of surrounding undisturbed forest, resulting in arrested succession. For this reason, the use of the *A.*

karroo successional pathway to rehabilitate disturbed coastal dune forests needs to be evaluated for each site, with particular emphasis on herbivore densities at the sites and their potential impact on seedling recruitment.

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Chapter 5

Summary and management recommendations for rehabilitation of coastal dune forests

The purpose of this study was to investigate factors limiting the establishment of forest tree species in anthropogenically disturbed areas within the coastal dune forest at Cape Vidal in northern KwaZulu-Natal. Although these sites have been undisturbed for 52 years and are surrounded by dune forest, they have not been colonised by mature coastal dune forest species. Monospecific *Acacia karroo* stands dominate these areas and they appear to be self-replacing. This gives rise to a management paradox because, while *A. karroo* is associated with arrested succession at Cape Vidal, at Richards Bay the *A. karroo* successional pathway is used successfully to rehabilitate mined dunes. Thus, the focus of this study is the efficacy of the *A. karroo* successional pathway for rehabilitating coastal dune forests. I compared the processes of natural coastal dune forest regeneration and succession via the *A. karroo* successional pathway in disturbed coastal dune forest at Cape Vidal with the managed rehabilitation of mined dunes at the Richards Bay Minerals mining lease areas (RBM) approximately 70 km south of Cape Vidal.

Recruitment success affects succession and is influenced by many factors, three of which were examined in this study: seed dispersal and seedling bank establishment (Chapter 2), soil nutrients (Chapter 3), and herbivory (Chapter 4). The specific purpose of this chapter is to apply the findings of this study to developing management practices and provide guidelines for current and future rehabilitation of coastal dune forests.

Coastal dune forest succession at Cape Vidal and RBM

Successful regeneration of disturbed habitats is most often achieved by the re-establishment of species that were present in the community prior to disturbance. This requires that propagules reach the habitat, are recruited into the seedling bank and later contribute to the mature vegetation. Recruitment occurs from the seed bank and seedlings are recruited through ingrowth from the seedling bank into bigger size classes. I examined the seed banks of the coastal dune forest and *A. karroo* stands at Cape Vidal and found that seed dispersal into the *A. karroo* stands is partially limited. The seed banks of the disturbed areas at Cape Vidal are dominated by *A. karroo* and *Adenopodia spicata*, a forest margin species, while common forest species such as *Cordia caffra, Diospyros natalensis, Mimusops caffra, Sideroxylon inerme* and *Teclea gerrardii* were only present in the forest seed bank. Dispersal limitation is potentially a consequence of the lack of fleshy-fruited species in the *A. karroo* stands, which would attract frugivorous birds and facilitate an influx of propagules. The composition of unprotected seedling banks are also significantly different between the *A. karroo* and forest habitats at Cape Vidal. However, when I protected the potential seedling bank by fencing so as to keep herbivores out, the richness of the seedling bank in the *A. karroo* stands doubled. I conclude that forest species can and will establish in the *A. karroo* stands and the difference in seed bank composition between the forest and the *A. karroo* stands is insufficient to explain why so few forest species have established in the *A. karroo* stands. While the low species richness of seeds detected in the seed bank experiments may be a consequence of the sampling methods, many tropical forests do not rely on a persistent soil seed bank for regeneration (Fenner & Thompson 2005), and there is naturally low sexual reproduction in many of the coastal dune forest tree species found at Cape Vidal (Nzunda et al. submitted). Together these findings point to a post-dispersal factor that reduces seedling recruitment and survival as the dominant cause of regeneration failure. Seedling establishment and survival may be influenced by the fertility and physical characteristics of the soil, and by herbivory.

Soil fertility is an important resource that influences seed germination and growth of established seedlings. I assessed soil quality in the *A. karroo* stands and forest at Cape Vidal, with particular emphasis on soil nitrogen availability because this nutrient is most often limiting in successional plant communities (Tilman 1986). However, the forest and *A. karroo* stands had comparable soil fertility, including nitrogen, and the observed nutrient levels are sufficient for establishment and growth of a range of forest tree species. This was confirmed by experiments where supplementary nitrogen was added to the soil and did not improve survival or growth of seedlings. The presence of high nitrate levels indicate that free nitrogen is available (little to no nitrate indicate that most free nitrogen is being taken up by plants as ammonium before it can be converted to nitrate ammonium. Thus, neither the *A. karroo* nor the forest habitats at Cape Vidal are limited by bottom-up forces, and soil fertility and quality can be excluded as factors limiting coastal dune forest succession. This finding narrows the focus on a post-emergence (as opposed to post-dispersal) factor affecting the seedling bank that is limiting forest regeneration on disturbed sites at Cape Vidal.

