

VAN DYK, PETRUS JOHANNES

**THE POPULATION BIOLOGY OF THE SWEETTHORN *ACACIA*
KARROO IN REHABILITATING COASTAL DUNE FORESTS IN
NORTHERN KWAZULU-NATAL, SOUTH AFRICA**

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FORESTS IN NORTHERN KWAZULU-NATAL, SOUTH
AFRICA**

by

Petrus Johannes van Dyk

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by
Petrus Johannes van Dyk

M.Sc. (Zoology)

Supervisor: Professor R.J. van Aarde
Mammal Research Institute
University Of Pretoria
0002, Pretoria
Republic of South Africa

Co-Supervisor: Doctor M.J. Coe
Department of Zoology
Animal Ecology Research Group
South Parks Road
Oxford OX1 3PS
United Kingdom

Abstract

The study investigated age-related trends in a *Acacia karroo* population and how these may relate to a developing woody broad-leaved community on rehabilitating coastal dunes. The results of the study showed that the *A. karroo* population in older stands are senescent (no recruitment is taking place) and that all attributes of the developing woody broad-leaved communities suggest that directional and cumulative changes are taking place. Although species richness and diversity are not yet comparable to those for “mature” dune forests, these are increasing with stand regeneration age. The results suggest that forest-type succession is taking place on previously mined stands at Richards Bay and that the rehabilitation programme has so far been successful.

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TABLE OF CONTENTS

Abstract	ii
Acknowledgements	iii
List of Tables	vii
List of Figures	ix

CHAPTER 1: INTRODUCTION

FROM PRESERVATION TO REHABILITATION	1
SUCCESION AND REHABILITATION	3
MODELS OF BIOLOGICAL SUCCESSION	4
The facilitation model	5
The tolerance model	6
The inhibition model	7
A choice between the models?	7
SPECIES DIVERSITY	8
COMPETITION	9
SUCCESION THEORY RECONSIDERED	11
CHANGES IN COMMUNITY ATTRIBUTES DURING SUCCESSION	15
OBJECTIVES AND AIMS OF THE PRESENT STUDY	17
Objectives of the study	18
The aims of the study	18

CHAPTER 2 STUDY AREA, MATERIALS AND METHODS

THE STUDY AREA	20
Locality and topography	20
Climate	20
Properties of coastal dune sands	23
The plant community	24
<i>General</i>	24
<i>Acacia karroo</i>	25
The mining and rehabilitation process	27

Description of stands	29
<i>Mined stands</i>	29
<i>Unmined but previously disturbed stand</i>	31
<i>Mature dune forest</i>	32
Relative ages of stands	32
MATERIALS AND METHODS	34

CHAPTER 3: MORPHOMETRIC VARIABLES OF *ACACIA KARROO*

INTRODUCTION	37
MATERIALS AND METHODS	39
RESULTS	41
Number of stems per tree	41
Height of the the canopy layer	42
Height of <i>A. karroo</i> juveniles in the shrub layer	43
Frequency distribution of heights	43
Crown and basal areas	45
Mass of trees	46
DISCUSSION	48

CHAPTER 4: POPULATION VARIABLES OF *ACACIA KARROO*

INTRODUCTION	52
MATERIALS AND METHODS	53
RESULTS	56
Density of trees in the canopy layer	56
Density of juveniles in the shrub layer	57
Life table and survivorship	57
Biomass	59
Productivity rate	59
Canopy cover and mean gap sizes	59
Flower-fall	61
Seed bank	63
DISCUSSION	64

CHAPTER 5: RELATIONSHIP BETWEEN MORPHOMETRIC, POPULATION AND SOME ENVIRONMENTAL VARIABLES OF *ACACIA KARROO*

INTRODUCTION	70
MATERIALS AND METHODS	72
RESULTS	74
Relationship between morphometric variables	74
Self-thinning	75
Classification of transects	76
Influence of rainfall on the population	78
Effects of aspect and dune slope on morphometric and population variables	79
DISCUSSION	81

CHAPTER 6: ATTRIBUTES OF THE WOODY PLANT COMMUNITY

INTRODUCTION	84
MATERIALS AND METHODS	84
RESULTS	86
Heights of broad-leaved species in the shrub and canopy layers	86
Height frequencies of the woody plant community	89
Density of broad-leaved species	91
Species richness and diversity of broad-leaved species	95
Similarity between mined stands and "mature" dune forests	96
Soil attributes	96
DISCUSSION	99

CHAPTER 7: SYNTHESIS

108

REFERENCES

113

OPSOMMING

123

SUMMARY

125

LIST OF TABLES

Table 1	Stand specific mean $\pm$ S.E. (C.V.) number of dead and alive stems per Acacia karroo individual	42
Table 2	Frequency distribution of single and multi-stemmed Acacia karroo individuals on mined and unmined stands. Only live stems are included. Frequencies are followed in brackets by the relative frequencies, expressed as percentages.	42
Table 3	Mean heights for Acacia karroo trees in the canopy layer and for juveniles in the shrub layer in mined and unmined stands.	43
Table 4	Mean crown and basal areas for Acacia karroo individuals on mined and unmined stands of different ages. All means are followed by the standard error of the mean ($\pm$ S.E.) and in brackets by the sample size and the coefficient of variation (%).	46
Table 5	Mass of Acacia karroo individuals calculated using the equation $y=0.864x - 1.445$ in mined and unmined stands of different ages.	48
Table 6	Density of Acacia karroo trees in the canopy layer and density of juveniles in the shrub layer for mined and unmined stands, based on the PCQ surveys conducted from January 1993 to July 1994. Means are followed by the standard error of the mean ($\pm$ S.E.) and in brackets by the number of individuals sampled and the coefficient of variation (%).	56
Table 7	Cohort life table for Acacia karroo in mined and unmined stands on coastal dunes at Richards Bay.	58
Table 8	Calculated biomass and productivity rate of the Acacia karroo population for different-aged mined and unmined stands at Richards Bay. Biomass figures are based on the density of trees per hectare (Table 6) and mean mass values per tree (Table 5). Productivity rates (% change) are based on annual changes in biomass.	60
Table 9	Canopy cover and mean gap size for Acacia karroo individuals on rehabilitating mined stands. Means are followed by the standard error of the mean ($\pm$ S.E.) and in brackets by the sample size and the coefficient of variation (%).	60
Table 10	Mean number of Acacia karroo flowers collected in different-aged rehabilitating stands at Richards Bay, showing the increasing flower production with age. Means are followed by the standard error of the mean ($\pm$ S.E.) and in brackets by the sample size and coefficient of variation (C.V.%).	61
Table 11	The mean number of Acacia karroo seeds per m ² in different-aged rehabilitating stands at Richards Bay, showing the increased number of seeds collected in the older stands. The means are followed by the standard error of the mean ($\pm$ S.E.), and in brackets by the sample size and coefficient of variation (%).	64
Table 12	The amount of rainfall recorded at RBM's Ecology Centre during the first year of each stand's rehabilitation, the percentage difference with the long term mean and the mean annual rainfall over the whole period of regeneration for a specific stand.	77

Table 13	Mean heights of woody broad-leaved species in the shrub layer of different-aged rehabilitating stands at Richards Bay. Means are followed in brackets by the maximum height and the number of individuals recorded in the survey.	83
Table 14	Mean heights of woody broad-leaved species in the canopy layer of different-aged rehabilitating stands at Richards Bay. Means are followed in brackets by the maximum height and the number of individuals included in the survey. (No individuals above 2m were recorded in the 2-year-old stand.)	83
Table 15	Density of broad-leaved woody species in the shrub layer of different-aged mined and unmined stands at Richards Bay as encountered on transects (see materials and methods). Densities of species (per hectare) are followed in brackets by relative densities.	87
Table 16	Density of broad-leaved woody species in the canopy layer of different-aged mined and unmined stands at Richards Bay. Densities of species (per hectare) are followed in brackets by relative densities. (No individuals above 2m were recorded in the 2-year-old stand.)	88
Table 17	Species richness and species diversity (Shannon-Wiener Index) of broad-leaved species in the shrub (<2m) and canopy layers (≥2m) of mined and unmined stands at Richards Bay.	90
Table 18	Bray-Curtis similarity index of different-aged mined stands with the 35-year-old unmined <i>Teclea gerrardii</i> stand at Zulti North. Density of woody broad-leaved species in the combined shrub and canopy layers were included in the calculation.	91
Table 19	Soil attributes of samples collected from stands of known age on rehabilitating coastal dunes in northern KwaZulu-Natal. Means are followed by the standard errors of the mean ($\pm$ S.E.), and in brackets by the coefficient of variations (%).	93

LIST OF FIGURES

Figure 1	Map of study area north of Richards Bay (28E43'S; 32E12'E) on the coast of KwaZulu-Natal, South Africa, illustrating the locations of the different stands.	21
Figure 2	Mean monthly rainfall (mm) and standard error of mean (illustrated as grid bars) as recorded by Paul Camp from 1976 to 1994 at the Ecology Centre of Richards Bay Minerals, Richards Bay.	22
Figure 3	Annual rainfall as recorded by Paul Camp from 1976 to 1995 at Richards Bay Minerals Ecology Centre, Richards Bay	23
Figure 4	Graphic representation of the mining and rehabilitation process, illustrating from left to right the removal of topsoil, the floating pond, the reforming of the dunes and the rehabilitation process.	27
Figure 5	A photo of a very young rehabilitating stand, illustrating the exotic cover crop and the shade cloth windbreaks.	28
Figure 6	An aerial view of the 2 to 6-year-old mined stands at Richards Bay. The 6-year-old stand is in the front of the photograph with the 2-year-old stand more towards the back. The stands comprise of Acacia karroo shrubland of 1m to 5m in height.	30
Figure 7	The layout of transects in the 14-year-old stand. The stand is used only as an example to explain the general layout of transects.	35
Figure 8	Scope constructed from a plastic pipe and water level to aid with the vertical projection of tree crowns down to ground level	40
Figure 9	Profile diagrams of frequencies of heights for Acacia karroo in different-aged mined and unmined stands at Richards Bay.	44
Figure 10	Fitted regression line to describe the relationship between $\log_e$ mass (y-axis) and $\log_e(\text{DBH}^2 \times \text{Height})$ (x-axis).	47
Figure 11	Survivorship curve for Acacia karroo in rehabilitating stands at Richards Bay, showing a type III curve (see Deevey, 1947).	58
Figure 12	Mean number of Acacia karroo inflorescences and seeds produced per kilogram of biomass in different-aged mined stands at Richards Bay.	62
Figure 13	Temporal trends in the mean number of Acacia karroo flowers collected during January 1994 in different-aged mined stands at Richards Bay.	63
Figure 14	Relationship between morphometric variables and age of Acacia karroo.	74
Figure 15	Regression of $\log_e$ height (m) on $\log_e$ DBH (mm) of Acacia karroo in 6 to 35-year-old mined and unmined stands at Richards Bay.	75
Figure 16	Regression line calculated for $\log_e$ density and $\log_e$ biomass of Acacia karroo. Four mined (3, 6, 9 and 14 year) stands and the Acacia karroo community of Venter (1972) were included in the calculations.	76
Figure 17	Dendrogram of cluster analysis (average method) for different-aged transects, based on density, height and basal area of Acacia karroo trees in the canopy layer.	77
Figure 18	Generalised dune profiles of mined stands at Richards Bay, showing relative densities (d1-d6) and heights (h1-h10) of Acacia karroo. Transects run from left to right and from the bottom to the top of the dunes.	80
Figure 19	Profile diagrams of height frequencies for the woody plant community of different-aged mined and unmined stands, at Richards Bay. The grey bars represent the frequencies for Acacia karroo and the black bars the frequencies for broad-leaved species.	90
Figure 20	Temporal trends in the percentage of maximum density for woody species in mined and unmined stands, at Richards Bay.	94

CHAPTER 1

INTRODUCTION

FROM PRESERVATION TO REHABILITATION

The establishment of conservation areas throughout the world is often motivated by the idea of setting aside "natural" areas and maintaining them in an "unchanged" state by limiting human impact (Hobbs & Huenneke, 1992). This static idea of conservation (more correctly named preservation) was supported by the belief that ecosystems are balanced systems that have existed for centuries in an almost unchanged state (Bruns & Gilcher, 1995). Under these conditions the task of ecologists was only to understand the intricate relationships between the elements within an ecosystem and to protect the balance between them.

However, as human impact on ecosystems increased at the beginning of this century, ecologists were increasingly faced with systems already altered or damaged by human dwelling and over-usage. Newly-created conservation areas were often degraded and simply proclaimed as conservation units because of their minimal value to agriculture (Stevenson-Hamilton, 1993). The mere preservation of these areas was therefore not possible, because the damage first had to be repaired (Cairns, 1995). Some corrective measures were therefore essential. Often, however, the damage could be rectified by merely limiting use, preventing soil erosion and by prohibiting hunting and poaching.

As the twentieth century "progressed", human activities became more destructive, often resulting in the destruction of large parts of ecosystems (Niering, 1987). The ability to restore or rehabilitate severely disturbed or destroyed ecosystems is therefore a major concern to contemporary ecologists (Cairns, 1995). This daunting task has led to the present emphasis on restoration ecology within the larger field of ecology. However, if the restoration of an ecosystem implies the exact

reparation of the system to its original state, it becomes an unattainable goal (Cairns, 1995). All ecosystems are constantly changing, therefore trying to duplicate any previous system is not possible, or even desirable (Kelly & Harwell, 1990). If one describes reparation to ecosystems on a continuum, re-vegetation (minimal success) can be seen as the one end, with restoration (total success) as the other end. Rehabilitation can then be defined as falling somewhere between these two extremes. Horticulturists, wishing to create colourful, interesting and attractive habitats for people, are often only interested in re-vegetation, while conservationists are trying to rehabilitate or restore ecosystems by encouraging natural succession (Baines, 1989).

The rehabilitation of ecosystems is directed at repairing the structure and function of the system, without pretending to restore a carbon copy of the original. The term "rehabilitation" expresses the notion that repair of ecosystems involves progress to the original state, but achieving only partial success (Bradshaw, 1990; Cairns, 1995). However, the more successful the rehabilitation, the more the rehabilitated ecosystems will resemble the original system.

The science of restoration ecology is a synthetic approach to ecological research and is described by Jordan (1995) as "...a second complementary phase of experimental (ecological) study". Restoration ecology is not only interested in finding out what works in rehabilitating ecosystems, but also why it works. The greatest value of restoration ecology is therefore the power it has to draw attention to what is important in a system (Jordan, 1995). Research on reclamation (especially reclamation of severely disturbed systems, following stripping for surface mining) has led to numerous insights into the interrelationships between plants and soils (Jordan, 1995). Restoration ecology provides a powerful tool for discrimination in the development of ecological concepts, for example, restoration can determine the mechanisms that account for changes in a community during the process of succession (Jordan, 1995). In the past restoration efforts were directed primarily towards the instalment of useable agricultural land, but recently the restoration of

ecosystems as habitat for indigenous animals and plants has rapidly gained importance (Bruns & Gilcher, 1995).

SUCCESSION AND REHABILITATION

In the case of major disturbances, rehabilitation is only possible through a process of biological succession or vegetational development (Inouye, 1995). Damaged or severely disturbed ecosystems often begin as monocultures or as systems containing a few species only (Barbour *et al.* 1987). The rehabilitation of badly damaged ecosystems is therefore slow and can only be accomplished when the species diversity of such a system has been restored. An increase in species diversity conveys two changes: first, an increase in species richness (number of species) and secondly, a decrease in the dominance of one or a small number of species (Magurran, 1988). Rehabilitating ecosystems can often only develop into complex and species-rich communities through a process of biological succession. The term "biological succession" refers to an indirect process or pathway by which an impoverished community may develop over time into a more diverse or "mature" community. It involves a series of directional and cumulative changes that leads to a sequence of seral communities that replace each other over time (Barbour *et al.*, 1987; Smith, 1990).

Some restoration ecologists (e.g. Niering, 1987) are critical of previous theories of succession and prefer the more neutral terms "biotic development" and "relative stability", to the problematic terms "succession" or "climax community" (Crawley, 1986). A growing scepticism over the whole notion of succession and the common practice of arranging communities in a temporal or successional sequence (e.g. Gleason, 1926; Crawley, 1986; Niering, 1995) complicate contemporary ecological theory. According to Niering (1995), the differences between neighbouring communities can often be explained in terms of zonation and are not necessarily the result of succession. These doubts about the importance of succession complicate the task of restoration ecologists and make it difficult to assess the success

of rehabilitation programmes. Studies dealing with rehabilitation of ecosystems should therefore first consider the various models for ecological succession and their implications for rehabilitation projects.

MODELS OF BIOLOGICAL SUCCESSION

The theory of biological succession was first devised to explain various conspicuous attributes of floral communities. These were as follows:

The similarity between communities. When Clements (1916) first formulated his theory of succession, he was impressed by the fact that many plant communities, occurring in separate but comparable localities, have so much in common. From this observation he deduced that similar climatic conditions produce the same "mature" vegetation.

The heterogeneity of plant communities. The theory of succession also attempted to describe the cumulative increase in species diversity during succession. Successive communities are progressively more complex and heterogeneous. Species diversity steadily increases during succession and this diversity was presumably closely correlated with the increasing stability of more complex communities.

Replacement of communities. Plant communities often replace each other in time, forming new associations, dominated (in terms of biomass) by different species. First, pioneer species colonise an area. They are characterised by a high growth and reproductive rate (r-selected). These pioneer communities are soon replaced by a series of so-called seral communities, consisting of secondary and primary species. Eventually the process ends in a "mature" or self-replacing community (Clements, 1916; Crawley, 1986).

Ecologists have proposed three basic models for biological succession. They categorise them in terms of the different mechanisms forwarded to explain the process by which communities replace each other. These are: facilitation, tolerance and inhibition (Connell & Slatyer, 1977; Crawley, 1986).

The facilitation model

The original version of this model was proposed by Clements (1916) and was called the "relay floristic model", because each seral community relays the site to the next community. According to Clements' theory of succession, the community is a super-organism with several closely-linked and balanced systems. Succession is an entirely predictable process, following the same course through specific seral communities, always ending in the same climax vegetation. The climax vegetation (usually dominated by a few species) is determined by climate and is in static equilibrium (Clements, 1936).

The facilitation model is a modern version of Clements' theory, but without the presupposition that a community is a super-organism. It states that succession involves several discrete (non overlapping) seral communities. The associated species of each community migrate, germinate and establish more or less at the same time in an area and eventually alter the habitat in such a way that new species (of the next seral community) are at an advantage and thus supplant the present community. Thus, the present community facilitates the establishment of the next community. The process is repeated until a climax community develops that propagates itself continually and therefore remains stable (Barbour *et al.*, 1987).

One would therefore expect groups of species to be replaced simultaneously by another set of species. Succession is also predictable, because a specific community (with very specific characteristics) is needed to facilitate the next community. Once climax vegetation is established, the same species coexist in an equilibrium state. This implies that an almost homogeneous climax community would exist and that this community (in contrast to the seral communities) could propagate itself.

Clements' description of the community in terms of a super-organism and his view that the climax community is almost homogeneous and in equilibrium, has been criticised by various scholars (e.g. Gleason, 1917; 1926; 1927; Tansley, 1935). Contemporary ecologists do not deny the fact that identifiable communities exist, but

the question is to what extent biological interactions (versus environmental factors) influence community structure (Crawley, 1986).

It has also been suggested that climax communities are in dynamic equilibrium (not static equilibrium) and thus may include stands of various successional stages. Within tree-fall gaps one may find, for example, juveniles of pioneer, seral and climax species. Crawley (1986) states that most of the evidence for facilitation comes from primary succession and not from secondary succession. It is also debatable whether one should talk about true interspecific facilitation, or simply of "enablement". In most examples so-called facilitation is the consequence of community-level processes affecting soils or light availability, and it is not the consequence of specific interactions between one plant species and another. The facilitation model was also criticised due to a lack of evidence on sufficient feedback mechanisms to maintain the climax state (Barbour *et al.*, 1987). However, it should be recognised that relatively late successional species (i.e. primary species) will in most cases not grow in disturbed or severe habitats before the habitat has been changed by other species to facilitate the growth of these primary species.

The tolerance model

The tolerance model is the modern equivalent of Egler's (1954) Initial Floristic Composition model. According to Egler, in the long term so-called climax species are merely better competitors, live longer, and are bigger than seral species. Climax (primary) and seral (secondary) species may therefore already coexist from the earliest stages of succession, although the climax species may only start to dominate at a much later stage. Different species tolerate each other and the life history of the species determines which species will dominate at which stage during succession.

In this model the exact course of succession is not predictable and the communities that exist during succession overlap (they are not discrete) and gradually replace each other. The exact direction of succession (which community is

going to replace the existing one) is largely determined by stochastic factors like the composition of the initial seed bank and when a species colonises an area.

The succession of communities is, therefore, not in the first place caused by facilitation or inhibition. This does not suggest that facilitation or inhibition plays no role, but merely that they are not the primary causes of succession. The tolerance model predicts that so-called pioneer, secondary and primary species will coexist at all stages of secondary succession.

The inhibition model

The inhibition model is the reverse of the facilitation model. Early species may inhibit the germination or establishment of later successional species by allelopathy. These early species are replaced only when they die or are damaged (see Barbour *et al.*, 1987). Climax species are initially inhibited (or stunned) by the fast-growing pioneer species, but when a suitable site later becomes available they germinate or emerge. Succession is, therefore, characterised by a set of species that initially inhibits a second set of species, but in the long term the first set is displaced by the second community. The earlier community, therefore, does not facilitate the next community, but stuns or prohibits its establishment for a certain time before giving way to the next community.

A choice between the models?

Crawley (1986) concludes that it will not be surprising if individual species have their own unique sets of rules governing invasion and extinction. This would imply that various combinations of facilitation, inhibition or tolerance can be operative during the history of a forest. Others have recently extended this idea by saying that the three general models should not be applied as alternatives to explain entire seres, but that they should be regarded as potentially testable alternatives for the effects of one mechanism (i.e. interspecific competition) (see Pickett *et al.*, 1987; De Steven,

1991a, 1991b). The importance attributed to interspecific competition in driving biological succession is, however, problematic (see the discussion below).

SPECIES DIVERSITY

The models of succession explain the way in which different communities replace each other and describe the associated increase in species diversity during succession. They do not, however, give reasons why species diversity tends to increase during succession. An additional explanation for the often increasing complexity of the seral communities during succession is therefore necessary. Tilman (1982; 1985; 1986a; 1986b) ascribes this increase in complexity to competition for limiting resources (scramble competition) and spatial heterogeneity in the supply rate of limiting resources. If, for example, there is one limiting resource the species that is the superior competitor for that resource, will eventually displace (out-compete) all the other species and exist in a monoculture. If, however, there are two limiting resources, it is theoretically possible for two species to coexist in equilibrium, three species if there were three resources, and so forth. This prediction is, however, only true when the species involved are limited by different resources and when the supply rates of the resources are constant (Tilman, 1982; 1985; 1986a; 1986b).

Usually the supply rate of limiting resources is not constant (Tilman, 1986a). Observations have shown that many more species can coexist in an ecosystem than predicted by the usual four or five limiting resources within the ecosystem (Tilman, 1986a). However, this high species diversity is explained by a high spatial heterogeneity in the supply rates of resources. Natural habitats are hardly uniform. For example, the aspect of a dune face may influence the availability of water, sunlight and nutrients. In a community many different microhabitats usually exist that favour different species (e.g. in terms of shade and humidity). This spatial heterogeneity affects resource availability, as well as the rate at which nutrients become available. During succession spatial heterogeneity increases; nutrients may accumulate in certain places, but may be very scarce in other places (Tilman, 1986a).

Humidity, available soil water, light and shade patterns, pH and other conditions may also greatly vary between plots only a few metres apart (Tilman 1982; 1985; 1986a; 1986b).

Another factor that may increase the heterogeneity of a community is low to moderate disturbances caused by herbivory and physical forces like fire, wind and floods (Hobbs & Huenneke, 1992). High-impact disturbances will, however, lower the species diversity of a community (see Barker *et al.*, 1989a, 1989b for the influence of dune encroachment and grazing on coastal communities). The more extreme an environment, the smaller the suite of species which initially invades the stand. Such species are usually fast growers, r-selected and can fix nitrogen (Barbour *et al.*, 1987). The death of a canopy tree also creates a totally different "gap" habitat in a forest. These random and mostly unpredictable disturbances, linked to stochastic factors (like seed dispersal) can create a mosaic of different patches within the community.

One important prediction of Tilman's (1986a) model is that the highest species heterogeneity will exist in moderately resource-poor habitats, while an average species heterogeneity will exist with an intermediate availability of resources. Nutrient-rich habitats have few limiting resources and therefore less competition for resources, resulting in a lower species diversity. In closed-canopy dune forests on moderately nutrient-poor soils with high spatial heterogeneity one can, therefore, expect a high plant species diversity (Tilman, 1982; 1985; 1986a; 1986b; Seely, 1991).

COMPETITION

Previously interspecific competition played an important role in the explanation of species diversity and the mechanisms for succession. However, especially among animal ecologists, much controversy presently exists over the importance that should be attributed to competition in explaining the structure of communities (Pimm, 1991).

Competition is a problematic term, because no coherent competition theory currently exists (Keddy, 1989). Some scholars limit competition to interference or contest competition (where organisms seeking a resource harm one another in the process, even if the resource is not in short supply). Others (e.g. Tilman, 1982) emphasise resource (scramble) competition where organisms utilise common resources which are in short supply (Krebs, 1985). Resource competition is a more indirect form of competition, because one individual is not directly harmed or attacked by another (e.g. by allelopathy), but is disadvantaged only because it cannot get its fair share of resources (e.g. light, nutrients or water).

Other ecologists limit the term competition to a situation where both individuals are disadvantaged by the biological interaction, and prefer the term amensalism to refer to interactions where one individual is advantaged (or not affected) while the other individual is damaged by the association (Barbour *et al.*, 1987). Because the exact interactions between individuals are usually not known, it is therefore better to use a broad working definition for competition. I will use the definition of Crawley (1986), who defines competition as "an interaction between two individuals that reduces the fitness of one or both of them". This broad definition includes both interference and resource competition.

Although Clements (1916) emphasised the importance of climatic factors for the outcome of successional pathways, interspecific competition plays an important role in explaining the way in which seral communities replace each other. The only difference between the previously described models of succession is when competition operates. In the facilitation model, no competition initially takes place between species with a mutualistic relationship between the pioneer species and the secondary and primary species making it possible for the latter to establish and survive. In the long term the pioneer species are, however, at a competitive disadvantage and therefore are replaced by species of the next community. Competition therefore follows mutualism.

In the tolerance model the concept of mutualism is replaced by tolerance, allowing all species to coexist from the start, without any significant interactions between them, either positive or negative. Later in the history of a community the populations of slower growing secondary and primary species do, however, start to compete with the pioneer species and eventually eliminate them. This may happen, for example, when primary species reach sufficient heights to cut off the sunlight to shade-intolerant pioneer species.

In the inhibition model competition is the primary agent, acting from the earliest history of the community. Pioneer species initially inhibit the establishment and fitness of secondary species, but are only successful in stunting their growth without eliminating them. When the short-lived pioneers start to die, the secondary species "take their chance" to out-compete and eventually eliminate the pioneers from the stand. In all three models interspecific competition therefore is the primary driving force in the replacement of species. However, in the United States a dispute has erupted in the last few decades among animal ecologists over the importance of competition in structuring communities (see Lewin, 1983). It is therefore important that ecologists should be very careful when assuming that competition plays an important role in communities and species replacement (succession).

SUCCESSION THEORY RECONSIDERED

Ecologists (e.g. Pimm, 1991; Cairns, 1995; Bruns & Gilcher, 1995) today recognise the shortcomings of static theories of ecosystems and their rehabilitation. They accept that so-called undisturbed or "climax" communities are often of recent origin and continually fluctuating (Kelly & Harwell, 1990). When studying communities, it is therefore important to take into account this fluctuation within ecosystems. Even when succession is accepted as an appropriate description of the development of a community, predictable pathways are not necessarily to be expected. Furthermore, most earlier successional studies were based on northern hemisphere temperate forests characterised by low species richness. In such situations predictable pathways

and stable "climax" communities are more probable than, for example, in species-rich tropical forests (see Barbour *et al.*, 1987). In tropical and subtropical communities with high species richness, stochastic factors may become more important, resulting in far less predictable outcomes of succession (Hubbell & Foster, 1986).

As mentioned earlier, the concept of succession is questioned by several contemporary scholars. Instead of organising neighbouring communities within a successional sere, Niering (1995) argues that different communities are merely the result of zonation due to different environmental factors, and that communities should therefore be classified according to the different responses of species to such factors. It should, however, be appreciated that mere zonation cannot explain the tendency of some communities to move more or less towards the same kind of species composition within a "mature" community. Clements (1916) proposed successional theory to explain the responses of a community towards environmental factors.

Life histories of individual species also reflect these responses towards environmental factors and have therefore been used by various models for the classification of populations. Three models have been proposed based on survivorship (Deevey, 1947), resource allocation (MacArthur & Wilson, 1967) and adaptive patterns depending on the availability of resources (Grime, 1977; 1979). Deevey's system of classification identifies three hypothetical survivorship curves, based on a species' adaptation to a specific environment and its reproductive strategy. A type I curve is typical of annual plants growing in open sites where most seedlings survive to reproduction. Type II is typical of annual plants on less open sites where intraspecific competition may cause mortality prior to reproduction. Forest trees often have a type III survivorship curve, with high initial mortalities of seeds and seedlings, followed by a more constant mortality rate leading to a situation where survivors may live for extended periods in the canopy (Krebs, 1985; Barbour *et al.*, 1987).

MacArthur & Wilson (1967) used a system based on resource allocation of species. Some species allocate most resources towards reproductive output (r-selected) while species on the other side of the spectrum allocate most resources towards carrying capacity (K-selected). Grime (1977; 1979) expanded the r and K concept to comprise three possible adaptive strategies. The first is ruderal (R) species, adapted to resource abundant and temporary habitats. R-selected species allocate most of their resources towards reproduction. They produce flowers early in their life, have a high frequency of flowering and usually produce many small seeds. Seeds may survive extended periods of dormancy. The second set of species is competitive (C) species which occur in resource abundant and permanent habitats. C-selected species use their resources primarily to gain a competitive advantage over other individuals by growing as fast as possible. They usually produce flowers every year, but allocate few resources towards seed production. The seeds of C-selected species may survive considerable periods of dormancy in the seed bank. The third group comprises stress tolerant (S) species (adapted for resource-stressed environments). They usually delay reproduction, flower intermittently over a long life history and produce few seeds. Seeds of S-selected species usually do not survive long within the seed bank.

