

A COMPARISON OF THE REPRODUCTIVE STRATEGIES OF KEY
SPECIES OF A PROGRADING DUNE SYSTEM IN THE MLALAZI
NATURE RESERVE, NATAL.

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ABSTRACT

The succession on the dunes of the Mlalazi Nature Reserve represents a classical example of primary succession. The reproductive strategies of eight key species were compared to determine some of the mechanisms affecting the community dynamics, at the population level, in the early stages of succession.

There is a temporal separation in the flowering and fruiting phenologies. *Passerina rigida*, *Stipagrostis zeyheri* and *Imperata cylindrica* produced small seeds with a low fruit/seed mass ratio within a short cycle. The seeds are suitable for wind-dispersal. The animal-dispersed species; *Eugenia capensis*, *Mimusops caffra* and *Scaevola plumieri*, produced large fleshy seeds with a high fruit/seed mass ratio within cycles of six months and more. *Chrysanthemoides monilifera*, also an animal-dispersed species, produced a large quantity of small fleshy seeds throughout the year. The fern, *Microsorium scolopendrium* produced spores throughout the year. The staggered fruiting and flowering phenology ensures a year-round availability of fruit in the dunefield.

The key species formed less than half of the species composition of the soil seed bank. The size and range of the soil seed bank differed between the species. *P. rigida* and *S. plumieri* formed a high proportion of the seeds in the soil with a wide distribution along the successional gradient. The other species had low soil seed densities with short distribution ranges, or

were not present. *P. rigida* and *S. plumieri* are easily dispersed species, whereas the other species may have a more restricted and clumped distribution due to the effect of foragers. A high density of *P. rigida* and *E. capensis* seeds were found under the parent trees. Only seeds of *P. rigida* and *S. zeyheri* were found in the soil in the open. Seeds of *P. rigida*, *S. zeyheri*, *E. capensis* and *M. caffra* were found under the canopies of *P. rigida*, *E. capensis* and *M. caffra*. No seeds of *C. monilifera* and *I. cylindrica* were found in the soil, possibly due to predation.

The period of the study (September 1991 to November 1992) was in a dry or drought cycle with only 56.8% of the mean annual rainfall falling. Seed germination and seedling survival of all the species were affected by these dry, warm climatic conditions. The species had seedling densities of less than 4 seeds/m². The environmental conditions along the successional gradient also had an effect on seed germination and seedling survival. Environmental factors of soil pH, light intensity and surface soil temperatures were higher in the open than under canopy. Soil pH and the understorey cover decreased as the light intensity decreased from under the canopy of *P. rigida* to *M. caffra*. Litter cover and plant height increased. *E. capensis* had measurements intermediate to the two species, but had higher surface soil temperatures and plant height than *P. rigida*. Seedlings of *P. rigida* in the open and under the canopy of the parent plants had died by the end of the monitoring period. 50% of the seedlings of *S. zeyheri* under the canopy of *P. rigida* and *M. caffra* died. The mortality rate of the seedlings of

E. capensis was lower under *M. caffra* than under the parent plants. *I. cylindrica* may be propagated vegetatively. However, the mortality of the propagules was greater under the canopy of *E. capensis* than under *P. rigida*. *M. caffra* only germinated under the canopy of *E. capensis* with a 100% mortality of the seedlings. *M. scolopendrium* only produced propagules through vegetative propagation under the canopy of *E. capensis* and *M. caffra*. The mortality of the young ferns was less than 50% and less under *M. caffra* than under *E. capensis*. No seedlings of *C. monilifera* or *S. plumieri* were found. The seed distribution range, seed germination requirements and the effect of the environmental conditions on the germination of the seeds and seedling establishment of the species appear to important factors of the reproductive strategies regulating the size of the species populations along the successional gradient.

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CHAPTER 1

Introduction

1.1 INTRODUCTION

The plant species diversity, growth form and structure, and community complexity of the vegetation found on the prograding dunes of the Mlalazi Nature Reserve increases with an increase in the age of the dunes, from the young foredune to the rear dunes inland (Moll 1972; Weisser *et al.* 1982; Weisser & Backer 1983; Avis 1992; Avis *et al.* in preparation). This directional change in the vegetation represents a classic example of primary succession (Weisser *et al.* unpublished; van Daalen *et al.* 1986). No studies have been undertaken on the actual mechanisms of successional change taking place in this vegetation, but the pathway of species change along the successional gradient suggests that the Facilitation Model proposed by Connell & Slatyer may be applicable here (Avis 1992; Avis *et al.* in preparation). This project is a study of the mechanisms of successional change, at the population level, of the vegetation growing on the prograding dunes of the Mlalazi Nature Reserve.

The Facilitation model is an attempt by Connell and Slatyer (1977) to explain the pathway of primary succession, based on mechanisms they suggest cause succession after a perturbation. Implicit in the model, is the importance that the life-history characteristics of individual species have in determining the

pathways of succession (Noble & Slatyer 1980). A pathway of succession is defined by Pickett *et al.* (1987) as the "the temporal pattern of vegetation change", and a mechanism of succession as "an interaction that contributes to successional change".

It is proposed in the Facilitation Model that the "early-succession species modify the environment so that it is more suitable for later-succession species to invade and to grow to maturity" (Connell & Slatyer 1977). The species modify the environment mainly by occupying space, by forming a litter layer and creating shade.

The life-history pattern of a species is commonly classified according to the 'r- and K-selected' resource allocation spectrum proposed by MacArthur and Wilson (Barbour *et al.* 1987). The characteristic features of the patterns at the extreme ends of the spectrum may be described with respect to the position of the species along the successional gradient (Colinvaux 1986; Barbour *et al.* 1987). The r-selected species are adapted to invading and colonizing bare areas where unpredictable conditions are experienced. The species are characterised by a high output of small seeds with effective dispersal mechanisms. The seeds form a persistent soil seed bank where the seeds remain dormant until favourable conditions for germination and growth occur. The seedlings have a rapid growth rate to maturity and are usually shade-intolerant. The species have short life-spans with a high

fecundity and mortality rate.

The K-selected species are adapted to stable environments, typical of the later-successional sequences, where competition with other already established species occurs. Low numbers of fleshy animal-dispersed seeds are produced. Persistent seedling banks are formed after the seeds have been in the transient soil seed banks for a short period. The seedlings have a slow growth rate and are shade-tolerant. The species have long life-spans with a low fecundity and mortality rate.

Succession is caused mainly by site availability, species availability in the area and the performance of the species (Pickett *et al.* 1987). The performance of the species is affected by, among other aspects listed (Pickett *et.al.* 1987), such as environmental stress, competition, herbivory, the life-history strategy. "Life-history differences among species in a sere are important causes for their differential behaviours" (Pickett 1976). Succession can therefore be seen as a phenomenon arising from the differential colonizing ability, and the growth and survival of species adapted to the different environments occurring along the successional gradient (Drury & Nisbet 1973).

An important aspect of the life-history of a species is the reproductive strategy, by which new propagules are successfully produced. Events experienced during seed dispersal, germination and seedling establishment determine the fate of the individuals

(Grubb 1974; Harper 1977), and hence, the development of the population. The strategies have, therefore, evolved to ensure that the seeds survive the environmental conditions experienced during germination and seedling establishment (Duke 1990).

This study is an investigation into the mechanisms of successional change, which influence the effectiveness of the reproductive strategies of the key plant species along the successional gradient. Pickett *et al* (1987) define a mechanism as "an interaction that contributes to successional change". It is necessary to relate the pattern of species change with the mechanisms of species change to understand how succession operates (Pickett *et al.* 1987).

1.2 LOCATION OF THE STUDY SITE

The study site (28°59'00" S; 31°49'30" E) is situated within the Mlalazi Nature Reserve adjacent to the farm "Twinstreams", south of the town of Mtunzini (Figure 1).

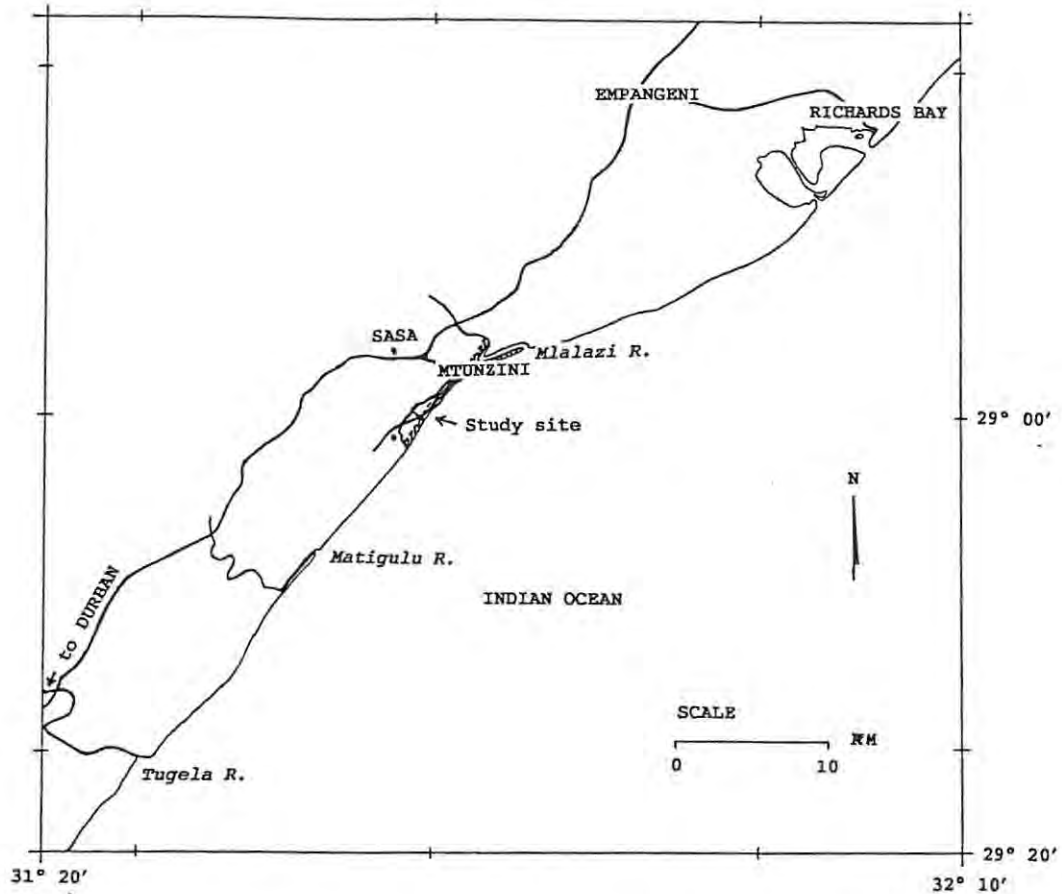


Figure 1. Location of the study site and the weather station (SASA). The hatched area indicates the location of the Mlalazi Nature Reserve.

1.3 CLIMATE

Climatic data from January 1966 to November 1992 was obtained from the South African Sugar Association Experiment Station (SASA), approximately 5 km north-west of Mtunzini. The monthly mean relative humidity recorded during the study period has been tabulated together with the mean of the data recorded monthly over the past twenty-six years and the mean of the data for the study period (September 1991 to November 1992) (Table 1).

Table 1. The monthly mean relative humidity for September 1991 to November 1992 is compared to the monthly mean for the past twenty-six years (January 1966 to November 1992). The monthly mean relative humidity was calculated from the mean of the readings taken at 8 a.m. and 2 p.m. daily.

MONTH	RELATIVE HUMIDITY (%)	
	STUDY PERIOD	1966 - 1992
September	86.5	71.0
October	90.5	71.5
November	87.0	72.5
December	77.0	72.0
January	82.5	72.5
February	81.5	74.5
March	76.0	74.0
April	68.5	74.0
May	65.0	72.5
June	58.5	70.0
July	67.0	69.5
August	69.5	70.0
September	71.0	71.0
October	67.5	71.5
MEAN	74.9	71.9

A climatogram has been constructed from the mean monthly rainfall and mean monthly temperatures, for the past twenty-six years and over the study period, for comparison (Figure 2).

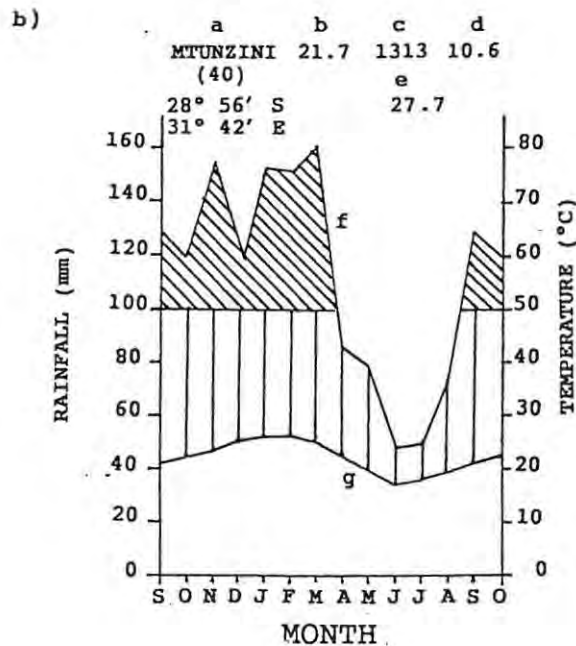
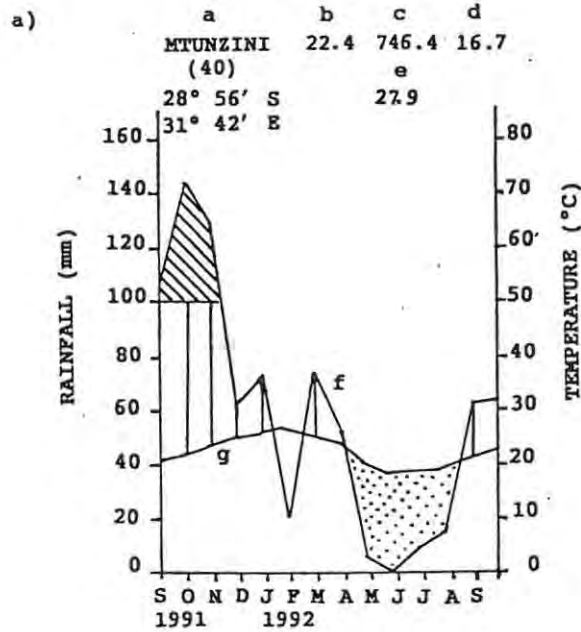


Figure 2. A Walter-Leith diagram of the mean monthly rainfall and temperature recorded from (a) September 1991 to November 1992 and, (b) January 1966 to November 1992 (a - elevation in metres; b - mean annual temperature; c - total mean precipitation; d - mean diurnal range in temperature; e - mean maximum annual temperature; f - rainfall curve; g - temperature curve). Diagram b has been presented for comparison with diagram a. Note the unusual dry period (stipuled).

The study area is warm to hot and humid in summer, and cool in winter (Schulze 1965). The prevailing winds alternate between north-easterly and south-westerly during the year.

A drier climate was experienced during the study period. In the past twenty-six years the area has had a high mean year-round rainfall of over 1000 mm, but only 56.8% was received during the study period (Figure 2a & b). The mean monthly rainfall figure is over 100 mm from August until April, but during the study period 100 mm per month was received only from September until December. The maximum amount of rainfall was received in October, the rainfall decreasing thereafter, until June when no rain was recorded (Figure 2a). Less than 100 mm per month were received to the end of the study period in November. The humidity was higher between September 1991 and April 1992, and lower for the rest of the study period than for the past twenty-six years (Table 1). The mean relative humidity between September 1991 and November 1992 was 3 % higher than the mean for the past twenty-six years. The mean monthly relative humidity ranged between 90.5 % in October 1991 to 58.5 % in June 1992. In comparison, the mean monthly relative humidity of the past twenty-six years ranged between 69.5 % in July to 74.5 % in February.

1.4 DUNE FORMATION AND SOILS

The dunefield in the study area is composed of a sequence of parallel ridges (Tinley 1985). Parallel dunes are formed as a

result of the seasonal silt load, which is washed down the Tugela River and other rivers south of the study area, being deposited onto the beach by the reverse inshore counter-currents of the Agulhas Current (Weisser & Backer 1983). The foredune is advancing at an approximate rate of 2.4 m per year (Weisser *et al.* 1982). Seventeen dune ridges extend from the most recent foredune colonized by *Scaevola plumieri*, of about two years old, to the oldest dunes covered by the Dune Forest, of about ninety years old (Weisser *et al.* 1982). The dune ridges have been numbered from 1, at the oldest dune ridge, to 17 at the foredune by Weisser. This dune number sequence has been adhered to in this study.