Herbivory was investigated as the post-emergence factor that most likely inhibits seedling recruitment. Herbivory by mammals can act as an ecological filter determining vegetation community composition (Augustine & McNaughton 1998). I examined the effect that large numbers of wild herbivores inhabiting the Cape Vidal coastal dune forest have on the successional dynamics. Exclusion experiments clearly demonstrated that large mammalian herbivore cause a decrease in the survival and growth of forest tree seedlings species such as *Celtis africana* in the *A. karroo* stands at Cape Vidal, thereby limiting recruitment and potentially altering the composition of the mature canopy at disturbed sites. Of the factors examined in this thesis, top-down pressure as a result of preferential use of *A. karroo* stands by herbivores was found to be the dominant force driving the vegetation dynamics at Cape Vidal, causing arrested succession in the *A. karroo* stands. The lack of regeneration at Cape Vidal is also partially associated with limited dispersal of forest species into the *A. karroo* stands. Together, these factors have arrested the *A. karroo* successional pathway at Cape Vidal, preventing community convergence with that of the surrounding undisturbed coastal dune forest.

Tree succession in the managed, regenerating coastal dune forest at RBM is more dependent on the seed bank than the natural system at Cape Vidal. However, successful regeneration at RBM is also strongly and more likely linked to a greater probability of seedling survival than at Cape Vidal because there are few naturally occurring herbivores at RBM. This study demonstrated that soil nutrients, specifically nitrogen, have continued to accumulate over time at RBM following mining and is supported by the findings of van Aarde et al. (1998). Soil nutrients, particularly nitrogen, accumulate rapidly following mining when *A. karroo* is present, promoting vegetation succession on mined dunes (Lubke et al. 1996). Combined with few wild herbivores at RBM, this soil fertility allows succession to proceed and vegetation to ultimately converge on benchmark levels for mature coastal dune forest (Wassenaar et al. 2005).

Top-down versus bottom-up ecosystem control

Gruner (2004) presented experimental results demonstrating that complex forest ecosystems are primarily driven by bottom-up forces, and top-down forces play a secondary role (Forkner & Hunter 2000). In these resource-controlled systems the impact of top-down forces increases with resource availability to plants (Dyer & Letourneau 1999a; Forkner & Hunter 2000). However, top-down control appears more widespread in terrestrial ecosystems than previously thought (Pace et al. 1999). For example, Dyer & Letourneau (1999b) demonstrated that increases in invertebrate herbivore numbers in a tropical forest decreased leaf area significantly.

Although top-down and bottom-up forces have been intensively studied in mature forest communities focusing on invertebrate herbivores (e.g. Dyer & Letourneau 1999b; Dyer & Letourneau 1999a; Forkner & Hunter 2000; Gruner 2004), to the best of my knowledge, this study is the first to investigate the relative roles of top-down and bottom-up forces in a non-equilibrium system where mammalian herbivores arrest vegetation succession.. The successional process at Cape Vidal is an example of a subtropical ecosystem driven by top-down herbivore dynamics. Vegetation establishment following disturbance is predominantly controlled by herbivore browsing and trampling that alters the seedling community composition. Productive ecosystems typically experience strong top-down forces (Hunter & Price 1992) and at Cape Vidal this has resulted in arrested succession and the vegetation community composition remaining in a monodominant, early successional state. At RBM, where the vegetation does not have such strong top-down pressure by herbivores, the pre-mining vegetation community may be restored within 54 – 80 years (Mentis & Ellery 1998; Wassenaar et al. 2005).

Management recommendations

The Cape Vidal coastal dune forests are under the management of Ezemvelo KZN Wildlife (EKZNW) authorities as part of the Greater St. Lucia Wetland Park (GSLWP), which was declared a World Heritage Site in 1999 (UNESCO 1999). The disturbances within the dune forests were isolated events, and in light of the region's conservation status, there is little threat of further loss of coastal dune forest habitat in the area. Stands of *A. karroo* occur naturally in northern KwaZulu-Natal (Weisser & Marques 1979) and the perpetuation of this habitat type appear to have been driven by populations of wild herbivores that occur in the GSLWP. Given the small extent of the disturbed areas and that no further disturbances are likely at Cape Vidal that would create conditions for *A. karroo* colonisation, no further management interventions are necessary there. However, if management interventions are deemed necessary by EKZNW, then these should be focused on excluding herbivores from affected areas. Large herbivore exclosure plots have been used to limit herbivore impacts in Kenya (Young et al. 1998) and in Hluhluwe-iMfolozi Park. A similar system could be used to promote succession of coastal dune forest in disturbed sites at Cape Vidal and in future rehabilitation of sites where herbivore levels are high.