Colonising species are usually R-selected, while secondary (seral) species are C-selected and primary ("climax") species are more S-selected (Barbour *et al.*, 1987). Classification of species according to their life histories (r and K) (MacArthur & Wilson, 1967), adaptive patterns (R, C, S) (Grime, 1977; 1979) or survivorship (Deevey, 1947) is informative, but is also of limited use when assessing vegetational development within forests. Species often display conflicting characteristics that make it difficult to classify them unambiguously into only one of these categories (Barbour *et al.*, 1987).

Other classification systems have been used to describe vegetational changes associated with treefall gaps in tropical forests (Hartshorn, 1980; Brokaw, 1985; Hubbell & Foster, 1986; Finegan, 1996) or in boreal forests

(Shugart, 1984; and Prentice & Leemans, 1990). Because light is usually the most critical limiting resource for plants, especially in forests, the classification systems of tree forest species should, according to these scholars, primarily be based on shade tolerance / intolerance of tree species and how this relates to germination and recruitment of juveniles, survival of saplings and growth rate (Hubbell & Foster, 1986). Reproductive patterns such as size and number of seeds produced, seed dormancy and relative reproductive ages, as well as architectural structure of individuals, are not primarily used to classify species. These attributes are, however, related to certain "guilds" or "roles" played by species according to their light preferences (Hubbell & Foster, 1986; Prentice & Leemans, 1990; Finegan, 1996).

Species should, therefore, preferably be classified into various guilds according to their environmental preferences. For instance, Hubbell & Foster (1986) distinguished three guilds of canopy tree species in neotropical forests (primary or "mature" forest species, late secondary species and early pioneer species), while Finegan (1996) distinguishes four phases of gap succession typified by early pioneers, short-lived pioneers, long-lived pioneers and shade-tolerant species.

Primary tree species (K-selected, according to MacArthur & Wilson, 1967) can germinate in shade or sun and can persist as suppressed juveniles until a gap opens in the canopy. They have moderate to high shade tolerance, low but variable growth rates and produce relatively few and large fruits with no dormancy. Late secondary species are typically shade-intolerant heliophiles with a fast growth rate like pioneers. However, they grow to a much larger stature (often being emergents which are taller than the general forest canopy) and persist longer in the canopy. They usually have no seed dormancy and rely on wind or ground mammals to disperse their seeds to newly created gaps.

Early pioneer species (r-selected) frequently persist for long periods as dormant seeds in the soil. They only germinate when a gap is formed and the light and heat increase in the gap. These pioneers have a high growth rate and respond

very fast to any favourable conditions. They are shade intolerant and their juveniles are usually found exclusively in gaps. Pioneers usually produce many small seeds that are widely dispersed by birds and bats (Hubbell & Foster, 1986).

These different guilds of species do not alternatively exist at different stages of a community's history, but occur in different zones within the community. On coastal dunes, these zones may be determined by availability of light, amount of salt spray, dune aspect and available soil water, or may be caused by stochastic events such as tree falls, fires, disease and herbivory.

The many unresolved issues related to succession theory make it difficult to assess when succession is taking place and if it is an appropriate model for rehabilitation. This state of affairs complicates the assessment of rehabilitation programmes (Niering, 1987).

CHANGES IN COMMUNITY ATTRIBUTES DURING SUCCESSION

According to "classical" succession theory several changes take place in a community during succession. Some 25 years ago Odum (1969) presented a list of 24 ecosystem attributes of plant communities, which he thought changed significantly during succession. Subsequent research resulted in this list being modified and reduced to 14 types of changes (Barbour *et al.*, 1987). However, many of these changes, when seen in isolation, are not unique to succession but can also be attributed to the mere maturation of a stand. In a monoculture (e.g. a commercial tree plantation) there is an initial increase in biomass and detritus. When individuals are not evenly spaced, a process of self-thinning is also to be expected as the individual plants get larger (Barbour *et al.*, 1987). A mere decrease in the density of one species should therefore not necessarily be seen as an indication of succession if it does not correlate with a decrease in biomass of the species. When studying possible successional changes it is thus important to distinguish between changes due to maturation and those unique to succession. "Maturation" changes are, however, an essential prerequisite for successional community changes. The community changes which may suggest

succession can be categorised into five broad, but closely related groups. These are as follows:

Replacement of communities. Closely associated with the increase in species diversity, is the replacement of communities during succession. Different sets of species will therefore dominate a stand at various stages of its development. Replacement can be shown directly by comparing the species composition of various seral communities, or can be suggested indirectly by a community's failure to replace itself. Such a failure may be suggested by low survival rates of current species while species of the next seral stage are increasing in dominance.

Increased species richness and diversity. An increase in species diversity tends to take place during succession, although diversity may again decrease in later seral stages (Kelly & Harwell, 1990). This suggests that from seral community to seral community the number of species present will increase in species richness, but also that the numerical dominance of one (or a few species) will progressively be broken.

A change in the life-histories from r to K . A gradual shift in the life histories of species from r to K takes place (Barbour *et al.*, 1987). At the later stages of succession a more predictable and/or constant environment linked to a longer life-span and slower development of individuals, will cause a shift from productivity to efficiency. This will cause a lower rate of net productivity and a decrease in the longevity of propagules. The vector of seed dispersal will also change from primarily wind-dispersed to primarily animal-dispersed seeds.

Increased structural complexity. As succession proceeds, structurally more complex communities are established (Terborgh & Petren, 1991). This is reflected in the increased complexity in physiognomy and leaf orientation of the individual trees in the community. At the community level more complex spatial and vertical structures are responsible for the development of diverse microhabitats, with an associated decrease in the importance of the macrohabitat (Barbour *et al.*, 1987).

A change in the availability of resources. With succession the increased spatial heterogeneity leads to a change in the supply of resources. The habitat quality, for example, changes from extreme to more mesic (Barbour *et al.*, 1987). Mineral cycles become slower and less leaky (more closed) and nutrients are increasingly stored in the plant material instead of in the soil. The role of detritus subsequently becomes more important in the supplying of nutrients (see Van der Merwe & McLachlan, 1991a; 1991b; on the increase of the organic content in dune sands where mature vegetation exists). Due to the increase in organic content, soil water also tends to increase during succession (Barbour *et al.*, 1987). In the last instance, the changes in nutrient levels usually cause the pH level to drop during succession (Barbour *et al.*, 1987).

When occurring together, these cumulative and directional changes may suggest a process of biological succession. When successive communities are increasingly similar to the "original" community (before disturbance), one can also deduce that a rehabilitation process is provisionally successful and may possibly end with a community closely akin to the original or surrounding (undisturbed) communities.

OBJECTIVES AND AIMS OF THE PRESENT STUDY

The present study focuses on temporal changes in the *Acacia karroo* population on rehabilitating stands of known age, recovering from disturbances caused by dune mining. These changes in the *A. karroo* population will be correlated with changes in the broad-leaved woody plant community. As part of a larger project on rehabilitating coastal dunes, the study also provides baseline information for studies on herbaceous plants, insects, millipedes, small mammal and bird communities (see Van Aarde *et al.*, 1996b).

Objectives of the study:

- To investigate age-related changes in the *A. karroo* population and how this may relate to woody plant succession on coastal dunes at Richards Bay.
- To investigate woody plant succession on coastal dune forests and how this may relate to various theories of biological succession.
- To assess the rehabilitation programme of Richards Bay Minerals.

The aims of the study are:

- *To investigate age-related changes in the morphometric variables of A. karroo individuals.* Key questions are:
 - a) Do the following variables change with the increasing regeneration age of stands: 1) the mean number of live stems per tree; 2) the mean number of dead stems per tree; 3) the mean height of trees in the canopy layer; 4) the mean height of juveniles in the shrub layer; 5) the frequency distribution of heights; 6) the mean crown and basal area of trees; 6) the mean mass of trees?
 - b) How do these changes reflect on the *A. karroo* population and possible woody plant succession?
- *To investigate age-related changes in the population variables of A. karroo.* Key questions are:
 - a) What temporal changes can be observed in the *Acacia karroo* population in terms of: 1) the density of trees in the canopy layer; 2) the density of juveniles in the shrub layer; 3) mortality and survivorship; 4) biomass; 5) productivity rate; 6) canopy cover and gap sizes; 7) flower-fall; 8) the seed bank?
 - b) How do these changes reflect on the future of the *A. karroo* population and possible woody plant succession?

- *To investigate the possible relationship (within the A. karroo population) between morphometric, population and some environmental variables, and how these relationships may change with time.* Key questions are:
 - a) How do height, basal and crown areas correlate with each other? b) Does self-thinning play a role in the population? c) Can transects be classified in terms of the characteristics of the *A. karroo* population? d) What was the influence of rainfall on the *A. karroo* population? e) Do the dune aspect and slope influence the characteristics of the population?

- *To investigate possible age-related changes in the broad-leaved woody plant community and how these changes may relate to the A. karroo population and possibly suggest succession.* Key questions are:
 - a) Can temporal changes be observed in terms of 1) the mean heights of broad-leaved species; 2) the height frequencies (vertical structure) of the whole woody plant community; 3) the density of broad-leaved species; 4) species richness and diversity; 5) similarities between mined and "mature" forests; 6) soil attributes?
 - b) How do these changes reflect on possible woody plant succession?

CHAPTER 2

STUDY AREA, MATERIALS AND METHODS

THE STUDY AREA

Locality and Topography

The study area is situated to the north east of the coastal town Richards Bay, KwaZulu-Natal, South Africa (28° 43' S and 32° 12' E) (Figure 1). The coastline primarily consists of recent sand deposits (Venter, 1972), with low-lying sand flats in the interior. These sand flats are separated from the sea by a series of high vegetated dunes of the bi-directional parabolic type, which run parallel to the coastline (Tinley, 1985). In the Richards Bay area the dunes are between 60 and 75m high and approximately 1-2km wide (Venter, 1972). Coastal sand dunes have distinct and unique geomorphic features and as a discrete community, consist of a mobile physical substrate stabilised by dense vegetation.

Climate

The climate in the study area is humid and warm to hot (Weisser, 1978; Majer & de Kock, 1992). Seasonal differences are not very pronounced, winter months are hotter and less extreme than in temperate regions and it rains throughout the year.

The warm Agulhas current close to the KwaZulu-Natal coast results in the temperature of the study area being relatively high throughout the year (Weisser, 1978). Annual fluctuations are small. The long-term temperature recorded at the Cape St. Lucia Weather Station (20km to the north of the study area) shows that maxima during the summer months are between 26-30°C. The mean minimum temperature is relatively high (13.4°C) and even extremes are never below freezing point.

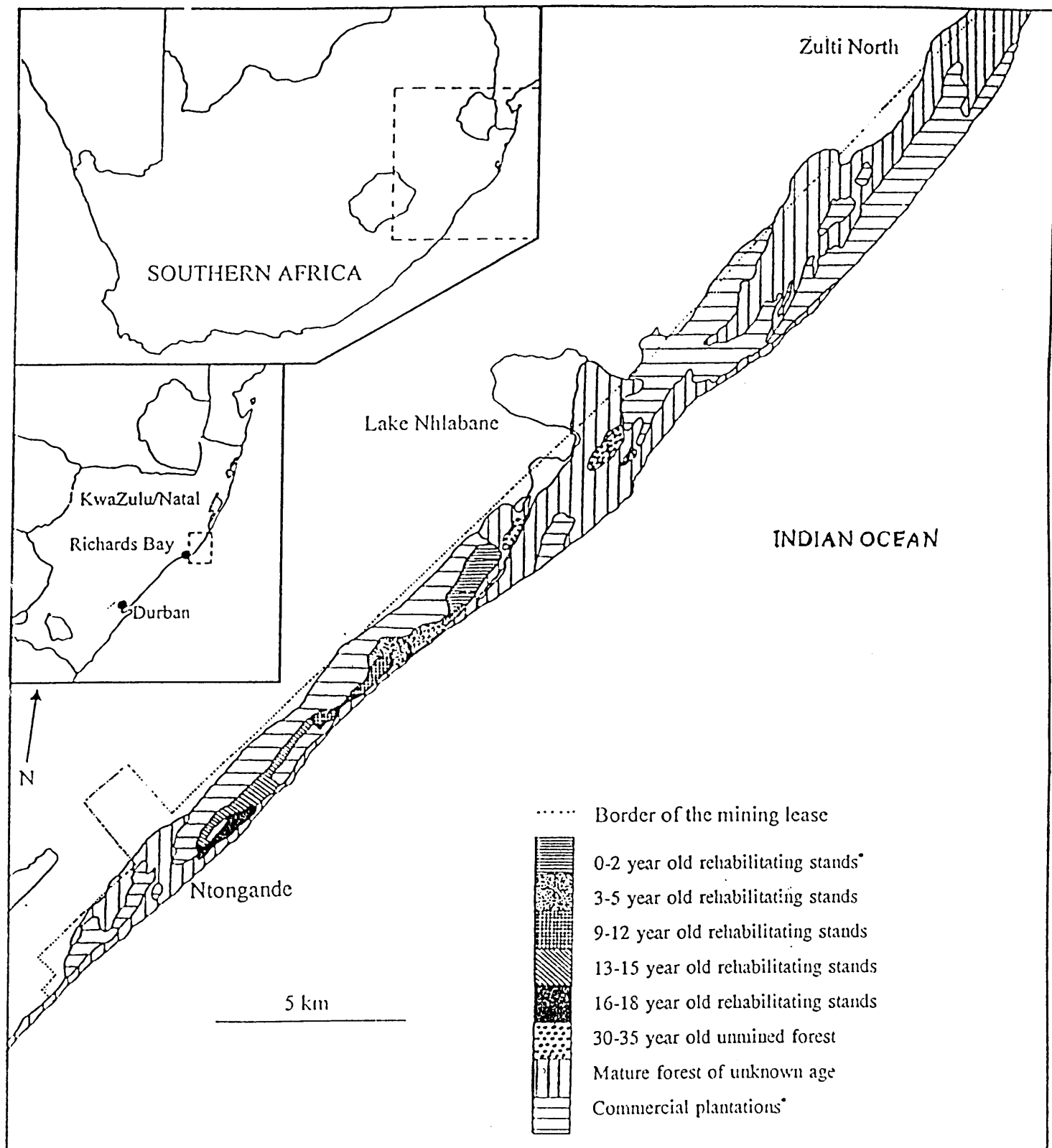


FIGURE 1: Map of study area north of Richards Bay ($28^{\circ}43'S$; $32^{\circ}12'E$) on the coast of KwaZulu-Natal, South Africa, illustrating the localities of the different stands.

Relative humidity in the study area is high (Weisser, 1978). Recorded humidities at 8h00 are between 79% and 88%, and at 14h00 between 61% and 74%. It is only in the winter months (between May and August) that relative humidities are sometimes below 70%. This high humidity is caused by the warm sea current and the abundant rainfall (Venter, 1972).

The mean rainfall measured at the Ecology Centre (within the study area) from 1976 to 1995 was $1575 \pm 107\text{mm}$ ($n=20$; $CV= 30.4\%$). Although the coastal dunes of KwaZulu-Natal receive rain throughout the year, it is evident from Figure 2 that in the winter months (April-August) and in midsummer (December) there is typically below average rainfall. February is the month with the highest average rainfall but with a high variability (mean= $211 \pm 47\text{mm}$; $n=20$; $CV=98.8\%$).

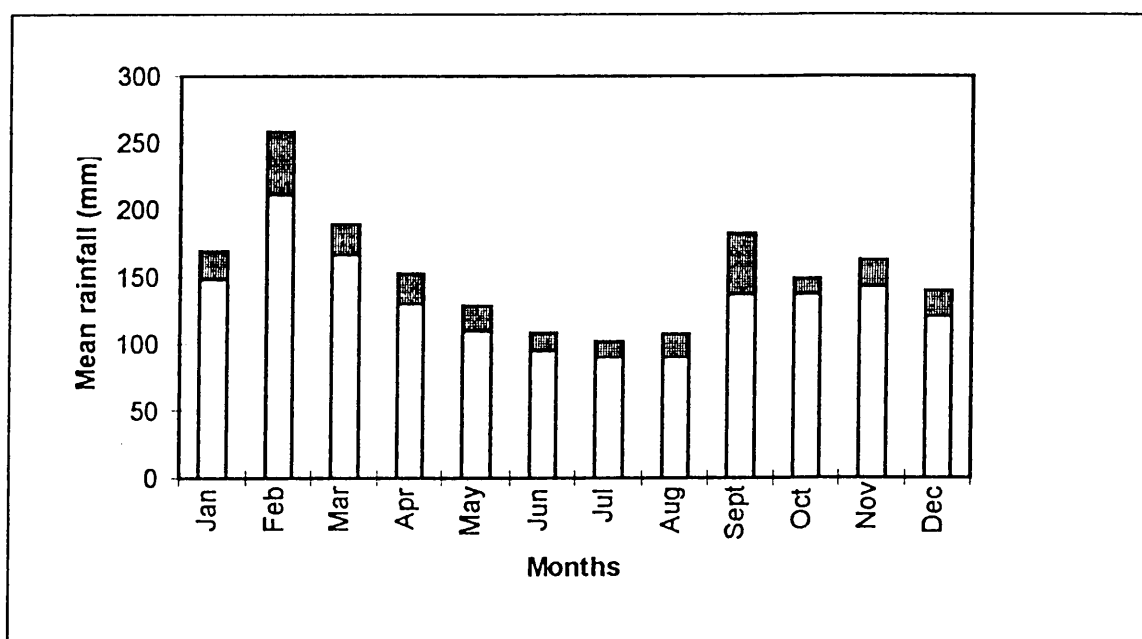


FIGURE 2: Mean monthly rainfall (mm) and standard error of mean (illustrated as grid bars) as recorded by Paul Camp from 1976 to 1994 at the Ecology Centre of Richards Bay Minerals, Richards Bay.

Extreme droughts and high temperatures are, however, a periodic feature (Venter, 1972). Such a drought was experienced during the study period (1992 to 1993). During this time the Ecology Centre recorded only 44.9% (1992) and 63.7%

(1993) of the mean annual rainfall reported for the area over the past 20 years (Figure 3).

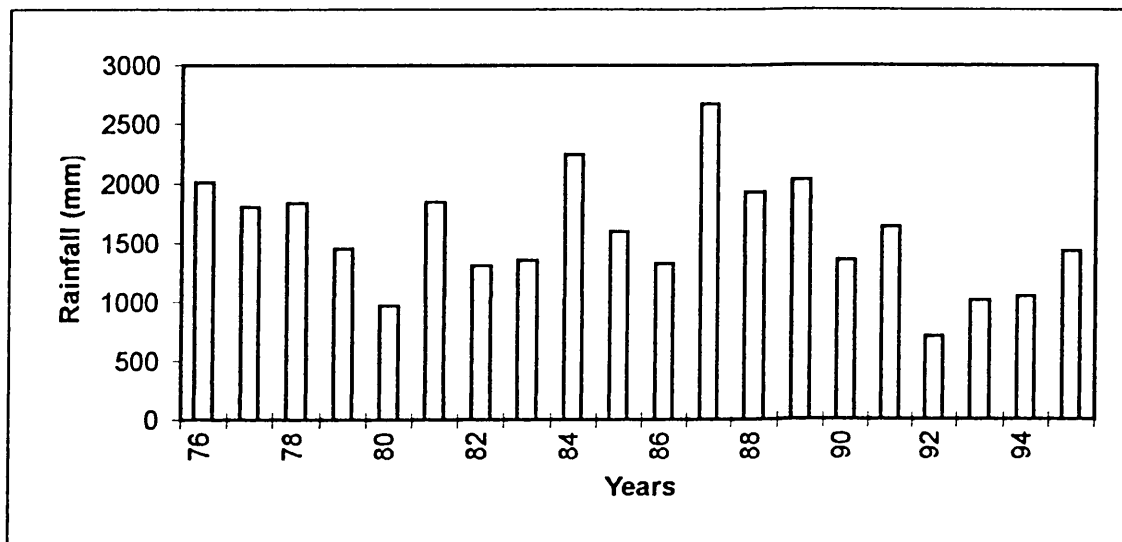


FIGURE 3: Annual rainfall as recorded by Paul Camp from 1976 to 1995 at Richards Bay Minerals Ecology Centre, Richards Bay.

The prevailing dry and warm north-westerly winds usually strengthen gradually before suddenly switching to a strong south-eastern that is often accompanied by rain. The strong south-westerly wind can sometimes cause extensive damage to trees in the dune forest (Venter, 1972).

Properties of coastal dune sands

Sands of coastal dunes are usually loosely packed with many air spaces between grains and thus experience drastic diurnal temperature fluctuations in the top layer. Sands are, however, poor conductors of heat, resulting in smaller of a temperature fluctuations deeper down in the substrate. Soils of a sandy nature have a low water retention capacity and are easily leached (Tinley, 1985). They are therefore usually poor in nitrogen, phosphorus and potassium (Hesp, 1991) and their productivity depends almost exclusively on nutrients derived from humus in the top 20cm of soil (Tinley, 1985; Lubke *et al.*, 1992a). The apparently low availability of nitrogen in younger dunes would presumably benefit plants that can fix nitrogen (e.g. legume

species such as *Acacia karroo*). Younger coastal dunes are typically alkaline (high pH) due to their generally high calcareous content from finely crushed shell fragments. High calcium and low nitrogen levels, however, increase the tolerance of plants to salt spray (i.e. decrease the toxicity of sodium) (Tinley, 1985).

Damage to coastal dunes usually results in bare and shifting sands which may create problems in dune stabilisation (Hesp, 1991). The deficient supplies of water and nutrients in coastal sand dunes should be taken into account when introducing plants to stabilise dunes (Hesp, 1991; Lubke *et al.* 1992a). The stabilisation of dunes by plants allows pedogenesis (soil formation) to take place. On coastal dunes this process comprises *inter alia* the leaching of carbonates and increasing acidification of the topsoil (Tinley, 1985). The acidification is caused by the solubilization of the calcium by hydrogen ions from humic acids and the build-up of humus in the topsoil. The accumulation of plant waxes in the topsoil further results in the formation of a water-repelling, hydrophobic layer. With the build-up of clay mineralization the texture and consistency of the soil also change. These combined processes of soil formation drastically alter the nutrient status and soil moisture balance of dune sands (Tinley, 1985).

The Plant Community

General

The plant community on the coastal dunes of northern KwaZulu-Natal is largely dominated by woody plants. Of the almost 400 dicotyledon species occurring in this region, 69.2% are trees or shrubs, 17.6% creepers and 13.2% are herbs (Weisser & Drews, 1980). These dune forests revert to grasslands when cleared and burnt regularly (Moll, 1992). For the Richards Bay region, Venter (1972) has described three distinct back-dune (second dune and further from the sea) woody plant communities. Venter's (1972) three communities are dominated by *Acacia karroo*, *Mimusops caffra* and *Celtis africana*. Venter (1972) also surveyed stands in the Kosi Bay and Sibaya area (further north along the coast) and came to the conclusion that

the forest vegetation in all these areas is relatively homogenous. From the seashore landwards, the dunes are characterised by a progressive ecocline with individual plants increasing in size and communities being older and more complex. Due to differences in dune aspect, distance from the sea (amount of salt spray) and edaphic influences, plants display a linear longshore pattern of distribution (Tinley, 1985; Hesp, 1991). Many endemic and specialised plants and animals occur on these dunes (Weisser & Marques, 1979).

When disturbed by either catastrophic events or human activity, the dune forests are often dominated by homogenous stands of even-aged *A. karroo* trees (Weisser & Marques 1979; Tinley, 1985; Barnes *et al.*, 1996). The *A. karroo* community represents an early stage of succession (Weisser & Marques, 1979; Mentis & Ellerly, 1994; Barnes *et al.*, 1996). In later seral stages *A. karroo* is often absent or occurs at very low densities. *A. karroo* is therefore an important component in the plant communities of coastal dune forests.

Acacia karroo

The genus *Acacia* Mill, is pantropical and some 1250 species are now recognised world-wide with 135 species occurring in Africa (Barnes *et al.*, 1996). The *Acacias* form a conspicuous component of the woody and shrub vegetation of southern Africa (Cresswell, 1981). The genus is widely distributed throughout Africa, occurring in some of the most arid regions, but is also present in wet and humid areas (Funston *et al.*, 1993). In Africa the *Acacias* belong to two subgenera: *Aculeiferum*, whose species are mostly diploid with prickles and spicate inflorescences, and *Acacia* whose species are mostly polyploids with thorns and capitate inflorescence.

Acacia karroo Hayne (Fam. Leguminosae), commonly known as the Sweet Thorn, is a shrub <2m, or a tree up to 25m high with a somewhat rounded or flattened crown (Barnes *et al.*, 1996). *A. karroo* is the most widespread tree in southern Africa (Barnes *et al.*, 1996) occurring over a diverse range of habitats. The species is therefore extremely variable, with some evidence that this variation may

constitute regional genetic differences (Ross, 1979). Swartz (1982) has proposed that the species should be divided into six subspecies. Although the extremes within the species are distinctive, they are, however, generally linked to the central type by numerous intermediate stages that become progressively less distinct, until it becomes impossible to delimit the variant (Barnes *et al.*, 1996). It is therefore probably better to regard *A. karroo* as an inherently variable polymorphic species in which no formal intraspecific categories are recognised (Ross, 1979; Barnes *et al.*, 1996).

The differences between specimens of *A. karroo* occurring on coastal dunes (in northern KwaZulu-Natal) and those occurring elsewhere, are especially pronounced. On coastal dunes *A. karroo* are large trees with greyish-white bark, spines up to 25cm long and long moniliform pods. Unlike "typical" *A. karroo*, the paired spines often persist on the trunk (Barnes *et al.*, 1996). The compound leaves are bipinnate with two to seven pairs of pinnae, each bearing eight to 20 pairs of small leaflets. The tree's inflorescences are golden-yellow globes and a tree may flower several times during the summer months, but with inflorescences more abundant between November and February (Barnes *et al.*, 1996). The fruits are thin-walled woody pods that ripen in winter. They split open while still on the trees when the seeds dangle from the pods by their funicles (Barnes *et al.*, 1996). Especially under favourable conditions trees flower profusely and produce copious amounts of seeds (Barnes *et al.*, 1996).

Acacia karroo is locally abundant, especially in previously disturbed areas where it sometimes forms dense homogenous stands of even-aged trees (Tinley, 1985; Barnes *et al.*, 1996). Belonging to the legumes, *A. karroo* is able to fix nitrogen in its rhizobial root nodules (Salisbury & Ross 1985; Barnes *et al.*, 1996).

The mining and rehabilitation process

Richards Bay Minerals (RBM) has for two decades dredged mined coastal dunes at Richards Bay in northern KwaZulu-Natal to extract heavy minerals (mainly ilmenite, rutile and zircon). The mining process has, since 1977, been followed by a rehabilitation programme directed at establishing indigenous coastal dune forests on one-third of the mining path. The remaining two-thirds of the area is revegetated with stands of exotic *Casaurina equisetifolia* for the development of a local charcoal industry (Van Aarde *et al.*, 1996a). A graphic representation of the mining and rehabilitation process is given in Figure 4.

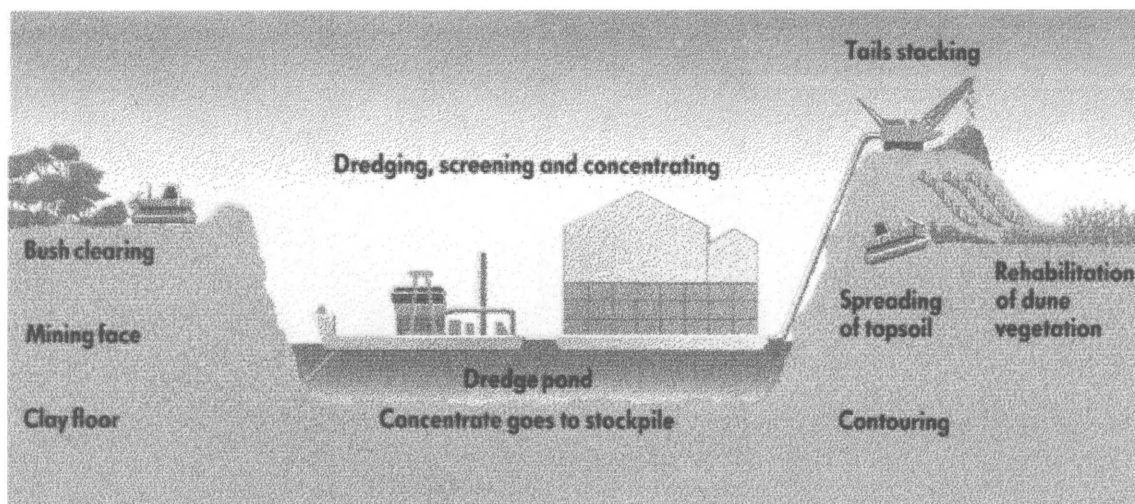


FIGURE 4: Graphic representation of the mining and rehabilitation process, illustrating from left to right the removal of topsoil, the floating pond, the reforming of the dunes and the rehabilitation process.

Before mining, vegetation is removed and the layer of topsoil is collected for later use. After the minerals have been removed from the sand, the dunes are reshaped to conform closely to the pre-mining topography. The next step in the rehabilitation programme is to spread topsoil over the mined sand to a depth of approximately 10cm and the placing of windbreaks (made from shade cloth) at approximately 5m intervals across the dunes. After good rains the topsoil is harrowed and a cover crop sown. A seed mixture of babala grass (*Pennisetum americanum*), sun hemp (*Crotalaria juncea*) and a *Sorghum* sp. together with indigenous seeds including *A. karroo*, are used to provide initial cover (Figure 5). The initial cover crop is short-lived and is replaced within a year by indigenous grass species, such as *Eragrostis curvula*, *Cymbopogon validus* and woody shrubs and trees with *A. karroo* dominating in the early years of rehabilitation. Management is limited to the initial topsoiling and seeding, after which the emergent *A. karroo* woodland is left to develop on its own accord (Lubke *et al.*, 1992b).



FIGURE 5: A photo of a very young rehabilitating stand, illustrating the exotic cover crop and the shade cloth windbreaks.

