The Life History Of Selected Coastal Foredune Species Of South Africa

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THE LIFE HISTORY OF SELECTED COASTAL FOREDUNE SPECIES OF SOUTH AFRICA

THESIS

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The beach is a stimulating place for humans,

but a stressful one for plants that must remain for a lifetime…

Barbour (1992)

ABSTRACT

South African dune fields are severely threatened by human expansion and in the long run the stabilisation of many dunes will be necessary. The alien grass *Ammophila arenaria* is the most important drift sand stabiliser at present in South Africa. Although not invasive, the current impact of *A. arenaria* on the dune systems of South Africa is considerable, and thus the stabilising benefit of the grass seemed to may be outweighed by its negative consequences. It is therefore preferable to use indigenous sand stabilising species. In order to define guidelines for the application of indigenous plants for stabilisation, their autecology should be studied first to enhance the chance of successful stabilisation results. The main aim of the present thesis was to gather information on the life history processes of selected indigenous, sand stabilising foredune species.

To investigate the growth of foredune pioneer species, the common pioneer *Scaevola plumieri* was followed over a three-year period to determine the growth season and leaf phenology. Soil-borne pathogens are known to influence the growth and vegetation dynamics of foredune species. To examine this effect on the South African foredunes the rhizosphere soil and the roots of several species were studied. To test the effect of the nematode fauna on succeeding plant species a transplantation experiment was carried out. The seed stage is the only life-cycle stage that can survive unfavourable conditions. Therefore, the seed ecology of several foredune species was studied extensively to determine the reproductive season, the seed production, the fate of seeds after shedding (germination, seawater dispersal), germination requirements and seed bank strategy. Seeds of the species *Arctotheca populifolia*, *Ipomoea pes-caprae, Myrica cordifolia,* and *Scaevola plumieri* were subjected to germination trials, field observations on seedling survival, and scarification and stratification experiments. This was done to obtain information about the germination requirements and to determine the reproductive season and growth season. The seed bank strategy of the foredune species, as well as the seed bank density, was determined by extensive sampling along the Cape coast.

The species *S. plumieri* thrived under sand accretion situations, which makes it a good candidate for stabilisation purposes. The growth of *S. plumieri* was seasonal, with the highest leaf production during spring and summer. The stem position on the foredune had a strong effect on the overall performance of *S. plumieri*, with the stems situated on the landward face of the foredune showing higher leaf and seed production. The

nematode survey of soil and roots of several foredune species showed that all plant species featured a specific nematode fauna in the rhizosphere soil and the roots. The specific nematode fauna affected the growth of foreign plant species in the transplantation experiment, resulting in a lower root and/or shoot biomass production.

Most of the foredune species produce seeds from spring to late summer. For *S. plumieri* the position of the stem on the dunes, as well as the predation of unripe seeds affected the number of seeds produced. The highest production was found for the landward faced stems. The *S. plumieri* seeds were able to float on seawater for at least three months without losing viability, as was observed for seeds of *I. pes-caprae.* The seeds of *M. cordifolia*, however, sank after a few days, but their viability was not affected. The rhizome fragments of *A. arenaria* and *S. virginicus* floated for 120 days, whereas the fragments of *E. villosa* sunk after one day. The viability of *S. virginicus* fragments was affected by the duration in seawater by an increase in sprouting time.

The seeds of all species tested germinated readily under controlled conditions, except *S. plumieri* seeds which required a long lag-phase before germination. In the field the seeds of *A. populifolia*, *I. pes-caprae* and *S. plumieri* germinated, producing many seedlings. Only the seedlings of *A. populifolia* and *S. plumieri* survived. Of the species found in the foredunes 57% was represented in the soil seed bank. For most species, the seeds that were found in the seed bank showed viability of at least 40%. Many of the seeds found were older than one year, suggesting a short-term persistent seed bank.

The present study is a start in filling the gap in information on dune pioneer and foredune species. The conclusion was that in general all species in the present study were easy to grow under controlled conditions, and thus could be used for stabilisation purposes. When the more rapidly growing pioneer species are planted in combination with succeeding foredune species, a functional and aesthetic ecosystem could be created.

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FOREWORD

Four years ago it all started with a missing postal package and six months later I was on a plane to South Africa, with as result this thesis on life history of coastal foredune species. My stay in South Africa has been a fantastic time and to work in the most amazing dune fields was a pure bonus. My project was part of an EU programme INVASS on invasive grass species in coastal and inland dunes of Southern Africa. Due to the work of Ursula Hertling most of the work on marram grass was already done, which left for me a big open space to choose a research direction supported by my supervisors Roy Lubke and Jan Bakker, who gave me room to find my own way. It was not always easy coming from Europe, being used to a certain 'luxury', to do everything yourself with not always the best equipment, but it makes you appreciate even more what you have.

Part of the work for this thesis I did not alone, for six months three Dutch students assisted me with some of the experiments and fieldwork. Thomas Lans thanks for all the nematode counting and identification. Meike Bulten and Harmen Venema thank you for counting all those seeds and rhizomes and all the help with the dispersal experiment. It was great fun having you guys in South Africa and sharing the fieldwork and the Saturday morning coffee ritual with you. Besides the help in South Africa I also had a nice back-up team at home. Wim van der Putten thank you for all the moral and scientific support and for being our fearless INVASS leader. Renée Bekker thanks for the all the support and of course the help on the seed bank fieldwork. We had a great trip visiting all the sandy beaches of the Cape coast. It was a shame that the wine estates were closed on our 'free' Saturday. Thanks also to Jan Bakker, my co-supervisor from Groningen, for all your help, support and a nice trip through KwaZulu-Natal. In my first three months in South Africa Ursula Hertling showed me around and made me feel a home. Thanks Ulla for being such a great friend and I wish we could have done our PhD's at the same time. After that my neighbour, colleague and friend (in no particular order!) Brad Ripley showed me the real African way of life with loads of braais. Thank you also for all the field trips together. It was nice and interesting to work on the same plant, but in totally different field. I will never forget the Old Woman's River trips when we stayed in the old stables ('our' beach cottage) and the lovely suppers with fresh fish on the braai. To set the record straight, I think that after four years of research at Old Woman's River it is your beach and your reef, but they are my dunes!

Lots of field trips I also made with Craig Peter. Thanks Craig for lots of fun and our around the Cape *Scaevola* trip. The after-dinner white chocolate and Jeripego sessions on cold winter field trip evenings are a good memory. Many times I drove around the Eastern Cape with Freyni Killer to do our fieldwork. We had a good deal, you helped me and I helped you, and it was always good fun. I will never forget those scorching February days at Bedford with no shade and no wind and the Magnum ice cream we deserved after that.

To all my other fellow students and all staff members I would like to say thank you for all the relaxing tea times and the Friday afternoon drinks. In particular I would like to thank Rachel and Claire for all the trips to your farms with the nice walks and picnics.

Further, a lot of non-work friends stimulated me and made my time in South Africa very pleasant, I would like to thank a few in particular. First of all Natalie Ripley, thank you for all the workouts, the chats over the fence and the walks with the boys and Felix. Alison Buswell and Janine Baart our Saturday morning coffees were to keep life in perspective. Eddie Baart corrected the English of my thesis. Thanks Eddie, compared to your field it must have been quite something else.

Last but not least I would like to thank Roy Lubke, my first supervisor, who made it all possible. My first few days in South Africa you took me on a trip to Die Mond to show me the marram dunes there. I will never forget the sight of these enormous dunes, my first braai, and my first swim in the Indian Ocean. It was the best start for four years of South Africa. Thanks for everything!

Irma

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CHAPTER 1

GENERAL INTRODUCTION

The coastal dune ecosystems of southern Africa are probably of greater importance, and therefore of greater value per unit area, than any other biome or ecosystems in the region.

Tinley (1985)

1.1. Dune stabilisation in South Africa

The movement of sand is a natural and intrinsic component of the dynamic coastal system, and the shape of dunes and beaches is constantly changing by erosion or accretion of sand in response to the variable climatic and environmental factors experienced along the coast. It was only when man started developing and exploiting the coastline that these natural drift sands posed a threat, and the need arose to prevent sand movement (Avis 1989). The dune plants play a vital role in stabilising dunes. Being well equipped with extensive underground stems or rhizomes or runners or stolons, the plants bind the sand, facilitate dune growth, and provide the first terrestrial habitat for animals and soil micro-organisms. Depending on the growth form of various dune plants quite different sand accumulations are developed (Ranwell 1972). Rhizomatous plants usually built a pronounced crest, whereas stoloniferous plants tend to form low undulating sand accumulations (Tinley 1985). Hence, the vegetation plays a dominant role in determining the size, shape and stability of foredunes. The aerial parts of the vegetation obstruct the wind and absorb wind energy. Wind velocity near vegetation is thus reduced below the velocity needed for sand transport, and the sand is deposited around and between the plants. A characteristic of dune vegetation, particularly the grasses, growing under these conditions is their ability to produce upright stems and new roots in response to sand covering. Successive stages of plant growth and sand deposition result in increased width and height of the dune (Chapman 1976, Tinley 1985, Hesp 1991). Vegetated foredunes are inherently flexible, because if they are damaged by storm waves, the remaining vegetation traps sand blown from the beach and the dune is reformed, thus providing protection against future wave attack (Tinley 1985, Carter 1993). During storm events vegetative plant parts and diaspores often are swept into sea, and subsequently dispersed via the currents to colonise new sites (Ridley 1930, Muir 1937).

The first attempts at stabilising drift sands in South Africa started around 1720 (Stehle 1981), after which in 1845 the first organised dune stabilisation projects began at the West coast with the introduction of the alien Australian *Acacia* species (Stehle 1981, Avis 1989). From 1892 onwards the interest in *Ammophila arenaria* as sand stabiliser increased and it was used in many drift sand stabilising projects (Hertling & Lubke 1999).

The threat to indigenous vegetation by the invasion of aliens used for sand stabilisation (e.g. *Acacia cyclops*) was raised for the first time in 1936 (Keet 1936 cited in Avis 1989). However the general consensus was that there were no indigenous species which could substitute for the aliens, despite the successful stabilisation in 1942 with the indigenous *Myrica cordifolia* and *Metalasia muricata*. It was not until 1974 that it was decided that only indigenous species and the non-invasive grass *Ammophila arenaria* could be used (Stehle 1987, Avis 1989, Hertling & Lubke 1999).

Nowadays *A. arenaria* is only used in connection with indigenous plants and according to Hertling (1997) the indigenous plants will replace *A. arenaria* within 10 years. Even though *A. arenaria* was not invasive (Hertling 1997) the use of *A. arenaria* has been criticised from 1980 onwards, mainly on the grounds of its foreign origin. During the 1980s South Africa experienced a green movement which highlighted more then ever the negative impact that alien species can have on South African ecosystems (Hertling & Lubke 1999). Concern about the use of *A. arenaria* has since than not only been based on the mere 'alienness' of the grass, but also on proven facts about its invasiveness in countries like North America, Australia and New Zealand where the grass also was introduced (Hewett 1970, Buell *et al.* 1995, Wiedeman & Pickart 1996, Hertling & Lubke 1999).

Is there a need for stabilisation?

It is apparent that the coastal dune systems are highly diverse and variable environments. They are often multifunctional systems of great importance to society, offering utility functions such as coastal defence, nature conservation, recreation, and housing areas (Avis 1992). Nowadays the African dune fields are severely threatened by human expansion, with the result that the stabilisation of many dunes will be unavoidable. By 1993 about 69% of the South African dune fields were affected by the development of houses, roads, car parks, camping facilities, sewage pipelines and other artificial structures (McGwynne *et al.* 1993, Moffett 1994). Since the Eastern Cape coastline is relatively sparsely populated, it is expected that the pressures of development will increase even more with time (Fabricius *et al.* 1991, Moffett 1994, Hertling & Lubke 1999). Rapid population growth as well as changing political and socio-economic conditions have resulted in an increased demand on coastal land for the development of holiday housing, recreation resorts and retirement purposes (Heydorn & Tinley 1980, Heydorn 1986, Moffett 1994). Besides the development on the

dunes and the subsequent stabilisation need, the mining of dunes sand is also having a large impact on the dunes ecosystem, and the dunes have to be rehabilitated after the sand has been mined (e.g. Van Aarde *et al.* 1996). Since the dune environment is extremely complex and varied in space and time, a dynamic approach towards stabilisation and rehabilitation management is required. Such an approach requires a clear understanding of the ecological processes active in the dune environment (Van Der Meulen *et al.* 1989).

1.2. Immediate cause of study

The coastal grass *Ammophila arenaria* has been one of the most important artificial drift sand stabilisers in South Africa since its introduction in the second half of the 19th century (Hertling & Lubke 1999). Analysis of the use *of A. arenaria* in earlier and recent days in relation to its present distribution does not indicate a tendency to spread unaided (Lubke *et al.* 1995*,* Hertling 1997, Hertling & Lubke 1999). Due to its many sand stabilising characteristics the grass was extensively used, but its use has been criticised mainly on grounds of its foreign origin and the proven facts of invasiveness in other parts of the world (Heyligers 1967,Buell *et al.* 1995, Wiedemann & Pickart 1996). The grass is presently still the primary and in most cases the only plant used in South African stabilising projects, and although not invasive the current impact of *A. arenaria* on the dunes system of South Africa is considerable, especially when intensively managed (Hertling 1997).

To determine the effect of *Ammophila arenaria* on indigenous vegetation and dune topography the international European Commission programme INVASS was initiated. The EC-INCO-DC program, INVASS (contract ERBIC18CT970145) is investigating "the impact of invasive grass species on the structure, functioning and sustainable use of coastal and inland dune ecosystems in Southern Africa". As far as the coastal sand dunes of South Africa are concerned, INVASS is primarily investigating the status of *A. arenaria* in South Africa. This species is indigenous to the temperate coasts of Europe and the Mediterranean where it has been used for stabilising mobile sands for a number of centuries. Broadly, the aims of this programme are:

1. To determine the natural behaviour of *A. arenaria* in South African and European dunes in different phases of its life history.
2. To investigate the current and likely future impact of *A. arenaria* on the dune systems of South Africa.

3. To compare the effect of soil-borne pathogens and arbuscular mycorrhizal fungi on vegetation succession in temperate European sand dunes with coastal and inland dunes in Southern Africa.
4. To provide management prescriptions for the wise use and, if appropriate, control of *A. arenaria* to maximise its beneficial properties for coast protection without concomitant threat to ecosystem function, biodiversity and wildlife.

The first two aims were answered by the study of Hertling (1997), who concluded that *A. arenaria* is a useful dune stabiliser and, although it is visibly alien to South Africa, it is neither aggressively spreading nor out-competing indigenous dune plants, as has been found in North America. In most cases *A. arenaria* stands were 'succeeded' by indigenous species within forty to fifty years; hence, *A. arenaria* was not classified as invasive and was not likely to become invasive in the near future, due to the unsuitable climate. But even though *A. arenaria* was not considered to be invasive, it remains alien and as such potentially dangerous as due to future climate change the South African rainfall could increase which would be favourable for *A. arenaria*.

1.3. Purpose of present study

South Africa has a long history of problematic alien plants, and it is important to control if not prohibit their use as far as possible. Hertling (1997) has extensively investigated the aspects of the first, second and fourth main objectives posed by INVASS, but with a climate change the non-invasive character of *A. arenaria* could change also.
Even though it is proven not to be invasive, the impact of *A. arenaria* on the aesthetics of dune environment is immense as shown in plate 1.1.

Plate 1.1. Hummock dunes formed by indigenous species (left) and *Ammophila arenaria* (right) at Tableview (Photo's by U.M. Hertling).

Both pictures were taken at the same site standing in the middle and turning 180 degrees to the *Ammophila* patch. On the left picture the indigenous vegetation builds little hummocks, whereas when *A. arenaria* was introduced to stabilise the sand, the whole appearance of the dunes changed dramatically (Plate 1.1). Together with the results from Hertling and Lubke (1999), the benefit of the grass as a stabilisation tool seems to be outweighed by its negative consequences for the structural and functional characteristics of the dune ecosystem where it has been introduced.

The present research will focus on the third and fourth aim of the INVASS programme. Within the fourth aim, the main focus will be on finding indigenous species to replace *A. arenaria* in its dune stabiliser role. h order to define guidelines for the application of indigenous plants for sand stabilisation and erosion control, the autecology and life-history processes should be studied to enhance the chance of successful stabilisation results.

Not much is known about the foredune species of the South Africa coast. Therefore the first step toward defining suitable species for stabilisation will be the study of the life history of the 'candidates'. Information on life-history traits of the indigenous species is vital for stabilisation purposes to be able for instance to determine when to collect seed, when to sow seeds, and when to plant seedling or stem cuttings.

Factors and processes that influence the life history of the indigenous foredune pioneers will be of importance in making any stabilising process a success; the reproduction phenology especially will give important information on when to collect seeds for instance. Therefore the main research questions of the present thesis are:

1. When and how rapidly do the foredune pioneer species grow?

To stabilise drift sand of a mobile dune the plant has to grow fast and withstand severe sand burial. The growth of *Scaevola plumieri*, the most common pioneer, has been followed over a period of three years to provide answers to this question (Chapter 3).

2. Do soil-borne pathogens influence the growth and vegetation dynamics of South African pioneer plant species?

The soil and roots of several pioneer species were investigated on infection with plant parasitic nematodes. In Europe the root zones of sequentional foredune plant species contain pathogens that were specific for their host and pre-successional plant species,

but that affect the next species in the successional sequence to a much lesser extent. To test the role of soil-borne pathogens in the vegetation dynamics of the South African foredunes, a transplantation experiment was carried out (Chapter 7).

3. What is the reproductive phenology of foredune pioneers?

To determine the development time for each reproductive stage and the number of seeds produced, the fruiting structures of *Scaevola plumieri* were followed for three subsequent reproductive seasons (Chapter 3).

4. What is the fate of dispersal units in the coastal foredune environment?

When the seeds were shed from the parent plants they could germinate (Chapter 4) or get secondarily dispersed by seawater, and could end up on a different surface at the same or a new site (Chapter 6). After high tides foredunes are often washed away and vegetative parts such as rhizomes often break off and are washed into the sea to be dispersed to new sites (Chapter 6).

5. Do the dispersal units germinate and establish seedlings in the field?

To test the viability of seeds of different pioneer species, germination experiments were carried out, and the seeds difficult to germinate were stimulated to germinate by scarification and stratification experiments (Chapter 3). The establishment of seedlings of various species was followed in the field and their growth rate recorded (Chapter 4). The seeds in the soil seeds bank were also tested for viability to determine their regeneration potential (Chapter 5).

6. Do foredune pioneer species form a soil seed bank?

Seeds that do not germinate or get dispersed have a high chance of ending up in the soil seed bank. According to the literature no soil seed bank exists in the foredune environment, but when the seed characteristics of certain species are examined and the fact that in a dynamic environment the seeds get easily buried, a soil seed bank should be present. The soil seed bank was sampled at different sites and the seed characteristics of selected foredune species were determined (Chapter 5).

During the present study a lot of attention was given to the seed ecology of foredune species. This is because seeds are an important part of the life history of plants, and have four main roles. Firstly, seeds are dispersal units and thus the primary means whereby plants colonise new sites (Van der Pijl 1972). Secondly, seeds represent a stage in the life cycle resistant to unfavourable environmental conditions by accumulating in the soil as a seed bank (Fenner 1985). Thirdly, seeds often carry a food supply to nourish the embryo and seedling, which is an important determinant of seedling success (Salisbury 1952). Lastly, because seeds arise from the production of gametes, they contain unique genetic information from the parent plant, and thus seeds maintain the genetic variation in a population in space and time (Harper 1977, Luken 1990).

1.4. General outline of the thesis

The introduced grass *A. arenaria* was not considered to be invasive, but did nevertheless show a large impact on the coastal foredunes when used for stabilisation purposes. Therefore the species should not be used for stabilisation, but rather indigenous stabilisers should be used. To find out which species are the best candidates to replace *A. arenaria*, the life history of selected foredune species was examined in the present study.

The general environment of the coastal dunes of South Africa is presented in chapter 2 with a description of the foredune plant species to give a framework to the present study. Knowledge of the plant phenology is of importance in habitats that require management reclamation or stabilisation, because this allows the identification of the fruiting periods for seed collection. Therefore, the phenology and growth of *Scaevola plumieri* was examined over a three-year period to assess how many flowers, and subsequently seeds, were produced (Chapter 3, Figure 1.1). *S. plumieri* was chosen because it is one of the dominant foredune species in the Eastern Cape.

When seeds are produced, can they germinate and establish seedlings in the field?

To answer this question the germination and seedling survival in the field was examined for *Scaevola plumieri* and *Ipomoea pes-caprae*, as well as the germination under controlled conditions for *Arctotheca populifolia, Ipomoea pes-caprae*, *Scaevola plumieri* and *Myrica cordifolia* (Chapter 4, Figure 1.1), the main sand binding foredune species of the Eastern Cape. Not all seeds produced germinated. Do the seeds enter the soil seed bank to wait for more favourable circumstances to germinate? To answer this question the soil seed bank of the foredunes of the Cape coast was examined (Chapter 5, Figure

1.1). Seeds that do not enter the soil seed bank often get secondarily dispersed by wind and would end up in the sea to be dispersed by hydrochory. After storm events rhizome pieces can also end up in the sea. Can the rhizomes float, and for how long, and what happens to the viability? The floating capacity and survival after floating was examined for the seeds of the species *Myrica cordifolia, Ipomoea pes-caprae*, *Scaevola plumieri*, *Ammophila arenaria*, and rhizomes of the species *Sporobolus virginicus*, and *Ehrharta villosa* (Chapter 6, Figure 1.1). The sea currents can disperse the dispersal units (seeds and rhizomes) over long distances to colonise other beaches to build new foredunes. The foredunes of the Eastern Cape do not represent clear successional stages dominated by a single plant species, but rather show a mixture of plant species. In Europe it was found that the root zones of sequential successional plant species contain pathogens that play a role in plant competition. This might be an important factor if a mix of indigenous species were used to stabilise a drift sand area. Therefore, the role of plant parasitic nematodes in the foredune vegetation was examined (Chapter 7, Figure 1.1).

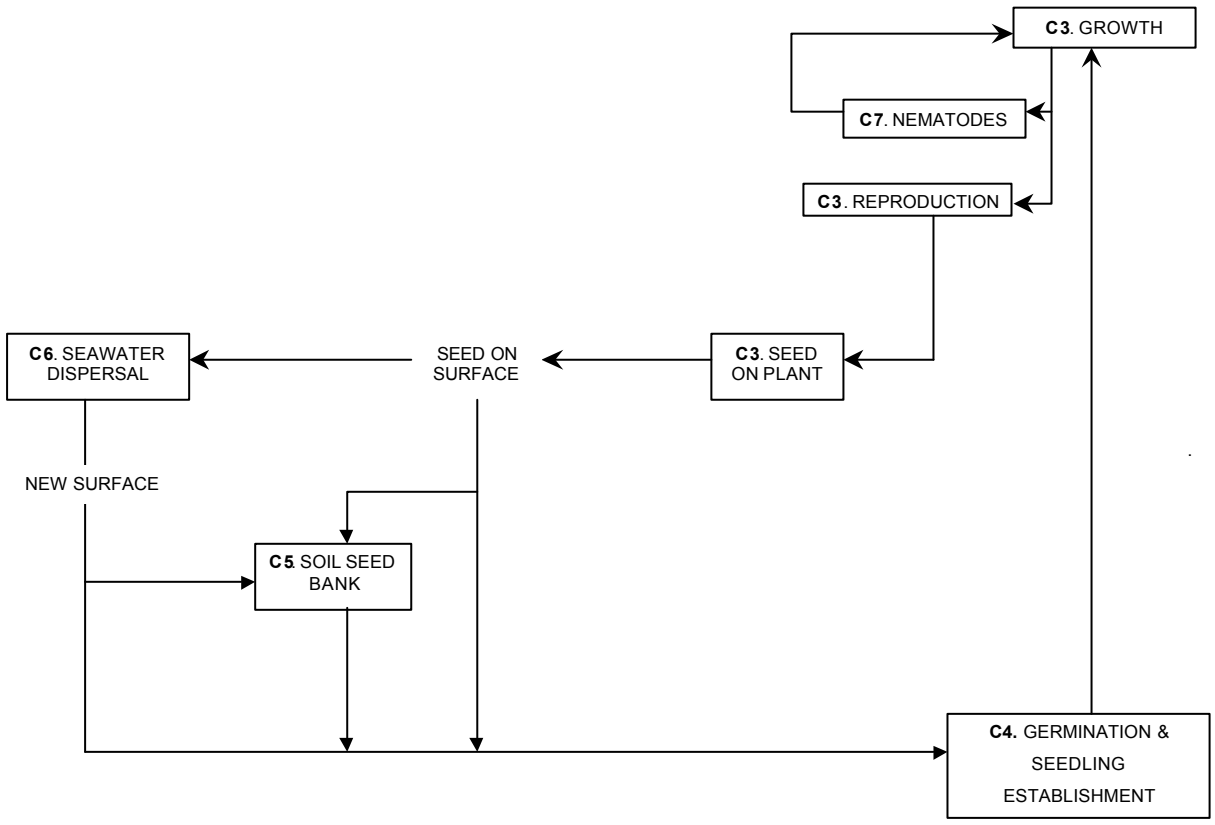


Figure 1.1. Flow diagram of chapters 3 to 7 of the present thesis.

CHAPTER 2

AN INTRODUCTION TO THE COASTAL DUNES OF SOUTH AFRICA

There is a general perception that all coastal dunes are highly sensitive to a number of impacts, and that coastal dunes should be left alone.

McGwynne and McLachlan (1992)

2.1. Geographical setting and ecological features

The South Africa coastline is very diverse, with a wide variety of habitats stretching over an area which is transitional between winter and summer rainfall climates (Avis 1992). The coastal landforms and types of shoreline can be divided into three main types, namely, the sandy beaches and dune fields, the rocky headlands and promontories, and thirdly, the estuaries and coastal lakes (Tinley 1985, Lubke 1998). Of those three coastal types, the sandy beaches and dune fields comprise over 70% (roughly 3000 km) of the South African coastline (Tinley 1985, Lubke & McLachlan 1998). The sandy beaches and dunes of the coastal zone can be divided into different zones: the beach, foredunes, primary dunes, and the rear dunes (see Figure 2.1).

Currents and winds

The coastline of Southern Africa forms a discontinuous U-shaped line of sandy beaches and sand dunes extending nearly 12^{o} of latitude south of the Tropic of Capricorn. It extends from Alexander Bay situated in the north-west on the Atlantic coast around Cape Agulhas to the Mozambique border situated in the north-east on the Indian ocean coast. The climate is largely subtropical and is affected by two major currents; the cold north-flowing Benguela Current of upwelled inshore waters along the west coast, and the warm south-flowing Mozambique-Agulhas Current of equatorial waters immediately offshore on the east and south-east coast (Tinley 1985, Lutjeharms 1998, Schumann *et al.* 1995, Schumann 1998). Due to its subtropical geographical position, weather processes in South Africa are dominated by the interaction of three major pressure systems, two semi-permanent highs alternate with a series of polar lows (Tinley 1985). As a result the major winds along the coast are bi-directional and quasi-parallel to the coastline. Hence, southerly winds alternate with north-westerly winds on the west coast, westerly with easterly wind along the south coast and south-westerly with north-westerly on the eastern coast. Gale force winds are common along the coast with the highest frequency from the south-west to south east (Tinley 1985, Stone *et al.* 1998).

Climate

The coastline traverses a number of climatic regions as it curves around from the moist, tropical east coast through the warm, temperate regions of the southern coast to the hyper-arid tropical west coast, categorised extreme arid at the north of the west coast,

to arid (Cape Agulhas to Mossel Bay), to mesic (Port Elizabeth to East London) and moist (Durban to St Lucia) (Tinley 1985).

The coastal extremes in temperature are in general damped by the influence of marine air, increased cloud cover, high atmospheric humidity, the cooling effect of land and sea breezes, and the cold and warm currents flowing offshore.

The annual variation in temperature is retarded on the coast so that maxima tend to occur in February and minima in August (Schulze 1965), during the same months when sea surface maximum and minimum temperatures occur. Amplitudes in diurnal variation are damped, and minimum temperatures tend to be stable, while maxima show large fluctuations due to the intervention of cold fronts, berg winds and the high variability of cloud cover (Schulze 1965). From the south-west Cape to the south-east coast where inshore temperatures are generally low, little rainfall occurs where the coastlands are low, and higher rainfall only occurs in areas of abrupt relief of the foreshore, e.g. Transkei Wild Coast. Four rainfall variation patterns are recognised in South Africa; summer rainfall, all season rainfall, winter rainfall and bimodal rainfall patterns, the latter being situated between the summer and winter rainfall regions (Tinley 1985, Kopke 1988).

Continental margins and soils (south to east)

The outstanding large-scale feature of the south coast is the series of large asymmetric half-heart embayments such as Struisbaai, Stilbaai, Mossel Bay, Plettenberg Bay and Algoa Bay. The low embayments are separated from each other by sectors of raised coastal plateaux with steep or cliffed shores, resulting in discontinuous coastal lowlands which are associated with river valleys. Active and fixed dune fields are most extensive against the half-heart bays and across their promontories (Tinley 1985). The south coast is fronted by the broad continental shelf of the Agulhas bank which was exposed by the lowering of sea level during the Würm glaciation 20,000 years ago (Rogers 1971). The south-east and east coasts shows a linear rocky coastline, indented with a much greater number of small bays at river mouths, and is characterised by nearly continuous dune cordons along the coast (Tinley 1985). The predominant soils of the south-east coastal region are shallow to deep gley-like podzols which are temporarily waterlogged in summer (Van der Merwe 1962, Rust 1995).

Coastal vegetation

The coastline in different parts of Southern Africa is colonised by various assemblages of vegetation. These assemblages are strongly influenced by the vegetation types of the adjacent hinterland and cannot be isolated from them (Lubke & Van Wijk 1998). The east-coast is strongly influenced by the Tongoland-Pondoland flora as well as the Afromontane flora (Lubke & Van Wijk 1998), and to some extent the Madagascan flora (Tinley 1985). The vegetation of the southern coast is dominated by elements of the Cape fynbos flora, and to a lesser extent the Karoo-Namib flora. All the floras listed above interact in a complex manner along the south-east coast of the Eastern Cape (Lubke & Van Wijk 1998). The west coast of Southern Africa, north of Cape Columbine, is dominated by the Karoo-Namib flora with elements of the Cape flora (Tinley 1985, Lubke *et al.* 1997, Lubke & Van Wijk 1998).

2.2. Coastal sand dune characteristics

Together with sandy beaches, dunes form a buffer zone and link between the marine system and the truly terrestrial stabilised land surfaces (Lubke 1998). The classic environmental factors and stresses associated with beach and foredune environments all over the world include, salt spray, intense solar radiation (incident and reflected), high substrate mobility, abrasive substrate, low water retaining capacity of the substrate, high wind speeds, large temperature fluctuations, high air and substrate temperatures, low concentration of macro-nutrients, and episodic over-wash and immersion (Salisbury 1952, Maun 1993, Barbour *et al.* 1985, Ignaciuk & Lee 1985, Rozema *et al.* 1985, Hesp 1991; Figure 2.1).

Many authors consider dunes as xeric environments with the aridity being considered an important synthetic stress as it is a product of several of the independent stresses mentioned above (Barbour 1992, Hesp 1991). In addition, dune plants often possess xeromorphic attributes often observed in desert plants, which contribute to the perception that this is a xeric environment (Pavlik 1983). For example, leaf hairs (*Arctotheca populifolia*; Ripley *et al.* 1999), leaf succulence, waxy cuticles (*Scaevola plumieri*; Pammenter 1983), leaf rolling, and sunken stomata (*Ammophila arenaria*; Peter 2000) are all traditionally associated with plants of dry environments. Yet there is little consensus as to whether it is a xeric environment, as there is still little information to which extent dune plants experience water stress (Peter 2000). Many species have extensive root systems and probably utilise the dune aquifer water (De Jong 1979,

Pavlik 1983, Peter & Ripley 2000). Shallow-rooted plants may utilise water in the superficial layers of sand resulting from precipitation, dew or fog (Salisbury 1952, Barbour *et al.* 1985, Kopke 1988).

Also important in these coastal systems are the high rates of sand movement and salt derived from sea spray and seawater (e.g. Barbour & De Jong 1977, Maze & Whalley 1992, Alpha *et al*. 1996). Vegetation has the effect of reducing wind speed, causing the deposition of sand. The vegetation needs to be able to outgrow high rates of sand accretion. Sand deposits of up to 90 cm per year can be tolerated by *Ammophila arenaria*, while *Abronia maritima* can withstand burial for up to 4 months (Barbour *et al.* 1985). While a number of species may tolerate sand burial, many species may be stimulated by high accretion rates (Martinez & Moreno-Casasola 1996) and species such as *A. arenaria* require high rates of sand deposition to escape from harmful soil-pathogens (Van der Putten & Peters 1997).

Salt contributes to the physiological desiccation of plants growing on sand dunes. In a number of cases the decreasing salt concentration gradient from the foredune inland correlates with the observed zonation patterns at a number of sites (Barbour & De Jong 1977, Donnelly & Pammenter 1983). Alpha *et al.* (1996) investigated the impact of salt spray and substrate salinity on the morphology and physiology of *Scaevola sericea* and concluded that these two variables contribute to limit its seaward expansion. Salt as an environmental variable may also be closely linked to such factors as wind which moves salt spray landward (Barbour *et al.* 1985, Avis & Lubke 1985). While salt spray may limit the seaward spread of many species, Rozema *et al.* (1985) noted that salt spray stimulates the growth of some dune species. De Jong (1979) found that the salinity of the sand was not very high, particularly deeper in the sand where salt concentrations were constant. In the dune aquifer and groundwater, the salinity was always less than 3% of seawater, and often less than 1% of seawater.

2.3. Dune formation and coastal vegetation

The wind and waves transport sand from offshore bars and the surf zone to the beach where the sand particles are loosely packed with intervening air spaces (Tinley 1985). Onshore winds of sufficient velocity to move sand particles erode sand from the dry parts of the beach and transport it landward onto the high water mark where it is trapped by debris and the vegetation (Heyligers 1985). The obstacles are responsible

for a sudden drop in wind velocity, hence the sand will drop and accumulate around the plant shoots and debris (Salisbury 1952, Gemmell *et al.* 1953, Tinley 1985). The burial will stimulate the plant to further growth up through the sand (Carter 1993), forming an embryo dune. This process can be repeated indefinitely, as long as sand accumulation continues, resulting in foredunes at the back of the beach (Gemmell *et al.* 1953).

Other pioneer species will colonise the dunes, hence further stabilising the sand (Lubke & Van Wijk 1998). The foredunes can become higher and wider as sand accretion continues. The foredunes act as barriers against the action of waves and tides, and are a source of sand for the beach during periods of erosion (Heyligers 1985, Tinley 1985).

During periods of shoreline advance, successive foredunes may develop, forming a series of dunes parallel to the shore (Gemmell *et al.* 1953), but during storms the seaward margin of a foredune might be trimmed down by high waves. During calm weather, waves build up a new beach ridge in front of and parallel to the original foredune, or to the trimmed margin of the foredune. As the new beach ridge develops, a low-lying swale is formed between the developing ridge and the original foredune. The dune plants colonise the new beach ridge and accumulate windblown sand, and a new foredune is built up (Tinley 1985, Carter 1993). In time the pioneer species will be replaced by other species in the successional sequence, mainly shrubs and thicket, but many successional stages can occur next to each other in a zone due to the highly unstable character of the dunes (Lubke & De Moor 1998; Figure 2.1). The coastline in different parts of Southern Africa is colonised by various assemblages of plant species. These assemblages are strongly influenced by the vegetation types of the adjacent hinterland and cannot be isolated from them (Lubke & Van Wijk 1998). Thus, the abundance of species within various coastal habitats is controlled by local habitat conditions. Only a few species of pioneer plants will be found on sand dunes. The pioneer dune-species, growing on beach and foredune, are highly specialised and are able to withstand extreme and unfavourable conditions. These species may have special morphological and/or physiological features enabling them to grow under adverse conditions (Rozema *et al.* 1985, Lubke 1998).

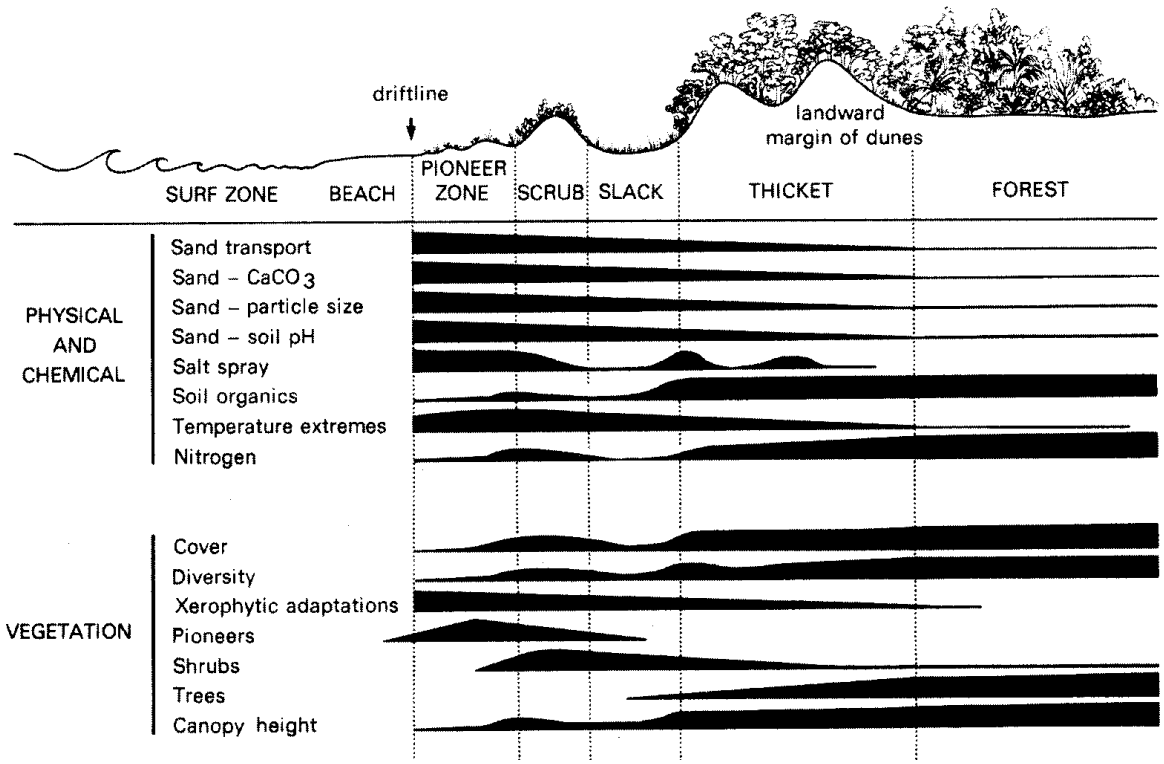


Figure 2.1. The zonation of a typical Cape coastal dune system with the importance of the physical and chemical factors, and vegetation type and parameters (From Brown & McLachlan 1990).

The vegetation of the embryonic dunes and foredunes is highly specialised and plays a vital role in stabilising the dunes of the pioneer zone. The coastal vegetation is often well equipped for sand stabilisation with many of the coastal plant species having extensive underground stems, rhizomes, runners, and stolons. The pioneer dune plants bind the sand and provide the first terrestrial habitat for animals and soil micro-organisms (Rozema *et al.* 1985, Tinley 1985; Figure 2.1). Even when covered with vegetation the newly established and colonised dunes are highly susceptible to human trampling and the effect of off-road vehicles. Lubke (1987) considered that a decrease in sensitivity to development, vehicles and trampling, is evident as one moves away from the sea towards a climax vegetation such as dune thicket, dune forest or dune fynbos. Thus the climax vegetation is less susceptible to damage compared to the newly colonised dunes, but even in established older dunes blowouts can develop caused by disturbance, even though they also occur naturally due to strong onshore winds (Daines 1991, Danin 1991, Carter 1993). In general the most sensitive areas, beaches and foredunes, are more in danger from heavy human traffic. Even barefoot

human traffic can be very destructive in the foredunes (Brown & McLachlan 1990, Moffett 1994). Thus, the balance between dune stabilisation by vegetation and dune instability resulting from physical forces is extremely delicate, and human intervention can throw the balance either way (Wallace & Hutton-Squires 1978, McAtee & Drawe 1980).

2.4. Eastern Cape coastal dunes

The main focus of the present research will be on the Southern and Eastern Cape coast, from Cape Agulhas to East London, with some more detailed studies carried out at Old Woman's River (near Great Fish River; Plate 2.1).

Plate 2.1. Overview from a high dune over the study site Old Woman's River with the *Scaevola plumieri* foredunes lying in a cordon between the sea and the older dunes, with the closed river mouth at the right.

In general this region is sub-tropical and the warm south-flowing Mozambique-Agulhas Current influences the coast of the Eastern Cape (Schumann *et al.* 1995, Schumann 1998). The Eastern Cape coastline is located at the western boundary of the south-east coastal climatic region (Schulze 1965). The area falls between the summer and winter rainfall regions and thus shows a bimodal rain pattern. The rainfall shows two distinct rainfall peaks, one in spring (October) and one in autumn (March) with the lowest rainfall in June. The average annual precipitation is 200-600 mm, with only 17 days of the year receiving more than 10 mm of rain. The maximum temperature of 22°C is experienced in December and January, the minimum of 14°C in July, with an annual average temperature of 18°C. Wind blows parallel to the coast and is predominantly north-easterly and south-westerly in summer, and westerly in winter. The net result of this wind regime is a 2-3 meter easterly movement of sand per annum (Tinley 1985, Kopke 1988, Avis 1995; Figure 2.2).

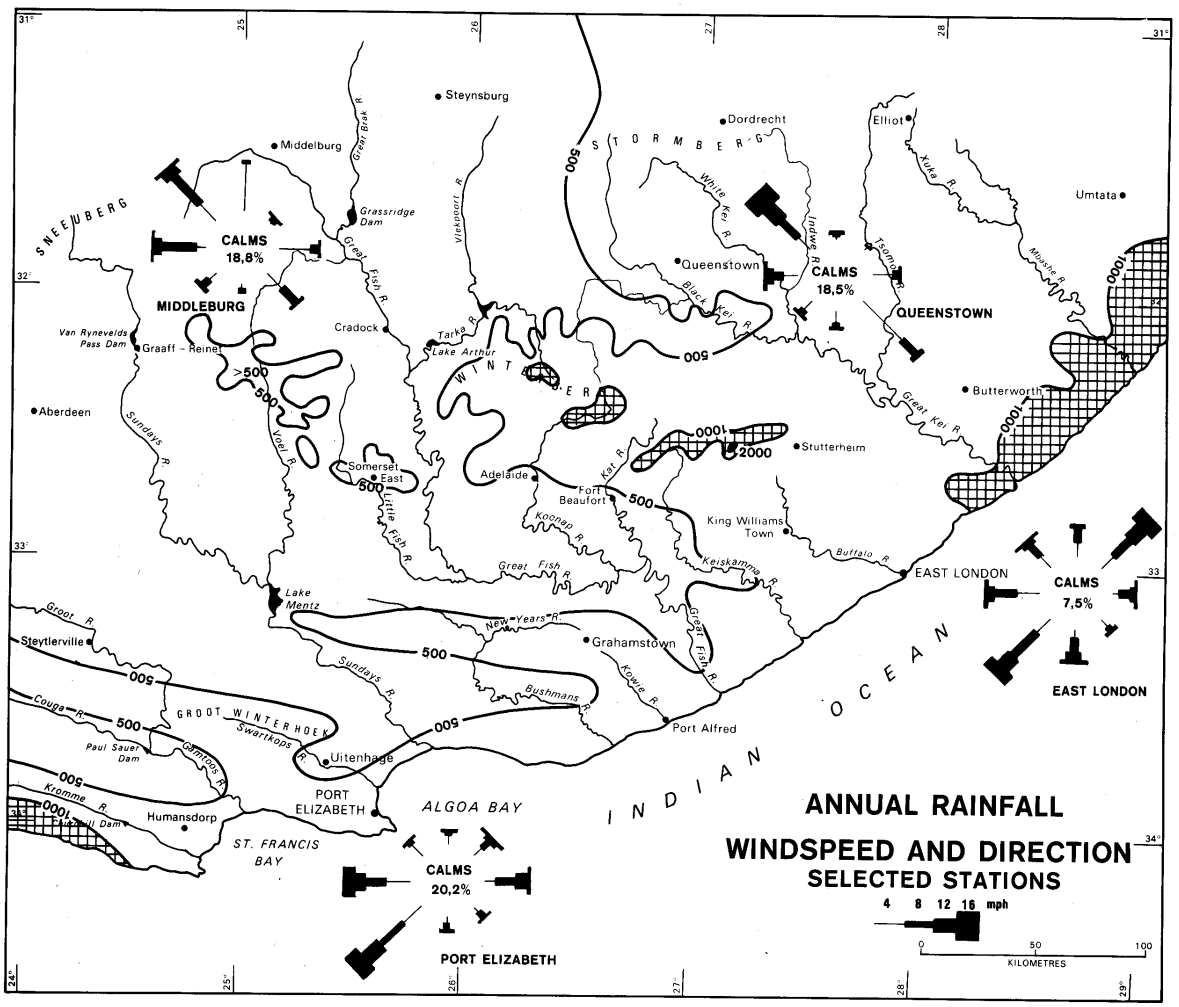


Figure 2.2. Annual rainfall and predominant winds of Eastern Cape region, with in the hatched areas a high rainfall of above1000 mm per annum (from Kopke 1988).

2.5. Zonation, succession and plant communities of the Eastern Cape coastal dunes

Vegetation regions on the South African coast generally reflect the climate of the region and this is certainly the situation along the southern and eastern Cape coast (Lubke 1998). Regional temperature and rainfall are the most important factors accounting for the distribution of different species and families over the eastern Cape region, and the assembling of plants into plant communities (Lubke 1998). Other factors such as geology, geomorphology, dune morphology and soils are more important on a local scale and will determine whether, for example dune thicket or dune fynbos is found is a particular environment (Tinley 1985, Lubke 1998, Bruton & Gess 1988).