Edaphic changes along the successional gradient occur from the beach into the Dune Forest. The soils of the frontal dunes are light in colour and sandy compared to the soils of the dunes covered by the late-successional stages (Moll 1972). The soil pH decreases as the age of the dune and the diversity and structure of the community increases. The mineral content (phosphate, potassium, sodium, calcium and magnesium) also increases (Avis 1992; Avis *et al.* in preparation). The organic matter content increases, forming a thicker layer in the later-successional stages than in the earlier stages (van Daalen *et al.* 1986).

1.5 STUDIES ON THE VEGETATION

The communities of the vegetation covering the dunes in the study

area were first described by Edwards (1967). Moll (1972) wrote a preliminary account of the structure of the communities and the environmental factors affecting the vegetation. He was the first to recognise the importance of the area as a classic example of primary succession. A description of the communities is given in section 1.6.

The rate at which dune advancement occurs and the vegetation-succession chronology has been determined from aerial photographs by Weisser *et al.* (1982) and Weisser & Backer (1983). They calculated the time taken for a community to become established and the approximate duration of each sere, using the estimated rate of advancement of the foredune from 1937 to 1977. These results are discussed in section 1.6.

Floristic and structural changes and processes occurring in forest succession were studied during the third annual Forest Biome Workshop (van Daalen *et al.* 1986). It was determined that the seres can be clearly distinguished using species composition, and that the succession is continuous. The development of the communities around bush clumps was identified as the main pathway of community development. Seed dispersal and edaphic processes were identified as the most important ecological processes affecting the vegetation change. Weisser has continued to monitor the vegetation change in the plots laid out during the workshop.

The community structure, floristic and edaphic changes along the

chronosequence were assessed by Avis (1992) and Avis *et al.* (in preparation), using the DECORANA and TWINSpan programs to determine whether the succession supports the Facilitation Model. The authors concluded that the change in species composition and diversity, with a corresponding development in the soil, from the foredune inland provide evidence in support of the Facilitation Model as the primary pathway of successional change.

Pamenter *et al.* (1985) assessed the regeneration of the forest following a fire by monitoring the regeneration of vegetation in permanent plots laid out in burnt and unburnt areas. The authors found that some species propagated only from seed and others only from clones. Only a few species utilized both methods.

Frost has made a study of the phenology of the Dune Forest species and avian dispersal of their seeds in the 1980's. This information is unseen and unpublished. This study represents the first autecological investigation on key species in this successional sequence.

1.6 COMMUNITY STRUCTURE

Moll (1972) described three community types: Pioneer, Dune Scrub and Dune Forest. Weisser & Backer (1983) described the Dune Scrub community as the Open Dune Scrub and the Closed Dune Scrub. Avis (1992) classified eight plant communities based on the Two Way Indicator Species Analysis (TWINSpan) procedure. The author

mention that only seven are easily identified in the field by using the differential species and the species composition of the communities.

The following is a description of the community types according to Moll (1972), Weisser and Backer (1983) and Avis (1992). Only the communities which can be identified in the field have been described here.

1. Foredune/Dune Pioneer

The pioneer dune colonizer, *Scaevola plumieri* is the dominant species. Other creeping herbaceous species are also present. The community has a single plant layer with a low species diversity and percentage plant cover.

2. Enriched Foredune

S. plumieri continues to be a dominant species. Other dominant species present are *Ipomoea pes caprae* and *Senecio littorosus*. The presence of these species indicates that the dunes have become relatively stable compared to the foredune. There is a greater variety of growth forms in the community. Plant cover increases to about 50% and the species richness to about 15.

3. Open Dune Scrub

This sere is dominated by *Passerina rigida*, *Stipagrostis zeyheri*, *Carpobrotus dimidiatus* and *Helichrysum asperum*. Plant cover is between 60 - 70% and the species richness is about 24. The

community has a field and a shrub layer.

4. Closed Dune Scrub

The dominant species are *Eugenia capensis*, *Helichrysum appendiculatum*, *Colpoon compressum*, *S. zeyheri* and *Imperata cylindrica*. Plant cover is between 70 - 80% and the species richness is about 23. Dune forest canopy species are now present and form a thicket with the shrub species. The fern, *Microsorium scolopendrium* forms a layer with the grass species, *S. zeyheri* and *I. cylindrica*.

5. Bushclump

The community has three strata. The field layer is dominated by *S. zeyheri*, *I. cylindrica* and *M. scolopendrium*. The shrub layer is dominated by *Maytenus heterophylla* and *E. capensis*. The tree layer is dominated by *Psydrax obovatum* and *Mimusops caffra*. Plant cover is almost 100% and the species richness is about 35.

6. Forest Margin

This community is similar in structure to the Bushclump community, but the early-succession species are now absent and the forest species predominate. Plant cover is over 100%, although the species richness has remained at about 35.

7. Dune Forest

In the young dune forest, the field layer is dominated by *M. scolopendrium* and the sub-canopy layer is dominated by

Peddiea africana and *Kraussia floribunda*. The canopy layer is dominated by *M. caffra*, *Sideroxylon inerme* and *Allophyllus natalensis*. Plant cover is over 100% and the species richness is greater than at the forest margin. In the older dune forest the species diversity remains high, but *M. scolopendrium* is replaced by *Isoglossa woodii*.

Weisser and Backer (1983) calculated the following succession chronology using the estimated rate at which the foredune advances annually. The pioneer community persists for about 13 years before the species of the Open Dune Scrub community become dominant; the Closed Dune Scrub community can be recognized after a longer period of about 58 years, and the Dune Forest can be recognized after about 119 years.

1.7 DESCRIPTION OF THE KEY SPECIES

Eight species were subjectively identified as key species of the first five communities, described in section 1.6. The species are locally common in the different seres and, therefore, have an influence on the structure of the seral communities. Species from the late-successional stages, the Forest Margin community and the Dune Forest community were excluded from the key species selection list for the study. Succession progresses along a relatively linear pathway in the early stages of succession, but appears to become a multiple-pathway in the later stages of succession (Avis 1992). The main mechanisms causing species

replacement becoming less distinct and more variable.

The following is a description of the attributes and distribution range of each of the selected species along the successional gradient. Their distribution range along the successional gradient is shown in Figure 3. The species are listed according to the order in which the community they influence, is situated along the successional gradient. The species are ordered from the Foredune community to the Bushclump community.

The descriptions of the shrubs and trees were taken from Dyer *et al.* (1963), Palmer & Pitman (1972) and Palmer (1977). The descriptions of the herbs were taken from Ross (1972) and Dyer (1976), and the description of the fern from Jacobsen (1983) and Schelpe & Anthony (1986). The descriptions of the grasses were taken from Gibbs Russell *et al.* (1990). The distribution range of the species in the study area were taken from Avis (1992).

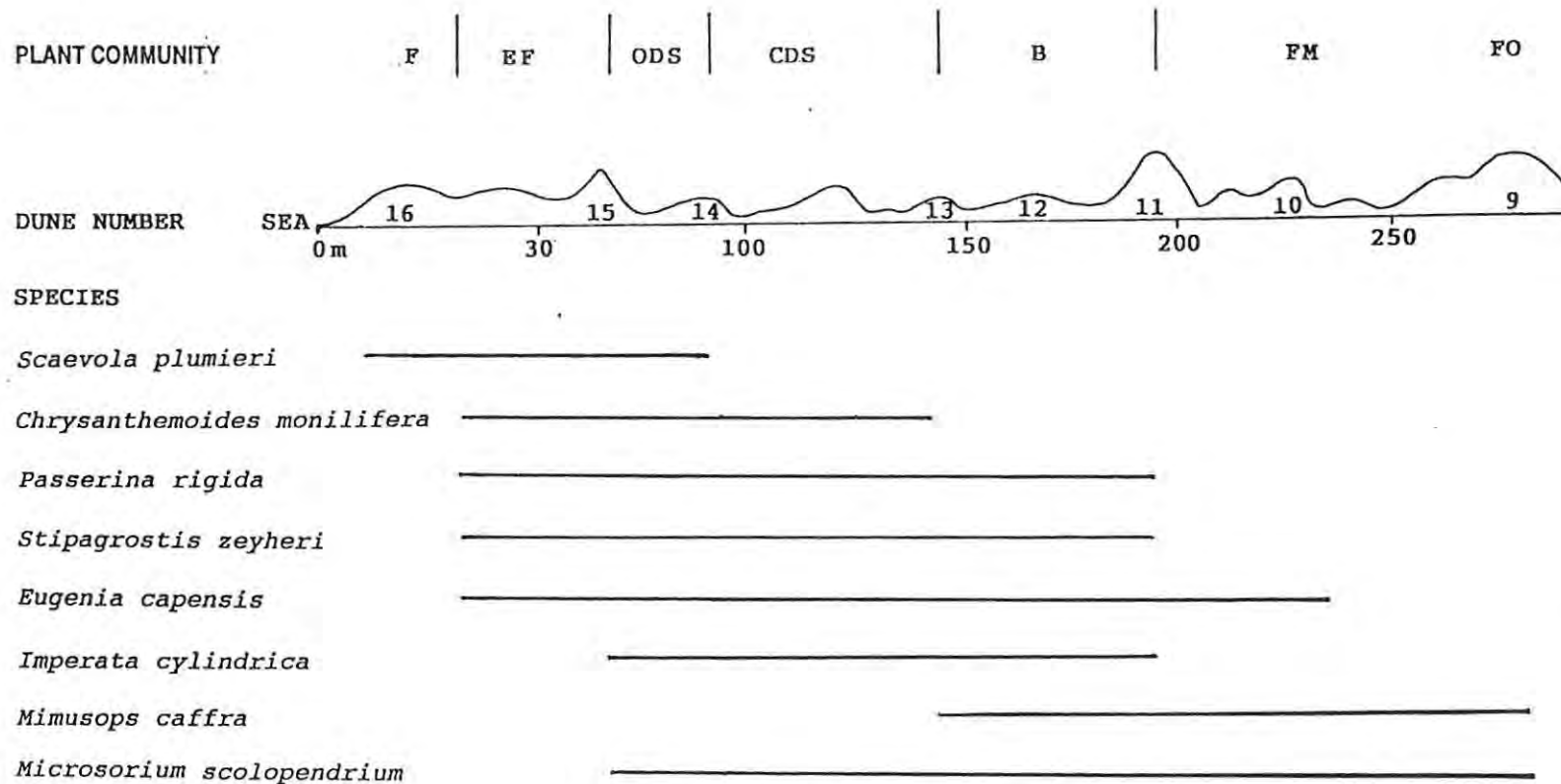


Figure 3. The distribution range of the species along the successional sequence according to the abundance values (Avis 1992) (F - Foredune; EF - Enriched Foredune; ODS - Open Dune Scrub; CDS - Closed Dune Scrub; B - Bushclumps; FM - Forest Margin; F - Dune Forest). The dune profile is adapted from transect three completed in 1987. Dune 17, which has developed since, is not included.

1. *Scaevola plumieri* (L.) Vahl (GOODENIACEAE) is pantropical and distributed from Somalia to the Cape Province (Thieret & Brandenburg 1986). The species is a common dune pioneer in Natal. It is a rhizomatous creeping shrub with erect stems. The dunes are formed by the moving sand being trapped by the creeping rhizomes of the plants (Steinke & Lambert 1986). The plants extend their range on the sand by stem elongation with adventitious roots, as well as by clonal and seed propagation. The species has no special physiological adaptations to the foredune environment, but is tolerant of salt-spray and sand abrasion (Pammenter 1983). The success of the species as a pioneer dune colonizer is possibly due to the ability of the plants to grow ahead of the sand accumulating between the stems (Pammenter 1983). White flowers and fleshy drupes are produced. The drupes are yellow and dark red in colour when ripe, and may contain one or two seeds. The fruits can be dispersed by water, wind and birds (Thieret & Brandenburg 1986). The species is distributed from the Pioneer zone on the foredune into the Open Dune Scrub community (Figure 3).

2. *Chrysanthemoides monilifera* (L.) T.Norl. subsp. *rotundata* (DC.) T.Norl. (ASTERACEAE) is a widespread creeping shrub. Plants are found along the coastal belt from Mozambique to the eastern Cape Province. Bright yellow flowers are produced on solitary flower heads, or as a group of a few flower heads in the axils of the leaves and at the ends of the branches. The outer florets of the flowers form the fruits. The fruits are fleshy and drupe-

like. When ripe the fruits are purple-black in colour and contain one kernel. The fruits are produced in a group within a flower head and are dispersed by birds (Bruton 1992). The species is distributed from the Enriched Foredune community into the Closed to the Forest Margin community (Figure 3)

3. *Passerina rigida* Wikstr. (THYMELAECEAE) is a woody shrub, which grows in the troughs of the dunes after they have been stabilized by *Scaevola plumieri*. The plants are distributed along the coast from Zululand to the Cape Flats in the Cape province. Small yellow, cream or reddish flowers are produced towards the ends of slender forked branchlets. Small round fleshy fruits are produced, which are orange when ripe and contain one seed which is bird-dispersed (Tinley 1985). The species occurs from the Enriched Foredune community into the Bush Clump/Forest Margin community (Figure 3).

4. *Stipagrostis zeyheri* (Nees) De Winter subsp. *barbata* (Stapf) De Winter (POACEAE) is a tufted perennial grass on coastal dunes, from northern Natal to the southern Cape Province. The leaf blades bend over and the inflorescence is paniculate and open. The glumes have three plumose awns. A hard projection, which aids dispersal, is found at the base of the floret. The spikelets are solitary and form a dispersal unit, the grain, which disarticulate above the glumes. The glumes are long compared to the awnless lemmas. The grain is slender and spindle shaped with a fused pericarp, and is dispersed by wind. The species is

distributed from the Enriched Foredune community to the Forest Margin community (Figure 3).

5. *Eugenia capensis* (Eckl. & Zeyh.) Harv. ex Sond. (MYRTACEAE) is an evergreen coastal tree species, with a distribution range from the eastern Cape Province to Mozambique. The plants can grow almost down to the water-level. Small white flowers with numerous stamens are produced. The fruit is a round tipped drupe with the remains of a calyx, and is purple-black in colour when ripe. Each drupe contains one stone which is dispersed by animals. The species is distributed from the Enriched Foredune community into the Forest Margin community (Figure 3).

6. *Imperata cylindrica* (L.) Raeuschel (POACEAE) is a perennial rhizomatous grass, common in southern Africa. The inflorescence is paniculate with short contracted branches and spikelets arranged in pairs. The species is dioecious with 2 florets per spikelet, of which only the female is fertile. The spikelet forms the dispersal unit, the grain, which is released from the inflorescence with the glumes attached. The glumes have long silvery hairs attached from the base. The species is distributed from the Open Dune Scrub community into the Bush Clump/Forest Margin community (Figure 3).

7. *Mimusops caffra* E.Mey. ex A.DC. (SAPOTACEAE) is a common coast forest tree, with a distribution range from the Eastern Cape to Mozambique. Slender oval rusty-brown flower buds form in small

groups of 2-4 in the leaf axils. The flowers are white and the fruits a fleshy round to oval drupe, crowned by a persistent calyx and style. When ripe the fruits are red and contain one seed which has a shining brown testa. The fruits are dispersed by animals. The species is distributed from the Bushclump community into the Dune Forest community (Figure 3).

8. *Microsorium scolopendrium* (Burm.f.) Copel. (FILICALES) is a coastal fern in southern Africa, common in the undergrowth of the dune scrub and the dune forests. The plants form colonies in shade and partial shade, sometimes covering the ground to the exclusion of other understorey species. Glossy fronds are produced along the widely creeping rhizome. The young fronds are occasionally simple. Propagules are produced through sexual and asexual propagation. Sori, containing spores, are produced at all times of the year, in one to two regular or irregular lines on either side of the costae. The species is distributed from the Open Dune Scrub community into the Dune Forest community (Figure 3).

1.8 AIM AND OBJECTIVES

The aim of the study was to obtain information on the community dynamics and ecological processes regulating species change along the successional gradient, at the population level. The objectives of the study were to compare the reproductive strategies of the eight key species described in section 1.7. The

species occupy different positions within the successional sequence and are ,therefore, expected to show differences in their reproductive strategies in ensuring seed germination and the establishment of the seedling in the different environments found along the successional gradient.

The key questions asked in this study were:

Do the species differ in:

1. the timing of the flowering fruiting phases during the reproductive cycle,
2. the size of seed and number of seeds produced,
3. the type and range along the chronosequence of the soil seed bank,
8. the response of the seed to environmental conditions, and
7. the seed germination and seedling establishment success rate.