The rehabilitation programme has resulted in the development of a series of known-aged stands, varying from young communities dominated by low growing *Acacia karroo* shrublands to woodlands, also dominated by *A. karroo* trees. Figure 6 is an aerial view of the 2 to 6-year-old stands, with older stands in the front and younger ones more towards the back of the photograph. If these different-aged stands are developing along a similar pathway, their simultaneous sampling should reveal successional or other forms of change, which are usually associated with ageing (Van Aarde *et al.*, 1996a).

Description of stands

In the present study three different kinds of stands were investigated. These were different-aged mined stands (at present being rehabilitated towards indigenous dune forest), a 35-year-old unmined (but previously disturbed) stand at Zulti North, and "mature" dune forest communities at Richards Bay, previously described in literature.

Mined stands

When mining started in 1977, the mine lease area comprised 60% *Eucalyptus saligna* plantations, 20% grassland and 20% coastal dune forest (Van Aarde *et al.*, 1996b). The mined stands are bordered on the seaward side by a 100 to 200m belt of unmined coastal dune forest, fragmented in places by plantation patches (mainly *Eucalyptus saligna* and *Cassaurina equisetifolia*). In the interior lies a narrow strip of *C. equisetifolia*, afforested at various stages following dune mining. The area also includes patches of sand dunes stripped of vegetation in preparation for mining, and dunes being reshaped and prepared for rehabilitation. The ages of stands were determined by using the mining map of RBM. On the mining map the mining path, direction of the mining process and the exact position of the mining ponds on specific dates are indicated. The date on which rehabilitation began on a particular stand, was taken as one year after mining.



FIGURE 6: An aerial view of the 2 to 6-year-old mined stands at Richards Bay. The 6-year-old stand is in the foreground of the photograph with the 2-year-old stand towards the background. The stands comprise of *Acacia karroo* shrubland of 1m to 5m in height.

Five different-aged stands were selected for sampling in the previously mined area. They were 2, 3, 6, 9 and 14 years old at the time of sampling. The 3-year-old stand is situated on the border with the 2-year-old stand and was initially surveyed as a transect falling within the 2-year-old stand. When the error was discovered the transect was assigned its proper age and treated as a separate stand. The 9-year-old stand was selected, because no suitable (comparable) 10-year-old stand was available. All sampling areas were located on the sea-facing aspect of the second parallel dune from the sea, and were covered with indigenous dune forest prior to mining.

Unmined but previously disturbed stand

Aerial photographs of the study areas, showed that the region was previously highly degraded due to grazing by domestic animals and shifting cultivation (Van Aarde *et al.*, 1996b). A patchwork of mature coastal forests, secondary *Acacia karroo* woodlands, commercial pine plantations, secondary grasslands and bare patches, existed at that time in the area. By the mid 1970's (before mining) some of the grasslands and disturbed areas had reverted to secondary dune forest or had been planted with *Cassaurina equisetifolia*, *Eucalyptus* spp. or *Pinus* spp. plantations (Weisser & Marques, 1979). Some of the approximately 35-year-old or secondary dune forests are as yet unmined and could therefore be sampled.

Two unmined sites in the Zulti North area (see Figure 1) were surveyed, although not as intensely as the mined stands. Due to political unrest at the time of the study, the number of possible sampling areas in this area was limited at the time of the study. The first stand is dominated by *Teclea gerrardii*, and aerial photographs suggest that it could be 35 years old. This age was confirmed by Gourlay (1995) who counted the year rings of an *A. karroo* tree, felled in this area.

A second unmined stand (dominated by *Apodytes dimidiata*) was earlier planted with pine trees, but the project was unsuccessful and therefore abandoned. The exact age of the stand is unknown. It is, however, clear that this stand follows a

different successional pathway than the mined stands or the unmined *Teclea gerrardii* stand (see Lubke *et al.*, 1992b). The *Apodytes* pathway is typical only of stands previously planted with exotic pine plantations (Lubke *et al.*, 1992b) and has therefore not been used in the present study for comparisons with the mined stands.

Mature dune forest

Several general vegetation surveys of the mature dune forests in the Richards Bay and northern KwaZulu-Natal area were previously conducted, for example by Venter (1972), Weisser & Marques (1979), Weisser & Drews (1980) and Tinley (1985). In addition to these, more recent surveys were done in the study area by Moll (1992), Lubke *et al.* (1992a; 1992b), Scott *et al.* (1993) and Mentis & Ellerly (1994). The results of these studies will be used to compare the woody plant composition of "mature" dune forests with the communities surveyed in the present study. The work of Venter (1972) will be used extensively, because he used comparable survey methods and presented his results in sufficient detail to make them directly comparable to the results of the present study. Venter's three back dune communities (*Acacia karroo*, *Celtis africana* and *Mimusops caffra*) will be compared with the communities in the present study. Due to the detailed description of mature communities by previous surveys and the political unrest at the time of the study, no further surveys of "mature" dune forests have been attempted.

Relative ages of stands

The absolute ages of Venter's (1972) three stands are not known. By using species ordination (Index Iteration) Venter (1972) calculated the successional order of the woody species. On an arbitrary scale from 1 to 10, 1 represented a species best adapted to severe habitat circumstances, while an index number of 10 was assigned to a species best suited for favourable environmental conditions. If it is accepted that more severe conditions prevail in younger seral communities (Barbour *et al.* 1987), one can deduce that younger communities will probably be dominated by species

having a lower index while later seral communities will contain a higher density of species favouring better conditions (i.e. with a higher index number). One can thereby organise stands into their *relative* ages by looking at the species dominating the various stands. Venter's (1972) Index Iteration resulted in the following successional order for woody species in the Richards Bay area:

<i>Acacia karroo</i>	=	1.0;
<i>Mimusops caffra</i>	=	5.0;
<i>Apodytes dimidiata</i>	=	6.4;
<i>Sideroxylon inerme</i>	=	6.9;
<i>Celtis africana</i>	=	7.6;
<i>Dovyalis longispina</i>	=	8.2;
<i>Teclea gerrardii</i>	=	9.7.

Mentis & Ellerly (1994) used correspondence analysis for the ordination of species in the Richards Bay area and their results showed a very similar order of species to those calculated by Venter (1972). They assigned the following successional order (from early to late): *Acacia karroo*, *Celtis africana*, *Teclea gerrardii*, *Draceana hookeriana*, *Deinbollia oblongifolia*, *Dovyalis longispina* and *Psychotria capensis*. These two independent ordinations of species were then used to estimate the **relative** ages of Venter's communities in relationship to the mined and unmined stand in Zulti North.

Venter's *Acacia karroo* community was probably younger than the unmined 35-year-old *Teclea gerrardii* stand surveyed in Zulti North. This can be deduced from the higher density of *A. karroo* in Venter's stand, the near absence of broad-leaved species in the canopy of his *Acacia karroo* stand, and the low densities or absence of 'later' species in the subcanopy layer of his stand. For example, *D. longispina* occurs at very low densities and the very important indicator species *Psychotria capensis* was absent in his *Acacia* stand (see also Scott *et al.*, 1993).

Venter's (1972) ordination differs from that of Mentis & Ellerly (1994) on the position of *Celtis africana*. However, Venter's *Celtis africana* stand was probably younger than his *Mimusops caffra* community. This can be deduced from the following: 1) The pioneer species *A. karroo* occurred at a density of 61 trees per

hectare in the *C. africana* stand, while it was totally absent from the *M. caffra* stand. 2) Two late species, *Psychotria capensis* and *Dovyalis longispina* occurred at very low densities in the *Celtis africana* community (6 /ha and 19/ha respectively) while *P. capensis* dominated the subcanopy layer of the *M. caffra* stand (density = 294/ha) and *D. longispina* also occurred (although at low densities) in the latter stand.

From young to old, the relative ages of all the unmixed stands can therefore be given as: 1) Venter's *Acacia karroo* community; 2) the 35-year-old *T. gerrardii* stand at Zulti North; 3) Venter's *C. africana* stand and 4) Venter's *M. caffra* stand.

MATERIALS AND METHODS

The Point-Centred Quarter method (Cottam & Curtis, 1956) was used to survey the canopy layer of the stands referred to above. Venter (1972) previously illustrated the appropriateness of this method as a fast and accurate method for surveying the coastal dune flora of northern KwaZulu-Natal. During the present study transect lines, 10m apart, were superimposed on a map of the study area and (depending on the dimensions of the stand) four to six of these were randomly selected for sampling. Each selected transect line was marked at 10m intervals and two thirds of these marks were randomly selected for sampling. Although the sampling method used was not completely random, it is considered an acceptable procedure (Jager & Looman, 1987) and during the present study ensured that the same individual plants were seldom included in more than one sample. It also reduced disturbance of the rehabilitating stands through sampling.

Transect lines or sampling points falling on roads were discarded and another transect line or point randomly selected in its place. All sampling points were permanently marked by wooden or metal poles. The transects were also used when collecting soil samples and when monitoring flower-fall. The transects were laid out perpendicularly to the coastline and therefore ran transversely across the dunes. All transects started in the valley between the first and second dunes from the beach and ran inland to the crest of the second dune. Figure 7 illustrates the layout of transects by using the 14-year-old stand as an example of such a layout.

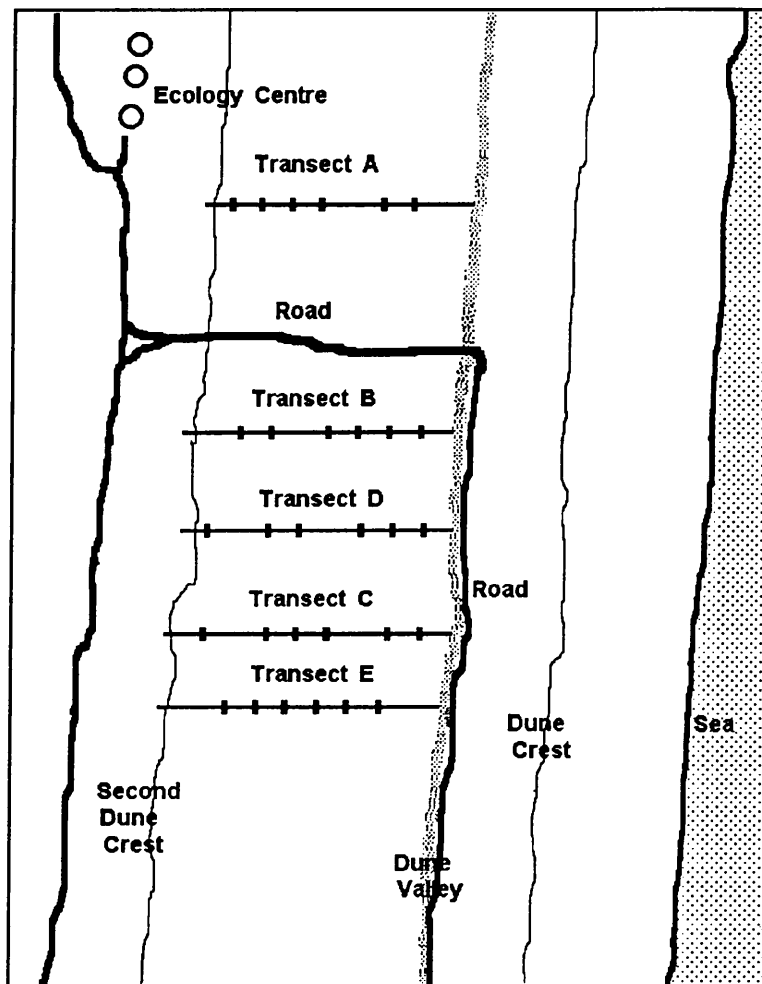


FIGURE 7: The layout of transects in the 14-year-old stand. The stand is used only as an example to explain the general layout of transects. Scale: 1cm:20m

At each sampling point the following physical features were recorded: 1) the dune aspect; 2) the dune slope, using a PM-5/1520 Suunto metre; 3) the distance from the starting point of the transect to the sampling point and 4) the distance from the transect line to the oldest border of the stand. Morphometric variables of *A. karroo* individuals, such as number of stems, height, crown area and basal area were recorded for the nearest individual to the centre point (as defined by the PCQ method) (see Chapter 3 for more details on the methods used). The measured or calculated population variables of *A. karroo* included density, biomass, canopy cover, canopy gap sizes, flower-fall and number of seeds in the seed bank (see Chapter 4 for details on methods) while the density, species and height of the nearest broad-leaved species were also recorded in each quarter, as defined by the PCQ method (see Chapter 6 for detail on the methods). Soil samples were taken and analysed for organic debris ($> 2\text{mm}$), organic content ($< 2\text{mm}$), pH and water content (see Chapter 6).

The Statistical Analysis System (SAS) and Statsgraphic statistical programmes were used for all calculations. In the results sections, means are followed by the standard error of the means ($\pm\text{S.E.}$) and in brackets by the sampling size (i.e. number of trees measured, or included in a calculation), and the coefficient of variation (C.V.%).

CHAPTER 3

MORPHOMETRIC VARIABLES OF *ACACIA KARROO*

INTRODUCTION

The morphology of individual plants may change during community development. These differences may reveal temporal trends that can be used to predict the future of a population and its fate during community development. *Acacia karroo* is considered an important species during early succession on coastal dunes in KwaZulu-Natal (Tinley, 1985; Barnes *et al.*, 1996) and morphometric attributes of individuals are therefore important when investigating age-related differences between stands.

Height of trees often correlates with age and height may therefore be used as an indicator of the age and age distribution of individuals within a population. Age distributions may indicate when a population is senescent, invading, or relatively stable. Senescent populations (which are not replacing themselves) usually comprise of mature trees, while invading populations contain seedlings and saplings of intermediate size. However, self-maintaining populations have many seedlings and saplings, but fewer adults (Barbour *et al.*, 1987). With long-lived trees it should be appreciated that the sporadic establishment of seedlings can be sufficient to replace a population. So-called senescent populations (with no juveniles) may therefore in future experience favourable conditions for recruitment, and by that establish a new cohort of individuals. Only one such recruitment in the lifetime of a cohort is needed to maintain a population (Barbour *et al.*, 1987).

The height of trees may also provide valuable information on the species' survival strategy. Growing to a great height to avoid interspecific competition is an important strategy for some species. The most important advantage of height, especially in dense forests, is the accessibility to light. Grime (1966) argued that

light must be a major component directing plant adaptations to specific habitats. Plants can accordingly be divided into heliophytes (sun loving plants) or sciophytes (shade-loving plants) (Krebs, 1985). Heliophytes have two possible strategies for survival — either they grow quickly, produce seeds and jump to the next open space, before conditions in the first stand become unfavourable for them (r-selected), or they may delay reproduction, grow fast and reach great heights to avoid shading by other individuals (more K-selected). Sciophytes grow slowly and make maximum use of the limited resources available to them (i.e. light and nutrients). They usually delay reproduction and allocate most resources towards maintenance (K-selected).

However, all life history strategies have trade-offs. Heliophytes using the r-selected option usually do not persist very long in a stand (unless the stand is regularly disturbed), but must continually "jump" to other suitable stands that become available. K-selected heliophytes may survive for extended periods within forests, but their seeds are usually susceptible to fungal attack in shaded environments (Krebs, 1985). Seeds from heliophytes may fail to germinate, or seedlings may not survive in a shaded environment. These factors may cause a low or a total lack in recruitment, eventually leading to the local extinction of the species.

Sciophytes need less light to reach CO₂ compensation points and can maintain a positive carbon balance in shade (Barbour *et al.*, 1987). Research has shown that sciophytes are very effective in using temporal and variable sun flecks in tropical forests, with 40-60% of their photosynthesis taking place during their short exposure to the sun (Barbour *et al.*, 1987). There is evidence that early seral species (which require full sunlight for optimal growth) do not exhibit the efficiencies and acclimation potentials of shade-tolerant species (Barbour *et al.*, 1987).

During succession the crown sizes of canopy tree usually steadily increase (Terborgh & Petren, 1991). Trees in the sunlit upper canopy usually have the largest diameters. Tall emergents with large crowns may cast vast shadows over

smaller trees and thus have a big influence on the community (Terborgh & Petren, 1991). Age-related trends in crown sizes may therefore be important when assessing a species effect upon a community. Basal area and the mass of individuals are two other morphometric variables which may differ between different-aged stands and which may be used to express the dominance of a species within a community. Variation of these two variables may also illustrate age-related trends, and when correlated with density (Chapter 4), may provide insight into the importance of self-thinning within a population.

MATERIALS AND METHODS

This chapter is based on information obtained at randomly selected survey points along transects lines, positioned in different-aged mined and unmined stands as described in Chapter 2. Unless stated otherwise, all results refer to *A. karroo* individuals. Within each quarter (as defined by the PCQ-method) all morphometric variables were recorded for the individuals nearest to the transect point. Individual heights were measured, either with a measuring rod, or for trees higher than 5m, with a PM5/1520 Suunto height metre. The Suunto metre measured the angle to the top of a tree (from a fixed distance of 15m or 20m) and then converted this to a measure of height. In stands older than 3 years, juveniles (defined as individuals <2m) were surveyed separately. The heights and number of juveniles were recorded within a 1m radius around each sampling point.

With canopy trees the longest and the shortest distances across each crown were measured and the crown area (*ca*) was then calculated as:

$$ca = \left(\frac{l/2 + s/2}{2} \right)^2 \times \Pi, \text{ where } l = \text{longest distance across crown (m), and } s = \text{shortest}$$

distance across crown (m). The diameters of small shrubs were measured directly. The crowns of big trees were measured by projecting their edges to ground level. For this purpose a "scope" consisting of a vertically held plastic pipe was constructed, with a water level on top (to assess its vertical aspect) (Figure 8). By looking upwards through the "scope" it was possible to project the edges of a tree's crown to ground level before measuring the diameter of a crown.

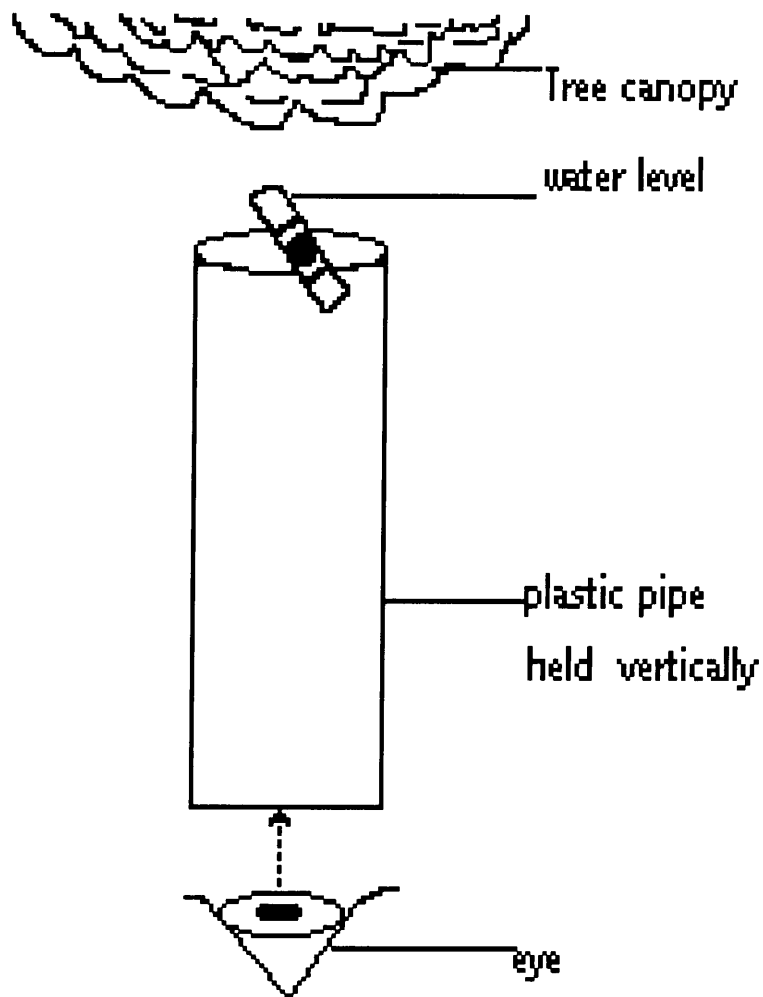


FIGURE 8: Scope constructed from a plastic pipe and water level to aid with the vertical projection of tree crowns down to ground level

Basal diameters of individuals in the 2 and 3-year-old stands were measured at ground level, but in the older stands (6 - 35 years) diameter at breast height (DBH = 1.2m above ground level) was recorded by using a measuring tape with a conversion of circumference to diameter. The basal area for each tree was calculated by summing the areas of all living stems.

To be able to calculate the individual mass of trees, the height and DBH of six randomly selected individuals were first measured as described above. They were then cut down and immediately weighed (to the nearest 0.01kg). Large trees were cut into smaller pieces before being weighed. For practical reasons, trees could not be dried to determine dry mass. An index was then calculated to relate wet biomass to DBH and height by using the equation: $\log_e y = a + b \log_e x$, where y = wet biomass, and $x = \text{DBH}^2 \times \text{height}$ (see Whittaker & Woodwell, 1968; Barbour *et al.*, 1987).

RESULTS

Number of stems per tree

Table 1 shows that the number of live stems per tree did not follow a clear age-related trend, although (if the 3-year-old stand is excluded) live stems had a weak negative correlation with age ($r = -0.15$; $n = 478$; $p < 0.0011$). Analysis of variance showed that there were significant differences in the frequency of live stems between the stands ($F = 6.68$; $df = 1, 3$; $p < 0.0001$), but Sheffe's test revealed that these significant differences were between the 2-year-old stand on the one hand and all the older stands (critical value of $F > 2.62$; $df = 469$; $p < 0.05$). The number of dead stems per tree increased with stand regeneration age as is suggested by the significant positive correlation between age and the number of dead stems in the mined stands ($r = 0.39$; $n = 478$; $p < 0.0001$). No dead stems were, however, recorded in the unmined 35-year-old stand. In the 6, 9 and 14-year-old stands more than 50% of *A. karroo* trees were single-stemmed (Table 2).

TABLE 1: Stand specific mean $\pm$ S.E. (C.V.) number of dead and live stems per *Acacia karroo* individual

Age of Stand (years)	Number of individuals in sample	Mean Number of Stems $\pm$ S.E. (C.V.)	
		Alive	Dead
2	126	2.14 $\pm$ 0.091 (48%)	0.040 $\pm$ 0.021 (588%)
3	28	1.46 $\pm$ 0.120 (44%)	0
6	108	1.70 $\pm$ 0.100 (61%)	0.222 $\pm$ 0.048 (225%)
9	128	1.55 $\pm$ 0.078 (57%)	0.492 $\pm$ 0.066 (151%)
14	112	1.74 $\pm$ 0.089 (54%)	0.768 $\pm$ 0.087 (120%)
35	5	1.40 $\pm$ 0.244 (39%)	0

TABLE 2: Frequency distribution of single and multi-stemmed *Acacia karroo* individuals on mined and unmined stands. Only live stems are included. Frequencies are followed in brackets by the relative frequencies, expressed as percentages.

Age of Stand (years)	Number of individuals	Number of Live Stems (%)					
		1	2	3	4	5	6
2	126	37 (29.4)	51 (40.5)	25 (19.8)	9 (7.1)	4 (3.2)	0
3	28	17 (60.7)	9 (32.1)	2 (7.1)	0	0	0
6	108	63 (58.3)	25 (23.1)	12 (11.1)	6 (5.6)	1 (0.9)	1 (0.9)
9	128	83 (64.9)	26 (20.3)	12 (9.4)	7 (5.5)	0	0
14	112	57 (50.9)	32 (28.6)	19 (17.0)	2 (1.8)	2 (1.8)	0
35	5	3 (60.0)	2 (40.0)	0	0	0	0

Height of the canopy layer

Although the mean heights of *A. karroo* in the 2 and 3-year-old stands were below 2m (Table 3) all individuals here were considered part of the canopy layer. Mean height increased with an increase in habitat regeneration age and the mean value of the 14-year-old stand differed significantly ($t=-7.526$; $df=115$; $p<0.0001$) from that of the unmined 35-year-old *Teclea gerrardii* stand (Table 3). The low coefficient of variation for canopy heights in the 14 and 35-year-old stands (15%

and 16% respectively) suggests that most individuals in these older stands were of comparable height. Height of trees furthermore significantly correlated with age ($r=0.94$; $n=514$; $p<0.0001$).

Height of *A. karroo* juveniles in the shrub layer

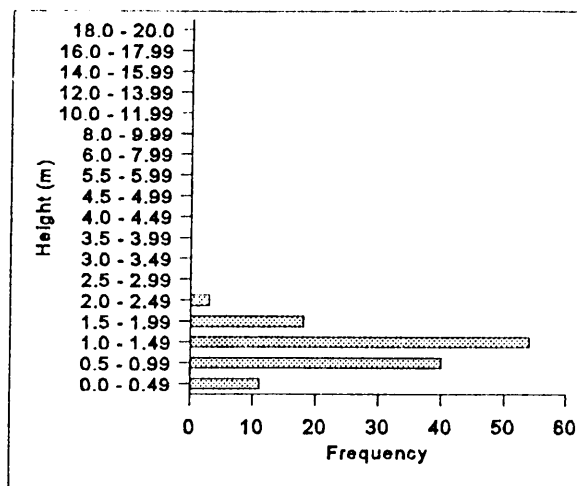
Mean heights of juveniles in the older stands (9 - 35years) were very small (below 20cm) (Table 3). There were no significant differences in the heights of juveniles between the 9 and 35-year-old or between the 14 and 35-year-old stands (Sheffe's test: $F<3.369$; $df=26$; $p>0.05$). The mean height of juveniles in the 6-year-old stand (1.37 ± 0.08) was relatively high in comparison with the older stands.

TABLE 3: Mean heights for *Acacia karroo* trees in the canopy layer and for juveniles in the shrub layer of mined and unmined stands.

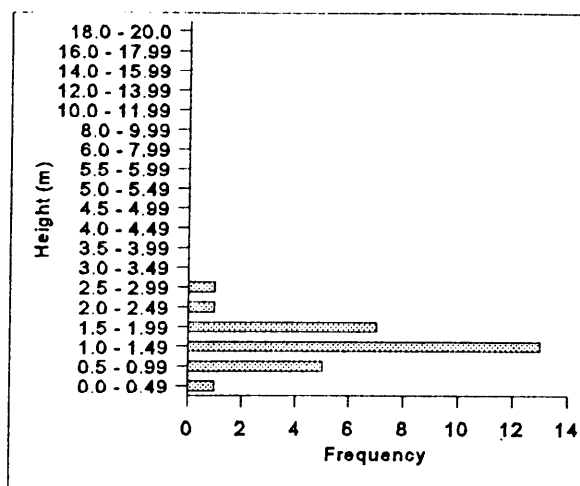
Age of stand (years)	Height of canopy layer (m)	Height of juveniles in shrub layer (m)
	Mean $\pm$ S.E. (n; C.V)	Mean $\pm$ S.E. (n; C.V.)
2	1.06 ± 0.04 (126; 40)	-
3	1.30 ± 0.09 (28; 36)	-
6	3.62 ± 0.07 (108; 21)	1.37 ± 0.08 (60; 45)
9	8.33 ± 0.15 (128; 20)	0.11 ± 0.02 (12; 64)
14	11.28 ± 0.16 (112; 15)	0.20 ± 0.01 (44; 35)
35	17.10 ± 1.21 (5; 16)	0.20 (1)

Frequency distribution of heights

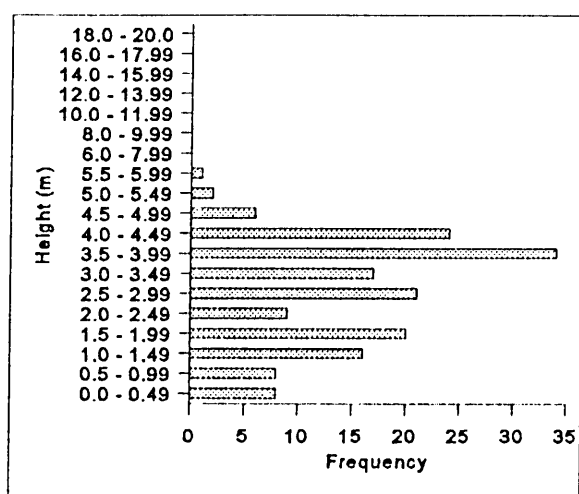
The frequency distributions of heights (including both the canopy and shrub layers) for each of the stands are represented in Figure 11a-f. In the 2 and 3-year-old stands all individuals were less than 3m high and the distribution in each of these stands were roughly bell-shaped. Heights in the 6-year-old stand ranged from 0.40 to 5.60m and the frequency distribution started to develop two



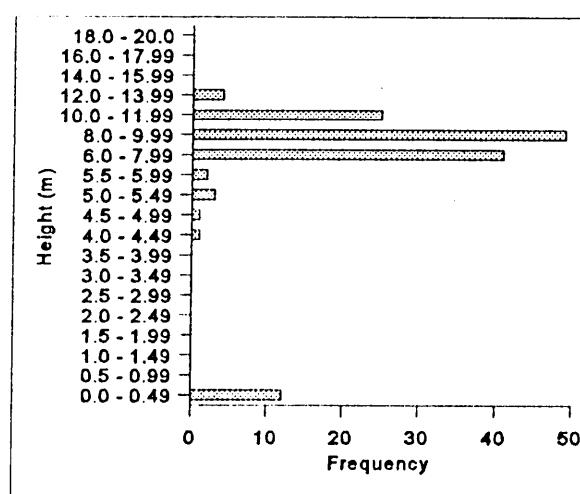
[a] 2-year-old stand.



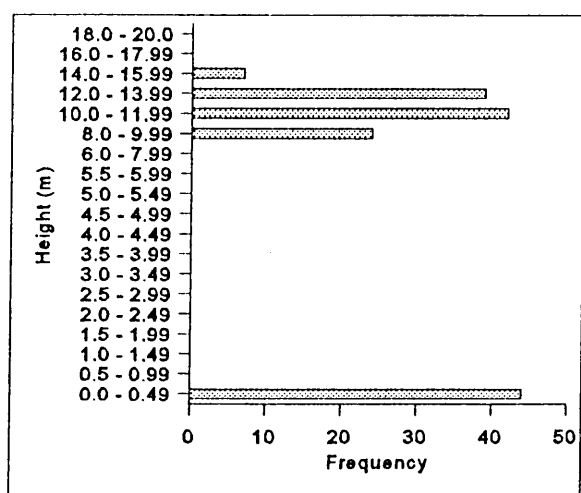
[b] 3-year-old stand.