In this area several distinctive plant communities can be identified extending from the back beach onto the dunes. Coastal sands are colonised and built up into wooded

dunes by the interaction of wind and plant growth in a seral succession of four communities (Tinley 1985). As most of the sand coast of the subcontinent is eroding, the zonation is rarely complete, and often only two of the zones are represented. At many beaches the strandline/foredune vegetation zone and thicket vegetation zone abut sharply against each other, the intermediate zones having being eroded away by sea and wind. Thus, the pioneer plants are subject to repeated phases of re-colonisation, growth and spread followed by erosion or elimination by storm events. Great variation in zone patterns is thus typical, and masks their seral successional relationships in South African dunes (Tinley 1985, Avis & Lubke 1996). The coastal pioneer communities form part of a multiple plant succession where many species coexist, in contrast to a single plant succession which is often observed in for instance Europe (Van der Putten *et al*. 1993). The strand plants (e.g. *Arctotheca populifolia*, *Sporobolus virginicus*) initiate the succession followed by pioneer species (e.g. *Ipomoea pes-caprae*, *Tetragonia decumbens*) that colonise bare mobile sand (Figure 2.3).

Through the stabilising effect and protection the plants can offer, a suitable habitat is provided for precursors from the next vegetation zone in the seral successional sequence until the closed climax (dune thicket, dune forest or fynbos) community is attained. Although the trend of succession is towards a dune thicket or dune forest, in dunes it is generally multidirectional as successional changes are taking place in response to erosion, accretion, secondary disturbances, and to the re-mobilisation of dune sand which provides new habitats and niches (Tinley 1985, Lubke *et al.* 1997). Thus dune plant communities are not static, but ever changing, especially in coastal dune systems where the environment is extremely dynamic and sand is easily moved leaving the plants in a constant danger of being buried or having their roots exposed (Tinley 1985).

The floristic compositions of dune plant communities around the South African coastline are ‘kaleidoscopically’ varying (Tinley 1985). On the South African coastal dunes six main plant communities occur, of which four form a seral suite of the four zones from pioneer to thicket/forest. The main communities are the Strand plant community (Zone I), the shrub community (Zone II), and the thicket community which often is the climax situation in Eastern Cape dunes (Zone III; Figure 2.3). The other two plant communities, grassland and heathland are mainly secondary (Tinley 1985). Many coastal plant

species are pantropical in their distribution as ocean currents disperse the seeds (Muir 1937, Good 1964, Sauer 1965). A total of 26 plant species have been recorded in zone I, of these 11 were considered to be principal or core assemblage of beach pioneers, of which nine species occurred on the Cape coast. The most important species are *Arctotheca populifolia*, *Scaevola plumieri*, *Ipomoea pes-caprae*, *Tetragonia decumbens*, and the grasses *Elymus distichus*, and *Sporobolus virginicus* (see Tinley 1985).

Zone I: ***Strand plant (or pioneer) community***

This littoral community is composed of low and often creeping plant species that are colonisers of mobile sand on the back beach and on the high water mark zone. It is an ephemeral or short-lived community, destroyed at intervals by sea erosion and reforming with phases of sand accretion (Tinley 1985).

The frontline strand plant community tends to be dominated by a single species, often water or wind dispersed, this appears to be related to seed availability coinciding with suitable conditions. The diaspores often end up in the swash zone where the debris is deposited. Where hummock dunes are able to persist for longer than a year additional species may become established to form a mixed herbaceous community (Tinley 1985, Lubke 1998).

In the south-west and on the south coast of South Africa the succulent herb *Tetragonia decumbens*, *Arctotheca populifolia*, and the introduced *Elymus distichus* (was *Thinopyrum disticum*) are the most important components of the strand plant zone, with locally the grasses *Sporobolus virginicus* and *Stenotaphrum secundatum* invading close to the beach. On the south-east coast of South Africa *Arctotheca populifolia* remains one of the most important strand plants, with an increasing predominance northwards of *Scaevola plumieri*, *Ipomoea pes-caprae*, and *Cyperus maritimus* (Tinley 1985).

*Zone II****: Shrub community***

This community is a mixture of zone I plants with the addition of a rich array of psammophytes. Psammophytes are less tolerant to the high salinity and extreme conditions on the strand line, and the community exhibits high species richness. The life forms of the zone II plants include annuals, forbs, creepers and climbers, geophytes, succulents, root-parasites and shrubs (Tinley 1985).

Most of these plants are generally not restricted to Zone II, but occur in nearly any site away from the beach where bare sand is exposed. The indicator shrub on the south-

east coast is *Passerina rigida*, where it is often associated with *Metalasia muricata* and *Myrica cordifolia*. The shrubs in Zone II are mainly wind dispersed (*Passerina rigida*, *Metalasia muricata*) or bird dispersed (*Myrica cordifolia*) (Tinley 1985, Avis 1992).

Zone III and IV: ***Shrub-Ticket and Forest community***

This is a dense community of multiple-stemmed dwarf trees and shrubs with a compact canopy. On eastern and southern coasts where steep foredunes rise immediately above the backshore the canopy is hedged by salt spray pruning (Tinley 1985). Typical shrub components of Zone III include *Diospyros, Euclea, Mimusops, Rhus, Eugenia, Cassine, Scutia, Dovyalis, Maytenus, Colpoon, Lycium* and *Olea* (Tinley 1985, Avis 1992). The variety of dune geomorphology determines the species content and height of the forest cover in zone IV, however this zone is not always present. The mature closed vegetation on coastal dunes is composed of 50% - 60% thicket species and some 30% - 40% species from forests of several kinds (e.g. Afrotemperate, equatorial, tropical sand forest). On the eastern and southern coasts of South Africa the canopy of the mature woody community is dominated by heliophytic thicket and savanna elements as exemplified by species of *Acacia, Aloe, Cassine, Eulcea, Euphorbia, Mimusops, Maytenus, Rhus*, and *Sideroxylon*. On the east and south cape dunes the dry sand slips and crests are colonised mainly by low fynbos heath communities composed of species such as *Helichrysum* spp., *Metalasia muricata*, *Myrica cordifolia*, *Restio eleocharis* and the grasses *Ehrharta villosa*, *Stipagrostis zeheri* and the sedge *Ficinia lateralis* (Tinley 1985, Avis 1992).

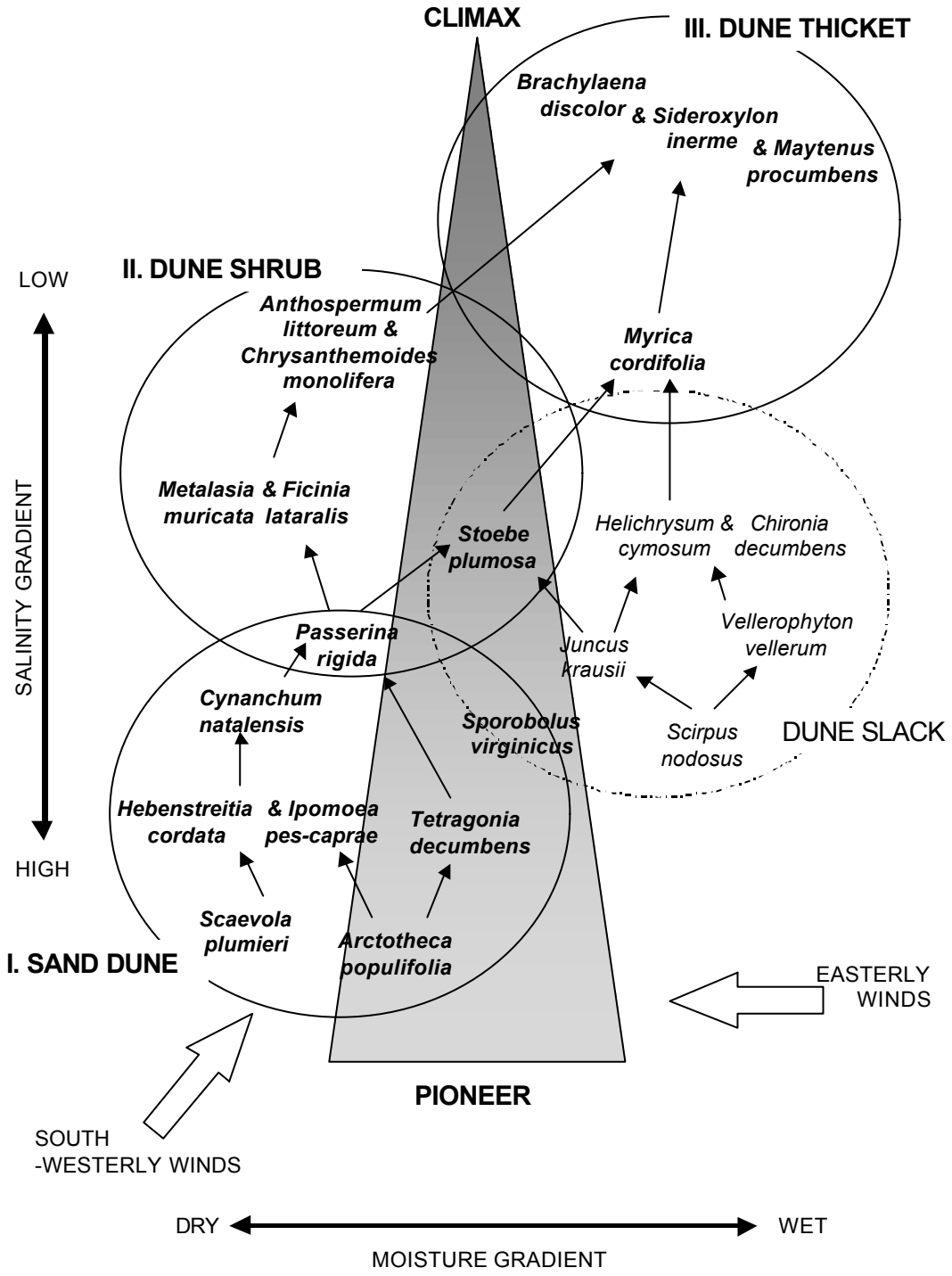


Figure 2.3. A model of plant succession of Eastern Cape coastal dunes from pioneer vegetation to the climax vegetation (dune thicket), with the predominant winds, and moisture and salt gradients. The circles represent the three vegetation zones (I to III) closest to the sea with the addition of the dune slack community which is mainly part of Zone I. The solid lines between the plant species show the most common successional pathways (After Lubke & Avis 1988).

2.6. Plant functional types of coastal dunes

Plant functional types have been widely proposed as an ecological alternative for traditional taxonomic entities, in effectively assessing the probable impact of the potential environment changes on ecosystems (Smith *et al.* 1997). A main consideration in using these non-phylogenetic plant groupings is their identification and the estimation of their abundance is highly relevant in predicting the dynamics of plant communities in regularly disturbed landscapes (Noble & Gitay 1999, Díaz & Cabio 1997). The way these groupings are constituted is related to the type of ecological response that is likely to be important (Hobbs 1997); thus the plant classification will depend on the chosen attributes (Westoby & Leishman 1997).

The foredune habitat is characterised by an array of geomorphological features, soil types and environmental factors (Tinley 1985, Barbour 1992). The coastal-ecological literature highlights the spatial variability of foredune vegetation in relation to geomorphological processes (Randwell 1972, Carter 1993). Foredune vegetation is dominated by species that are limited to beaches and coastal foredunes, and which usually show a wide geographical distribution (Barbour 1990, Tinley 1985). All over the world the major stresses and disturbances on coastal foredunes are similar (see Chapter 2.2). In this context, functional types might permit ecological comparison among foredune plant communities on a much larger scale than would be possible through traditional taxonomic approaches (García-Mora *et al.* 1999). It might also offer a tool for assessing the foredune status through evaluation of the vegetation, since both physical and biological factors can affect plant morphology (Lewis *et al.* 1987).

The vegetation of the beach and foredune can be related to foredune dynamics and the main environmental stress factors that determine the structure and function of the ecosystem. By identifying characteristic plant traits related to the foredune dynamics and stresses, the species can be allocated to different plant functional types (Box 1996; Smith *et al.* 1997, García-Mora *et al.* 1999; Table 2.1). Plant functional types are groups of plant species that share similar structural and functional attributes, and that exhibited a comparative response to environmental conditions (García-Mora *et al.* 1999). The concept of plant functional types (PFT) is that it summarises the role that plants perform in ecosystem processes and the functionally different responses to environmental changes (Walker 1997).

Table 2.1. Plant functional types (PFT) of the foredunes of SW Spain categorised according to plant traits (after García-Mora *et al.* 1999).

Plant traits	Plant functional type		
	Type I	Type II	Type III
Life span:	annual	perennial	perennial
Canopy height:	≤15 cm	indifferent	>15 cm
Below-ground structures:	shallow fibrous	thick spreading or deep	thick spreading or deep
Leaf adaptations :	absent (thin and soft)	present (tough/succulent/ pubescent)	present (tough/succulent/ pubescent)
Adaptations to sand burial:	absent	absent	present
Seawater dispersal:	absent	absent	present

On the basis of plant traits significant for exposed coastal environments, the foredune vegetation can be divided into three plant functional types (García-Mora *et al.* 1999; Table 2.1). All associated traits are not fully represented in every species belonging to a functional type (García-Mora *et al.* 1999), e.g. *Ammophila arenaria* is a type III PFT with the plant trait that it can withstand deep sand burial but without the seawater dispersal trait. Most of the zone I plant species of the Eastern Cape foredunes showed four or five of the six traits of plant functional type III, and although lacking adaptation to seawater dispersion, were considered to be of this type. Species that lacked adaptations to either seawater dispersal or severe sand burial were considered to be plant functional type II (Table 2.2).

Table 2.2. Selected species of the foredunes environment of South Africa, divided into zone I (strandline species) and zone II (shrub zone) with life form, plant functional type (PFT), and distribution along the Cape coast. The species marked with * are alien species according to Tinley (1985).

Dune pioneer plants			Distribution [3]			
Species [1]	Life form [1]	PFT[2]	Natal	E. Cape	S. Cape	W. Cape
Zone I:						
Arctotheca populifolia	herb	III	+	+	+	+
Dasispermum suffructicosum	herb	III	+	+	+	+
Elymus distichus	grass	III		+	+	+
Gazania rigens	herb	III		+	+	
Hebenstreitia cordata	herb	II		+	+	
Ipomoea pes-caprae	creeper	III	+	+	+	
Scaevola plumieri	shrub	III	+	+	+	
Sporobolus virginicus	grass	III	+	+	+	+
Tetragonia decumbens	herb	III		+	+	+

Table 2.2 continued.

Dune pioneer plants			Distribution [3]			
Species [1]	Life form [1]	PFT[2]	Natal	E. Cape	S. Cape	W. Cape
Zone II:						
Acacia cyclops *	shrub	II		+	+	+
Ammophila arenaria *	grass	III		+	+	+
Chrysanthemoides monilifera	shrub	II	+	+	+	+
Ehrharta villosa	grass	III		+	+	+
Metalasia muricata	shrub	II		+	+	+
Myrica cordifolia	shrub	II		+	+	+
Passerina rigida	shrub	II	+	+	+	+
Stoebe plumosa	shrub	II		+	+	+

[1] Species and life form nomenclature according to Tinley (1985) and Lubke and Van Wijk (1998).
[2] Plant functional types according to García-Mora *et al.* (1999).
[3] Distribution according to Tinley (1985).

2.7. Description of coastal foredune species

In the present research the focus will be on pioneer species of the strand and foredune area (Zone I) and on the enriched foredune zone located between zone I and II, which is often a mixture of species from both zones (Avis 1992). Only a few dune plant species belong to the foredune pioneers group. For the Eastern Cape the species include the grasses *Sporobolus virginicus*, *Ehrharta villosa*, *Elymus distichus*, the sedge *Cyperus natalitium* (Cyperaceae), the herbaceous *Arctotheca populifolia*, *Ipomoea pes-caprae* and *Tetragonia decumbens*, and the shrubs *Scaevola plumieri* and *Chrysanthemoides monilifera* (Tinley 1985, Avis 1992, Lubke & Van Wijk 1998). The shrub *Myrica cordifolia* is also frequently found on the foredunes, but is not considered a pioneer species (Lubke & De Moor 1998), although it is a very good sand stabiliser in other zones (Avis 1992, Knight 1999). There are a lot of herbaceous species growing in between the main foredunes species, but they are of no significance in dune building (e.g. *Gladiolus gueinzii*, *Senecio elegans*, *Cynanchum natalitium*, *Zalusianskya maritima*, *Silene primuliflora*; Lubke & De Moor 1998). The pioneer species of interest in the coastal environment of the Eastern Cape are described below in more detail. All species were polycarpic perennials unless stated otherwise.

Ammophila arenaria (marram grass - PFT III): The alien *Ammophila arenaria* (L.) Link (Poaceae) is a zone I grass, native to Europe. The grass forms a densely tufted stand and is a rhizomatous perennial up to 1.3m tall. The inflorescence is erect, dense, spike-like and cylindrical, pale green to straw coloured (Lubke & Van Wijk

1998; Plate 2.3). Although the grass produces flowers, it rarely produces seeds (Hertling 1997). The leaves are grey-green, stiff and tough with strongly in-rolled margins. It has been extensively planted to bind drift sand on the beaches along the Cape coast, and has become naturalised, and flowers in spring and early summer. In general flowers produced viable caryopses, each containing one elongated seed (Hertling 1997).

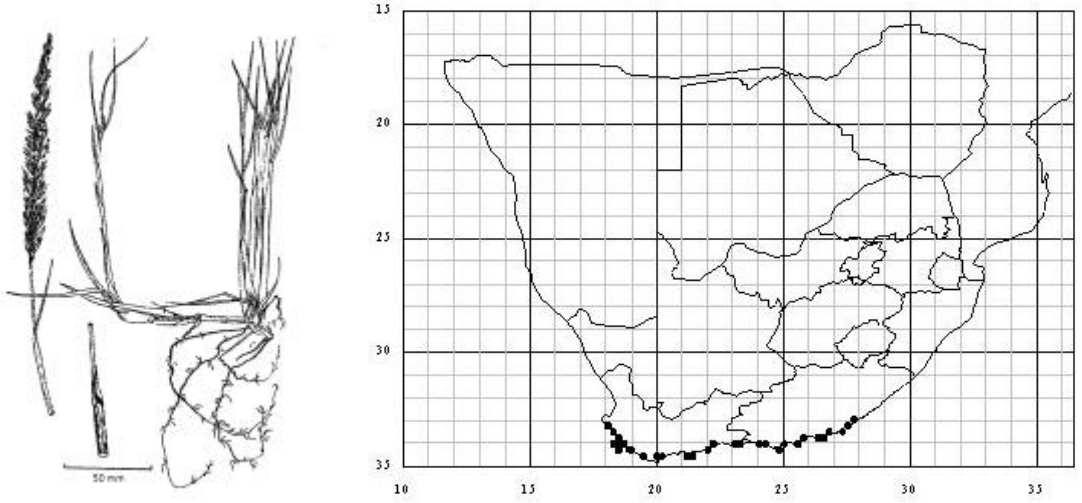


Plate 2.2. Drawing of the alien grass *A. arenaria* (Lubke & Van Wijk 1998), with the distribution of *A. arenaria* in South Africa (Gibbs Russell *et al.* 1990).

Elymus distichus (was *Thinopyrum distichus*; sea wheat - PFT III): *Elymus distichus* (Thunb.) Melderis (Poaceae) is a creeping, rhizomatous perennial grass of zone I, which can grow up to 50cm tall. The grass flowers from October to January producing dense, erect, and green panicles of spikelets of approximately 15cm long, in late spring and early summer. It is used to stabilise coastal dunes and is not native to South Africa (Melderis 1978, Gibbs Russell *et al.* 1990).

Ehrharta villosa (Pipe grass - PFT III): *Ehrharta villosa* Schult. f. var. *maxima* Stapf (Poaceae), is a robust perennial grass up to 15 cm tall. The grass forms single culms or small tufts (about 90 cm tall) from long creeping rhizomes, and flowers from September to March (Gibbs Russell *et al.* 1990). The grass is common on the rear dunes and dune slacks, but often found on the foredunes (Zone I to II; Lubke & Van Wijk 1998).

Sporobolus virginicus (Seaside rush grass - PFT III): *Sporobolus virginicus (L.)* Kunth. (Poaceae) is a mat-forming perennial grass with stolons and extensive creeping rhizomes of coastal areas (dunes and salt marshes). The branches are erect and can grow up to 770 mm tall (Gibbs Russell *et al.* 1990). The grass flowers from

October to April, producing many small seeds. *Sporobolus* is a common dune grass and produces stable dunes in zone I, but frequently occurs in dune slacks and in zone II (Avis & Lubke 1985; Plate 2.3).

Plate 2.3. A typical *S. virginicus* hummock dune at Old Woman's River, with *S. plumieri* foredunes situated in the background of the photo.

Arctotheca populifolia *(Beach daisy* - PFT III): The semi-succulent herb *Arctotheca populifolia* (Berg.) T. Norl. (Asteraceae, Compositae) is a strand plant with a thick stem and a low and spreading growth habit. The species is confined to unstable littoral habitats such as beaches and mobile dunes where it is a good sand binder forming small round hummock dunes on beach and foredune (Zone I; Heyligers 1983, Lubke & Van Wijk 1998; Plate 2.4). The herbaceous *A. populifolia* forms a dense perennial clump with ovate grey leaves densely covered with woolly hairs. The flowers, produced from winter through spring to early summer, are about 3cm across and both disc and ray florets are golden yellow. The flowers produce small achenes, covered in greyish wool (inadequate to keep the seed air borne) each containing one sunflower-like seeds. After seed ripening the flowerheads bend down and get covered by wind blown sand (Tinley 1985; Plate 2.4).

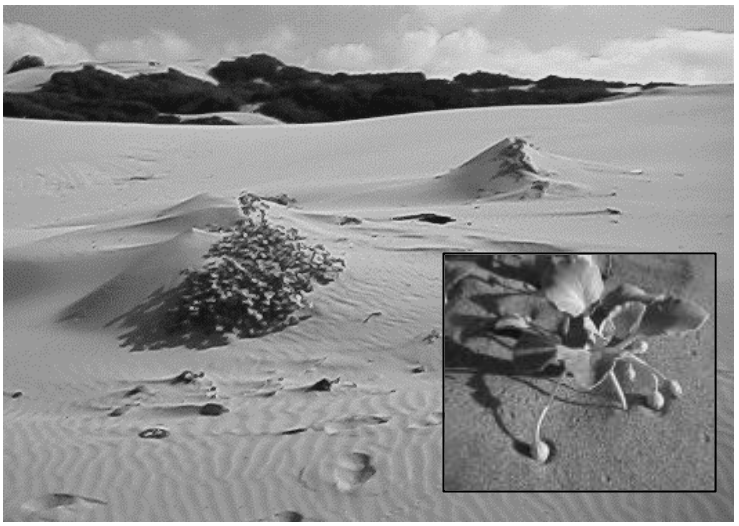


Plate 2.4. An example of an *A. populifolia* dune on the beach of Kleinemonde, and the burying of flowerheads after flowering (inset).

Ipomoea pes-caprae (Goat's foot - PFT III): One of the most common foredune and strand plants is the pantropical herbaceous *Ipomoea pes-caprae* (L.) R.Br. subsp. *brasiliensis* (L.) Van Ooststr. (Convolvulaceae) (Zone I; Sykes 1970, Tinley 1985). *I. pes-caprae* is a creeper with extensive red stems, which can grow up to 10 metres long and which are usually growing towards the sea (Bach 1998, Devall 1992; Plate 2.3).

Plate 2.5. The long runners of *I. pes-caprae* covering long distances, with flowering plants on the inset.

I. pes-caprae is a common and abundant pioneer of the eastern and southern Cape foredunes, especially around river mouths along the whole coast (Lubke & Van Wijk 1998, Lonard & Judd 1999). The species flowers from spring to

summer, with each of the purple mauve flowers producing a 4-valved, subglobular capsule containing one to four seeds per capsule (Tinley 1985, Devall & Thein 1991, Lonard & Judd 1999; Plate 2.5). The seeds have a hard seed coat covered with hairs that are lost during sand abrasion. The species is one of the best known examples of oceanic dispersal (e.g. Guppy 1907, Ridley 1930, Muir 1937) with buoyant seeds, fruits and vegetative fragments (Lonard & Judd 1999). The larvae of the tortoise beetle (*Aspidomorpha puncticosta*) frequently eat the leaves of *I. pes-caprae* (Bach 1998, Lubke & De Moor 1998).

Myrica cordifolia (Wax berry - PFT II): The branching shrub *Myrica cordifolia* L. (Myricaceae) is not a real pioneer species but is often found growing on the foredunes, even though the species is a zone II plant (Lubke & Van Wijk 1998). *M. cordifolia* is endemic to the southern coasts of South Africa (east to south-west Cape; Tinley 1985). The scrambling stems can grow up to 2 m tall and support small heart-shaped leaves with serrated margins. Tiny inconspicuous male and female flowers are borne on different plants blooming from September till March. It bears many round dark berries (crop size 5,000-10,000; Knight 1986) covered with grey wax that are eaten and dispersed by birds. A few months after flowering fruiting takes place, which is slow, but continuous throughout the summer. The fruits stay on the branches for months, thus forming an aerial seed bank (Knight 1986). The roots of *M. cordifolia* are associated with mycorrhizal fungi and possess root nodules containing endophyte bacteria capable of fixing nitrogen (Tinley 1985, Knight 1999).

Plate 2.6. The fine-leafed shrub *M. cordifolia* growing in between *S. plumieri* in the foredune area.

Scaevola plumieri (Seeplakkie - PFT III): *Scaevola plumieri* (L) Vahl. (= *Scaevola thunbergii* Eckl. & Zeyh.) (Goodeniaceae) is a pantropical species of the strand and foredune area (Zone I) which can grow up to 1.5m tall (Pammenter 1986, Lubke & Van Wijk 1998). *S. plumieri* produces a woody stem, which ramifies and branches as sand is deposited. This is resulting in large extensive beach ridge hummock dunes parallel to the coast (Tinley 1985, Lubke & De Moor 1998). The perennial shrub forms bright green succulent leaves and during the flowering season (September-October), with the flowering structures (peduncles) carrying multiple buds that will form white fan flowers that each produce a single fruit from November till January (Steinke & Lambert 1986). The black drupes roll down the dune when shed, and are often subsequently dispersed by wind and sea. The drupes contain a single stone fruit with a hard endocarp and can float for months on seawater (Ridley 1930, Muir 1937).

Plate 2.7. Foredunes formed by *S. plumieri* at Old Woman's River.

Tetragonia decumbens (Sea spinach - PFT III): The herbaceous *Tetragonia decumbens* Mill. (Aizoaceae) is a prostrate or scrambling, soft and semi-succulent perennial with a low, ground-covering growth habit. The plants grow mainly in zone I, and flower in spring. The small four-lobed yellow flowers produce numerous stamens and brown, winged fruits containing usually four to six small seeds (Tinley 1985, Lubke & Van Wijk 1998). The fruits are dropped by the plants, after which the winged fruits are secondarily dispersed by the wind by blowing over the (wet) sand surface (Tinley 1985).

Beside these main species, *Acacia cyclops*, *Chrysanthemoides monilifera*, *Dasispermum suffructicosum*, and *Gazania rigens* are also of importance in dune building and sand trapping.

Acacia cyclops (Rooi krans - PFT II): The shrub *Acacia cyclops* A. Cunn ex G. Don (Fabaceae) a very aggressive alien from Australia. It has spread rapidly in the Cape Province due to natural dispersal and due to the use of *A. cyclops* brushwood in stabilising programmes. This nitrogen-fixing shrub is invading coastal areas from the foredunes to the fynbos and dune thicket (zones I to IV) and is a fast grower, which forms dense, pure stands, overshadowing other plants, thus eliminating competitors and replacing the native flora (Tinley 1985, Stehle 1987). The seeds are contained in a coiled pod and take over a year to mature, forming an aerial seed bank with the seeds attached to the open pods for months (Milton & Moll 1982). *A. cyclops* produces a crops size of over 10,000 smooth, elongated and brown-black seeds per season. Birds, attracted by the bright-red aril that surrounds each seed disperse the seeds (Tinley 1985).

Dasispermum suffructicosum (was *Heteroptilis suffructicosum*; Dune parsley - PFT III): *Dasispermum suffructicosum* (Berg.) B.L. Butt (Apiaceae) is a branched perennial herb with a low growth habit, mainly occurring in zone I. The species produces small white flowers mainly in spring, but can be found throughout the year (Tinley 1985, Lubke & Van Wijk 1998). The winged seeds are very small and dispersed by wind.

Chrysanthemoides monilifera (Bitou or Bush-thick berry - PFT II): *Chrysanthemoides monilifera* (L.) T. Norl. subsp. *rotundifolia* (DC.) T. Norl. (Asteracea) is a zone II shrub with bright-green semi-succulent leaves, with the young leaves being covered by fine cobweb-like hairs. The flowers are bright-yellow with five or six yellow ray florets (petals) surrounding a few brown disk florets. Flowers are up to 3 cm in diameter and are formed in clusters at the end of branches, and flower throughout the year with a peak during the rain season. Each flowerhead produces up to eight spherical fleshy achenes, resulting in a crop size of over 10,000 fruits per season (Knight 1986). The berry-like achene consists of a soft-fleshy coat surrounding a hard, single bone-like seed (Tinley 1985, Todd 1994). The seeds stay on the plant after ripening, but are dropped from the plant at the end of the season, if not eaten by birds (Knight 1986).

Gazania rigens (Dune Gazania PFT III): *Gazania rigens* (L.) Gaertn. var. *uniflora* (L.f.) Roessl. (Asteraceae) is a perennial herb of beach and foredune. The dark-green leaves are white and woolly underneath, with big yellow flowers. The plants are able to build small hummock dune in zone I, where usually grow in between the other pioneers (Tinley 1985, Lubke & Van Wijk 1998).

Hebenstreitia cordata (Dune cats tail - PFT III): *Hebenstreitia cordata* L. (Selaginaceae) is an erect branched perennial herb of the foredune area, mainly growing in between the other pioneers of zone I. The stems support small oval leaves, closely clasping and adpressed to the stem. The species flowers in early spring, showing small white flowers inconspicuously situated in the axils of the leaves. The fruit is a swollen capsule (or coci; Muir 1937) that easily splits in two and is mainly dispersed by wind (Lubke & Van Wijk 1998).

Metalasia muricata (Blombos or White bristle bush - PFT II): *Metalasia muricata* L.) D. Don (Asteraceae) is a tall shrub of zone II and III, growing up to 2 m high. The species flowers all year round with big flowerheads that contain numerous greenish-white floral bracts. The shrub has tiny grey to green leaves that look as if they should belong to the Ericaceae rather than the Asteraceae. The small achenes contain a single seed, which is wind dispersed (Tinley 1985, Lubke & Van Wijk 1998).

Stoebe plumosa (Slangbossie - PFT II*)*: *Stoebe plumosa* (L.) Thunb. (Asteraceae) is a branched shrub of zone II and III that can grow up to 1.5 m tall. The grey ericoid-like leaves are closely adpressed to the stem. The white and woolly flowerheads appear in spring and produce small wind dispersed seeds (Tinley 1985, Lubke & Van Wijk 1998).

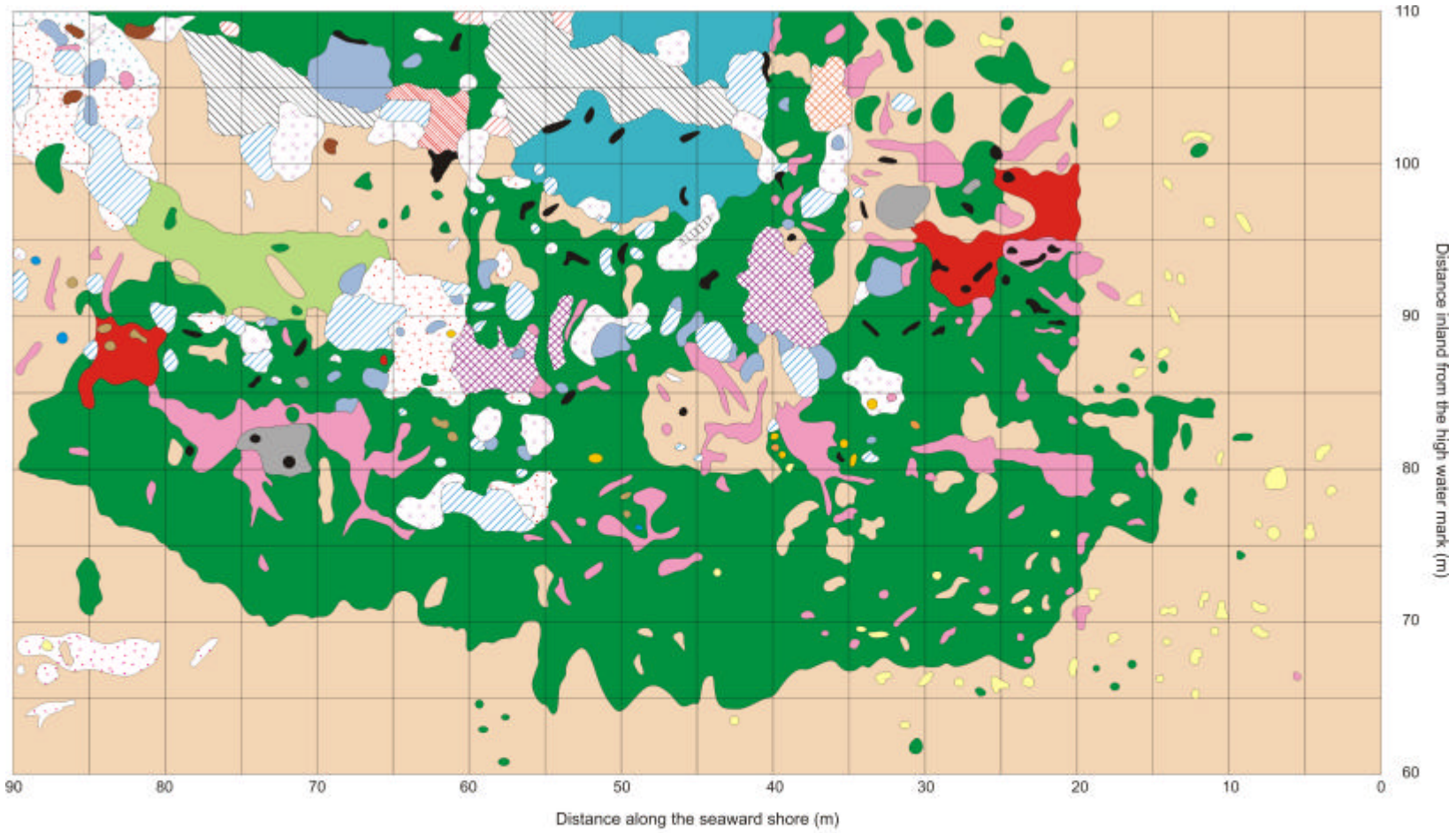
Passerina rigida (Dune-string - PFT II): *Passerina rigida* Wikstrom *(*Thymelaeaceae) forms a gangly bush up to 2 m tall in zone II. It has very small triangular leaves adpressed closely to the stem. For most of the year it is a uniform bright green plant, but during the spring it bears clusters of reddish flowers situated at the ends of branches. The orange-yellow fruit is small, lemon shaped and dispersed by birds (Tinley 1985, Lubke & Van Wijk 1998).

To give an impression of the vegetation composition of the Eastern Cape foredunes, a vegetation map of one of the study sites, Old Woman's River was drawn (Figure 2.4). At Old Woman's River the foredunes consist of typical *Scaevola plumieri* dunes mixed with

species such as *Ipomoea pes-caprae*, and are often preceded by patchy *Arctotheca populifolia* hummocks and *Sporobolus virginicus* hummocks. After the foredune ridge, the enriched foredune zone shows a mixture of species of zone I and II, including the species *Passerina rigida*, *Chrysanthemoides monilifera*, *Myrica cordifolia*, and *Cynanchum natalitium*.

Next Page:

Figure 2.4. A vegetation map of the sample site near the Old Woman's River mouth.


110
100
90
80
70
60
Distance inland from the high water mark (m)
90
80
70
60
50
40
30
20
10
0
Distance along the seaward shore (m)
Acacia cyclops
Acacia cyclops & Rhus crenata
Arctotheca populifolia
Carpobrotus sp.
Chrysanthemoides monilifera
Cynanchum natalitium
Gazenia rigens
Hebenstreitia cordata
Helichrysum cymosum
Ipomoea pes-caprae
Metalasia muricata
Myrica cordifola
Myrica cordifolia & Ehrharta villosa
Myrica cordifolia & Passerina rigida
Rhus crenata
Passerina rigida
Scaevola plumieri
Scaevola plumieri & Chrysanthemoides monilifera
Scaevola plumieri & Ipomoea pes-caprae
Scaevola plumieri & Myrica cordifolia
Senecio elegans
Silene primuliflora
Sporobolus virginicus
Stoebe plumosa
Zalusianskya maritima
Sand
Dead A. cyclops

CHAPTER 3

PLANT PERFORMANCE OF THE COASTAL FOREDUNE PIONEER *SCAEVOLA PLUMIERI* (L.) VAHL. IN THE EASTERN CAPE, SOUTH AFRICA

The zone above the high tide line of the beaches may be one of the most physically stressful places in which a plant can begin life.

Hesp (1991)

3.1. INTRODUCTION

Primary colonisers of the coastal dunes play a major role in the stabilisation and successional stages involved in the formation and growth of dynamic dune fields common to this environment. The fan flower *Scaevola plumieri* (L.) Vahl. is thought to be one of the major (if not the key) species involved in the colonisation of South African foredunes (Ward 1960, Tinley 1985, Steinke & Lambert 1986). *S. plumieri* is a sturdy clonal perennial shrub, responsible for building dunes by trapping the drifting sand with stems and leaves (Harte & Pammenter 1983, Pammenter 1985, Steinke & Lambert 1986, Lubke & Van Wijk 1998).

The foredune habitat is very unstable, hence plant survival and performance can be affected by many factors that vary significantly with dune position (Martin 1959, Van der Valk 1974, Koehler *et al.* 1995, Houle 1997). The prevailing factors include rainfall (Alpha *et al.* 1996), sand movement and salt spray (Oosting & Billing 1942, Barbour & De Jong 1977, Maun & Lapierre 1984, Moreno-Casasola 1986, Maze & Whalley 1992, Carter 1993, Houle 1997), soil salinity and seawater inundation (Alpha *et al.* 1996), and nutrient and other resource levels (Pemasada & Lovell 1974, Pavlik 1983, Dougherty *et al.* 1990, Olff *et al.* 1993). These factors may be particularly restrictive for plant growth on the coastal foredunes (Hesp 1991, Pakeman & Lee 1991, Houle 1997). Sand movement especially is of importance and can affect plant (and seedling) distribution, morphology, biomass, and flowering and fruiting phenology (Wallen 1980, Maun & Riach 1984, Maun & Lapierre 1984, Moreno-Casasola 1986, Primack 1987, Alpha *et al.* 1996). Some coastal foredune species exhibit high vigour following partial burial (Wallen 1980, Eldred & Maun 1982, Zhang & Maun 1990, Van der Putten *et al.* 1993), presumably due to altered soil temperature, increased space for root development, and higher moisture availability in the root zone (Olson 1958, Marshall 1965, Zhang & Maun 1992). However, little is known about the effect of the above mentioned factors on the performance of South African dune pioneer plants, and of *Scaevola plumieri* in particular.

S. plumieri displays both vegetative and sexual reproduction, which is often observed for clonal perennial species (Eriksson 1997, Price & Marshall 1999), especially in unstable, frequently disturbed habitats where flowering plants must overcome many problems for successful reproduction to take place. Therefore, reproduction by seed is expected to have limited success in disturbed areas (Fitter & Hay 1992, Jones & Gliddon 1999), and is consequently an important aspect of the life history of the plant

species (Harper 1977). Flowering and fruiting timing is a trait that could be critical to plant success through its effect on reproductive processes such as pollination and timing of seed dispersal. Environmental factors such as the seasonal changes in temperature, moisture and photo-period have a significant effect on the timing of flowering and fruiting (Pierce & Cowling 1984, Rathke & Lacey 1985, Zimmerman *et al.* 1989). Other factors of importance are the availability of pollinators (Waser 1979, Rathke & Lacey 1985), and the availability of resources (in the past and present). The latter affects the physiological condition of the plant, which determines the amount of resources that will be allocated to reproduction and growth during a cycle (Fenner 1985).

Given the role of *Scaevola plumieri* in the dune environment and the need for indigenous sand stabilisers for South Africa's coastal dunes, an analysis of its leaf and reproductive phenology was carried out. This was done because knowledge of the plant phenology is important in habitats which require management reclamation such as in drift sand areas of dunes fields. This to identify the fruiting periods for seed collection, and the growth/production period coupled with the mean annual rainfall indicates the best planting times (Tinley 1985).
The aim of the present study was to investigate the performance of *S. plumieri*, focussing on patterns in leaf and reproductive phenology; to relate these to climate and soil conditions so as to establish the potential use of *S. plumieri* as a dune stabiliser. The following key questions were addressed:

For leaf phenology:

- *How many leaves are produced per stem?*
- *What is the birth rate and death rate of leaves?*
- *Are there differences in leaf production and birth/death rates for stems according to dune position (seaward or landward), season or sample year?*
- *How does leaf production and leaf birth/death rates of adult stems relate to those of* S. plumieri *seedlings?*
- *Is there a relation between the leaf production and soil characteristics?*
- *Is there a relation between the monthly rainfall/temperature and leaf production?*

For reproductive phenology:

- *How many peduncles (reproduction structures) are produced per stem?*
- *How many buds, unripe seeds and ripe seeds are produced per stem?*
- *What is the duration of the reproduction in total and per stage (bud/flower/unripe seed/ripe seed)?*
- *Are there differences between the number of buds/unripe seed/ripe seed and duration per dune position (seaward or landward), season and sample year?*
- *Is there a relation between the different reproduction stages and soil characteristics?*
- *Is there a relation between the monthly rainfall and temperature and the different reproduction stages?*

The work on *S. plumieri* will concern leaf and reproduction phenology observations from June 1998 to June 2001, and linking the results obtained with climate and soil conditions.

3.2. MATERIAL AND METHODS

3.2.1. Species description

Taxonomy

The genus *Scaevola* (family Goodeniaceae) is centred in Australia and includes over 400 species and is the only genus within the family Goodeniaceae that has radiated into the Pacific Basin (Dyer 1967). Twenty-nine species of *Scaevola* comprise a monophyletic group, of which only two species are dune pioneers and which are found circumtropically (Dyer 1967). This includes the Indo-Atlantic species of interest in the present study *Scaevola plumieri* (L.) Vahl., also known under the name *Scaevola thunbergii* Eckl. & Zeyh. (Jeffrey 1979).

Ecology and distribution

Scaevola plumieri is found along many of the tropical sandy beaches in the Indo-Atlantic region. It is found along the east coast of the Americas, the Caribbean Islands (Guppy 1917, Koontz *et al.* 1996), the Gulf of Mexico and central America (Espejel 1987), Brazil (Guppy 1917, Doing 1985), Sri Lanka, Mauritius and Madagascar (Ridley 1930), the west and east coast of Africa as far south as Arniston in South Africa (Tinley 1985, Doing 1985, Peter 2000; Figure 3.1).

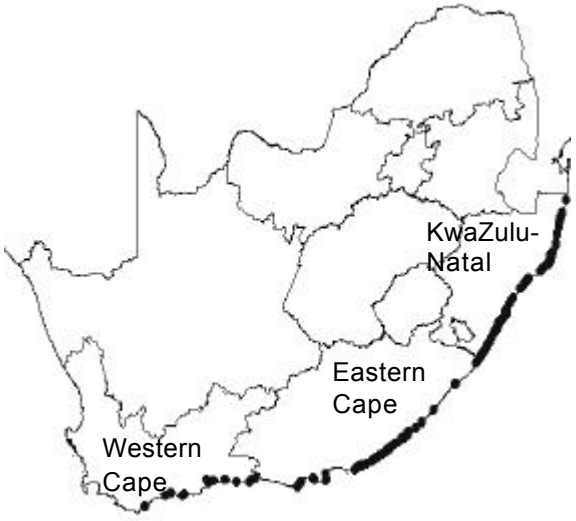


Figure 3.1. Occurrence of *S. plumieri* in South Africa represented by dots along the coastline of the Western Cape, Eastern Cape and KwaZulu-Natal (After Peter 2000).

Morphology and reproduction

The shape of the dunes formed by *Scaevola plumieri* suggests that it forms an "underground tree", with the surface stems (or plantlets) connected by subterranean branches. Adventitious roots are produced from the stems as they become buried. A *S. plumieri* foredune can be up to 8-10 meter high, and may have originated from one or two individuals (Pammenter 1986, Harman 2000; Plate 3.1). The stems stand up to 80 cm above soil level and show apical growth. During the reproduction season the stems carry multiple fertile structures or peduncles, producing big purple-black fruits called drupes. The drupes consist of a hard stone seed (1.3 cm radius, 0.53 gram; see Chapter 5) covered with a corky-like structure surrounded by a fleshy mesocarp (Ridley 1930, Peacock 1962, Carolin 1966). To be consistent with chapters 3 to 5 the drupes of *S. plumieri* will be referred to as seeds from here onward.

The reproduction period starts in November and ends in April-May, and includes a short flowering phase and a long fruiting phase (Peacock 1962, Steinke & Lambert 1986, Todd 1994). In South Africa *S. plumieri* can be found on the foredunes of the Western Cape, Eastern Cape and KwaZulu-Natal (Plate 3.1).

Plate 3.1. *Scaevola plumieri* foredunes with some *Arctotheca populifolia* (grey leaves) at the study site Old Woman's River, Eastern Cape, South Africa.

3.2.2. Study site

The study was carried out on the foredunes near the Old Woman's River mouth (27◦ 08' 49" E - 33◦ 28' 59" S), two kilometres east of the Great Fish River mouth in the Eastern Cape (Figure 3.2). Port Alfred is located 25 kilometres to the west of the study site, and East London is located 125 kilometres to the east. For further site details see Chapter 2.