CHAPTER 2

Phenology and seed production

2.1 INTRODUCTION

Phenology is "the study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species" (Leith 1974).

The timing of the phases, such as the flowering and fruiting phases, are regulated by the endogenous rhythm and the environment. Environmental factors, such as the seasonal changes in temperature, moisture and photoperiod have the most significant effect on the timing of the phases (Rathcke & Lacey 1985). Other environmental factors may include the availability of pollinators and dispersal vectors, the availability of and competition for resources and the avoidance of predators (Pierce 1984; Rathcke & Lacey 1985). The past and prevailing environmental conditions and availability of resources affect the physiological condition of the plant. The physiological state of the plant determines the amount of resources that will be allocated to reproduction and growth during a cycle (Fenner 1985).

Seed number and seed size are characteristics of the life-cycle strategies of species (Fenner 1985). The resources allocated to

reproduction are related to the predictability of the environment (Fenner 1985). Colonizing species which invade unstable environments have a high output of seeds. The survival of the propagules are independent of density. The species of the later-successional stages differ from the colonizing species by producing fewer seeds, and the survival of the propagules is density-dependant. Seed size and seed number are, however, alternate strategies in the allocation of resources to reproduction (Harper *et al.* 1970), and are a compromise with the environmental factors for dispersal (Fenner 1985). Species which are wind-dispersed produce many small seeds, whereas animal-dispersed species produce fewer and larger seeds. Seed number is a phenotypic character (Harper 1977), whereas seed size and shape are genotypic, and are relatively constant within a species (Rathcke & Lacey 1985).

Seed size is related to the environmental conditions for germination, seedling establishment (Stebbins 1971) and the successional status (Fenner 1985). Large seeds are more shade-tolerant, but have a lower dispersal capability and growth rate than small seeds. Large seeds are, therefore, more successful with a higher survival rate in the later stages of succession than in the earlier stages, where the small seeds are more successful.

The aim of this section is to compare the regenerative capabilities of the species relative to their location in the

successional sequence. The objectives of this section are to compare the phenological patterns of the species, and to compare the seed output and the seed size, for surviving the different environmental conditions experienced along the successional gradient.

2.2 METHODS

2.2.1 Phenology

The flowering and fruiting phenology of seven species (described in section 1.7); *Scaevola plumieri*, *Chrysanthemoides monilifera*, *Passerina rigida*, *Stipagrostis zeyheri*, *Eugenia capensis*, *Imperata cylindrica*, and *Mimusops caffra* were monitored for thirteen months.

The start of the reproductive cycle, and consequently seed production, has been found to vary along a successional gradient within a species (Roos & Quinn 1977; Cartica & Quinn 1982; Escarré & Thompson 1991). The individuals of each species were, therefore, selected from the zones in which they dominate, to ensure that an adequate number of individuals showing reproductive activity could be randomly selected in the same area. This reduced the effect of spatial variation on the timing of the reproductive phases within the species, and ensured that the selected individuals were reproductively active when the majority of individuals of the species were active.

The zones from which the individuals were selected for each species were identified in the field according to the descriptions of the communities (section 1.6, Chapter 1) given by Moll (1972), Weisser and Backer (1983) and Avis (1992).

Ten individuals of each species were selected. Three side-branches, on different sides of the trees and shrubs, were selected at random on each individual. One flowering-head, defined in this study as the branches carrying the flower and fruit inflorescences, on each side-branch was selected, and tagged with coloured electrical tape. The tape marked the length of the flowering-head to be monitored for reproductive activity. The lengths differed between species due to the differences in growth form. The lengths varied from 5 cm in *P. rigida* to 40 cm in *S. plumieri*. *P. rigida* has ericoid leaves, whereas *S. plumieri* has leaves over 5 cm long. Three inflorescences from each of the ten individuals of the two grass species, *S. zeyheri* and *I. cylindrica* were tagged. *M. scolopendrium* was only observed for the presence of ripe sori.

A phase of phenology is a phenophase, which is defined as "an observable stage of plant development...that is accomplished by an individual in a given site...during a precise period of observation" (Monasterio & Sarmiento 1976). The phenophases monitored in this study were defined as follows:

Flowering : a) buds or flowers closed or partially open.
 : b) open flowers, stigma, style and anthers exposed.

Fruiting : a) immature or unripe fruits, usually green or yellow.
: b) ripe fruits, usually red or purple-black.

Phenological records were obtained every three to four weeks, from September 1991 to October 1992. Data on the number of buds, open flowers, immature fruits and ripe fruits were obtained by counting the number on the marked flowering-heads on each visit.

A phenodiagram of the number of individuals in each phenophase was constructed. A species was considered to be in a particular phase at a certain time when at least 30% of the individuals had buds, open flowers, immature fruits or ripe fruits.

2.2.2 Seed production

The total number of seeds produced per plant per m² in one year was calculated for each species. The fruiting phase data collected during the monitoring period, when the fruits were unripe, was used for this calculation. At this stage of fruit development there is less chance that seeds could be lost, which would affect the accuracy of the calculation. The following formula was used:

$$TS/30 \times FH = SO$$

where, TS = total number of seeds counted for 10 plants
30 = total number of tagged flowering heads per plant
FH = mean number of flowering heads per individual
SO = number of seeds produced per plant

The estimated number of flowering-heads (FH) was determined by counting the number of branches to, and including, the flowering-heads in a branch order starting from ground level (Figure 4). A single branch was followed from the base of the plant to the approximate size of the tagged sections of the species, the branching order increasing as the branch divided further.

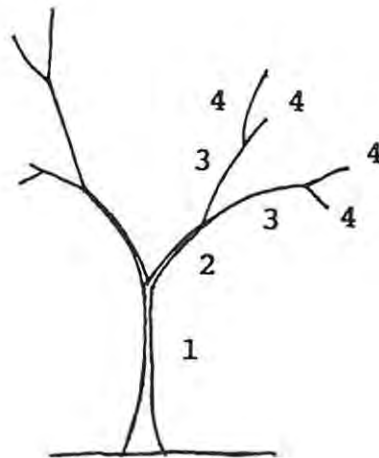


Figure 4. The branching order of the plants used to make an estimate of the seed output. 1 refers to the main stem. The branch order increases each time as the branches divide until the last division ends in the flowering-head section.

The total number of seeds produced in a year was multiplied by the number of plants per m². The number of plants per m² of each species was obtained from the raw data collected by Avis (1992), calculated from the number of plants counted in 36 sample plots, each with 25 quadrats of 1 m², along three transects from the foredune into the Dune Forest community. The results were plotted on a graph.

2.2.3 Seed size

A sample of fruits was collected from each species when the fruits were ripe. The fruits were collected from a number of individuals of each species. One hundred fruits of each of the species were collected at random and weighed with the flesh, as a fruit, and without flesh. Weight is used as an index of size as seed shapes are variable and seed volume is, therefore, difficult to measure (Willson 1983). A ratio of the fruit to seed mass was calculated, and all these results tabulated.

2.3 RESULTS

2.3.1 Phenology

The timing of the phenophases are shown in the phenodiagrams in Figure 5, and rainfall and temperature in Figure 2. The phenology of each species will be considered separately.

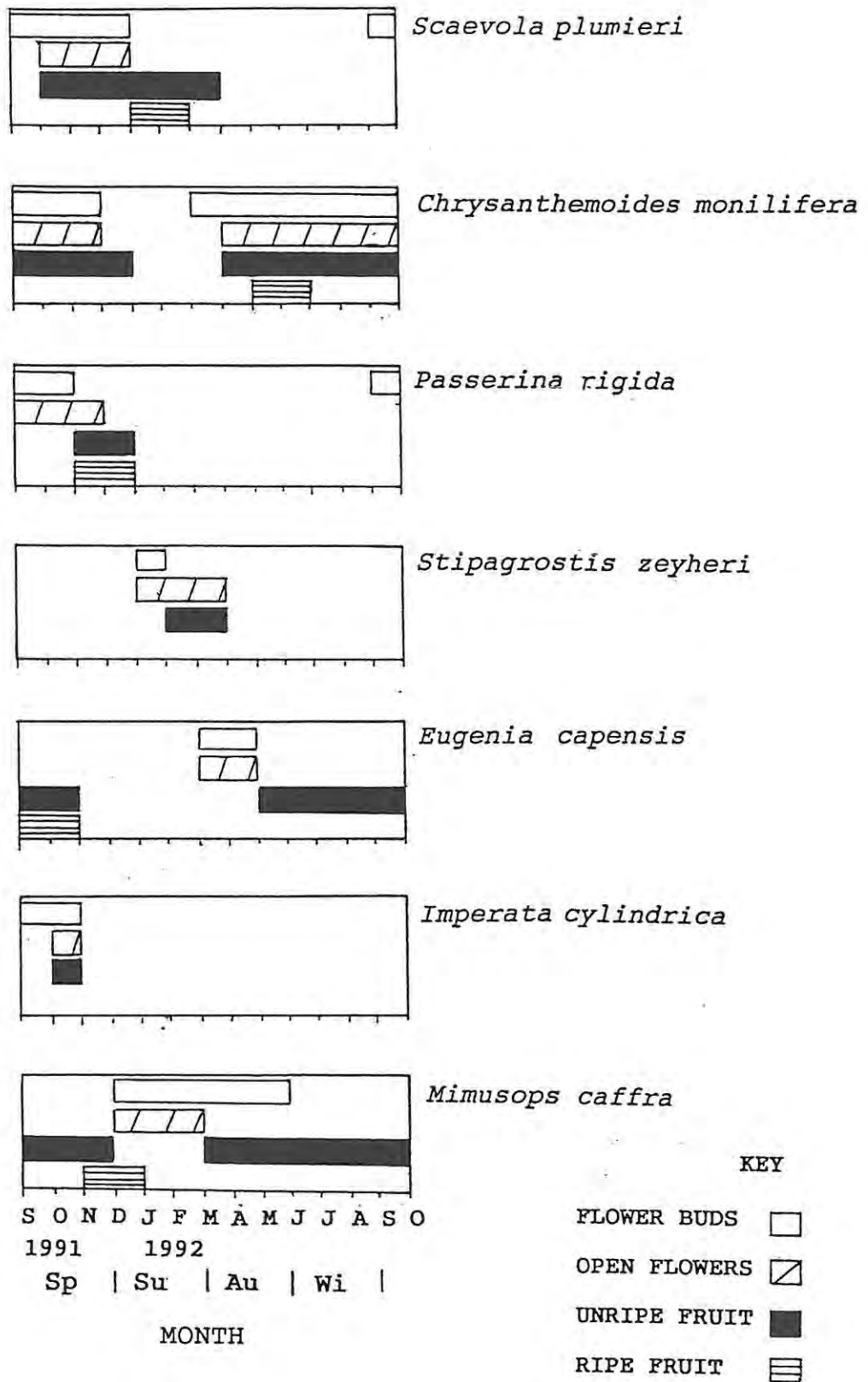


Figure 5. Phenodiagrams of the flowering and fruiting phenology of the key species. The monitoring period began in September 1991 and ended in October 1992. (Sp - Spring; Su - Summer; Au - Autumn; Wi - Winter).

Scaevola plumieri (L.) Vahl

Flower buds were on the plants when the monitoring period began in early-spring. The flowers were open by mid-spring and fruits had begun to develop. The fruits started to ripen in mid-summer and were only ripe six months later. Ripe fruits were available in January and February. The cycle continued from the beginning of spring until mid-autumn, when rainfall and the ambient temperatures were high.

Chrysanthemoides monilifera (L.) T.Norl. subsp. *rotundata* (DC.)
T.Norl.

Flower buds, open flowers and unripe fruits were present when the monitoring period commenced, and were present simultaneously for most of the year, but ripe fruits were abundant for only a few months, in late-autumn/early winter. Ripe fruits were observed and counted during the cycle, but were low in number or were not present on the tagged branches at the time of collecting the data. No reproductive activity was evident from mid-summer until the beginning of autumn. The cycle continued from autumn until the end of spring. The climate during this period was drier and cooler than the rest of the year. New flowering-heads had to be selected at times during the monitoring period as the tagged flower-heads were lost through browsing by animals.

Passerina rigida Wikstr.

Flower buds were present and flowers were open in early-spring, when the monitoring period commenced. Fruits were produced and

were ripe from late-spring. Ripe fruits were available in November and December, and had been dispersed by mid-summer. The cycle began in early-spring when the rainfall was increasing, but the ambient temperatures were still low. The cycle was completed by mid-summer.

Stipagrostis zeyheri (Nees) De Winter subsp. *barbata* (Stapf) De Winter

The cycle began in mid-summer, and was completed by the beginning of autumn when the rainfall and ambient temperatures had begun to decrease. The grains were released in February and March.

Eugenia capensis (Eckl. & Zeyh.) Harv. ex Sond.

Unripe and ripe fruits were on the plants when the monitoring period began in early-spring. The seeds had been dispersed by late-spring. A new cycle started with flower buds appearing in early-autumn. The individuals initially selected became reproductively inactive after the cycle had ended, and new individuals had to be selected to continue the monitoring. Fruits were produced towards the end of autumn, and were ripe from the beginning of spring, in September and October. The cycle continued from early-autumn until late-spring the following year.

Imperata cylindrica (L.) Raeuschel

The cycle began in early-spring, in September, when flower buds were present. Open flowers and unripe fruit appeared the following month, and the cycle was completed before the end of

spring. Grains were dispersed in October. No reproductive activity was noted during the rest of the monitoring period.

Mimusops caffra E.Mey. ex A.DC.

Unripe fruits were counted at the beginning of the monitoring period, in September. The fruits were ripe by the end of spring, in November, and were available until December. The next cycle started in early summer, before the last cycle had been completed. Flower buds began to develop at the beginning of summer. Open flowers were present during summer and fruits were counted from early-autumn. The fruits were still immature by the end of the monitoring period.

Microsorium scolopendrium (Burm.f.) Copel.

Unripe and ripe sori were observed on different individual plants throughout the monitoring period, on different individuals, suggesting that the plant is reproductively active throughout the year.

2.3.2 Seed production

The estimated total number of seeds produced by each species, during the twelve months of the monitoring period, is shown in Figure 6.

The results are estimated values. It was difficult to obtain an accurate count of the fruits during the monitoring period for the

following reasons: fruits persisted on the plants and were therefore counted more than once on different recording days; and, fruits developed and became ripe or were lost from the plant in the interval between recording days. The results are, therefore, an underestimate rather than an overestimate of the annual output of seeds.

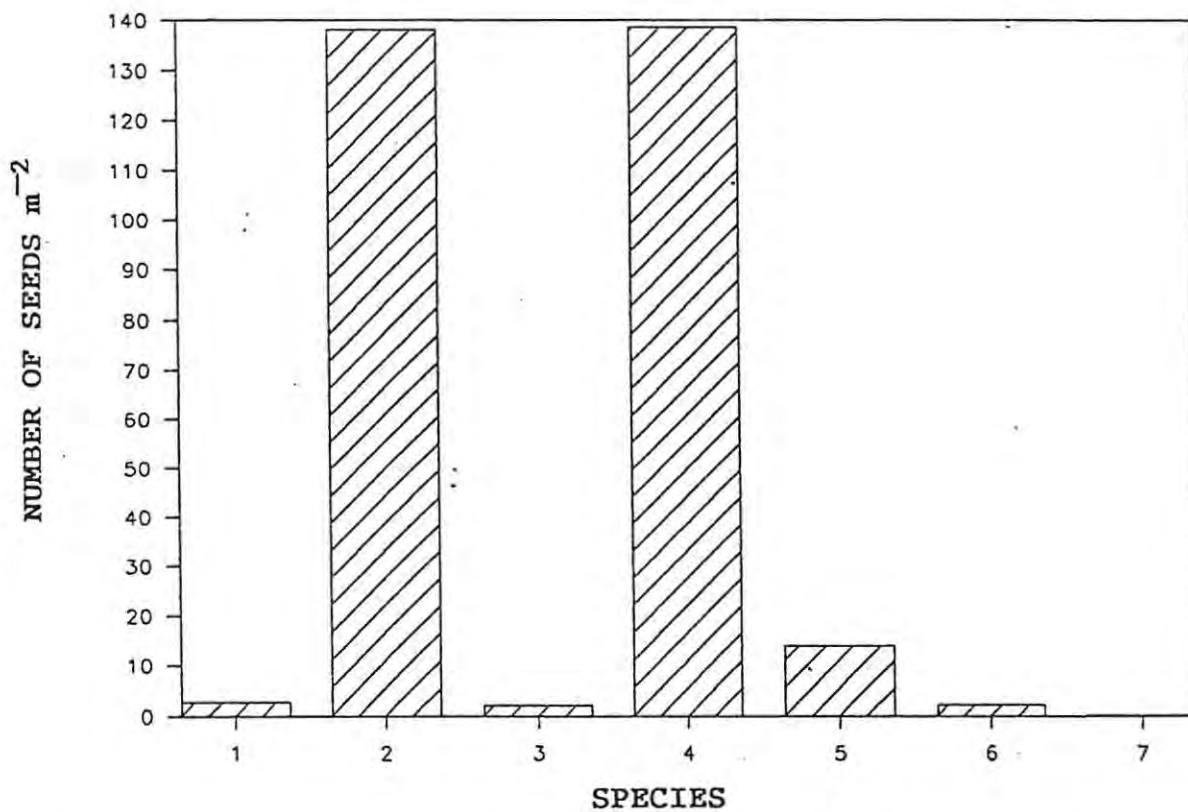


Figure 6. The estimated seed output after one year (1 - *Scaevola plumieri*; 2 - *Chrysanthemoides monilifera*; 3 - *Passerina rigida*; 4 - *Stipagrostis zeyheri*; 5 - *Eugenia capensis*; 6 - *Imperata cylindrica*; 7 - *Mimusops caffra*).