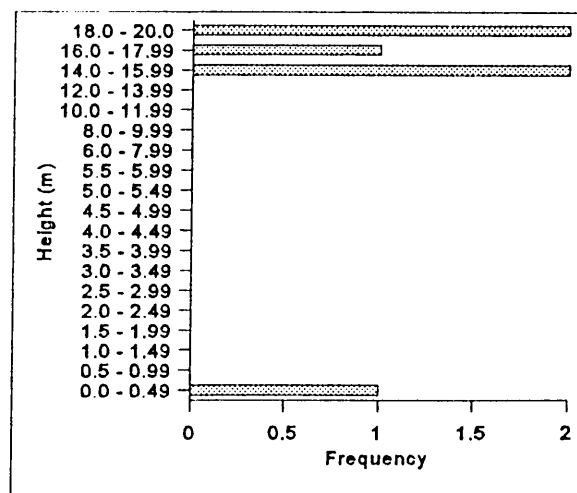
[c] 6-year-old stand.



[d] 9-year-old stand.



[e] 14-year-old stand.



[f] 35-year-old *Teclea gerrardii* stand.

FIGURE 9: Profile diagrams of frequency of heights for *Acacia karroo* in different-aged mined and unmined stands at Richards Bay

distinctive peaks. The frequency distributions in the 9, 14 and 35-year-old stands (Fig.4d-f) were similar in the sense that they had two distinct peaks. The low peak comprises of juveniles below 30cm and the high peak consists of all the canopy trees. With stand regeneration age, an increasing gap with no *A. karroo* individuals in it developed between these two peaks. All juveniles in these older stands should therefore be considered seedlings.

Crown and basal areas

Mean crown areas (3-year-old stand excluded) increased with stand age (Table 4) and there was a significant positive correlation between crown areas ($\log_e$ scale) and stand age ($r=0.72$; $n=384$; $p<0.0001$). Stand specific crown area over the first six years was characterised by high variability (C.V.=116-126%), but this variability decreased slightly with an increase in stand age (Table 5).

Mean basal area of individuals also increased with stand age (Table 5) and there was a significant positive correlation between basal area ($\log_e$ scale) and stand age ($r=0.7832$; $n=439$; $p<0.0001$). Variability was again high in all the younger stands (C.V. between 84% and 98%), but slightly lower in the 14-year-old stand (C.V.=62%) and much lower in the 35-year-old unmined stand (C.V.=26%). The 3-year-old stand was an exception to the general increase in basal area with stand age since its mean was lower than the value for the 2-year-old stand. Basal areas differed significantly between stands ($F = 178.47$; $df = 1,3$; $p<0.0001$). Means were significantly higher between the following age groups: 6 and 9 years; 9 and 14 years; 14 and 35 years (Scheffe's test: $F>3.53$; $df=439$; $p<0.05$). This increase in basal area continued beyond the oldest mined stand (14 years) as is evident from the fact that there was also a significant difference between the 14-year-old stand and the unmined 35-year-old *Teclea gerrardii* stand.

The mean basal area for the 14-year-old stand (300.3cm^2) was also smaller than the value of 765.2cm^2 recorded by Venter (1972) for his *Acacia karroo* community of unknown age (Table 4).

TABLE 4: Mean crown and basal area for *Acacia karroo* individuals on mined and unmined stands of different ages. All means are followed by the standard error of the mean ($\pm$ S.E.) and in brackets by the sample size and the coefficient of variation (%).

Age of stand (years)	Crown area (m ²)	Basal area (cm ²)
2	1.49 $\pm$ 0.18 (111; 124%)	9.18 $\pm$ 0.69 (125; 84%)
3	0.86 $\pm$ 0.20 (28; 126%)	5.84 $\pm$ 0.97 (28; 88%)
6	2.45 $\pm$ 0.32 (80; 116%)	18.5 $\pm$ 1.84 (99; 98%)
9	10.82 $\pm$ 0.90 (112; 88%)	99.9 $\pm$ 7.87 (114; 84%)
14	26.09 $\pm$ 2.72 (67; 85%)	300.3 $\pm$ 18.87 (100; 62%)
Acacia*	-	765.2
35	-	872.6 $\pm$ 312.1 (5; 36%)

* Venter's (1972) *Acacia karroo* stand of unknown age.

Mass of trees

The relationship between $\log_e$ mass and $\log_e(\text{DBH}^2 \times \text{height})$ was best described by the equation $y = 0.864x - 1.445$ ($r^2=0.99$; $df=5$; $p<0.0001$) (Figure 10). The significant correlation between $\log_e$ mass (y-axis) and $\log_e(\text{DBH}^2 \times \text{height})$ (x-axis) suggested that the index is reliable and can be used to give a reasonably accurate estimate of the wet mass of *A. karroo* individuals.

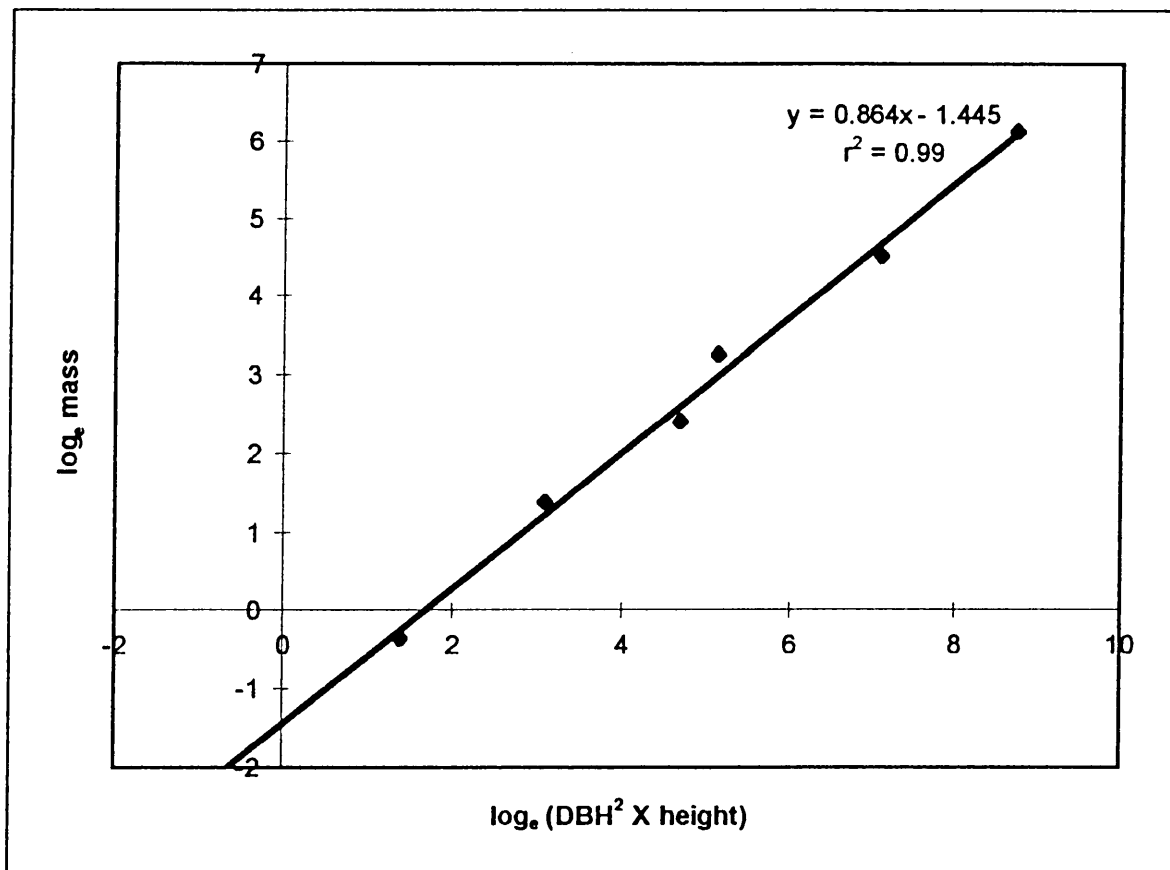


FIGURE 10: Fitted regression line to describe the relationship between $\log_e$ mass (y-axis) and $\log_e (\text{DBH}^2 \times \text{height})$ (x-axis)

The mean mass increased with stand age (Table 5) and there was a significant positive correlation between stand age and mass ($r=0.8035$; $n=470$; $p<0.0001$). Individuals in the unmined *Acacia karroo* stand surveyed by Venter (1972), were much heavier than those in the oldest 14-year-old mined stand and there was also a significant difference ($t= -10.9291$; $df=115$; $p<0.0001$) in the mass between the 14-year-old and the 35-year-old unmined stand at Zulti North. The coefficients of variation decreased consistently with age.

TABLE 5: Mass of *Acacia karroo* individuals calculated using the equation $y=0.864x - 1.445$ in mined and unmined stands of different ages

Age of Stand (years)	Number of trees included in calculation	Mass of individuals (kg) mean $\pm$ S.E. (C.V.%)
2	121	1.82 $\pm$ 0.14 (84%)
3	28	1.74 $\pm$ 0.35 (108%)
6	108	10.44 $\pm$ 0.84 (84%)
9	124	91.01 $\pm$ 5.85 (72%)
14	112	278.83 $\pm$ 15.52 (59%)
Acacia*	-	1054.6
35	5	1157.3 $\pm$ 167.6 (32%)

* From Venter (1972)

DISCUSSION

The lack of any clear trend in the mean number of live stems per tree suggests that they cannot be predicted by the age of a stand. For example, the 2 and 14-year-old stands had the highest mean number of stems per tree, while the 3, and 9-year-old stands had on average fewer stems per tree. The low number of stems in the dense 3-year-old stand (see Chapter 5) is probably due to the high rainfall during its year of rehabilitation, causing a higher density of trees in that stand. Such a high density would probably limit the number of stems per tree due to crowding. In the mined stands (excluding the 3-year-old stand) the number of dead stems per tree increased with stand age, showing that mortality of stems coincides with mortality of individuals (see Chapter 4).

Although *A. karroo* is often a multi-stemmed tree (Barnes *et al.*, 1996), most individuals (>50%) in the rehabilitating stands were single-stemmed. It is only in the youngest 2-year-old stand where more than 50% of individuals were multi-stemmed. The higher number of single-stemmed trees and the lower mean

number of live stems in the stands older than 2 years, are probably caused by density-dependent mortality. This suggestion is supported by the higher number of dead stems in the older stands (Figure 8), where crowding may play a significant role as is suggested by the self-thinning rule (Chapter 5).

The trees in the oldest mined stand (14 years) have clearly not yet reached their maximum heights as is suggested by the significant difference in height between the trees in the 14-year-old stand and the 35-year-old stand. The positive correlation between stand age and height illustrates the continual increase in trees' heights during the first 35 years, suggesting that trees probably keep growing throughout their lifetime. *Acacia karroo* therefore probably allocates a significant amount of resources towards growth. This agrees with Hubbell & Foster's (1986) definition of late secondary forest trees with high growth rates. The low variability in heights (see C.V.'s in Table 1) further suggests that trees in the canopy layer are more or less of equal height, with most of the variability attributable to the different heights of trees occurring on the various aspects of dunes (see Chapter 5).

In the 6-year-old stand the mean height of 1.37m for *A. karroo* juveniles in the shrub layer and the relatively high coefficient of variation (45%) indicate that recruitment was still taking place at that age. However, all juveniles in the shrub layer of the older stands (9-35 years) were seedlings less than 30cm high. Venter (1972) did not measure any heights during his surveys, but based on DBHs he divided the vegetation into canopy, subcanopy and herb layers. One can therefore compare the height frequencies of juveniles in the present study by inspecting the relative frequencies of saplings and seedlings in his subcanopy and herb layers. In Venter's *Acacia karroo* stand the relative frequencies of *A. karroo* in the subcanopy and herb layers were 26.7% and 0.5% respectively. In his *Celtis africana* stand the frequency was 1.3% (subcanopy) and 0.4% (herb layer). However, in the *Mimusops caffra* community *A. karroo* was absent from both layers. It is therefore clear that few *A. karroo* juveniles of intermediate heights were recorded in Venter's more "mature" stands. The relative frequency of juveniles in the 35-year-old unmined stand (surveyed in the present study) was also low. As argued in Chapter 2,

Venter's three communities are probably older than the mined stands of the present study. The low frequency (or absence) of *A. karroo* juveniles in the subcanopy and herb strata of Venter's "mature" communities therefore confirms the conclusion that no (or a very low) recruitment of *A. karroo* is taking place in more mature stands during later stages of succession.

The initially high and consistent increase in the heights of *A. karroo* individuals throughout their life-span, suggests that *A. karroo* can maintain itself for extended periods in the canopy layer of the community. The lack of saplings of intermediate heights in the older stands, suggests that they have difficulty surviving in a shaded environment.

In the 2- to 6-year-old stands juveniles of all heights (=ages) occurred, but no adults, suggesting that during the first six years *A. karroo* can be described as an invading population. In the older stands (≥ 9 years) an increasing spatial gap developed between the small seedlings on the forest floor on the one hand and the *A. karroo* trees in the canopy on the other hand. No saplings of intermediate heights (0.5m - 8.0m) were recorded in the older stands, suggesting that the *A. karroo* population is senescent and that, if no future recruitment takes place, the local population will not replace itself (Barbour *et al.*, 1987).

If no major disturbance takes place in future, it is unlikely that the mined stands will experience any mass recruitment of *A. karroo*, or go through another *A. karroo* phase (vs. Barnes, 1996). This is supported by the low frequency or absence of subcanopy individuals in the 35-year-old unmined *Teclea gerrardii* stand as well as in the "mature" communities surveyed by Venter (1972). Although the canopy cover comprising of *A. karroo* individuals has already become very sparse in the 35-year-old *Teclea gerrardii* stand, there was no increase in the frequency of saplings of intermediate heights in this stand. This lack of *A. karroo* recruitment in the "mature" stands is probably the result of shading caused by the multispecies broad-leaved canopy (see Chapter 6).

The complexity of the vertical structure of the *A. karroo* population increased with the stand age (Figure 9). In the 2 and 3-year-old stands a mono-

layer of vegetation extends from ground level to about 2.5m. In the 6-year-old stand this mono-layer has increased in width from ground level to just below 6m, with a possible tendency towards developing a two-peak profile, as is suggested by the low frequency between 2.0m and 2.49m. In the 9-year and older stands a definite two-peak structure is observed with a discrete canopy stratum and a shrub stratum below 0.5m. This two-peak vertical structure is typical of early and late seral communities (Terborgh & Petren, 1991), but a more comprehensive picture will emerge when all woody species are considered in Chapter 6.

There was no further increase in the number of strata comprising *A. karroo* towards the older 35-year-old *Teclea gerrardii* stand, suggesting that the vertical complexity of the *A. karroo* population will probably not increase after 14 years. The extent of the gap between the canopy stratum and the shrub stratum has, however, increased with stand age and will probably further increase as the mined stands grow older. The heights of *A. karroo* individuals, relative to other species will be investigated in Chapter 6.

The increases in the mean crown sizes, basal areas and mass with stand regeneration age, suggest that individuals are becoming larger over time, without any (or few) smaller individuals being added to the older stands. This is supported by the decreasing trend (after six years) in the variability (C.V.'s) of crown sizes, basal areas and mass, and shows that individuals in the older stands are increasingly similar in size. The much higher basal area of trees in Venter's (1972) *Acacia karroo* stand and the significant difference in basal area of *A. karroo* individuals between the oldest mined stand (14 years) and the unmined 35-year-old stand, shows that trunks in the mined stands have not yet reached their maximum thickness. Over the next few decades the stems of surviving individuals will therefore probably further increase in thickness. All indications are that *A. karroo* therefore is probably a heliophyte that avoids shading by maintaining a high growth rate throughout its lifetime.

CHAPTER 4

POPULATION VARIABLES OF *ACACIA KARROO*

INTRODUCTION

After the initial recruitment phase of *A. karroo* on disturbed stands, mortality becomes an important factor in determining population density. With primary producers (i.e. plants), population density is often limited by density-dependent mechanisms due to the limitation of resources (Hairston *et al.*, 1960). Control mechanisms may either influence reproduction or mortality rates of a species. Few organisms in nature die of senescence. Plants may be eaten by herbivores and die of disease or lack of resources long before they reach old age (Krebs, 1985).

The density of a population is an important population variable, but on its own cannot adequately express the dominance of a plant species. Canopy cover, basal area and biomass are also important variables which may shed light on the trends within a population and, when investigated over time, can be predictors of the future dominance of a species. When dealing with the canopy layer, the temporal trends in percentage canopy cover and the sizes of gaps within the canopy will be investigated. Percentage canopy cover and the sizes of gaps can show how the cover of a species is developing with time, for example, if it is increasing or decreasing in older stands. Gaps in the canopy may also become bigger or smaller or may become more variable as the age of a stand increases. In a forest the amount of canopy cover and the size and variability of gaps may be critical in the survival of heliophyte seedlings or the opening up of the canopy may offer a chance to sciophyte saplings to take their place in the canopy and eventually dominate a forest community.

Basal area is often used to express a species' dominance, especially when biomass figures are not available. On the other hand the biomass of a population is often calculated from basal area (or DBH) or from both the basal area and the height of an individual (Whittaker & Woodwell, 1968; Barbour *et al.*, 1987). The biomass per hectare of a species is the most important indication of a species' dominance, because it not only takes the density, but also the sizes of individuals into account. The rate at which biomass accumulates can also be used as an index of productivity (Barbour *et al.*, 1987).

Flower and seed production is important when assessing the reproductive strategies of a population. In the present study production of flowers and seeds was measured indirectly by assessing flower-fall during the height of the flowering season and by sampling the seed bank in early winter. Although seed survival was not specifically assessed in the present study, the occurrence of seeds in the seed bank of immature (non-seed producing) stands may show how *A. karroo* seeds are surviving. The age at which trees start to flower and the general pattern of flowering and seed production can further shed light on the reproductive strategy of the species and its life history in general. Questions that will be addressed in this chapter are: 1) Is the proportion of resources allocated by *A. karroo* towards reproduction fixed or does it change with age? 2) Is reproduction negatively influenced by stressful situations such as droughts (Harper, 1967)?

MATERIALS AND METHODS

Estimates of tree densities are based on Point-Centred Quarter surveys (Cottom & Curtis, 1956) at randomly selected survey points (see Chapter 2). Each quarter (as defined by the PCQ-method) was considered one sample. All individuals, irrespective of height, in the 2 and 3-year-old stands were considered part of the canopy layer. In stands 6 years and older, density estimates for *A. karroo* juveniles (<2m) were based on actual counts of individuals in a circle with a radius of 1m

around each sampling point. The relationship between the density of trees (in the canopy layer) and the age of a stand was calculated by correlating the mean of the four distances (within each quarter) at each sampling point, with the age of the stand. The reason for this is because the density at any given point can be expressed better in terms of the average of all four distances rather than by the individual distances within each quarter.

Mortality rates were calculated for 3-year intervals. Because no density figures were available for 12 and 15 years, the rates for these two intervals (9 to 12 and 12 - 15 years) were estimated by using the equation $d_x = \log_e[1/(1-q)]$, where d = mortality and q = mortality rate (based on the 5-year period from 9 to 14 years). The mortality rate (q_x) for a 3 year period was then calculated by using the following equation: $q_x = 1 - e^{-d \times 3/5}$ (Caughley, 1977). The same method was used to estimate the mortality rate for the 32 to 35 year interval (i.e. the last 3-year interval), but in this case it was based on the mortality rate for the 21-year period between 14 and 35 years. The mortality rates for the other 3-year intervals between 14 and 32 years were not calculated because they would be based on the same data and hence be the same than the 32 to 35-year interval. When calculating the cohort life table and survival rate of *A. karroo*, only the canopy layers were taken into account, because they represent even-aged cohorts. No discrete cohorts of *A. karroo* juveniles existed in the shrub layers. The 3-year-old stand was taken as the starting point, because the population has reached its maximum density there. Of the older unmined stands only the 35-year-old *Teclea gerrardii* stand was included in the calculations, because the absolute ages of the other stands are unknown.

The biomass of the *A. karroo* population was calculated from the density and the mean mass of individuals by using the equation: $bm = d \times \bar{m}$, where bm = biomass kg / hectare; d = density of *A. karroo* individuals per hectare and $\bar{m}$ = the mean mass (kg) of *A. karroo* individuals in a specific stand.

The percentage canopy cover was determined by measuring the length of gaps in the canopy along a transect line of known length. Percentage cover (c) for a given stand was calculated using the equation: $c = \frac{t - \sum g}{t} \times \frac{100}{1}$, where t = the total length of all the transects in a stand, and $\sum g$ = the sum of the gap lengths in the canopy. In the 2 and 3-year-old stands the length of gaps were measured directly with a measuring tape, but in the older stands the gaps were first projected to ground level before measuring. This was facilitated by using the "scope" described in Chapter 3.

Circular baskets with a diameter of 0.42m were constructed from wire and shade cloth to record flower-fall. Ten baskets were randomly placed at 1m above ground level in each stand. Baskets in all stands were emptied on the same day, usually at three-day intervals. In total seven collections were made. The baskets were first placed in the stands on 5 January 1994 and the last collection was completed on 27 January 1994. The collection period coincided with the height of the flowering season for *A. karroo*. Flower-fall /m² / day (ff) for each

collection point was calculated by using the equation: $ff = \frac{n/d}{r^2 \times \Pi}$, where n = number of flowers per a basket; d = number of days for which flowers were collected and r = radius of collection basket. Mean flower-fall (m² / day) for each stand per collection period and for the whole month was also calculated.

During June 1993, 25 soil samples were taken at random points along transects within each stand using a corer with a diameter of 7.3cm and a depth of 10cm. Between 12 and 16 randomly selected points were again sampled during June 1994, using a corer with a diameter of 10cm and a depth of 10cm. Each sample comprised two sub-samples taken within 1m from a selected transect point. The sub-samples were mixed and treated as one sample. The soil was sieved through a sieve with 2mm apertures and the *A. karroo* seeds (remaining behind) were counted. The density of seeds per square metre (d) for each sampling point was calculated using the equation: $d = \frac{n}{r^2 \times \Pi \times 2}$, where n = number of seeds per collection point and r = the radius of the corer (with the second survey the area of the corer was multiplied by two, to account for the fact

that two samples were taken at each collection point). The density of seeds for a whole stand was extrapolated from these results.

RESULTS

Density of trees in the canopy layer

In the canopy layer, the mean density of *A. karroo* reached a peak in the 3-year-old mined stand (20724 ± 2143), after which it declined quickly to a value of 737 ± 35 individuals per hectare in the 14-year-old stand (Table 6). There was not a significant difference in the density of the 14-year-old mined stand and that of the 35-year-old unmined stand ($t=0.0025$; $df=115$; $p<0.9976$), although the density of *A. karroo* (mean= 141 ± 11) was much lower in the 35-year-old stand than in the 14-year-old stand (mean= 737 ± 35). The densities of *A. karroo* in Venter's (1972) three back-dune communities were all considerably lower than those recorded for the mined stands. There was a significant negative correlation between stand age and density ($r=-0.88$; $n=87$; $p<0.0001$).

TABLE 6: Density of *Acacia karroo* trees in the canopy layer and density of juveniles in the shrub layer for mined and unmined stands, based on the PCQ surveys conducted from January 1993 to July 1994. Means are followed by the standard error of the mean ($\pm$ S.E.) and in brackets by the number of individuals sampled, and the coefficient of variation (%).

Stands	Density of trees in the Canopy layer (>2.0m)	Density of juveniles in the Shrub layer (<2.0m)
2 years old	3861 ± 176 (140; 54%)#	-
3 years old	20724 ± 2143 (28; 55%)#	-
6 years old	9031 ± 609 (108; 70%)	8754 ± 1043 (80; 107%)
9 years old	1997 ± 104 (128; 59%)	341 ± 93 (112; 290%)
14 years old	737 ± 35 (112; 50%)	5968 ± 1021 (96; 168%)
<i>Acacia</i> *	379	90
35 years old	141 ± 11 ; (40; 51%)	142 ± 19 (1; 82%)
<i>Celtis</i> *	61	13
<i>Mimusops</i> *	0	0

Although *A. karroo* has not yet reached a height above 2m in the 2 and 3-year-old stands, the populations in these two younger stands should be compared with the canopy layer of the older stands, as argued in Chapter 2.

* From Venter (1972)

Density of juveniles in the shrub layer

The mean density of *A. karroo* juveniles (<2.0m) in mined stands (Table 6), peaked in the 6-year-old stand, but did not follow an age-related trend as suggested by the low and non-significant correlation between age and density ($r=-0.043$; $n=72$; $p=0.72$). Juveniles occurred at low densities, or were absent in the 35-year-old stand and in Venter's (1972) three communities. The coefficient of variation for the mean was in most stands very high (>100%) and precluded statistical analysis.

Life table and survivorship

The cohort life table (Table 7) and survival curve (Figure 11) for *A. karroo* are based on the number of individuals in the canopy layer. Table 7 shows that the mortality rate (q_x) (calculated for 3-year intervals) is high in the mined stands (>0.45), and especially so in the 6 to 9-year interval (0.78). After 9 years only 9.6% of the initial cohort was still alive (l_x), with an estimate 2.9% still alive after 15 years. The estimated mortality rate of 0.2093 from 32 to 35 years (probably an over-estimate) is much lower than in the mined stands. After 35 years less than 1% of the initial cohort was still alive.

The survivorship curve for *A. karroo* is illustrated in Figure 11. The first data point ($\log_{10} 8\,960\,000$) is an estimate of the number of *A. karroo* seeds in the initial seed bank, based on the number of seeds present in the 14-year-old stand (see Table 11). The graph clearly shows a type III curve (Deevey, 1946; Krebs, 1985), indicating that mortality is initially very high but that some *A. karroo* individuals may survive for an extended period of time within the population.

TABLE 7: Cohort life table for *Acacia karroo* in mined and unmined stands on coastal dunes at Richards Bay.

Age x	Frequency f_x	Survival l_x	Mortality d_x	Mortality rate q_x	Survival rate p_x
3	20724	1.0000	0.5642	0.5642	0.4358
6	9031	0.4358	0.3394	0.7788	0.2212
9	1997	0.0964	0.0434	0.4502	0.5498
12	1099*	0.0530	0.0240*	0.4528	0.5472
14	737				
15	604*	0.0290*			
:	:	:			
32	178 [#]	0.0086 [#]	0.0018 [#]	0.2093 [#]	0.7907 [#]
35	141	0.0068 [#]			

* Based on mortality rate from 9 to 14 years.

[#] Based on mortality rate from 14 to 35 years.



FIGURE 11: Survivorship curve for *Acacia karroo* in rehabilitating stands at Richards Bay, showing a type III curve (see Deevey, 1947).

Biomass

Wet biomass (kg/ha) increased in the mined stands from a value of 7 204 kg/ha in the 2-year-old stand to a value of 197892 kg/ha in the 14-year-old stand (Table 8). In the mined stands there was a significant positive correlation between stand age and stand biomass ($r=0.95$; $n=5$; $p<0.0001$). A biomass of 366000 kg/ha was calculated for the *Acacia karroo* community surveyed by Venter (1972), which was considerably higher than that for the 14-year-old mined stand. The biomass for *A. karroo* in the 35-year-old unmined stand at Zulti North (162273) was, however, lower than those calculated for the 14-year-old mined stand or for Venter's (1972) *A. karroo* community.

Productivity rate

Productivity rates (based on the percentage annual change in wet biomass) were positive in the mined stands, but the rate slowed considerably as the regeneration age of stands increased (Table 8). The negative productivity rate between 14 and 35 years suggests that the population has become senescent.

Canopy cover and mean gap sizes

Percentage canopy cover increased from 59% in the 2-year-old stand to a peak value of 92.8% in the 6-year-old stand, and decreased thereafter to a value of 81% in the 14-year-old stand (Table 9). Variability (C.V.) of canopy cover in the 3, 6 and 9-year-old stands remained below 10%, but increased to 14% in the 14-year-old stand. Differences in the canopy cover of the different-aged stands were significant ($F=47.40$; $df=1,3$; $p<0.0001$), but Sheffe's test reveal that these differences were all between the 2-year-old stand and all the other stands (Sheffe's test: $F > 2.688$; $df=109$; $p<0.05$). No comparable values are available for unmined stands. Mean gap sizes decreased from 1.28m (C.V.=59%) in the 2-year-old stand to 0.46m (C.V.=95%) in the 6-year-old stand, and increased thereafter to a value of 0.95m in the 14-year-old stand (C.V. =72%) (Table 9). Analysis of variance showed that differences in gap sizes were significant ($F=20.00$; $df=1,3$; $p<0.0001$), but again these difference were primarily between the 2-year-old stand and all the other stands. There was, however, also a

significant difference in gap sizes between the 6-year-old and 14-year-old stand (Sheffe's test: $F > 2.688$; $df = 1,3$; $p < 0.05$).

TABLE 8: Calculated biomass and productivity rate of the *Acacia karroo* population for different-aged mined and unmined stands at Richards Bay. Biomass figures are based on the density of trees per hectare (Table 6) and mean mass values per tree (Table 5). Productivity rates (% change) are based on annual changes in biomass.

Stand age (years)	Calculated biomass kg /ha	Annual productivity rate (%)
2	7 204	
3	36 121	+401.4
6	94 287	+53.7
9	181 715	+30.9
14	197 892	+1.77
<i>Acacia</i> *	366 000	-
35	162 273	-0.86

* From Venter's (1972) *Acacia* community.

TABLE 9: Canopy cover and mean gap size for *Acacia karroo* individuals on rehabilitating mined stands. Means are followed by the standard error of the mean ($\pm$ S.E.) and in brackets by the sample size and the coefficient of variation (%).