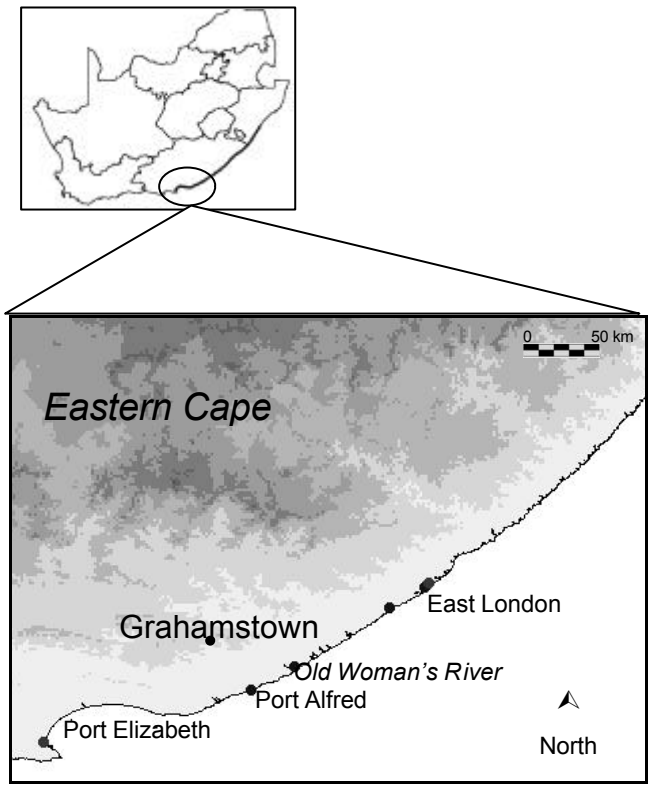


Figure 3.2. The study site Old Woman's River, situated near Port Alfred at the Eastern Cape coast (Map after Peter 2000).

At the study site the main foredune building species is *S. plumieri*, mixed with *Ipomoea pes-caprae* and *Arctotheca populifolia* (See Chapter 2 for species description). Along the first foredune row of *S. plumieri*, twelve plots of 1 m^2 were randomly chosen. Six plots were situated on the seaward face of the foredune and six plots on the landward face of the foredune (Dune position nomenclature after Steinke & Lambert 1986; Figure 3.3). Unfortunately one plot on the landward face was buried completely after 3 months and therefore excluded from further analysis.

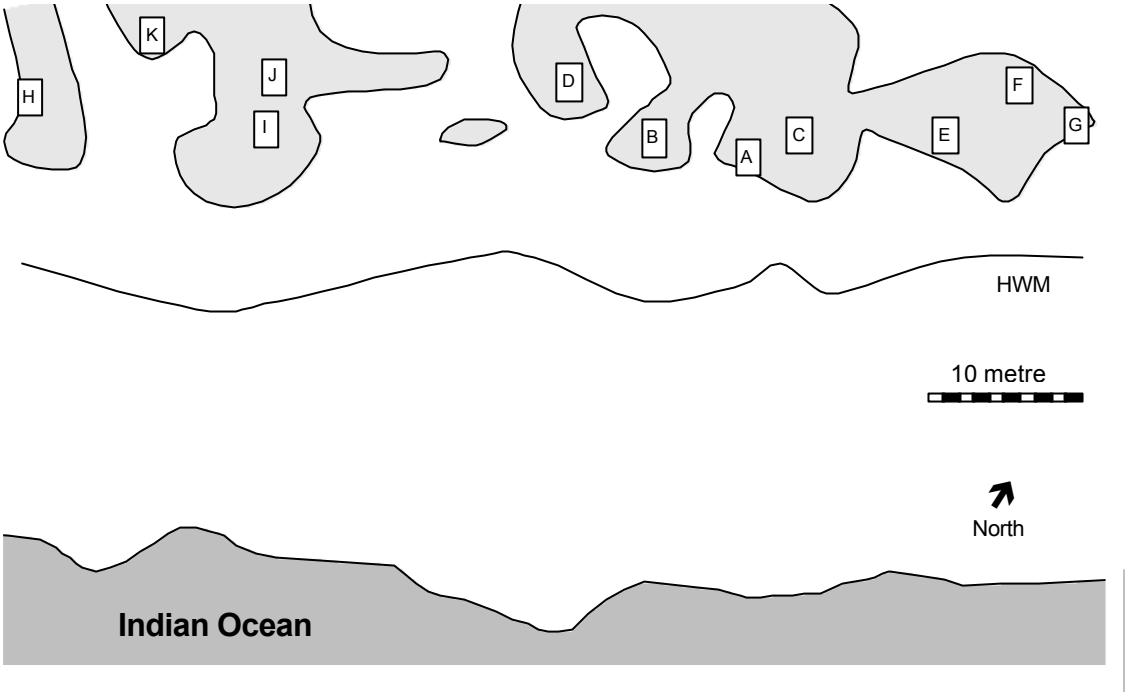


Figure 3.3. Schematic drawing of the Old Woman's River study site with the eleven plots, each of one square metre, situated on the seaward (plots A B D E G K) and on the landward face (plots C F H I J) of the *S. plumieri* foredunes, with the high water mark line (HWM).

The plots were situated at different distances from the high water mark line and at least three meters apart (Table 3.1).

Table 3.1. Plots situated on the seaward or landward face of the foredunes, with the distance to high water mark (HWM) in meters.

Foredune position of plots			
Seaward side		Landward side	
Plot	HWM (m)	Plot	HWM (m)
A	9	C	12
B	9	F	11
D	11	H	12
E	6	I	10
G	9	J	14
K	17		

3.2.3. Sampling procedure *Scaevola plumieri*

The total number of stems of each of the eleven plots were counted at the beginning of the sampling period (June 1998) and subsequently before the beginning of the flowering season in July. Eight stems of *S. plumieri* were tagged in each plot with wire covered with coloured plastic.

Leaf production - Adult stems

The coloured tag was placed around the stem with at least four leaves below the tag. Approximately every 4-8 weeks the number of leaves above and below the tag were counted and the tag moved up the stem if less than four leaves were present beneath the tag. For each tagged stem the number of leaves per stem were counted, as well as the appearance of new leaves (birth rate) at the top of the stem and abscission of senescent leaves (death rate) at the base of the stem.

Leaf production - Seedlings

In the second sampling year many seedlings emerged. To monitor the seedling growth (leaf production) in the field a belt transect (3 by 12 meter) was established on the landward face of a *S. plumieri* foredune (after Westerlaken & Maun 1985). The belt transect was divided in 36 grid cells of 1 m^2 each, and the seedlings from ten randomly chosen grid cells were tagged and mapped. At approximately 4-8 weekly intervals the total number of leaves was counted for the period April 2000-June 2001. When the tag could be fitted between the leaves, the number above and below the tag was recorded to determine the birth/death rate of the leaves (Plate 3.2.).

Plate 3.2. Young *Scaevola plumieri* seedling emerging on the beach near a *Sporobolus virginicus* foredune. The new leaves appearing at the top and the dried leaves shedding at the bottom.

The tag moved when less than two leaves were below the tag. For the presence/absence and survival of the seedlings see Chapter 4.

Reproductive phenology

The reproduction of *S. plumieri* includes a short flowering and a long fruiting phase. The plants were considered to be in the flowering phase when buds were closed, partially open or when the flowers were exposing stigma, style and anthers. The fruiting phase started when unripe seeds (green to yellow) or ripe seeds (purple to black) were observed.

For each tagged stem the total number of reproduction structures or peduncles was counted at approximately 4-8 weekly intervals from June 1998 to June 2001. Each newly developed peduncle was colour tagged with plastic covered wire so as to be able to follow the development of buds into ripe seeds (see Plate 3.3). The data on the reproduction stages were obtained by counting the number of buds, open flowers, unripe seeds and ripe seeds per peduncle of the tagged stems. All the buds produced developed into flowers, therefore only the numbers of buds, unripe seeds and ripe seeds produced were determined per stem, as well as the numbers of unfertilised flowers and aborted unripe seeds. For the ripe seeds the numbers were also determined per m^2 plot. For each reproduction stage the duration was determined in days per plot for each sample year.

Plate 3.3. *Scaevola plumieri* stem with peduncles supporting multiple buds and flowers (right) and unripe green seeds (left).

Ripe seed collection

In the first sample year (1998-1999) ripe seeds of *S. plumieri* were collected at three different sites (Old Woman's River, Kleinemonde and Wavecrest) to be used in the study in chapter 5 from which the infection rate with fruit fly larvae was determined.

3.2.4. Sand movement

To mark the plot and to measure the sand movement in the plots two 50 cm long metal poles with a diameter of 2 cm, approximately the stem diameter of *S. plumieri*, were placed in two opposite corners of each m^2 plot. The length of the poles above the sand surface was measured at approximately at 4-8 weekly intervals and the sand movement determined in cm for each sample date. When less than 10 cm of the pole was left above the sand surface, a new pole was inserted.

3.2.6. Soil analysis

Approximately 60 grams of soil was collected (n = 3) for soil analysis at a depth of approximately 10 cm in each plot to avoid the sampling of recently deposited sand. The following parameters were determined: pH (H_2O), chloride ions, conductivity (salinity), soil moisture and organic matter (MacKereth *et al.* 1978, Van Vliet *et al.* 1988, Avis 1995, Hertling 1997):

pH: To determine the pH (H_2O), 20 grams of fresh soil was placed in a 250ml flask with 100ml distilled water. The solution was shaken for one minute, allowed to settle, after that the shaking was repeated for three more times. The pH was measured at 18◦C with a cyberscan 100 pH meter.

Conductivity (or salinity): After the pH measurement the soil solution of each sample was filtered over a Whatman no 1 filter paper to prepare the soil solution for the conductivity measurement. The filtered solution was placed in a plastic beaker and the conductivity was measured in μS/cm at 25◦C with a digital conductivity meter (HI 8820 Hanna Instruments). The calibrating was done using a 0.01 mol/l potassium chloride solution.

Chloride: Because chloride contributes greatly to salinity, this anion is determined separately. For the chloride ion measurement, 100 ml of the soil solution was placed in a beaker on a magnetic stirrer and the chloride ion concentration measured in mV with a Eutech chloride-ion electrode (EC-CLO-03) at 20◦C (Eutech 2000).

Soil moisture and organic matter: To determine the moisture content of the soil 10 grams of soil was placed in a 70◦C oven for 48 hours, weighed (oven-dry weight), with the difference in weights given in percentage moisture. After this procedure, the soil was placed in a muffle furnace to be burned at 400◦C for 24 hours (ash-free dry weight). The percentage organic matter (loss on ignition) is the difference between the oven-dry weight and the ash-free-dry weight, divided by the oven-dry weight.

3.2.7. Climate data

The climatic data on rainfall, and minimum and maximum temperatures were obtained from the South African Weather Services from the stations Fish Point and Port Alfred situated nearest to the study site. The data from Port Alfred was used to fill in the missing data from Fish Point (February 1998 to December 1998).

3.2.7. Data analysis

The independent variables were tested for normality and homogeneity of the variance by using the Kolmogosov-Smirnov and Levene's test, respectively. When these assumptions failed, non-parametric procedures were carried out. The mean number of stems and the sand movement (quantity and direction) were analysed per plot, dune position (seaward or landward) and sample year using analysis-of-variance (ANOVA). The different soil parameters were analysed per plot and position using ANOVA and with a regression analysis to obtain the relationships between the soil parameters. For the leaf production of adult stems the mean number of leaves and the birth and death rate of leaves per stem was normalised to 30 days and analysed per plot, position and sample year using ANOVA. The leaf production data and birth rate and death rate of the seedlings were analysed using Kruskal-Wallis followed by a Newman-Keuls test for the comparison of means (Zar 1996).

For the reproduction, the mean number of peduncles per stem was analysed per plot, position and year using ANOVA. The mean numbers of buds, unripe seeds and seeds were calculated per stem and per peduncle and analysed per plot, position and year using the non-parametric Kruskal-Wallis test. The percentage of buds that developed into unripe and ripe seeds was determined and the mean number of unfertilised flowers, and aborted unripe seeds (per peduncle) was also analysed per plot, position and year with ANOVA. The relationships between the unfertilised flowers and aborted seeds with

the number of buds/unripe seeds/ripe seeds produced were determined with a regression analysis.

For each reproduction stage (bud, flower, unripe seed, ripe seed) the mean duration per position for each year was plotted in a phenogram. The mean duration per reproduction stage was calculated and analysed per plot, position, and year, as well as the total duration per stage (over all years) using ANOVA.

To relate the number of stems, sand movement, mean number of leaves, peduncles, buds and seeds per stem with each other and with the soil parameters a regression analysis was used. After all ANOVA analyses, a Tukey comparison-of-means test was conducted, whereas the non-parametric Kruskal-Wallis analyses were followed by a Newman-Keuls comparison-of-means test.

For all data analyses the standard error (± S.E.) and number of replicates (*n*) was given and the differences between the analysed data is pointed out by different letters (abc, pqr, xyz) behind the values in tables or above the columns or data points in graphs. For each analysis the level of significance was specified with the following system: * = $P<0.05$, ** = $P<0.01$, and *** = $P<0.001$. The ** are placed next to the highest value of the analysed parameter. All statistical tests were performed at a 95% confidence interval using the statistical program Statistica 5.5. (Statsoft Inc). For details of the ANOVA analysis see Appendix III.

3.3. RESULTS

For the analysis of the leaf phenology and reproductive phenology results, the seaward face plot D was excluded due to the fact that the plot was buried most of the time. Plot B was also buried on occasions and excluded from the reproduction phenology analysis due to an incomplete data set.

3.3.1. Number of stems per plot

For all plots, variations in the number of stems were observed over the years, with in general a mean of 18.2 ± 2.6 stems/m^2. The significant highest mean number of stems was found for plot B compared to the other plots (ANOVA, $P<0.001$; Table 3.2).

For landward plot I, the significant lowest mean number of stems was observed, compared to seaward plot B and landward plot F ($P<0.001$; Table 3.2). The mean number of stems per plot showed a high variation for the different positions. No significant difference were observed with a mean number of stems on the seaward face 19.4 ± 1.4 stems/m^2 and the landward face 17.0 ± 0.8 stems/m^2 of the foredune (ANOVA, $P>0.05$; Table 3.2). Overall the mean number of stems per plot was not significantly different between the sample years (P>0.05; Table 3.2.C). The variation observed in number of stems per plot per year, although not significant (Table 3.2.A), was due to the fact that the dune system was unstable, hence the plots went through phases of sand accretion and erosion over the years. The movement of the sand pushed stems in and out the sample plots (see also Figure 3.16 and Table 3.9).

Table 3.2. Number of stems (per m^2) given by plot (A), by position (B) and by sample year (C) measured in July of each sample year with the *n* and standard error (± S.E.). Any value with the same letter does not differ significantly in mean number of stems per plot, position or year. Contrast obtained by Tukey after analysis by ANOVA. Level of significance: *** - $P<0.001$.

A)

Plot	Dune position	*n*	Number of stems				Mean	(± S.E.)
			1998	1999	2000	2001		
A	Seaward	8	17	11	13	15	14.0	(1.29) bc
B	Seaward	8	34	26	30	26	29.0	(1.91) a ***
E	Seaward	8	14	19	15	11	14.8	(1.65) bc
G	Seaward	8	20	20	19	18	19.3	(0.48) bc
K	Seaward	8	26	20	18	16	20.0	(2.16) bc
C	Landward	8	20	19	16	14	17.3	(1.38) bc
F	Landward	8	21	20	18	24	20.8	(1.25) b
H	Landward	8	18	15	16	16	16.3	(0.63) bc
I	Landward	8	13	10	18	11	13.0	(1.78) c
J	Landward	8	18	16	21	16	17.8	(1.18) bc
Total	All	80	20.1	17.6	18.4	16.7	18.2	(2.55)

B)

Position	*n*	Number of stems				Mean	(± S.E.)
		1998	1999	2000	2001		
Seaward	40	22.2	19.2	19	17.2	19.4	(1.38) a
Landward	40	18.0	16.0	17.8	16.2	17.0	(0.77) a

C)

Sample year	*n*	Mean	(± S.E.)
1 (1998-1999)	20	17.60	(1.22) a
2 (1999-2000)	10	18.40	(1.42) a
3 (2000-2001)	10	16.70	(1.56) a

3.3.2. Leaf phenology adults and seedlings

Mean number of leaves per stem

The overall mean number of leaves was 16.3 ± 0.14 leaves per stem, with landward plot I showing a significantly higher number of leaves per stem compared with the other plots, with the exception of landward plot J (ANOVA, $P<0.001$; Figure 3.4A). The highest number of leaves was observed for the stems of landward plots I and J compared to seaward plots E, B and K ($P<0.001$; Figure 3.4A). In general the plots on the landward face of the foredune showed significantly more leaves per stem with a mean of 16.8 ± 0.25 leaves per stem compared to the seaward face with a mean of 15.8 ± 0.09 leaves per stem ($P<0.001$; Figure 3.4B). In year 1 and 2 significantly more leaves per stem were observed as compared to year 3, with a difference of 3 leaves per stem between year 1 and 3 ($P<0.001$; Figure 3.4C).

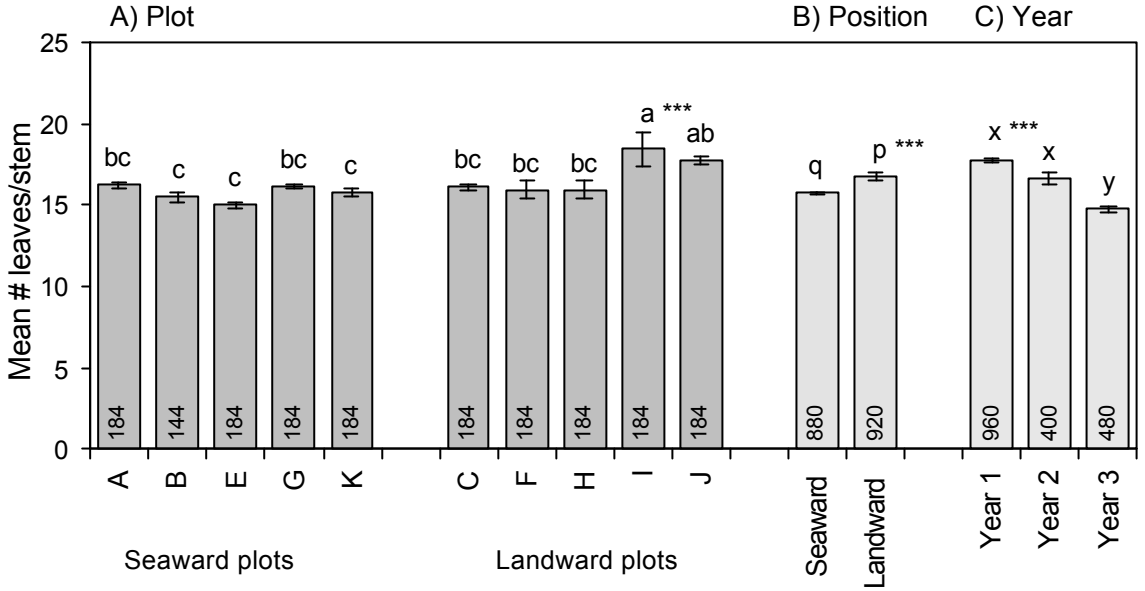


Figure 3.4. Mean number of leaves per stem (± S.E.) given by plot (A), by dune position (B), and by sample year (C) with the *n* mentioned at the base of each column. Any column with the same letter for plot ^{abc}, position ^{pq} or year ^{xy} does not differ significantly in mean number of leaves. Contrast obtained by Tukey analysis by ANOVA. Level of significance: *** - P<0.001.

When analysed per season (over all plots and years), the highest number of leaves per stem was observed in summer compared to the other seasons, followed by spring and autumn, with the lowest mean number of leaves per stem found in winter (Figure 3.5).

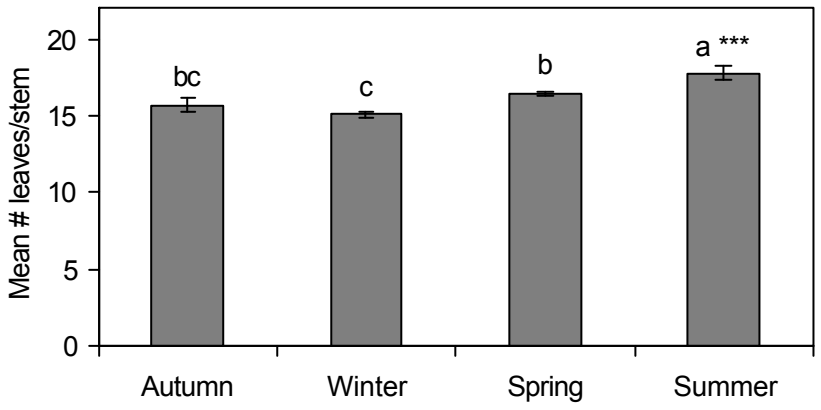


Figure 3.5. Mean number of leaves per stem given by season over all plots and years (± S.E.). Contrasts obtained by Tukey after analysis by ANOVA. Any column with the

same letter does not differ significantly in mean number of leaves. Level of significance: *** - $P<0.001$.

Birth and death of leaves

Between the different plots and positions no significant differences were found in the mean number of birth and mean number of death of leaves per stem (Kruskal-Wallis, $P>0.05$; Table 3.3A and 3.3B). However, the mean birth rate and death rate showed significant differences for the sample years. A significantly higher leaf birth rate and death rate was found for the first sample year, compared to years 2 and 3 ($P<0.001$; Table 3.3C). For the death rates year 2 showed significantly higher rates compared to year 3 ($P<0.001$; Table 3.3C).

Between the total mean birth rate (1.6 ± 0.02 leaves/30 days) and death rate (1.5 ± 0.02 leaves/30 days) no significant differences were observed, hence the number of newly produced leaves and older dying leaves seemed to be in a sort of balance ($P>0.05$; Table 3.3D).

Table 3.3. The mean leaf birth rate and death rate per stem per 30 days, by plot (A), position (B) and by sample year (C) with the total mean (D), with the *n* and standard error (± S.E.). Birth rates or death rates with the same letter do not differ significantly for plot, position or year. Contrasts obtained by Newman-Keuls test after Kruskal-Wallis analysis. Level of significance: *** - $P<0.001$.

A)

Plot	Position	*n*	Mean rate stem (per 30 days)			
			Birth	(± S.E.)	Death	(± S.E.)
A	Seaward	128	1.59	(0.06) a	1.50	(0.06) a
E	Seaward	153	1.68	(0.06) a	1.43	(0.05) a
G	Seaward	155	1.60	(0.05) a	1.48	(0.05) a
K	Seaward	140	1.63	(0.06) a	1.44	(0.06) a
C	Landward	143	1.61	(0.06) a	1.51	(0.05) a
F	Landward	132	1.62	(0.06) a	1.49	(0.05) a
H	Landward	157	1.76	(0.05) a	1.60	(0.05) a
I	Landward	122	1.63	(0.06) a	1.39	(0.05) a
J	Landward	136	1.69	(0.05) a	1.48	(0.05) a

B)

Position	*n*	Mean rate stem (per 30 days)			
		Birth	(± S.E.)	Death	(± S.E.)
Seaward	576	1.63	(0.03) a	1.46	(0.03) a
Landward	690	1.67	(0.03) a	1.50	(0.02) a

Table 3.3 continued.

C)

Sample year	*n*	Mean rate stem (per 30 days)			
		Birth	(± S.E.)	Death	(± S.E.)
1	665	3.38	(0.10) a ***	3.09	(0.08) a ***
2	188	1.92	(0.08) b	2.02	(0.10) b
3	414	1.80	(0.07) b	1.63	(0.06) c

D)

Parameter	*n*	Rate (per 30 days)	
		Mean	(± S.E.)
Birth rate	1266	1.64	(0.02) x
Death rate	1266	1.48	(0.02) x

When examined per season, the significant highest leaf birth rate and death rate were found in spring and the lowest in winter (Figure 3.6). The order for the birth and death rate (high to low) for the seasons was spring>summer>autumn>winter (Figure 3.6). When compared to the order of the leaves per season (summer>spring>autumn>winter; Figure 3.6) the order is almost the same with the difference that the highest number of leaves was observed in summer. In general the highest leaf production was in the warmer months of summer and spring.

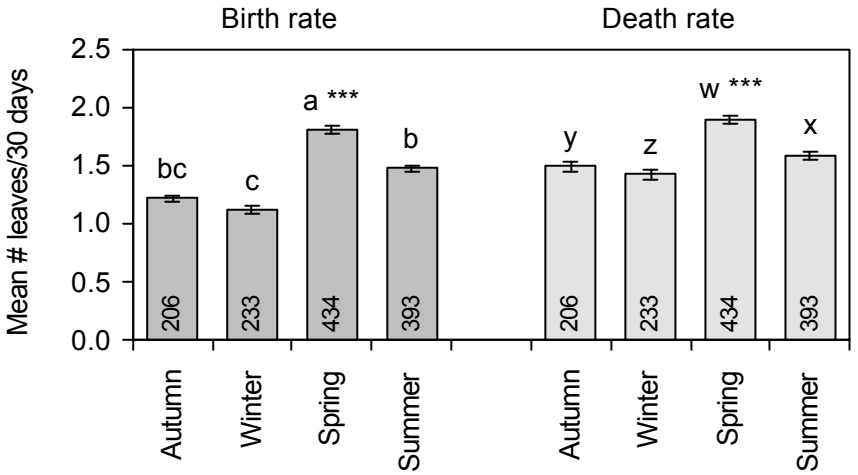


Figure 3.6. Mean birth rate and death of leaves per stem by season over all plots (± S.E.), with the number of replicates (*n*) mentioned at the base of each column. Any column with the same letter does not differ significantly in birth rate or death rate. Contrasts obtained by Newman-Keuls after analysis by Kruskal-Wallis. Level of significance: *** - $P<0.001$.

Seedling leaf phenology

The mean number of leaves per seedling in the period April 2000 to June 2001 was 9.4 (± 0.29), with no significant difference between the new (8.9 ± 0.60, n = 23) and older seedlings (9.5 ± 0.34) (Kruskal-Wallis, *P*>0.05; Figure 3.7).

On the last sampling date the number of leaves of the older seedlings was significantly higher compared to the other dates (Kruskal-Wallis, P<0.001; Figure 3.7). In Between June and August all newly emerged seedlings died due to a high tide in June 2000. The seedlings were either washed away or wilted away as a result of saltwater inundation (see Figure 3.7).

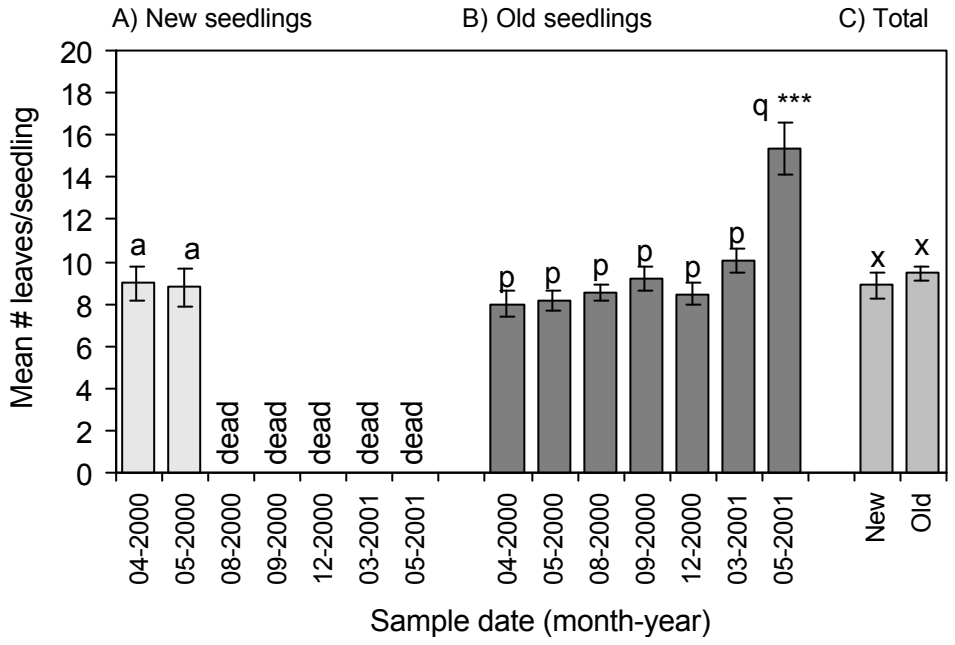


Figure 3.7. Mean leaf production per stem (± S.E.) for seedlings newly emerged (new; A) and older seedlings (old; B), with the total mean number of leaves (C) per seedling age given by sample date. Any column within a graph (A, B or C) with the same letter does not differ significantly in number of leaves. Contrast obtained by Newman-Keuls test after analysis by Kruskal-Wallis analysis. Level of significance: *** - *P*<0.001.

Some of the older seedlings were also damaged due to the effect of seawater inundation, but most of the older seedlings survived, although a decrease in leaf rate was observed between date 2 and 3 (June to August 2000; Figure 3.8). The death rate was significantly lower compared to the previous period, whereas the birth rate was not significant due to high variation between the seedlings (Kruskal-Wallis, *P*<0.01; Figure 3.8). Between September and December another high sea washed over the seedlings,

with a further inhibiting effect on the leaf production of the older seedlings compared to the first date (Figure 3.7 and 3.8). After March 2001 the seedlings started to grow with significantly higher mean birth rates (3.1 ± 0.44) and death rates (1.3 ± 0.30) per seedling; the birth rate especially was very high compared to the birth rates of the other dates (P<0.001; Figure 3.8). When compared to the mean birth/death rate of adult stems (1.7 ± 0.02 and 1.5 ± 0.02 leaves/30 days, respectively) the rates of the seedlings (0.9 ± 0.10 and 1.3 ± 0.11 leaves/30 days, respectively) were lower (Figure 3.8 and Figure 3.6).

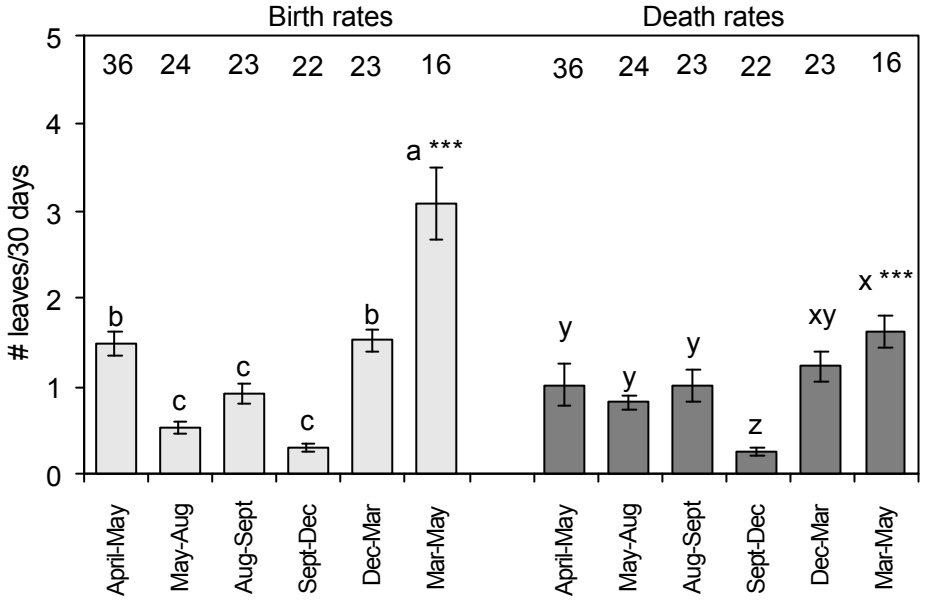


Figure 3.8. Mean birth and death rates of leaves of older seedlings per stem from April 1999 to May 2000, normalised to 30 day periods between succeeding sample dates with the number of seedlings (n) mentioned above each column (± S.E.). Any column with the same letter does not differ significant in birth rate^{abc} or death rate^{xyz}. Contrast obtained by Newman-Keuls test after analysis by Kruskal-Wallis. Level of significance: * - P<0.05, ** - P<0.01, *** P<0.001.

3.3.3. Reproductive phenology

3.3.3.1. Mean number of peduncles per stem

Overall an average of 9.5 ± 0.30 peduncles was produced per stem, but the mean number of peduncles formed per stem was very variable between the different plots (Figure 3.9A). In landward plot C a significantly higher mean number of peduncles was found, compared to the other plots, with exception of landward plots I and J (ANOVA,

P<0.001; Figure 3.9A). Whereas the significantly lowest number of peduncles was found for the seaward plot G compared to all plots except seaward plot K (*P*<0.001; Figure 3.9A). Overall, the plots situated on the landward face of the foredune produced more peduncles per stem (10.7 ± 0.97) compared to the seaward plots (8.3 ± 0.78) (ANOVA, *P*<0.001; Figure 3.9B). No significant differences in mean number of peduncles per stem were observed between sampled years (ANOVA, *P*<0.05; Figure 3.9C). Thus, as with the number of leaves (see Figure 3.4B), the highest number of peduncles per stem was observed on the landward side of the foredune.

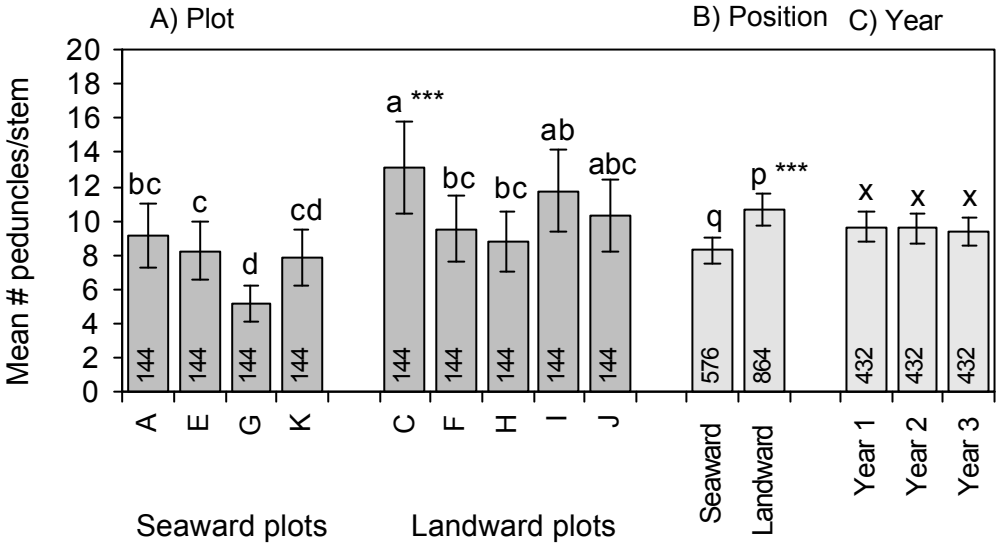


Figure 3.9. Mean number (± S.E.) of peduncles per stem presented by plot over all years (A), by dune position over all years (B) and by sample year over all plots (C), with the *n* mentioned at the base of each column. Any column with the same letter does not differ significantly in mean number of peduncles. Contrasts obtained by Tukey after analysis by ANOVA. Level of significance: *** - *P*<0.001.

3.3.3.2. Mean number of buds, unripe and ripe seeds produced per stem

Not all the buds produced per peduncle developed into seeds (Table 3.4). Per stem a mean of 42.9 ± 1.85 buds, 8.4 ± 0.37 unripe seeds and 2.9 ± 0.11 ripe seeds were produced (Table 3.4A). Only the buds were mentioned in table 3.4. because all buds developed into flowers. The stems of landward plots C and J formed the highest number of buds, unripe seeds and ripe seeds (Kruskal-Wallis, *P*<0.001; Table 3.4A). The lowest

number of buds per stem was produced in seaward plot G, whereas the lowest number of unripe seeds was produced in landward plot F compared to all plots, except seaward plots E, G and K (*P*<0.001; Table 3.4A). For the ripe seeds produced per stem, the seaward plots E and K and landward plots F and H produced significantly lower seed numbers compared to landward plots C, I and J (*P*<0.001; Table 3.4A). Although the lowest number of buds and seeds were found on both the seaward and landward face of the foredunes, the overall trend showed that significantly more buds, unripe and ripe seeds were found on stems situated on the landward face of the foredune (Kruskal-Wallis, *P*<0.001; Table 3.4B). For the different sample years there were no differences in mean numbers of buds, unripe seed and ripe seed produced per stem (Kruskal-Wallis, *P*>0.05; Table 3.4C).

Table 3.4. Mean number of buds, of unripe seeds and of ripe seeds produced per stem given by plot over all years (a), by dune position over all years (b), and by sample year over all plots (c) (± S.E.). Any value for bud, unripe seed or ripe seed with the same letter does not differ significantly per plot, position or sample year. Contrasts obtained by Newman-Keuls after analysis by Kruskal-Wallis. Level of significance: *p*<0.001.

A)

Plot	Position	*n*	Bud		Unripe seed		Ripe seed	
			Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
A	Seaward	18	49.79	(5.40) abc	10.62	(1.74) ab	3.24	(0.39) ab
E	Seaward	22	29.35	(2.58) bcd	5.72	(0.51) cd	2.09	(0.16) b
G	Seaward	18	20.35	(2.09) d	5.89	(0.67) cd	2.87	(0.38) ab
K	Seaward	22	35.88	(3.98) bcd	7.47	(0.51) cd	2.42	(0.15) b
C	Landward	24	73.15	(5.30) a ***	12.98	(1.12) a ***	3.94	(0.34) a ***
F	Landward	24	25.71	(1.75) cd	4.78	(0.37) d	2.31	(0.15) b
H	Landward	23	36.45	(3.83) bcd	6.80	(0.73) b	2.23	(0.14) b
I	Landward	21	50.20	(5.89) ab	8.84	(0.95) a	3.49	(0.30) a
J	Landward	23	61.68	(5.47) a	12.29	(1.28) a	3.77	(0.42) a
Mean		195	42.94	(1.85)	8.40	(0.37)	2.93	(0.11)

B)

Position	*n*	Bud		Unripe seed		Ripe seed	
		Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
Seaward	80	33.72	(2.14) b	7.34	(0.50) b	2.62	(0.14) b
Landward	115	49.42	(2.60) a ***	9.14	(0.51) a ***	3.14	(0.14) a ***

Table 3.4 continued.

C)

Sample year	*n*	Bud		Unripe seed		Ripe seed	
		Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
1	65	45.45	(3.55) a	8.51	(0.69) a	2.89	(0.17) a
2	62	45.10	(3.43) a	8.84	(0.80) a	2.95	(0.21) a
3	68	38.69	(2.59) a	7.89	(0.40) a	2.94	(0.16) a

When the mean number of seeds produced was calculated per one m^2 plot, the overall mean was 47.8 ± 1.8 seeds /m^2, with a significantly higher number of seeds produced in plot J and C, compared to plots E and H (Kruskal-Wallis, P<0.001; Figure 3.10). Even though the lower seed production in individual plots was observed on the landward and seaward face of the dunes, the overall means showed that significantly more seeds were produced on the landward faced plots (51.7 ± 2.5 seeds/m^2) when compared to the seaward plots (42.3 ± 2.8 seeds/m^2) (P<0.001; Figure 3.10B). Between the different sample years no significant difference in seed production/m^2 was observed (P>0.05; Figure 3.10C).

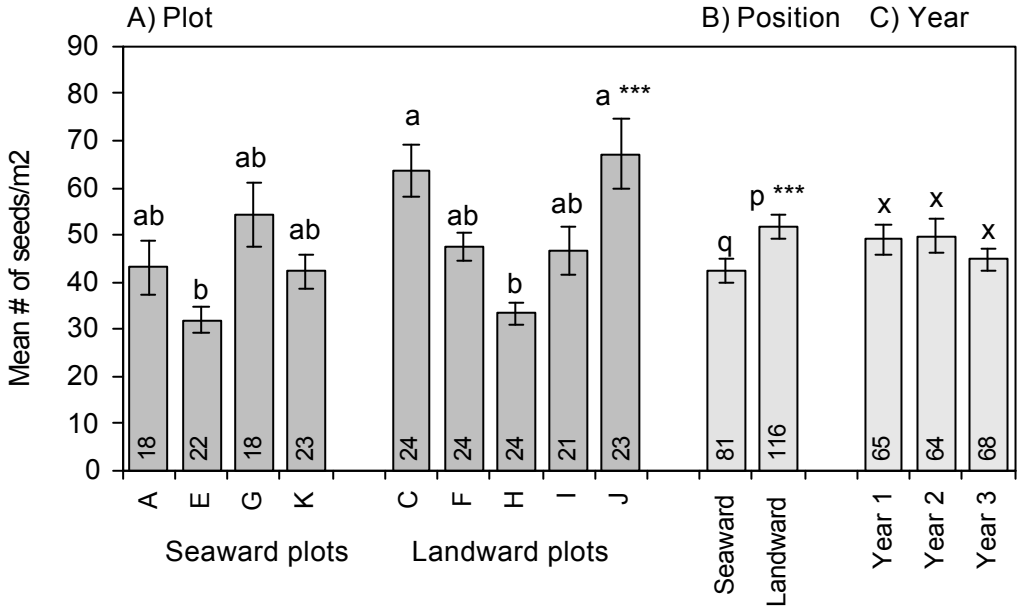


Figure 3.10. Mean number of seeds produced/m^2 given by plot, position and sample year with the *n* given at the base of each column (± S.E.). Any column with the same letter does not differ significantly in mean number of seeds. Contrasts obtained by Newman-Keuls after analysis by Kruskal-Wallis. Level of significance: *** - P<0.001.

The plots C and J that produced the highest number of seeds per plot and showed an average stem number of 17.3 and 17.8, respectively. However, the highest number of

stems, 20.8, was observed for plot F (see Table 3.2). No relation was found between the number of stems per plot and seed production (Regression, P>0.05; Table 3.5). When the parameters were compared to each other, several relationships turned out to be significant, with correlation coefficients (R^2) ranging from 0.14 to 0.69. The strongest relationships were found between the number of peduncles and seeds produced per stem (R^2 = 0.69), the number of peduncles and the number of buds (R^2 = 0.55), and the number of buds and seed produced (R^2 = 0.53) (Regression, *P*<0.001; Table 3.5). The correlations between the number of leaves with the number of seeds (R^2 = 0.15), buds (R^2 = 0.23) and peduncles (R^2 = 0.14) were lower, but also significant (*P*<0.001; Table 3.5).

Table 3.5. Correlations between the parameters, number of leaves, peduncles, buds, and seeds per stem, and the number of stems per plot. Contrasts obtained by regression analysis. The significant correlations are marked with the level of significance: *** - *P*<0.001.

Parameter	*n*	Leaves	Peduncles	Buds	Seeds
Stem	30	0.0001	0.0077	-0.0677	-0.0162
Seeds	25	0.1513 ***	0.6907 ***	0.5272 ***	
Buds	25	0.2289 ***	0.5508 ***		
Peduncles	190	0.1362 ***			

When the total production (all tagged stems) of the unripe and the ripe seeds was plotted per month, the peak of unripe seed production was in January, whereas for the ripe seeds the peak was approximately 2 months later in March (Figure 3.11).

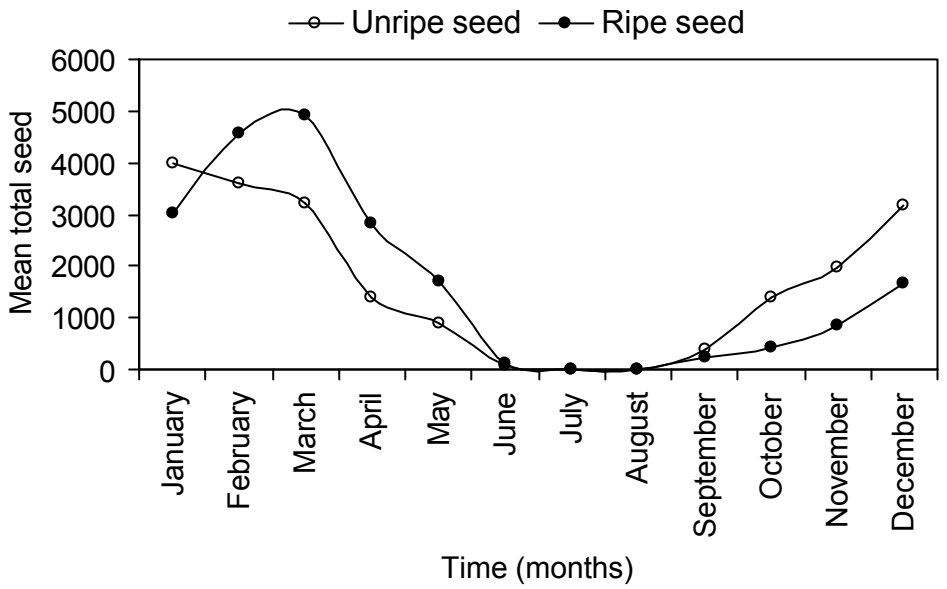


Figure 3.11. Mean of the total numbers of unripe and ripe seeds produced by all the tagged stems, over all sample years presented by month (*n* = 3).

3.3.3.3. Unfertilised flowers and aborted seeds

In general a mean of 20.3 ± 1.2% of the buds produced per stem developed into unripe seed and 7.6 ± 0.88% into ripe seed (Figure 3.12).

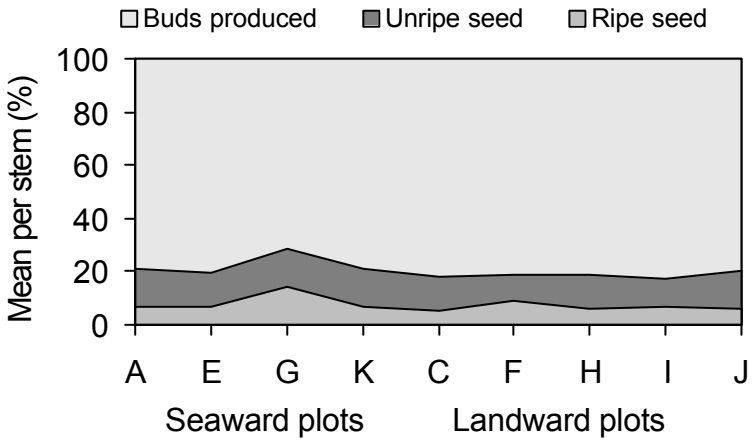


Figure 3.12. Development of buds (set to 100%) into unripe and ripe seeds (in %) on the seaward (A E G K) and landward face (C F H I J) of the foredune.

The ratio between the numbers of buds and unripe seeds for each plot was the proportion of flowers that were not fertilised, whereas the ratio between the number of unripe and ripe seed was the proportion of aborted unripe seeds. In total 77.4 ± 1.0% of

the flowers were unfertilised, and 61.1 ± 0.97% of the unripe seeds were aborted (Table 3.6A). For the mean number of unfertilised flowers only seaward plot G showed a significantly lower mean number compared to the other plots, with exception of plot K (ANOVA, *P*<0.001; Table 3.6A). Even though on both positions high numbers of unfertilised flowers were observed, the highest number was observed on the more protected landward face of the foredune (ANOVA, *P*<0.001; Table 3.6B).