S. zeyheri and *C. monilifera* produced the greatest number of seeds during the monitoring period. They both had an output more than 9 times the output of *E. capensis*, *S. plumieri*, *P. rigida*, *I. cylindrica* and *M. caffra*. *E. capensis* had an output more than 7 times greater than *S. plumieri*, *P. rigida*, *I. cylindrica* and *M. caffra*. *M. caffra* had the lowest output of less than 1 seed per plant per m².

2.3.3 Seed size

The results of the mass measurements of the seeds and the fruit/seed mass ratio are presented in Table 2.

Table 2. Seed mass (mean \pm 1 S.E., n = 10) and fruit mass to seed mass.

SPECIES	MASS (g)	RATIO (g)
<i>Scaevola plumieri</i>	0.44 \pm 0.04	71.1
<i>Chrysanthemoides monilifera</i>	0.03 \pm 0.004	28.0
<i>Passerina rigida</i>	0.003 \pm 0.001	13.3
<i>Stipagrostis zeyheri</i>	0.006 \pm 0.002	-
<i>Eugenia capensis</i>	0.21 \pm 0.03	33.5
<i>Imperata cylindrica</i>	0.002 \pm 0.001	-
<i>Mimusops caffra</i>	0.20 \pm 0.02	80.0

S. plumieri produced the heaviest seed of the seven species. *M. caffra* and *E. capensis* produced lighter seeds of a similar size,

but *M. caffra* had a higher fruit to seed mass ratio than *E. capensis* or *S. plumieri*. *E. capensis* had a lower fruit to seed mass ratio than *S. plumieri*, but which was higher than *C. monilifera* or *P. rigida*. *P. rigida* produced a light seed smaller, than *C. monilifera*, and with the lowest fruit to seed mass ratio. *S. zeyheri* and *I. cylindrica* also produced light seeds. The grain mass of *S. zeyheri* and *I. cylindrica* is the same as the seed mass, as the pericarp was inseparable from the seed. The ratio was therefore, not calculated.

2.4 DISCUSSION

A comparison of the phenodiagrams of *S. plumieri*, *C. monilifera*, *P. rigida*, *S. zeyheri*, *E. capensis*, *I. cylindrica* and *M. caffra* show that the flowering and fruiting phases commenced at different times of the year (Figure 5). Three groups of strategies were evident. Group 1 consists of *P. rigida*; *I. cylindrica* and *S. zeyheri*, which have short flowering and fruiting phases completed in spring and summer. Group 2 consist of *M. caffra*; *E. capensis* and *S. plumieri*. These species have a short flowering phase with a long fruiting phase of half a year and more. The ripening of the fruits occurs gradually over many months. *C. monilifera*, which forms group 3, produces flowers and fruits simultaneously throughout most of the year.

There are several advantages to this observed temporal separation in the phases between the species. Competition for pollinators

and dispersers is reduced (Rathcke & Lacey 1985), seed predators may be avoided (Willson 1983), and the seeds are disseminated at that time of year when conditions meet the germination requirements of the seeds, which do not become dormant on being dispersed.

The timing of the phases are closely associated with climatic factors, such as rainfall (Etherington 1982; Willson 1983), and many studies have shown the relationship between phenophases and climate (Monasterio & Sarmiento 1976; van Rooyen *et al.* 1979; Opler *et al.* 1980; Cordazzo and Seeliger 1988). Although, the data size was too small to obtain significant correlations with climate, it appears that the timing of the phases in this study is connected to rainfall, temperature and humidity when the phases (Figure 4) are visually compared to the climatic data (Figure 2 & Table 1). Most of the species, except *C. monilifera* and *E. capensis*, began to flower when rainfall, humidity and the ambient temperatures were high in spring and summer. *E. capensis* began to flower when the rainfall and ambient temperatures were increasing after the cool dry winter period. The fruits of most of the species, except *S. zeyheri* and *C. monilifera*, began to ripen in spring and summer. The fruits of *S. zeyheri* began when the rainfall and ambient temperatures were decreasing. Only the phenology *C. monilifera* did not appear to be influenced by climate. Flowers and fruits were produced simultaneously throughout the year, except during the months of January and February when the highest ambient temperatures were recorded.

Although, climatic factors, such as photoperiod, temperature and moisture initiate the onset of flowering, ensuring synchrony between the species, they have a greater effect on the rate of fruit maturation, and less on the onset of fruiting (Rathcke & Lacey 1985). The timing of the fruiting phase shows a greater difference between the species than in the timing of the flowering phase, in this study, which may be related to how the seeds are dispersed.

There is a compromise between the seed production and seed size (Harper et al. 1970) as large seeds are more expensive to produce than small seeds (Harper 1977). There is thus, also a compromise between the number of seeds produced and the method of dispersal (Fenner 1985).

The results of the number of seeds produced in one year (Figure 6), the mass measurements (Table 2) and phenological cycle (Figure 4) and dispersal mechanisms, of each species, is discussed with respect to the position of the species along the successional gradient (Figure 3).

Scaevola plumieri (L.) Vahl

The seed output for the year was lower than is expected for a colonizing species (Fenner 1985), the seed is, however, large and has a high fruit/seed mass ratio. The large food reserve in the fruit enables the seed to be independant of the soil until a good root system has been developed (Harper 1977; Fenner 1985). Large

seeds also tend to produce seedlings, which attain the adult form more quickly than small-seeded species (Harper 1977), which is advantageous on the frontal dune where the young plants may be buried by the shifting sand. The species will, therefore, have an advantage over the smaller-seeded species with higher seed outputs, to colonize and become established on the frontal dune.

The duration of the phenological cycle is intermediate to the species which are wind-dispersed, and those which are animal-dispersed. The fruit maturation period is about six months. A long fruit maturation phase is characteristic of large-seeded species (Willson 1983), in which the fruits undergo many physiological changes before they are ripe (Stebbins 1971). The fruits can be dispersed in a number of ways such as by water, wind, animals (mainly birds) or by rolling down a dune slope (Thieret & Brandenburg 1986). The seeds are, therefore, more easily dispersed than other animal-dispersed species, *E. capensis* and *M. caffra*.

Chrysanthemoides monilifera (L.) T.Norl. subsp. *rotundata* (DC.)
T.Norl.

This species is the most prolific seed producer of all the species. The drupe-like fruits are produced for most of the year. The seeds are contained in a drupe-like fruit with a fruit/seed mass ratio intermediate to the large-seeded species, and the small seeded species. The seed is, therefore, able to survive in the conditions of hot dry sands of the early stages of succession

for a short period of time.

The species has opted for a strategy, in which many small seeds are produced, but which still have a high nutritive value to attract foragers (Dirzo & Domínguez 1986). Thus, the species has adapted to animal-dispersal instead of wind-dispersal, but has the potential to invade areas as fast as the small-seeded wind-dispersed species and into areas where wind-dispersal is inefficient, with a higher seed output.

Flower and fruits are produced simultaneously. This has been observed in populations in the south-western Cape (Knight 1986). Knight concluded that the prolonged fruit display of *C. monilifera* provides the frugivores with a supply of fruits for the frugivores when other fruiting species are reproductively inactive.

The phenodiagrams show that ripe fruits are only available for a few months of the year, however ripe fruits are present though usually in low numbers for most of the year. The low ripe fruit count obtained in this study may be due to a short maturation period. Large seeds require a longer maturation period than small seeds (Willson 1983). Knight noticed that the fruits abscised 48 hours after ripening. In addition, the fruits might be removed by animals as soon as the fruits become ripe. A larger quantity of fruits were counted on the plants during the two months of the year, in mid-late summer, when frugivore activity in the area was

low. Thirdly, many of the plants showed evidence of browsing at the ends of the branches where the flowering heads were located. During periods of intense browsing the seed output of plants are reduced (Harper 1977).

Passerina rigida Wikstr.

Small seeds with a low fruit/seed mass ratio are produced in low quantities. The species has a short reproductive cycle which is completed within four months. The seed is adapted for wind-dispersal, with a hook at the one end of the seed for hooking onto vegetation as the seed is blown along by the wind.

Stipagrostis zeyheri (Nees) De Winter subsp. *barbata* (Stapf) De Winter

This species has characteristics of colonizing species with a high seed output of small, light wind-dispersed grains (Fenner 1987). The species is therefore easily and widely dispersed in the early-successional stages, where wind is still a factor. The grains are produced during a short reproductive cycle during the summer as small seeds do not require a long maturation period.

Eugenia capensis (Eckl. & Zeyh.) Harv. ex Sond.

The species produces drupes, which are smaller and have a lower fruit/seed mass ratio than *S. plumieri*, but are in a higher quantity. The species occurs in successional communities later in the successional sequence than *S. plumieri*, and extends into the young Dune Forest. The species has therefore adopted a

strategy suited to the establishment of the species in areas where there is already vegetation and shade present. The food reserve enables the seedling to tolerate shade, where the growth rate is slower than in the open (Harper 1977). The large reserve also enables the seedling to develop an extensive root system and canopy, thereby out-competing the seedlings of the small-seeded species for resources, such as nutrients, water and space. The drupes are produced during the cycle which continues for over a year.

The fruit maturation period required by the seed is over six months, however, the species may avoid competition with *S. plumieri* and *M. caffra* for dispersers by producing ripe fruits in early spring, before either *S. plumieri* or *M. caffra*.

New plants had to be selected when a new cycle started during the monitoring period. More of the plants' resources are been allocated to reproduction than to growth during the reproductive phases of the life-history of the plant. Consequently, different individuals produce seed in different years, depending upon the age and condition of the plants at the time of year when the species starts to flower (Harper 1977).

Imperata cylindrica (L.) Raeuschel

The grains produced are small and light with a plume to assist with wind-dispersal. However, the number produced is low for a colonizing species. This species has a phenological cycle as

short as *P. rigida* and *S. zeyheri*, which also produced wind-dispersed seeds. The cycle commences in spring before *S. zeyheri* begins the cycle. The temporal separation in the availability of the grains of the two species increases the period during which food is available for foragers, such as rodents and ants, thereby, reducing the number of foragers attracted to the food and, therefore, reduces the effect of predation on the soil seed bank.

***Mimusops caffra* E.Mey. ex A.DC.**

This species produced the lowest number of seeds, and the largest seeds with the highest fruit/seed mass ratio of all the species in the study. This species, therefore, has the greatest capacity to out-compete species with smaller seeds, and tolerate a lower light intensity. A low light-intensity tolerance is advantageous for the survival of the species in the community of the young Dune Forest, where the species has been found growing (Avis 1992). The species occurs in communities later in the successional sequence than the other species, including *E. capensis*, which may account for the larger seed size and food reserve than the seeds of *E. capensis*.

***Microsorium scolopendrium* (Burm.f.) Copel.**

Spores are produced throughout the year, and because they are small and light are probably widely distributed throughout the dunefield.

The temporal separation of the species with ripe fruits ensures that the foragers have a supply of food throughout the year (Guy *et al.* 1979; Knight 1986; Castley 1992). This also attracts foragers into the dunes when food is scarce elsewhere in the adjacent habitats. The separation also ensures that the foragers eat the fruits of a number of species throughout the dune system, and not only a select few at the forest margin, where fleshy-seeded species are common. Buck and other footprints have been seen around the foredune, indicating that animals forage along the entire successional gradient, and are not limited to the forest and forest margin.

The effect of predators on the distribution of species in the study area needs to be determined, as predation is important in reproductive strategies (Harper 1977). In the Alexandria Dunefield, Bruton (1992) found that most of the fleshy fruits of the dominant thicket and bushpocket species, such as *Myrica cordifolia*, *Rhus crenata*, *Euclea racemosa* dispersed by birds, are produced in winter. The fruits of most of these species remain on the trees for at least four months. Other bird-dispersed species such as *Colpoon compressum*, *C. monilifera* and *Scutia myrtina* produce fleshy fruits for most of the year. These fruits invade the bushpocket communities after the colonizing species have stabilized the dunes (Bruton 1993).

CHAPTER 3

The soil seed bank

3.1. INTRODUCTION

The soil seed bank is formed by seeds produced from plants in the vicinity of adult plants and by seeds relocated into the area by dispersal agents (Harper 1977). "All viable seeds present on or in the soil or associated litter constitutes the soil seed bank" (Leck *et al.* 1989).

Seed banks are an alternative strategy to vegetative propagation. In habitats which experience disturbances such as drought and periods of adverse conditions, seed banks are an advantage. The seed bank maintains the genetic diversity of the species and is a source of new propagules for increasing the size of the population, or for the colonization of new areas (Fenner 1985). Vegetative propagation is restrictive as it lacks genetic diversity and only maintains the present population growth rate of a species.

The composition and the size of the seed bank is affected by many factors. These factors include changes in seed production, predation, dispersal, germination, climatic factors and the micro-environment. They alter the rate of input and output of seeds into the seed bank (Harper 1977; Bewley & Black 1985;

Parker *et al.* 1989). Predation and dispersal affect the spatial distribution of the seeds, whereas seed production, germination and abiotic environmental factors affect the temporal distribution of the seeds.

Seed banks are described as being transient or persistent according to the dormancy-germination strategy displayed by the species. Seeds which germinate or die within one year from dispersal form transient seed banks, whereas seeds which accumulate in the soil over more than one year form persistent seed banks (Leck *et al.* 1989). Thompson & Grime (1979) have expanded the classification into four categories for the different strategies shown by the flora in northern Britain.

Persistent seed banks are characteristic of early-succession species. Seeds which form persistent seed banks are small and form large soil seed banks. The seeds are usually light-insensitive and have a high seedling growth rate. Transient seed banks, formed by later-succession species, are smaller (Harper 1977). The transient seed banks are formed in predictable habitats, which experience little disturbance (Fenner 1985). The seeds have a short dormancy period, or remain for a long period on the plant. They germinate rapidly to become part of the seedling bank, and are generally large, with large food reserves, but are prone to predation (Louda 1989). The seedlings have a slow growth rate and are often shade-tolerant (Fenner 1985). Seeds of most species are in a dormant state on reaching the soil

(Parker *et al.* 1989). Burial and shading may induce dormancy in some species and initiate germination in others.

The aim of this section is to determine the seed bank strategy of the key species. The objectives were to assess the distribution and size of the seed bank of each species, from the foredune to the forest margin, and in the open and under the canopy.

3.2 METHODS

The soil seed banks of the following species selected as key species (refer to section 1.7) were investigated; *Scaevola plumieri*, *Chrysanthemoides monilifera*, *Passerina rigida*, *Stipagrostis zeyheri*, *Eugenia capensis*, *Imperata cylindrica* and *Mimusops caffra*.

3.2.1. The seed bank along the chronosequence

It is necessary to take many small samples or sub-samples rather than a few large samples to obtain an accurate estimate of the seed abundance in the soil (Bigwood & Inouye 1988; Benoit *et al.* 1989). As there was no information on the number of samples required for the seed range found in the key species of this study in a sandy dry environment, it was decided to take replicate soil samples at random from within quadrats placed systematically along a transect.

Soil samples were collected from forty-four points along a transect in January 1992. The transect extended from the top of the foredune (dune 17) to the forest margin (dune 11). The soil samples were taken from the upper 10-15 cm of the ground with a soil auger (15 cm x 86 cm²). Three samples were taken from within a 1 m² quadrat every 2 m for 174 m. The dunes were dry at the time of collecting the samples, with the result that the samples were variable in size. The samples varied between 680 g and 1349 g. It was therefore decided to combine the replicate samples to form one sample per quadrat, and to take a sub-sample for analysis. The replicate samples were shaken together to form one sample, from which one sub-sample of 1000 g was weighed off.