Age of stand (years)	Canopy cover (%)	Mean Gap Sizes in Canopy (m)
2	59.2 $\pm$ 2.30 (116; 50%)	1.28 $\pm$ 0.072 (108; 59%)
3	84.1 $\pm$ 1.36 (28; 9%)	0.74 $\pm$ 0.020 (24; 13%)
6	92.8 $\pm$ 0.91 (96; 9%)	0.46 $\pm$ 0.046 (92; 95%)
9	89.5 $\pm$ 0.68 (112; 8%)	0.53 $\pm$ 0.023 (116; 47%)
14	81.2 $\pm$ 1.13 (108; 14%)	0.95 $\pm$ 0.066 (108; 72%)

Flower-fall

The results of the flower-fall during the height of the flowering season of 1994 for different-aged stands are summarised in Table 10. Variability in flower-fall was very high in the 6-year-old stand (CV=210.6%) since only a few trees produced flowers. In the 9 and 14-year-old stands the coefficients of variation were lower (65.7% and 59.0% respectively), suggesting that more trees produced flowers at much less variable rates. No flowering occurred in the immature 2 and 3-year-old stands and no comparable flower-fall figures are available for the unmined stands. There was a significant positive correlation between flower-fall and the age of a stand ($r=0.63$; $n=240$; $p<0.0001$).

TABLE 10: Mean number of *Acacia karroo* flowers collected in different-aged rehabilitating stands at Richards Bay, showing the increasing flower production with age. Means are followed by the standard error of the mean ($\pm$ S.E.) and in brackets by the sample size and coefficient of variation (C.V.%).

Age of Stand (years)	Mean number of flowers / m ² / day
2	0
3	0
6	6.11 $\pm$ 1.54 (70; 210.6%)
9	58.87 $\pm$ 4.63(70; 65.7%)
14	102.38 $\pm$ 7.23 (70; 59.0%)

The number of flowers produced per kilogram of biomass increased with age, suggesting that the *A. karroo* population allocates a higher percentage of resources towards flower production at a later stage of its life (Figure 12).

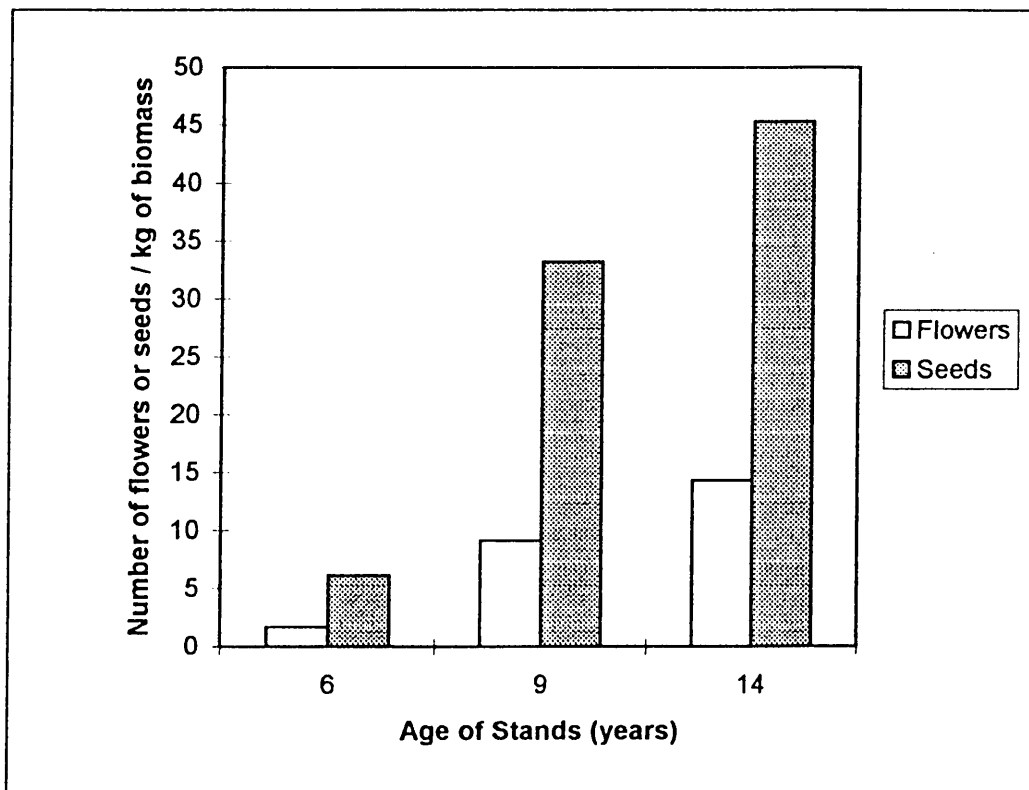


FIGURE 12: Mean number of *Acacia karroo* inflorescences and seeds produced per kilogram of biomass in different-aged mined stands at Richards Bay.

Figure 13 illustrates the temporal differences in flower-fall from 5 January to 27 January 1994. Flower-fall was initially high in the 9 and 14-year-old stands with a second smaller peak around 20 January. No linear temporal trend in flower-fall was observed in the 9-year-old stand ($r=0.08$; $n=80$; $p=0.4632$). A weak negative correlation between date sampled and flower-fall was recorded in the 14-year-old stand ($r= -0.32$; $n=80$; $p<0.0037$) suggesting that flower-fall declined somewhat towards the end of January. The graph confirms, however, that there was no clear linear relationship between date sampled and flower-fall as was to be expected from such a relatively short sampling period. A somewhat

stronger positive correlation between the date sampled and flower-fall was recorded in the 6-year-old stand ($r=0.38$; $n=80$; $p<0.0006$), suggesting that flower-fall increased towards the end of the sampling period.

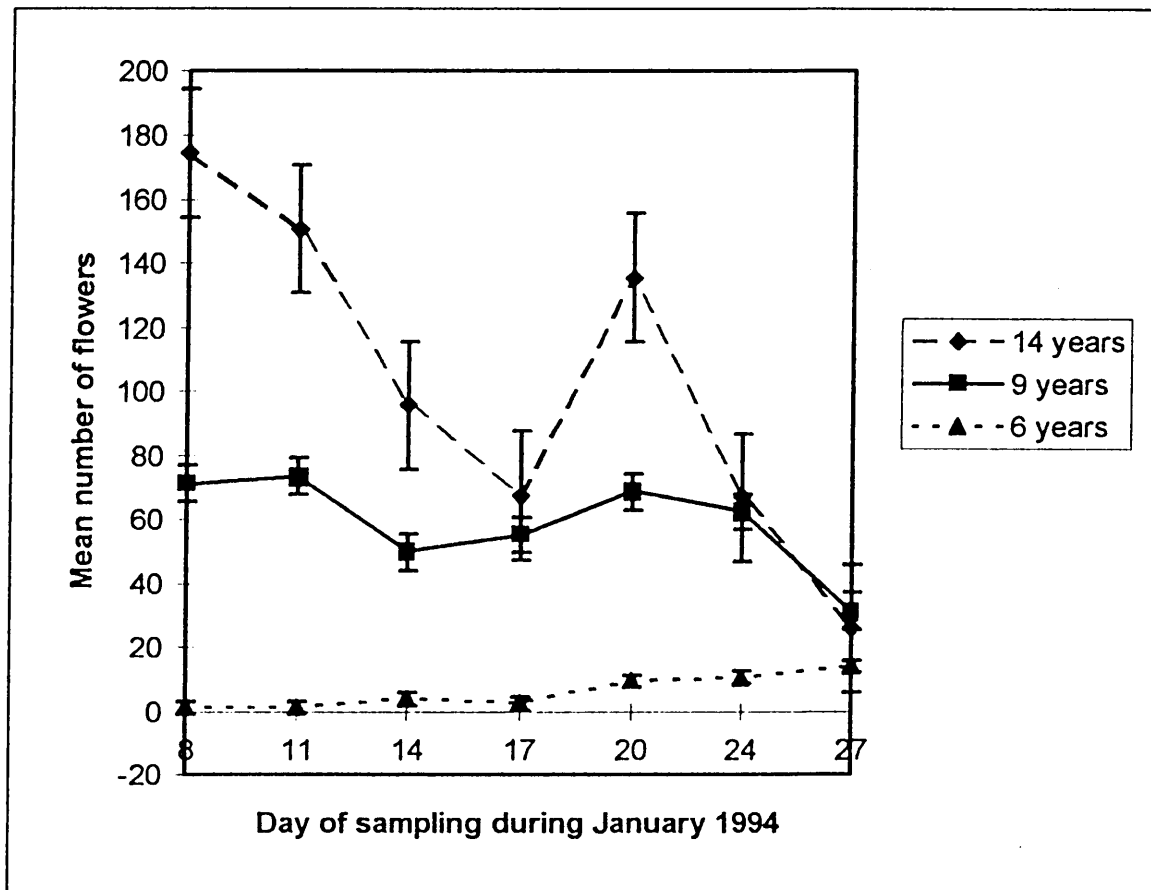


FIGURE 13: Temporal trends in the mean number of *Acacia karroo* flowers collected during January 1994 in different-aged mined stands at Richards Bay.

Seed bank

Due to the high variability in the results of the 1993 survey (Table 11), only the results for the 1994 survey were used in statistical analyses. However, the 1993 results showed the same increasing trend with stand age in the mean number of seeds / m^2 (although the means were much lower), than the 1994 survey. When the results for the two surveys of the 2/3-year-old stand are compared it also

becomes clear that during the 1993 sampling (when the youngest stand was 2 years old) a few *A. karroo* seeds still survived in the stand from those occurring in the initial topsoil or scattered over the dunes at the start of the rehabilitation programme (see Chapter 2 for details). However, only a year later (June 1994) no *A. karroo* seeds were found in the same stand. This could be due to germinated, seed predation or fungal attack.

There was a significant positive correlation between the number of seeds in the seed bank and stand age ($r=0.75$; $n=37$; $p<0.0001$) (1994 survey only), suggesting that the older stands produce more seeds than younger stands. The mean number of seeds produced per kilogram of biomass, increased with stand regeneration age (see above, Figure 12).

TABLE 11: The mean number of *Acacia karroo* seeds per m² in different-aged rehabilitating stands at Richards Bay, showing the increasing number of seeds collected in the older stands. The means are followed by the standard error of the mean ($\pm$ S.E.), and in brackets by the sample size and coefficient of variation (%).

Stand age (years)	June 1993	June 1994
2/3	4.8 $\pm$ 4.8 (25; 705%)	0 (n=16)
6/7	28.7 $\pm$ 28.7 (25; 708%)	57.8 $\pm$ 23.4 (11; 134%)
9/10	119.5 $\pm$ 30.7 (25; 182%)	603.2 $\pm$ 90.4 (15; 58%)
14/15	124.2 $\pm$ 24.8 (25; 141%)	896.2 $\pm$ 64.2 (11; 27%)

DISCUSSION

Moll (1992) and Mentis & Ellerly (1994) have shown that there are no significant differences between rehabilitating mined and unmined stands. According to Mentis & Ellerly (1994) the mined stands developed faster towards "mature" forest than the unmined areas recovering from other forms of disturbance. Comparing densities (and other attributes) between mined and unmined stands

may therefore be appropriate. Due to the possible differences in time to rehabilitate between mined and unmined stands, it would, however, not be possible to construct an accurate time scale for predicting future densities. Predictions of rehabilitation times are further complicated by the fact that except for the 35-year-old *Teclea gerrardii* stand, the absolute ages of the other unmined stands are not known (see Chapter 2) and the high density of *A. karroo* in the 3-year-old stand, is probably unusual due to an above-average rainfall during the year of rehabilitation or because of denser seeding during initial rehabilitation (see Chapter 5).

The density of *A. karroo* was lower in the older unmined stands than in the mined stands. For example, Venter (1972) reported a density of 379 trees per hectare in his *A. karroo* community, and in the unmined 35-year-old *Teclea gerrardii* stand the density of *A. karroo* trees was only 141 ± 11 trees per hectare. In Venter's *Celtis africana* stand the density of *A. karroo* was even lower (61 trees / ha) and in the most mature stand (Venter's *Mimusops* community) *A. karroo* was absent. These figures suggest that with increasing stand age *A. karroo* densities will continue to decrease in the canopy layer of the rehabilitating mined stands, but that it will remain an important species for at least 35 years. It will probably take 40-50 years (Moll, 1992; Barnes *et al.*, 1996) for the last individuals of the initial cohort to die out, and hence for the species to become rare or absent in the canopy layer of rehabilitating stands.

The density of juveniles in the mined stands showed no clear temporal trend. It is possible that the relative increase in density in the 14-year-old stand (in comparison with the 9-year-old stand) was only a temporary phenomenon, caused by an almost total defoliation of the canopy trees of the 14-year-old stand by *Sphingomorpha chlorea* caterpillars just prior to sampling. The defoliation (of the 14-year-old stand) caused a sudden increase in the amount of light reaching the forest floor and thereby probably caused better germination and survival of *A. karroo* seedlings. The relatively high density of small seedlings in the 14-year-

old stand is therefore probably no indication of better recruitment of *A. karroo* juveniles in older stands. The high coefficients of variation for the densities in the 9 and 14-year-old stands (290% and 168% respectively), illustrate the patchy distribution of *A. karroo* juveniles in the older mined stands.

Very low densities (or the absence) of *A. karroo* juveniles in the 35-year-old *Teclea gerrardii* stand at Zulti North, and in the communities surveyed by Venter (1972), further suggest that *A. karroo* recruitment is not very successful in "mature" stands. The low heights of juveniles and the increasing vertical spatial gap between juveniles and the canopy layer with age support this conclusion (see Chapter 3).

The results showed that the mortality rates (q_x) were high during the first 9 years (especially in the age interval between 6 and 9 years), but then started to gradually slow down. The survivorship curve (Figure 11) is therefore close to a type III curve (Krebs, 1985) which is typical of forest trees. Forest trees often have very high initial rates of seed mortality due to frugivory and granivory, then a period of almost constant mortality as self-thinning takes place, and finally an extended period of low mortality as the surviving trees occupy positions in the canopy (Barbour *et al.*, 1987). A type III curve (as has been recorded for *A. karroo* in the present study) is typical of populations where intraspecific competition initially plays an important role by causing density-dependent mortality.

Although the density of *A. karroo* in the mined stands has decreased considerably with stand age, this cannot be taken as a decrease in the dominance of the species, because the biomass of the population has steadily *increased* during rehabilitation of the mined stands. The slower increase in the productivity rate, as individuals grew older, is also typical of the maturation process within a population. Younger individuals allocate more resources towards growth (increase in biomass) than older individuals, who allocate more resources towards maintenance and/or reproduction (Barbour *et al.*, 1987). The slower

increase in the productivity rate of *A. karroo* is therefore not a sign that the species is losing its dominance, but only that (in the older stands) it is allocating more resources towards reproduction and maintenance. This conclusion is supported by the increasing flower and seed production per kilogram of biomass in older mined stands (Figure 11).

The decline in the canopy cover of the mined stands ≥ 6 years, suggests that the canopy layer reaches a maximum density at a relatively early stand age (6 years), after which it starts to gradually become thinner. Mean gap sizes decreased from two to six years, but there was a significant increase between the 6 and the 14-year-old stand. Variability in gap sizes during recruitment (first two years) was relatively high, when compared with the 3 to 9-year stands, but increased again as the canopy became less dense in the oldest stand (14 years). Due to the bigger and more variable gap sizes, an increasing amount of light could probably reach the forest floor in the older mined stands and this may stimulate the growth of subcanopy *A. karroo* seedlings and other broad-leaved species. This possible relationship between canopy cover and densities of *A. karroo* and broad-leaved species will be investigated in Chapters 5 and 6.

If it is accepted that flower-fall reflects flower production (which seems reasonable, since flower-fall was measured for a whole month and under various climatic conditions) then the older mined stands produced more flowers than the younger ones. The results suggested that not only the number of flowers produced per unit area increased in the older stands, but also the number of flowers produced per kilogram of biomass. From the productivity rates it became clear that *A. karroo* initially allocates most resources towards growth (biomass accumulation), but that productivity increased at a slower rate in older stands. The increase in flower production in these stands may therefore suggest that *A. karroo* trees allocate increasingly more resources towards reproduction as they grow older (as also suggested by the positive correlation between age and flower production). It also became clear that once the species started to produce flowers

at approximately six years, it gradually produced more and more flowers throughout its lifetime.

The number of seeds in the seed bank showed the same increasing trend with stand age. This suggests that flower production and the number of seeds in the seed bank are related. The results for the 2 to 3-year-old stand are of special interest. At this young stage the shrubs in the stand had not yet started to produce flowers or seeds. The very low density of seeds after two years and the lack of any seeds, when sampled again a year later, suggest that very few *A. karroo* seeds probably survive more than two to three years in the seed bank. Most seeds collected in the older stands were fresh (undamaged and sometimes still in their pods) and were probably produced in the previous season. Only a few older seeds were found in the samples and they were usually badly damaged by fungi. Granivory by small mammals and birds may also contribute to the quick loss of seeds in the seed bank.

The lower number of seeds collected during the 1993 season, in comparison with the 1994 season, was probably because of the drought in that year. *A. karroo* is an opportunistic species that can immediately utilise resources available to it (Barnes *et al.*, 1996). This also implies that the species will immediately respond to unfavourable conditions by producing less flowers and seeds during a drought. However, during the 1994 season both flower and seed production suggest that the *A. karroo* population is not showing any signs of senescence in terms of reproductive productivity. The possibility that this may, however, be the population's "last gasp" before becoming senescent cannot be ruled out.

Following MacArthur & Wilson's (1967) r and K classification system, *A. karroo* cannot be classified with any certainty. It has a high growth rate, but almost disappeared from the subcanopy strata of mined stands within nine years, suggesting that it may be an r-selected species. However, in the canopy layer the species did survive for an extended period, suggesting the contrary classification

as a more K-selected species. The species' high growth rate, but inability to survive in resource-stressed environments (e.g. shade), makes it, however, more appropriate to classify *A. karroo* as a C-selected species (competitive life history) according to Grime's (1977) threefold classification system. In terms of succession theory, *A. karroo* may then be seen as a secondary species. However, the species probably fits the definition of Hubbell & Foster (1986) for a late secondary forest species best, in that it is shade-intolerant, with a fast growth rate like pioneers, but differing from pioneers in that it grows much larger in stature.

CHAPTER 5

RELATIONSHIP BETWEEN MORPHOMETRIC AND POPULATION VARIABLES OF *ACACIA KARROO* AND SOME ENVIRONMENTAL VARIABLES

INTRODUCTION

During the maturation of a stand, increases in the morphological dimensions of individuals (such as height, basal area and crown size) are usually (but not always) correlated with each other (Barbour *et al.*, 1987). The way in which these morphometric variables increase, relative to each other, may reveal survival strategies of the species (Waller, 1986). For example, in the case of heliophytes, individuals may prevent being shaded by others by growing as fast and as high as possible. This may result in high trees with relatively thin trunks. On the other hand an individual may try to expand its crowns maximally in a horizontal direction and thereby prevent smaller individuals to fill gaps in the canopy. These relative increases in the morphological dimensions of individuals are therefore important when considering the life-history of a species (Hutchings, 1987).

Three different models have been proposed to explain the relationship between the heights and diameter of trees. These are the elastic similarity, geometric similarity and constant stress models (O'Brien *et al.*, 1995). Of these the constant stress model is probably the most generally applicable model, assuming that the local environment is sufficiently windy (O'Brien *et al.*, 1995).

With even-aged monocultures (natural or commercial), the density of a population can often be explained by relating density to biomass. Yoda *et al.* (1963) proposed the self-thinning rule to explain this relationship whereby density decreases as sizes (mass) of individuals increase. When mortality in a population is primarily due to such a process of self-thinning, lower densities cannot be interpreted as a decline in the dominance of the species, because the

biomass of the species may actually have increased in spite of lower numbers. The relationship between the biomass and density of *A. karroo* should therefore be assessed when considering the species' present and possible future dominance on mined coastal dunes.

Cluster analysis will be used to classify transects and identify possible differences in the *A. karroo* population within and between stands (Van Tongeren, 1987). For these purposes the density, height and basal area of *A. karroo* will be used to compare transects with each other. Because *A. karroo* dominates the canopy layer of all mined stands, such a classification may reveal important temporal trends within the population.

Climatic variables may have a pronounced influence on plant populations (Barbour *et al.*, 1987). In the subtropical climate of the study area, rainfall is probably an important climatic variable that may explain growth patterns of individuals and the resulting density of tree populations. During the rehabilitation process, the rainfall received in the first year of rehabilitation may have an important influence on the success of seed germination and the survival of seedlings. With more established forest stands, droughts may have a less severe influence on individuals due to the shading effect of the canopy, more protection from desiccation by winds, the better water holding capacity of mature soils (see Chapter 6) and the more extensive root systems of larger individuals. Due to the limitations of the present study (see Materials and Methods below) the influence of rainfall on rehabilitating stands will be investigated in general terms only.

Some of the variation in population attributes within the *A. karroo* population may be explained by differences in the physical environment. On coastal dunes the aspect of the dune or the position on the dune (e.g. dune valley, sideslope or ridge), steepness of the dune slope and the distance from the individual to the sea, are important factors that may effect a plant's growth (Venter, 1972; Tinley, 1985; Hesp, 1991). These factors may influence the extent of exposure to salt spray, the availability of nutrients and water, and the stability of the substrate. For example, in contrast with individuals located in the dune

valleys, individuals growing on the steep upper sea-facing slope of a dune may be more exposed to salt spray, have less water and nutrients available to them, and the slipping sands on the steep slope may make for a less stable substrate (Tinley, 1985; Hesp, 1991). However, Venter (1972) showed that the effect of salt spray on vegetation quickly diminishes as the distance from the sea increases. He also illustrated that the vegetation in the dune valley (behind the first dune) is to a large extent shaded from salt spray, while trees on the higher slopes (e.g. at the top of the second dune) are more exposed. The effects of salt spray at the top of the second dune are relatively small ($< 1\text{mg salt}/100\text{cm}^2/\text{day}$) in comparison with the high salt spray received by the fore dune ($\pm 3\text{mg salt}/100\text{cm}^2/\text{day}$), but should not be ruled out as a factor influencing the vegetation in the area (Venter, 1972).

MATERIALS AND METHODS

The vegetation was surveyed by using the Point-Centre Quarter method on randomly selected transects and transect points, as described in Chapters 2, 3 and 4. The ratio between height and stem diameter was determined by correlating the $\log_e$ height (in metres) to the $\log_e$ stem diameter (in millimetres) of all trees in the 6 to 14-year-old stands (O'Brien *et al.*, 1995). The 2 and 3-year-old stands were not included in the calculation because the models proposed (for explaining the ratio between height and DBH) are only appropriate for closed-canopy forests (O'Brien *et al.* 1995). In the case of multi-stemmed trees, the DBH of all live stems was correlated with the height of the tree.

As explained in Chapter 2, all transects sampled in the present study started in the dune valley (between the first and second dune) and ran perpendicularly to the coastline towards the top of the second dune. Three different dune aspects can therefore be distinguished within the sampling areas; they are: the dune valley between the first and second dune, the sea-facing slope of the second dune, and the dune ridge of the second dune.

An increasing distance from the starting point of a transect coincided with a higher position on the dune slope, while a smaller distance would coincide with

localities in the dune valley, or on the lower slope of a dune. The distance from the starting point of a transect (that is the locality on the dune) may be important in terms of the availability of water and nutrients and the effects of salt spray. Distances from the starting point of a transect to each sampling point were measured with a measuring tape when transects were laid out.

Dune slopes were measured at every sampling point by using the PM-5/1520 Suunto height metre. At each sampling point the slope was measured for a 10m length along the transect line, with the sampling point in the middle. A generalised dune profile was constructed by averaging the degrees of the slopes for all transects within a stand. In the dune profiles, absolute heights are not illustrated, but the differences between heights. This has the advantage that it maximally displays differences in heights, while true heights (when represented on such a small scale) may have masked many of the smaller differences in heights. However, in the profile diagrams distances and slopes of dunes are true and represented on a scale of approximately 1 : 1000 (i.e. 10mm equals 10m). Densities were always represented on a scale from 1 to 6, and the differences in heights on a scale from 1 to 10. The actual scales depended on the range of densities or heights within a specific stand. Densities and differences in heights are therefore not comparable between stands.

Cluster analysis (average method) was used to classify transects according to the density, height and basal area of *A. karroo* individuals in the canopy layer. For this analysis transect lines were subdivided into equal halves (a = lower half; b = higher up the dune) and treated as separate transects. The transects in the 6-year-old stand were, however, not subdivided, because of their relatively short length and the fact that they ended well below the dune ridge.

Rainfall in the study area has been measured since 1976 by P C Camp (Chief ecologist, RBM) at the Ecology Centre, located within the study area. The possible effect of rainfall on the *A. karroo* population will be considered in general terms by investigating the amount of rainfall received by each stand in its

first year of rehabilitation, how this amount differed from the long term mean, and the mean annual rainfall received by each stand since rehabilitation.

RESULTS

Relationship between morphometric variables

There were significant and positive correlations between the heights and the $\log_e$ of basal areas ($r=0.87$; $n=439$; $p<0.0001$), and between heights and the $\log_e$ of crown areas ($r=0.78$; $n=384$; $p<0.0001$). The $\log_e$ of basal areas also significantly correlated with the $\log_e$ of crown areas ($r=0.93$; $n=359$; $p<0.0001$). These relationships (on a non-log scale) are illustrated in Figure 14.

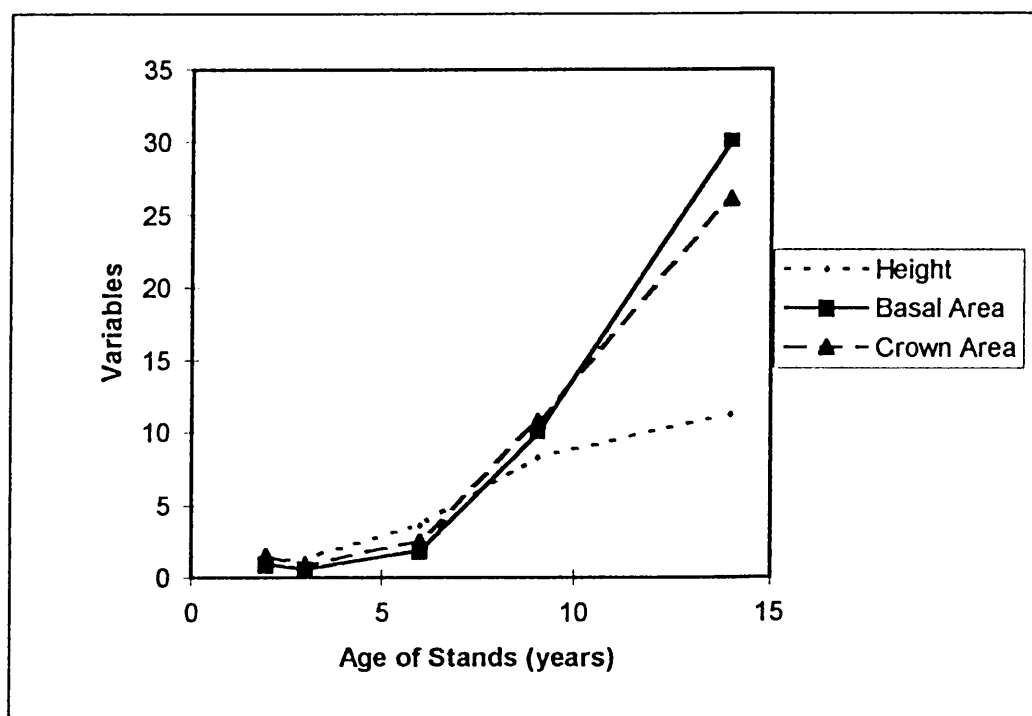


FIGURE 14 Relationship between morphometric variables and age of *Acacia karroo*.

The ratio of height to diameter ($\log_e$ scale) for trees can be explained by the elastic similarity, constant stress or geometric similarity theories (O'Brien *et al.* 1995). The ratio (slope) of 0.659 ($r^2=0.80$; $n=557$; $p<0.0001$) calculated for *A. karroo* in the 6 to 14-year-old stands (Figure 15) is similar to the ratio of 0.67 predicted by the elastic similarity model (O'Brien *et al.*, 1995).

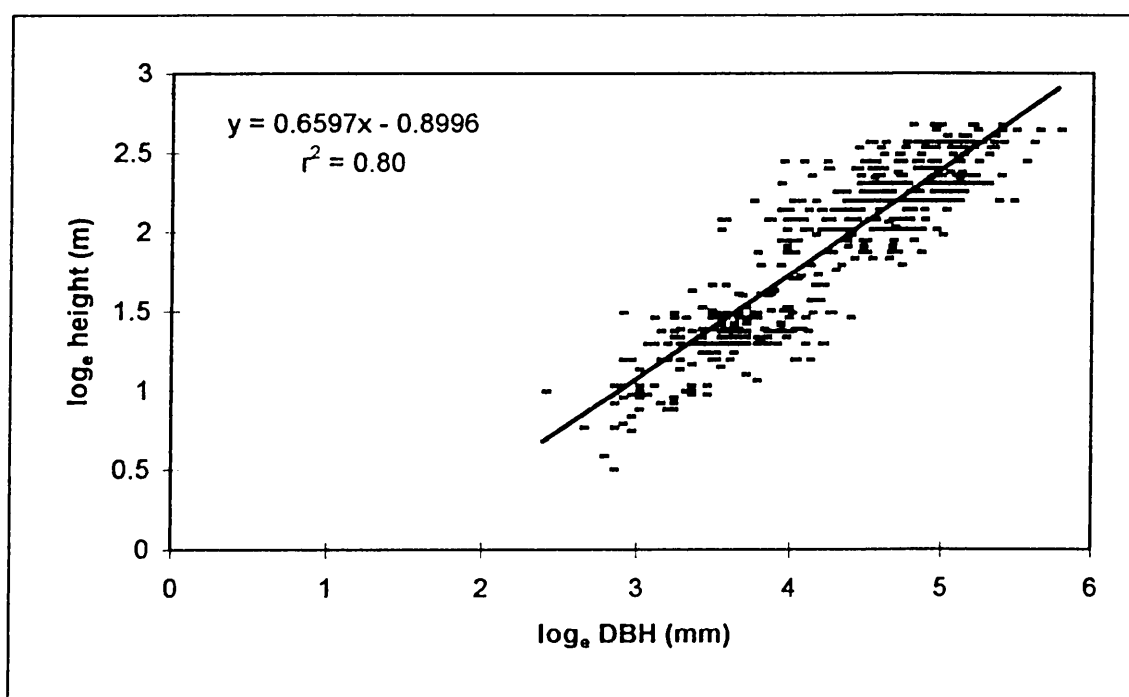


FIGURE 15: Regression of $\log_e$ height (m) on $\log_e$ DBH (mm) of *Acacia karroo* in 6 to 35-year-old mined and unmined stands at Richards Bay.