The lowest numbers of aborted unripe seeds were found in landward plot F and seaward plot G, when compared with the other plots, with the highest value found for landward plot J (*P*<0.001; Table 3.6A).

No differences between the positions as far as number of aborted unripe seeds were observed (P>0.05; Table 3.6B). For both the number of unfertilised flowers and as the number of aborted unripe seeds no significant differences between the sample years were observed (ANOVA, *P*>0.05; Table 3.6C).

Table 3.6. Mean percentages (± S.E.)of unfertilised flowers and aborted seeds per stem given per plot (A), position (B) and sample year (C). Any value with the same letter does not differ significantly in the number of non-fertilised flowers or aborted unripe seeds. Contrasts obtained by Tukey after analysis by ANOVA. Level of significance: * - *P*<0.05, ** - *P*<0.01, *** - *P*<0.001.

A)

Plot	Position	*n*	Unfertilised flowers (%)		Aborted unripe seed (%)	
			Mean	(± S.E.)	Mean	(± S.E.)
A	Seaward	18	79.1	(1.27) a	65.4	(2.92) ab
G	Seaward	18	64.5	(5.95) b	48.7	(2.49) c
C	Seaward	24	82.0	(0.89) a ***	67.8	(2.02) ab
J	Seaward	23	80.1	(1.68) a	69.0	(1.72) a ***
E	Landward	22	74.8	(4.36) a	61.8	(2.44) ab
K	Landward	22	71.9	(4.21) ab	66.6	(1.51) ab
F	Landward	24	80.8	(1.29) a	47.7	(3.10) c
H	Landward	23	80.0	(1.47) a	63.1	(2.93) ab
I	Landward	21	80.3	(2.34) a	58.5	(2.42) b
Total mean		195	77.4	(1.02)	61.1	(0.97)

B)

Position	*n*	Unfertilised flowers (%)		Aborted unripe seed (%)	
		Mean	(± S.E.)	Mean	(± S.E.)
Seaward	72	72.7	(2.19) b	60.9	(1.38) a
Landward	112	80.6	(0.69) a **	61.1	(0.69) a

Table 3.6 continued.

C)

Sample year	*n*	Unfertilised flowers (%)		Aborted unripe seed (%)	
		Mean	(± S.E.)	Mean	(± S.E.)
1	64	80.3	(0.92) a	60.5	(1.87) a
2	57	76.7	(2.26) a	61.2	(1.74) a
3	65	75.1	(1.86) a	61.4	(1.44) a

The number of unfertilised flowers was directly related to the number of buds, whereas the number of aborted unripe seeds was related to the number of ripe seeds, as expected (Regression, $P<0.001$; Table 3.7). Between the other parameters no significant differences were observed.

Table 3.7. Correlations between the numbers of unfertilised flowers and aborted seeds with the numbers of buds, unripe seeds and ripe seeds produced per stem. Regression analysis wit level of significance of *** - $P<0.001$.

Parameter	Correlation coefficient per stem		
	# Buds	# Unripe seeds	# Ripe seeds
# Unfertilised flowers/stem	0.91 ***	0.04	0.05
# Aborted unripe seed/stem	0.06	0.45 ***	0.01

In most cases the unripe seeds were aborted due to the predation of the fruit coat and the still-soft stone fruit of the unripe seed by an unidentified fruit fly larvae. The larvae would empty the seed until only the fruit coat remained and dropped off the peduncle. The fruit fly also infected ripe seeds. The proportion of infected ripe seeds was high on some sites, whereas on other sites no infected seeds were found (Figure 3.13). Almost a third of the seeds collected at Old Woman's River (36%) and Kleinemonde (27%) were infected with fruit fly, whereas at Wavecrest no infected seeds were collected (Figure 3.13). No significant differences were observed in the dry weight of uninfected and infected seeds. This was due to the fact that the stone fruit hardened during the ripening of the seeds, the larvae could only eat the fruit layer and the seed remained undamaged and (if viable) capable of germination (ANOVA, $P>0.05$; Figure 3.13).

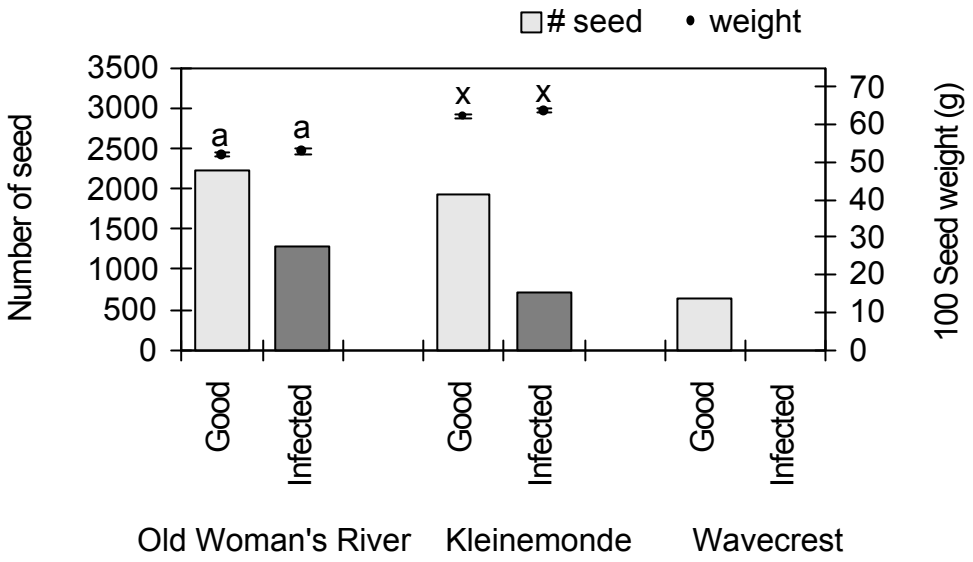


Figure 3.13. The numbers of uninfected (good) and infected ripe seeds of *S. plumieri* collected in 1999 at Old Woman's River, Kleinemonde and Wavecrest with the dry weight of 100 seed (*n* = 5, ± S.E.) in grams. Any seed weight points with the same letter does not differ significantly. Seed weight contrasts obtained by Tukey after analysis by ANOVA (*P*>0.05).

3.3.3.4. Duration of reproduction stages

The total reproduction (first bud to last seed) lasted in the first year 229 days, 252 days in the second year, and 213 days in the third year (Figure 3.14). In the first two years the development of buds (over both positions) started around day 233 (August), but in the third year the development started 45 days later round day 255 (September; Figure 3.14). The development of seeds started on average 57 ± 10.0 days after bud development and had an average duration of 172 ± 9.9 days. In total the mean duration of the bud stage was 108 ± 7.2 days, the flower stage 114 ± 6.2, the unripe seed stage 133 ± 7.3 and the ripe seed stage 149 ± 4.4 days (Figure 3.14).

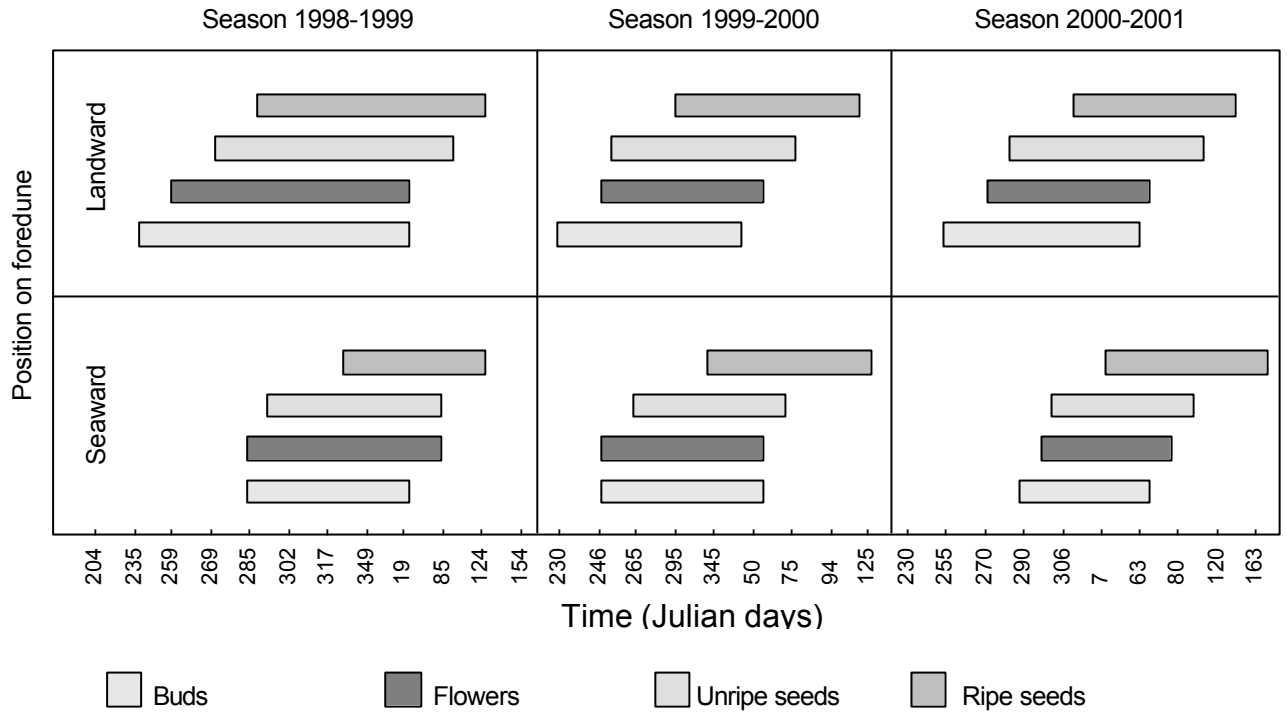


Figure 3.14. Phenogram with the duration of the different reproduction stages (bud, flower, unripe seed, ripe seed) in Julian days given by seaward and landward position. Note that the separation in days on the x-axis is not uniform.

Only for the duration of the ripe seed stage were significant differences observed for the different plots, with the highest duration found for plot C. Compared to plot C the seaward plots E and K, and landward plots H and J showed a significant lower duration of the ripe seed stage (ANOVA, $P<0.01$; Table 3.8A). For the other three reproduction stages (bud, flower and unripe seed) no significant differences between the plots were observed ($P>0.05$; Table 3.8A). On average the landward plots started 34 $\pm$ 9.8 days sooner with the development of buds (see Figure 3.15), but no overall significant differences were observed for the duration of the different reproduction stages per position (ANOVA, $P>0.05$; Table 3.8B). Between the different sample years significant differences were found for the bud to unripe seed stage (Table 3.8C). For the bud, flower and unripe seed stages the longest duration (or development period) was observed for the third year (2000-2001) compared to the first year (1998-1999)(ANOVA, $P<0.05$; Table 3.8C). No significant differences were found between the years for the duration of the ripe seed stage ($P>0.05$; Table 3.8C).

Table 3.8. Mean duration (± S.E.) of the reproduction stages by plot (A) and by position (B), and by sample year (C). Any value within a reproduction stage with the same letter does not differ significantly for plot, position or year. Contrasts obtained by Tukey after analysis by ANOVA. Level of significance: * - $P<0.05$, ** - $P<0.01$, *** - $P<0.001$.

A)

Plot	Position	*n*	Reproduction stage			
			Bud	Flower	Unripe seed	Ripe seed
			Mean (± S.E.)	Mean (± S.E.)	Mean (± S.E.)	Mean (± S.E.)
A	Seaward	3	128.7 (15.2) a	135.3 (20.3) a	143.0 (22.7) a	162.3 (12.7) ab
E	Seaward	3	96.3 (16.0) a	125.0 (4.0) a	139.0 (3.5) a	134.7 (15.6) b
G	Seaward	3	101.7 (20.5) a	103.0 (18.0) a	117.0 (25.1) a	147.7 (3.7) ab
K	Seaward	3	71.7 (14.1) a	81.7 (9.0) a	96.7 (23.5) a	131.7 (11.7) b
C	Landward	3	162.3 (7.1) a	150.7 (13.2) a	183.3 (5.6) a	192.7 (7.3) a ***
F	Landward	3	111.7 (22.5) a	113.0 (24.4) a	127.0 (31.7) a	151.7 (3.3) ab
H	Landward	3	95.7 (25.5) a	100.3 (12.1) a	121.0 (11.7) a	127.7 (7.7) b
I	Landward	3	116.7 (17.5) a	123.3 (21.0) a	137.3 (28.3) a	148.3 (3.3) ab
J	Landward	3	90.0 (25.7) a	96.7 (21.0) a	136.0 (15.6) a	146.7 (8.3) b
	Mean	72	108.3 (7.2)	114.2 (6.2)	133.4 (7.3)	149.3 (4.4)

B)

Position	*n*	Bud	Flower	Unripe seed	Ripe seed
		Mean (± S.E.)	Mean (± S.E.)	Mean (± S.E.)	Mean (± S.E.)
Seaward	12	99.6 (9.4) a	111.3 (8.8) a	123.9 (10.4) a	144.1 (6.2) a
Landward	15	115.3 (10.4) a	116.8 (8.8) a	140.9 (9.9) a	153.4 (6.2) a

C)

Year	*n*	Bud	Flower	Unripe seed	Ripe seed
		Mean (± S.E.)	Mean (± S.E.)	Mean (± S.E.)	Mean (± S.E.)
1	8	128.7 (15.2) a *	135.3 (20.3) a *	143.0 (22.7) a***	162.3 (12.7) a
2	8	162.3 (7.1) ab	150.7 (13.2) ab	183.3 (5.6) a	192.7 (7.3) a
3	8	96.3 (16.0) b	125.0 (4.0) b	139.0 (3.5) b	134.7 (15.6) a

The ripe seed stage was the significantly longest reproduction stage compared to the bud and flower stages (ANOVA, $P<0.001$; Figure 3.15). The duration of the unripe seed stage was significantly higher compared to the bud stage but not compared to the other stages ($P<0.001$; Figure 3.15).

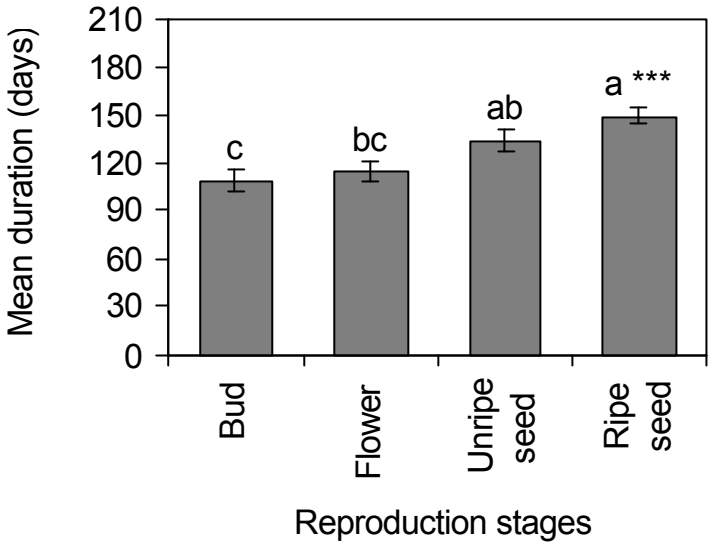


Figure 3.15. Mean duration (± S.E) of the reproduction stages bud, flower, unripe seed and ripe seed over all sample years and plots. Any column with the same letter does not differ significantly. Contrasts obtained by Tukey after analysis by ANOVA. Level of significance: * - $P<0.05$, ** - $P<0.01$, *** - $P<0.001$.

3.3.4. Sand movement

The sand movement (in cm) was very variable per year for all plots, but over the three-year sampling period the main trend was erosion (Figure 3.16). Almost from the beginning the landward plots showed negative sand movement resulting in sand erosion, whereas the seaward plots showed positive sand movement (accretion) for the first 105 days after which, from 23 November 1998 onwards, the sand movement changed from accretion to erosion (Figure 3.16).

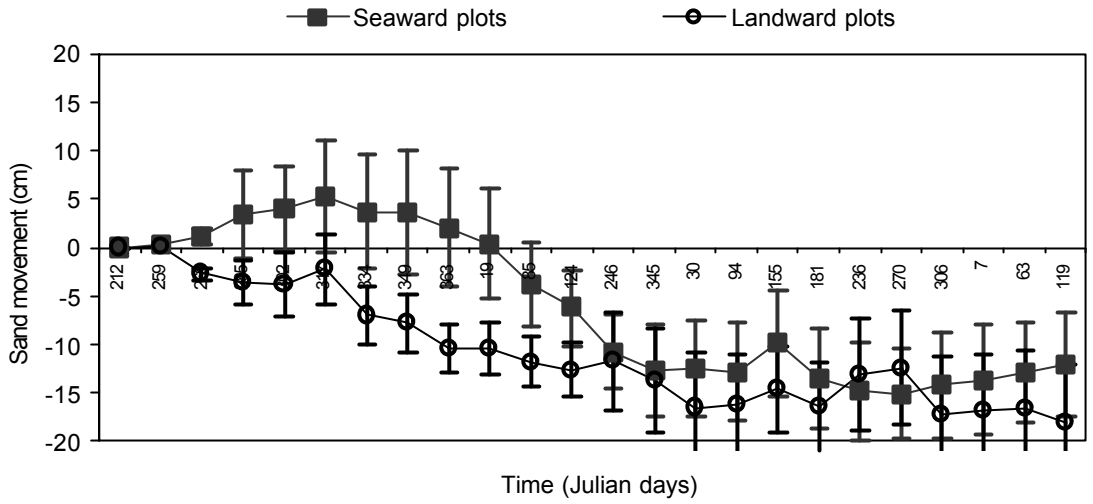


Figure 3.16. Mean sand movement (in cm) during the period July 1998 to May 2001 in Julian days given by seaward position and landward position of the foredunes (*n* = 12, ± S.E.).

The positive sand movement in the seaward plots mainly occurred in plots E and K, the only plots that showed an overall positive sand movement. The accretion was not strong enough to compensate for the negative sand movement in the other plots, resulting in an overall negative sand movement of 13.9 ± 0.77 cm (Table 3.9A). The highest mean sand movement of over 25 cm was observed in seaward plot B and landward plot J (Kruskal-Wallis, *P*<0.001; Table 3.9A). The stems of plot B were buried during most of the sample time, but the poles were still visible, so the movement could be recorded. The lowest mean sand movement was observed for seaward plot E and landward plot C and H (*P*<0.001; Table 3.9A). This was reflected in the lower net sand movement in those plots (Table 3.9A). The sand movement was not related to the position on the foredunes (P>0.05; Table 3.9B), probably because the shape of the dune and plant cover has a stronger influence on sand movement and deposition. There were, however, differences in sand movement between the different seasons and the sample years. The highest sand movement was observed during the winter and autumn and in years 2 and 3 (Table 3.9C and D).

Table 3.9. The net sand movement (accretion and erosion summed), total movement (all sand moved), direction of movement (+ = sand accretion, - = erosion), and the average movement given by plot (A), by position (B), by season (C) and by sample year (D) (± S.E.). Any value with the same letter does not differ significantly in sand movement per plot, position, season or year. Contrasts obtained by a Newman-Keuls test after analysis by Kruskal-Wallis. Level of significance: * - $P<0.05$, ** - $P<0.01$, *** - $P<0.001$.

A)

Plot	Position	*n*	Sand movement (cm)				
			Net movement	Total movement	Direction	Mean	(± S.E)
A	Seaward	46	-197	445	-	19.34	(1.92) ab
B	Seaward	46	-616	620	-	26.93	(1.77) a ***
E	Seaward	46	81	110	+	4.78	(0.61) d
G	Seaward	46	-182	190	-	8.25	(1.39) cd
K	Seaward	46	208	220	+	9.57	(1.94) cd
C	Landward	46	-41	117	-	5.09	(0.70) d
F	Landward	46	-330	331	-	14.40	(1.33) bc
H	Landward	46	114	143	+	6.20	(1.01) d
I	Landward	46	-429	437	-	19.00	(2.69) ab
J	Landward	46	-590	590	-	25.63	(1.79) a
Total		460	-1981	3201	-	13.92	(0.77)

B)

Position	*n*	Sand movement (cm)				
		Net movement	Total movement	Direction	Mean	(± S.E)
Seaward	230	-1436	3092	-	15.61	(1.10) a
Landward	230	-1253	2513	-	10.38	(1.09) a

C)

Season	*n*	Sand movement (cm)				
		Net movement	Total movement	Direction	Mean	(± S.E)
Autumn	100	-615	781	-	15.61	(1.15) a
Spring	100	-284	726	-	10.38	(0.95) a *
Summer	130	-559	1027	-	14.68	(1.04) b
Winter	130	-524	667	-	16.68	(1.10) ab

D)

Sample year	*n*	Sand movement (cm)				
		Net movement	Total movement	Direction	Mean	(± S.E)
1	232	-347	1104	-	9.69	(0.92) b
2	100	-626	827	-	16.55	(1.62) a
3	128	-1008	1270	-	19.24	(1.55) a ***

No significant correlation was found between the sand movement and the number of stems per plot, as well as between the sand movement and the numbers of peduncles, buds, and ripe seeds (Table 3.10).

Table 3.10. Relationships between the sand movement and the parameters, numbers of leaves, peduncles, buds, and seeds per stem, and the number of stems per plot. Contrasts obtained by regression analysis. Regression analysis (P>0.05).

Parameter	*n*	Sand
# Stems/m^2	30	0.1014
# Leaves per stem	30	-0.0001
# Peduncles/stem	30	0.0001
# Buds/stem	25	0.0026
# Unripe seeds/stem	25	0.0024
# Seeds/stem	25	0.0021

3.3.5. Soil analysis

The pH, conductivity, chloride content and organic matter content of the soil were variable per plot. The pH, chloride content, organic matter and conductivity showed significant differences between the sampled plots (ANOVA, P<0.05; Table 3.11A). Slight differences were observed for the pH with higher values found for the plots E, G, F and I compared to plot C, for which the lowest pH of 9.34 was observed (P<0.001; Table 3.1A). For the chloride content of the soil only plot K and F showed significant differences, with plot F showing the higher chloride content (P<0.001; Table 3.1A). The organic matter of the soil varied a bit more between the plots, with the soil of plots J and G showing a significantly higher organic matter content compared to plot A and C (P<0.001; Table 3.11A). The lowest percentage of organic matter was found in plot C.
The conductivity of plots A and B was significant higher compared to all other plots, with the exception of plot E, C and F (P<0.001; Table 3.11A). In general no direction in the soil analysis results was observed between the plots. This was supported by the means per dune position, where only the moisture content showed significant differences, with the highest moisture content found for the seaward facing side (ANOVA, P<0.001; Table 3.11B).

Table 3.11. Mean soil parameter data with standard error (± S.E) given by plot (A) and by position (B) with the distance to the high water mark (HWM) in metres. Any value within a soil parameter with the same letter does not differ significantly per plot or position. Contrasts obtained by Tukey after analysis by ANOVA. Levels of significance: * - $P<0.05$, ** - $P<0.01$, *** - $P<0.001$.

A)

Plot	HWM (m)	Soil parameter means (± S.E.) with *n* = 3				
		Moisture (%)	pH	Chloride (mg/100 g soil)	Organic matter (%)	Conductivity (µS/cm)
A	9	0.12 (0.01) a	9.51 (0.08) ab	0.75 (0.09) ab	0.30 (0.02) bc	67.33 (5.33) a
B	9	0.16 (0.03) a	9.39 (0.01) ab	0.65 (0.08) ab	0.42 (0.03) abc	71.00 (4.00) a***
E	6	0.19 (0.05) a	9.55 (0.04) a	0.71 (0.02) ab	0.42 (0.03) abc	66.67 (2.40) ab
G	9	0.12 (0.02) a	9.56 (0.04) a	0.64 (0.05) ab	0.65 (0.12) a	53.67 (2.73) bcd
K	17	0.15 (0.03) a	9.45 (0.01) ab	0.84 (0.08) a***	0.52 (0.05) ab	52.00 (2.08) cd
C	12	0.10 (0.01) a	9.34 (0.07) b	0.63 (0.030 ab	0.20 (0.01) cc	66.00 (2.08) ab
F	11	0.11 (0.01) a	9.56 (0.02) a***	0.55 (0.08) b	0.56 (0.03) ab	64.33 (0.88) abc
H	12	0.11 (0.02) a	9.50 (0.02) ab	0.57 (0.04) ab	0.56 (0.02) ab	50.00 (1.00) d
I	10	0.08 (0.03) a	9.56 (0.02) a	0.73 (0.04) ab	0.60 (0.02) a	50.00 (1.00) d
J	14	0.11 (0.01) a	9.40 (0.04) ab	0.76 (0.02) ab	0.68 (0.08) a***	43.00 (1.53) d

B)

Position	HWM (m)	Soil parameter means (± S.E.) with *n* = 15				
		Moisture (%)	pH	Chloride (mg/100 g soil)	Organic matter (%)	Conductivity (µS/cm)
Seaward	10.0	0.15 (0.01) a**	9.49 (0.09) a	0.72 (0.12) a	0.46 (0.15) a	62.13 (9.84) a
Landward	11.8	0.10 (0.01) b	9.47 (0.11) a	0.64 (0.11) a	0.52 (0.18) a	54.67 (9.49) a

When the soil parameters were compared with the distance to the high water mark (HWM) the conductivity and the moisture content showed significant negative correlation with a R^2 of -0.34 and -0.18, respectively. Thus the plots situated closer to the sea show, in general, higher soil conductivity and soil moisture (Regression, $P<0.001$; Table 3.12). The only other significant correlation was found between organic matter and conductivity. The organic matter showed a negative significant correlation with the conductivity with an R^2 of -0.399 (Table 3.12). The remaining soil parameters showed no significant correlation with the other parameters or the distance to high water mark.

Table 3.12. Regression coefficients (R^2) of the relations between the high water mark (HWM) and soil parameters, organic matter, conductivity, chloride, pH and moisture (n = 30). Contrast obtained by Regression analysis. Level of significance: * - $P<0.05$, *** - $P<0.001$.

Soil parameters	Organic matter	Conductivity	Chloride	pH	Moisture
Distance	0.074	- 0.344 ***	- 0.001	- 0.063	-0.182*
Moisture	0.016	0.098	0.003	0.010	
pH	0.106	- 0.006	0.016		
Chloride	- 0.005	- 0.002			
Conductivity	- 0.399 ***				

When the leaf and reproduction phenology parameters were correlated to the soil parameters, four significant relations were found with an R^2 ranging from 0.23 to 0.59 (Table 3.13). The strongest correlation was found between the number of stems and the soil moisture (R^2 = 0.59) (Regression, P<0.001; Table 3.13). For the number of peduncles two negative correlations were found, one with the pH (R^2 = -0.33) and one with the organic matter content (R^2 = - 0.28) (P<0.001; Table 3.13). The last correlation found, was between the number of buds and the pH, with a R^2 of 0.23 the correlation was not strong (P<0.05; Table 3.13). The results of these regressions were not pointing in one direction, with the exception perhaps of the peduncles, but the soil samples were only taken once during the sampling period of three years. It was therefore not possible to say how the chemical soil conditions changed throughout the year to show relationships between biological parameters and soil parameters. To be able to say more about the relations the sampling should be carried out at least every season.

Table 3.13. Correlations between the parameters, number of leaves, peduncles, buds, and seeds per stem and the number of stems per plot with the soil parameters pH, chloride, conductivity, organic matter content and soil moisture. Contrasts obtained by regression analysis. The significant relationships are marked with the level of significance: * - P<0.05, *** - P<0.001.

Parameter	*n*	pH	Chloride	Conductivity	Organic matter	Moisture
# Leaves	30	-0.0586	0.1247	-0.1417	0.0208	-0.0038
# Peduncles	30	-0.3311 ***	0.0530	0.0259	-0.2799 ***	-0.0008
# Buds	25	0.2259 *	0.0669	-0.0001	0.1700	-0.0029
# Seed	25	0.1385	0.0773	-0.0079	0.1181	-0.0002
# Stem	30	0.0455	0.1310	0.0437	0.0038	0.5945 ***

3.3.6. Climate data

The temperature showed a clear pattern with the lowest temperature measured in July-August, whereas the higher temperatures were measured for the months December to March, with the highest peak in February (Figure 3.17). The total rain per week

measured for the period June 1998 to June 2001 fluctuated strongly and did not show any pattern (Figure 3.17).

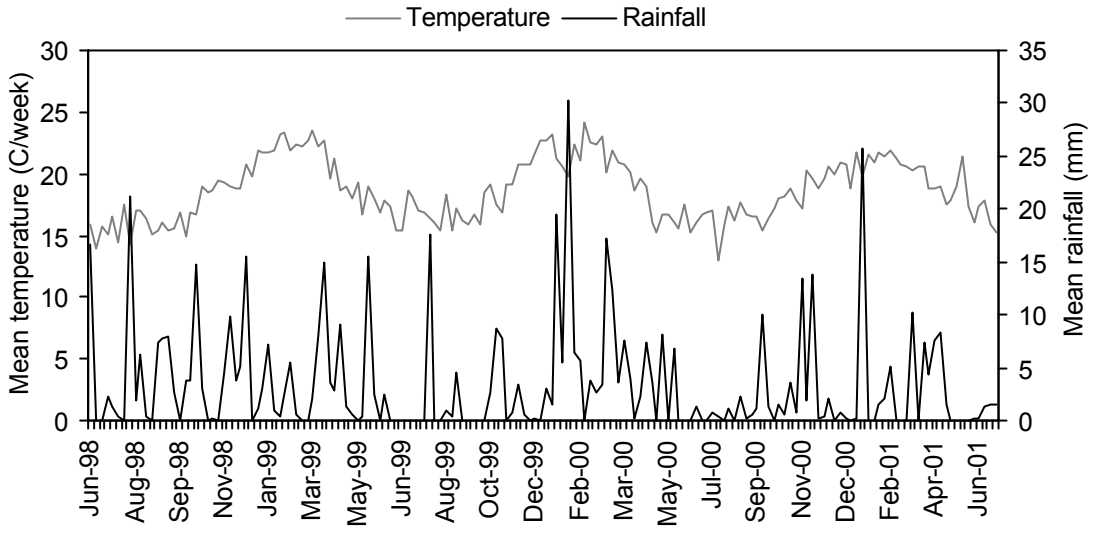


Figure 3.17. Mean weekly temperature and total weekly rainfall (in mm) for the period June 1998 to June 2001.

The mean average temperature analysed per month showed the same pattern as observed in figure 3.17, showing that the pattern was seasonal (Table 3.14). The highest temperature was observed in February followed in order by December, January, March, November, April, May, June, July, August, and September (Kruskal-Wallis, $P<0.001$; Table 3.14A). Between the different seasons the highest average temperature was observed for summer followed in order by autumn, spring, and winter ($P<0.01$; Kruskal-Wallis; Table 3.14B). For the different years the years 2000 and 2001 showed the highest mean average annual temperature, with the lowest temperature found for 1998 ($P<0.01$; Table 3.14C). Over the period January 1998 till July 2001 it rained on 315 of the 1266 days (24.9%) (Table 3.14A).

The annual rainfall was on average 385.3 mm per annum. The year 2001 was excluded because only data till July were measured (see Table 3.14C). No significant differences were observed between the months, seasons and for the mean average rainfall and mean total rainfall (Kruskal-Wallis, $P>0.05$; Table 3.14A-C).

Table 3.14. Mean monthly rainfall and mean total rainfall (in mm) with the number of days rainfall occurring in the period January 1998 to June 2001, and the mean temperature given by month (A), by season (B) and by year (C) collected at Fish Point and Port Alfred. Any value with the same letter does not differ significantly in mean rainfall, total rainfall, or temperature. Contrasts obtained by Newman-Keuls after analysis by Kruskal-Wallis. Level of significance: ** - $P<0.01$, *** - $P<0.001$.

A)

Month	Rainfall (mm)					Average temperature (◦C)	
	# Days	Average		Total			
		Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
January	39	6.89	(1.40) a	61.05	(23.38) a	21.60	(0.17) b
February	28	2.77	(0.44) a	18.70	(3.53) a	22.24	(0.14) a ***
March	42	7.90	(1.37) a	78.00	(22.90) a	21.29	(0.17) b
April	44	4.65	(0.81) a	52.25	(9.38) a	19.04	(0.16) c
May	12	5.35	(1.77) a	15.55	(5.15) a	17.69	(0.20) d
June	13	2.80	(1.22) a	9.10	(4.09) a	16.25	(0.21) e
July	16	9.94	(3.84) a	53.00	(26.06) a	16.29	(0.31) e
August	20	3.26	(1.37) a	21.73	(13.96) a	16.49	(0.26) e
September	19	6.11	(1.48) a	38.67	(12.94) a	16.12	(0.19) e
October	28	7.77	(2.50) a	72.50	(11.40) a	18.02	(0.21) d
November	29	4.42	(1.17) a	42.73	(15.25) a	19.46	(0.19) c
December	25	3.69	(1.45) a	30.73	(17.94) a	21.02	(0.19) b
Total	315	5.59	(0.47) a	40.87	(5.17) a	18.91	(0.09)

B)

Season	Rainfall (mm)					Average temperature (◦C)	
	# Days	Average		Total			
		Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
Summer	92	4.77	(0.75) a	37.38	(10.62) a	21.67	(0.10) a **
Autumn	98	6.13	(0.73) a	48.60	(10.85) a	19.35	(0.13) b
Winter	49	5.32	(1.46) a	26.06	(9.90) a	16.33	(0.15) d
Spring	76	6.07	(1.09) a	51.30	(8.52) a	17.88	(0.14) c

C)

Year	Rainfall (mm)					Average temperature (◦C)	
	# Days	Average		Total			
		Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
1998	55	7.03	(1.36) a	55.26	(6.84) a	17.17	(0.20) c
1999	119	4.83	(0.59) a	31.17	(5.61) a	19.68	(0.13) b
2000	106	5.51	(0.86) a	48.65	(14.15) a	18.53	(0.16) a
2001*	35	6.18	(1.55) a	36.03	(13.12) a	19.45	(0.19) a **

* Only until July

3.3.7. Summary

The summary of all the leaf and reproductive statistics is listed in table 3.15. Landward plots C and J show (over all parameters) the most significant highest parameters compared to the other plots, hence those were the plots showing the highest performance. In general, from the data summarised in table 3.15, it is obvious that the stems growing on the landward face of the foredune showed the overall highest performance, with the highest numbers of leaves, peduncles, buds and seeds produced. The highest performance was observed in the warmer season's spring and summer, whereas the highest sand movement was observed in the colder months of autumn and winter. There were distinct differences between the sample years with sample year three (2000-20001) showing the lowest leaf performance, the shortest reproduction time (duration), the highest mean temperature, and the highest overall sand movement (Table 3.15).

Table 3.14. Summary of the statistics of the parameters measured given by plot, position, year and season. Any value within a parameter with the same letter does not differ significantly, with values marked with 'a' being the significant highest value.

Parameter	Details	HWM (m)	Rain fall	Temperature	# Stem/m^2	Leaves			Reproduction/stem					# Seed/m^2	Duration				Sand			
						Mean per stem	Birth rate	Death rate	# Peduncles	# Bud	# Seed	Unfertilised flowers	Aborted unripe seeds		Bud	Flower	Unripe seed	Ripe seed	Organic matter	Conductivity	Movement	Direction
Plot A	Seaward	9			bc	bc	a	a	bc	abc	ab	a	ab	ab	a	a	a	ab	bc	a	ab	-
B	Seaward	9			a	c	a	a	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]			a	-
E	Seaward	6			bc	c	a	a	c	bcd	b	a	ab	b	a	a	a	b	abc	ab	d	+
G	Seaward	9			bc	bc	a	a	d	d	ab	b	c	ab	a	a	a	ab	a	bcd	cd	-
K	Seaward	17			bc	c	a	a	cd	bcd	b	ab	ab	ab	a	a	a	b	ab	cd	cd	+
C	Landward	12			bc	bc	a	a	a	a	a	a	ab	a	a	a	a	a	c	ab	d	-
F	Landward	11			b	bc	a	a	bc	cd	b	a	c	ab	a	a	a	ab	ab	abc	bc	-
H	Landward	12			bc	bc	a	a	bc	bcd	b	a	ab	b	a	a	a	b	ab	d	d	+
I	Landward	10			c	a	a	a	ab	ab	a	a	b	ab	a	a	a	ab	a	d	ab	-
J	Landward	14			bc	ab	a	a	abc	a	a	a	a	a	a	a	a	b	a	d	a	-
Position	Seaward	10.0			a	b	a	a	b	b	b	b	a	b	a	a	a	a	a	a	a	-
	Landward	11.8			a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	-
Year	1		a	c	a	a	a	a	a	a	a	a	a	a	a	a	a	a			b	-
	2		a	b	a	a	b	b	a	a	a	a	a	a	ab	ab	a	a			a	-
	3		a	a	a	b	c	b	a	a	a	a	a	a	b	b	b	a			a	-
Season	Autumn		a	b		bc	bc	c													a	-
	Winter		a	d		c	c	d													a	-
	Spring		a	a		b	a	a													b	-
	Summer		a	c		a	b	b													ab	-

[1] Missing data due to irregular burial of stems.

3.4. DISCUSSION

In coastal foredunes, primary colonisers such as *Scaevola plumieri* play a major role in the formation and growth of dunes by their influence on stabilisation and succession (Ranwell 1972, Tinley 1985, Steinke & Lambert 1986). Only a few studies (Harte & Pammenter 1983, 1986, Steinke & Lambert 1986, Todd 1994, Peter & Ripley 2000) have dealt with *S. plumieri*, but those were mostly focussed on the (eco)physiology. To use foredune species for drift sand stabilisation, information on the growth patterns and the timing and duration of reproduction is of importance. Information of the growth period(s) for instance is essential to determine when best to plant stem cuttings or seedlings in the field, whereas information on the reproduction cycle is needed to know when to collect seeds. Therefore, the aim of the present research was to establish the growth period (leaf phenology) and reproduction phenology of *S. plumieri* growing on the foredunes.

The dune environment is very hazardous, especially in the foredune area. The sand movement, sand abrasion, impact of wind, salt spray and the chance of seawater inundation were higher on the seaward side of the foredunes (Ranwell 1972, Donnelly & Pammenter 1982, Crawford 1989, Carter 1993, Fahrig *et al.* 1993, Houle 1997). It was therefore not surprising that the stems of *S. plumieri* situated on the landward face of the foredunes showed an overall higher performance compared to the stems on the seaward face of the foredunes.

Leaf phenology

The stems of *S. plumieri* situated on the landward face showed the overall highest numbers of leaves per stem, whereas Pammenter (1986) found more leaves on the seaward face of the foredune. In the present research a mean range of 14-18 leaves per stem was observed which fell within the leaf range found by Steinke and Lambert (1986) in KwaZulu-Natal, but was narrower compared to Pammenter (1986). New leaves were produced throughout the year with distinct differences in the mean number of leaves between seasons and sample years. The number of leaves per stem showed a distinct peak during the summer, with the lowest number of leaves produced in winter, as found by other research (Pammenter 1986, Steinke & Lambert 1986). Hence, the lowest number of leaves was observed during the cooler months, when radiation levels are lower. During the spring and summer months, when radiation levels are high, there

is more demand for photosynthates for reproduction (Steinke & Lambert 1986), corresponding to the higher number of leaves per stem.
The different stems situated on the seaward and landward dune position showed no differences in the birth rates and the death rates of leaves between plots and/or dune positions, due to the fact that the birth rates and death rates were lying close together. Indicating that there was some sort of balance between the appearance and senescence of leaves. Steinke and Lambert (1986) also found similar birth and death rates, but the mean birth and death rates observed for the present study were on average 0.5-1.1 leaves lower compared to Steinke and Lambert (1986). Even though in the present study no differences between plot and position were observed for birth and death rates of leaves, a seasonal trend was observed for the birth and death rate of leaves, as seen for the number of leaves per stem. The main difference was that the birth and death rates peaked in spring, whereas the leaf growth peaked in summer. In general the death rate seemed slightly higher when compared to the birth rate, but this might be due to the factors like sand movement, temperature, rainfall pattern during the studied period.

Because the foredune environment was such an unstable habitat, the establishment of seedlings was difficult due to high sand movement, sand abrasion, salt spray, high tides and high solar radiation (e.g. Barbour 1992, Carter 1993). Nevertheless *S. plumieri* seedlings were frequently observed on the beach and base of the foredunes, showing a reasonable survival rate (see Chapter 4). Besides sand burial, one of the biggest dangers to seedlings was seawater inundation. The high seas could kill or injure seedlings by washing the seedlings into the sea, by bury the seedlings by sand deposited during the overwash, or by the effect of seawater inundation (Lee & Ignaciuk 1985, Fahrig *et al.* 1993). During the present study several big seas occurred resulting in the death of younger seedlings, and a standstill in leaf production of the older seedlings. The standstill in leaf production was reflected in a decrease in leaf birth and death rates the (older) seedlings that survived the inundation, which was also observed by Cavers and Harper (1967). The ability to survive seawater inundation without serious leaf (or root) damage is an important property for a coastal plant.
In general the mean birth/death rates of the seedlings were lower compared to adult stem rates. A reason for the lower birth/death rates could be, apart from seawater injuries, the fact that seedlings have periods that they invest more in root than leaf

growth. Whereas, the adult stems were part of the big below-ground structure with roots probably reaching the groundwater, as suggested by Peter and Ripley (2000). Besides differences between seasons and positions, differences were also found between the sample years. In general the production of *S. plumieri* was higher in the warmer months with a maximum life span of a leaf of approximately 150 days (Pammenter 1986). The leaf shedding was highest in summer, and hence the leaves from the cooler months remained on the plant for longer periods. The seasonal variations in appearance and senescence of leaves in the present study were marked, and in this respect appeared to behave in a similar way to other coastal species (Steinke & Charles 1984).

Seasonal leaf appearance of *S. plumieri* might suggest that the plants would not be effective in combating moving sand. Usually a high rate of sand mobility inhibits growth, but a few specialised plant species withstand or flourish under sand accretion (Salisbury 1952). For instance the plants of the sand-binding coastal grass *Ammophila arenaria* exhibit high vigour following burial (Wallen 1980, Eldred & Maun 1982, Moreno-Casasola 1986, Zhang & Maun 1990, Van der Putten *et al.* 1993). The vigorous growth due to sand accretion was probably due to altered soil temperatures, increased space for root development, and higher moisture/nutrient availability in the root zone (Olson 1958, Marshall 1965, Zhang & Maun 1992). The stems of *S. plumieri* that were growing in a prograding system with sand accretion showed more and bigger leaves and a more elongated stem than stems from degrading dunes (Plate 3.4). This suggests that *S. plumieri* belongs to the small group of plant species that prosper under sand accreting situations.

Plate 3.4. Stems of *Scaevola plumieri* from a prograding dune (top) and degrading dune (bottom). Note the difference in stem length between the leaves and the leaf size.

Reproductive phenology

Apart from the higher leaf production, the output of the different reproduction stages was also higher for the stems situated on the landward face of the foredunes. The reproduction would start in August-September and would end when all the seeds were shed in May-June. The duration of the different reproduction stages (bud, flower, unripe seed and ripe seed) showed no differences between the plots and was not related to dune position; however, between the sample years some differences in duration of the different stages was observed. The first sample year showed a longer duration for the reproduction stages bud, flower and unripe seed, whereas the seed stage was equally long for the three sample years.

The mean numbers of buds and seeds produced on the landward face plots were higher compared to the seaward plots. Per stem many buds were produced which all developed into flowers, but only 24% of the flowers per stem were fertilised on average. There were considerable inter-plot variations, but the highest number of unfertilised flowers was found on the landward face of the foredunes, where the highest number of buds per stem was produced. Several studies suggest that natural and artificial (by hand) pollination did not result in 100% seed set in many species, and that the number of flowers usually exceeds seed set even when all the flowers were pollinated (see Stephenson 1981). The low ovule maturation found for *S. plumieri* could have been caused by resource limitation (Stephenson 1981, Fenner 1985), but it was probably caused by inadequate pollination due to for instance a low number of pollinators (Schaal 1980, Bierzychudek 1981). The flower of *S. plumieri* showed traits indicating that the flower required animal pollination, e.g. large visible, sturdy flowers and nectar supply.

S. plumieri has white flowers which are generally indicative of moth or butterfly pollination. However, many close relatives of *S. plumieri* have dark-blue to purple flowers, which implies Hymenopteran pollinators (Faegri & Van der Pijl 1979).

Trevelyan (1995) found that birds (Stephen's lori) were foraging mainly on *Scaevola taccada*, making birds a possible candidate for pollination of *S. plumieri*. Personal observations during the fieldwork revealed that small bees were often robbing the flowers of nectar by entering the flower to the side without touching the reproductive organs. Thus the pollinator of *S. plumieri* remains unknown as observations during the present study have failed to detect a pollinator for *S. plumieri*.

The average seed production of 3 seeds per stem was much lower compared to the mean seed production measured by Pammenter (1986; 7 seeds/stem), but near the range found by Steinke and Lambert (1986; 3-4 seeds/stem) in KwaZulu-Natal. The fact that many flowers were not fertilised could have resulted in this low seed set, which was much lower than the potential seed set (number of buds/flowers). Apart from the number of pollinated flowers, the resources might also have an influence on the number of seeds produced (Stephenson 1981). For the numbers of seeds, unripe seeds and buds no differences in output were observed, even though the duration of the bud, flower and unripe seed stages showed differences between the sample years. Thus the longer duration did not result in a higher output because no differences were observed between the sample years for reproductive output. The mean number of seeds produced per stem per sample year ranged from 2.89 in year 1 to 2.95 in year 2 and 3, suggesting that the observed seed output was quite similar even though the duration of the reproductive periods per year differed greatly.
The between-year differences could be due to many factors including, sand movement, salt spray, temperature and rainfall before and during sample period (Carter 1993, Ranwell 1972). The longer duration in the first sample year concords with the higher leaf production that sample year.

The region of the Eastern Cape where the study sites were located on the coastal lowlands, is situated in the sub-region between the summer and winter rainfall regions, resulting in a spring dominant bimodal rain pattern. The bimodal pattern usually showed a double maximum of rainfall in spring/early summer and autumn, followed by dry periods in summer and winter (Tinley 1985, Kopke 1988). The lowest rainfall during the present study was observed in the months February, May and June, but due to large fluctuations no significant differences were noticed in mean and total rainfall per month. The rainfall at the SW to SE Cape coast is usually low, and perhaps the rain extremes were less pronounced at the coast due to the ever-blowing wind and the low inshore temperatures, as was observed for temperature and humidity by Tinley (1985).