Two methods are used in analyzing the soil seed banks. 1) germination and, 2) flotation/sieving method. It has been found that the most accurate results are obtained when both methods are used (Ball & Miller 1989; Pierce & Cowling 1991). The advantage of the flotation/sieving method is that the method can recover all the seeds in the sample, but the disadvantages are that the method is time consuming and not always suitable for small seeds (Bigwood & Inouye 1988). The germination method is more sensitive to seed size, but the conditions for germination in the greenhouse need constant attention, and it is not always possible to obtain the correct germination conditions for all the species (Malone 1967).

The sub-sample of 1000 g taken from each sample was treated as follows:

1) Germination

Plastic containers containing a mixture of the soil sample and potting soil (1:4) were maintained in a greenhouse until germination had ceased. The containers were watered regularly and the soil turned over every four to five weeks for six months. Seedlings began to emerge after six weeks for the next four months. As the seedlings reached an identifiable size, they were identified as to species, counted and then removed. The soil was washed after six months.

2) Flotation/sieving method

The soil was treated according to the following method described by Malone (1967) to extract the seeds remaining in the soil samples.

A soil sample was added to a solution in a 10-l plastic bucket. The solution consisted of 10 g of sodium hexametaphosphate, 5 g of sodium bicarbonate and 25 g of magnesium sulphate dissolved in 200 ml of tap water for 100 g of soil. The chemicals induce the separation of soil particles and organic matter more effectively than with only water (Malone 1967). The soil sample was agitated for about two minutes in the solution. The organic matter, which floated to the top was decanted through a 3 mm sieve held over a 1 mm sieve. The 3 mm sieve retained the large seeds, whereas the 1 mm sieve retained the small seeds.

The procedure was repeated three or four times with the same

solution until all the seeds had been extracted from the soil samples. It was found that the solution made up for 100 g of soil was still effective for two or three samples of 1000 g of sandy soil. A new batch of solution was made after every two or three samples had been washed, depending on the amount of litter contained in the soil sample and the soil consistency. The extracts containing the seeds were rinsed with tap water to remove any remaining soil particles and foam. The process was repeated until no organic matter was extracted. The extracts were air-dried. The seeds were identified to species and counted with the aid of a 10x magnification dissecting microscope and a lamp.

The seed counts obtained using method 1) and method 2) were combined. The number, relative frequency and density of seed of each species found in the sample obtained from 1000 g of soil were calculated and the results tabulated. The data was also grouped according to the community zones from which the samples were collected. The density of seed of the key species in each community group found in 1000 g of soil was calculated and tabulated.

3.2.2 The seed bank in the open and under canopy

Soil samples from the upper 10 - 15 cm of soil were taken using the soil auger (15 cm x 86 cm²). Three samples were taken from the open sites and three from under the canopies of three individuals of *Eugenia capensis*, *Mimusops caffra* and *Passerina*

rigida outside the monitoring plots used to monitor seed germination and seedling establishment (Chapter 4). The samples were taken in July 1992. The samples were treated using the flotation-sieving method (described in section 3.2.1) to obtain a seed count. The seed soil density under canopy and in the open were calculated for each of the key species and the results tabulated.

3.3 RESULTS

3.3.1. The seed bank along the chronosequence

The results of the number of seeds and density of all of the species identified in the soil samples are presented in Table 3. The data must be interpreted with care as the values presented in Table 3 and 4 may be an underestimate of the seed abundance in the soil seed bank. The results obtained do, however, give an indication of which key species contributed to the soil seed bank.

Only a total of seventy-six seedlings were counted in the six month period, of which only sixteen were key species. Fifteen seedlings were identified to *S. zeyheri* and one to *M. caffra*. The germination method was, therefore, considered to be an ineffective method for such a study when the germination requirements of the seeds for the species under study are not known.

Fourteen species were identified. The key species accounted for 97.7% of the seeds and 35.7% of the species composition.

Table 3. Species composition and density of the soil seed bank in soil samples (n = 44) taken along the chronosequence from the foredune to the forest margin.

SPECIES	NUMBER OF SEEDS	SEEDS/m ²
<i>Passerina rigida</i>	2605	59.20
<i>Scaevola plumieri</i>	50	1.14
<i>Helichrysum decorum</i>	33	0.75
<i>Chironia baccifera</i>	18	0.41
<i>Ipomoea pes caprae</i>	13	0.30
<i>Stipagrostis zeyheri</i>	11	0.25
<i>Canavalia purpurea</i>	6	0.14
<i>Senecio</i> sp.	3	0.07
<i>Senecio</i> sp.	2	0.05
<i>Eugenia capensis</i>	2	0.05
<i>Carpobrotus dimidiatus</i>	1	0.02
<i>Indigohopra spicata</i>	1	0.02
<i>Mimusops caffra</i>	1	0.02
TOTAL	2749	

P. rigida had the highest soil seed density of all the species, at approximately 59 seeds per 1000 g of soil. *S. plumieri* had a density of approximately 1 seed per 1000 g of soil. The remaining species had a density of less than 1 seed per 1000 g of soil.

No seeds of *I. cylindrica* and *C. monilifera* were found in the soil samples.

Scaevola plumieri (L.) Vahl

Seeds were found in soil samples from the foredune into the Closed Dune Scrub community. The seed density was generally low, ranging from 1 to 2 seeds per 1000 g of soil. The highest density occurred in the Open Dune Scrub community, possibly because the seeds have been blown into this community and have not germinated.

Chrysanthemoides monilifera (L.) T.Norl. subsp. *rotundata* (DC.)

T.Norl.

There were no seeds found in the soil samples.

Passerina rigida Wikstr.

Seeds were found in the soil samples from all the successional stages. The density increased from 1 seed per 1000 g of soil in the Enriched foredune community to 123 seeds per 1000 g of soil in the Bushclump community.

Stipagrostis zeyheri (Nees) De Winter subsp. *barbata* (Stapf) De

Winter

Seeds were found in soil samples from the Open Dune Scrub community into the Bushclump community. The density ranged between 1 seed per 1000 g of soil in the Closed Dune Scrub community to less than 1 in the other communities.

Table 4. Seed density (mean \pm 1 S.E.) in 1000 g of soil and range of the species in the soil seed bank along the successional gradient.

COMMUNITY	SAMPLE NUMBER	SEEDS/m ²				
		<i>Scaevola plumieri</i>	<i>Passerina rigida</i>	<i>Stipagrostis zeyheri</i>	<i>Eugenia capensis</i>	<i>Mimusops caffra</i>
Enriched foredune	6	1.5 \pm 3.67	0.7 \pm 0.41	0	0	0
Open Dune Scrub	15	2.1 \pm 5.28	15.4 \pm 42.9	0.27 \pm 0.80	0	0
Closed Dune Scrub	9	1.1 \pm 2.70	95.0 \pm 99.9	0.56 \pm 1.01	0.22 \pm 0.67	0
Bushclump	14	0	123.3 \pm 98.9	0.14 \pm 0.50	0	0.07 \pm 0.27

Eugenia capensis (Eckl. & Zeyh.) Harv. ex Sond.

Seeds were found in soil samples taken from the Closed Dune Scrub community, but not from any of the other communities. The seed density was lower than 1 seed per 1000 g of soil.

Imperata cylindrica (L.) Raeuschel

No seeds were found in the soil samples.

Mimusops caffra E.Mey. ex A.DC.

Seeds were only found in the soil samples taken from the Closed Dune Scrub community. The seed density was less than 1 seed per 1000 g of soil.

Microsorium scolopendrium (Burm.f.) Copel.

The spores were not found in the soil samples. The sieve sizes used were too large to retain the microscopic spores therein.

3.3.2 The soil seed bank in the open and under canopy

The results of the seed abundance of the key species in the soil under the canopy and in the open are presented in Table 5.

Scaevola plumieri (L.) Vahl

Seeds were found in the soil of the open sites and under the canopy of *P. rigida*. The number of seeds in the soil was higher under the canopy of *P. rigida* than in the open. The density ranged from 65 seeds per m² under the canopy of *P. rigida* to 13 in the open.

Table 5. Soil seed density under the canopy (1 - *Passerina rigida*; 2 - *Eugenia capensis*; 3 - *Mimusops caffra*) and in the open (mean \pm 1 S.E., n = 9).

SITE	SEEDS/m ²				
	<i>Scaevola plumieri</i>	<i>Passerina rigida</i>	<i>Stipagrostis zeyheri</i>	<i>Eugenia capensis</i>	<i>Mimusops caffra</i>
OPEN	12.9 \pm 38.8	2196 \pm 2900.0	0	0	0
CANOPY 1	64.6 \pm 131.4	6653.8 \pm 9304.0	0	0	12.9 \pm 38.7
CANOPY 2	0	2403.1 \pm 3657.3	25.8 \pm 77.5	206.7 \pm 620.2	12.9 \pm 38.7
CANOPY 3	0	5917.3 \pm 5624.4	0	51.7 \pm 84.5	12.9 \pm 38.8

Chrysanthemoides monilifera (L.) T.Norl. subsp. *rotundata* (DC.)
T.Norl.

No seeds were found in the soil samples taken from the open or from under the canopy.

Passerina rigida Wikstr.

Seeds were found in the soil samples taken from the open and from under the canopies. The highest seed density was found in the soil under the parent plants. The lowest density of seeds occurred in the soil samples taken from the open. The seed density ranged from 2196 to 6654 seeds per m².

Stipagrostis zeyheri (Nees) De Winter subsp. *barbata* (Stapf) De Winter

Seeds were only found in the soil samples taken from under the canopy of *E. capensis*.

Eugenia capensis (Eckl. & Zeyh.) Harv. ex Sond.

Seeds were found in the soil samples taken from under the canopy of the parent plants and under *M. caffra*. The highest number of seeds occurred in the soil under the canopy of the parent plants.

Imperata cylindrica (L.) Raeuschel

No seeds were found in the soil samples taken from the open or from under the canopies.

Mimusops caffra E.Mey. ex A.DC.

Seeds were found in the samples taken from under the canopy of *P. rigida*, *E. capensis* and under the canopy of the parent plants. The seed density in the soil was the same under the canopy of all three species.

3.4 DISCUSSION

3.4.1 The seed bank along the chronosequence

The soil seed bank between the foredune and the forest (Table 3) is composed mainly of early-succession species (57%), which produce small wind-dispersed seeds (Fenner 1985; Silvertown 1982). The larger fleshy-seeded species of *M. caffra* and *E. capensis* found in the soil samples, had a low seed density in the soil.

The results of the soil seed density is lower than those obtained in other habitats (Harper 1977; Silvertown 1982). The number of soil samples collected may have been inadequate, but Pierce & Cowling (1991) found low densities for some species of the dune fynbos which would equate with the densities found in this study.

The results of the seed density of each of the key species in the soil of the successional stages along the chronosequence is discussed with reference to each species (Table 4).

Scaevola plumieri (L.) Vahl

The seeds were found from the early-successional stages into the mid-successional stages. The soil seed density was higher in the Open Dune Scrub community, probably due to the seeds accumulating, due to the unfavourable conditions for germination. These seeds are considered to be of no demographic value (Clark & Clark 1984).

The seed density in the soil was low, however, which may have been due to the current season of seeds not yet being part of the soil seed bank. The species was in the fruiting phase of the phenological cycle (Chapter 2) when the soil samples were collected. Some fleshy fruits were found in the soil samples, but the majority had been abraded by the sand and were bare of flesh, indicating that they were seeds from previous seasons.

Many of the seeds may have become inviable with time, or were still in a dormant state. The low density of seeds in the soil, however, suggests that the species forms a transient seed bank, with the seeds germinating shortly after reaching the soil. This hypothesis would need to be tested in field germination trials.

Chrysanthemoides monilifera (L.) T.Norl. subsp. *rotundata* (DC.)

T.Norl

No seeds were found in the soil samples, though seeds were noted to be present by van Daalen *et al.* (1986). The seeds are animal-dispersed and may, therefore, have a clumped distribution (Louda

1989). The seeds may have been present in the soil, but were absent from where the soil samples were collected. One would expect seeds to be present, since ripe fruits are available for most of the year. More soil analyses are required to determine whether this species forms a transient or persistent seed bank.

Passerina rigida Wikstr.

The species had a high seed density in the soil relative to the other species. *P. vulgaris*, of the dune fynbos on the south-eastern Cape coast, was also found to have a higher seed density in the soil than the other species present (Pierce & Cowling 1991).

The fruits of the last phenological cycle had been disseminated a few months prior to the soil samples being collected (Chapter 2), which may have been the reason for the high density of seeds in the soil. The high number of seeds in the later stages of succession could, however, not have been due to the recent phenological cycle as the species is predominantly an early-succession species. The seeds are small and light (Chapter 2). They may have been blown into this zone and have accumulated due to the conditions not being favourable for germination. Also, plants would have occurred here prior to the development of the later-successional stages, and thus the seeds may represent an accumulation from past generations. Germination trials need to be conducted to determine whether the species would germinate here.

The high number of seeds in the soil suggests that this species forms a persistent soil seed bank, but it is not known how many of the seeds were viable.

Stipagrostis zeyheri (Nees) De Winter subsp. *barbata* (Stapf) De Winter

The seed density in the soil was low. The species was in the flowering phase of the phenological cycle, and the seeds had not yet been formed to be released into the soil seed bank, which occurs in February and March (Chapter 2). The low number of seeds in the soil suggests that the species may, therefore, form a transient seed bank.

Eugenia capensis (Eckl. & Zeyh.) Harv. ex Sond.

The soil seed density was low, and seeds were only found in the Closed Dune scrub community, though seeds were noted by van Daalen *et al.* (1986) to occur in the later-successional stages, including the Dune Forest. The phenological cycle had been completed a few months before the soil samples had been collected (Chapter 3). Seeds were therefore expected to be in the soil samples.

The low number of seeds may be due to the seeds being dispersed by animals, and may therefore have a clumped distribution. A pile of seeds consisting mainly of this species was seen on a tuft of *S. zeyheri*. The flesh had been removed from the seeds, which suggested that the seeds had passed through the gut of an

animal. The low seed density suggests that the species forms a transient seed bank.

Imperata cylindrica (L.) Raeuschel

The phenological cycle had been completed a few months before the soil samples were collected, however, no seeds were found in the soil samples. The absence of the seeds in the soil samples may have been due to the seeds germinating shortly after reaching the soil, or the seeds may have been removed by predators. The seeds may also have been trapped in the vegetation into a clumped distribution. The result suggests that the species may form a transient seedbank.

Mimusops caffra E.Mey. ex A.DC.

The seeds were only found in the soil samples from the Bushclump community, where the species is a dominant species in the tree layer (Chapter 1). The phenological cycle had been completed a month before the soil samples were collected and yet, the species had a low seed density in the soil. The reasons given for the low density of *E. capensis* seeds may also apply here. The results suggest that the species forms a transient seedbank.

A soil seed bank survey from the Dune Scrub zones into the Dune Forest zone was completed during a Forest Biome workshop in 1985 (van Daalen *et al.* 1986). This survey showed similar results in the distribution of the seeds of *S. plumieri* and *P. rigida* to those obtained in this study. The survey found that the range of

seeds of *E. capensis* and *M. caffra* extended into the Dune Forest community. The results of the survey did not include *S. zeyheri* or *I. cylindrica*. Seeds of *C. monilifera*, which were not found in this study, were noted by van Daalen *et al.* (1986) as having a range extending from the Dune Scrub community into the Bushclump community.

The results show that most of the species appear to form transient seedbanks, although the species in the early stages of succession appear to form persistent seed banks. If correct, these conclusions would concur with the theory of Fenner (1985) that, colonizing species produce small seeds with a wide distribution range, and which form persistent seed banks, whereas the seeds of the larger-seeded species have a smaller range and form transient seedbanks.

Seed density is variable with time (Fenner 1985; Pierce & Cowling 1991). Several years of sampling the soil seed banks is, therefore, necessary to determine an accurate estimate of the seed bank, and to determine whether the species form a transient or persistent soil seed bank.

The effect of predation is also unknown. Predation affects the seed bank strategies (Harper 1977), and a seed of *P. rigida* was seen to be carried away from under the canopy of *P. rigida* by an ant.

3.4.2 The seed bank in the open and under the canopy

The survey of the soil seed bank completed by van Daalen *et al.* (1986), showed that the seed density in the open, relative to under the canopies, decreased as the vegetation changed from the Open Dune Scrub community into the Dune Forest community. The results of the soil seed bank survey of the key species in the open and under the canopy of *P. rigida*, *E. capensis* and *M. caffra* showed a similar pattern (Table 5).