Self-thinning

Figure 16 illustrates the relationship between the $\log_e$ density and $\log_e$ biomass of *A. karroo* for the four mined stands and the *A. karroo* community described by Venter (1972). The regression line had a similar slope (-0.5122) to the $-\frac{1}{2}$ suggested by the self-thinning rule, and density explained 92% of the variance for biomass. The density (in the canopy layer) correlated negatively with size variables such as height ($r = -0.78$; $n=348$; $p<0.0001$) and basal area ($r = -0.67$; $n=314$; $p<0.0001$), but not significantly with crown area ($r = -0.11$; $n=259$; $p<0.073$).

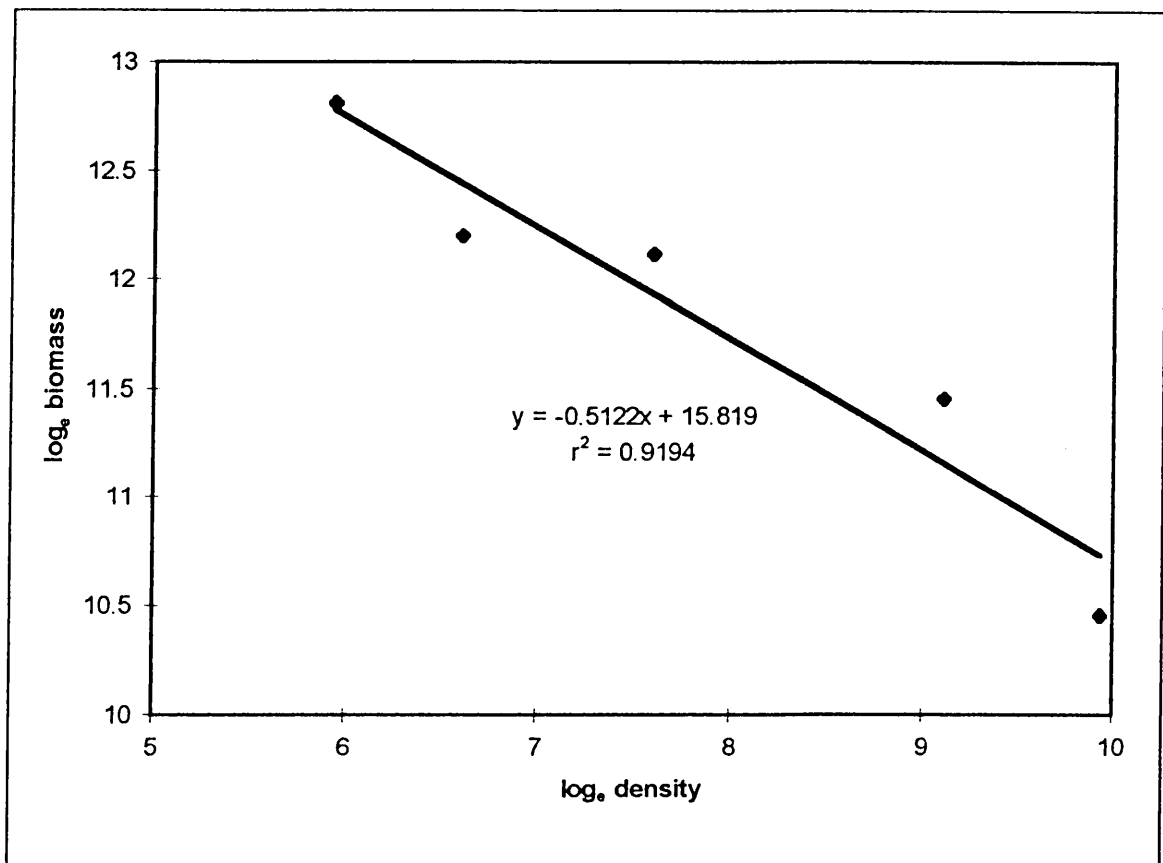


FIGURE 16: Regression line calculated for $\log_{10}$ density and $\log_{10}$ biomass of *Acacia karroo*. Four mined (3, 6, 9 and 14 year) stands and the *Acacia karroo* community of Venter (1972) were included in the calculations.

Classification of transects

Cluster analysis (average method) based on density, height and basal area of trees in the canopy layer are illustrated in the dendrogram of Figure 17. Above the 0.595 distance (in Figure 17) five clusters can be identified. With a few exceptions these clusters largely coincide with the different-aged stands. One of the clusters (middle of the graph) comprised only one transect (2a in the 14-year-old stand), while two 14-year-old transects (1a and 1b) were included in the 9-year-old cluster (left side of the diagram).

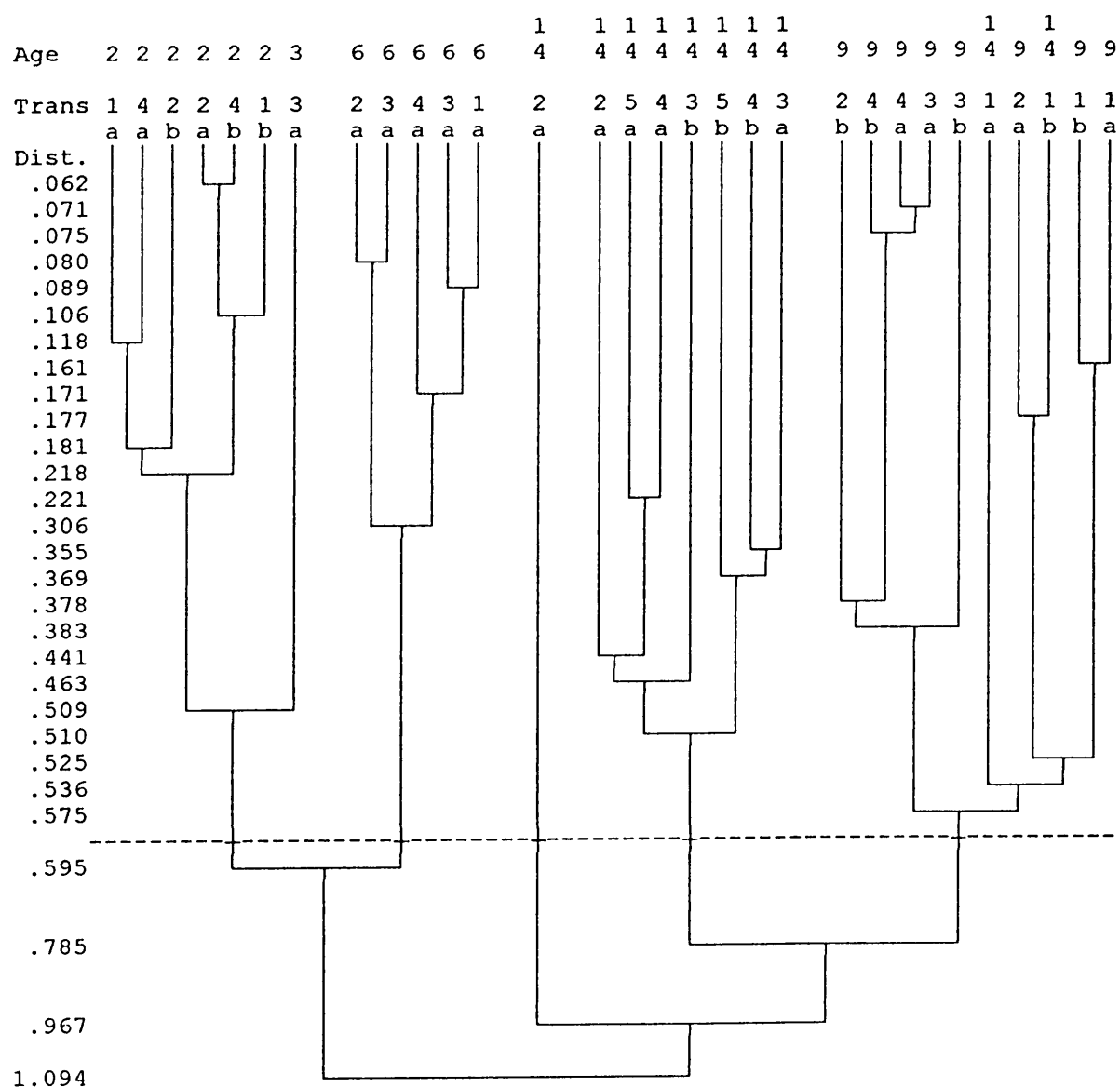


FIGURE 17: Dendrogram of cluster analysis (average method) for different-aged transects, based on density, height and basal area of *Acacia karroo* in the canopy layer.

The 3-year-old transect (3a) was categorised with the 2-year-old cluster, but is connected at a much further distance (0.509), indicating that it could also be seen as a separate cluster. Figure 17 also shows that the younger transects (2 to 6 years, left side) were grouped closer together, while the older transects (9 and 14 years) formed part of more loosely grouped clusters.

Influence of rainfall on the population

To assess the possible influence of rainfall on stand-specific densities the amount of rain that fell during the year that rehabilitation commenced, the percentage difference with the long term mean, and the mean annual rainfall experienced by a specific stand, are presented in Table 12. From these figures it follows that the 3-year-old stand received 2025mm (28.3% above the long term mean of 1578mm) during its first year of rehabilitation, while the 2, 6 and 9-year-old stands received about 15% less rain than the long term mean. The 14-year-old stand, on the other hand received 1881mm (19.2% above the long term mean) during its first year of rehabilitation. The two youngest stands (2 and 3-year-old) received a below average annual rainfall since rehabilitation commenced, while the three oldest stands were only slightly higher than the long term mean of 1578mm.

TABLE 12: The amount of rainfall recorded at the RBM's Ecology Centre during the first year of each stand's rehabilitation, the percentage difference with the long term mean and the mean annual rainfall over the whole period of regeneration for a specific stand.

Stand Age (years)	Year when rehabilitation commenced	Total amount of rain in first year of rehabilitation (mm)	Percentage difference from long term mean (1578mm)	Mean±S.E. annual rainfall over period of regeneration (n = years)
2	1990	1349	-14.5%	1211±288 (2)
3	1989	2025	+28.3%	1414±288 (3)
6	1986	1327	-15.9%	1654±241 (6)
9	1983	1343	-14.9%	1677±208 (9)
14	1978	1881	+19.2%	1612±131 (14)

Effects of aspect and dune slope on morphometric and population variables

The dune profiles in Figure 18 illustrate the relationship between dune aspect, the density and heights of *A. karroo*. In the diagrams dune profiles are represented on a comparable scale (1 : 1000 cm) for all the stands, but heights and densities are not comparable between stands (see Materials and Methods). Starting points of transects are located at the bottom of the dunes on the left side of the graph (seaward side), with transects running directly inland to the top of the dune ridge. The profile diagrams show that the steeper dune slopes were usually in the middle ranges along transects, with more level slopes in the dune valleys and on the ridges.

In the 2, 9 and 14-year-old stands, distance from the bottom of the dune significantly correlated (negatively) with the heights of *A. karroo* in the canopy layers ($r = -0.315$; $n=126$; $p<0.0003$; $r = -0.314$; $n=128$; $p<0.0003$; and $r = -0.672$; $n=112$; $p<0.0001$ respectively). These negative correlations indicated that trees tended to be higher, closer to the start of transects and therefore lower down the dune slopes (see Figure 18). In the 6-year-old stand there was no significant correlation between the height of trees and the distance from the bottom of the dune. There were also no significant correlations (in all the stands) between the distance from the starting point of a transect and flower-fall, or between distance and seed density in the seed bank.

Steepness of the dune slopes correlated negatively with the size of gaps in the canopy ($r = -0.22$; 79; $p<0.0417$) and positively with the density ($r=0.31$; 72; $p<0.0071$) and height ($r=0.61$; 29; $p<0.0004$) of *juveniles* in the shrub layer. These correlations (although weak) indicate that canopy gaps tended to be smaller on the steeper slopes, while juveniles were denser and higher on steeper dune slopes. No other physical variable correlated significantly ($p<0.05$) with any morphometric or population variable in the mined stands.

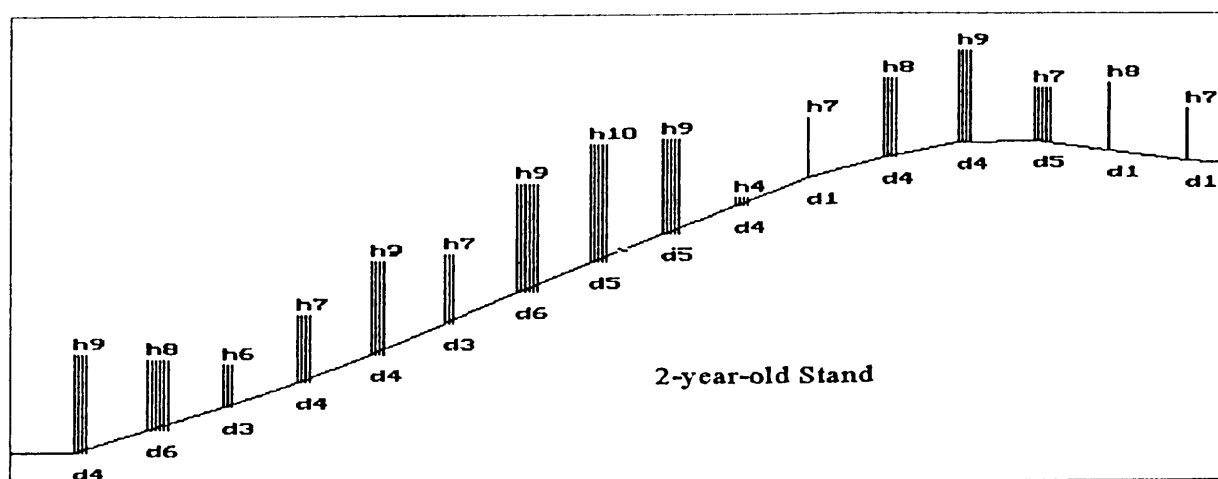
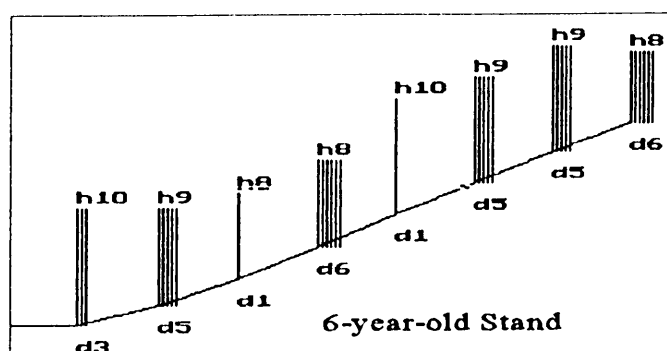
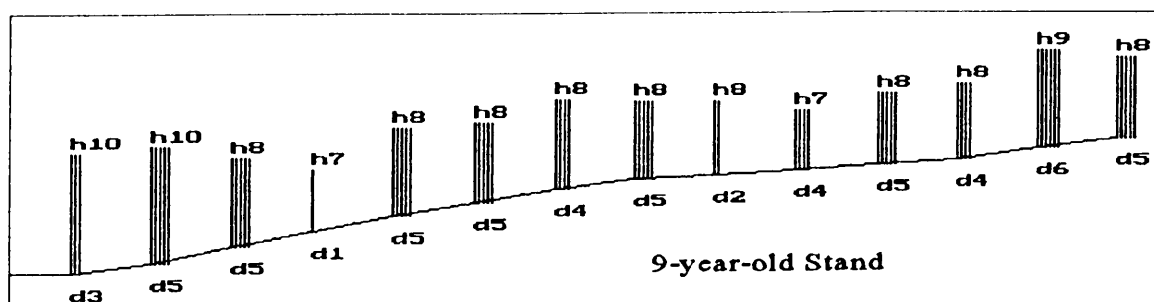
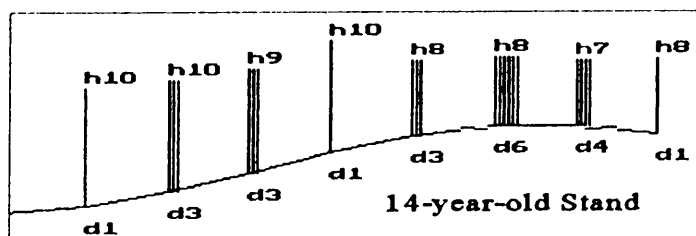


FIGURE 18: Generalised dune profiles of mined stands at Richards Bay, showing relative densities (d1-d6) and heights (h1-h10) of *Acacia karroo*. Transects run from left to right and from the bottom to the top of the dunes.

DISCUSSION

The positive correlations between height, basal area and crown area of *A. karroo* suggest that the various size dimensions of individuals increased in tandem. An increase in all dimensions may be an important strategy of *A. karroo* in the dense cohorts of even-aged stands, where intraspecific competition may be severe, especially for sunlight (Condit *et al.*, 1994). The highest individuals with the largest crowns therefore have the biggest chance to avoid shading by others and thereby may have a better chance of survival. The simultaneous increase in the basal area of individuals may be necessary to support the increasing size and weight of individuals. The 0.65 ratio between height and diameter of *A. karroo* suggests that the species needs to allocate sufficient resources towards support structures (thickness of stems), which would limit its vertical growth (O'Brien *et al.*, 1995). This is probably important on coastal dunes with an almost constant wind which often reaches high speeds. The initial high growth rate and the consistent increases in size throughout the lifetime of *A. karroo* fit the definition for a late secondary forest species (Hubbell & Foster, 1986). It should therefore not be seen as a pioneer species.

In a crowded population, intraspecific competition causes the density of a population to decrease with the increasing size of individuals (Barbour *et al.*, 1987). This relationship between size (e.g. biomass) and density is described by the self-thinning rule proposed by Yoda *et al.* (1963). The rule states that above a certain density, crowding will determine the mortality rate of the population to such an extent that there will be a linear relationship (with a slope of -0.5) between the $\log_e$ of the density and the $\log_e$ of the size (e.g. biomass) (Watkinson, 1986). Originally Yoda *et al.* (1963) used the equation $w = KD^{-3/2}$ to describe the self-thinning rule (where w = mean weight of individuals, K = constant, and D = density). In the present study, the derived equation $B = CN^{-1/2}$ of Barbour *et al.* (1987) was used: where B = $\log_e$ biomass per unit area, C = constant, N = $\log_e$ number of survivors per unit area, and $-1/2$ describe the slope of the line.

The results of the present study suggest that the decrease in the density of the *A. karroo* population in the mined stands can be explained entirely by the self-thinning rule and that the decrease in density is therefore not an indication of any decrease in the dominance of the species. In the foreseeable future self-thinning is probably going to continue to play an important role in the mined stands, as is suggested by the fact that the 14-year-old stand has only reached a density of 737 trees per hectare while self-thinning was still evident in Venter's (1972) *A. karroo* stand with a density as low as 379 trees per hectare. It was only in the youngest (2-year stand) and oldest unmined (35 years) stands where self-thinning did not play any significant role within the *A. karroo* population.

Cluster analysis showed that transects within the same stand were similar to each other in terms of density, height and basal area of the trees in the canopy layer. The only real exceptions were transects 1a and 1b in the 14-year-old stand which were classified with the 9-year-old transects. This may be explained by these two transects being located on the border between the 9 and 14-year-old stands. The results suggest that the individuals within same-age stands were similar, if compared with stands of different ages. Age of a stand was therefore an important determining factor in the development of *A. karroo* populations in the mined stands.

The potential influence of rainfall on rehabilitating stands is illustrated by the very dense population of *A. karroo* shrubs on the 3-year-old stand, with individuals having fewer stems and smaller basal and crown areas than those in the younger 2-year-old stand. These differences between the 2 and 3-year-old stands could, however, be explained, if the 3-year-old stand had from the beginning a denser population of seedlings than the 2-year-old stand. This could have resulted from better germination and survival of seedlings due to an above average rainfall in the year of rehabilitation. Since the 2-year-old stand received a below average rainfall during its first year (-14.5%) while the 3-year-old stand received 28.3% more than the long term mean, annual differences in rainfall seem plausible as a possible explanation for these differences between the

populations. Rainfall may thus be an important confounding effect when investigating different-aged populations, but the effects of differential rainfall would probably become less important with increasing age, self-thinning and below and above average rainfall years occurring during the history of a stand.

Tinley (1985) showed that the height of forest vegetation on coastal dunes may vary considerably depending on the dune aspect and distance from the sea. Trees on dune ridges are more exposed to salt pruning and may have less nutrients available to them (Van den Merwe & McLachlan, 1991; Hesp, 1991) resulting in smaller individuals than those in the more protected and nutrient-rich dune valleys. The present study showed that in the older stands, *A. karroo* individuals were smaller on the dune ridges than in the valleys, with the effect most pronounced in the oldest 14-year-old stand. This is probably due to the leaching of nutrients and organic matter.

Steepness of the dune slope did not have an important effect on the *A. karroo* population. The results were, however, unexpected in the sense that one would have thought that the steeper dune slopes would have a more unstable substrate, which would have a negative impact on most vegetation. However, the correlations (although mostly weak) showed a favourable relationship between steeper dune slopes and population variables such as gap sizes, heights and density of *A. karroo*. The negative correlation between gap size and steepness of the dune slope (with smaller gaps occurring on the steeper slopes) shows that steeper slopes did not have any negative effect on the canopy layer. In the shrub layer *A. karroo* juveniles were also higher and denser on the steeper slopes. The influence of dune slope on *A. karroo* may, however, be indirect. The less stable substrate on steeper slopes may impact negatively on the establishment of broad-leaved species and herbs and may thereby allow *A. karroo* seedlings to establish in these more open places.

CHAPTER 6

ATTRIBUTES OF THE WOODY PLANT COMMUNITY

INTRODUCTION

During succession (or vegetational development) community attributes such as species composition, relative density of species and other community attributes change (Odum, 1969). Woody plants comprise an important component of forested sand dunes in the Richards Bay area and the development taking place within the woody community can therefore reflect on the success of rehabilitation (see Chapter 1).

MATERIALS AND METHODS

For the purposes of this study broad-leaved woody species were defined as all non-*Acacia karroo* and non-herbaceous species, which according to Palgrave (1983), Moll (1981) and Pooley (1993) may potentially reach a height of at least 2m, without the support of another individual or structure. Species such as *Rhus nebulosa* and *Rhoicissus digitata*, that often are scramblers (Venter, 1972) were included in the survey because they may in some cases have the growth habit of a small shrub or tree higher than 2m.

The PCQ-method (Cottam & Curtis, 1956) was used on randomly selected transects and sampling points as described in detail in Chapter 2. In the 2 and 3-year-old mined stands, broad-leaved species and *A. karroo* were surveyed together, because of the low density of broad-leaved species. In the older mined and unmined stands broad-leaved species were surveyed separately from the *A. karroo* population. In the 6, 9 and 14-year-old mined stands no distinction was made during the survey between the shrub (<2m) and canopy layers (≥2m) in the broad-leaved community, due to the fact that very few individuals were above 2m. During the analysis the broad-leaved vegetation was, however, divided into a shrub and canopy layer on the basis of individuals' height. In the 35-year-old

unmined stand at Zulti North the shrub and canopy layers were surveyed separately. The distance to the nearest individual within each quarter (as defined by the PCQ-method), the height, and the species were recorded.

Species richness was taken as the number of species occurring in a stand and species diversity was calculated using the Shannon-Wiener Index (H') as $H' = -\sum (p_i) (\ln p_i)$, where p_i = the proportion of all individuals in the sample that belong to species i , and $\ln p_i$ the natural log of these proportions. Similarities in species composition between the different-aged mined stands and the 35-year-old unmined stand at Zulti North, were calculated using the Bray-Curtis similarity coefficient (Bray & Curtis, 1957), also called Steinhaus' Similarity Coefficient (Legendre & Legendre, 1983). The index was calculated as $s = 2w/(a+b)$, where s is the similarity coefficient, w is the sum of the minimum densities of species occurring in the stands compared, and a and b are the total densities of the relevant species in each stand respectively.

Soil samples were collected at 11 to 16 randomly selected sampling sites along existing line transects (see Chapter 4) placed on the second dune slopes of the 2, 6, 9 and 14 year old stands. A circular corer with a 10cm diameter and a 10cm height was used to collect the samples and two samples were taken at each sampling point. These two samples were mixed and treated as a single sample. All samples were taken on the same day between 8:00 and 13:00. Half of the samples were collected between 8:00 and 10:30 and the remainder between 10:30 and 13:00. The first session of sampling started in the oldest (14-year-old) stand and ended in the youngest (2 year old) stand. Sampling for the rest of the morning took place in a reverse order (starting with the youngest stand). The time of sampling for each sample was recorded and the samples were stored in plastic bags at 4°C until analyzed for the following characteristics: percentage organic debris (>2mm) primarily consisting of dead litter that accumulated on top of the ground, percentage organic matter content (<2mm) representing the organic material (humus) in the soil which is an indication of the productivity and fertility of the soil (Scott *et al.*, 1993), percentage soil water and pH of the soil.

The procedures and sequence as suggested by Moore & Chapman (1986) were followed to analyze the soil samples. These can be summarized as follows: the whole sample was weighed (total wet mass = twm). A sieve with 2mm apertures was used to sieve each sample. Pieces of stems, roots, leaves and other bigger pieces of organic debris were thus sieved out and weighed separately (wet mass of debris = wmd). Due to the large quantities of organic debris, the debris was not dried. The percentage organic debris (od), larger than 2mm, was calculated by using the following equation: $\%od = \frac{wmd}{twm} \times \frac{100}{1}$.

The soil sample was then thoroughly mixed and through continual subdivision, two representative sub-samples were taken from the mixture. The first sub-sample was mixed with distilled water in 1:2 ratio of soil to water (volume : volume) and after 2 hours the pH was recorded with a pH meter. The second sub-sample was weighed (wet mass of sub-sample = wm) and dried in a ventilated oven at 105°C and weighed again (dry mass of sub-sample = dm). Percentage Water Content ($\%wc$) was calculated by using the following equation: $\%wc = \frac{wm - dm}{wm} \times \frac{100}{1}$.

The dry sample was then burned in an oven at 450°C for 2 hours. After cooling the sample was weighed again (burned mass = bm). The percentage organic matter content of the soil ($\%mc$) was calculated by using $\%mc = \frac{dm - bm}{dm} \times \frac{100}{1}$.

RESULTS

Heights of broad-leaved species in the shrub and canopy layers

The mean heights of broad-leaved species in the shrub (<2m) and the canopy layers (≥2m) are given in Table 13 and Table 14 respectively. The data for the *Apodytes dimidiata* stand are not given because the stand probably represents a different successional pathway than the other stands (Lubke *et al.*, 1992b).

TABLE 13: Mean heights of woody broad-leaved species in the shrub layer of the different-aged rehabilitating stands at Ric Bay. Means are followed by the standard error of the mean and in brackets by the number of individuals recorded in the survey.

Species	Mean heights of broad-leaved species in different-aged stands (m)				
	2 years	6 years	9 years	14 years	35 years
1. <i>Dodonaea angustifolia</i>	0.18± 0.03 (4)	1.21± 0.16 (11)	0	0	0
2. <i>Brachylaena discolor</i>	0.30± 0 (1)	0.87± 0.09 (35)	0.68± 0.07 (44)	1.09± 0.08 (34)	0
3. <i>Rhus nebulosa</i>	0.45± 0 (1)	0.30± 0 (1)	0.47± 0.08 (15)	0.65± 0.08 (18)	0
4. <i>Canthium inerme</i> *	0	0.38± 0.11 (8)	0.95± 0.21 (4)	1.17± 0.15 (10)	1.70± 0 (1)
5. <i>Scutia myrtina</i>	0	0.40± 0.05 (4)	0.83± 0.12 (13)	0.82± 0.17 (7)	1.14± 0.09 (5)
6. <i>Kraussia floribunda</i>	0	0	0.66± 0.11 (8)	0.97± 0.03 (2)	1.70± 0 (1)
7. <i>Tricalysia sonderiana</i>	0	0	0.93± 0.17 (10)	1.05± 0 (1)	0.60± 0 (1)
8. <i>Eugenia capensis</i>	0	0	0.35± 0.10 (2)	0.40± 0 (1)	0
9. <i>Apodytes dimidiata</i> *	0.49± 0.13 (5)	1.19± 0.20 (6)	0	0.40± 0 (1)	0
10. <i>Mimusops caffra</i> *	0	0.15± 0 (1)	0.40± 0 (1)	0	0
11. <i>Rhoicissus digitata</i>	0	0.40± 0.20 (2)	0.35± 0.08 (5)	0	0
12. <i>Draceana hookeriana</i>	0	0.70± 0 (1)	0	0.59± 0.10 (5)	0.55± 0.11 (11)
13. <i>Allophylus natalensis</i> *	0	1.50± 0 (1)	0.55± 0.10 (5)	0.57± 0 (1)	0
14. <i>Vepris lanceolata</i> *	0	0.57± 0.05 (20)	0.52± 0.16 (3)	0.80± 0 (1)	0
15. <i>Sideroxylon inerme</i> *	0	0	1.70± 0 (1)	0.50± 0 (1)	0
16. <i>Trichilia emetica</i> *	0	0	0.60± 0 (1)	0	0
17. <i>Clerodendrum myricoid</i>	0	0	1.28± 0.03 (2)	0	0
18. <i>Peddiea africana</i>	0	0	1.01± 0.29 (2)	0	0
19. <i>Carissa macrocarpa</i>	0	0	0	0.77± 0.52 (3)	0
20. <i>Phoenix reclinata</i> *	0	0	0	1.50± 0 (1)	0
21. <i>Antidesma venosum</i>	0	0	0	0.90± 0 (1)	0
22. <i>Trema orientalis</i> *	0	0	0	1.65± 0 (1)	0
23. <i>Rhus rehmanniana</i>	0	0	0	1.65± 0 (1)	0
24. <i>Rhus natalensis</i>	0	0	0	0.50± 0 (1)	0
25. <i>Celtis africana</i> *	0	0	0	0	0.70± 0 (1)
26. <i>Clausena anisata</i>	0	0	0	0	1.00± 0.27 (6)
27. <i>Deinbollia oblongifolia</i>	0	0	0	0	1.17± 0.38 (3)
28. <i>Teclea gerrardii</i> *	0	0	0	0	1.85± 0.05 (2)
29. <i>Turraea floribunda</i>	0	0	0	0	1.10± 0 (1)
30. <i>Grewia occidentalis</i>	0	0	0	0	1.30± 0 (1)
31. <i>Acacia kraussiana</i>	0	0	0	0	0.45± 0.05(2)

* Potential high canopy species

TABLE 14: Mean heights of woody broad-leaved species in the canopy layer of the different-aged rehabilitating stands at Richards Bay. Means are followed by the standard error of the mean and in brackets by the number of individuals recorded in the survey.(No individuals above 2m were recorded in the 2-year-old stand.)