Seed abortion

Not all the fertilised flowers developed into ripe seeds, overall 61% of the unripe seeds aborted. The proportion of matured seeds was mainly dependent on the weather conditions, seed predation, and the ability of the parent plant to provide the resources

necessary for growth and development (Udovic & Aker 1981, Wilson & Price 1980, Wyatt 1980). But according to Stephenson (1980, 1981) plants selectively abort seeds because they initiate more seeds than can be developed to maturity with the available resources, and the 'surplus' seeds would abort. This was true for some of the aborted seeds of *S. plumieri*, but the main reason for the seed abortion for *S. plumieri* seemed to be predation by the larvae of an unidentified fruit fly. The seed of *S. plumieri* is a drupe consisting of a thick fruit layer surrounding a stone seed. In unripe young seeds of *S. plumieri* the fruit layer and the soft stone seed were eaten, whereas in ripe mature drupes the stone seed hardened and was left undamaged by the predators. The larvae of the fruit fly was predated by a wasp and the wasp larvae were found in a 1:5 ratio to its host, the fruit fly larvae, in infected ripe seeds. The proportion of infected ripe seeds was high at some sites, whereas at other sites no infected seeds were found. Clearly, the level of predation was more related to the occurrence and density of the predators than for example the position of the plots; this was supported by the fact that no differences between the positions or sample years were found for the number of aborted seeds.

Comparison with other research

The differences in leaf production and reproduction within the present research might be due to a combination of differences in degree of exposure of the stems (salt spray, wind, sand abrasion), sand movement, plant age and climate between the plots, positions, seasons and years. Sand movement is a complex factor, and only high wind velocities (Ranwell 1972) accomplished substantial sand movement. Apart from the direct mechanical effect of burying and erosion, sand movement increases the amount of nutrients, as well as the availability of moisture (Salisbury 1952, Willis *et al.* 1959, Moreno-Casasola 1986), but between the sand movement and the leaf/reproduction parameters no correlations were observed. This was probably due to the fact that the main effect of the sand movement was erosion.

Abiotic conditions, e.g. sand parameters, pH, conductivity and organic matter, can vary significantly over short distances from the foot of the foredune to, for instance, the ridge (Martin 1959, Van der Valk 1974, Koehler *et al.* 1995, Houle 1997). This was not observed during the present study, as in general the soil properties had hardly any effect on plant performance. The soil samples were taken at a depth of approximately 10 cm to avoid sampling recently deposited sand. Between the soil parameters and the

leaf/reproduction parameters a few weak correlations were found, with the strongest relation between soil moisture and number of stems (R^2 0.59).

The contradicting results found by Pammenter (1986) probably would have been due to variation in the degree of sand movement, salt spray, wind, sand abrasion, plant age and climate between the two sites. The climate in KwaZulu-Natal where the research of Pammenter (1986) and Steinke and Lambert (1986) took place, is overall warmer and more humid (Tinley 1985, Todd 1994). The mean annual temperature was more than 4°C lower in the Eastern Cape, and with a difference in rainfall of more than 800 mm/year (200-600mm/year compared to 1000-1600mm/year; Tinley 1985, Kopke 1988, Peter & Ripley 2000). The Eastern Cape is a much drier area and the difference in climate had a big influence on plant performance, resulting in a higher leaf production and reproduction effort in KwaZulu-Natal compared to the Eastern Cape.

Apart from climate, sand movement probably was the other major determinant in the differences in plant performance. The dunes at Old Woman's River were overall degrading, with the negative sand movement resulting in erosion on the seaward and landward face of the foredune. *S. plumieri* stems seemed to thrive during sand accretion (Pammenter 1986) and the fact that the stems in KwaZulu-Natal were situated in a prograding system could explain the differences in leaf production and reproduction effort in the Natal dunes. Clearly the leaf phenology and reproduction success was strongly correlated with the habitat in which the plants were growing, accounting for the differences between the Eastern Cape and KwaZulu-Natal plants.

Sexual versus vegetative reproduction

In the coastal environment flowering plants must cope with many problems for successful reproduction to take place (Tinley 1985, Fitter & Hay 1992, Molau 1992, Carter 1993). These environmental conditions can affect reproductive success through their effect on flowering and fruiting phenology, which could influence seed size and seed maturation, for example (Primack 1987, Totland & Birks 1996).

Reproduction by seed œnsequently has limited success because of the difficulties of establishing seedlings under such conditions (Fenner 1985, 1987, Jones & Gliddon 1999). Many perennials overcome these difficulties through vegetative reproduction. Clonal species are generally thought to propagate mainly by vegetative rather than sexual means. The latter process is however by no means insignificant (Eriksson 1997), proven by the fact that *S. plumieri* allocates up to 36% of its primary production to fruits

(Pammenter 1986). This was supported by the observation that the potential output of reproduction (number of buds produced) of *S. plumieri* was more than 15 times higher compared to the realised output (number of seeds) in the present research. Why does *S. plumieri* put so much energy into sexual reproduction?

A long-lived clonal species might exhibit phenotypic plasticity in response to environmental conditions with the ability to benefit from sexual reproduction, a strategy which confers survival potential on a species inhabiting a harsh environment (Jones & Gliddon 1999). Such a strategy is important, as a heavy reliance on clonal growth, rather than sexual reproduction, can reduce intra-specific genetic diversity enough to threaten long-term survival in a changing environment (Jones & Gliddon 1999). Perhaps so many seeds are produced because the plants are unsuccessful in establishing via seedlings. Many clonal plants produce seeds to establish 'every now and then' from seeds, but this is on an event basis rather than a regular pattern as observed by Huiskes (1977) for *A. arenaria*.

Is Scaevola plumieri *a clonal plant?*

Harman (2000) found that all sampled populations of *S. plumieri* were resolved as being genetically distinct from each other and suggested that there was sexual reproduction between populations. If however one is regarding vegetative growth within a dune as clonal reproduction, then it must be concluded that *S. plumieri* is locally clonal but broadly sexual. Sexual reproduction is the driving force behind diversity and also acts as a repressive force preventing the formation of local variants through extended isolation (Ellstrand & Elam 1993). This low diversity detected within the South African range is both what allows *S. plumieri* to be so successful within its range and what prevents it from extending its range into the various other niches available (Harman 2000). It was concluded that individual isolated dunes consisted of individual plants or clones, but reproduction between dunes and populations was more of a sexual nature and thus, strictly speaking *S. plumieri* cannot be taken as an obligate clonal plant (Harman 2000).

Concluding remarks

In general the stems situated on the landward face of the dunes show the best overall plant performance, even though the duration of the different reproduction stages was not affected by the position. A lot of unripe seeds were aborted due to seed predation,

but enough would be available to germinate in February-March, approximately a year after shedding at the base of the foredune. The seedling, once established survived well and could stand severe seawater inundation. All this makes *Scaevola plumieri* a good candidate to use for drift sand stabilisation.

3.5. ACKNOWLEDGEMENTS

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CHAPTER 4

GERMINATION OF SELECTED COASTAL FOREDUNE SPECIES OF THE EASTERN CAPE, SOUTH AFRICA

Though I do not belief that a plant will spring up where no seed has been, I have great faith in a seed. Convince me that you have a seed there, and I am prepared to expect wonders.

Thoreau (1999)

4.1. INTRODUCTION

The life history traits of plant species can determine their occurrence and abundance in certain habitats. For instance in the coastal foredune environment unusual combinations of life history are apparent in the population structure and reproductive biology of the plant species, as the plant species live in a narrow maritime habitat (Martinez *et al.* 1992, Devall *et al.* 1989, Crawley 1997). An important factor in the life history of plants is the reproduction phase, a crucial and sensitive phase in the life cycle of plants, especially the period from seed to adult where mortality is high during the germination-seedling recruitment phase (Grubb 1977, Harper 1977, Cavers 1983). This interface between seed pool and seedling establishment is often referred to as an environmental sieve in which seed germination is the determinant process (Harper & White 1971).

Germination requirements of dune species

Germination ecology studies of dune species have shown that there are wide ranges of response to factors that affect germination (Seneca 1972, Van der Valk 1974, Pemasada & Lovell 1975, Schat 1983, Martinez *et al.* 1992, among others). Including, dormancy, moisture, temperature, light, and seed (Stebbins 1971, Pemasada & Lovell 1975, Fenner 1985, Priestly 1986, Bewley & Black 1994, Crawley 1997, Baskin & Baskin 1998). The requirements and tolerances of the seeds during this phase of the life cycle can have a strong effect on the natural distribution within the habitat and are therefore of interest in the process of drift-sand stabilisation. The dune plants *Arctotheca populifolia*, *Ipomoea pes-caprae*, *Myrica cordifolia* and *Scaevola plumieri* produce very different diaspores in the same habitat, which all probably have different requirements for germination and seedling establishment. The flowerheads of *A. populifolia* produce many achenes, each containing soft seeds, whereas each flower of *I. pes-caprae* produces a capsule that contains up to four hairy seeds protected by a very hard seed coat. The shrub *S. plumieri* produces drupes consisting of a big stone seed surrounded by a thick fleshy fruit layer, whereas *M. cordifolia* produces berries surrounded by a thick wax layer and containing a single hard seed.

Seed dormancy

Seeds from unpredictable environments are often subjected to seed dormancy. Seed dormancy prevents the seeds from germinating under conditions unfavourable for establishment, by reducing the metabolic activities in the seed (Fenner 1985, Baskin &

Baskin 1998). Harper (1977) recognises three types of dormancy depending on how the dormancy arises - innate, enforced and induced. A seed which is innately dormant is incapable of germination when freshly dispersed, even in conditions suitable for germination. This may be due to various factors, e.g. the embryo is immature at time of dispersal, a thick impermeable seed coat inhibits water and oxygen uptake, chemical compounds in the seed coat or embryo inhibit germination, or the seeds need special environmental conditions (e.g. fluctuating temperature, chilling period, photo period). Enforced dormancy occurs in general when seeds are deprived of their requirements for germination, for example, insufficient moisture, light, oxygen, or suitable temperature. No special physiological mechanism is involved. If newly dispersed seeds have no innate dormancy, but fail to meet suitable conditions, they acquire an induced (or secondary) dormancy (Fenner 1985, Baskin & Baskin 1998). The environmental factors known to influence the development of seed dormancy during maturation are nutrient deficiency (Baskin & Baskin 1998) and drought stress (Sawhney & Naylor 1982). Seeds of some of the South Africa dune species are known to be difficult to germinate (Muir 1937, Tinley 1985, Wrigley & Fagg 1988), and thus suspected of dormancy. When seeds are under dormancy, the dormancy needs to be broken to get the seeds to germinate: this can be done by scarification of the seed coat or seed stratification (Baskin & Baskin 1998).

To use seedlings in the process of dune stabilisation, the requirements of the germination and establishment are of great importance. Therefore, the general aim of the present study is to determine the germination requirements of seeds of *A. populifolia*, *I. pes-caprae*, *M. cordifolia* and *S. plumieri*, and to find out if the seeds that germinate in the field can emerge and survive over time. Since all four species produce numerous seeds, the expectation is that the seeds will germinate and that seedlings will survive under field conditions, but that survival will be low due to the heterogeneity of the habitat and the instability of the substrate. To test this hypothesis different germination, scarification and stratification experiments were carried out with the seeds of *A. populifolia*, *I. pes-caprae*, *M. cordifolia* and *S. plumieri* under controlled conditions, as well as observations on germination and seedling emergence and survival in the field.

4.2. MATERIAL AND METHODS

4.2.1. Seed collection and drying

The diaspores of the species *Arctotheca populifolia*, *Ipomoea pes-caprae*, *Myrica cordifolia*, and *Scaevola plumieri* which were used, were of different categories and were collected at different sites in 1998 and 1999:

Arctotheca populifolia: For *A. populifolia* whole flowerheads were collected at Port Alfred and put on trays in the sun. The sun dried the flowerheads, which opened and the released the soft sunflower-like diaspores (see Plate 4.1). After the diaspores were released, the diaspores were collected and were spread out in a single layer on trays and dried at room temperature (18-23°C) for approximately 7 days. After the drying period the diaspores were kept in paper bags at room temperature until used.

Ipomoea pes-caprae: The seed capsules of *I. pes-caprae* containing up to four seeds were collected at Fish River from the standing vegetation. Only the brown and dried capsules were selected which were ready to crack open and release the hairy seeds (Plate 4.1). The diaspores of *I. pes-caprae* have a hard seed coat that protects the embryo and prevents predation in mature seeds. Apart from fresh seeds, older seeds were collected from the soil seed bank, which had accumulated in a dune valley covered in *I. pes-caprae* plants. The older seeds of *I. pes-caprae* lost the hairs due to sand abrasion in the field, leaving the seed smooth and bare (Plate 4.1). Directly after collection the seeds were removed from the capsule and spread out in a single layer on trays and dried at room temperature (18-23°C) for approximately two weeks. The dry seeds were kept at room temperature in paper bags until used.

Myrica cordifolia: The diaspore of *M. cordifolia* are berries that consist of hard 'nut' that is surrounded by a fruit coat which is surrounded by a thick wax layer (Plate 4.1). The diaspores were collected at Old Woman's River from the stems where the diaspores form an aerial seed bank and were bird dispersed. After collection the diaspores were spread out on trays in a single layer and placed at room temperature (18-23°C) for approximately four weeks. After drying the diaspores were kept in paper bags at room temperature till further use.

Scaevola plumieri: For *S. plumieri* only the ripe black drupes were selected from the plants at Old Woman's River and Kleinemonde. The drupe contains a hard seed

(stone) which is surrounded by a thick fleshy fruit layer. To dry the drupes without getting fungi infections, the diaspores were put in a single layer on a tray containing absorbing paper and placed in a wooden drying cabinet at approximately 25°C for four weeks.

From here onward all the fruits and drupes and will be called seeds, even when not true seeds. For more detailed information on the species see chapter 2.

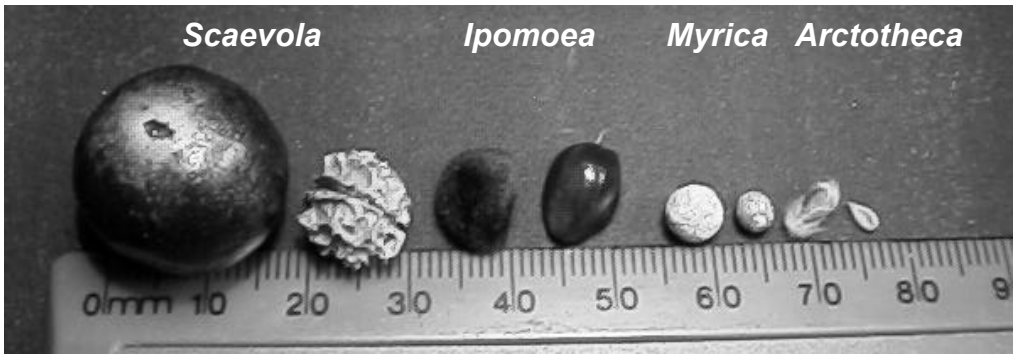


Plate 4.1. From left to right the two diaspores of each species: *Scaevola plumieri* (fresh and air-dried without fruit layer), *Ipomoea pes-caprae* (fresh air-dried and old seeds scarified in the field), *Myrica cordifolia* (with and without wax and fruit layer), and *Arctotheca populifolia* (with and without the seed coat).

4.2.2. Germination under controlled conditions

Disinfecting of seeds

The seeds of *A. populifolia*, *I. pes-caprae*, *M. cordifolia*, and *S. plumieri* used in the germination experiment were washed beforehand in a 70% bleach solution (JIK household bleach consisting 3.5% sodium hypochlorite) to prevent fungi infections, after which the seeds were rinsed vigorously five times with tap water (Hertling 1997). For the species *I. pes-caprae*, *M. cordifolia*, and *S. plumieri* different seed types were tested in the germination experiment besides the fresh air-dried seeds (see Plate 4.1). For the species *I. pes-caprae* and *S. plumieri* old and often sand scarified smooth seeds, were collected in the field by sieving the soil of dune hollows, whereas *M. cordifolia* seeds were set to germinate with and without the wax layer (1.5 mm) that surrounds the seed (see Plate 4.1).

Germination test controlled environment

For germination in the controlled environment cabinet (conviron) 50 seeds (30 for

S. plumieri) of the each of the four species five replicates were placed on filter paper saturated with distilled water in 9 cm plastic petri dishes. The seeds were set to germinate under a 25°C day and 15°C night temperature regime and a light regime of 16 hours light and 8 hours dark (Fenner 1985, Hertling 1997) for a period of 7 weeks (for *S. plumieri* 14 weeks). The petri dishes were randomised for position every 2-3 days when checked for moisture status and germination. The germinated seeds were counted and removed from the petri dish when the radicle was approximately 1 cm long. After termination of the germination test, the ungerminated seeds where tested for viability by either squeezing the seeds upon a hard surface or cutting the seeds in half to check the embryo. The soft and easy to squeeze seeds with brown embryos were considered dead, whereas the hard seeds with white embryos were considered viable (Baskin & Baskin 1998, Bekker *et al.* 1998a).
The germination tests were conducted in 1998 after seed collection and drying. The seed batches collected in 1998 were also used to grow seedlings for experiments during the present study (e.g. Chapter 7); thus the germination success of the seeds was also tested after different periods of dry-storage.

The greenhouse (polythene tunnel) is temperature controlled with a mean day temperature of 28.5°C and night temperature of 15.5°C without extra light sources. For the germination experiment the fresh air-dried seeds of the four species and old seeds of *I. pes-caprae* were placed 1 cm deep in trays filled with moistened beach sand and covered with perforated plastic sheets to prevent evaporation. The trays were checked every 2-3 days for moisture status and germinated seeds (appearance at soil surface), counted and removed.

For the seeds that germinated, the coefficient of the rate of germination was calculated per species (Scott *et al.* 1984):

$$\text{Coefficient Rate Germination CRG} = \frac{\Sigma (n_i)}{\Sigma (n_i * t_i)} X\ 100$$

with n_i the number of germinated seeds at time i, and t_i the number of germination days at time i. The coefficient of rate of germination (CRG) gives an indication of how uniformly the seeds have germinated.

4.2.3. Seed scarification

Any process of breaking, scratching, or mechanically altering the seed coat to make it permeable to water and gases is known as scarification (Baskin & Baskin 1998). The fresh air-dried seeds of *I. pes-caprae* and *S. plumieri* have a hard seed coat, especially the seeds of *S. plumieri* (Wrigley & Fagg 1988, Donnelly & Pammenter 1983, Lubke & De Moor 1998). To test if the dormancy was seed coat induced, experiments were carried out using boiling water or wet heat, and sulphuric acid or mechanical scarification. Other seeds need a temperature-related stratification period before germination can take place, therefore a cold stratification and heat stratification experiments have been conducted for the species *I. pes-caprae* and *S. plumieri*.

After each experiment the seeds were tested for viability by means of a germination test in the controlled environmental cabinet (conviron) under the conditions as mentioned in Chapter 4.2.2. One control was used for all the experiments because the tests were run simultaneously. After all the experiments the (dried) fruit coat surrounding the seed of *S. plumieri* was removed to prevent fungi infections during the germination test.

Wet-heat scarification

Boiling water was used to break the seed coat in the wet heat scarification (Baskin & Baskin 1998). Five replicates of 20 seeds each of *I. pes-caprae* and *S. plumieri* were submersed in distilled water and kept at boiling point for periods of 1, 5, 15, 30, 60 and 240 minutes. After the scarification the seeds were placed on filter paper saturated with distilled water in 9 cm plastic petri dishes in the conviron to germinate at a 25/15°C day/night temperature regime with a 16 hour day length (Fenner 1985, Hertling 1997). The petri dishes were randomised and checked every 2 to 3 days on germination and moisture. After 40 days (60 for *S. plumieri*) the germination experiment was terminated and the ungerminated seeds where tested on viability as before in the germination test.

Acid scarification

To make the seed coat thinner and permeable for water and gases, five replicates of 20 seeds each of *I. pes-caprae* and *S. plumieri* were soaked in 0.5 M sulphuric acid for periods of 5, 15, 30 minutes and 2, 8 and 24 hours (after Hardcastle 1978). After submersion the seeds were rinsed thoroughly with tap water to remove the sulphuric acid. The rinsed seeds were placed on moist filter paper in petri dishes and treated as mentioned for the wet-heat scarification experiment.

Mechanical scarification

To break the seed coat and to make it possible for the embryo to take up water, part of the seed coat was cut off for the species *I. pes-caprae* and *S. plumieri* so that the embryo was exposed (Baskin & Baskin 1998). For each species, five replicates of 20 seeds each were mechanically scarified in this way. Subsequently, the seeds were placed on moist filter paper and treated the same way as described for the wet heat stratification.

4.2.4. Seed stratification

Cold stratification

Seeds of the species *A. populifolia*, *M. cordifolia*, *I. pes-caprae* and *S. plumieri* were placed between moist filter papers in petri dishes in a dark fridge at 5ºC for a period of 6 weeks. For each species six replicates of 40 seeds each were used, except for *S. plumieri* where replicates of 25 seeds were used, the maximum number of seeds fitting in a 9 cm petri dish. After the stratification period the petri dishes with the seeds were moved to the conviron and set to germinate in the conviron by a 25/15°C day/night temperature regime with a 16 hour day length (Fenner 1985, Hertling 1997). The petri dishes were randomised and checked every 2 to 3 days on germination and moisture. After 40 days (60 for *S. plumieri*) the germination experiment was terminated and the ungerminated seeds where tested on viability as described for the germination test.

Heat stratification

In this experiment, conditions in the top layer of sand in the foredunes during summer were simulated in the laboratory. Five replicates of twenty seeds of *I. pes-caprae* and *S. plumieri* were placed 2 cm deep in crucibles filled with dry sterilised dune sand and placed in an electric oven at a regime of 8 hours at 45°C and 16 hours at 20°C for a period of two weeks. The crucibles were wrapped in thick aluminium foil and placed in random order on asbestos plates in the oven to ensure that only the top surface of the sand would be heated. The temperature of 45°C was chosen after observations made at the upper leeward side of a foredune in November 2000. Five replicates of twenty seeds per crucible of each species were placed at room temperature to serve as a control.

After the stratification period, the fruit layers were removed from the *S. plumieri* seeds and the crucibles were placed in the conviron to germinate under the same conditions

as described in the boiling-water scarification experiment. After termination of the experiment the viability of the seeds was tested as described previously in the germination test.

4.2.5. Seed germination, seedling emergence and survival in the field

To monitor seed germination and seedling survival in the field, a belt transects of 3 by 20 meter were set out at the front and at the back of the foredune for the species *I. pes-caprae* and *S. plumieri* (after Westelaken & Maun 1985, Todd 1994).
The species *A. populifolia* and *M. cordifolia* were excluded from the field trial because for *A. populifolia* the seedlings were too scattered to be able to produce transects with enough replication, whereas for *M. cordifolia* no seedlings were observed in the field.

Each transect was divided into plots of 1 m^2 and ten plots were randomly chosen and the seedlings present marked with colour tags and mapped. At intervals of 1 to 2 months, the seedlings were monitored and newly-emerged seedlings in the ten plots were marked and colour tagged. From the other plots of the transect 15 newly-emerged seedlings (only cotyledons present) were exhumed and the length of the hypocotyls measured to determine the emergence depth of the seedlings.
After 166 days of observation only the seedlings of *S. plumieri* at the back of the dune survived. An extra ten $1m^2$ plots were randomly chosen in the 3 by 20 meter transect, and the seedlings mapped, colour tagged and followed at 1 to 2 monthly intervals.

4.2.6. Climate

The climatic data was obtained from the South African Weather Services form the stations Fish point and Port Alfred situated nearest to the study site. The weekly rainfall and weekly minimum and maximum temperatures were used. The climate data from Port Alfred was used to fill in the missing data from February 1998 to December 1998 of Fish point.

4.2.7. Data analysis

The independent variables were tested for normality and homogeneity of the variance by using the Kolmogosov-Smirnov and Levene's test, respectively. When these assumptions failed, non-parametric procedures were carried out. The data of the germination experiment and scarification-germination test were analysed with a one-

way analysis-of-variance (ANOVA) for the numbers of germinated, viable and dead seeds per species and within the species per treatment, as well as the rate of germination within and between species. The contrasts within and between the species were obtained by a Tukey comparison-of-means test (Zar 1996).

The data of the scarification-germination experiments did not show a normal distribution, and therefore a Kruskal-Wallis ANOVA was used followed by Newman-Keuls test to compare the means of germination of different aged seeds and of the total viable seeds (germinated + ungerminated seeds) per species per experiment (Zar 1996). To test the relation between the number of seedlings in the field with time a regression analysis was used. For the germinated seeds of the experiment a coefficient of rate of germination (CRG) was calculated.

For all data analyses, the standard error (± S.E.) and the number of replicates (*n*) is given and the differences between the analysed data was pointed out by different letters (abc, pqr, xyz) behind the values in tables or above the columns or data points in graphs. For each analysis the level of significance was specified using the following system: * = $P<0.05$, ** = $P<0.01$, and *** = $P<0.001$. The ** are placed next to the highest value of the analysed parameter. All statistical tests were performed at a 95% confidence interval using the statistical program Statistica 5.5. (Statsoft Inc.). For details of the ANOVA analysis see Appendix III.

4.3. RESULTS

4.3.1. Seed germination under controlled conditions

For the different species seeds were germinated under controlled conditions in the conviron and the greenhouse.

Conviron germination

Of all the species and seed types only the seeds of *I. pes-caprae* showed significant differences in germination, with a significant higher germination for the old seeds (scarified in the field) compared to the fresh air-dried seeds (ANOVA, $P<0.001$; Figure 4.1). Only a few *I. pes-caprae* seeds of the fresh air-dried type germinated, but 87% of the ungerminated were viable (Figure 4.1). The seeds of the species *A. populifolia* and *M. cordifolia* showed overall mean percentages of 53 ± 6.5% and 34 ± 5.6%, respectively (Figure 4.1). No differences in percentage of germinated seeds were observed for either of the species between the different seed types (P>0.05; Figure 4.1). For *S. plumieri* not one seed germinated, but all seeds were considered viable (Figure 4.1).

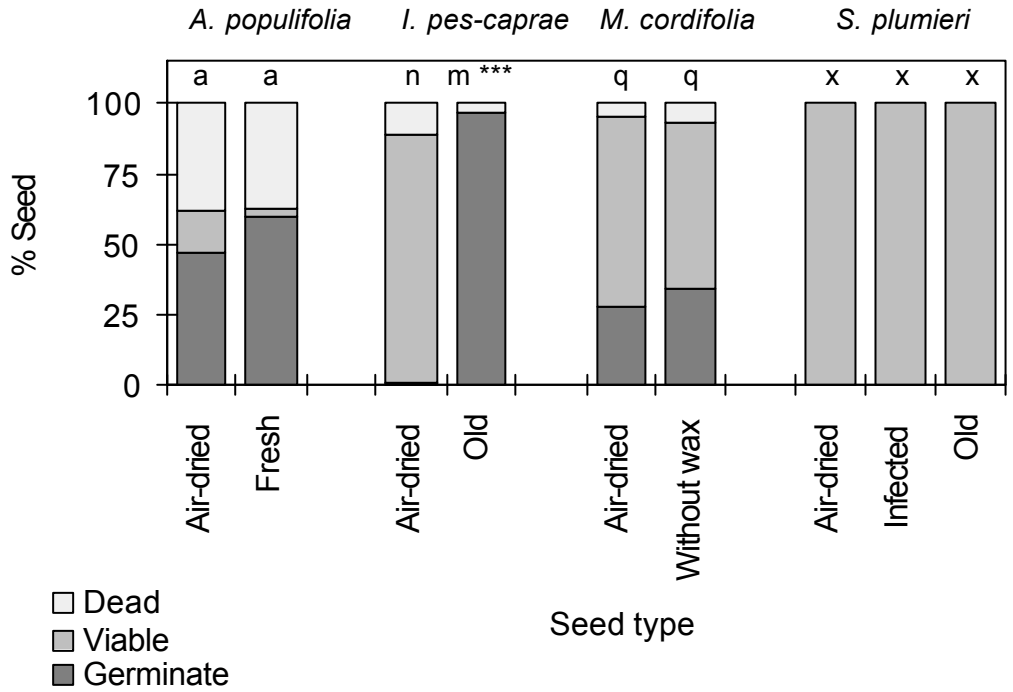


Figure 4.1. The germination response different seeds types of *A. populifolia*, *I. pes-caprae, M. cordifolia* and *S. plumieri*, with the mean percentage of germinated, ungerminated viable and ungerminated dead seeds (n = 5). Any column within a

species with the same letter does not differ significantly in the number of germinated seeds. Contrast obtained by Tukey after analysis by ANOVA. Level of significance: *** $P<0.001$. Seed types: Air-dried - Air-dried fresh seeds; Fresh - Fresh seeds and not air-dried; Old - Older seeds (> 1 year) collected from the seed bank and scarified in the field; Without wax - Fresh air-dried seeds with the outer wax layer removed; Infected - Fresh air-dried seeds infected by fruit fly.

The coefficient of rate of germination (CRG) indicates that the seeds of *A. populifolia* showed the most uniform germination compared to *I. pes-caprae* (ANOVA, $P<0.001$; Table 4.1). For *I. pes-caprae* almost 97% of the seeds germinated, but the rate of germination was very low due to the spread in germination over the 130 days. Within the three species no significant differences in germination rate was observed between the different seed types ($P>0.05$, Table 4.1).

Table 4.1. The mean (± S.E.) coefficient of the rate of germination (CRG) of *A. populifolia*, *I. pes-caprae*, *M. cordifolia* and *S. plumieri* given by seed type, with the total mean CRG per species. Any two values with the same letter does not differ significantly for the CRG per seed type ^{abc} or per species ^{xyz}. Contrasts obtained by Tukey after analysis by ANOVA. Level of significance: *** - $P<0.001$.

Seed type	*n*	*A. populifolia*	*I. pes-caprae*	*M. cordifolia*	*S. plumieri*
		Mean (± S.E.)	Mean (± S.E.)	Mean (± S.E.)	Mean (± S.E.)
Air-dried	6	5.52 (0.825) a	0.41 (0.279) a	2.31 (0.156) a	0.00
Fresh seeds	3	5.82 (0.306) a	-	-	
Old seeds	6	-	2.42 (1.091) a	-	0.00
Without wax	6	-	-	2.25 (0.140) a	
Infected	6				0.00
Total mean	>9	5.62 (0.66) x ***	1.42 (0.87) y	2.28 (0.14) xy	

After different dry storage periods all species germinated, with exception of *S. plumieri* (Table 4.2). The seeds of *A. populifolia* and *M. cordifolia* showed a significantly higher germination percentage after dry storage of respectively 1.5 and 3 to 4 years (Kruskal-Wallis, $P<0.001$; Table 4.2). For *M. cordifolia* the air-dried seeds showed a significant decline in the number of viable seeds ($P<0.001$; Table 4.2). This was mainly due to the fact that a high percentage of the nonviable seeds were empty, without a viable embryo. The same had been observed for the seeds from *A. populifolia* in the first year, which accounts for the significantly higher percentage of nonviable seeds in year 1 (Table 4.2). The seeds of *I. pes-caprae* showed the highest germination percentage, but no significant differences were observed between the seeds of different age for each seed

type (*P*>0.05; Table 4.2). The seeds of *I. pes-caprae* showed a low, but significant decline in viability of 2 to 5 % after 3 to 4 years in dry storage, but the fact that the total number of viable seed was only declining slightly, points to the fact that the seeds might be long-lived. No seed germinated for *S. plumieri*, but the number of viable seeds declined significantly after 3 years in storage at a rate of 4 ± 1.0% (*P*<0.01; Table 4.2).

Table 4.2. Germination response of air-dried seeds of *A. populifolia*, *M. cordifolia*, *S. plumieri* and old seeds of *I. pes-caprae* after different dry storage periods (age). Any seed status within a species with the same letter does not differ significantly. Contrasts obtained by Newman-Keuls after analysis by Kruskal-Wallis. after arcsine transformation. Level of significance: ** - *P*<0.01.

Species	Age (years)	*n*	Seed status (%)					
			Germinated		Ungerminated Viable		Ungerminated Dead	
			Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
A. populifolia	<1	6	60.0	(1.16) b	2.9	(1.17) b	37.1	(2.33) a ***
	1.5	10	73.0	(2.83) a ***	17.5	(2.24) a ***	9.5	(1.48) b
I. pes-caprae	>1	6	96.2	(1.78) a ns	0.0	(0.00) b	3.8	(1.37) a ***
	>3	9	95.0	(1.10) a	5.0	(1.10) a ***	0.0	(0.00) b
	>4	7	96.1	(0.91) a	2.0	(0.89) a	1.7	(0.55) a
M. cordifolia	<1	6	27.6	(2.92) b	67.6	(3.88) a ***	4.8	(2.29) b
	3	10	50.7	(4.71) a ***	3.8	(1.13) b	45.5	(4.49) a ***
S. plumieri	<1	6	0.0		100.0	(0.00) a ***	0.0	(0.00) b
	2	10	0.0		97.5	(0.79) ab	2.5	(0.79) ab
	3	6	0.0		97.1	(0.95) b	4.0	(1.02) a

Greenhouse germination

All the species germinated under greenhouse conditions, although for the species *S. plumieri* and *I. pes-caprae* needed a longer germination period of 147 days (Figure 4.2). The seeds of *A. populifolia*, *M. cordifolia*, and *S. plumieri* germinated well (>70%), only the fresh air-dried seeds of *I. pes-caprae* showed a very low performance (Figure 4.2). The seeds of *M. cordifolia* and *A. populifolia* germinated within 25 days and showed the most uniform germination with rates of respectively 10.8 and 12.2 (Figure 4.2). The old seeds of *I. pes-caprae* and fresh air-dried seeds of *S. plumieri* also showed high germination percentages, but much more spread over time, and therefore showed much lower CRG's of 2.43 and 1.09, respectively (Figure 4.2). Most of the

ungerminated seeds were viable, with 10% dead or empty seeds for *M. cordifolia* and *A. populifolia*, 5% for *I. pes-caprae* (air-dried and old) and 4% for *S. plumieri*.

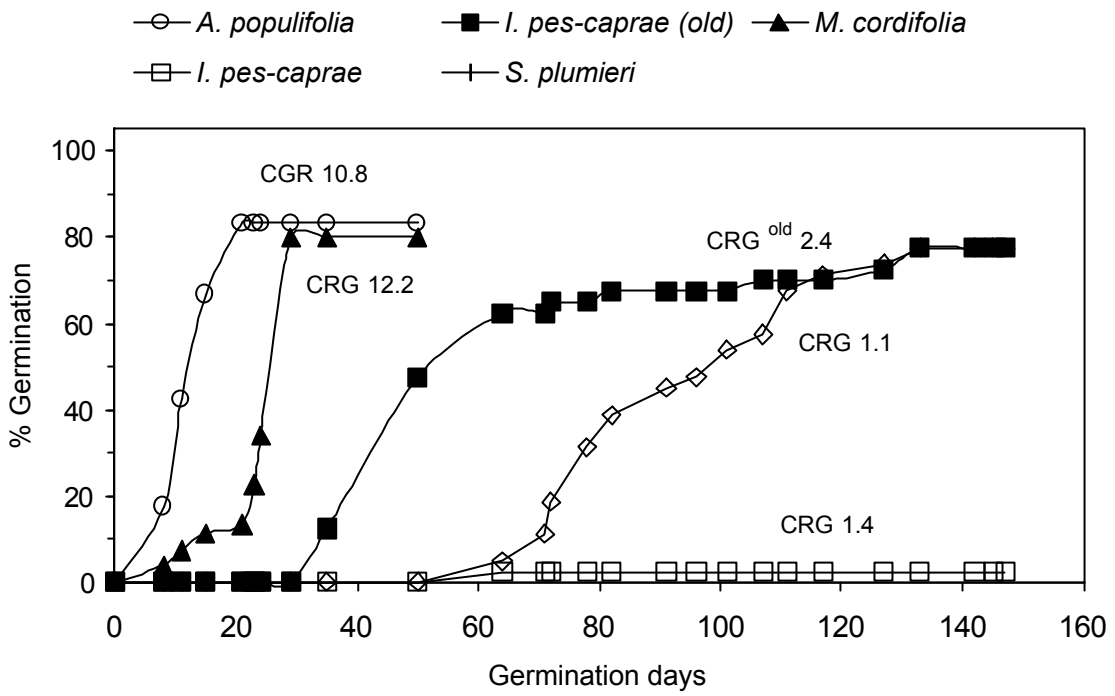


Figure 4.2. Greenhouse germination and rate of germination (CRG) of fresh air-dried seeds of *A. populifolia*, *I. pes-caprae*, *M. cordifolia* (without wax layer) and *S. plumieri*, as well as the old seeds of *I. pes-caprae*.

4.3.2. Scarification

Wet-heat scarification

Only *I. pes-caprae* seeds showed germination after the boiling water scarification, but the germination was not significantly higher compared to the control (Kruskal-Wallis, $P>0.05$; Figure 4.3A). Most of the non-germinated seeds of *I. pes-caprae* were viable for the control and the treatment of 1 minute, but after 60 minutes or more in boiling water the total number of viable seeds declined significantly ($P<0.001$; Figure 4.3A). The decline in viability was due to the fact that the seeds that stayed in the boiling water for more than 15 minutes cracked open completely and became fungus infected during the germination period after the scarification. Apparently, seeds of *I. pes-caprae* could not survive more than 30 minutes in boiling water.

None of the seeds of *S. plumieri* germinated within the germination period of 62 days (Figure 4.3B). Most of the remaining seeds were viable but for some seeds the two halves of the seeds started to separate during the viability test after scarification,

exposing the embryo, which started to decompose within a week. In most cases these were seeds from the 30 and 240 minute treatment, which showed a significant lower number of viable seeds compared to the control (*P*<0.001; Figure 4.3B). Within the treatments only the 1 minute treatment showed a significant higher number of viable seeds when compared to the 30 and 240 minute treatment (*P*<0.001; Figure 4.3B).

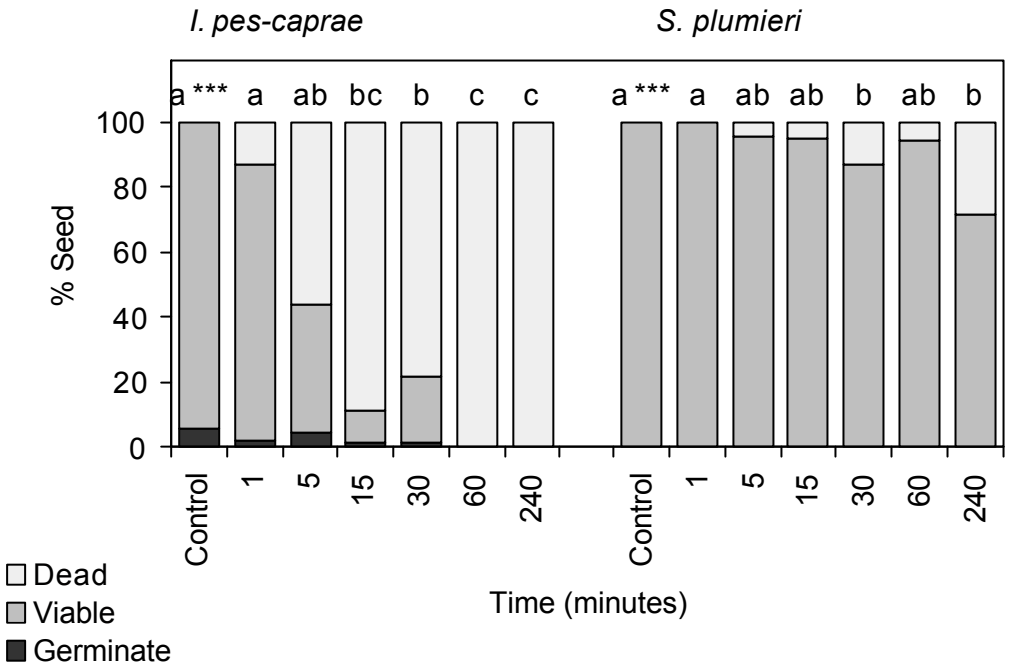


Figure 4.3. Mean percentage of germinated and ungerminated (viable and dead) seeds after boiling water scarification for fresh air-dried seeds of *I. pes-caprae* and *S. plumieri* (*n* = 5). Any column within the species with the same letter does not differ significantly in the total number of viable seeds (germination + ungerminated). Contrast obtained by Newman-Keuls after analysis by Kruskal-Wallis. Level of significance: *** - *P*<0.001.

Acid scarification

Of all 600 *I. pes-caprae* seeds immersed, only eight germinated; four seeds from the 15 minute treatment, three from the 480 minute treatment and one from the 1440 minute treatment (Figure 4.4). There were no significant differences within the treatments or between the treatments and the control for the number of germinated seeds (Kruskal-Wallis, *P*>0.05; Figure 4.4). For the total number of viable seeds (germination + ungerminated) also no significant differences were observed (*P*>0.05; Figure 4.4). Of the ungerminated seeds, none seemed to have imbibed, but 96 ± 2.4 % were

considered viable. The remaining seeds were dead, mainly due to fungi infections. When cut open the seeds When the ungerminated seeds were cut open to check the viability, the seeds were empty (see Figure 4.4). None of the seeds of *S. plumieri* germinated within the 60 days of the germination period. Of the remaining seeds 91 ± 21% were considered viable, except for the seeds of the 1440 minute treatment, which showed a significant lower number of seeds that survived the acid scarification (Kruskal-Wallis, $P<0.001$; Figure 4.4).

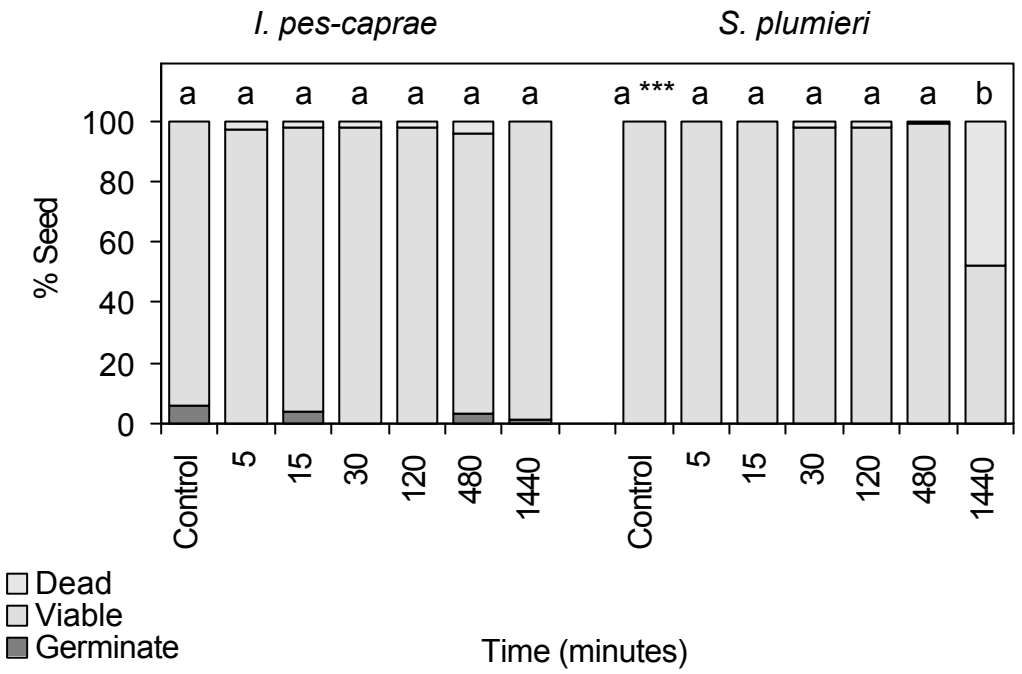


Figure 4.4. Mean percentage of germinated and ungerminated (viable and dead) seeds after sulphuric acid scarification for fresh air-dried seeds of *I. pes-caprae* and *S. plumieri* (n = 5). Any column within a species with same letter does not differ significantly for the total number of viable seeds (germination + ungerminated). Contrast obtained by Newman-Keuls test after analysis by Kruskal-Wallis. Level of significance: *** - $P<0.001$.

Mechanical scarification

The seeds of *S. plumieri* all were dead within 40 days after mechanical scarification due to fungi infection after the embryo was exposed by means of apical cutting. Only the scarified seeds of *I. pes-caprae* germinated (Figure 4.5). After mechanical scarification 90 ± 3.5% of air-dried *I. pes-caprae* seeds germinated within six days (Figure 4.5). Compared to the control the germination percentage after the scarification treatment was highly significant (ANOVA, $P<0.001$; Figure 4.5). The remaining seeds were mostly

viable, but 3.0 ± 1.3% of the seeds were soft and fungi infected and therefore considered dead. Due to the fast and uniform germination of the scarified seeds the coefficient germination rate was significantly higher with a value of 21.3 compared to control value of 0.9 (P<0.001; see Figure 4.5).

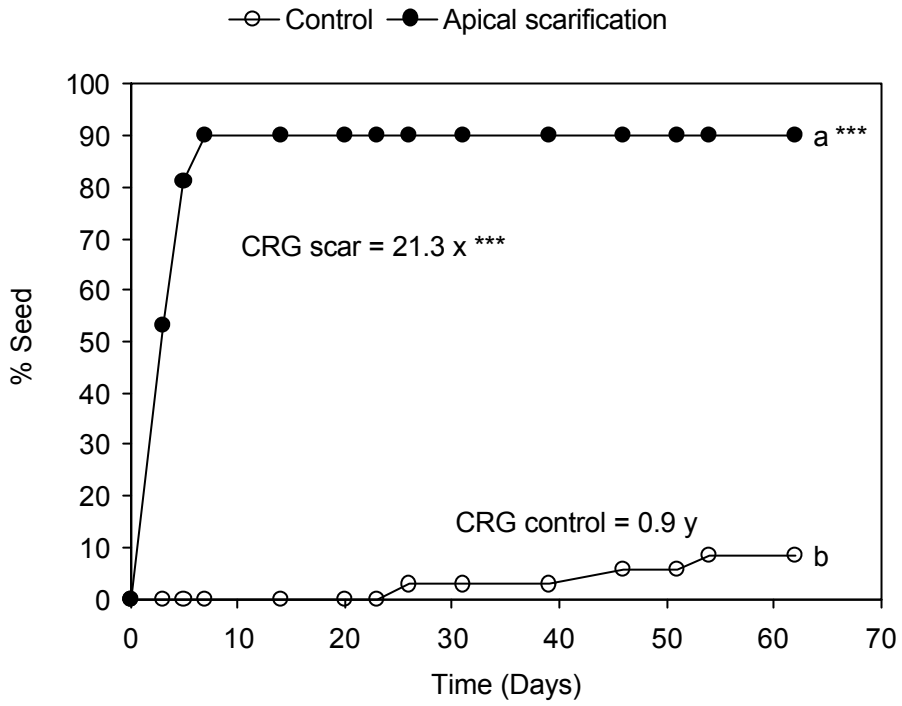


Figure 4.5. Mean germination percentage and germination rate (CRG) of mechanical scarified fresh air-dried seeds of *I. pes-caprae* and non-scarified (control) seeds (n = 5). Contrasts obtained by Tukey after analysis by ANOVA. Level of significance: *** - P<0.001.