Seeds of the early-succession species, *S. plumieri* and *P. rigida* occurred in the soil in the open and under the canopy of *P. rigida*. The seed density of *P. rigida* was higher under the canopies of the parent plants, but seeds were also found in the soil under the canopies of *E. capensis* and *M. caffra*. Seeds of *S. zeyheri*, *E. capensis* and *M. caffra* were not found in the open, and were only found under the canopy of *E. capensis*. Seeds of *E. capensis* were also found under the canopy of *M. caffra*, while its' seeds were found under the canopies of *P. rigida*, *E. capensis* and under the canopies of the parent plants. The results of the Forest Biome survey found that seeds of *E. capensis* and *M. caffra* also occurred in the open.

The greater seed density of *P. rigida* and *E. capensis* under the canopies of the parent plants indicates that many of the seeds are not disseminated great distances away from the parent plants.

CHAPTER 4

Seed germination and seedling establishment in the open and under canopy

4.1 INTRODUCTION

Seedling emergence pattern is a result of the interaction between the response of seeds to seasonal heterogenous environmental conditions, and the endogenous rhythm of the seed which releases it from dormancy. Factors which affect the interactions between the dormancy-releasing agents and the germination requirements of the seed include seed burial, shade, temperature, water, interactions between these factors, secondary dormancy (Bewley & Black 1985), minerals, competition avoidance, soil microtopography, predation and desiccation (Koller 1972; Fenner 1985).

A seed which germinates has found a "safe site". A safe site is defined by Harper (1977) as "that zone ... which provides (a) the stimuli required for breakage of seed dormancy, (b) the conditions required for the germination processes to proceed and (c) the resources (water and oxygen) which are consumed during germination". Hazards such as predators, competitors, toxic soil constituents and pre-emergence pathogens should be absent. The greatest hazards seedlings encounter during establishment are drought, burial and predation (Stebbins 1971; Fenner 1985). Successional species differ in their requirements for germination (Luken 1991).

Survival in the shade is related to the successional status of the species (Augsburger 1984), with a difference in growth between species which require light, and those which are shade-tolerant. Seedlings under shade have a slower growth rate than those growing in light. A large food reserve, characteristic of large seeds, is advantageous in the shade, whereas the smaller seedlings of small-seed species are at an advantage in the open, since they have a faster growth rate. The large-seeded species are therefore generally found in the later-successional stages, and the small-seeded species in the more open early stages of succession (Fenner 1985), although exceptions do occur (eg. *Scaevola plumieri*).

Seeds of some species can germinate over a wide range of temperatures, but the range of is usually species specific (Bewley & Black 1985). Temperature may release a seed from primary dormancy or induce secondary dormancy, and therefore has a regulatory influence on the rate of germination (Bewley & Black 1985).

Moisture affects both the rate and percentage germination, and water stress can delay germination. As with temperature species have specific tolerance ranges (Bewley & Black 1985).

Canopy light also has an effect on germination. Only wavelengths greater than 720 nm are transmitted through the leaves of the canopy (Bewley & Black 1985), the quality of the light therefore

decreases since the red/far-red light ratio decreases as the shorter wavelengths of red light (<700 nm) are blocked. The far-red form of phytochrome inhibits germination, as a result of a low germination spectral energy distribution, which is insufficient to break dormancy. The effect on germination varies between different trees due to the variation in leaf density (Bewley & Black 1985).

Many species require a combination of factors to ensure germination, and if one factor is insufficient it may result in secondary dormancy. These dormancy and germination controlling environmental factors result in a temporal distribution in the seedling emergence times, which are important for competition avoidance and the colonization of new open sites. Date of seedling emergence has been found to influence the survival rate of the seedlings, with respect to competition with older seedling cohorts and the seasonal change in environmental conditions (Fenner 1985; Silvertown 1982).

The aim of this section is to compare the germination characteristics of the species along the successional gradient. The germination and seedling growth requirements of the seeds change as the vegetation changes from an open aspect to a more closed aspect. It is suggested that the germination and seedling growth requirements will change in response to local environmental conditions. The objectives were to assess the effect of selected environmental factors on the germination and

establishment of the key species.

4.2 METHODS

Seed germination and seedling establishment of the following species was investigated (refer to section 1.7, Chapter 1); *Scaevola plumieri*, *Chrysanthemoides monilifera*, *Passerina rigida*, *Stipagrostis zeyheri*, *Eugenia capensis*, *Imperata cylindrica*, *Mimusops caffra* and *Microsorium scolopendrium*.

4.2.1 Seed germination and seedling establishment

Permanent plots were used to monitor seedling emergence and survival in the shade of three canopy species, and in open sites from September 1991 until January 1993.

Four individuals of each of the three main shading species in the early- and mid-successional stages, *Passerina rigida*, *Eugenia capensis* and *Mimusops caffra* were selected. A group containing an individual of each species was selected from between the foredune and the Dune Forest community where possible. The representative individuals of each species were selected in the vicinity of each other, provided there was no canopy interference. This was done to minimize the differences in the soil structure and composition of the understorey between the species.

Three 0,5 m x 0,5 m plots were placed under each individual. The plots were placed at approximately 45 degrees to each other, and 0,5 m away from the tree base where possible. Twelve plots were placed in the sunlight in adjacent open areas. Refer to Figure 7 for the plot lay-out.

The distribution of the *P. rigida* individuals differed from the other two species, as individuals without canopy interference were only found closer to the foredune and in the early-successional stages.

The Cartesian co-ordinate method, used by Westelaken & Maun (1985) and van Rooyen *et al.* (1979) in similar studies, was used to record new seedlings and to monitor their survival in their first year. The plots were marked with two steel rods in opposite corners, over which the quadrat (0.5 m x 0.5 m) could be placed when the plots were surveyed. This ensured that the same area was sampled at each visit. The quadrat was sectioned into 10 cm squares with string so that the location of each seedling could be mapped accurately.

The species composition, percentage cover and height range of the existing plants growing in each plot were recorded at the start of the monitoring period. The estimated percentage cover and plant height of the understorey plant species in the open and under each canopy species was tabulated. The location of seedlings already present in the plots were also recorded.

FOREST MARGIN

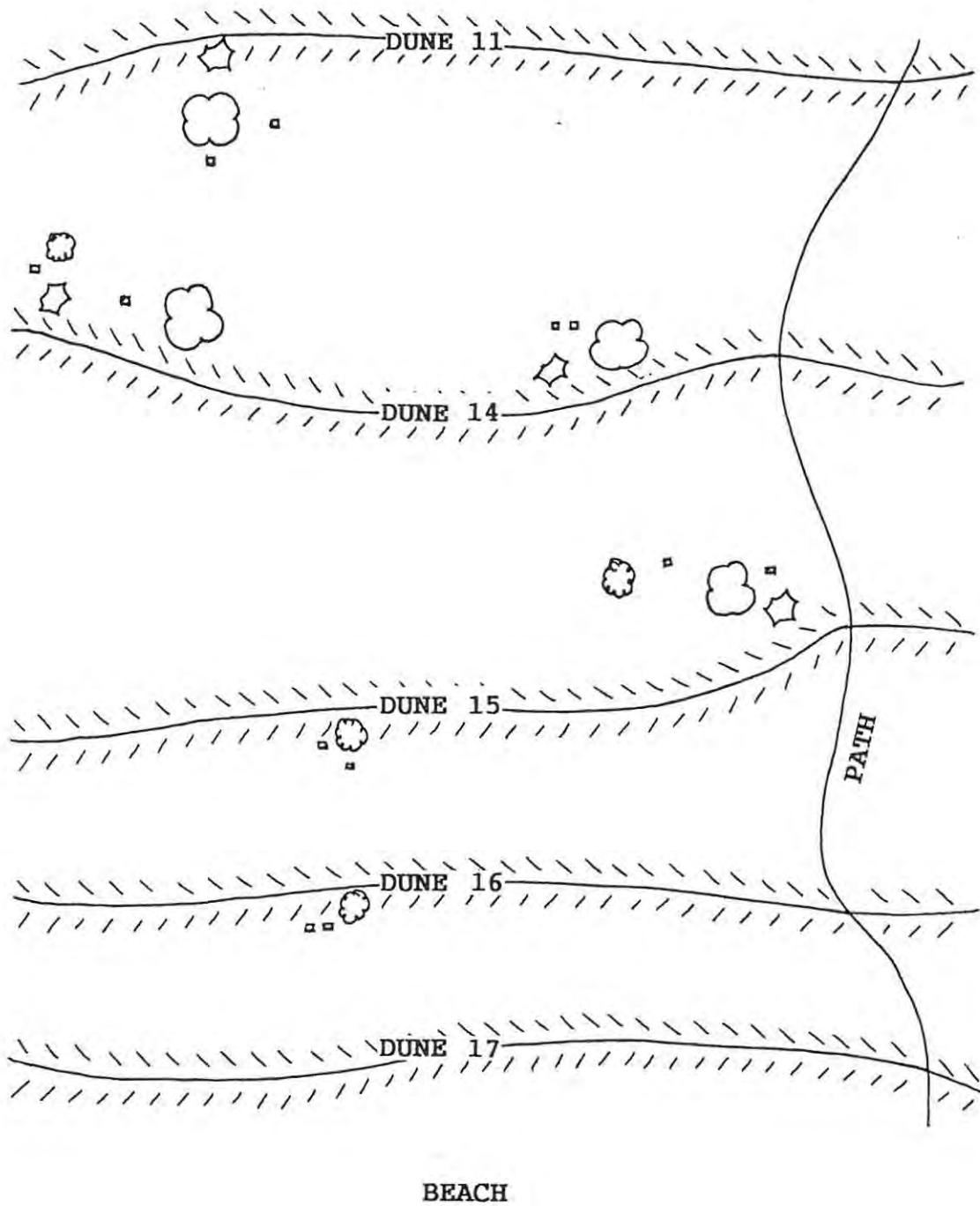


Figure 7. The approximate location of the canopy species (*Passerina rigida*; *Eugenia capensis* and *Mimusops caffra*) and the plots placed in the adjacent open areas (□ open) in the dunefield. The hatching represents the dune slopes.

The plots were checked every four weeks, from October 1991 until December 1992. New seedlings and dead or missing seedlings were recorded on the plot maps of the previous survey each visit, with a different coloured marker.

The number of seedlings of each of the key species which had germinated and died by the end of the monitoring period were counted. The seedling counts were too low to show a Poisson or binomial distribution, and descriptive statistical analysis of the results were therefore done. The percentage germination and seedling survival for the year was calculated for each of the species under each shade species and in the open. The results were tabulated.

4.2.2 Environmental factors

Species composition, plant height and percentage cover, as well as percentage litter cover in each plot were recorded at the start of the monitoring period. The mean maximum understorey plant height, percentage understorey plant cover and litter cover for each shade species and open site were calculated, and all these results tabulated.

Soil samples for pH analysis were collected from the plots in July 1992. The pH analysis procedure described by the Fertilizer Society of South Africa (1974) for electrode analysis was followed: 50 ml of distilled water was added to 20 g of soil in

a 100 ml beaker. The solution was stirred with a glass rod until the soil was completely wet. The soil was stirred again after 50 minutes and the soil left to stand for a further 10 minutes. The soil was stirred vigorously again and the pH measured with a Beckmann electrode. Six readings were obtained for each tree. The mean pH for each canopy species and open site was calculated and the results tabulated.

A Li-Cor integrating quantum photometer Li-188B was used to measure the photosynthetically active radiation (PAR), expressed as $\mu\text{E m}^{-2} \text{s}^{-1}$, under the canopy of *P. rigida*, *E. capensis* and *M. caffra* and in the full sunlight. Nine light readings were taken under the plant canopies and six in the open. The readings were taken between 10:00 am and 2:00 pm on a clear day in April 1992. An integrating time of 10 seconds was used. The average light intensity was calculated for each canopy species and for the measurements taken in the open and the results tabulated.

An MCS 120-02 Data Logger was used to measure and record the surface soil temperatures under the canopy and in the open. The surface soil temperatures were recorded under the canopy of *P. rigida*, *E. capensis* and *M. caffra*, and in the open, over a twenty-four hour period for five days in April 1993. Two MCS 151 temperature sensors were placed under the canopy of each species and in the open on the soil surface. Litter present had been cleared away from where the sensor was placed. The mean temperature for a half hour log period was recorded every half

hour. Figure 8 shows the locations of the tree species and the lay-out of the sensors.

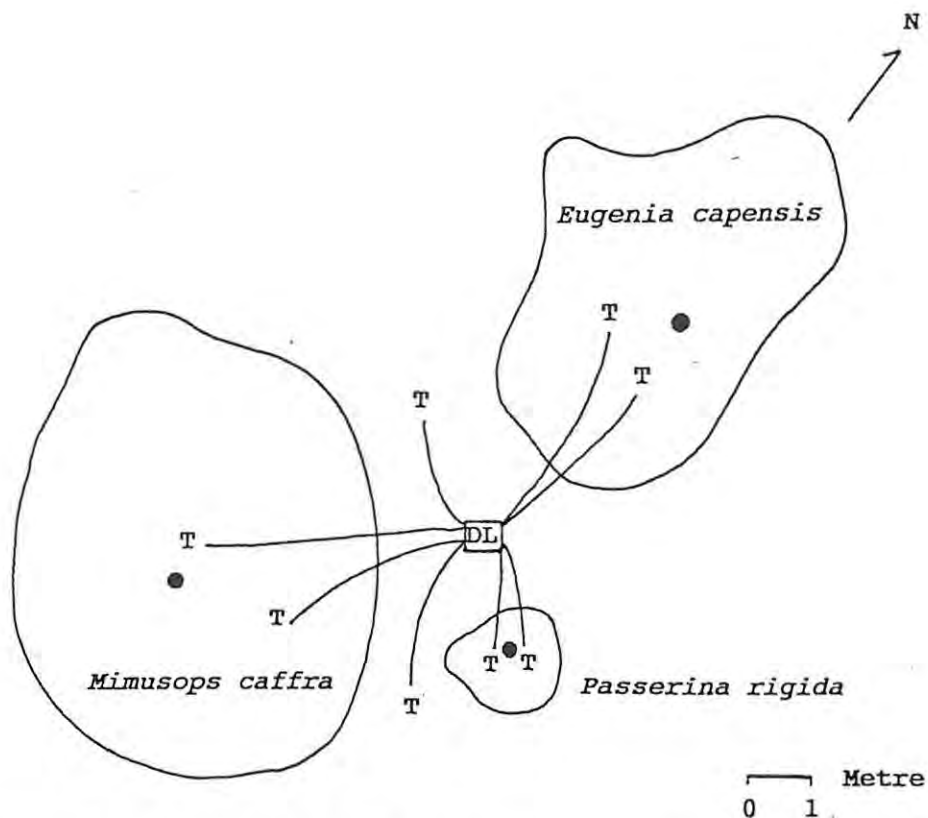


Figure 8. The relative position of the canopy species (*Passerina rigida*; *Eugenia capensis* and *Mimusops caffra*) and the canopy size of plants used to determine seed germination and seedling survival of the key species under different conditions. The layout of the temperature sensors (T) used to measure the diurnal surface soil temperatures and the location of the data logger (DL) is also shown.

A graph of the mean of the temperature measurements recorded over twenty-four hours for five days under the canopy species and the open sites was plotted to show the diurnal temperature change. The mean maximum and minimum temperatures and temperature range were calculated for each species and the open site, and the results tabulated.

4.3 RESULTS

4.3.1 Seed germination and seedling establishment

The seedling emergence density for the year is shown in Table 6. The number and percentage of seedlings which had died by the end of the monitoring period are presented in Table 7. The results for each species will be considered separately.

Table 6. Density of the seedlings (number m⁻²) in the open and under the canopy of *Passerina rigida* (1); *Eugenia capensis* (2) and *Mimusops caffra* (3) (mean \pm 1 S.E., n = 4).

SPECIES	OPEN	CANOPY 1	CANOPY 2	CANOPY 3	TOTAL
<i>Passerina rigida</i>	0.08 \pm 0.20	2.68 \pm 3.77	0.00	0.30 \pm 0.65	3.10
<i>Stipagrostis zeyheri</i>	0.00	0.66 \pm 1.33	0.00	0.30 \pm 0.65	1.00
<i>Eugenia capensis</i>	0.00	0.00	0.65 \pm 0.75	2.00 \pm 2.50	2.30
<i>Imperata cylindrica</i>	0.33 \pm 0.52	0.30 \pm 0.65	2.33 \pm 2.75	0.00	3.10
<i>Mimusops caffra</i>	0.00	0.00	0.30 \pm 0.65	0.00	0.30
* <i>Microsorium scolopendrium</i>	0.00	0.00	1.33 \pm 2.66	2.00 \pm 3.28	3.33

* spores

Scaevola plumieri (L.) Vahl

No seedlings were found from September 1991 until January 1993 in the open plots or in the plots under the canopy species.