Species	Mean heights of broad-leaved species in different aged stands (m)			
	6 years	9 years	14 years	35 years
1. <i>Dodonaea angustifolia</i>	2.60±0 (1)	0	0	0
2. <i>Brachylaena discolor</i>	2.19±0.05 (8)	2.61±0.25 (12)	2.32±0.13 (11)	0
3. <i>Canthium inerme</i> *	0	0	2.56± 0.22 (5)	3.66± 0.66 (5)
4. <i>Scutia myrtina</i>	0	0	2.10±0 (1)	2.50±0 (1)
5. <i>Celtis africana</i> *	0	0	3.05± 1.05 (2)	4.30±1.70 (2)
6. <i>Carissa macrocarpa</i>	0	0	2.40±0 (1)	3.00±0 (1)
7. <i>Kraussia floribunda</i>	0	0	2.20± 0 (2)	5.00±0 (1)
8. <i>Apodytes dimidiata</i> *	2.18± 0.07 (5)	0	0	9.00±0 (1)
9. <i>Rhoicissus digitata</i>	2.30±0 (1)	0	0	0
10. <i>Vepris lanceolata</i> *	2.30±0 (1)	0	0	0
11. <i>Allophylus natalensis</i> *	0	0	0	5.50±0 (1)
12. <i>Sideroxylon inerme</i> *	0	0	0	8.50±0 (1)
13. <i>Clausena anisata</i>	0	0	0	2.55±0.50 (2)
14. <i>Olea capensis</i>	0	0	0	6.50±0 (1)
15. <i>Peddiea africana</i>	0	0	0	3.20±0.80 (2)
16. <i>Deinbollia oblongifolia</i>	0	0	0	3.25±0.75 (2)
17. <i>Turraea floribunda</i>	0	0	0	2.70±0 (1)
18. <i>Teclea gerrardii</i> *	0	0	0	3.24±0.29 (8)
19. <i>Strychnos henningsii</i>	0	0	0	3.70±0 (1)
20. <i>Zanthoxylum capense</i>	0	0	0	2.70±0 (1)
21. <i>Grewia occidentalis</i>	0	0	0	5.75±0.25 (2)

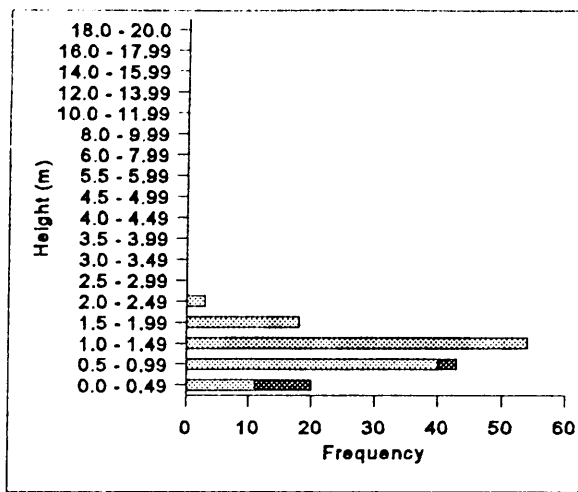
*Potential high canopy species

The mean height of *Dodonaea angustifolia* increased from two to six years, but this species was absent on all the older stands. *Brachylaena discolor* was highest in the oldest mined stand (14-year-old), but absent in the 35-year-old stand. *Rhus nebulosa* (a scrambling shrub) was present in all the mined stands, but its mean height showed no age-related trend, although the maximum heights were higher in the 9 and 14-year-old stands than in the younger stands. The species was absent in the 35-year-old unmined stand. Five species (i.e. *Canthium inerme*, *Scutia myrtina*, *Kraussia floribunda*, *Tricalysia sonderiana* and *Eugenia capensis*) were initially absent but in the older stands showed an increasing height with age. Other species showed no age-related trend in their heights (e.g. *Allophylus natalensis* and *Draceana hookeriana*). The maximum heights of some broad-leaved species in the shrub layer (*B. discolor*, *R. nebulosa*, *C. inerme*, Table 13) increased with regeneration age.

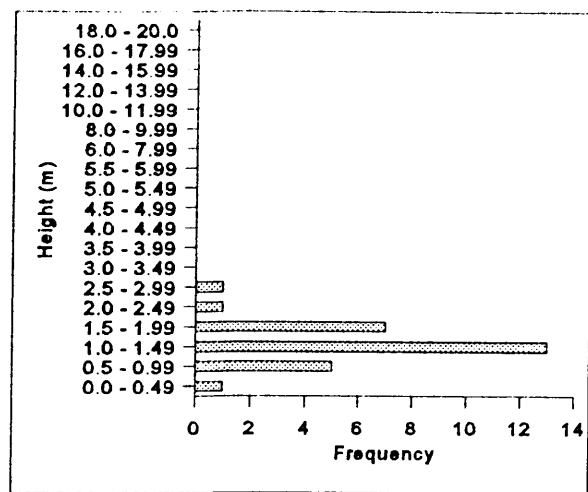
In the canopy layer *Dodonaea angustifolia* was present only in the 6-year-old stand while *Brachylaena discolor* was initially absent with some relatively high individuals occurring in the 9 and 14-year-old stands (e.g. a maximum height of 5.0m was recorded in the 9-year-old stand). *Canthium inerme*, *Scutia myrtina*, *Celtis africana*, *Carissa macrocarpa* and *Kraussia floribunda* were initially absent in the canopy layer, but in the older stands showed an increasing mean and maximum height with age. Many broad-leaved species (no. 11-21) occurring in the 35-year-old stand were absent in the canopy layer of the mined stands.

Height frequencies of the woody plant community

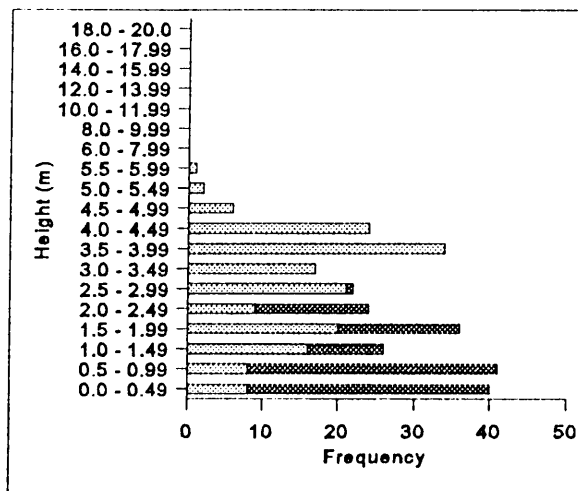
The vertical structure (frequencies of height) for the woody plant community of different-aged mined and unmined stands, is presented in Figure 19. In the 2 and 3-year-old stands a single layer of vegetation existed, comprising primarily of *A. karroo* shrubs below 3.0m in height. In the 6-year-old stand a more bimodal vertical structure has developed with a canopy peak between 3.5m and 4.49m high, consisting of *Acacia karroo* only, with a mixture of *A. karroo* and



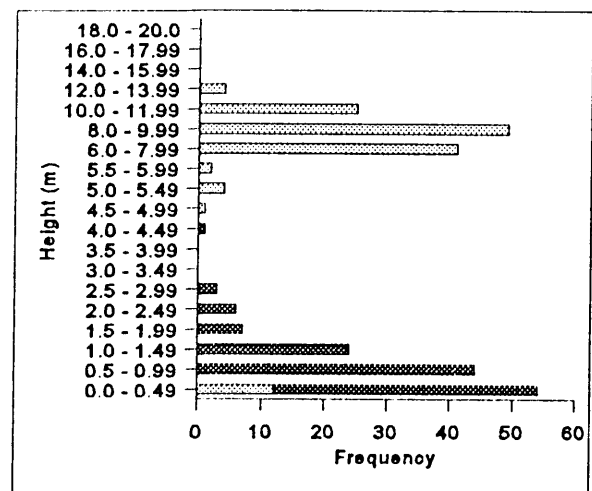
[a] 2-year-old stand.



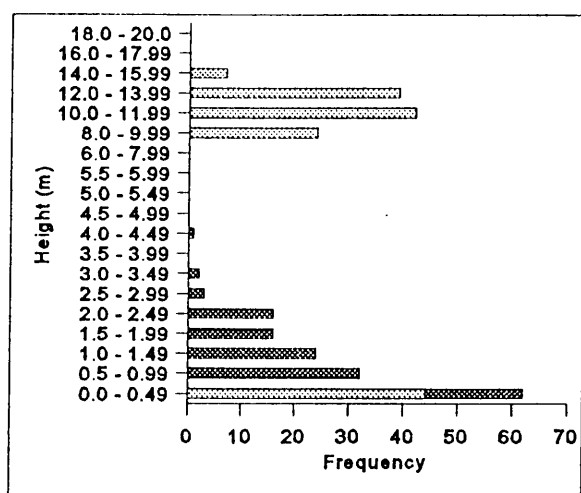
[b] 3-year-old stand.



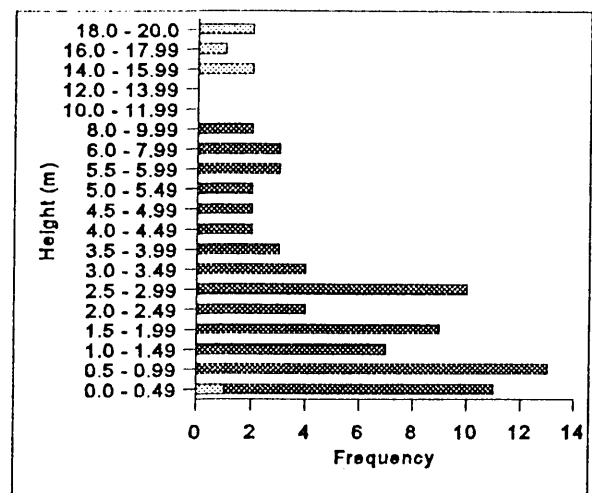
[c] 6-year-old stand.



[d] 9-year-old stand.



[e] 14-year-old stand.



[f] 35-year-old unmined *Teclea gerrardii* stand.

FIGURE 19: Profile diagrams of height frequencies for the woody plant community of different-aged mined and unmined stands at Richards Bay. The grey bars represent the frequencies for *Acacia karroo* and the black bars the frequencies for broad-leaved species.

broad-leaved species forming a second peak below 2.5m. In the 9 and 14-year-old mined stands the gap between the *A. karroo* canopy and the primarily broad-leaved lower layers has increased, but both the *A. karroo* canopy and the broad-leaved strata are higher than in the younger stands. In the 35-year-old unmined stand, *A. karroo* individuals are emergents (14m-20m) above a lower canopy of broad-leaved species (5.5m-9.99m). Except for the gap between the *A. karroo* emergents and the broad-leaved canopy, no big gaps in the vertical structure of the 35-year-old stand were evident.

Density of broad-leaved species

The total densities of broad-leaved species increased in both the shrub and canopy layers with an increase in the regeneration age of stands. The density of broad-leaved species in both the shrub (Table 15) and canopy layers (Table 16) of the oldest mined stand (14 years) was still much lower than in the unmined 35-year-old stand at Zulti North. In both the shrub and canopy layers the density of *Dodonaea angustifolia* decreased with stand age until it was absent from the older stands. *Brachylaena discolor*, *Rhus nebulosa*, *Canthium inerme* and *Scutia myrtina* invaded the mined stands relatively early (they were already present in the 6-year-old stand) and increased in density with stand regeneration age. *B. discolor* and *R. nebulosa* were, however, absent in the 35-year-old unmined stand. In the shrub layer *Trichilia emetica*, *Clerodendrum myricoides* and *Peddiea africana* were only present in the 9-year-old stand, while *Carissa macrocarpa*, *Phoenix reclinata*, *Antidesma venosum*, *Trema orientalis*, *Rhus rehmanniana* and *Rhus natalensis* were only present in the shrub layer of the 14-year-old stand. In the shrub layer *Celtis africana*, *Clausena anisata*, *Deinbollia oblongifolia*, *Teclea gerrardii*, *Turraea floribunda*, *Grewia occidentalis* and *Acacia kraussiana* were not recorded in any of the mined stands, but were present in the unmined 35-year-old stand. Typically high canopy forest species such as *Canthium inerme*, *Apodytes dimidiata*, *Mimusops caffra*, *Allophylus natalensis*, *Vepris lanceolata*, *Sideroxylon inerme*, *Trichilia emetica*, *Phoenix reclinata*, *Trema orientalis* and *Celtis africana* were present in the shrub and/or canopy layers of the mined stands ≥ 6 year of age.

TABLE 15: Density of broad-leaved woody species in the shrub layer of different-aged mined and unmined stands at Richards Bay as encountered on transects (see materials and methods). Densities of species (per hectare) are followed in brackets by relative densities.

Species	Density per hectare				
	2 years	6 years	9 years	14 years	35 years
1. <i>Dodonaea angustifolia</i>	110.3 (33.3%)	57.6 (12.2%)	0	0	0
2. <i>Brachylaena discolor</i>	55.2 (16.7%)	183.1 (38.9%)	701.5 (37.9%)	721.0 (37.8%)	0
3. <i>Rhus nebulosa</i>	27.6 (8.3%)	5.2 (1.1%)	238.7 (12.9%)	381.7 (20.0%)	0
4. <i>Canthium inerme</i> *	0	41.9 (8.9%)	62.9 (3.4%)	212.1 (11.1%)	142.7 (2.9)
5. <i>Scutia myrtina</i>	0	20.9 (4.4%)	207.3 (11.2%)	148.4 (7.8%)	714.7 (14.3%)
6. <i>Kraussia floribunda</i>	0	0	127.7 (6.9%)	42.4 (2.2%)	142.7 (2.9)
7. <i>Tricalysia sonderiana</i>	0	0	158.4 (8.6%)	21.2 (1.1%)	142.7 (2.9%)
8. <i>Eugenia capensis</i>	0	0	31.5 (1.7%)	21.2 (1.1%)	0
9. <i>Apodytes dimidiata</i> *	137.9 (41.6%)	31.4 (6.7%)	0	21.2 (1.1%)	0
10. <i>Mimusops caffra</i> *	0	5.2 (1.1%)	15.9 (0.86%)	0	0
11. <i>Rhoicissus digitata</i>	0	10.5 (2.2%)	79.6 (4.3%)	0	0
12. <i>Draceana hookeriana</i>	0	5.2 (1.1%)	0	106.0 (5.6%)	1572.2 (31.4%)
13. <i>Allophylus natalensis</i> *	0	5.2 (1.1%)	79.6 (4.3%)	21.2 (1.1%)	0
14. <i>Vepris lanceolata</i> *	0	104.7 (22.2%)	48.1 (2.6%)	21.2 (1.1%)	0
15. <i>Sideroxylon inerme</i> *	0	0	15.9 (0.86%)	21.2 (1.1%)	0
16. <i>Trichilia emetica</i> *	0	0	15.9 (0.86%)	0	0
17. <i>Clerodendrum myricoid.</i>	0	0	31.5 (1.7%)	0	0
18. <i>Peddiea africana</i>	0	0	31.5 (1.7%)	0	0
19. <i>Carissa macrocarpa</i>	0	0	0	63.6 (3.3%)	0
20. <i>Phoenix reclinata</i> *	0	0	0	21.2 (1.1%)	0
21. <i>Antidesma venosum</i>	0	0	0	21.2 (1.1%)	0
22. <i>Trema orientalis</i> *	0	0	0	21.2 (1.1%)	0
23. <i>Rhus rehmanniana</i>	0	0	0	21.2 (1.1%)	0
24. <i>Rhus natalensis</i>	0	0	0	21.2 (1.1%)	0
25. <i>Celtis africana</i> *	0	0	0	0	142.7 (2.9)
26. <i>Clausena anisata</i>	0	0	0	0	857.4 (17.1%)
27. <i>Deinbollia oblongifolia</i>	0	0	0	0	428.7 (8.6%)
28. <i>Teclea gerrardii</i> *	0	0	0	0	286.0 (5.7%)
29. <i>Turraea floribunda</i>	0	0	0	0	142.7 (2.9)
30. <i>Grewia occidentalis</i>	0	0	0	0	142.7 (2.9)
31. <i>Acacia kraussiana</i>	0	0	0	0	285.9 (5.7%)
Total	331.0 (99.9%)	470.9 (99.9%)	1850.6 (99.7%)	1908.5 (101%)	5001.1 (100.2)

*Potential high canopy species

TABLE 16: Density of broad-leaved woody species in the canopy layer of different-aged mined and unmined stands at Richards Bay. Densities of species (per hectare) are followed in brackets by relative densities. (No individuals above 2m were recorded in the 2-year-old stand.)

Species	Density per hectare			
	6 years	9 years	14 years	35 years
1. <i>Dodonaea angustifolia</i>	5.2 (6.2%)	0	0	0
2. <i>Brachylaena discolor</i>	41.9 (50.1%)	191.4 (100%)	233.3 (50.0%)	0
3. <i>Canthium inerme</i>	0	0	106.0 (22.7%)	140.8 (14.3%)
4. <i>Scutia myrtina</i>	0	0	21.2 (4.5%)	28.2 (2.9%)
5. <i>Celtis africana</i>	0	0	42.4 (9.1%)	56.3 (5.7%)
6. <i>Carissa macrocarpa</i>	0	0	21.2 (4.5%)	28.2 (2.9%)
7. <i>Kraussia floribunda</i>	0	0	42.4 (9.1%)	28.2 (2.9%)
8. <i>Apodytes dimidiata</i>	26.2 (31.3%)	0	0	28.2 (2.9%)
9. <i>Rhoicissus digitata</i>	5.2 (6.2%)	0	0	0
10. <i>Vepris lanceolata</i>	5.2 (6.2%)	0	0	0
11. <i>Draceana hookeriana</i>	0	0	0	56.3 (5.7%)
12. <i>Allophylus natalensis</i>	0	0	0	28.2 (2.9%)
13. <i>Sideroxylon inerme</i>	0	0	0	28.2 (2.9%)
14. <i>Clausena anisata</i>	0	0	0	56.3 (5.7%)
15. <i>Olea capensis</i>	0	0	0	28.2 (2.9%)
16. <i>Peddiea africana</i>	0	0	0	56.3 (5.7%)
17. <i>Deinbollia oblongifolia</i>	0	0	0	56.3 (5.7%)
18. <i>Turraea floribunda</i>	0	0	0	28.2 (2.9%)
19. <i>Teclea gerrardii</i>	0	0	0	225.2 (22.9%)
20. <i>Strychnos henningsii</i>	0	0	0	28.2 (2.9%)
21. <i>Zanthoxylum capense</i>	0	0	0	28.2 (2.9%)
22. <i>Grewia occidentalis</i>	0	0	0	56.3 (5.7%)
Total	83.7 (100.0%)	191.4 (100.0%)	466.5 (99.9%)	985.8 (100.4)

Figure 20 summarizes the trend in the total density of the more important woody species, by expressing densities in terms of a percentage of the total density of the species. The graphs clearly show the different regimes of increase and decline of species with time (see Finegan, 1996).

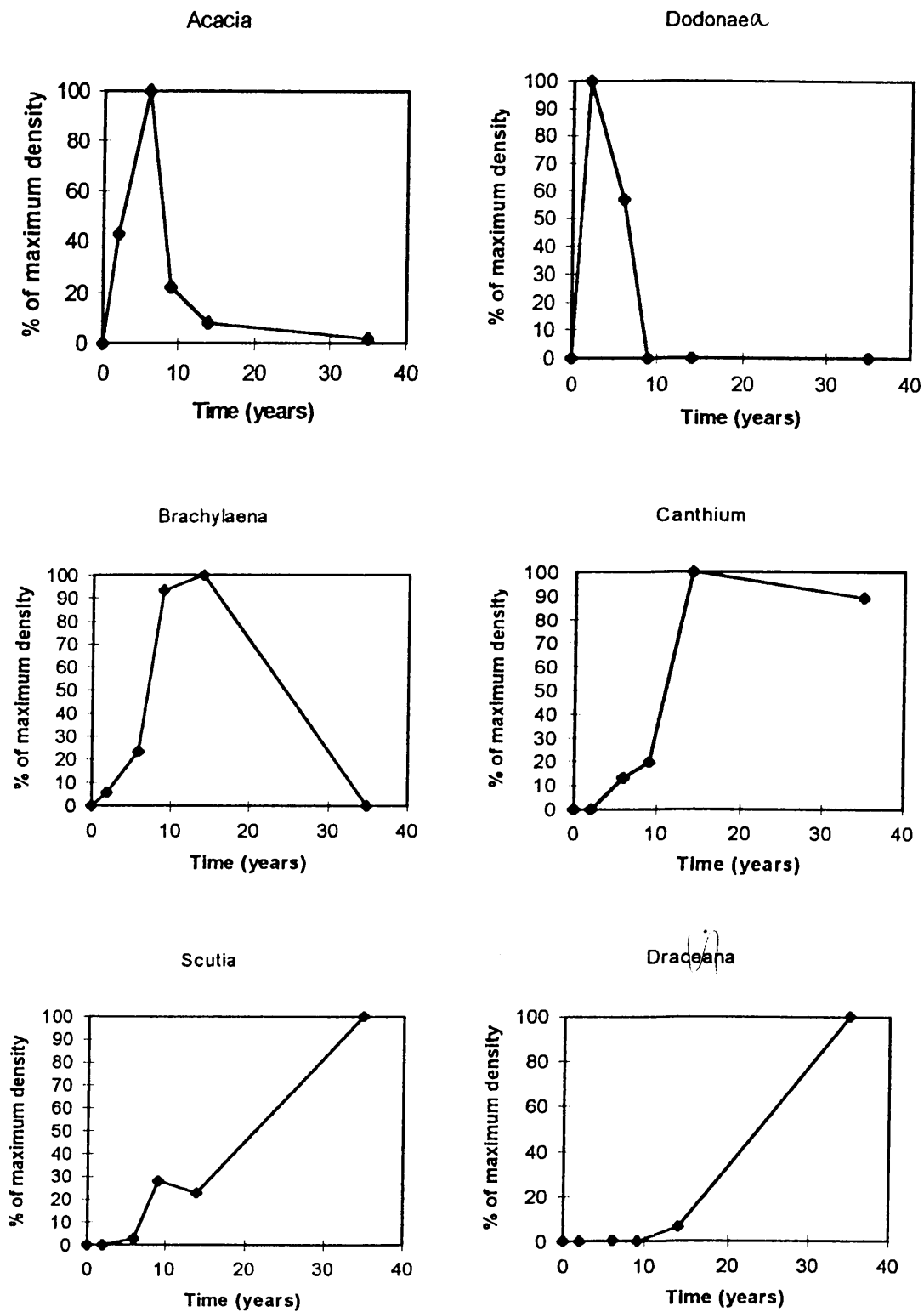


FIGURE 20: Temporal trends in the percentage of maximum density for woody species in mined and unmined stands at Richards Bay.

Species richness and diversity of broad-leaved species

In the shrub layers of the mined stands (2 to 14 years) species richness increased with stand regeneration age, but decreased towards the 35-year-old unmined stand (Table 17). Species diversity (Shannon-Wiener Index) in the shrub layer generally increased with age, although the diversity in the 14-year-old stand was slightly lower than in the 9-year-old stand. In the canopy layer species diversity was zero in the 9-year-old stand, because only one species (*B. discolor*) has reached a height above 2m, but otherwise there was also an age-related tendency towards an increase in species richness and diversity. When the two layers of broad-leaved species are combined, both the species richness and diversity increased (without exception) with regeneration age. With the ages transformed to a $\log_{10}$ scale, age (y) significantly correlated with species diversity (x) in the combined layers ($y = 1.646x - 0.2$) ($r^2 = 0.976$; $F=121.32$; $df=1,4$; $p<0.0016$).

TABLE 17: Species richness and species diversity (Shannon-Wiener Index) of broad-leaved species in the shrub (<2m) and canopy layers (≥2m) of mined and unmined stands at Richards Bay.

Stand Age (years)	Shrub layer		Canopy layer		Both layers	
	Species richness	Species diversity	Species richness	Species diversity	Species richness	Species diversity
2	4	1.78	-	-	4	1.78
6	11	2.56	5	1.77	11	2.54
9	15	3.00	1	0	15	2.85
14	18	2.94	6	2.02	19	2.93
35	13	3.19	18	3.78	21	3.90

Similarity between the mined stands and "mature" dune forest

The species in both the canopy and shrub layers of the mined stands were included in the calculation, because all broad-leaved species (also those above 2m) were still well below the higher canopy of *A. karroo* trees (see Figure 19) and therefore more comparable to the subcanopy layer of the 35-year-old stand. Similarities (as calculated by the Bray-Curtis similarity index) between the different-aged mined stands and the 35-year-old unmined *Teclea gerrardii* stand increased with an increase in stand regeneration age (Table 18). This suggests that the mined stands, in terms of species composition and relative densities, are developing towards the more mature unmined *Teclea gerrardii* stand at Zulti North.

TABLE 18: Bray-Curtis similarity index of mined stands with the 35-year-old unmined *Teclea gerrardii* stand at Zulti North. Density of woody broad-leaved species in the combined shrub and canopy layers was included in the calculation.

Age of stand (years)	Bray-Curtis similarity index with mature unmined <i>Teclea gerrardii</i> stand at Zulti North
2	12.3
6	26.3
9	28.0
14	39.0

Soil Attributes

There was a definite trend in the accumulation of organic debris (>2mm) (Table 19, column 3) with age as illustrated by the significant positive correlation between the age of the stands and the amount of organic debris ($r=0.77$; $n=54$; $p<0.0001$). Significant differences in the organic debris between stands were recorded ($F=52.762$; $df=1,3$; $p<0.0001$) with the biggest difference between the 6

and 9-year-old stands. In the older mined stands (6, 9 and 14 years) there was a significant negative correlation between the amount of organic debris and the distance from the starting point of a transect ($r=-0.47$; $n=40$; $p<0.0001$), showing that there was a thicker layer of debris in the dune valleys (and on the lower slopes of the dunes) than closer to the dune crests.

The organic matter content ($<2\text{mm}$) of the soil increased gradually with an increase in stand age (Table 19) as was also illustrated by a significant positive correlation between the age of the stand and the amount of organic matter content in soil samples ($r=0.65$; $n=54$; $p<0.0001$). There were also significant differences in the organic matter content between stands ($F=89.162$; $df=1,3$; $p<0.0001$).

When the values for the youngest (2-year-old) stand were excluded, there was a significant negative correlation between organic matter content and the distance from the starting point of a transect ($r=-0.47$; $n=40$; $p<0.0001$), suggesting that organic matter content (like organic debris) accumulated faster in the dune valleys and lower slopes than on the higher slopes or dune crests. A positive correlation existed between the organic matter content of the soil and the amount of organic debris that had accumulated on top of the soil ($r=0.68$; $n=54$; $p<0.0001$).

The water content of the soil increased with the age of the stand (Table 19). The 6-year-old stand, however, had the lowest percentage soil water. There were positive correlations between organic debris and soil water ($r=0.61$; $n=54$; $p<0.0001$) and between organic matter content and soil water ($r=0.58$; $n=54$; $p<0.0001$). A significant negative correlation existed between the amount of soil water and the distance from the starting point of a transect ($r=-0.51$; $n=40$; $p<0.0001$) suggesting that the soils in the dune valleys and lower slopes contained more water than the areas closer to dune crests. There was a significant difference in soil water content between stands ($F=18.627$; $df=1,3$; $p<0.0001$).

TABLE 19: Soil attributes of samples collected from stands of known age on rehabilitating coastal dunes in northern KwaZulu-Natal. Means are followed by the standard errors of the mean ($\pm$ S.E.), and in brackets by the coefficient of variations (%).

Age of stand (years)	Number of samples	Mean % organic debris >2mm	Mean % organic matter content <2mm	Mean % soil water	Mean soil pH
2	16	1.28 $\pm$ 0.095 (30.0%)	0.88 $\pm$ 0.063 (28.4%)	2.52 $\pm$ 0.133 (1.0%)	7.97 $\pm$ 0.028 (1.4%)
6	11	1.55 $\pm$ 0.121 (25.5%)	1.39 $\pm$ 0.066 (15.8%)	2.09 $\pm$ 0.274 (43.6%)	6.98 $\pm$ 0.057 (2.7%)
9	15	5.68 $\pm$ 0.333 (22.7%)	2.63 $\pm$ 0.137 (20.2%)	3.05 $\pm$ 0.165 (20.9%)	6.97 $\pm$ 0.044 (2.4%)
14	14	5.82 $\pm$ 0.575 (36.9%)	3.65 $\pm$ 0.208 (21.4%)	4.34 $\pm$ 0.307 (26.4%)	7.04 $\pm$ 0.059 (3.1%)

In the first two to three years following initial rehabilitation the soil had a relative high pH (Table 19): in the 2-year-old stand the pH of the soil was 7.97, with a relative low coefficient of variation (1.4%). In the older stands (6-14 years) the pHs were similar (between 6.97 and 7.04) with higher coefficients of variation (2.4%-3.1%) than in the 2-year-old stand. The pH differed significantly between stands ($F=119.624$; $df=1,3$; $p<0.0001$). Significant negative correlations existed between the pH and organic debris ($r=-0.58$; $n=54$; $p<0.0001$) and between the pH and the organic matter content ($r=-0.52$; $n=54$; $p<0.0001$) in the stands. In the 9 and 14-year-old stands there were positive correlations between the pH and the distance from the starting point of the transect ($r=0.79$; $n=14$; $p<0.0001$ and $r=0.57$; $n=15$; $p<0.0004$ respectively) suggesting that in the older two stands the pH was higher at the top of the dunes (further along the transect) than lower down the dunes.

DISCUSSION

From the results of the heights of broad-leaved species it appears that *D. angustifolia* is an early colonizing species that increased in height over the first 6 years of rehabilitation, but was absent in all the older stands. The mean and maximum heights of *B. discolor* and *R. nebulosa* also increased with regeneration age, but these species were absent from the unmined 35-year-old stand. The consistent increase in the mean and maximum heights of some broad-leaved species with stand regeneration age of the mined stands (e.g. *C. inerme*, *S. myrtina*, *T. sonderiana*, *E. capensis* and *K. floribunda*) suggests that these species are surviving in the rehabilitating stands. However, few broad-leaved individuals have reached the canopy layer (>2m) in the mined stands although some individuals of *B. discolor*, *C. inerme* and *C. africana* have reached heights of more than 3 meters.