4.3.3. Stratification

After cold stratification the seeds of *A. populifolia*, *I. pes-caprae* and *M. cordifolia* showed a higher germination percentage, but due to high variability between the replicates, the difference was not significant (ANOVA, P>0.05; Figure 4.6). A trend was observed for the total number of viable seeds (germinated + ungerminated), but again no significant differences between the control and the cold stratification treatments (P>0.05; Figure 4.6). After heat stratification only the seeds of *S. plumieri* showed a significant increase in germination percentage compared to the control (P<0.001; Figure 4.6). Most of the ungerminated seeds of all the treatments were viable, except for *A. populifolia* where most of the ungerminated seeds were dead (Figure 4.6).

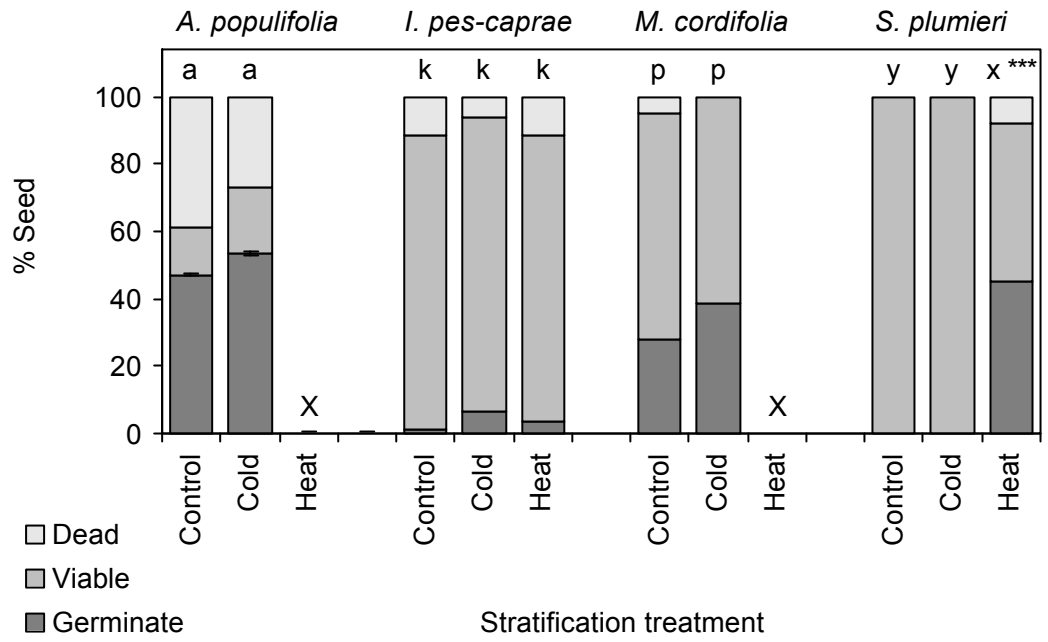


Figure 4.6. Mean percentage of germinated and ungerminated (viable or dead) seeds after cold or heat stratification for *A. populifolia*, *I. pes-caprae*, *M. cordifolia*, and *S. plumieri*. Any column within a species with the same letter does not differ significantly for the total number germinated seeds. Contrasts obtained by Tukey after analysis by ANOVA. Level of significance: *** - $P<0.001$.

The highest overall germination rate was found for cold stratified seeds of *A. populifolia* (Kruskal-Wallis, P<0.001; Table 4.3). Within the species *A. populifolia* the seeds from the cold treatment showed a significantly faster and more uniform mean germination rate (9.5) compared to the control (5.5; $P<0.001$; Table 4.3A). Thus, the period of cold stratification resulted in a more uniform germination, even though the total number of seeds germinated was not significantly different between the treatment and the control (see also Figure 4.6). For *M. cordifolia* the cold-stratified seeds also gave a significantly higher germination rate compared to the control (4.8 and 2.3 respectively; $P<0.001$; Table 4.3A). No significant differences in germination rate were observed for *I. pes-caprae* because only a few seeds germinated per treatment (Table 4.3A and see Figure 4.6). For *S. plumieri* no seeds germinated for the control and cold treatment, but after heat stratification the rate of germination increased significantly ($P<0.001$; Table 4.3A). Between the species, *A. populifolia* showed the most uniform germination for the control and the cold treatment ($P<0.01$; Table 4.3B). The order of germination rate was, from high to low, *A. populifolia, M. cordifolia, I. pes-caprae, S. plumieri* (Table 4.3B). For the

heat stratification no significant difference between germination rates were observed between *I. pes-caprae* and *S. plumieri* (*P*>0.05; Table 4.3), even though the germination percentage of *S. plumieri* was much higher (see Figure 4.6). In general cold or heat stratification was did not enhanced the number of seeds that germinated (except *S. plumieri*), but did shorten the lag phase before germination and resulted for some species in a more uniform germination pattern.

Table 4.3. Coefficient germination rate (CRG) within (A) and between (B) fresh air-dried seeds of *A. populifolia*, *I. pes-caprae*, and *M. cordifolia* after cold stratification or heat stratification. Any value within a species with the same letter does not differ significantly in the rate of germination. Contrasts obtained by Newman-Keuls after analysis by Kruskal-Wallis. Level of significance: *** - *P*<0.001.

A)

Treatment	*n*	CRG within species			
		A. populifolia	*I. pes-caprae*	*M. cordifolia*	*S. plumieri*
		Mean (± S.E.)	Mean (± S.E.)	Mean (± S.E.)	Mean (± S.E.)
Control	6	5.52 (0.82) b	0.41 (0.28) a	2.31 (0.16) b	0.00 (0.00) b
Cold	6	9.52 (0.96) a ***	0.77 (0.16) a	4.75 (0.43) a ***	0.00 (0.00) b
Heat	5		0.65 (0.39) a		0.89 (0.04) a ***

B)

Species	CRG between species								
	Control			Cold			Heat		
	n	Mean	(± S.E.)	*n*	Mean	(± S.E.)	*n*	Mean	(± S.E.)
A. populifolia	6	5.52	(0.82) a ***	6	9.52	(0.96) a ***			
I. pes-caprae	6	0.41	(0.28) bc	6	0.77	(0.16) c	5	0.65	(0.39) a
M. cordifolia	6	2.31	(0.16) ab	6	4.75	(0.43) b			
S. plumieri	6	0.00	(0.00) c	6	0.00	(0.00) d	5	0.89	(0.04) a

4.3.4. Germination and survival under field conditions

The seedlings of *I. pes-caprae* and *Scaevola plumieri* emerged on the seaward and landward sides of the foredune in almost a monostand. When seedlings were exhumed (*n* = 15) the seedlings of *I. pes-caprae* and *S. plumieri* emerged from approximately the same depth. The mean emergence depth of *I. pes-caprae* was 6.8 ± 2.4 cm, whereas the seedlings from *S. plumieri* emerged from a mean depth of 5.4 ± 1.6 cm. The number of seedlings found per plot was highly variable with 0 to 21 seedling per plot for *S. plumieri* and 0 to 177 for *I. pes-caprae*. The high variability in number of seedlings per plot found for *I. pes-caprae* (see Table 4.4) was due to the fact that on the seaward

transect most seedlings emerged in dense clusters. The seedlings of the seaward transect of *I. pes-caprae* were approximately the same height and only the cotyledons were present, suggesting the seedlings were approximately of the same age and probably all germinated and emerged around the same time. After day 36 no new emergence was recorded for *I. pes-caprae* (Table 4.4). For *S. plumieri* the seedlings at the start of the observation were of different age with differences in size and number of leaves. For *S. plumieri* the seedling emergence was more continuous, and up to day 110 seedlings emerged in both transects (Table 4.4).

For both species the number of seedlings declined gradually over time, with the exception of the seaward transect of *I. pes-caprae* where the seedlings died within a period of 20 days (Table 4.4). On day 36 all seedlings were dead, probably due to a combination of sand abrasion and heat stress because the leaves all looked sand blasted, dry and brown on day 36. After 166 days of observation only the seedlings of *S. plumieri* survived at the back of the foredune. Due to a few big storms the *S. plumieri* seedlings at the front and back of the foredunes were buried by sand or washed away by the sea. These factors were probably the two major factors responsible for the death for *S. plumieri* seedlings.

Table 4.4. The mean number of seedlings that emergence and survived per plot (n = 10) of *I. pes-caprae* and *S. plumieri* situated on the seaward or landward side of foredunes at Old Woman's River, presented by number of days of observation.

Species	Transect position	Days	Present	New	Gone
			Mean (± S.E.)	Mean (± S.E.)	Mean (± S.E.)
I. pes-caprae	Seaward	0	33.3 (16.7)	0.0	0.0
		16	33.3 (16.7)	0.0	0.0
		36	0.0	0.0	33.3 (16.7)
		67	0.0	0.0	0.0
		110	0.0	0.0	0.0
		166	0.0	0.0	0.0
I. pes-caprae	Landward	0	4.0 (1.33)	0.0	0.0
		16			
		36	4.0 (1.33)	4.9 (1.70)	0.9 (0.50)
		67	8.0 (1.60)	0.0	6.0 (1.10)
		110	2.0 (0.77)	0.0	2.0 (0.77)
		166	0.0	0.0	0.0

Table 4.4 continued.

Species	Transect position	Days	Present		New		Gone	
			Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
S. plumieri	Seaward	0	2.6	(0.56)	0.0		0.0	
		16	3.1	(0.78)	0.5	(0.40)	0.0	
		36	3.6	(1.11)	0.1	(0.10)	0.3	(0.21)
		67	3.4	(0.95)	0.2	(0.20)	0.3	(0.15)
		110	2.6	(0.65)	0.2	(0.20)	0.4	(0.16)
		166	0.0		0.0		2.6	(0.65)
S. plumieri	Landward	0	5.3	(2.39)	0.0		0.0	
		16	5.5	(2.40)	0.2	(0.13)	0.0	
		36	5.7	(2.41)	0.4	(0.22)	1.7	(1.07)
		67	4.6	(1.95)	0.8	(0.51)	1.2	(0.85)
		110	4.4	(1.84)	0.1	(0.10)	0.3	(0.21)
		166	2.7	(1.22)	0.0		1.7	(0.72)

The *S. plumieri* seedlings that survived at the back of the foredune (landward face) were continued to be observed after the 166-day period. With an extra ten plots, each of 1 m^2. In total 20 m^2 were observed for another 760 days (Figure 4.7). After day 121 in 1999 the number of seedlings started to decline, with some new emergence on day 154 in 2000, after which the mean number of seedling declined even further, until a mean of 1 seedling per plot was left (Figure 4.7A). But due a high standard error no significant differences were observed between the number of seedlings per m^2 over time (Kruskal-Wallis, $P>0.05$; Figure 4.7). The significant decline in seedling numbers over time was mainly due to the death of younger seedlings because of the high tides and the subsequent seawater inundation ($R^2 = 0.17$) (Regression, $P<0.001$; Figure 4.7).

Other reasons for seedling death were sand burial and root predation.

During the period November 1999 to February 2000 most of the seedlings were buried, exposed and buried again (open symbols in Figure 4.7A), but after February all seedlings were exposed again.

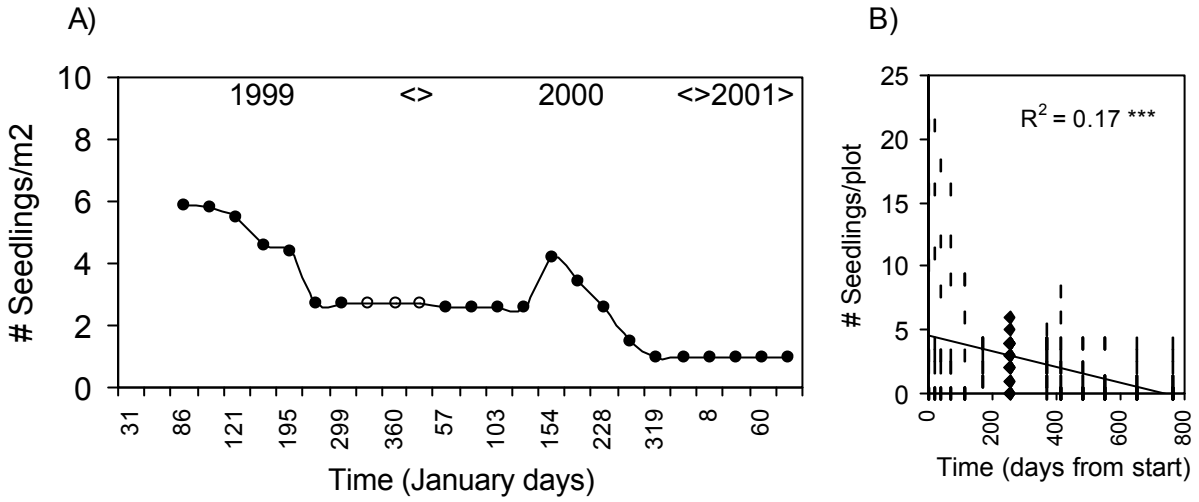


Figure 4.7. The number of seedlings that survived per plot (*n* = 20) of *S. plumieri* situated at the base of a landward faced foredune for in the period January 1999 to April 2001(A), with the relationship between the number of seedlings per plot over time (B). Regression analysis with level of significant of *P*<0.001(***). The open symbols in figure A represent a period of strong sand movement and seedling burial.

4.3.5. Climatic data

The temperature showed a seasonal pattern with the lowest temperatures measured in winter (June-July). The rainfall fluctuated, but some distinct peaks could be observed in autumn (March) and spring (October-November) (Figure 4.8).

For both species the seedlings emerged after a period of higher rainfall in March 1999 (Figure 4.8). The seedlings of *I. pes-caprae* did not survive for long, and no new seedling emerged after August 1999. For *S. plumieri* the mean number of seedlings was also declining, but maintained a level of approximately one seedling per plot, with a slight increase in after a high rainfall period in March 2000 (Figure 4.8). The seedlings were buried over the period November 1999 to February and this is represented with open symbols in figure 4.8.

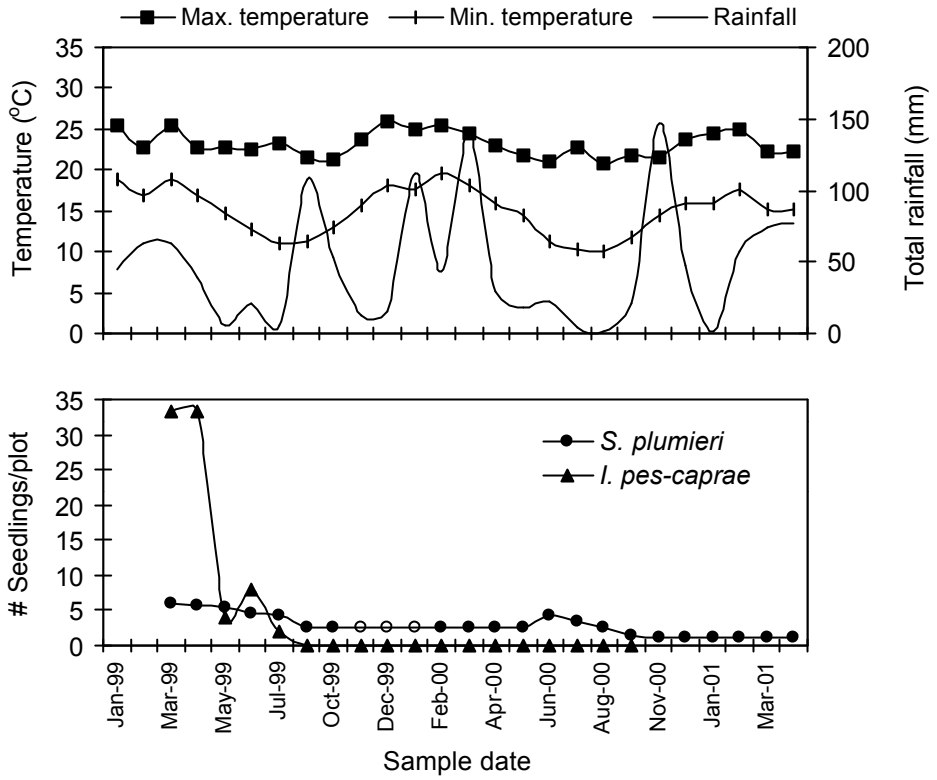


Figure 4.8. Mean maximum and minimum temperature, and rainfall combined with the mean number of seedling per plot for *I. pes-caprae* and *S. plumieri* over time (*n* = 20).

4.4. DISCUSSION

Reproduction is a crucial and sensitive phase in the life cycle of plants, especially the period from seed to adult where mortality is high during the germination-seedling recruitment phase (Grubb 1977, Harper 1977, Cavers 1983). In the coastal environment most of the dune pioneer plant species produce seeds, which germinate in the field. But only a few seedlings establish, and even fewer mature to adult plants. For some species no seedlings were observed in the field for species that produced many seeds. The requirements of seeds during germination, and the tolerances of seedlings during emergence and establishment have a strong influence on plant distribution of the coastal dunes, and consequently on the process of dune building and drift sand stabilisation (Barbour 1992, Crawley 1997). The aim of the present study was to determine the germination requirements of several sand-binding foredune species and to find out if the seeds that germinate in the field can emerge and establish seedlings that survive over time. Given the fact that all the foredune pioneers used in the present study produced masses of seeds, the expectation was that seeds would germinate well under controlled conditions as well as in the field. However, the expectation was that establishment and survival in the field would be low due to the heterogeneity of the habitat and the instability of the substrate. This hypothesis was proven to be true because all species germinated under controlled conditions during the present study with an increase in rate of germination due to scarification/stratification for some of the species. Only the seedlings of *A. populifolia* (observation) and *S. plumieri* survived in the field. Seedlings of *I. pes-caprae* emerged and established in the field but none survived for longer than a few weeks, whereas for *M. cordifolia* no seedlings were observed in the field.

The germination and scarification/stratification results are discussed per species in the following paragraphs.

Arctotheca populifolia

The soft seeds of *A. populifolia* showed an intermediate germination success in the conviron, but when placed in soil in the greenhouse the germination percentage enhance by 30% and the germination rate by 5.2. The high germination rate suggests that the seeds of *A. populifolia* showed a uniform germination pattern within a relative short period. This indicated that the seeds were not subjected to dormancy. This is supported by the fact that Heyligers (1983) found no innate dormancy for *A. populifolia*,

as the seeds readily germinated with a high success rate. The seeds of *A. populifolia* were usually buried close to the parent plant because the seed-bearing flower bend down and got buried by wind blown sand (Tinley 1985). Desert plants also show this 'active' seed burial or geocarpy which according to Van der Pijl (1972) was to protect seeds against predators as well as a system to keep the plants in the right spot in a inhospitable environment. In other words the site where the parent grow was considered a safe site, and if the parent can survive there, the seedlings also would have a better chance to survive.

To germinate as soon as possible was probably the best solution to prevent seed predation and deep burial, and is often observed in unstable habitats (Fenner 1985). The soft seeds of *A. populifolia* were probably not capable of forming a persistent seed bank, although after one year in dry storage the germination success was still high. After cold stratification the mean germination percentage was not enhanced, but the seeds were germinating with a much higher rate after cold stratification. Seeds in dry storage in general showed a longer lag phase to germination according to Harrington (1973). This because dry seeds require more water, thus a longer time to imbibe compared to seeds from the cold-stratification treatment which were kept moist during the stratification.

In general *A. populifolia* reproduced throughout the year (Tinley 1985), and thus seedlings could be found all year round. After rainfall periods, especially many seeds would germinate, often clustered in groups scattered over the strandline and foredune zone in the vicinity of the parent plant, resulting in even-aged cohorts due to the simultaneous germination of seeds (Plate 4.2). This could explain the fact that the plants of *A. populifolia* usually grow for about two years after which the plants would die back en mass as observed by Tinley (1985). Due to the fact that the clumps of *A. populifolia* seedlings were very scattered over the beach and foredunes, it was difficult to find *A. populifolia* seedling transect with enough replication.

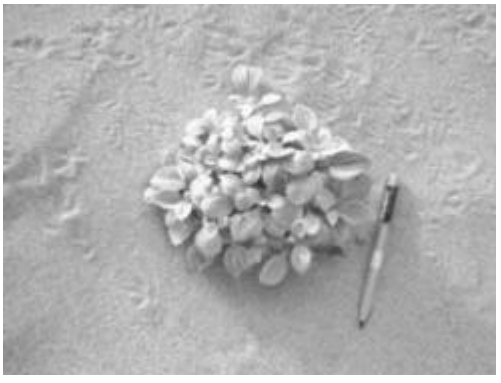


Plate 4.2. A stand of even-aged *A. populifolia* seedlings emerging from the soil where as single flowerhead was buried.

Ipomoea pes-caprae

The germination rate of older *I. pes-caprae* under controlled conditions was much lower compare to *A. populifolia* due to a high spread in germination, even though the older scarified seeds of *I. pes-caprae* showed a higher germination percentage. The seeds of *I. pes-caprae* have a hard seed coat and probably would be able to survive in the soil seed bank and therefore did not need to germinate in a 'rush' as do the *A. populifolia* seeds. This was supported by the fact that seeds of at least four years old were not declining in viability, and showed a mean germination success of over 95%.

However, fresh air-dried seeds of *I. pes-caprae* showed hardly any germination in the conviron or greenhouse. Several authors (Gomes *et al.* 1978, Devall *et al.* 1989, Martinez *et al.* 1992) also noted a low germination for fresh air-dried seeds of coastal and non-coastal *Ipomoea* taxa. The hard seed coat seemed impermeable to water and gases, resulting in innate dormancy, preventing the seeds from germinating until the seed coat was altered physically (Fenner 1985, Bewley & Black 1994, Baskin & Baskin 1998).

The older *I. pes-caprae* seeds from the soil seed bank had lost their hairs due to natural mechanical scarification by sand abrasion in the field, making the seed coat thinner and permeable for water and/or gases (Keddy & Constable 1986, Priestly 1986, Shipley & Parent 1991). When the fresh air-dried seeds of *I. pes-caprae* were mechanically scarified, the germination improved with 88%, which proved the fact that the dormancy was seed coat induced. Several other authors obtained similar results in that mechanical scarification of the seed coat of *Ipomoea* broke dormancy and increased germination in air-dried fresh seeds (e.g. Hardcastle 1978; needle pricking, Devall *et al.* 1989; sand paper). During the wet heat scarification the seed coat of *I. pes-caprae* cracked open to make it permeable for water and gases, but the embryos did not survive this treatment. It is possible that the temperature of the water was too high for the *I. pes-caprae* seeds. Teketay (1997) and Thapliyal *et al.* (1998) found that *Acacia* seeds soaked in water of 80ºC for 600 seconds resulted in high germination percentages, whereas when soaked in water of 100ºC for more than 90 seconds the germination would decline strongly, indicating that embryos might have been damaged. The acid scarification gave no increase in germination, but the remaining seeds were viable. Maybe the sulfuric acid concentration was not strong enough as Gomes *et al.* (1978) and Misra (1963) found high germination percentages for *Ipomoea* sp. after scarification with concentrated sulphuric acid. The cold stratification and heat

stratification showed the same effect as the acid scarification in that no increase in germination was observed, and that most seed were viable after stratification. Of the scarification and stratification experiments, the mechanical scarification of the seed yielded the best results for *I. pes-caprae.*

In March the seedlings of *I. pes-caprae* started to emerge almost simultaneously within a 2-week period mainly form older, scarified seeds from the seed bank (Plate 4.3).

Plate 4.3. A dense patch of even-aged seedlings of *I. pes-caprae* that emerged within a period of two weeks at Old Woman's River.

This explosive germination pattern was also observed for *I. pes-caprae* at the Gulf of Mexico (Devall *et al.* 1989). From the seed coast still attached to the cotyledons it was obvious that all were smooth, and scarified by sand abrasion. When exhumed, the newly emerged seedlings (only cotyledons present) of *I. pes-caprae* showed that the seedlings could emerge from depths over 10 cm. Seedlings derived from large-seeded species like *I. pes-caprae* (0.5-1 cm) tend to have higher shoot to root ratios, suggesting that their priority was to capture light rather than minerals (Fenner 1985). In the dune environment the sand in which the seeds germinated dries out rapidly from the surface downwards. In order to survive, the seedlings had to maintain root elongation. Thus being large-seeded in the dune environment had two advantages for *I. pes-caprae* seedlings: shoots could emerge from greater depths and roots grew more quickly (Fenner 1985).

Compared to *A. populifolia* the *I. pes-caprae* plants showed a different strategy, with a distinct germination peak in March, a strategy observed in many other species (Mayer & Poljakoff-Mayber 1982, Roberts & Boddrell 1985). The strategy resulted for *I. pes-caprae* in more or less a monostand of seedlings on the seaward or landward sides of the foredunes, even when the dune is a mixed community (Plate 4.3).

Although the seeds of *I. pes-caprae* showed good germination in the field and many seedlings emerged and established themselves, none of the seedlings survived over time. This was probably due to sand abrasion in combination with heat stress (sand and sun) and the low moisture conditions on the beach (Lesko & Walker 1969), resulting in brown leaves after which the whole seedling would desiccate. This low field survival of seedlings of coastal *Ipomoea* species was also observed by Devall *et al.* (1989). The surviving seedlings each year will have been subjected to a different set of environmental conditions and have been selected for a different set of characters. In a changing environment, like the coastal foredunes, highly specialised adaptations in seedlings to particular mortality factors might not have been expected (Fenner 1987). Many demographic studies indicate that even within a single species, the causes of seedling mortality may vary markedly from season to season and from place to place (see Fenner 1987).

Myrica cordifolia

The seeds of *M. cordifolia* showed an intermediate germination success, but the remaining seeds were mostly viable. The lower germination success could have been due to the 1.5 mm wax layer surrounding the seed, which could have inhibit the water uptake. However, seeds without the wax layer showed the same germination percentage, hence the wax layer did not inhibit germination. After cold stratification, the seeds of *M. cordifolia* showed an enhanced rate of germination, but no enhancement in germination was observed as was observed for *A. populifolia*. However, when seeds without the wax layer were set to germinate in the greenhouse, the germination percentage increased by more than 50%, and appeared to germinate much faster with a rate of 12.2, compared to 1.4 in the conviron.

After three years in dry storage the seeds of *M. cordifolia* showed a 23% increase in germination percentage. Perhaps the seeds were immature when collected since in general the seeds stayed on the parent plant for months, creating an aerial seed bank. The fact that the seeds were immature probably imposed innate dormancy on the seeds, which was broken over time when the seed matured. This maturing of the seeds resulted in higher germination after two years of dry storage, probably because the seed coat had become more permeable when stored dry at room temperature (Egley 1976, Morrison *et al.* 1992). On the other hand the number of dead seeds had increased over the same period by 41%. This could have been due to the fact that immature seeds die

when dried out (Harrington 1972), and the three year dry-storage period might be too long for these seeds. Another reason could have been the fact that the seeds were bird dispersed (Tinley 1987), and might therefore need to pass through the bird to break dormancy (Baskin & Baskin 1998).

Even though the seeds were germinating well under controlled conditions, no seedlings of *M. cordifolia* were noticed in the foredunes or backdunes (personal observation & Lubke personal comment). Most plants of the genus *Myrica* have roots with nodules that contain nitrogen-fixing bacteria. The roots are also associated with arbuscular mycorrhizal fungi (Tinley 1987). The absence of especially mycorrhizae in a new environment might explain the absence of seedling establishment in the field in combination with the effect of seed mass, soil type and soil compaction on the emergence (Harper *et al.* 1970, Sheldon 1974, Weller 1985, Maun & Lapierre 1984).

Scaevola plumieri

The fresh air-dried, infected and old seeds of *S. plumieri* were all difficult to germinate, as cited in literature (Tinley 1985, Wrigley & Fagg 1988). This in contrast to the dune shrub *Scaevola taccada* which showed no dormancy, and germinated within four weeks when put in soil (Lesko and Walker 1969). For *S. plumieri* after 14 weeks in the conviron and a subsequent 8 weeks in the greenhouse the seeds germinated, and showed a high germination percentage. The period in which the seeds germinated was several weeks, even when excluding the lag phase, hence leading to a low germination rate. The fact that the seeds of *S. plumieri* needed about 3 months to germinate indicated innate dormancy that prevented the seeds from germinating. The *S. plumieri* drupes were ripe when collected from the plant, but the embryos might have needed after-ripening period after dispersal as has been observed for other species (Pemadasa & Lovell 1975, Baskin & Baskin 1998). However, the seeds that had been in dry storage for two and three years, enough time to ripen, were showing the same germination behaviour as the fresh air-dried seeds. On the other hand the hard seed coat of *S. plumieri* seeds might indicate seed coat induced dormancy, but the boiling water scarification, sulphuric acid scarification and mechanical scarification did not result in any germination. Perhaps the dormancy was more temperature related? The cold stratification showed no germination, but the heat stratification enhanced the germination in the greenhouse by 43%, but again after a long lag phase resulting in a low germination rate.

The seeds of *S. plumieri* were shed in the period February to May, and the first seedlings appeared from February onwards. When the seedlings emerged in the greenhouse the seeds of *S. plumieri* were approximately 10 months old, and germinated in approximately the same period that the seeds would have germinated in the field. This could have been a coincidence, but occurred twice during the present study. Perhaps a certain combination of temperature and photoperiod was needed to trigger the seeds to germinate.

At the end of March the seedlings of *S. plumieri* started to emerge, and produced seedlings continuously over a period of 15 weeks instead of an explosion of seedlings as observed for *I. pes-caprae.* This strategy was likely to be favourable in unpredictable environments because seedlings were available for establishment over a long period, preventing massive mortality due to, for instance, sand burial as observed by Balarin (1996; Plate 4.4). Thus, the low rate of emergence due to a spread in germination observed in the greenhouse was also observed in the field. As noted for *I. pes-caprae*, the seeds of *S. plumieri* were also large, and thus capable of emerging from depths over 10 cm. Similar results were reported by Van der Valk (1974), Maun and Lapierre (1981; dune grasses), Garner and Witowski (1997), and Lonard and Judd (1999; *Ipomoea* spec.).

Plate 4.4. Newly-emerged and older seedlings of *S. plumieri* situated on the landward base of a foredune.

In general pioneer species produce many small seeds, but in the beach environment the pioneer species have large seeds (e.g. Fenner 1985, Barbour 1992). The large seed size could also have been an adaptation to drought-avoidance by conferring on the seedling the ability to grow rapidly (Buckley 1982). Having big seeds, especially in the unstable dune habitats, would ensure successful seedling establishment. By providing an ample nutrient reserve, the seedling was enabled to reach the critical size to survive (Buckley 1982, Fenner 1985).

The seedlings of *S. plumieri* on the seaward side of the foredune also showed poor survival after 110 days, which was mainly due to salt water inundation and hypocotyl predation. The remaining seedlings were buried by sand. Only the seedlings of *S. plumieri* on the landward side of the foredune survived. Many demographic studies indicate that even within a single species, the causes of seedling mortality may vary markedly from season to season and from place to place (see Fenner 1987), but in the unstable dune environment sand burial usually was the main cause of death (Fenner 1985, Tinley 1985). In total, 20 seedlings survived up to the termination of the observations and some are now more than two years old and stand a good chance of surviving.

Concluding remarks

Germination is a key process in determining plant distribution and the study of its ecology will add greatly to our understanding of plant ecology in its wider aspects. The results show that the seeds of the four species germinated well when the right conditions were met only the seedling survival was very low. For *Scaevola plumieri* it was not clear what the conditions were, but they are probably temperature related. A high number of seedlings of *A. populifolia, I. pes-caprae* and *S. plumieri* were observed the field, but note that the number of seeds germinated in the field might be underestimated because the number of seeds in the soil was unknown. This is because the number of emerging seedlings was counted and the seeds that germinated but failed to reach the surface were not recorded. The same is true for the number of seedlings. Even though the seedlings were colour tagged, the number of seedlings that emerged could have been an underestimation, due to unrecorded emergence and mortality between the observation periods.

CHAPTER 5

THE SOIL SEED BANK AND SEED CHARACTERISTICS OF COASTAL FOREDUNES SPECIES

Almost every part of the earth's surface is filled with seeds of various kinds, and in some cases seed dug up from far below the surface will still retain their virility. The earth itself is a granary and a seminary…

Thoreau (1999)

5.1. INTRODUCTION

The seed occupies a critical position in the life history of higher plants. From the time that the seed is formed, it becomes liable to a succession of hazards. It may germinate in unsuitable places, be eaten by predators or attacked by pathogens (Bewley & Black 1994). The seeds that do not germinate might accumulate in the soil seed bank (Harper 1977, Cook 1980, Thompson 1987). The incorporation of seeds in the soil seed bank is often related to seed characteristics such as seed shape and size, which can be crucial factors in the dispersal and seed bank behaviour of seeds (Fenner 1985, Thompson *et al.* 1993). Seed banks play a role in preserving genetic diversity (Fenner 1985, Cabin *et al.* 1998), and are an advantage in surviving unfavourable conditions in habitats that experience disturbances such as drought and periods of adverse conditions (Tinley 1985, Thompson 1992, Baskin & Baskin 1998). In general two types of seed banks are distinguishable; transient seed banks with seeds that remain viable for less than one year, and persistent seed banks with seeds that remain viable for more than one year (Thompson & Grime 1979). Transient seed banks are often formed in predictable habitats with little disturbance, where seeds have a short dormancy period or remain for a long period on the plant. Persistent seed banks are often large and are characteristic of early-successional species (Fenner 1985, Louda 1989). Persistent seed banks can be divided into short-term persistent and long-term persistent seed banks. In the short-term persistent seed banks the seeds stay viable for at least one year, but less than five years, whereas in the long-term persistent seed bank the seeds stay viable for at least 5 years (Bakker *et al.* 1996a).

The time seeds stay viable in the soil (longevity) is very variable and often species dependent. Seeds of some species can remain viable in the soil for periods of at least 100 years (Thompson *et al.* 1997). The longevity of seeds can be obtained from the vertical distribution in the soil. There is abundant evidence that deeply buried seeds are older than shallow ones, allowing the ratio of deeply buried to shallow seeds to be used as an index of seed longevity (Bakker 1989). Besides burial depth, the longevity of seeds can also be assessed using by their size and shape (Harper 1977, Thompson & Grime 1979, Leck *et al.* 1989, Thompson *et al.* 1993). Persistent seeds tend to be small and compact, whereas transient seeds seem to be larger (heavier) and either elongated or flattened. The proposed basis for this relationship is that larger seeds do not

penetrate into deeper soil layers, whereas small and rounded seeds do so easily (Bakker *et al.* 1996a).

Seeds that remain viable in the soil in large numbers and for many years can play a significant role in determining the future vegetation (Poschlod & Jackel 1993, Warr *et al.* 1993). The seeds in the soil seed bank are therefore considered to be part of the 'community pool' according to the species pool concept, with the soil seed bank as an important part of the life cycle of plant species of many different habitats (Fenner 1985, Zobel *et al.* 1998). Species from fast-changing environments are usually good dispersers and have persistent seed banks (Fenner 1985), but little is known of the seed bank dynamics of the fast -changing coastal foredune environment. It has been proposed that sand dune systems do not have a persistent soil seed bank because the shifting and dynamic nature of the substrate does not favour a significant carryover of seeds from one season to the next (Planisek & Pippen 1984, Ehrenfeld 1990). Studies of the seed biology of several annual and biennial species have confirmed this supposition (Barbour 1972, Mack 1976, Watkinson 1978a, 1978b, Boorman & Fuller 1984, Crawford & Young 1998). However, two studies have showed that buried seeds of sand dune species can remain viable for more than two years, thus providing the potential to form a persistent seed bank (Pemadasa & Lovell 1975, Zhang & Maun 1994). The aim of the present study is (1) to determine the seed bank strategy of coastal foredune species of the Cape coast, (2) to assess the distribution and size of the soil seed bank of foredune systems, and (3) to determine and relate seed characteristics to seed bank persistence. This to test the hypothesis that there is a potential (persistent) soil seed bank in the South African coastal foredune system.

The work on the soil seed banks of the coastal foredune environment will consist of sampling the soil seed bank of sites situated along the Eastern and Southern Cape coast (from Fish river to Cape Agulhas). The seeds found will be identified, counted, and tested for viability. Furthermore, seed shape measurements of the foredune species will be obtained to relate seed shape and seed size to seed bank behaviour.

5.2. THE LONGEVITY OF SEEDS: SOIL SEED BANK CLASSIFICATION AND SEED ATTRIBUTES

5.2.1. The soil seed bank

The re-appearance of plants may depend on the persistence of seeds in the soil seed bank (Thompson *et al.* 1997). If species have been lost from the persistent seed bank, they have to be dispersed into the site from the local or regional species pool by some vector (e.g. water, wind) and become incorporated into the fresh seed bank (Bakker *et al.* 1996a, 2000). Without the presence or arrival of seeds no plant establishment will be possible, and therefore the seed bank is an important part of the life cycle of plants and of the existence of plant communities.

Changes in seed production, seed germination, micro-environment (temporal distribution of seed), seed predation and dispersal (spatial distribution) affect the composition of the seed bank, and alter the rate of seed input into and output of seeds from the seed bank (Harper 1977, Bewley and Black 1985). The causes of depletion of buried seeds often are germination, predation, fungal attack and loss of viability (Roberts 1970). The relative importance of these sources of mortality is usually unknown, and must vary with species, habitat and depth of burial (Warr *et al.* 1993).

Thompson and Grime proposed a widely used scheme for soil seed bank classification in 1979. Their scheme was based on the observed viability of seed in the soil revealed by seasonal sampling over the period of one year. Bakker (1989) and Bakker *et al.* (1996a) proposed a modified version of seed bank classification. This classification defines three types of soil seed bank; transient, short-term persistent, and long-term persistent. The species that form a **transient** seed bank persist in the soil for less than one year, often much less. **Short-term persistent** seeds can persist for at least one year, but less than five years. This type may play a role in the maintenance of plant populations after a bad event. **Long-term persistent** seeds survive in the soil for at least five years. This seed bank type could contribute to regeneration of destroyed habitats or plant communities (Thompson *et al.* 1997).

There is a wide range of possible criteria that could be employed in allocating species to a seed bank type. To appoint a species found in the soil seed bank to a certain longevity class Thompson *et al.* (1997) developed a dichotomous key (Figure 5.1). The key uses

both direct and indirect evidence of seed longevity with the assumption that all species found in the seed bank were also present in the vegetation. The direct evidence might be provided by the studies of natural buried seeds of disappeared plant species, provided the time the species last grew at the site is known. Another source of longevity information is the vertical distribution of seed in the soil. There is evidence that deeply buried seeds are older than shallow ones, under the assumption that it takes time for seeds to become deeply buried in the soil (Thompson *et al.* 1993). Any species in the vegetation but not detected in the seed bank is considered to be transient (see figure 5.1). Occasionally a species does not produce seed at a particular site and will then appear as transient even if its seeds are in fact persistent.

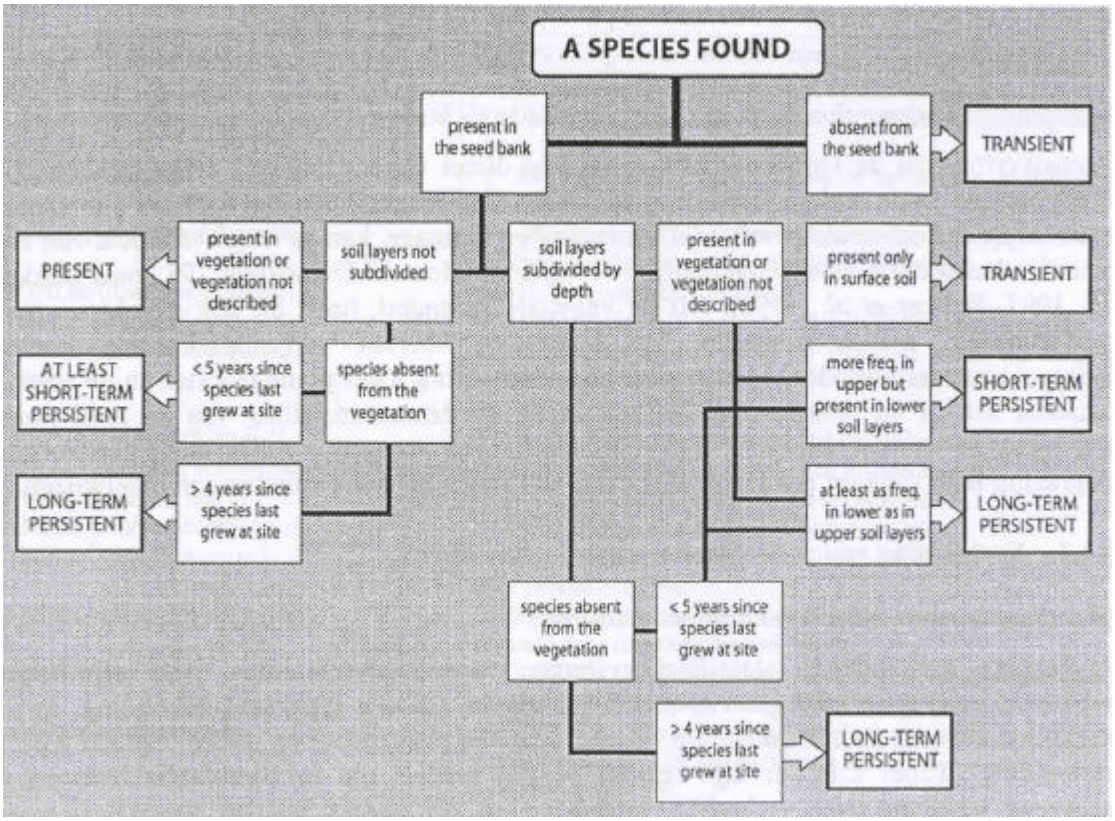


Figure 5.1. The dichotomous key to the three seed bank types (Thompson *et al.* 1997).

Another valuable but less direct source of evidence for seed longevity is the vertical distribution of seeds in the soil. In general deeper buried seeds are older than shallow ones. A potential obstacle to the general application of this method is the wide variety of soil depths employed by different researchers. To obtain information on longevity related to soil depth, the soil seed bank should be sampled in at least two layers (Thompson *et al.* 1997).

An alternative way to allocate longevity to a species is by means of different seed attributes. Thompson *et al.* (1993) found a combination of shape and weight of seeds to be correlated with seed persistence. Other research points in the same direction. Bakker *et al.* (1996b) showed that transient seed banks of Alvar grasslands species in Sweden had significantly heavier seeds and a higher shape variance compared to persistent species. Also a group of species of flooded meadows in England, that were classified as having a transient seed bank, showed a significantly higher variance of seed shape than persistent classified species (McDonald *et al.* 1996). In the Argentine flora similar results have been found (Funes *et al.* 1999).

5.2.2. Ecological seed attributes

Seeds exhibit a great diversity in shape, colour, size, surface sculpturing, hairiness, appendages, anatomical structures and chemical composition, often typical to the species (Hodgson & Grime 1990, Werker 1997). Some features, like the seed coat structure, are more stable in a species, whereas others, like colour, may be more variable (Werker 1997). In ripe and mature seeds the seed coat has many functions; it serves as protection against physical, chemical, or biological damage, acts as regulator for water uptake, and plays a role in dispersal by specialised structures attached to the seed coat (Werker 1997).

The characteristic shape and size of seeds are crucial factors in the dispersal behaviour of these seeds and the chance of incorporation in the soil seed bank, and can influence levels of predation, depth of burial and persistence in the soil (Silvertown 1981, Garner & Witkowski 1997). Thompson *et al.* (1993) classified the persistence of seeds by combining seed shape and weight. Bakker *et al.* (1996a), following Thompson *et al.* (1993), concluded that seeds that weigh <3 mg with a shape variance of <0.093, i.e. small and nearly spherical seeds, are persistent.

The **shape** of a seed is determined genetically but it is finally moulded by the seed packaging and number of seeds in the fruit/pod, or by the shape of the embryo within the seed. The external form of a seed may determine the orientation of the seed when it falls on the ground and it may play a crucial role in seed dispersal. For example, when dispersed by water, flat seeds have more chance of floating than more rounded ones, whereas compact seed shapes without appendages (hairs or teeth) are characteristics associated with rapid burial (Thompson *et al.* 1993a). It seems likely that if seeds are very

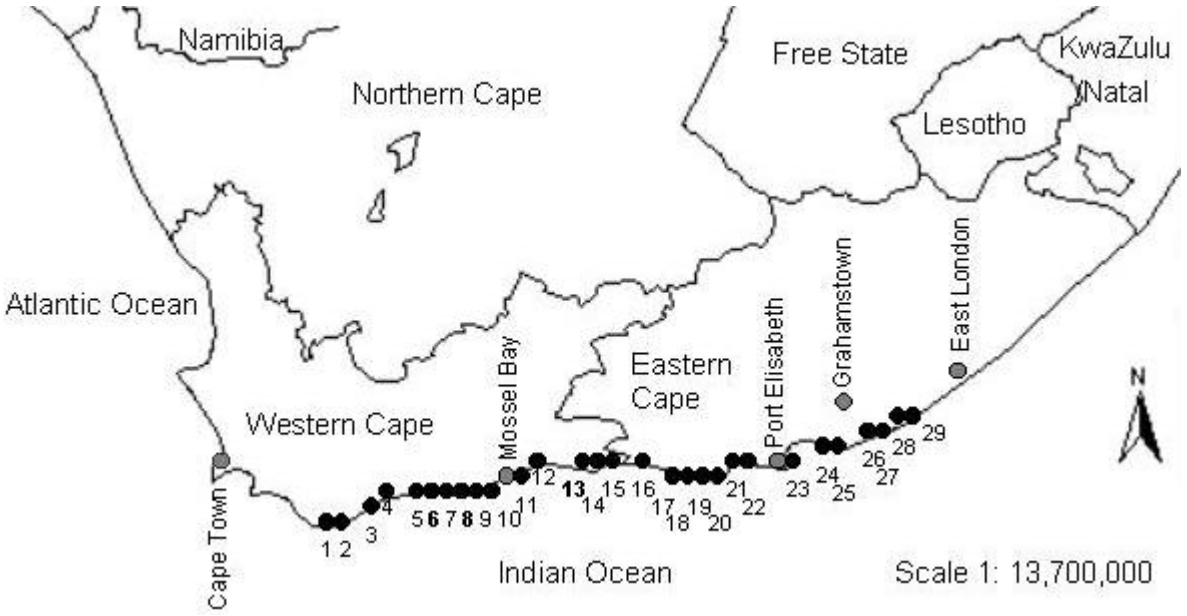
small, shape will not have a large effect on incorporation into the soil. However, if seeds are large and heavy it seems likely that rounded seeds will penetrate the soil more easily than awkwardly-shaped seeds.