Table 7. The total number of seedlings (per 0.25 m²) in the open and under the canopy of *Passerina rigida* (1); *Eugenia capensis* (2) and *Mimusops caffra* (3). The percentage mortality is in parentheses.

SPECIES	OPEN	CANOPY 1	CANOPY 2	CANOPY 3
<i>Passerina rigida</i>	5 (100)	6 (100)	-	1 (0)
<i>Stipagrostis zeyheri</i>	-	2 (50)	-	1 (0)
<i>Eugenia capensis</i>	-	-	1 (100)	6 (17)
<i>Imperata cylindrica</i>	3 (0)	1 (100)	3 (33)	-
<i>Mimusops caffra</i>	-	-	1 (0)	-
<i>Microsorium scolopendrium</i>	-	-	4 (25)	6 (33)

Chrysanthemoides monilifera (L.) T.Norl. subsp. *rotundata* (DC.)

T.Norl.

No seedlings were found in the plots during the monitoring period.

Passerina rigida Wikstr.

Seeds germinated in the open sites, under the canopy of the parent plants and under the canopy of *M. caffra*. The highest seedling density occurred under the parent species. No seedlings were counted under the canopy of *E. capensis*.

All the seedlings which emerged in the open sites and under the canopy of the parent species had died by the end of the monitoring period. Only the seedling under the canopy of *M. caffra* survived.

Stipagrostis zeyheri (Nees) De Winter subsp. *barbata* (Stapf) De Winter

Seeds germinated under the canopy of *P. rigida* and *M. caffra*. None germinated in the open sites or under the canopy of *E. capensis*. The number of seedlings which were still alive at the end of the monitoring period was half the total number which had germinated under the canopy of *P. rigida*. The seedling under the canopy of *M. caffra* was still alive.

Eugenia capensis (Eckl. & Zeyh.) Harv. ex Sond.

Seeds germinated under the canopy of the parent species and under the canopy of *M. caffra*. None germinated under the canopy of *P. rigida* or in the open sites. A higher seedling density was counted under the canopy of *M. caffra*. The seedlings under the canopy of the parent plants had died by the end of the monitoring period, whereas the majority of seedlings under the canopy of *M. caffra* had survived.

Imperata cylindrica (L.) Raeuschel

It was unclear if the seedlings were asexual tillers sprouting, since most arose near adult plants of the species. The seedlings were left undisturbed so as not to cause damage which may have

resulted in an early death.

Seedlings were counted under the canopy of *P. rigida* and *E. capensis*, but not under the canopy of *M. caffra*. Seeds also germinated in the open sites. The highest density of seedlings was counted under the canopy of *E. capensis*. The seedling under the canopy of *P. rigida* had died by the end of the monitoring period, whereas less than half the number had died under the canopy of *E. capensis* and none had died in the open sites.

Mimusops caffra E.Mey. ex A.DC.

One seedling was recorded under the canopy of *E. capensis*. No seeds germinated under the canopy of *M. caffra* or *P. rigida* or in the open sites. The seedling was still alive at the end of the monitoring period.

Microsorium scolopendrium (Burm.f.) Copel.

All the new ferns counted were clonal in origin. Young plants were found in the plots under the canopy of *E. capensis* and *M. caffra*, but not under the canopy of *P. rigida* or in the open sites. Less than half the number of young plants had died in the plots under the canopy of *E. capensis* and *M. caffra* by the end of the monitoring period.

4.3.2. The environmental factors

The composition of the understorey of the plots was similar in

all the plots in the open and under canopy cover, generally. There was only one plot in the open which was devoid of any vegetation. Herbaceous species occurred more often in the plots in the open, whereas the fern, *M. scolopendrium*, and succulent plants occurred more frequently in the plots under the canopy of the three species. Grasses, either *S. zeyheri* or *I. cylindrica*, occurred in most of the plots under the canopy of *P. rigida*, *E. capensis* and *M. caffra*. The plots in the open also had a grass cover, with the exception of a few plots in the early-successional stages, which contained a low plant cover of mainly herbaceous species.

The height of the understorey was due to the grasses (*S. zeyheri* and *I. cylindrica*) in the plots of *P. rigida* and in the open, and due to the fern (*M. scolopendrium*) in the plots of *E. capensis* and *M. caffra*. *S. zeyheri* forms a tussock providing shade, whereas *I. cylindrica* has a few erect broad leaf blades providing minimum shade. *M. scolopendrium* grows to a height of approximately 50 cm, and provides deep shadow.

The measurements of the environmental factors recorded in the plots in the open and from under the canopy of *P. rigida*, *E. capensis* and *M. caffra* are shown in Table 8 and the mean surface soil temperatures in Table 9. The average surface soil temperature measured for five days in the open plots and under the canopy of the three species is presented in Figure 9.

Table 8. Environmental factors measured in the open and under the canopy of *Passerina rigida* (1); *Eugenia capensis* (2) and *Mimusops caffra* (3) (mean \pm 1 S.E.).

FACTOR	OPEN	CANOPY 1	CANOPY 2	CANOPY 3
MEAN MAXIMUM PLANT HEIGHT OF THE UNDERSTOREY (cm) (n=12)	28.4 \pm 23.8	24.8 \pm 20.9	40.5 \pm 14.1	30.0 \pm 30.5
MEAN PLANT COVER OF THE UNDERSTOREY (%) (n=12)	42.5 \pm 42.4	38.9 \pm 26.7	38.6 \pm 31.8	19.4 \pm 31.8
MEAN LITTER COVER (%) (n=12)	10.5 \pm 8.9	30.0 \pm 27.3	60.1 \pm 37.6	61.4 \pm 20.0
MEAN SOIL pH (n=3)	8.36 \pm 0.22	7.97 \pm 0.18	7.73 \pm 0.22	7.17 \pm 0.47
MEAN CANOPY LIGHT (PAR) ($\mu\text{E m}^{-2} \text{s}^{-1}$) (n=4)	1579.2 \pm 337.7	797.0 \pm 18.2	389.0 \pm 181.8	160.0 \pm 84.8

Table 9. The mean diurnal surface soil temperatures recorded over 5 days in April 1993 from under the canopy of *Passerina rigida* (1); *Eugenia capensis* (2) and *Mimusops caffra* (3) and in the open (mean \pm 1 S.E.).

TEMPERATURE ($^{\circ}\text{C}$)	OPEN	CANOPY 1	CANOPY 2	CANOPY 3
MEAN MAXIMUM	42.1 \pm 2.05	32.2 \pm 0.6	34.6 \pm 1.2	31.0 \pm 1.32
MEAN MINIMUM	21.7 \pm 0.3	23.1 \pm 0.2	22.6 \pm 0.5	22.9 \pm 0.8
RANGE	20.4 \pm 1.83	9.0 \pm 0.52	12.0 \pm 0.7	9.1 \pm 0.7

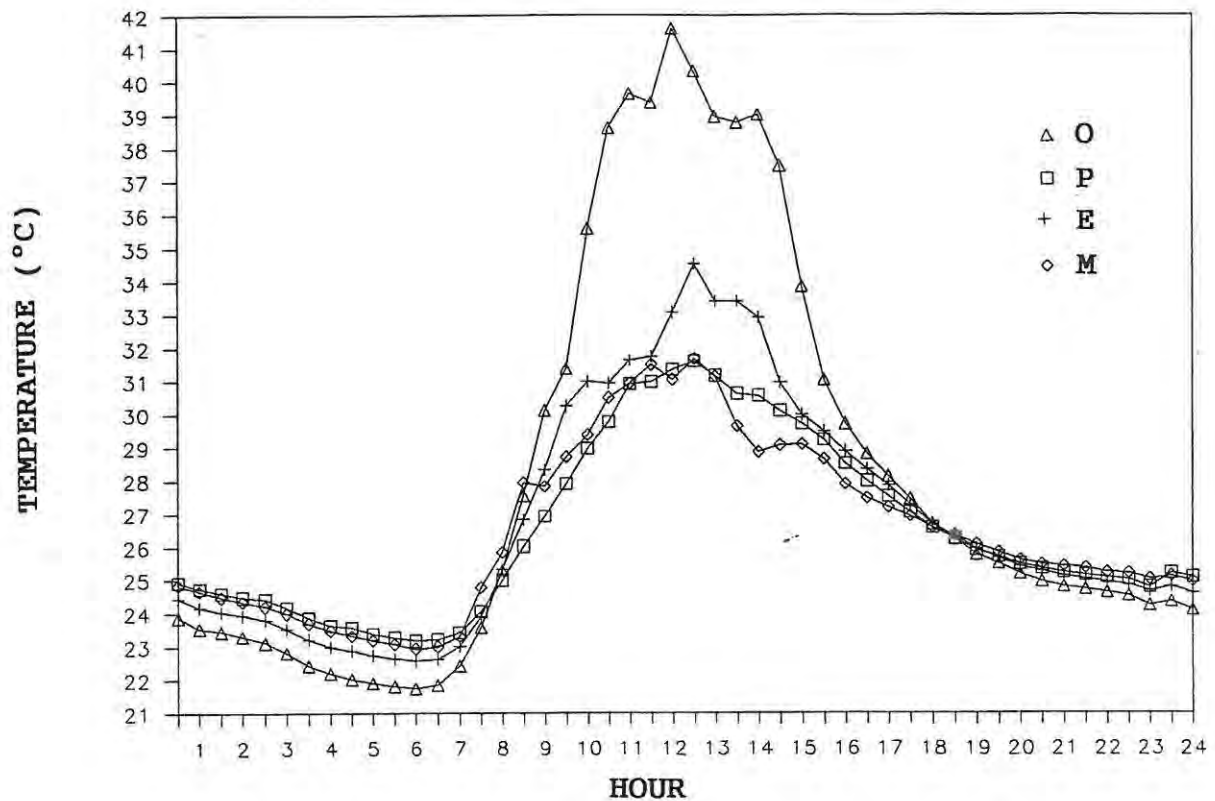


Figure 9. The mean diurnal surface soil temperatures (n = 5) measured under the canopy of *Passerina rigida* (P); *Eugenia capensis* (E) and *Mimusops caffra* (M), and in the open (O).

The three canopy species predominate from the early- to the mid-succession communities, with *P. rigida* occurring in the earlier zones and *M. caffra* in the mid-successional zones (section 1.6, Chapter 1). The results show the following trends in the environmental condition in the plots.

The understorey plant cover and the canopy light intensity decreased with an increase in the canopy cover density of

P. rigida to *E. capensis* and to *M. caffra*. Leaf and twig litter increased as the plant cover decreased. Soil pH decreased towards the forest.

The surface soil temperatures were higher in the open at midday than under the canopy of the three species. The temperature range over twenty-four hours was also greater. The highest temperatures were recorded under the canopy of *E. capensis* of the three canopy species. The maximum temperatures were higher under the canopy of *E. capensis* than *P. rigida*, which had a similar temperature range to *M. caffra*.

The litter content and soil temperature measurements followed the same trends as those obtained in the Forest Biome Workshop survey (van Daalen *et al.* 1986). The results of the pH analysis of the soil were also similar to those obtained by Avis (1992).

4.4 DISCUSSION

No seedlings appeared after 26 April 1992, after seven months of monitoring the plots. The main cause of the low total seedling count (75) may have been due to the low rainfall experienced during the monitoring period (Figure 2). Other studies have observed the importance of rainfall for successful regeneration (Davidson & Barbour 1977; Weller 1985).

Germination ceased from the end of December in the open plots,

and from the end of February under the canopy of *P. rigida*, when the ambient monthly mean maximum temperature reached a peak of about 32 °C (Figure 2a). Germination continued until the end of March under the canopy of *E. capensis* and until the end of April under the canopy of *M. caffra*. In the past twenty six years, the mean monthly maximum ambient temperatures for February, March and April were 2 °C to 3.5 °C cooler (Figure 2b). Germination is affected by light, soil moisture and temperature (Harper 1977; Bewley & Black 1985).

Seeds of some species can germinate under a wide range of temperatures, however high soil temperatures reduce the reserves due to more rapid respiration than cool temperatures (Daubenmire 1974).

The results of the number of new seedlings (Table 6), and the survival of the seedlings after about one year (Table 7), are discussed below with respect to the environmental factors measured under the canopies of the three species and in the open sites (Table 8 & 9; Figure 9).

Scaevola plumieri (L.) Vahl

This species has specific germination requirements that appear to be met only on the frontal dune where the species stabilizes the moving sand. No seedlings were expected in the plots monitored and none were found.

Chrysanthemoides monilifera (L.) T.Norl.

The zero germination result obtained for this species may be due to a low soil seed density, or because the species has a clumped seed distribution.

Passerina rigida Wikstr.

Seedlings appeared under the canopy of *P. rigida* and *E. capensis*, but not under the canopy of *E. capensis*. The seeds may have been out-competed by the seedlings of the larger-seeded species, such as *E. capensis*. The highest density of seedlings occurred under the parent plants. A high soil seed density (Chapter 3) has been found under the parent species, and the germination of the seeds appear not to be inhibited by the parent plant.

The seedlings, which appeared in the plots which experienced high soil temperatures and high light intensity, had all died by the end of the monitoring period. Those under *M. caffra*, which had the lowest light intensity and low mean surface soil temperature, had survived. The litter layer under *M. caffra* was more compact than under the canopy of the other two species. This observation suggests that the soil moisture content is higher here due to the lower evaporation rate due to the dense canopy. Thus, the seedling may be sensitive to desiccation.

Stipagrostis zeyheri (Nees) De Winter subsp. *barbata* (Stapf) De Winter

Seeds germinated under *P. rigida*, an early-succession species and

under *M. caffra*, a mid-succession species. The result indicates that the species can tolerate a wide range of temperatures and soil moisture conditions. No seeds germinated in the open sites possibly as a result of the hot dry soil conditions experienced due to a low rainfall.

Eugenia capensis (Eckl. & Zeyh.) Harv. ex Sond.

No seedlings appeared in the high light intensities of the open sites and under the canopy of *P. rigida*. The result indicates that the species is shade-tolerant. Seedlings were however observed in the Enriched Fore-dune zone of a size which indicated that they had germinated in previous years. The seeds can possibly tolerate a wide range of conditions, provided there is sufficient moisture in the soil. The highest density of seedlings and lowest mortality rate was obtained under the canopy of *M. caffra*.

Imperata cylindrica (L.) Raeuschel

Seedlings were counted under all the light intensities, except under the lowest intensity under the canopy of *M. caffra*. The result suggests that the species requires a high light intensity for germination. The fern, *M. scolopendrium*, which predominates under the canopy of *M. caffra*, may out-compete the grass for resources such as space and light. Seeds germinated in the open sites and survived, whereas the seeds which germinated under the canopy of *E. capensis* and *P. rigida* died.

The seedlings counted in the open sites had germinated in the shade of established grass plants of *S. zeyheri* and *I. cylindrica*, whereas the amount of grass was lower under the canopy of *E. capensis* and *P. rigida*. This suggests that the seedlings were tillers from the parent plants.

Mimusops caffra E.Mey. ex A.DC.

Seed germination occurred only under *E. capensis*. The low germination success rate may have been due to the germination requirements not being met by the low rainfall conditions experienced during the monitoring period. The seedlings under the canopy of *E. capensis* had died by the end of the monitoring period. No seeds germinated under the parent species, either because the plants selected had not been reproductively active recently, or the seeds had been removed by frugivores to another location.

Microsorium scolopendrium (Burm.f.) Copel.

The number of young plants showed a decrease in number as the light intensity under the canopy of the three species increased, from *E. capensis* to *M. caffra*. The result suggests that the species is shade-loving, though plants are also found growing in open light at the edge of canopies (personal observation). The mortality of half the number of young plants suggests that the young plants are susceptible to desiccation. It was found that the fronds are easily damaged, which may be fatal for the plant.

The results show that more seedlings survived under the canopy of *M. caffra* than under any other species or in the open. Other factors such as soil nutrients and competition for resources may also have had an effect on germination, but to a lesser extent during this dry year. The litter layer under *E. capensis* and the more compact litter layer of *M. caffra* may have reduced the soil moisture evaporation rate under these species, having a positive influence on seed germination and seedling survival.