This study highlights the importance of a seed source from which recruitment and subsequent regeneration can occur. Considering that *A. karroo* does not encourage visitation to disturbed sites by birds, it does not facilitate avian seed dispersal. Where succession is proceeding via the *A. karroo* successional pathway, other early succession species with fleshy fruits and that are protected from herbivory could be interspersed with *A. karroo* individuals. A good species for this purpose may be *Ziziphus mucronata* (Griffiths & Lawes 2006). If large-scale disturbance of the forest habitat is unavoidable, it is essential to preserve fragments of coastal dune forest as a source of propagules within easy dispersal distance. This will ensure that recruitment does not become compromised due to limited dispersal opportunities (Janzen 1970; Clark et al. 1999).

A recent study by Wassenaar et al. (2005) shows that not all original coastal dune forest species are found in rehabilitated areas at RBM. However, compared to the persistent *A. karroo* stands at Cape Vidal, the *A. karroo* successional pathway at RBM has been very successful. Should permanent species loss at RBM become apparent in time, further management may be necessary. Manual introduction of threatened tree species into the system via seeding of the top soil is possible, but caution would need to be taken to ensure that seeds from the pre-existing vegetation only are sewn to prevent the introduction of non-native genotypes and species. Grazing by livestock can affect coastal dune forest vegetation (Wassenaar & van Aarde 2001), so it is also important that domestic herbivores be kept out of rehabilitating coastal dune forests to ensure that top-down forces do not interfere with rehabilitation.

The bush-clump pathway is a natural successional process occurring on old fields or grasslands adjacent to coastal dune forest in northern KwaZulu-Natal. The bush-clump pathway is advocated by von Maltitz et al. (1996) as a potential rehabilitation process. However, this pathway is only successful where a site is left undisturbed for a long time and has a nearby source of propagules. Little is known about how to initiate this pathway and the establishment of scattered clumps of forest species is not a suitable approach for rehabilitating mined or otherwise disturbed coastal dune fields. Further research is needed before the bush-clump pathway can be considered a viable management alternative to the *A. karroo* successional pathway.

Early successional species characteristically have fleshy fruits eaten by birds, high rates of growth under sunny conditions, light, non-durable wood, multilayered, diffuse crowns and are usually short-lived in comparison to later successional species (Raven et al. 1992). Many of these traits are displayed in *A. karroo*, contributing to its success as a colonising species. This legume is capable of establishing in infertile soil, it has a rapid growth rate particularly in high light conditions, it is well defended against herbivory and produces large numbers of seeds which are persistent in the seed bank. Although these traits aid in colonization, they also promote longevity (particularly the heavily defended recruits) of the species in habitats with high herbivore density. Species that share some similar life history traits with *A. karroo*, may also be suited to initiating succession in herbivore-dominated ecosystems, and should be considered for future restoration of coastal dune forests. For example, *Ziziphus mucronata* is common at Cape Vidal and produces large numbers of fleshy fruits that germinate easily (Griffiths & Lawes 2006) and would attract frugivorous birds into disturbed sites.

Conclusions

Rehabilitation of coastal dune forest following disturbance is not always achieved when the *A. karroo* successional pathway is initiated. This study highlights that succession is not necessarily a unidirectional process (Raven et al. 1992). The *A. karroo* successional pathway has resulted in very different plant communities at Cape Vidal and RBM. At these two sites, subtle differences in abiotic and biotic conditions during the successional progression have altered the end-point of this dynamic process. Both von Maltitz et al. (1996) and West (2000) found that using the *A. karroo* successional pathway to rehabilitate protected coastal dune forests could lead to significant tree species loss. On the other hand Mentis & Ellery (1998) and Wassenaar (2003) claim that under certain conditions the same successional pathway leads to convergence on dune forest composition within 50-80 years. Thus, the *A. karroo* successional pathway is not a panacea and must not be implemented without careful consideration of site-specific factors. This study shows that distance to a source of propagules, soil fertility, and the intensity of herbivory all deserve consideration, but with particular emphasis placed on the role of herbivory in the system. Ironically, the *A. karroo* pathway appears to be least effective in protected areas where natural herbivore densities are highest. Although the *A. karroo* successional pathway has the potential to rehabilitate coastal dune forests successfully in some sites, the presence of high densities of herbivores at a site will require management interventions to ensure that succession does not become arrested as it has at Cape Vidal.

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