The **size** of seeds is also determined genetically and is partly a function of the size of the parent plant, but may be affected by environmental factors during development (Fenner 1985). Seed size varies within a species, but is also correlated with habitat (e.g. larger seeds in drier habitats) and successional status. The mean seed weight of all species increases with maturity of the vegetation from open habitats to woods, but also within a species occurring in those habitats (Fenner 1985). Seed weight is perceived to be a key quantity linked with both competitive and colonisation success, and negatively correlated with abundance (Rees 1995). The number of seeds or fruits of a plant is usually inversely proportional to their size, compensating small size with large number. The seed size can be a characteristic feature of a family like, for instance, the very small seeds of the Orchideaceae. This while other families show a great variability in seed size, for example the Legiminosae show seed sizes varying from 18 cm (*Mora olefera*) to 1 mm (*Pynospora butescens*; Werker 1997; Thompson 1993). In families with a range of seed size, the smaller seeds are correlated with the more herbaceous species. In addition to inter-specific variation in seed size there may also be intra-specific variation, although less extreme. Differences in seed size may be the result of various factors. They partly depend on the conditions prevailing during seed development, external conditions (e.g. day length), internal conditions (e.g. food reserves), and genetic condition (e.g. pollen donor). As for seed shape, seed packaging within the fruit or pod also influences the size and the weight. In spite of intra-specific variation in seed size, it still can serve, for many taxa, as a diagnostic feature. The total weight of a seed is determined primarily by its size, seed coat, the structure and contents of the cells.

5.3. MATERIALS AND METHODS

5.3.1. Seed bank sampling

The soil seed bank was sampled at along the Cape coast of South Africa, from Cape Agulhas (south) Old Woman's River (south-east) (Figure 5.2). The vegetation around the sampled plots and at the different locations was recorded using the 'presence/absence' method and related to species found in the soil seed bank.



No.	Location	No.	Location	No.	Location
1	Struisbaai	11	Mossel Bay	21	Jeffreys Bay
2	Arniston/Waenhuiskrans	12	Klein Brak Rivier	22	Seaview
3	De Hoop	13	Glentana (2x)	23	Blue water Bay
4	Witsand	14	Wilderness	24	Alexandria
5	Jongensfontein	15	Sedgefield	25	Kenton-on-Sea
6	Stilbaai (2x)	16	Plettenberg Bay	26	Port Alfred
7	Vleesbaai	17	Keurboom	27	Kleinemonde
8	Dana Bay (2x)	18	Nature's Valley	28	Fish River
9	Jeffreys Bay	19	St Francis	29	Old Woman's River
10	Hartenbos	20	Aston Bay		

Figure 5.2. Map of the Eastern and Western Cape with the sample locations. At each location one sample site was located, except for the locations represented by bold numbers, where two sample sites were situated.

When sampling heterogeneous populations, stratified random sampling was appropriate because separate values for mean seed densities can be calculated for different parts

of the sample and the distribution of sampling units is more even (Sampford 1962, Bigwood & Inouye 1988, Benoit *et al.* 1989, Simpson *et al.* 1989).
The dune system is known for its instability and variable sand accretion rates. Thus for reliable estimates of seed banks in dune systems, large soil samples of a known volume should be obtained from shallow and deep locations (Zhang & Maun 1994). Given that Zhang and Maun (1994) showed that most seeds end up in depressions, the samples were taken in the depressions in front of or behind the foredunes.

A pilot seed bank sampling test of the seed bank was carried out at the sites Kleinemonde, Fish River and Old Woman's River to determine the sampling depth. At these sites multiple layers were sampled, Kleinemonde 0-90 cm (Plate 5.1.D), Fish River 0-50 cm and Old Woman's River 0-50 cm, to determine the maximum sampling depth for the majority of the sites. The pilot test resulted in a maximum sampling depth of 20 cm. The top layer of the sample plots was too dry to subdivide it into two layers of 5 cm (Benoit *et al.* 1989), so two layers of 10 cm were chosen to be sampled at the other sites.

Seed bank sampling procedure
At each site ten plots were sampled, five at the front and five at the back of the foredunes. In each sample plot an area of 30 x 30 cm was sampled (after Auld 1986). The sample was divided into layers of 10 cm (volume: 9 dm^3) by means of a sample tray (see Plate 5.1.A-B).
The first layers (0-10 cm) of many of the samples were collected in paper bags, and transported to the lab for detailed research after being sieved in the field over a 5 mm mesh. When only a few seeds were present in the sample, the seeds were counted and identified in the field. In the lab the collected samples were sieved over a 2 mm mesh to remove roots, shells and stones, after which the seeds were identified and counted. The second layer (10-20 cm) was sieved over 5 mm and 2 mm mesh sieves at the site (Plate 5.1.C). After sieving the seeds were collected in paper bags and transported to the lab where the seeds were stored in a dark cold room (5°C) until further use. The seeds collected from each layer were sorted separately on the number of species and the number of seeds per species. After counting the seeds were tested for viability.

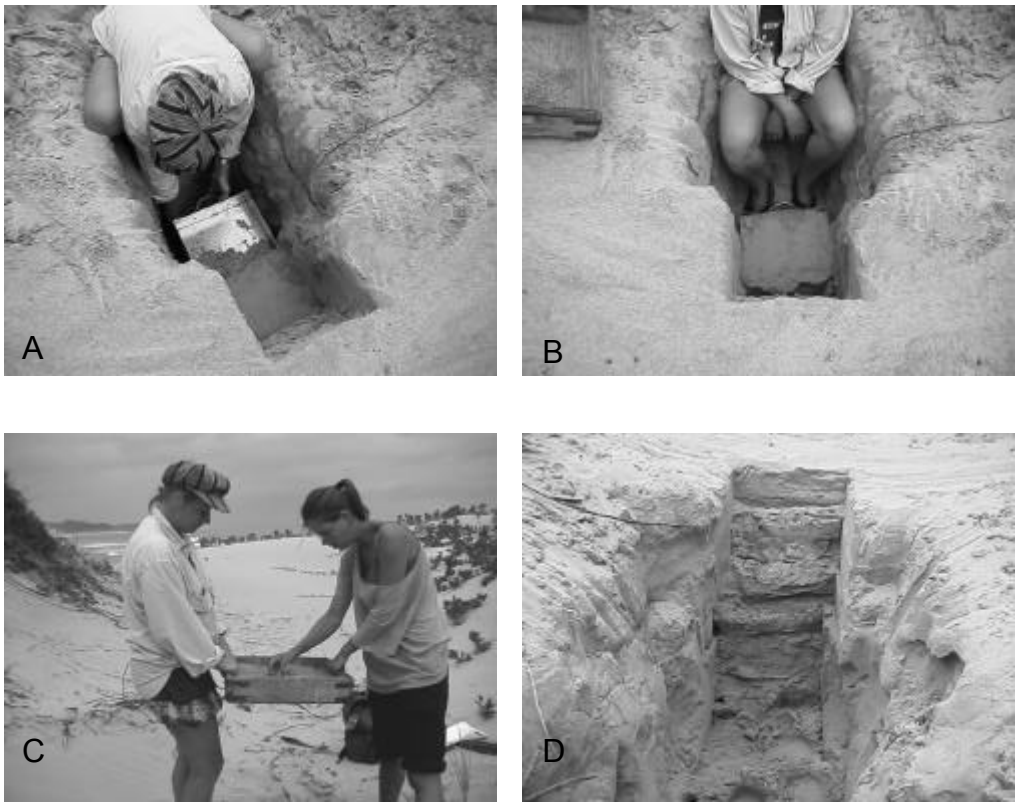


Plate 5.1. The soil seed bank sampling procedure to remove a layer of soil (A-B) after which the layer was sieved (C) and the seeds collected. At Kleinemonde a maximum of nine layers was sampled at one of the plots (90cm; D).

5.3.2. Seed viability test

The seeds were tested for viability by squeezing the seeds onto a hard surface for the soft seeds, and by cutting the seeds in half to expose the embryos for the seeds with hard seed coats. The soft and easy-to-squeeze seeds with brown embryos were considered dead, whereas the hard seeds with white embryo's were considered viable (Baskin & Baskin 1998, Bekker *et al.* 1998a). Intact seeds from the species *Acacia cyclops, Chrysanthemoides monilifera, Dasispermum suffructicosum, Hebenstreitia cordata, Ipomoea pes-caprae, Scaevola plumieri,* and *Tetragonia decumbens* collected at different sites were set to germinate in a temperature controlled greenhouse under a day/night regime of 28°C/15°C, without additional light sources (see Table 5.1). The seeds were placed 1 cm deep in trays filled with beach sand and covered with perforated plastic sheets. The trays were checked every 3-5 days for moisture status and germinated seeds were counted and removed. After four months the germination experiment was terminated and the ungerminated seeds where tested for viability.

Table 5.1. Species used in the germination viability test sampled originating from different sites and layers.

Site	Layer		Species
	0-10 cm	10-20 cm	
Alexandria	X	X	***Acacia cyclops***
Blue water Bay	X		*Tetragonia decumbens*
Fish River	X	X	*Ipomoea pes-caprae*
Jeffreys Bay	X	X	*Hebenstreitia cordata*
Jongensfontein	X		*Dasispermum suffructicosum*
Kleinemonde	X	X	*Scaevola plumieri*
Old Woman's River	X		*Chrysanthemoides monilifera*
Plettenberg Bay	X		*Tetragonia decumbens*
Struisbaai	X	X	*Tetragonia decumbens*
Stilbaai	X		*Tetragonia decumbens*

5.3.3. Soil seed bank diversity and vegetation

For each site the species richness and diversity of the soil seed bank was calculated. Diversity indices provide more information about community composition than simply species richness, as the relative abundance is also taken into account. For the species diversity the Simpson's diversity index and the Shannon diversity index were used (Begon *et al.* 1996, Stiling 1996).

The Simpson's diversity index D is calculated by determining, for each species, the proportion of individuals that contributes to the total of the sample (Begon *et al.* 1996). The proportion (P_i) of a species *i* relative to the total number of species is calculated and squared. The squared proportions for the all the species are summed and the reciprocal is taken:

$$\text{Simpson's index } D = \frac{1}{\sum_{i=1}^{S} P_i^2}$$

where S is the total number of species in the community (richness). The value of the index depends on both the species richness and evenness with which the individuals are distributed among the species and ranges from 0 to 1. If a species has an index of 0, the species showed no dominance, whereas a value of 1 indicates total dominance. The Simpson's diversity index is a dominance index and is less sensitive to species richness, and thus places more weight on the dominant species than the Shannon index.

The Shannon index is a species richness index and thus more sensitive to richness than to evenness (Stiling 1996, Begon *et al.* 1996, Fragstats 2001). For the Shannon index (*H'*) the proportion (P_i) of species *i* relative to the total number of species is calculated and than multiplied by the natural logarithm of this proportion. The resulting

$$\text{Shannon index } H' = -\sum_{i=1}^{S} P_i \ln P_i$$

product is summed across species and multiplied by -1:

The range of the Shannon index is positive and without limit, but real communities score between 1 and 6.

Both indices increase as the number of species increases and/or the proportional distribution of species becomes more equitable (Fragstats 2001).

5.3.4. Seed characteristics

Species can be classified according to diaspore (whether true seed or fruit) size and shape (Thompson *et al.* 1993, Thompson 1993). For the species *Ammophila arenaria, Acacia cyclops, Arctotheca populifolia, Chrysanthemoides monilifera, Dasispermum suffructicosum, Gladiolus gueinzii, Hebenstreitia cordata, Ipomoea pes-caprae, Myrica cordifolia, Scaevola plumieri, Silene primuliflora*, and *Tetragonia decumbens* seed weight and shape was determined. Not all diaspores of these species have represent true seeds. The drupes of *S. plumieri* contain a stone seed which is surrounded by a fleshy layer, whereas the fruits of *M. cordifolia* contain a single nut and is surrounded by a 1.5 mm thick wax layer. The diaspores of *T. decumbens* are winged fruits with a hard core that contains up to 6 seeds, each situated in its own compartment. The fruits of *T. decumbens* were treated as one diaspore because the seeds do not leave the seed pod when germinating or dispersing. The other species have bare seeds or have seed coats that were easily removed during dispersal. For more details about the species, diaspores and means of dispersal see chapter 2. For convenience all diaspores of the measured species will be referred to as seed, even if not true seed. All seeds were measured without detachable appendages.

Seed weight

The seed weight (**W**) of all the species was measured using a Cahn balance, model TA 4100 reading four decimal points. The air-dried seeds (Hodkinson *et al.* 1998) were

measured in batches of 50 or 100 seeds. To determine a weight-shape correlation for different species, the weight of individual seeds was measured (one seed weight). All the seed weights were obtained from diaspores with appendages removed.

Seed shape and volume

The seed shape was defined by the extent to which it differs from a sphere. The shape can be quantified by measuring length, width and height of a seed, and by normalising the values so that the length was unity. The shape variance (**Vs**) had a minimum of 0 for perfectly spherical seeds, and a maximum of 0.2 for elongated or flattened seeds (Thompson *et al.* 1993 with modifications of Bakker *et al.* 1996a).

The seed dimensions length, width and height were measured for 50 seeds per species using a digital slide-calliper accurate to 0.05mm. A measure for seed volume was obtained by multiplying length, width and height of the seeds.

Weight, shape, and volume combinations

To correlate seed weight with seed shape the graph of Thompson *et al.* (1993; with the modifications of Bakker *et al.* 1996a) was used (Figure 5.3). The lighter and more compact seeds with a seed weight of less than 3 mg and a shape variance of less than 0.093, will fall within the dotted square of figure 5.3. This area is called 'the persistent area', and the species that fall within this area are assumed to be persistent.

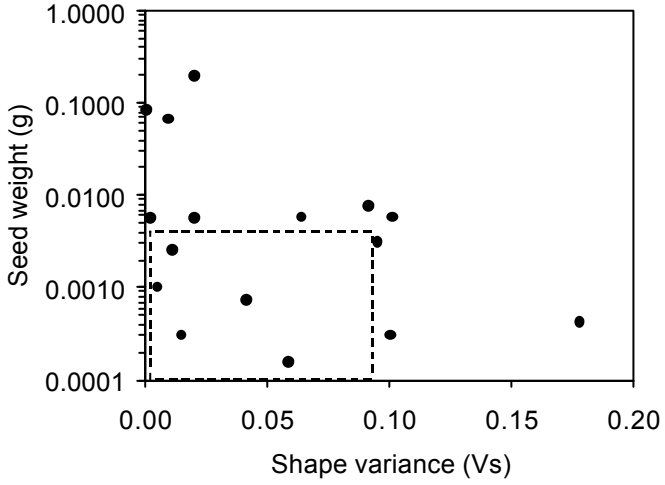


Figure 5.3. The weight-shape (Vs) of Thompson *et al.* (1993) with modifications of Bakker *et al.* (1996a). The dotted square represents the persistent area.

To find other correlations between seed longevity and different seed characteristics, the weight, shape variance and seed volume were combined into a single parameter (Table 5.2).

Table 5.2. The seed parameters weight (W), shape (V_s) and volume (Vol) were combined in an attempt to find a single parameter accounting for seed longevity.

Combinations:	Weight and Shape	Weight and Volume
	W * √ Vs[1]	W * √ Vol
	√ W * Vs	√ W * Vol
	W * Vs	W * Vol

[1] After Bekker *et al.* 1998b

5.3.5. Seed longevity, species longevity and successional status

Each species found in the soil seed bank will be attributed a seed longevity, species longevity and successional status obtained from the literature. It is difficult to distinguish between short-term and long-term persistence on the basis of one sample event (Thompson *et al.* 1997). Therefore, in the present research the species will be classified as transient (short-lived) or persistent (long-lived). To allocate the species to a seed bank type the key of Thompson *et al.* (1997) presented in figure 5.1 was used.

The successional status of the species is divided into pioneer, early successional, or mid-successional status and was obtained from the literature, as was the species longevity (annual, biennial or perennial) (Table 5.3A). The seed weight, shape variance, volume and the different combinations were each divided into six classes and were obtained by measurement (Table 5.3B).

Table 5.3. Species (A) and seed (B) attributes divided into categories of classification associated with each attribute (After Grandin & Rydin 1998).

Ecological characteristics	Classification category	
	Code	Description
A) Species attributes:		
Seed bank type	1	Transient (≤ 1 year)
(Thompson *et al.* 1997)	2	Persistent (> 1 year)
Successional status	1	Pioneer species
(Tinley 1985, Lubke & Van Wijk 1998)	2	Early successional species
	3	Mid-successional species
Species longevity	1	Annual
(Tinley 1985)	2	Biennial
	3	Perennial
B) Seed attributes:		
Weight (gram)	1	≤ 0.050
	2	0.051-0.150
	3	0.151-0.250
	4	0.251-0.350
	5	0.351-0.450
	6	0.451-0.550
Shape variance	1	≤ 0.025
	2	0.026-0.050
	3	0.051-0.075
	4	0.076-0.100
	5	0.101-0.150
	6	0.151-0.200
Volume (mm^3)	1	0-250
	2	251-500
	3	501-750
	4	751-1000
	5	1001-1250
	6	1251-1500

5.3.6. Data analysis

The independent variables were tested for normality and homogeneity of the variance by using the Kolmogosov-Smirnov and Levene's test, respectively. When these assumptions failed, non-parametric procedures were carried out. The observations made in the vegetation and soil for the different sites, such as the mean number of seeds, mean seed density and mean species richness per layer for pilot-sampling seed bank test at Kleinemonde, Fish River and Old Woman's River, were analysed with a Kruskal-Wallis test followed by a Newman-Keuls test for the comparison of means (Zar 1996). A

regression analysis was used to find a relationship between the number of seeds found per layer in the pre-sampling seed bank test, and the seed weight, shape variance and volume of the foredune species. The percentage similarity between the dominant species of the vegetation and seed bank, based on the presence or absence of a species, was calculated. For the species found at the different sites the species richness was determined and the Simpson's and Shannon diversity indices were calculated. For all data analyses the standard error (± S.E.) and number of replicates (*n*) was given and the differences between the analysed data was pointed out by different letters (abc, pqr, xyz) behind the values in tables or above the columns or data points in graphs. For each analysis the level of significance was referred to using the system: * = $P<0.05$, ** = $P<0.01$, and *** = $P<0.001$. The ** were placed next to the highest value of the analysed parameter. All statistical tests were performed at a 95% confidence interval using the statistical program Statistica 5.5. (Statsoft Inc.). For details of the ANOVA analysis see Appendix III.

5.4. RESULTS

5.4.1. Pilot seed bank sampling test

At the first three sites sampled, Kleinemonde, Fish River and Old Woman's River, the sampling depth for the entire experiment was determined by sampling multiple layers of 10 cm each. At Old Woman's River and Fish River the maximum sample depth was 50cm (5 layers), whereas at Kleinemonde the seed bank was sampled to a maximum of 90cm (9 layers) at one plot (Figure 5.4.A). The number of seeds found was bulked per layer for the three sites, and the mean number of seeds per layer was determined. For the bulked samples of the three sites seeds the significant highest number of seeds were found in the 0-10 cm layer (Kruskal-Wallis, $P<0.001$; Figure 5.4A). The mean number of seeds declines significantly with depth with a R^2 of 0.13 ($P<0.001$; Figure 5.4A+B). The R^2 was significant, but low due to the lower number of seeds found in the deeper layers.

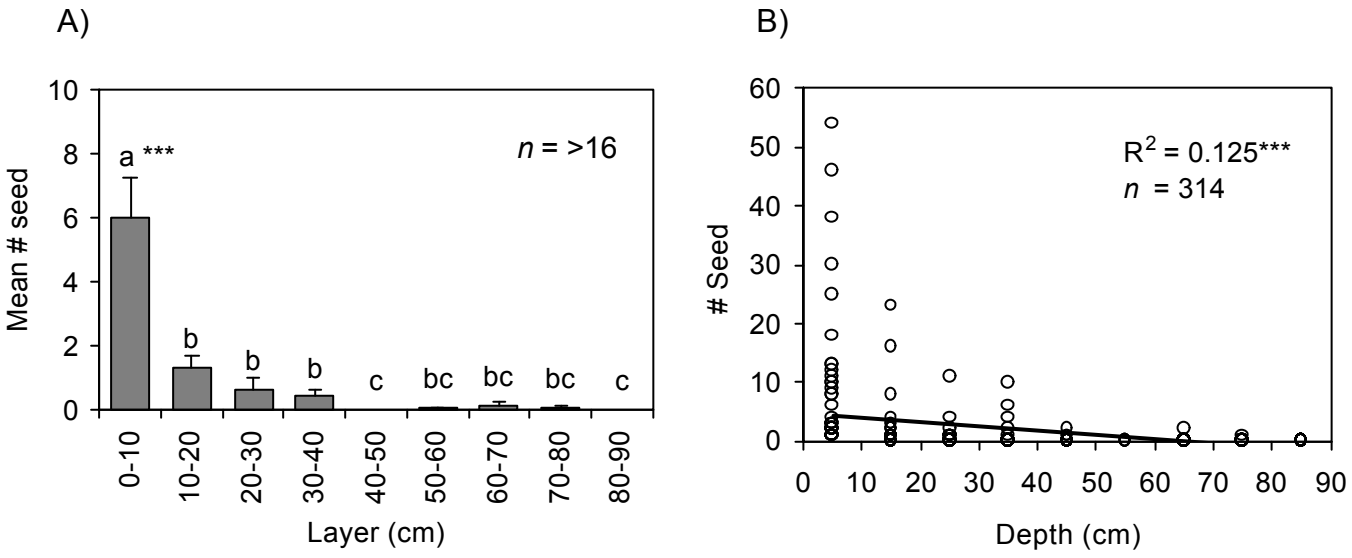


Figure 5.4. The mean (± S.E.) number of seeds per 10 cm layer in the bulked samples from Kleinemonde, Fish River and Old Woman's River (A), and the linear relationship between number of seeds and sample depth (B). Statistics used: Kruskal-Wallis followed by a Newman-Keuls test (graph A) and regression analysis (graph B). Level of significance: *** - $P<0.001$. The *n* in graph A was ranging from 70 for the 0-10 cm layer to 17 for the 80-90 cm layer.

Of all the plots sampled in the three sites, the observations (hits) were observed in the first layer (Table 5.4). After which the number declined with no seeds found at the 40-50

cm layer and the 80-90 cm layer (Table 5.4). The maximum number of seeds and mean seed density per m^2 was significantly higher for the first layer, and declined significantly after that (Table 5.4). The same was found for the maximum number and mean number of species per layer (Kruskal-Wallis, $P<0.01$; Table 5.4).

Table 5.4. Summary of number of seeds of all species found per layer in the bulked samples of Kleinemonde, Fish River and Old Woman's River. The maximum and mean (± S.E.) seed density (per m^2) and species richness is given by layer, with the number of times seeds were found in a layer (number of hits). Any value with the same letter does not differ significantly in density or species richness. Contrasts obtained by Newman-Keuls after Kruskal-Wallis test. Level of significance: ** - $P<0.01$.

Layer (in cm)	# Hits	Seed density per m^2			Species richness		
		Maximum	Mean	(± S.E.)	Maximum	Mean	(± S.E.)
0-10	41	3956	96.5	(21.9) a **	11	7.7	(0.7) a **
10-20	23	856	37.2	(12.6) b	11	5.6	(0.8) b
20-30	11	544	49.5	(24.9) b	5	1.3	(0.4) b
30-40	6	267	44.4	(15.9) b	2	2.0	(0.0) b
40-50	0	0	0.0	(0.0) c	0	0.0	(0.0) c
50-60	2	11	11.1	(0.0) b	1	0.1	(0.0) bc
60-70	1	22	22.2	(0.0) b	1	0.1	(0.0) bc
70-80	1	11	11.1	(0.0) b	1	0.1	(0.0) bc
80-90	0	0	0.0	(0.0) c	0	0.0	(0.0) c

Because of the relationship found between number of seeds and soil depth (Figure 5.5), and the seed density and species richness with sampling depth (Table 5.4), the maximum sample depth was set at 20 cm.

5.4.2. Vegetation versus soil seed bank

There were not real foredunes present at all the sites, probably due to high seas that washed away the foredunes. Often only mid- and late-successional species were growing on the steep dunes that were left, so only 14 sites were sampled (Figure 5.5). The frequency of a species found in the vegetation and soil seed bank was recorded per site. The category 'seed bank only' represents the number of observations of a species found only in the seed bank. The observations from the category 'both' represent the number of times a species was found in both the vegetation and the seed bank, whereas the category 'vegetation only' represent the observations of a species found only in the established vegetation (see Figure 5.5).

Between the sites significant differences for all three categories were found (Kruskal-Wallis, $P<0.05$; Figure 5.5). For the category 'seed bank only' the highest number of mean observations was made at Plettenberg Bay. These observations were significantly higher only when compared to Kleinemonde ($P<0.05$; Figure 5.5). For Plettenberg Bay and Fish River significantly more observations were made in the category 'vegetation only' when compared to Witsand, Struisbaai, Stilbaai and Alexandria (Kruskal-Wallis, $P<0.05$; Figure 5.5).

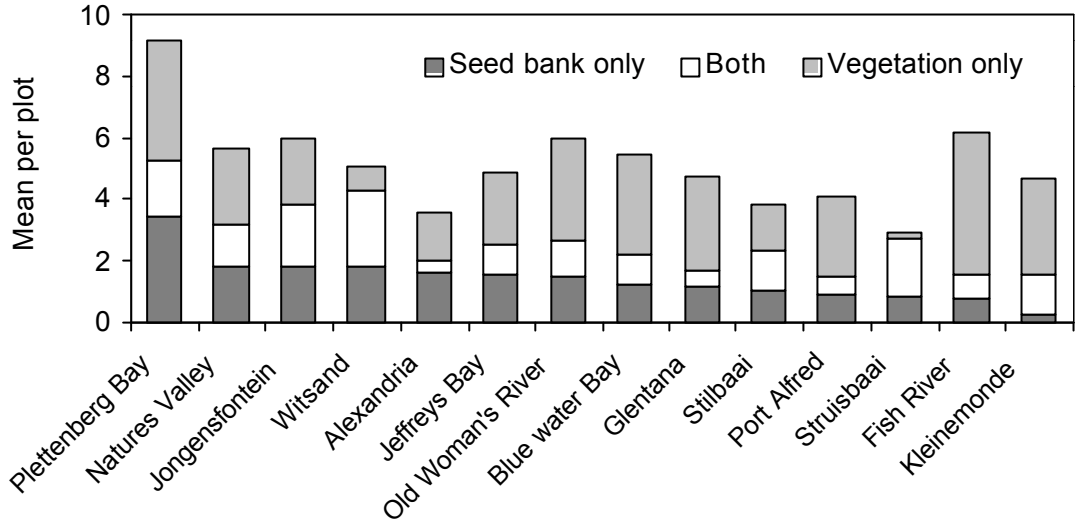


Figure 5.5. The mean number of observations per plot given per site for the species found in the categories seed bank only, both (found in vegetation and seed bank), and vegetation only at the 14 sites sampled. The sites are ranked according to the number of seed bank observations (high to low). Contrasts obtained by Newman-Keuls after analysis by Kruskal-Wallis. Level of significance: * - $P<0.05$. All sites $n = 10$, with exception of Alexandria ($n = 6$), Blue water bay ($n = 6$), and Fish River ($n = 9$).

In total, 40 species were found in the vegetation and/or soil seed bank of the sampled sites, of which 25 species were part of the foredune community, including the alien *Acacia cyclops*. The remaining 15 species were species foreign to the foredune environment and were grouped together as 'non-foredune species' (Table 5.5). The common weed *Datura stramonium* was the most frequently found non-foredune species at nine of the fourteen sites with up to 23 seeds per sample. The frequencies and seed densities of the other non-foredune species found were much lower.

The species were categorised as mentioned above in the group's 'vegetation only', 'seed bank only' and 'both' (Table 5.5). In total 36% of the observations were made for

the category ‘vegetation only’, 37% for ‘both’ and 27% for ‘seed bank only’ with most of the species well represented in the sampled sites. Only *R. crenata* and *S. nodosus* were observed in only 1 site, whereas the species from the non-foredune group were all absent from the vegetation (Table 5.5). Of the foredune species 48% (12 species) were found in the soil seed bank when not present in the vegetation (category ‘seed bank only’) (Table 5.5). The highest number of ‘seed bank only’ observations of the foredune species were made for *C. monilifera, A. populifolia*, and *H. cordata*, with few observations for *I. pes-caprae, S. plumieri* and *A. cyclops* (Table 5.5). The species represented in the ‘seed bank only’ category, were also represented in the category ‘both’. Seeds of *S. plumieri, T. decumbens and E. distichus* were most often recorded, with the lowest occurrence for *A. cyclops, G. gueinzii,* and *M. cordifolia* (Table 5.5). Besides the seeds of *G. gueinzii*, in 13 plots of the 124 plots sampled (10%) corms of *G. gueinzii* were recorded without plants being present in the vegetation (Table 5.5). In total seeds of the foredune species *A. populifolia, S. plumieri* and *T. decumbens* were recorded in more than 45% of the plots sampled, whereas in 44% of the plots sampled non-foredunes seeds were found.

Table 5.5. The number of plots where the foredune species and non-foredune species observed in the categories vegetation only, seed bank only, and both (in the vegetation and seed bank) with the number of sites where the species was found, given by species. For each species the number of sites where the species was found, and the total number of plots where the species was found is presented. The species found in the category ‘seed bank only’ are highlighted.

Species	# Sites	# Plots			
	(Max =14)	Vegetation only	Both	Seed bank only	Total (max = 124)
Acacia cyclops	12	14	2	4	20
Ammophila arenaria	3	8	-	-	8
Arctotheca populifolia	12	24	12	21	57
Chrysanthemoides monilifera	13	3	10	32	45
Cynanchum natalitium	2	7	-	-	7
Cyperus natalitium	2	4	-	-	4
Dasispermum suffructicosum	7	5	13	6	24
Ehrharta villosa	3	13	-	-	13
Elymus distichus	10	17	22	9	48
Gazania rigens	3	13	-	-	13
Gladiolus gueinzii - seed	7	15	2	4	21
- corm	4	-	-	13	13
Hebenstreitia cordata	9	1	9	19	29
Ipomoea pes-caprae	5	17	12	1	30
Metalasia muricata	6	16	-	-	16
Myrica cordifolia	5	2	2	7	11
Passerina rigida	9	40	-	-	40
Pentaschistis heptamera	2	4	-	-	4
Rhus crenata	1	1	-	-	1
Scaevola plumieri	9	28	38	4	70
Scirpus nodosus	1	1	-	-	1
Senecio elegans	5	10	-	-	10
Silene primuliflora	3	3	-	-	3
Sporobolus virginicus	6	15	-	-	15
Stoebe plumosa	2	6	-	-	6
Tetragonia decumbens	10	24	29	7	60
Non-foredune species	11		-	55	55

At most of the sites the dominant species of the vegetation was not the dominant species found in the soil seed bank (Table 5.6). Only for Struisbaai a 100% overlap was found for the three dominant species found in the vegetation and the seed bank. At most sites the third dominant species was present in low numbers, compared to the first two dominant species. At Plettenberg Bay, Jeffreys Bay, Alexandria and Port Alfred only one of the dominant species of the vegetation was found as a dominant species in the seed bank. The remaining nine sites showed an overlap of two of the three dominant species in the vegetation. At Fish river *S. plumieri* seeds were the third dominant species to be found in the soil seed bank, which was the only time a dominant seed bank species was not present in the vegetation (see Appendix II). At Jongensfontein and Nature's Valley the species *H. cordata* and *D. suffructicosum* were the dominant species found in the seed bank. This was due to the fact that the species had started to shed seeds, hence a high number was found in the seed bank.

Table 5.6. Comparison between the three dominant species found in the vegetation and the soil, with the percentage overlap between the vegetation and soil seed bank community. The dominant species in the soil were the species with the highest number of total seeds**.**

Site	Community	Dominant species			Overlap (%)
		1	2	3	
Struisbaai	Vegetation Soil	*T. decumbens* *E. distichus*	*E. distichus* *T. decumbens*	*A. populifolia* *A. populifolia*	100.0
Witsand	Vegetation Soil	*S. plumieri* *H. cordata*	*E. distichus* *C. monilifera*	*C. monilifera* *E. distichus*	66.7
Jongensfontein	Vegetation Soil	*S. plumieri* *D. suffructicosum*	*D. suffructicosum* *H. cordata*	*C. monilifera* *C. monilifera*	66.7
Stilbaai	Vegetation Soil	*A. arenaria* *T. decumbens*	*T. decumbens* *E. distichus*	*H. cordata* *A. populifolia*	66.7
Glentana	Vegetation Soil	*S. plumieri* *E. distichus*	*T. decumbens* *T. decumbens*	*E. distichus* *A. populifolia*	66.7
Plettenberg Bay	Vegetation Soil	*A. populifolia* *T. decumbens*	*T. decumbens* *S. plumieri*	*A. arenaria* *G. gueinzii*	33.3
Nature's Valley	Vegetation Soil	*A. populifolia* *D. suffructicosum*	*T. decumbens* *E. distichus*	*E. distichus* *T. decumbens*	66.7
Jeffreys Bay	Vegetation Soil	*S. plumieri* *G. gueinzii*	*E. distichus* *H. cordata*	*C. monilifera* *E. distichus*	33.3
Blue water Bay	Vegetation Soil	*T. decumbens* *S. plumieri*	*A. populifolia* *T. decumbens*	*S. virginicus* *A. populifolia*	66.7
Alexandria	Vegetation Soil	*I. pes-caprae* *A. cyclops*	*A. populifolia* *C. monilifera*	*A. arenaria* *I. pes-caprae*	33.3
Port Alfred	Vegetation Soil	*S. plumieri* *S. plumieri*	*T. decumbens* *C. monilifera*	*A. arenaria* *A. populifolia*	33.3
Kleinemonde	Vegetation Soil	*S. plumieri* *S. plumieri*	*C. monilifera* *C. monilifera*	*S. virginicus* *I. pes-caprae*	66.7
Fish River	Vegetation Soil	*E. villosa* *I. pes-caprae*	*I. pes-caprae* *C. monilifera*	*C. monilifera* *S. plumieri*	66.7
Old Woman's River	Vegetation Soil	*S. plumieri* *C. monilifera*	*I. pes-caprae* *S. plumieri*	*A. populifolia* *I. pes-caprae*	66.7

5.4.3. Soil seed bank sampling

For five of the fourteen sites sampled only the front or back of the foredune could be sampled due to the lack of a proper front or back dune environment. In general the plots sampled at the back of the foredune tend to have a higher number of observations (hits), seed density, total number of seed and number of species (Table 5.7). Due to the high variation between the samples, none of the parameters was significantly higher when compared to the plots at the front of the foredune (Kruskal-Wallis, $P>0.05$).

Table 5.7. The mean seed density per m^2 (± S.E.) in the top 20 cm of the soil, with the total number of seeds, and the number of species found is given per sample area (front or back of foredune) and by site. The number of plots sampled per site and the number of times seeds were found in a sample (hits) is also given per sample area and by site. The number of non-foredune species found at a site is given in brackets in the species column (- is used for 'not sampled').

Site	# Plot		# Hits		Seed density per m^2 (0-20cm)				Total seed		# Species	
					Front		Back					
	Front	Back	Front	Back	Mean	(± S.E.)	Mean	(± S.E.)	Front	Back	Front	Back
Struisbaai	6	0	18	-	87.2	(21.6)	-		212	-	4 (2)	-
Witsand	0	6	-	45	-		213.3	(71.5)		1344	-	11 (2)
Jongensfontein	5	5	17	23	82.0	(19.5)	131.9	(73.3)	155	380	5 (2)	6 (4)
Stilbaai	10	0	24	-	101.6	(55.1)	-		320	-	7 (3)	-
Glentana	10	0	18	-	62.2	(45.1)	-		112	-	7 (1)	-
Plettenberg Bay	4	6	24	14	72.6	(23.1)	50.4	(17.4)	187	68	8 (6)	8 (1)
Nature's Valley	5	5	12	20	26.2	(5.6)	28.5	(5.8)	33	59	5 (1)	7 (4)
Jeffreys Bay	1	9	2	20	137.0	(73.0)	73.4	(30.3)	37	152	1 (1)	8 (1)
Blue water Bay	1	5	8	5	84.4	(52.9)	28.6	(11.1)	76	18	4	3
Alexandria	0	6	-	10	-		103.9	(69.5)	-	131	-	4 (1)
Port Alfred	7	3	12	6	38.0	(13.8)	35.8	(18.1)	41	29	5	3
Kleinemonde	5	4	8	6	27.2	(9.2)	103.2	(50.8)	22	65	5	3 (1)
Fish River	6	5	5	13	37.8	(16.3)	151.5	(51.4)	17	152	2 (2)	4 (1)
Old Woman's River	5	5	11	15	73.6	(19.9)	70.2	(34.7)	55	120	3 (2)	6 (2)
Total mean	**4.6**	**4.2**	**13.3**	**16.1**	**72.6**		**120.6**		**105.6**	**228.9**	**4.7**	**5.7**
± S.E.	0.9	0.7	1.9	3.0	10.7		20.6		25.3	102.3	0.6	0.7

Witsand was the only site where all 11 foredune species were observed. The sites Blue Water Bay, and Port Alfred were the only sites where no non-foredune species were found, whereas in Plettenberg Bay 6 non-foredune species were found in the seed bank (Table 5.8). In total 11 species were found in the top 20 cm of the soil sampled at the 14 sites. For *E. distichus, D. suffructicosum* and *H. cordata* the highest total mean densities were found, with the lowest for *M. cordifolia* and *A. populifolia* (Table 5.8). The highest number of species was found at Witsand and Plettenberg Bay, whereas only 4 species were found at the sites Struisbaai, Blue water Bay, Alexandria and Port Alfred (Table 5.8). For the species *C. monilifera,* seeds were found at all the sites, with the exception of Struisbaai, whereas *A. populifolia, S. plumieri* and *T. decumbens* were found in 10 out of the 14 sites sampled (Table 5.8). For *D. suffructicosum* and *I. pes-caprae,* at less than 50% of the sites were seeds found in the seed bank, but in some samples the densities were very high. For *D. suffructicosum* more than 430 seeds/m^2 were found at

the sites Witsand and Jongensfontein, whereas for *I. pes-caprae* 276 seeds/m^2 were found at Fish River (Table 5.8). The other species with high seed densities of over 200 seeds/m^2 were *A. cyclops* (Alexandria), *C. monilifera* (Witsand), *E. distichus* (Struisbaai, Witsand, Stilbaai), *G. gueinzii* (Jeffreys Bay), *H. cordata* (Witsand), and *T. decumbens* (Plettenberg Bay). Besides being the site with the highest species richness, Witsand also showed the highest seed densities for 36% of the species. Only *A. populifolia, M. cordifolia* and *S. plumieri* did not show high seed densities at any of the sites sampled, but for all species the number of seeds found per species was highly variable per site. For instance at Witsand a density of 478 seeds/m^2 was found for *C. monilifera*, whereas at Nature's Valley only 11 seeds/m^2 were found (Table 5.8).

Table 5.8. Mean densities of seeds per m^2 in the top 20 cm of the soil listed per site and species. The sites where more than 200 seeds/m^2 were found are marked bold. The number of sites at which a species is found (n^{site}) is given below each row, and the number of species found at a site species (n^{sp}) is given after the columns. Species marked with a * are pioneer foredune species.

Site	Species (mean density/m^2)											n^{Sp}
	A. cyclops	*A. populifolia* *	*C. monilifera*	*D. suffructicosum* *	*E. distichus* *	*G. gueinzii*	*H. cordata*	*I. pes-caprae* *	*M. cordifolia*	*S. plumieri* *	*T. decumbens* *	
Struisbaai		47			**256**	44					178	4
Witsand	94	27	**478**	**678**	**459**	178	**911**	11	51	76	44	11
Jongensfontein			134	**434**	**216**		114		33	28		6
Stilbaai	22	37	33		**304**				22	11	168	7
Glentana		20	11	92	47	44	11				22	7
Plettenberg Bay	22	38	50	17	67	72	50		22	137	**326**	10
Nature's Valley	39	20	11	92	47	44	11				22	8
Jeffreys Bay		26	22	11	128	**356**	133			48	72	8
Blue water Bay		30	33							214	49	4
Alexandria	**889**		31				11	56				4
Port Alfred		20	22			22				107		4
Kleinemonde	11		176				33	22	22	128	11	7
Fish River	11	11	17					**276**	11	56		6
Old Woman's River			141				22	52	11	73	22	6
n^{site}	7	10	13	6	8	7	9	5	7	10	10	
Total density	1089	275	1019	1324	1522	761	1275	365	162	804	892	

In general the number of species found in the soil seed bank was also variable per site, and this was reflected in the species richness and diversity indices of the different sites

(Table 5.9). The highest Simpson's index was found for the site Alexandria, even though only four species were recorded. The high index was due to the dominance of one species (*A. cyclops*; see Table 5.8) since Simpson's diversity index is a dominance index that is heavily weighted toward the most abundant species (Table 5.9). The Shannon diversity index for the site Alexandria was low due to the fact that for the Shannon diversity index the species richness is included in the calculations, and only 4 species were observed at Alexandria. A low species richness was also observed for Struisbaai, Alexandria, Blue water Bay, Port Alfred, Jongensfontein, Fish River and Old Woman's River, but not all these sites showed a low Shannon diversity index (Table 5.9). For the Shannon diversity index the values ranged from 1.0 to 6.0 stand for real communities, but only for Struisbaai, Alexandria and Fish River were the values less than 1.0, suggesting that the samples do not represent real communities. Even the sites showing a high species richness have a maximum Shannon index of 1.9 (Table 5.9).
In general for the sites with the highest Shannon index, low Simpson diversity indices, and a high species richness were observed due to the fact that at these sites no dominant species was observed. For instance at Nature's Valley 8 species were observed, all with similar seed densities (Table 5.9, see also Table 5.8).

Table 5.9. The species diversity and species richness of the foredune soil seed bank communities over all plots given by site in geographical order.

Site	Simpson's Diversity Index	Shannon Diversity index	Species richness
Struisbaai	0.4	0.9	4
Witsand	0.2	1.7	11
Jongensfontein	0.3	1.4	6
Stilbaai	0.3	1.4	7
Glentana	0.2	1.7	7
Plettenberg Bay	0.2	1.9	10
Nature's Valley	0.1	1.9	8
Jeffreys Bay	0.3	1.6	8
Blue water Bay	0.5	1.0	4
Alexandria	0.8	0.4	4
Port Alfred	0.4	1.1	4
Kleinemonde	0.3	1.5	7
Fish River	0.7	0.9	6
Old Woman's River	0.3	1.5	6

For most species the highest seed densities were found in the top 10 cm of the soil, except for the non-foredune species (Table 5.10). For the foredune species the highest seed density was found for *D. suffructicosum, H. cordata* and *I. pes-caprae* in the 0-10

cm layer, whereas for *A. populifolia* and *M. cordifolia* much lower densities were found (Table 5.10). The same species mentioned for the 0-10 cm layer, also showed the highest and lowest densities in the 10-20 cm layer, with an addition of *G. gueinzii* for the lower density group (Table 5.10). The total densities of the species per layer showed a high total number of seeds for *D. suffructicosum, H. cordata and E. distichus* in the 0-10 cm layer and for the 10-20 cm layer *H. cordata* showed the highest total density (Table 5.10). The high densities for *H. cordata* and *D. suffructicosum* were partly due to the fact that these species started shedding their seeds at some sites during the sampling period, resulting in a high standard error. However, a high variation in number of seeds found per site was also found for *A. cyclops* (Table 5.10). The non-foredune species (bulked results from 15 species) showed low seed densities in both sampled layers, but higher than *A. cyclops, A. populifolia, G. gueinzii*, and *M. cordifolia* in the 10-20 cm layer (Table 5.10).

Table 5.10. Mean seed densities (± S.E.) over all sites and plots given by layer by species with the state of the seeds. In each sampled layer the total density and the number of plots (n) where a species was found is listed.

Species	State of seeds [1]	Seed density per layer (per m^2)							
		0-10 cm layer				10-20 cm layer			
		N	Mean	(± S.E.)	Total	N	Mean	(± S.E.)	Total
A. cyclops	1≥	6	175.9	(133.2)	1055.6	2	25.9	(18.1)	77.8
A. populifolia	1≥	27	29.0	(4.6)	811.1	11	15.2	(3.1)	166.7
C. monilifera	1≥	40	123.3	(57.7)	4933.3	16	61.8	(17.1)	988.9
D. suffructicosum	<1≥	20	325.6	(118.9)	6511.1	3	88.9	(6.4)	266.7
E. distichus	1≥	30	187.8	(66.2)	5633.3	10	106.7	(35.2)	1066.7
G. gueinzii	1≥	5	53.3	(31.7)	266.7	3	18.5	(7.4)	55.6
H. cordata	<1≥	27	207.0	(104.1)	5588.9	13	135.0	(49.3)	1755.6
I. pes-caprae	1≥	11	144.4	(53.7)	1588.9	3	100.0	(78.0)	300.0
M. cordifolia	1≥	7	33.3	(8.0)	233.3	6	22.2	(9.1)	133.3
S. plumieri	1≥	39	77.2	(16.0)	3011.1	24	30.4	(6.3)	700.0
T. decumbens	1≥	34	75.8	(19.0)	2577.8	24	62.2	(14.7)	1555.6
Non-foredune species	1≥	29	33.0	(6.9)	955.6	17	35.7	(15.9)	677.8

[1] State of seeds: 1≥ - Only seeds from previous season(s) were found (seeds equal or more than 1 year old); <1≥ - Mixture of seeds from present and previous season(s) found (seeds less than, equal or more than 1 year old).