The litter layer usually determines the seed germination size order (Molofsky & Augspurger 1992). The larger seeds germinate earlier and the seedlings become established more rapidly than the seedlings of small seeds. Many of the adult grass plants of *S. zeyheri* and *I. cylindrica*, which formed a large component of the understorey died, possibly due to the dry conditions. The die-back in the grass exposed seedlings to the sun. In the wet years, the grass would have protected the seedlings from desiccation until they had become established. Many studies have shown that the light intensity affects seed germination and seedling growth (Davidson & Barbour 1977; Bell 1993).

The combination of the immediate environment of the seed and the seed germination requirements depends on whether the seed will germinate (Harper 1977). Seed germination and seedling survival in this study was probably controlled mainly by the regularity and amount of rainfall received, and surface soil temperature experienced during the monitoring period. In wetter years, other

factors such as soil nutrients and competition for resources may have a greater influence.

A survey of the seedling density under the bushclumps by van Daalen *et al.* (1986) in the study area, found a higher density of seedlings of *E. capensis* and *M. caffra* under the bush clumps. Seedlings of *C. monilifera* which were not found in this study were found in the survey.

Further monitoring of the germination and seedling survival success rate of the key species is needed. The results of the germination success rate under the canopies obtained in this study are inadequate to comment on the ability of the species to germinate in the environmental conditions experienced along the successional gradient. The results did, however, show that the seedlings of the small-seeded species, *P. rigida* and *S. zeyheri* are susceptible to desiccation. The larger-seeded species, *E. capensis* and *M. caffra* and seedlings growing under shade are less susceptible.

CHAPTER 5
General discussion

The phenological, soil seed bank, seed germination and seedling establishment data obtained in a year of monitoring *Scaevola plumieri*, *Chrysanthemoides monilifera*, *Passerina rigida*, *Stipagrostis zeyheri*, *Eugenia capensis*, *Imperata cylindrica* and *Mimusops caffra* and observations on *Microsorium scolopendrium* have shown that the species differ in their reproductive strategies.

The main features of the reproductive strategies, summarized in Table 10, are discussed for each species with respect to its position along the successional gradient.

Scaevola plumieri (L.) Vahl is found growing in the Foredune, the Enriched Foredune and Open Dune Scrub communities (section 1.6 & Figure 3). It is the dominant species in the Foredune and the Enriched Foredune communities, where it traps the wind-blown sand, which accumulates to form dunes (Steinke & Lambert 1986). The phenological cycle, which begins in early-spring and is completed in mid-autumn (Figure 4), is of a similar duration as *E. capensis* and *M. caffra*, which also produce large, heavy fruits. The species produces the largest fleshy drupes of the fleshy-seeded species in the study (Figure 6 & Table 2), which ripen slowly over six months. The drupes, which are available in January and February, can be dispersed in several ways including

Table 10. Summary of the main features of the reproductive strategies relating to succession

SPECIES	PHENOLOGY		SOIL SEED BANK		SEED GERMINATION & SEEDLING ESTABLISHMENT	
	CYCLE	SEED	Zone	Open/Canopy	Germination	Seedling mortality
<i>Scaevola plumieri</i>	long fruiting phase	low output of large heavy drupes	Foredune into the Closed Dune Scrub	both	nil	?
<i>Chrysanthemoides monilifera</i>	simultaneous flower & fruiting phases	high output of small drupe-like fruits	?	?	nil	?
<i>Passerina rigida</i>	short flowering & fruiting phases	low output of small light fruits	Foredune into the Bushclump	both	low	high in the open & under canopy
<i>Stipagrostis zeyheri</i>	short flowering & fruiting phases	high output of light grains	Open Dune Scrub into the Bushclump	under canopy only	low	high in the open & under canopy
<i>Eugenia capensis</i>	long fruiting phase	low output of large heavy drupes	Closed Dune Scrub	under canopy only	low	high
<i>Imperata cylindrica</i>	short flowering & fruiting phases	low output of grains	?	?	nil	higher under low light intensities
<i>Mimusops caffra</i>	long fruiting phase	low output of large heavy drupes	Bushclump	under canopy only	low	nil
<i>Microsorium scolopendrium</i>	continuous	microscopic spores	?	?	low	lower under low light intensities

water, wind and animals (Thieret & Brandenburg 1986). The seeds can, therefore, be dispersed over a wide area. Pioneer colonizing species often have several means for disseminating their fruits, increasing their ability to disperse widely, which is important in a colonizing environment (Fenner 1985). The soil seed density, which is high relative to the other species, except *P. rigida*, (Table 3) is generally low in the soil, ranging from the Foredune community into the Closed Dune Scrub community (Table 4), but, although seeds were found in the soil in the open and under the canopies of shade species (Table 5), none germinated. Thus, the seeds are widely dispersed, but the conditions for germination in the seral stages after the Foredune possibly do not meet the germination requirements of the seed. The plants found in the later seral stages are past generations, which have been surrounded by other species as the dunes have become stable as a consequence of the vegetative lateral growth of *S. plumieri*. These plants may eventually die due to disease, predation or old-age, and because seeds are not germinating, thereby maintaining the populations in the Enriched Foredune and Open Dune Scrub communities, the species will eventually disappear from these zones.

Chrysanthemoides monilifera (L.) T.Norl. subsp. *rotundata* (DC.) T.Norl. is found growing in the Enriched Foredune community and the Dune Scrub communities (section 1.7 & Figure 3). Small fleshy drupe-like fruits are produced for most of the year, simultaneously with the production of flowers (Figure 4), which

results in a high seed output for the year (Figure 6). The fruits appear to have a short ripening period of about 48 hours (Knight 1986). Despite the high seed output and the nutritive value of the fleshy fruits, which attract frugivores such as birds and bushbuck (Castley 1992) into the Enriched Foredune and Dune Scrub communities, no seeds were found in the soil along the entire successional gradient. Seeds were, however, found by van Daalen *et al.* (1986) in the open and under canopied species in the Dune Scrub and Bushclump communities, and seedlings were seen in the dunefield by the author and van Daalen *et al.* (1986) under the bushclumps in the Dune Scrub communities. This suggests that the foraging behaviour of the frugivores may cause a clumped effect in the distribution of the seeds. The seeds are released into the bushclumps when the birds are resting on a bush, but it is difficult to reach a conclusion on the behaviour of the species in succession with the results obtained. The species is important, however in attracting frugivores into the Enriched Foredune with its' fleshy fruits.

Passerina rigida Wikstr. occurs in the communities from the Enriched Foredune zone to the Forest Margin zone (section 1.7). It is one of the dominant species of the Open Dune Scrub community (section 1.6). The phenological cycle is short, commencing in early-spring and is completed by mid-summer (Fig.4). Small, light seeds (Table 2) are available in November and December. The seeds have a hook at one end to assist with wind-dispersal, and although, the seed output for the year is low

(Figure 6), the seed density in the soil is higher than all the species present (Table 3), and have a wide distribution range from the Foredune to the Bushclump community (Table 4). The distribution range is similar to the range of the adult plants. Seedlings were recorded in the open and under the canopy of the parent plants and *M. caffra* (Table 8), suggesting that the seeds can tolerate the high light intensities and surface soil temperatures measured, in the open and under the canopy of the parent plants (Table 8 & 9; Figure 9) and germination is not inhibited by the parent plants. The high mortality of the seedlings recorded show that the seedlings are susceptible to desiccation (Table 7). The rainfall and therefore the soil moisture content was low during the study period (Figure 2). The plants of this species may, therefore, be prevented from extending its' range into the foredune zone by moisture stress. It is expected that in wetter years, the germination rate and seedling survival in the early stages of succession will be higher than during the study period. The plants may be important in providing perches for birds attracted to the frontal dune by the fleshy seeds of *C. monilifera*, and for providing shade for other foragers such as bushbuck.

Stipagrostis zeyheri (Nees) De Winter subsp. *barbata* (Stapf) De Winter has the same distribution range along the chronosequence as *P. rigida* (Figure 3). It is one of the dominant species in the Open and Closed Dune Scrub communities, where it forms a field layer with *I. cylindrica* and *M. scolopendrium* (section 1.6). The

phenological cycle, which commences in mid-summer and is completed by autumn. The phenology cycle and the grain size is similar to *P. rigida* (Table 2), but the output of the grains is higher (Figure 6). The grains are released in February and March. However, the soil seed density is lower (Table 3), but soil seed bank range is as extensive as *P. rigida*, from the Open Dune Scrub community into the Bushclump community (Table 4). Seeds were found in the soil under the canopy of *E. capensis* (Table 5), and seedlings were recorded under the canopy of *P. rigida* and *M. caffra*, as well as in the open (Table 6). The grains are, therefore, widely distributed within the early stages of succession and the seeds appear to have a wide temperature and light tolerance range. However, half the number of seedlings under the canopy of *P. rigida* (Table 7) died, possibly due to desiccation as a consequence of the low rainfall received during the study period (Figure 2). It appears that the species has a similar reproductive strategy as *P. rigida*, and may also be prevented from expanding the population range into the Foredune zone by moisture stress. Once established, the plants may be important in trapping seeds blown by the wind.

Eugenia capensis (Eckl. & Zeyh.) Harv. ex Sond. has a wide distribution range, from Foredune to the Dune Forest zone (section 1.7 & Figure 3). It is one of the dominant species in the Closed Dune Scrub community, and is one of the dominant species in the shrub layer of the Bushclump community (section 1.7). The phenological cycle is longer than the cycle of

S. plumieri (Figure 4), but the species also produces a low output of large fleshy drupes (Figure 6 & Table 2), which require a long maturation period. Ripe fruits are available in September and October, before the fruits of *M. caffra* are ripen. Although, the standing populations of *E. capensis* have a wide distribution range, seeds were found at a low density (Table 3) only in the soil seedbank of the Closed Dune Scrub zone (Table 4), and only under the canopy of the parent plants and *M. caffra* (Table 5). The distribution pattern of the seeds appears to be determined by the foraging behaviour of the frugivores, and may therefore, have a clumped distribution. A large quantity of fruits were recorded under the canopy of the parent plants, indicating the species is dependant upon frugivores to extend the range of its populations into the early-successional stages. Seedlings were only recorded under the canopies of the parent plant and *M. caffra* (Table 6), although seedlings have been seen by the author in the open in the Enriched Foredune zone. The seeds may have a wide light and temperature tolerance range, however, the seedling recorded under the parent plant died, whereas the seedling under the canopy of *M. caffra* survived (Table 7), suggesting that the seeds are sensitive to a low soil moisture level. Seed germination maybe higher in the early-successional stages, where the seeds will have a growth advantage over the seeds of small-seeded species which have little food reserve to sustain them before a root system is developed.

Imperata cylindrica (L.) Raeuschel has a range from the Enriched

Foredune zone to the Forest Margin zone (section 1.7 & Figure 3), and is one of the dominant species in the Open Dune Scrub and Bushclump communities, where it forms a field layer with *S. zeyheri* and *M. scolopendrium* (section 1.6). The phenological cycle is as short as *S. zeyheri*, but commences in early-spring and is completed by the end of Spring before the cycle of *S. zeyheri* begins (Figure 4). This may reduce the impact of granivory on the soil seedbank of the two grass species. A low output of small, light grains are produced (Figure 6 & Table 2) in October (Figure 4), which have plumes to assist with wind-dispersal. The seeds are similar in size to the seeds of *S. zeyheri*, but whereas *S. zeyheri* has a relatively high soil seed density, no seeds of *I. cylindrica* were found. This suggests the predators, such as ants and rodents, may have removed a large number of the seeds from the soil seedbank, reducing the number of potential new propagules. Compared to *S. zeyheri*, *I. cylindrica* appears to be less successful in extending the range of its populations into new areas. Vegetative propagation may be an important reproductive strategy for this species as the seedlings found in the open and under the canopy of *P. rigida* and *E. capensis*, appeared to be clones.

Mimusops caffra E.Mey. ex A.DC. is found growing in the Bushclump community and in the young Dune Forest community (section 1.7 & Figure 3). It is one of the dominant species of the tree layer in the Bushclump community (section 1.6). The phenological cycle is longer than either *S. plumieri* or *E. capensis*, due to the long

fruit maturation period of nine months (Figure 4). The species has the lowest output of large, heavy fleshy drupes (Figure 6 & Table 2), which are available in November and December (Figure 4). Seeds were found only in the Bushclump zone soil seedbank (Table 4), and at a low density (Table 3). Seeds were also only found under the canopy of *P. rigida*, *E. capensis* and the parent plants (Table 5). This suggests that the seed distribution pattern of the species is also apparently determined by the foraging behaviour of the frugivores as *E. capensis*. However, as only one seedling was recorded under the canopy of *E. capensis* (Table 6), where it survived (Table 7), the seeds may be less tolerant of high surface soil temperature and light intensity than *E. capensis*. Thus, the expansion of the populations of the species appears to be dependant upon the presence of other species which will provide shade for the seedlings.

Microsorium scolopendrium (Burm.f.) Copel. is found growing in all the seres, except the Foredune and Enriched Foredune (section 1.7 & Figure 3). It forms a field layer with the grasses, *S. zeyheri* and *I. cylindrica* in the Closed Dune Scrub and Bushclump communities (section 1.6). Spores were observed on the plants throughout the year, suggesting that the species is continually in a reproductive state. The spores are too small to detect in the soil samples with the seed extraction technique used, but young plants, clonal in origin, were found under the canopy of *E. capensis* and *M. caffra*. None were found in the open, suggesting that the species prefers shade conditions where the

light intensity and the surface soil temperatures are lower than in the open (Table 8 & 9; Figure 9).

5.4 CONCLUSION

The pathway of species change suggests that the Facilitation model is applicable in this study area (Avis 1992). One of the assumptions of the Facilitation Model is that the species first to colonize an area after a perturbation, such as wind, are specific species that are able to tolerate the adverse conditions (Connell & Slatyer (1977)). *S. plumieri* is the first species to colonize the dunes in the Mlalazi Nature Reserve. The other colonizing species (eg. *C. monilifera*, *P. rigida*) appear only after *S. plumieri* become established.

Connell & Slatyer (1977), propose in their models of mechanisms that the colonizing species modify their environment, so that it becomes more suitable for later-successional species to invade and become established in than for the colonizing species. The results of the investigations of Avis (1992) and in this study on the succession on the prograding dunes of the Mlalazi Nature Reserve, suggest that the species do modify their environment. Changes, which included changes in the species composition of the communities, together with changes in the soil such as pH, mineral and organic content (Avis 1992; Avis *et al.* in prep.), as well as changes in the micro-environment in which seeds germinate in the open and under the canopies of species, such as

P. rigida, *E. capensis* and *M. caffra* occur along the successional gradient. Differences in environmental factors, such as light intensity, surface soil temperatures, the amount of litter and plant cover of the understorey were also found between the environment in the open and the canopied species, *P. rigida*, *E. capensis* and *M. caffra*, and between the species (Table 8 & 9; Figure 9).

A model has been proposed by van Daalen *et al.* (1986) to explain the pathway of succession of the vegetation on the prograding dunes in the Mlalazi Nature Reserve, based on the establishment and growth of bushclump species, such as *C. monilifera*, *P. rigida* and *E. capensis*. As the species diversity increases around the bushclumps and the canopy closes as the canopy species reach maturity, pioneer species are replaced by later-successional species. The species replacement occurs until the forest community has developed, and the early-succession are no longer present. A similar succession pattern was found in the vegetation of the Alexandria Dunefield, where the fleshy-seeded species established in the bush pocket communities after the colonizing species had stabilized the dunes (Bruton 1992).

The results obtained of the main features of the reproductive strategies of phenology, soil seedbanks and seed germination and seedling establishment, investigated in this study provide evidence to support the model. The importance of the canopy species, *P. rigida*, *E. capensis* and *M. caffra* in providing

favourable environments for later-successional species was emphasized during the study by the low soil moisture conditions, which prevailed as a consequence of the low rainfall and high ambient temperatures experienced from September 1991 until November 1992. The mean surface soil temperature was lower under the canopies than in the open due to the lower light intensities, and the moisture evaporation rate from the seeds and the soil would therefore have been lower than in the open.

Pickett *et al.* (1987) suggest that the main causes of succession are the availability of sites for establishment, the differential availability of seeds of the different species and the differential response of the species to the environment. The results of the seed output and the soil seedbank density obtained in this study suggests that these causes may be important in the succession investigated in this study.

Other studies involving primary succession have found that the life-history characteristics, including the reproductive strategies of the dominant species and their response to the environmental conditions, help determine the path and rate of succession (van Tooren *et al.*; Walker *et al.* 1986).

The results obtained in this study has shown that the species have different reproductive strategies for producing new propagules through seed. The strategies are adapted to the seed characteristics of the species. The establishment of a species

in a site depends upon the availability of seed and the response of the seed according to its characteristics to the local environment, to become part of the successional sequence (Luken 1991).

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