The profile diagrams drawn from the height frequencies of the woody plant community, show the typical pattern of rehabilitating woody communities with an increasing number of broad-leaved species starting to fill up the lower vegetation layers of the mined stands (Terborgh & Petren, 1991). These profiles suggest an increasing similarity between the mined and the unmined 35-year-old stand with time. The gap between the upper *A. karroo* canopy and the broad-leaved subcanopy persisted but with an increasing dominance of broad-leaved species in the lower vegetation strata both in terms of frequency and height.

Mature tropical rain forests have complex vertical structures with several distinct layers of vegetation (Terborgh & Petren, 1991). Such multi-layers of vegetation are absent from the rehabilitating mined stands with only two layers (i.e. canopy and subcanopy layers) present. In the 35-year-old unmined stand a more complex multi-layered vegetation (similar to mature forests) was recorded. It is, however, clear that the mined stands are developing towards a more complex vertical structure (Figure 19). The rehabilitating mined stands will in future probably develop a lower broad-leaved canopy, with various lower layers

of broad-leaved strata nearer to the ground. The *A. karroo* canopy may continue to increase in height but will probably thin out to form a discontinuous layer of tall emergents above the broad-leaved canopy.

The age-related increase in the density of broad-leaved species is complex, with many species showing no clear trend. This is probably due to stochastic factors effecting their establishment on rehabilitating stands. However, the results suggest that *D. angustifolia*, *R. nebulosa* and *B. discolor* are early invaders (the position of *A. dimidiata* is not clear). *D. angustifolia* is a sun-loving species frequenting forest margins (Pooley, 1993) and therefore decreases in density with the formation of a canopy and soon disappears from older stands. *Brachylaena discolor* and *R. nebulosa* increased in density with an increase in regeneration age of mined stands, but were absent from the 35-year-old unmined stand, suggesting that they are also secondary successional species that are not common in older communities. This is supported by the fact that *B. discolor* often had a climbing growth-form in the two older mined stands (9 and 14 years), sometimes extending up to 5m (see Table 14) into the branches of the *A. karroo* canopy trees.

Canthium inerme, *S. myrtina*, *K. floribunda* and *C. africana* increased in density with stand regeneration age. It is, however, significant that the total density of broad-leaved species in both the shrub and canopy layers increased considerably with an increase in the regeneration age of stands. The results suggest that species have different regimes of increasing and declining in dominance (Figure 20). For example, *D. angustifolia* colonizes stands very early, but soon declines in density. Early in its life it produces large clusters of small to medium sized papery-winged seeds (15-19mm) that are widely distributed by the wind (Palgrave, 1983; Pooley, 1993). It can therefore be classified as an early pioneer (Finegan, 1996) and one would not expect to find it in a forest. On the other hand *R. nebulosa* and *B. discolor* also colonize stands early, but take longer to reach their maximum densities and persist longer in stands. *B. discolor*

(Asteraceae) produces large quantities of wind-dispersed seeds while *R. nebulosa* also produces large quantities of spherical fruit (up to 4.5mm in diameter) which are dispersed by birds and animals (Palgrave, 1983; Pooley, 1993). Their regime is therefore typical of short-lived pioneers (according to Finegan's [1996] classification) or can also be described as early pioneers (according to Hubbell & Foster's [1986] classification). However, *R. nebulosa* is a typical undercover forest species, while the wind-dispersed *B. discolor* is usually not associated with older forests.

Acacia karroo colonizes stands early, produces somewhat larger seeds of shorter viability (see Chapter 5), but persists for long periods in the canopy of stands. It can therefore be classified somewhere between a long-lived pioneer species (Finegan, 1996) and a late secondary species (Hubbell & Foster, 1986). Other species such as *D. hookeriana* and *S. myrtina* produce larger succulent fruit (8mm and 20mm respectively) (Pooley, 1993) which are animal-dispersed. They therefore tend to colonize stands later (as was evident from the results) and were still increasing in density after 35 years. They, and many other species first recorded in the 35-year-old stand, can therefore be described as shade-tolerant or primary species typical of Finegan's (1996) fourth phase of secondary forest succession. It is therefore clear that species typical of different phases of succession (or vegetational changes) are present in the mined stands, which suggests that succession is taking place. There is, however, no indication of discreet communities replacing each other on a relay basis, as was suggested by Clements (1916) and "classical" succession theory. During the present study it was also observed that early colonizing species (e.g. *D. angustifolia* and *B. discolor*), which were absent from under the shaded canopy of older stands, were still present in relatively large numbers on the borders of stands (personal observation). The present study therefore confirms that forest succession on coastal dunes should be described in terms of those changes observed in gap succession of species-rich, closed-canopy tropical forests (Hubbell & Forest,

1986; Finegan, 1996) rather than in terms of models of succession developed for species-poor temperate climates.

Many ecologists reject diversity indices, based on species abundance distributions (e.g. the Shannon-Wiener Index) in favour of simple counts of number of species (species richness) (see Magurran, 1988). Although species richness may in many cases be an informative measure, a considerable degree of ecological insight can be gleaned from more detailed investigations of the variety of abundances of species (Magurran, 1988). During rehabilitation, changes in diversity may alert the ecologist to a shift in the distribution of species abundance or a decrease in dominance, often associated with succession (Barbour *et al.*, 1987).

On the mined stands increases in species richness and diversity with stand age (in association with addition and replacement of species), suggests that succession is taking place. Although the dominance of *A. karroo* in terms of biomass (see Chapter 5) has not declined in the mined stands, the increasing number of broad-leaved species and the associated increase in the abundance of broad-leaved individuals in older stands, are typical of succession (Odum, 1969; Barbour *et al.*, 1987). Species richness and diversity for the combined layers (Table 17) are probably more informative than those for either the shrub or canopy layers. Most broad-leaved species in the mined stands are still below 3m and well below the higher canopy consisting of *A. karroo*. The split of the broad-leaved species into shrub and canopy layers is therefore somewhat arbitrary for the mined stands. The consistent increase in the species diversity in the combined layers is therefore an indication of both the increasing number of species occurring in the older stands and the fact that the stand is not dominated by only one or two species. Although *B. discolor* is the dominant species in all the mined stands older than 2 years, other species such as *R. nebulosa*, *C. inerme*, *S. myrtina* and *D. hookeriana* are also fairly abundant in the older stands.

Both in terms of species richness and diversity, the mined stands have not yet reached the diversity of the 35-year-old unmined stand at Zulti North. There was a decrease in the species richness of the shrub layer from the 14-year-old to the 35-year-old stands. This may either be ascribed to the decrease in species richness that is sometimes associated with later stages of succession (Barbour *et al.*, 1987) or to the small sample size ($n=40$) in the 35-year-old stand. However, in spite of the decrease in species richness, species diversity in the shrub layer increased from 14 to 35 years. This is an indication of the lesser extent to which the 35-year-old stand was dominated by only a few species.

During rehabilitation the direction of succession is important when assessing the success of such a project. Although the densities and relative dominance of species may change with time, rehabilitation can only be successful if rehabilitating stands are increasingly similar in terms of species occurrence and abundance, with "mature" unmined stands. The increasing similarity (Bray-Curtis Index) with age between the woody broad-leaved plants in the mined stands and the more "mature" stand at Zulti North, suggests that the mined stands are developing towards the "mature" forest. This is supported by Mentis & Ellerly (1994) who found that there was no difference in the composition of the woody plant communities of rehabilitating mined and unmined (but previously disturbed) stands in the Richards Bay area. This increasing similarity between the woody species of mined and "mature" forest is also mirrored by an increase in the similarity of species in the herbaceous plant layer, millipedes, beetles and birds (Van Aarde *et al.*, in press; Van Aarde *et al.*, 1996).

Earlier soil researchers in the Richards Bay area usually dug one or two pits in each stand to collect soil samples. Venter (1972) dug pits to a depth of 1m in 64% of his stands to analyze the soil profiles and various soil attributes. More recently Scott *et al.* (1993) investigated changing soil attributes in mined and unmined stands in the Richards Bay area. They chose 14 sites in the mined stands (ranging from one month to 14 years in age) located on the sea-facing

aspect of the second dune from the sea. Their sampling sites are therefore comparable to the stands in the present study. They dug two soil pits of 1m² and 1.2m deep at each site. Their A-horizon, or so-called topsoil, is comparable to the samples taken in the present study.

Although this sampling method is appropriate when trying to identify different soil horizons it has, however, two important disadvantages: Firstly, because of the extreme variability of soil characteristics, one or two samples within a stand may not be representative of the stand as a whole and secondly, the method cannot identify any soil gradients along the dune slopes. Another point of criticism against the methods of Scott *et al.* (1993) is that they equate the A-horizon in all the stands with the cover soil initially spread over the dunes at the start of rehabilitation. This may be true for the very young stands, but is inappropriate for the older stands where important changes in the top soil may have taken place with the maturation of a stand. It is conceivable that any changes in soil attributes taking place during succession, will first be observed in the top layer and will become visible in the lower soil layers only later. The present study, therefore, concentrated on the top 10cm of soil.

During the process of succession the accumulation of organic debris (>2mm) on top of the soil is important for soil formation. Important nutrients are gradually released into the soil from this decomposing debris layer and the layer also forms a protective barrier on top of the soil, decreasing the rate of evaporation from the soil. Both factors are essential in eventually creating a more fertile and damp soil that is conducive for the establishment of secondary broad-leaved species. The clear trend in the accumulation of plant debris (with increasing stand age) may be because of self-thinning in the *A. karroo* populations (see Chapter 4) causing a lot of dead branches and leaves to litter the older stands. The warm and humid climate speeds up the decomposition of this organic debris that may lead to an almost continual supply of organic matter content to the soil.

This trend was confirmed by the analysis of the organic matter content (<2mm) of the soil which increased with the increased regeneration age of stands. Venter (1972) reported a low organic matter content in his younger *A. karroo* community (1.06%) while his more "mature" communities contained much higher percentages (e.g. *Mimusops* = 4.74%; *Celtis* = 3.16%). The percentage organic content in the topsoil of the 14-year-old stand (3.65%) was already comparable to the more mature stands of Venter. This is an indication of the soil becoming increasingly more fertile as nutrients become available from the decomposing organic material. This may support the notion that facilitation (or enablement) may play some role (although it may be indirect) during succession.

The failure of Scott *et al.* (1993) to detect any clear trends in the accumulation of organic matter content is probably due to their sampling method. Their samples may not be representative, and they emphasized the lower B-horizon where soil changes may take much longer to occur. The general increase in the organic content of the soil in the rehabilitating stands with time, was confirmed by the study of Van Aarde *et al.*, (1996c).

The 6-year old stand contained the smallest percentage of soil water, but there was otherwise a general increase in soil water with stand age. The dryness of the 6-year-old stand could probably be explained by the dense canopy cover (Chapter 4) (shielding the ground from dew and salt spray), the thin top layer of organic debris (offering only limited protection from evaporation), and the low organic matter content (reducing the soil's water-holding capacity) (Barbour *et al.* 1987). Although predicted by theory, the low water content of the 2-year-old stand was also surprising, since during the sifting process the soil from this stand "appeared" to be the wettest: it was wet to the touch and repeatedly clogged the sieve. This apparent wetness of the soil is, however, probably due to the low organic content of these young soils. Sandy soils with low organic content bind water not very well, giving the false impression that the sand is wetter. The significant positive correlations between organic debris and organic matter

content on the one side, and water content on the other, suggest that these conclusions are probably right (see Venter, 1972). Venter (1972) reported a relatively low soil water percentage of 0.10% in his *A. karroo* community, but much higher figures in the more mature stands (e.g. *Celtis* = 1.92% and *Mimusops* = 4.24%). The water content of the 14-year-old stand (4.34%) was comparable to that of Venter's mature *Mimusops* community. Soil water may, however, be highly variable with time, depending on the amount of rain, dew, wind, time of sampling and other factors, which make it difficult to compare results especially because the exact time of Venter's sampling is not known.

From the present study it is clear that the biggest drop in *pH* takes place at the earlier stages of rehabilitation (before 6 years), after which it stays almost the same. Scott *et al.* (1993) found similar results in their B-horizon, suggesting that the *pH* of the soil drops (become marginally more acidic) with an increase in stand age. According to Tinley (1985) the soil *pH* of coastal dunes on the east coast of southern Africa is generally high. He reported a *pH* of 7.7 for the top 10cm layer at Kosi Bay. Venter (1972) also reports relatively high *pH* levels for the coastal dunes in the Richards Bay area, ranging mostly between 6 and 8. This high *pH* is caused by a characteristic high concentration of sodium in the top soil and an equivalent high concentration of calcium in the subsoil (Tinley, 1985). The decrease in *pH* with stand age is probably due to the leaching of carbonates and the accumulation of organic acids in the soil during succession (Barbour *et al.*, 1987). It is therefore clear that at the initiation of the rehabilitation process the soil is relatively homogeneous (as is suggested by the relatively low coefficient of variation in the 2 -year-old stand) with a high *pH*. Within six years the *pH* drops considerably and the soil becomes less homogeneous with lower *pH* levels reported in the dune valleys.

Soil attributes display the trends associated with the cumulative changes during succession (Odum, 1969; Barbour *et al.* 1987). All these physical changes in the soil contribute to a more fertile and mesic environment, preferred by the

broad-leaved species usually associated with the later stages of succession. At least in the top soil layer the percentage organic matter content, soil water and pH have reached levels comparable to those reported for more mature forests. Although not investigated in the present study, it was confirmed by Van Aarde *et al.* (1996c) that some nutrients and minerals still occur at relatively low concentrations in the mined areas, but that there is a cumulative effect with time.

Discrete communities (that alternatively occupy a site), as predicted by extreme exponents of the facilitation model, were not observed in the present study, although *A. karroo* probably facilitated (or at least enabled) some understory specialists to establish (Welden *et al.*, 1991). The tolerance model can explain the coexistence of some pioneer, secondary and primary species during earlier stages of vegetational development, but cannot explain how "tolerance" can cause some species to be absent from younger stands and others to become absent at later stages. The original name for this model (i.e. the "Initial Floristic Composition" model) was therefore probably a more appropriate name. The Inhibition model can explain why some species are slow to dominate in the developing dune communities (e.g. *C. africana* and *M. caffra*), but ignores the positive role that may be played by *A. karroo* in the establishment and survival of others. On the other hand, the gap-phase successional model, primarily developed by ecologists working in more species-rich forest communities (see, for tropical forests: Hartshorn, 1980; Brokaw, 1985; Hubbell & Foster, 1986; Finegan, 1996; and for boreal forests: Shugart, 1984; and Prentice & Leemans, 1990), enabled the unambiguous description of vegetational development on these coastal dunes.

CHAPTER 7

SYNTHESIS

The rehabilitation of mined stands by Richard Bay Minerals on the coastal dunes of northern KwaZulu-Natal resulted in the development of known-age stands from a few months old to 14 years, at the time of the present study. Age-related trends in the *Acacia karroo* population on these stands, and the population's relationship to the developing woody broad-leaved community, were investigated. Possible woody plant succession on coastal dune forests was studied and how this may relate to various models proposed for succession. In the light of these results, the rehabilitation of the woody plant community (i.e. of the programme by Richards Bay Minerals) can be assessed.

This study revealed various trends in the morphometric variables of *A. karroo*. More than 50% of the trees in the mined stands were single-stemmed with no temporal trend in the mean number of live stems per tree. Rainfall during the year of rehabilitation may influence the initial densities of *A. karroo* trees and thereby produce such "unexpected" results. The increase (in the older mined stands) of the number of dead stems per tree, suggests that competition between stems is severe, causing stems that are outgrown by others (and therefore shaded) to die. Trimming of lower stems and branches is typical of heliophytes that are shade-intolerant (O'Brien *et al.*, 1995).

Acacia karroo trees in the canopy layer ($\geq 2\text{m}$) showed a high and sustained growth rate. Comparisons with the unmined 35-year-old stand at Zulti North suggest that trees in the oldest mined stand (14 years) have not yet reached their maximum heights and will in future further lengthen to avoid shading. Its relatively high and sustained growth rate is typical of a long-lived pioneer species (or late secondary forest species) as defined by Finegan (1996) and Hubbell & Foster (1986) respectively. On the 35-year-old unmined stand, the few surviving *A. karroo* trees are tall emergents, high above the lower developing broad-leaved

canopy, which is also typical of late secondary canopy species (Hubbell & Foster, 1986; Leemans & Prentice, 1987).

Other morphometric variables of *A. karroo* (i.e. crown area, basal area and mass) showed an age-dependent increase, as is to be expected during the maturation of a stand. The size distributions of all size variables suggested that trees tend to be more or less similar-sized in the older stands, with no trees of intermediate sizes occurring in these stands. An increasing gap therefore develops (with increasing stand age) between the small seedlings and the higher canopy layers of *A. karroo*. A more complex vertical structure is typical of "mature" forest and should develop with further vegetational development (Terborgh & Petren, 1991).

Recruitment of *A. karroo* juveniles was still taking place in the 6-year-old stand, as is suggested by the range of heights in the shrub layer (<2m). In the 9 and 14-year-old stands, however, only small seedlings occurred, with no juveniles or trees of intermediate heights (see Finegan, 1996). This suggests that although *A. karroo* seeds germinate in the older stands, seedlings only survive for a few months. The absence of juveniles of intermediate heights (i.e. between 3cm and the canopy layer) indicates that the older mined stands have a senescent *A. karroo* population. This is typical of shade-intolerant short-lived and long-lived pioneers (Finegan, 1996). The absence (or very low densities) of *A. karroo* juveniles in the more "mature" stands surveyed by Venter (1972) supports the conclusions of the present study that recruitment of *A. karroo* juveniles is almost absent in later successional stages on coastal dune forests.

The density of *A. karroo* in the canopy layer substantially decreased with stand age, due to density-dependent mortality and the lack of recruitment. Saplings of heliophytes have a slim chance of reaching maturity in the shaded environment below a closed-canopy forest (Welden *et al.*, 1991). This was also the case with the *A. karroo* population as is evident from the absence of saplings of intermediate height in the older stands. All *A. karroo* individuals occurring in the 9 to 35-year-old stands were small seedlings less than 30cm high.

However, the increasing biomass, productivity and flower and seed production of *A. karroo* in the older mined stands, show that the dominance of the species has not yet declined, but is actually increasing. It is only in the unmined 35-year-old stand at Zulti North where a decline in the biomass of *A. karroo* was recorded. Highly productive, even-aged stands of long-lived pioneer trees typically persist for extended periods in secondary forests and are therefore indicative of forest succession (Finegan, 1996). The initially high mortality rate, but very low mortality amongst older *A. karroo* trees (type III survivorship curve) is also typical of forest trees that may survive for extended periods in the canopy of "mature" forests (Barbour *et al.*, 1987).

Morphometric variables of *A. karroo* such as height, basal area and crown area are correlated with each other and increased with age. These relationships further illustrate the sustained growth of *A. karroo* throughout its potential lifespan of about 40 years (Barnes *et al.*, 1996). The calculated slope (ratio) of 0.659 for the relationship of *A. karroo*'s height to basal diameter (log scale), indicates that the species invests an appreciable amount of carbon in building supportive structures as predicted by the elastic similarity model (see O'Brien *et al.*, 1995). This shows, that although *A. karroo* is able to increase relatively quickly in height, its vertical growth rate is reduced by the need for also developing sturdy and thick stems for support on wind-swept coastal dunes (O'Brien *et al.*, 1995).

The self-thinning rule (Yoda *et al.*, 1963) predicts the relationship of density to size within the *A. karroo* population well and suggests that intraspecific competition is a determining factor in mortality. On the 35-year-old unmined stand, self-thinning did not play a significant role, although it cannot be ruled out entirely. In species-rich forest communities (where conspecific species are seldom neighbours) self-thinning may still play a role as suggested by the results of Condit *et al.* (1994).

Cluster analysis based on density, height and basal area of *A. karroo* trees in the canopy layer, showed that transects within same-age stands are generally

closer grouped together. This suggests that there is definite vegetation development with increasing stand age, and that there is no evidence of this development becoming "stuck" at any stage within the mined area.

Rainfall during the year of rehabilitation probably has an important effect on the density, number of stems and basal area of *A. karroo* trees in younger stands. This effect would, however, decrease with the age of a stand as good and bad rainfall years cancel each other out, and after the effects of self-thinning. Locality of *A. karroo* trees on a dune slope had only minor effects on the population: trees tended to be smaller on dune crests and steeper dune slopes coincided with larger gaps in the canopy and with more dense stands of juveniles. These relationships with locality were, however, in most cases weak and more pronounced in the oldest mined stand (14 years).

On mined stands, all attributes of the developing woody broad-leaved communities, and the associated changes in soil characteristics, suggest that directional and cumulative changes are taking place. "Classical" species replacement was, however, not recorded, but vegetational development was in line with those described for gap succession in species-rich neotropical forests (see Hubbell & Foster, 1986 and Finegan, 1996). Although species richness and diversity are not yet comparable to more "mature" dune forests, especially in the shrub layers, the number of species has already reached those for "mature" forests. This is in agreement with Finegan's (1996) findings that species richness in shrub layers tends to recover fairly quickly after a disturbance. Finegan (1996) warns, however, that mere increases in species richness and diversity should not be used in isolation as indicators of the recovery of an ecosystem. Species composition in secondary forests is equally important, because long after species richness may have retained levels comparable to "mature" forests, species composition (especially in the canopy layers) may be significantly different. The present trend in ecological research to use species richness and diversity as the only indices for a community's health or successful rehabilitation, should therefore be avoided (Finegan, 1996). In terms of species composition and

density, the mined stands are, however, developing towards the 35-year-old stand, as indicated by the Bray-Curtis Similarity Index.

Classification of species, according to their life histories (r and K) (MacArthur & Wilson, 1967), adaptive patterns (R, C, S) (Grime, 1977; 1979) or survivorship (Deevey, 1947) is informative, but is sometimes inappropriate as is indicated by the difficulty to unambiguously classify *A. karroo* according to these models (see Barbour *et al.*, 1987). Previous succession models were primarily based on northern hemisphere species-poor forests (Barbour *et al.*, 1987) and are therefore not necessarily applicable to highly diverse coastal dune forests in subtropical areas. All three "classical" models of succession can probably be applied to some aspects of the vegetational development on coastal dunes (see Pickett *et al.*, 1987; De Steven, 1991a; 1991b), but they failed to supply an integrated explanation of the whole process.

Recent gap-phase successional theory, developed to explain vegetational changes in closed-canopy forests, described the changes during rehabilitation of coastal dunes better (see for tropical forests: Hartshorn, 1980; Brokaw, 1985; Hubbell & Foster, 1986; Finegan, 1996; and for boreal forests: Shugart, 1984; and Prentice & Leemans, 1990). This model is primarily based on shade tolerance / intolerance of species and how these relate to the germination and recruitment of juveniles, survival of saplings and growth rate (Hubbell & Foster, 1986).

The results of the present study further suggest that forest-type succession is clearly evident within the mined stands at Richards Bay, and that mined stands are developing towards a more "mature" dune forest. Rehabilitation of the woody plants on mined stands is therefore taking place and the rehabilitation programme by the mining company (RBM) could be considered successful. Should the woody plant community keep on developing in the same direction (which is to be expected if no major disturbance takes place) the rehabilitation programme will be successful. It is, however, imperative that the vegetation is monitored on a continual basis to ensure that any future problems are identified early.

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OPSOMMING

Die mynbou-aktiwiteite van Richard Bay Minerals op kusduine in die noordelike dele van KwaZulu-Natal het gelei tot die ontstaan van rehabiliterende stande wat wissel in ouderdom van 'n paar maande tot 14 jaar (tydens die huidige studie). Ouderdom-verwante veranderinge in die *Acacia karroo* populasie en hoe dit moontlik verband hou met die ontwikkeling van die houtagtige breëblaar gemeenskap, is ondersoek. Houtagtige plantsuksessie op duinewoude en hoe dit verband kan hou met verskillende modelle van suksessie, is verder bestudeer. Ten slotte is die moontlike sukses van Richards Bay Minerals se rehabilitasie van die houtagtige plantgemeenskap beoordeel.

Die resultate van die studie het getoon dat *Acacia karroo* bome in die boonste plantegroeilaag 'n hoë en volgehoue groeitempo vertoon, tipies van langlewende pionierspesies (soos gedefinieer deur Finegan, 1996) of van sekondêre spesies (soos gedefinieer deur Hubbell & Foster, 1986). Ander morfometriese eienskappe van *A. karroo* (naamlik kruinarea, basale area en massa) het ouderdom-verwante toenames getoon. In die 9- en 14-jaar-oue stande het slegs saailinge kleiner as 30cm voorgekom. Dit suggereer dat hoewel *A. karroo* sade ontkiem die saailinge nie oorleef in die skaduryke onderbos van ouer rehabiliterende stande nie en dat dit lei tot 'n seniele populasie van *A. karroo*. Seniele populasies is tipies van skadu-intolerante pioniers tydens woudsuksessie (Finegan, 1996).

As gevolg van self-uitdunning en die gebrek aan oorlewing van saailinge, toon die digtheid van *A. karroo* in die boonste laag 'n drastiese afname tydens toenemende stand ouderdom. 'n Toename in biomassa, produktiwiteit en blom en saad produksie van *A. karroo* (in die ouer stande) illustreer egter die dominansie van die spesie. Die hoë mortaliteit van onvolwassenes en die lae mortaliteit van volwassenes (tipe III oorlewingskurwe) is tipies van woudbome wat vir lang tydperke in die blaredak van "volwasse" woude kan oorleef (Barbour *et al.*, 1987).

Cluster-analise (bereken vir digtheid, hoogte en basale area van *A. karroo* bome) het in die algemeen gelei tot die saamgroepering van transekte met vergelykbare ouderdomme. Dit is 'n verdere aanduiding van plantegroei ontwikkeling wat plaasvind tydens veroudering. Reënval gedurende die jaar van rehabilitasie het waarskynlik 'n invloed gehad op die aanvanklike digtheid, getal stamme en basale area van *A. karroo* bome. Die posisie van 'n boom op die duin het slegs 'n geringe invloed gehad op die individu. Veral in die 14-jaar-oue stand was individue egter geneig om kleiner te wees hoër op en bo-op die duine as in die duinvalleie.

In die gemynde stande dui alle eienskappe van die ontwikkelende houtagtige plantgemeenskappe en die geassosieerde veranderinge in grondeienskappe daarop dat direkte en kumulatiewe veranderinge besig is om plaas te vind. "Klassieke" spesieverplasing en voorspelbare opeenvolging van min of meer diskrete serale gemeenskappe is egter nie waargeneem nie. Hoewel spesierikheid en diversiteit toeneem het met die ouderdom van stande, is rikheid en diversiteit nog nie vergelykbaar met "volwasse" duinewoud nie. Die Bray-Curtis Similarity Index het verder aangetoon dat beide in terme van spesiesamestelling en digtheid die gemynde stande nader beweeg aan 'n meer volwasse 35-jaar-oue stand.

Die huidige studie het getoon dat plantegroei ontwikkeling, soos beskryf vir spesierike neotropiese woude (Hubbell & Foster, 1986; Finegan, 1996), vergelykbaar is met ontwikkelings op die rehabiliterende kuswoude van Richardsbaai. Die resultate suggereer dat woud-tipe suksessie besig is om plaas te vind op voorheen gemynde stande en dat die rehabilitasieprogram van Richards Bay Minerals sover suksesvol was.

SUMMARY

The mining activities of Richards Bay Minerals on coastal dunes of northern KwaZulu-Natal, resulted in stands of known-age, ranging from a few months to 14 years in age (at the time of the study). Age-related trends in the *Acacia karroo* population and how these may relate to the developing woody broad-leaved community, were investigated. Possible woody plant succession on coastal dune forests and how this may relate to various models proposed for succession, was investigated. Considering the results, the possible success of Richards Bay Minerals in rehabilitating the woody plant community was assessed.

The results of the study showed that *Acacia karroo* trees in the canopy layer had a high and sustained growth rate, typical of long-lived pioneer species (as defined by Finegan, 1996) or late secondary species (as defined by Hubbell & Foster, 1986). Other morphometric variables of *A. karroo* (i.e. crown area, basal area and mass) showed age-dependent increases. In the 9 and 14-year-old stands only small seedlings of less than 30cm occurred. This suggests that although *A. karroo* seeds germinate in the older stands, seedlings do not survive in the shaded undercover of rehabilitating stands and that these previously mined stands have senescent populations that are typical of shade-intolerant pioneers during forest succession (Finegan, 1996).

Due to self-thinning and the lack of recruitment, the density of *A. karroo* in the canopy layer showed a substantial decrease with stand age. However, the increasing biomass, productivity rate and flower and seed production of *A. karroo* in older mined stands, illustrated the dominance of the species. The high mortality rate among juveniles and low mortality among adults (type III survivorship curve) is typical of forest trees that may survive for extended periods in the canopy of “mature” forests (Barbour *et al.*, 1987).

Cluster analysis (calculated from density, height and basal area of *A. karroo* trees in the canopy layer) generally resulted in transects of similar ages

to be grouped together. This further suggests that vegetational development is taking place with age. Rainfall during the year of rehabilitation probably effected initial density, number of stems and basal area of *A. karroo* trees. Position of trees on a dune slope had only minor effects on the population. However, in the 14-year-old stand, individuals tended to be smaller towards the dune crests than those in dune valleys.

In mined stands all attributes of the developing woody broad-leaved communities and the associated changes in soil characteristics suggest that directional and cumulative changes are taking place. However, “classical” species replacement with predictable pathways and more or less discrete seral communities was not evident. Although species richness and diversity are not yet comparable to those for “mature” dune forests, these are increasing with stand regeneration age. The Bray-Curtis Similarity Index further showed that both in terms of species composition and density the mined stands are developing towards a more mature 35-year-old unmined stand.

The present study showed that vegetational development described for species-rich neotropical forests (Hubbell & Foster, 1986; Finegan, 1996) is similar to developments on the coastal dune forests in the Richards Bay area. The results also suggest that forest-type succession is taking place on previously mined stands at Richards Bay and that the rehabilitation programme has so far been successful.