Seeds of the non-foredune group and the alien *A. cyclops* were found at 79% and 50% of the sites sampled, respectively. An exceptional high number of alien seeds were found at Alexandria, whereas for Kleinemonde and Fish River only a few alien seeds

were found (Figure 5.6). At Blue water Bay and Port Alfred no seeds of the non-foredunes species group were found. Between the other 11 sites no significant difference in number of non-foredune seeds was observed (Kruskal-Wallis, $P>0.05$; Figure 5.6). At Jongensfontein, Plettenberg Bay and Old Woman's River the non-foredune seeds were found in more than 50% of the plots sampled at the sites. The number of non-foredune seeds found per site seemed lower compared to the foredune species, but due to the high standard deviations of both groups no significant differences were shown ($P>0.05$; Figure 5.6).

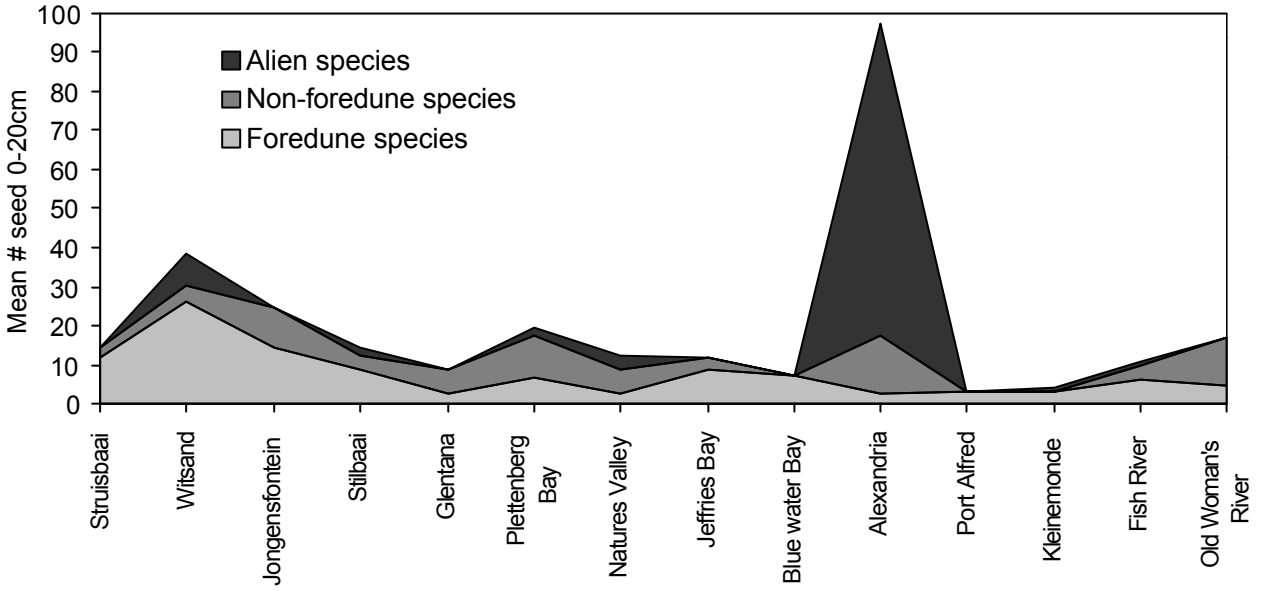


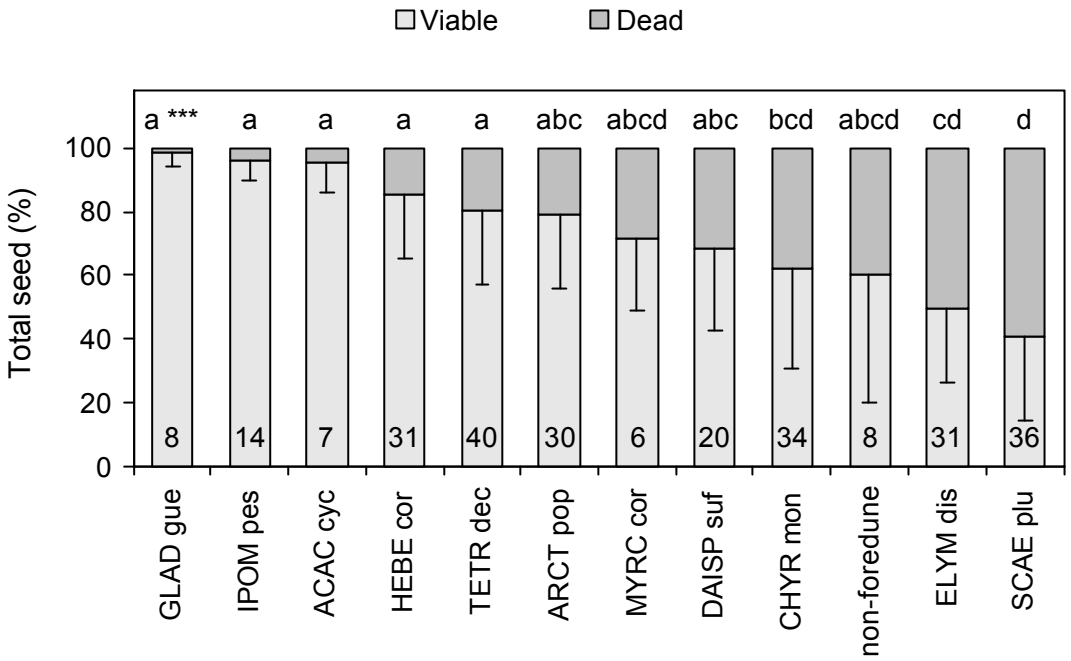
Figure 5.6. Distribution of the mean number of seeds of foredune species, non-foredune species and alien species (*A. cyclops*) found per plot in the top 20 cm given per site in geographical order (west to east).

5.4.4. Viability of seeds found in the soil

The mean number of seeds found in the soil for each species at the sampled sites fluctuated strongly (see Table 5.8), as was found also for the viability of the seeds found in the seed bank (Figure 5.7). The seeds of *G. gueinzii, I. pes-caprae, A. cyclops, H. cordata* and *T. decumbens* showed the highest number of viable seeds when compared to the number of viable seeds of the species *C. monilifera, E. distichus* and *S. plumieri* (Kruskal-Wallis, $P<0.001$; Figure 5.7). The high number of *H. cordata* could be explained by the fact that the seeds found were a mixture of seeds from the present

and previous seasons. The seeds of *S. plumieri* were the only ones showing a viability percentage of less than 50% (Figure 5.7).

Figure 5.7. Mean percentage (± S.E.) of viable and dead seeds by species (over all sites) in the top 20 cm of the soil seed bank with the number of plots (*n*) mentioned at



the base of each column. Any column with the same letter does not differ significantly in number of viable seeds. Contrast obtained by Newman-Keuls after analysis by Kruskal-Wallis. Level of significance: *** - $P<0.001$. Species: ACAC cyc - *Acacia cyclops*, ARCT pop - *Arctotheca populifolia*, CHRY mon - *Chrysanthemoides monilifera*, DAIS suf - *Dasispermum suffructicosum*, ELYM dis - *Elymus distichus*, GLAD gue - *Gladiolus gueinzii*, HEBE cor - *Hebenstreitia cordata*, IPOM pes - *Ipomoea pes-caprae*, MYRI cor - *Myrica cordifolia*, SCAE plu - *Scaevola plumieri*, TETR dec - *Tetragonia decumbens*, Non-foredune - Species not belonging to the foredune environment, mainly weeds.

The seeds were tested for viability by cutting the seeds in half, but for seven of the species some of the seeds were set to germinate in the greenhouse (Table 5.11). Only the seeds of the species *A. cyclops, C. monilifera, I. pes-caprae, S. plumieri* and *T. decumbens* germinated; the *A. cyclops* seeds especially showed a high germination percentage. The ungerminated seeds of the species *H. cordata, I. pes-caprae* and *T. decumbens* were more than 50% viable, whereas of the ungerminated seeds of *C. monilifera, D. suffructicosum,* and *S. plumieri* more than 60% were dead.

An analysis of data of figure 5.7 showed that the seeds of *A. cyclops, I. pes-caprae* and *T. decumbens* had a high number of germinated and/or viable seeds, whereas

S. plumieri and *C. monilifera* recorded a high percentage of dead or non-viable seeds (Table 5.11 and Figure 5.7).

Table 5.11. Mean percentage of germinated, viable and dead seeds (± S.E.) of the 0-10 cm layer (A) and the 10-20 cm layer (B) found in the soil seed bank of different sites with the number of replicates (N) per species.

A)

Species 0-10 cm layer	*n*	Germinated		Viable		Dead	
		Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
A. cyclops	1	85.3		6.67		8.0	
C. monilifera	3	5.3	(4.6)	19.5	(16.9)	75.1	(21.6)
D. suffructicosum	1	0.0		40.0		60.0	
H. cordata	3	0.0		44.4	(16.3)	55.6	(16.3)
I. pes-caprae	4	22.6	(23.7)	77.4	(23.5)	0.00	
S. plumieri	4	0.0		31.3	(47.2)	68.8	(47.3)
T. decumbens	12	18.2	(12.7)	53.5	(18.5)	27.4	(18.5)

B)

Species 10-20 cm layer:	*n*	Germinated		Viable		Dead	
		Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
A. cyclops	1	80.0		20.0		0.0	
C. monilifera							
D. suffructicosum							
H. cordata	1	0.0		88.9		11.1	
I. pes-caprae	2	0.0		100.0		0.0	
S. plumieri	1	25.0		12.5		62.5	
T. decumbens	5	2.7	(3.8)	64.5	(25.9)	32.8	(26.6)

5.4.5. Seed characteristics

The seed weight and shape (length, width and height) were measured for the species *A. arenaria, A. cyclops, A. populifolia, C. monilifera, D. suffructicosum, G. gueinzii, H. cordata, I. pes-caprae, M. cordifolia, S. plumieri, S. primuliflora,* and *T. decumbens.* All diaspores measured were single seeds, with exception of *T. decumbens* which was measured as a dispersal unit (containing >1 seed) since the seeds do not leave the seed pod during dispersal and burial. For the species *A. populifolia, I. pes-caprae* and *M. cordifolia* a second seed type was measured: for *A. populifolia* seeds without the seed coat, for *M. cordifolia* seeds without the wax layer, and for *I. pes-caprae* old and scarified seeds of the seed bank were measured. The second seed type were marked with an * and presented as an open symbol in figure 5.8. None of the foredune seeds measured fell within the persistence area (Figure 5.8). The seeds of *A. cyclops, G. gueinzii, I. pes-caprae, M. cordifolia, S. plumieri,* and *T. decumbens* fall within the shape variance boundary, but were too heavy (>3 mg). The remaining species were either too flat or too elongated to fall within the shape variance boundary and were also too heavy (Figure 5.8).

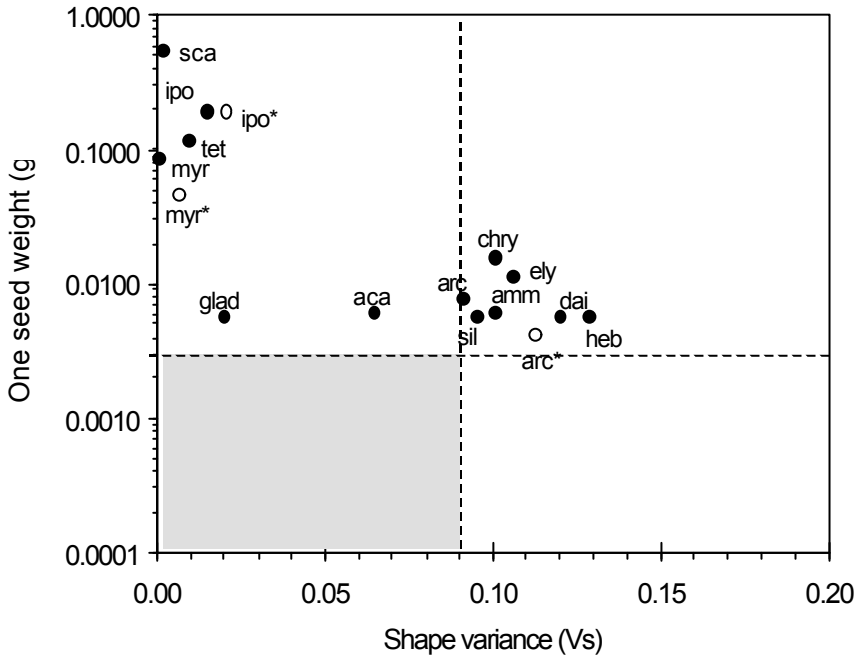


Figure 5.8. The weight-shape variance (Vs) graph of the species found in the soil seed bank. The dots represent the mean values of the species (*n* = 50) with the grey area in the graph representing the persistence area of Thompson *et al.* (1993), with dotted lines representing the weight (3 mg) and shape variance (0.093) boundary (with

adjustment of Bakker *et al.* 1996a). All the diaspores measured were true seeds with the exception of *T. decumbens* which was measured as dispersal unit.

Species: amm – *A. arenaria*, aca – *A. cyclops*, arc – *A. populifolia*, arc* -*A. populifolia* without seed coat, chry – *C. monilifera*, dai – *D. suffructicosum*, ely – *E. distichus*, glad – *G. gueinzii*, heb – *H. cordata*, ipo – *I. pes-caprae*, ipo* – *I. pes-caprae* old seeds, myr – *M. cordifolia*, myr* - *M. cordifolia* without wax layer, sca – *S. plumieri*, sil – *S. primuliflora*, tet – *T. decumbens*.

The relation between seed weight and the seed shape variance was significant, but showed a weak correlation with a correlation coefficient of 0.24 (Figure 5.9).

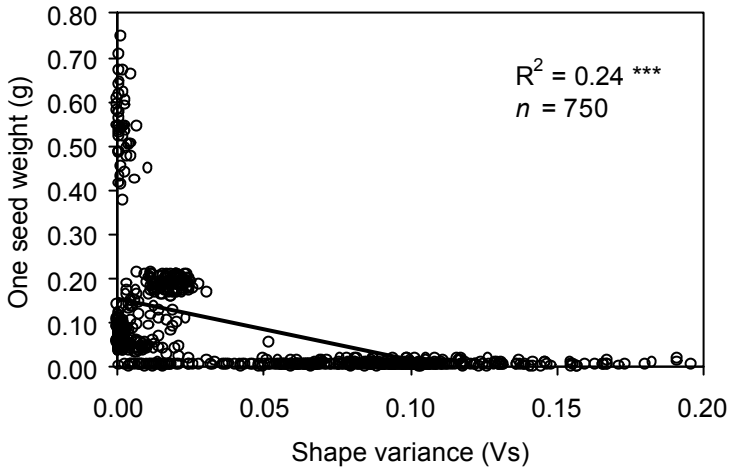


Figure 5.9. The regression between seed weight (g) and shape variance (Vs) for all seeds measured (*n* = 750). Contrast obtained by regression analysis. Level of significance: *** - *P*<0.001.

From figure 5.8 and 5.9 it was clear that the weight and shape variance boundaries set for north-western European species (3 mg and 0.093), were not applicable for the bigger foredune seed.

A certain combination of the weight, shape, and volume might give a better prediction of seed longevity, therefore for eight characteristic foredune species suspected of being either persistent or transient, various combinations were calculated using weight, shape and volume (Table 5.12). To compare the different measures the measures of the different parameters were allocated to four classes from low (+) to high (++++). All the transient seeds showed a low seed weight, but the persistent seeds of *A. cyclops* and *C. monilifera* were also found in the lowest weight classes (Table 5.12). The shape variance was fluctuating within the persistent and transient groups. The transient seeds all showed high shape variances, with exception of the almost perfectly round seeds of *G. gueinzii.* The shape variances of the persistent seeds were represented in each

shape variance class, with the highly persistent *A. cyclops* in the highest class as was seen for the volume of the seeds. In general seed weight, shape variance and volume as a single predicting seed characteristic were not a good prediction tool. When combining the weight and shape variance to one characteristic by multiplying or taking the square root of one of the characteristics the result was the same, too much variation was observed to find a trend to predict longevity. The same was observed when weight and volume were combined (Table 5.12). Perhaps the seeds do not follow any principle in a changing environment such as the foredunes.

Table 5.12. The predicted and expected longevity of four persistent and four transient species found in the soil seed bank of the foredunes. The longevity was predicted using the seed characteristics seed weight (W), shape variance (Vs) and volume (Vol). The expected longevity was obtained from the present research and the literature. Classes: ++++ - very high values, +++ - high values, ++ - intermediate values, + - low values.

Seed characteristics	Transient (≤ 1 year)				Persistent species (> 1 year)			
	A. populifolia	*A. arenaria*	*G. gueinzii*	*D. suffructicosum*	*A. cyclops*	*C. monilifera*	*I. pes-caprae*	*T. decumbens*
Predicted longevity:								
Weight (W)	+	+	+	+	+	+	+++	+++
Shape variance (Vs)	++++	++++	+	++++	+++	++++	++	+
Volume (Vol)	++	+	+	+	++	++	++++	+++
Weight + Shape variance:								
W * Vs	+	+	+	+	+	+++	++++	+++
W * √ Vs	+	+	+	+	+	++	++++	++
Vs * √ W	+++	+++	+	+++	++	++++	++	+
Weight + Volume:								
W * √ Vol	++	++	+	++	++	++	++++	+
Vol * √ W	+	+	+	+	+	++	++++	++
Vol * W	++	++	+	++	+	++	++++	+
'Expected' longevity:								
Years	<1	<1	1-2	<1	>5	>5	>5	1-5

5.4.6. Summary

When all results of the seed characteristic were combined, no clear trend in predicting seed longevity could be found (see Table 5.12), but the seed weight seemed to be important in the burial chance of a seed. With the results obtained by sampling the seed bank in different layers and testing the seeds on viability, the longevity of the species could be determined (Table 5.13). The expected longevity in Table 5.13 was based on the literature and seed coat structure (present/absent or soft/hard).

The species *D. suffructicosum* and *H. cordata* were expected to be part of the transient seed bank due to the fact that the seed had a soft and thin seed coat. The seeds of *D. suffructicosum* were found more often in the seed bank when also present in the vegetation, whereas many of the seeds of *H. cordata* were found only in the seed bank. For both species relatively high densities of the light-weighted seeds were found in both layers of the seed bank which was suggesting a transient seed bank.
The percentages of viable seeds for *D. suffructicosum* and *H. cordata* were 68% and 86%, respectively. The seeds of *D. suffructicosum* and *H. cordata* started shedding during the sampling period, explaining the high viability found. Therefore, the *D. suffructicosum* and *H. cordata* seeds were considered to be transient, as expected (Table 5.13). *A. populifolia, E. distichus,* and *G. gueinzii* were expected to be part of the transient seed bank, again due to the fact that the seeds were soft and not protected by a hard seed coat. Seeds of all three species showed low seed weights and were found in both layers of the seed bank. The densities of *A. populifolia* and *G. gueinzii* were low, but showed a high viability, whereas the *E. distichus* seeds were found in with a higher density but with a lower percentage of viability. The seeds of *E. distichus* were most often found when also present in the vegetation. This was not the case for *A. populifolia* and *G. gueinzii*, for which the seeds were found most often in the 'seed bank only' category. Unlike *E. distichus* and *G. gueinzii, A. populifolia* produces seeds throughout the year, but during the sampling period the plants were flowering and no 'new' seeds were found. Seeds found looked battered and were believed to be at least a few months old and assumed to be from previous season(s). With the information in Table 5.13, *A. populifolia, E. distichus* and *G. gueinzii* were moved from the expected transient class to the short-term persistent class (Table 5.13).

M. cordifolia was the only species expected to have a short-term persistent seed bank, due to the fact that, even though the seeds do look like persistent seeds, no seedlings were observed in the field. Most of the hard, heavier, round seeds of *M. cordifolia* were found in the seed bank in a low density (22-33 seeds/m^2) in both layers, but not in the vegetation. The seeds found all looked scarified and were without the thick waxy fruit layer and showed a high viability. Considering all the facts the seeds of *M. cordifolia* were definitely part of the short-term persistent seed bank.

The remaining species *C. monilifera, I. pes-caprae, S. plumieri, T. decumbens* and *A. cyclops* were considered to be long-term persistent. All those species have reasonably big seeds with very tough seed coats. The seeds of *A. cyclops* and *C. monilifera* were found most often only in the seed bank, whereas *I. pes-caprae, S. plumieri* and *T. decumbens* seeds were found in the seed bank and in the vegetation. Also seeds of all five species were found in both layers of the seed bank in densities ranging from 30 to 144 seeds/m^2. The seeds that were found in the soil for *I. pes-caprae, T. decumbens* and *A. cyclops* showed a very high percentage of viability (80% - 96%), whereas the viability of *S. plumieri* and *C. monilifera* was much lower.
The seeds of *I. pes-caprae* and *S. plumieri* were very heavy compared to the other species. The seeds of *T. decumbens* were of intermediate weight, whereas the elongated seeds of *A. cyclops* are light in weight.
Considering the fact that the seed viability of *S. plumieri* and *C. monilifera* was lower than to be expected if they were long-term persistent, the species were considered to be short-term persistent. The species *A. cyclops, I. pes-caprae* and *T. decumbens* showed a high viability and therefore were considered to be long-term persistent as expected from the literature and the percentage of viable seeds found in the soil (Table 5.13).

Table 5.13. Summary of results from seed bank sampling and seeds with additional species information.

Description of species						Seed bank sampling									Seed characteristics				
Species	Life form	Successional status [1]	Species longevity [2]	**Expected seed longevity [3]**	# Sites species found	Vegetation only (%)	Seed bank only (%)	Both (%)	**Seed longevity [3]**	Density 0-10 cm	Density 10-20 cm	% Viable	State of seeds found [4]	**Seed longevity [3]**	Seed shape [5]	Seed weight (mg) [6]	Volume (mm3) [7]	**Seed longevity [3]**	**Final longevity [3]**
A. populifolia	Herb	1	2	**1**	10	32	37	21	**2**	29	15	79	1>	**1-2**	5	1	1	**1**	**2**
C. monilifera	Shrub	2-3	3	**3**	13	7	71	22	**2**	123	62	61	1>	**2**	5	1	1	**1**	**2**
D. suffructicosum	Herb	1-2	3	**1**	6	21	25	54	**2**	326	89	68	<1>	**1-2**	5	1	1	**1**	**1**
E. distichus	Grass	1	3	**1**	8	35	19	46	**2**	188	107	50	1>	**2**	5	1	1	**1**	**2**
G. gueinzii	Herb	1-2	1	**1**	7	71	19	10	**2**	53	19	98	1>	**3**	1	1	1	**1**	**2**
H. cordata	Herb	1-2	3	**1**	9	3	66	31	**2**	207	135	86	<1>	**1-2**	5	1	1	**1**	**1**
I. pes-caprae	Herb	1-2	3	**3**	5	57	3	40	**2**	144	100	96	1>	**3**	1	3	2	**2**	**3**
M. cordifolia	Shrub	2-3	3	**2**	7	18	64	18	**2**	33	22	71	1>	**2**	1	2	1	**2**	**2**
S. plumieri	Shrub	1-2	3	**3**	10	40	6	54	**2**	77	30	41	1>	**2**	1	6	6	**2**	**2**
T. decumbens	Herb	1	3	**3**	10	40	12	48	**2**	76	62	80	1>	**3**	1	2	1	**2**	**3**
Alien *A. cyclops*	Shrub	2-3	3	**3**	7	70	20	10	**2**	176	26	96	1>	**3**	3	1	1	**1**	**3**
Non-foredune species	-	-	-	**-**	11	0	100	0	**2**	33	36	60	1>	**2**	-	-	-	**-**	**-**

[1] Successional status: 1 - pioneer species, 2 - Early successional species, 3 - Mid-successional species, 4 - Late successional species (Tinley 1985, Lubke & Van Wijk 1998).
[2] Species longevity: 1 - Annual species, 2 - Biennial species, 3 - Perennial species (Tinley 1985, Lubke & Van Wijk 1998).
[3] Seed longevity, including final longevity: 1 - Transient (< 1 year), 2 - Short-term persistent (1-5 years), 3 - Long-term persistent (> 5 years) (Nomenclature Bakker *et al.* 1996a).
[4] State of the seeds: <1 - New seeds, from present season (< 1 year old), 1> - Older seeds, from previous seasons(s) (≥ 1year old), <1> - mixture of new and older seeds.
[5] Seed shape: 1 = ≤ 0.025, 2 = 0.026-0.050, 3 = 0.051-0.075, 4 = 0.076-0.100, 5 = 0.101-0.150, 6 = 0.151-0.200.
[6] Seed weight (gram): 1 = ≤ 0.050, 2 = 0.051-0.150, 3 = 0.151-0.250, 4 = 0.251-0.350, 5 = 0.351-0.450, 6 = 0.451-0.550.
[7] Volume (mm^2): 1 = 0-250, 2 = 251-500, 3 = 501-750, 4 = 751-1000, 5 = 1001-1250, 6 = 1251-1500.

5.5. DISCUSSION

Most of the available reports suggest that persistent seed banks may not be present in dune systems (Barbour 1972, Watkinson 1978b, Boorman & Fuller 1984, Planisek & Pippen 1984). However, a few studies have shown that seeds of several buried dune species remained viable for two years, suggesting a potential to build a soil seed bank (Pamadasa & Lovell 1975, Zhang & Maun 1994). The survival of seeds in the soil (longevity) is highly variable and species dependent (Roberts 1970, Warr *et al.* 1993). The general consensus is that seeds have irregularly clustered spatial distributions, dictated by both biotic and abiotic environmental factors (Major & Pyott 1966, Graber & Thompson 1978). The post-dispersal movement of seeds may cause seeds to become aggregated, because wind scatters the diaspores and they accumulate in sites where wind velocity is low, such as the leeward sites of the foredune (Harper 1977, Danin 1991). Therefore, the seed bank was sampled in depressions in front and behind the first foredunes as a first step in proving that the foredune species do form a seed bank.

Seed bank and established vegetation

At all sites sampled seeds of different foredune species were found in both layers of the soil seed bank. In total 27 foredune species were recorded in the vegetation of the sample sites, from which 11 species were present in the soil seed bank, including the alien *A. cyclops*. Besides the foredune species, 15 non-foredune species were found in the soil seed bank of 78% of the sites sampled. None of these species grew at the site or in the vicinity of the sampled plots and the seeds were very small and usually present in low densities. Only the common roadside weed *Datura stramonium* was found in higher numbers (up to 32 seeds/sample). These seeds were probably dispersed to the site by the wind or by birds. This means that many of the non-foredune species also have at least short-term persistent seeds.

For most sites the front and the back of the foredunes was sampled. At the front of the foredunes the environment is usually more unstable (Hesp 1991) and the seeds ending up at the front of a foredune probably have a higher chance of being secondarily dispersed by the wind before being buried by the fast moving sand (Danin 1991, Looney & Gibson 1995). This observation was supported by the fact that at 56% of the sites the plots situated at the back of the foredunes showed higher seed densities and higher species richness.

The foredune species found in the soil seed bank were all perennial species of the pioneer to mid-successional stage. No annuals were observed in the soil seed bank or the established standing vegetation, as was also observed by Looney and Gibson (1995). Not all species found in the vegetation of the sampled plots were represented in the soil seed bank (e.g. *Ammophila arenaria*, *Passerina rigida* were missing). According to Thompson *et al.* (1997) these species would be transient because they were absent from the seed bank, but present in the vegetation. This absence from the seed bank could be due to the fact that a species was really absent, or does not produce seed at a site (e.g. *A. arenaria*) and will then appear as transient. The absence could also be due to the fact that the seeds were not detected due to the small size, which might be the case for the small wind-dispersed seeds of *P. rigida*.

In 27% of the plots sampled seeds of species occurred in the soil seed bank that were absent from the vegetation. A comparison between the three dominant species found in the vegetation and the seed bank showed the highest similarity (100% overlap) for Struisbaai. The seed bank dominant species were often only represented with one or two species in the vegetation, or as seen at Fish River for *S. plumieri,* absent from the vegetation. This is in contrast to the findings of other research where the principal strand and dune species found in the seed bank were strongly associated with the vegetation dominance (e.g. Looney & Gibson 1995). Whereas, Ungar and Woodell (1993) found a high correlation between vegetation and seed bank for annuals, but a low correlation for perennials.

The seeds of *C. monilifera* were found most often in the soil seed bank without being present in the vegetation, which could be explained by the fact that the seeds are bird-dispersed (Tinley 1985, Weis 1986). The big and heavy seeds of I *pes-caprae* and *S. plumieri* were mainly found in the seed bank when also present in the vegetation. The other seeds found in the seed bank are relative smaller and lighter compared to *I. pes-caprae* and *S. plumieri.* The lighter seeds are more easily blown across the sand surface and secondarily dispersed to other parts of the dunes, which could explain the low numbers of observations in the 'seed bank only' category for *I. pes-caprae* and *S. plumieri*. The few 'seed bank only' observations of *I. pes-caprae* and *S. plumieri* could be explained by the fact that the seeds can be dispersed by seawater (Ridley 1930, Tinley 1985). Another explanation is that the seeds could be a remnant of

previous vegetation (Bakker *et al.* 1996a, Thompson *et al.* 1997). The seeds of *I. pes-caprae* have very hard seed coats and would probably be able to survive for years in the soil seed bank after the plants have died. According to the key of Thompson *et al.* (1997) those species should be described as at least short-term persistent. The same was observed for *A. cyclops* at Alexandria. In general at 63% of the sampled sites the alien *A. cyclops* was found in the soil seed bank where it was also present in the vegetation. Only at Alexandria did the species occurred solely in the seed bank as previous stand had been cut down and removed. Birds disperse the seeds *of A. cyclops* (Tinley 1985, Stehle 1987), but the densities found were much too high for bird dispersal. The samples were probably taken at a plot where *A. cyclops* used to grow and this was supported by buried *A. cyclops* brushwood at the site.

The waxy seeds of *M. cordifolia* were in general poorly represented in the seed bank, even though birds (Tinley 1985) disperse the seeds. The lack of seeds in the seed bank might be explained by the fact that the species forms an aerial seed bank (Tinley 1985), where the seeds stay on the plant. Seeds in long-term aerial seed banks usually are non-dormant and germinate readily when dispersed. This might be the reason why soil seed banks of these species are not developed all that well (Baskin & Baskin 1998).

In general the Simpson's and Shannon diversity indices found for the seed bank were in the same order as found by Pierce and Cowling (1991) for seed banks of the coastal dune grassland, fynbos and thicket vegetation, but usually with lower species richness.

Sampling depth

Several authors (Kellman 1978, Young 1985, Young *et al.* 1987) stated that the seeds often show an almost uniform distribution with depth, whereas the foredune species in general showed a strong decline with depth for seed density and species richness. The first 10 cm showed the highest density and species richness compared to the 10-20 cm layer. Normally the seed bank of, e.g. grasslands, will be sampled to a depth of 10 cm, but, because of the unstable sandy substrate, samples from greater depths were taken. In general deeply buried seed is assumed to be older than seed near the soil surface, because the seeds need time to get to greater depths (Chippendale & Milton 1934, Kellman 1978, Hill & Stevens 1981, Thompson *et al.* 1993, Bakker *et al.* 1996a). This seems not to hold for the dune environment. For example the seeds of *I. pes-caprae* lose the hairs on the seed coat due to sand scarification. The older, scarified (≥ 2 year old) and newer hairy seeds (< 1 year old) were found at all layers, even up to 40 cm

deep at Fish River, proving how mobile the dune system can be. In fact the chance that a seed will remain unburied on the sand surface is rather low (Maun & Riach 1981, Looney & Gibson 1995; see Plate 5.2).

Plate 5.2. Seed accumulation of *S. plumieri* at the base of a landward facing foredune.

Seed longevity: Evidence from seeds and seed banks

For all species found in the seed bank at least 40% were viable, but variation was found between and within species and sites. The fact that for all species viable seeds were found indicates that the species form at least a transient seed bank, since most seeds were from the previous season (≥1 year old). The longevity of seeds of different species is very variable and the seeds of some species can retain viability in the soil for periods up to a 100 years (Warr *et al.* 1993). The main causes of depletion of the seed bank are germination, predation, fungal attack and loss of viability (Roberts 1981b). The relative importance of these sources of mortality is usually unknown, and must vary with species, habitat and depth of burial (Warr *et al.* 1993).

The seeds found for *C. monilifera* were known to persist in the soil for years (Tinley 1985, Weis 1986), but showed a low viability. Many of the seeds were found at plots without vegetation and probably arrived at the sites via bird dispersal (Tinley 1985).

The passage through the bird's digestive tract might have damaged/softened the seed coat (Ridley 1930, Stiles 1992), making the seed susceptible to pathogens and predators (Bewley & Black 1994). There is some evidence that seed viability is retained longer with increasing depth of burial in the soil (Pons 1989), perhaps because losses due to predation and germination are less at greater depths in the soil (Rampton & Ching 1970, Warr *et al.* 1993). However, a lot of seed halves and damaged seeds have been found at greater depths for *C. monilifera* indicating that predation could have occurred at deeper depths at the South Africa foredunes.

Little is known about the relations between different seed characteristics and distribution in the soil with regard to seed longevity of the dune environment. Seed characteristics like weight, shape, seed coat structure are linked with the longevity and seed bank behaviour of species in Europe (Shen-Miller *et al.* 1995, Werker 1997, Thompson *et al.* 1997) and Argentina (Funes *et al.* 1999). Thompson & Grime (1979), Leck *et al.* (1989) and Thompson *et al.* (1993) suggested that seed size and shape might predict persistence in the soil. The variance in shape and weight of diaspores varies little between individual seeds of the same species (Thompson *et al.* 1993, Garner & Witkowski 1997). The relation found between seed weight and shape defined as a persistence area (Thompson *et al.* 1993) translates to the fact that small compact seeds are persistent and larger flattened or elongated seeds are transient.

None of the seeds found in the soil seed bank of the foredunes fell within the persistence area of Thompson *et al.* (1993) because the seeds were all too heavy and/or too flattened and/or elongated. The persistent seeds of the foredune species were not smaller and more compact than transient seeds, when compared across all species. This could be due to the fact that due to the abiotic conditions at the coast the seeds follow a different pattern. Or because some species measured were not herbaceous like the woody shrubs *S. plumieri* and *M. cordifolia*, but the herbaceous slightly elongated, heavy seeds of *I. pes-caprae* also did not fit the 'rules'. Any combination of shape or volume with weight did not lead to a variable that separated persistent from transient. Leishman and Westoby (1998) also failed to find a relationship between seed size/shape and persistence in the soil for Australian species from a range of habitats.

That no evidence was found for any relationship between weight, shape and volume, even as a single characteristic, might result from the fact that the conditions of burial at

the foredunes are different from those of the species measured by Thompson *et al.* (1993). For instance the seed of foredune and beach species are in general heavier (Cavers & Harper 1966, Fenner 1985, 1992, Rees 1995). This might suggest that seed weight was of more importance than shape in a very mobile sandy environment when seed bank behaviour and seed longevity is concerned. The heavier seeds tend to stay more in depressions where they end up after secondary dispersal and might therefore have a higher chance of being buried compared to lighter seeds that are more easily blown away (Maun & Riach 1981, Looney & Gibson 1995). The heavy seeds of *I. pes-caprae, S. plumieri* and *T. decumbens* were all considered to be at least short-term persistent (soil survival of 1-5 years).

In general little is known of how seeds enter the soil. Oosting and Humphreys (1940) suggested a gradual process in which seeds are buried as a result of litter accumulation and soil-forming processes. However, more rapid incorporation of seeds in the soil is likely to occur as a result of rainwater percolation, and the activity of burrowing animals and soil fauna such as ants, termites and earthworms (Harper 1977, Guo *et al.* 1998). But, in the dune environment, the chance of getting buried is more related to the unstableness of the environment than the shape or weight of the seeds, or factors mentioned above.

Comparison with other systems

Comparisons of seed banks of communities analogous to foredunes are limited. Zhang and Maun (1994) found 0 to 2165 seeds/m^2 in the sand dunes of the great Lakes, whereas Pierce and Cowling (1991) found for the coastal grasslands, thicket and fynbos seed densities of 4273, 3417 and 1683 seeds/m^2, respectively.

The coastal marsh seed bank was much larger with seed densities ranging from 0 to 140,000 seeds /m^2 (Jefferies *et al.* 1981, Ungar & Woodell 1993, 1996, Todd & Ungar 2000). Halophytic shrubs that dominate the coast of the Arabian sea have seed banks ranging up to 940,000 seeds/m^2 (Khan & Gul 1999), whereas the seed bank sizes for saline desert community's range from 0 to 981 seed/m^2 (Khan 1990).

Although methodological differences make a direct comparison difficult, it would seem that the seed bank of the coastal foredunes is not exceptional with densities of 0 to 2,778 seed/m^2. In the present study the seed bank was sampled in dune depressions, due to the fact that the aim was to prove that foredune species do form a soil seed bank. Therefore, with random sampling the seed densities found would be lower since

developing dunes provide a poor habitat for seed bank development because the low plant cover permits high levels of sand movement (Looney & Gibson 1993, 1995).

Concluding remarks

The conclusion of the present study is that foredune species of South Africa foredunes form at least a short-term persistent seed bank with seed surviving at least a year in the soil. The seeds of all main foredune species were well represented in the soil seed bank with few having the potential to be long-term persistent, based on the seed characteristics and field observations. In general it is difficult to distinguish between short- and long-term persistence without burial experiments of at least 5 years. The failure to detect dune seed banks by other authors may have been due to improper sampling techniques, inadequate sample size or sampling depths. The dune system is variable with high sand accretion rates; thus for reliable estimates of seed banks in dune systems relatively large soil samples should be obtained from shallow and deep locations.

CHAPTER 6

LONG DISTANCE DISPERSAL OF SELECTED COASTAL FOREDUNE SPECIES OF SOUTH AFRICA

The seashore is a uniform easy pathway leading to its own rapid migration of its own characteristic flora of strand plants.

Bews (1925)

6.1. INTRODUCTION

An important feature of plants, and a significant phase in the life history of plants is seed dispersal. The importance is indicated by the fact that many resources are invested in moving seeds through space with the benefit of spreading genetic material by colonisation of new habitats (Van der Pijl 1982). It is also a critical stage in the survival of plant species and communities, especially in unpredictable habitats (Van der Pijl 1982, Armstrong 1998), as successful regeneration depends upon seeds being dispersed to a 'safe site', where the seeds can germinate and establish seedlings (Harper 1977, Fenner 1985). The characteristic pattern in which an individual deposits the seeds depends in general on the size and shape of the seed, the height of the parent plant, and the density of the surrounding vegetation (Fenner 1985). Plants produce many different shapes and sizes of diaspores (Werker 1997), hence within a plant community a wide range of dispersal mechanisms can be found including dispersal by wind, water, by the plants self, and via dispersal agents like birds and ants (Van der Pijl 1982). The proportion of species using particular agencies varies between plant communities (Fenner 1985).

The type of surface the seeds land upon after dispersal is the primary determinant of their subsequent secondary dispersal movement or phase II dispersal (Chambers & MacMahon 1994, Marone *et al.* 1998). Phase II dispersal is in the coastal dune environments is often a major factor due to the smooth sand surface (Watkinson 1978a). During this phase the diaspores (seeds, fruits or rhizomes) are frequently blown into the swash zone and carried away to sea by the waves. It is known that seeds of certain beach species, especially, can stand seawater dispersal for different periods of time, or even have special adaptations to float on seawater (Ridley 1930, Muir 1937). That seawater dispersal is important for colonising new habitats was demonstrated by the fact that at the Pacific Ocean islands the seeds of sea-drift species were mainly responsible for colonising the islands (Carlquist 1967). Over time the successful establishment after seawater dispersal shows in general a low rate, but sea transport does not have to be frequent to be effective (Carlquist 1967). The likelihood of seeds arriving at a new site will be influenced by the distance from the nearest seed source, the direction of prevailing winds, the currents, and the buoyancy of the seeds (Fenner 1985).

Is seawater dispersal also of importance for the Cape coastal foredune species? To answer this question the buoyancy of the dispersal units (fruits, seeds and rhizome

fragments) of strand and foredune species was tested, as well as the survival after seawater dispersal.

It is known from the literature that the seeds of the dune pioneers *Ipomoea pes-caprae* and *Scaevola plumieri* are equipped with a floating device (Ridley 1930, Muir 1937), in contrast to the unspecialised or non-buoyant dispersal units of *Myrica cordifolia.* The rhizome fragments of pioneer grasses like *Sporobolus virginicus* are known to be seawater dispersed, but will only stay buoyant for a few days (Muir 1937).

Therefore the expectation is that only the specialised seeds of *I. pes-caprae* and *S. plumieri* will float for prolonged periods and will survive the dispersal, whereas the non-buoyant species might be able to float for a few days but would not survive long floating periods. To test this hypothesis dispersal units of *Ipomoea pes-caprae*, *Myrica cordifolia*, and *Scaevola plumieri* and rhizome fragments of *Ammophila arenaria*, *Ehrharta villosa*, and *Sporobolus virginicus* were put in artificial seawater to test buoyancy and viability after different floating periods.

6.2. DISPERSAL MECHANISMS AND STRATEGIES

The advantages of dispersal emphasises on avoiding disproportionate seed and seedling mortality near the parent (Escape hypothesis), colonising disturbances (Colonisation hypothesis), or locating habitats suitable for establishment and growth (Directed dispersal hypothesis). The 'Escape hypothesis' implies a disproportionate success for seeds that escape the vicinity of the parent, as compared to the ones that fall nearby. Most seeds fall near the parent plant (Levin & Kerster 1974) and they have a higher density-dependent mortality due to predation (Janzen 1970), pathogen attack (Antonovics & Levin 1980), and seedling competition (Harper 1977). The 'Colonisation hypothesis' assumes that habitats change, and dispersal in space and time allows a parent to produce offspring capable of taking advantage of uncompetitive environments as they open. The 'Directed dispersal hypothesis' assumes that adaptation ensures that diaspores reach localised sites suitable for establishment by, for instance, using a dispersal agent such as in the case of the dispersal of *Viola* species by ants (Culver & Beattie 1980). The alternatives are not exclusive, but may differ in importance from one population to the other. In the ever-changing environment of the coastal dunes the plants probably are adapted to a combination of the Colonising and Directed dispersal hypotheses (Howe & Smallwood 1982).

Watkinson (1978a) distinguished two aspects of seed dispersal: phase I and phase II. Phase I dispersal involved movement of diaspores from the infructescence to the soil surface, whereas phase II dispersal consists of subsequent movement of diaspores along the soil surface. Phase II dispersal is a major factor on smooth soil surfaces with bare soil (Watkinson *et al.* 1979), as found in the coastal environment.

Dispersal mechanisms

Dispersal can be defined as the means with which higher plants reach different sites to establish new generations. The units of dispersal, the diaspores, are in general nude seeds, seeds liberated from dehiscent fruits, simple fruits (one ovary), aggregated fruits (many ovaries), a multiple collective of fruits, or vegetative parts of the plant (Van der Pijl 1982). The dispersal of these diaspores often involves an external agent such as wind (anemonochorous), water (hydrochorous), and animals (zoochorous), whereas plant species which disperse their own seeds are classified autochorous (Howe & Smallwood 1982, Van der Pijl 1982, Fenner 1985). The fruit and seed morphology may indicate the general means of dispersal (Howe & Smallwood 1982). The various

dispersal modes include adaptations such as nutritious fruit adapted to attract (in)vertebrate consumers (Van der Pijl 1982, Stiles 1992), the buoyancy of coconuts that float thousands of miles (Ridley 1930), dust-like seeds wind-dispersed seeds of the orchids (Ridley 1930), wings and plumes capable of aerial transport (Burrows 1975), and ballistic fruits that can toss seeds for several metres (Beattie & Lyons 1975). Most diaspores are deposited near the parent plant and in many cases there is a negative relationship between density of deposited seeds and the distance from the parent plant (Werner 1975). An obvious modification for dispersal may not imply the actual process used, nor does the absence of an obvious mechanism preclude dispersal by a certain agent; the syndromes are only a general organising tool (Van der Pijl 1982).

The fate of dispersed seeds

When the seeds land on the soil surface, the seeds can either (i) remain where landed, (ii) move along the soil surface (phase II dispersal); (iii) become buried; (iv) be predated on the soil surface; (v) removed from the soil surface and carried long distances by dispersal agents; (vi) be killed by pathogens; (vii) germinate or die on or beneath the soil surface (Sagar & Mortimer 1976, Hutchings 1989). Some seeds may experience more than one of these fates, whereas predation, death and germination are terminal from the dispersal point of view.

6.2.1. Strategies of South African foredune species

The foredune species of the Eastern Cape coast show different dispersal strategies. But many of the foredunes species have no primary means of phase I dispersal, as for most of the foredune and strand species the seeds fall from the parent plant and roll down the dune (Autochory - phase I dispersal). After phase I, the diaspores could be blown across the sand surface to end up in depressions at the base of the dunes to germinate, to get buried, or to end up in the swash zone to be washed into sea by phase II dispersal. This sequence of phase I and phase II dispersal was observed for the nearly spherical diaspores of the species *Hebenstreitia cordata*, *Gladiolus gueinzii*, *Ipomoea pes-caprae*, *Scaevola plumieri*, and *Tetragonia decumbens*, as well as for the light and elongated seeds of *Arctotheca populifolia, Dasispermum suffructicosum*. The diaspores of *G. gueinzii*, *D. suffructicosum,* and *T. decumbens* have winged seeds. Winged seeds are a modification for wind dispersal (Table 6.1), but due to the heavy weight of the seeds, only the seeds of *D. suffructicosum* could be air-dispersed. The wings in the

case of *T. decumbens* are more an enhancement for phase II surface-wind dispersal and might also assist in short-distance water dispersal; this in contrast to the small seeded *Metalasia muricata* and *Stoebe plumosa*, which are considered to be true wind dispersed species (Tinley 1985).

The seeds of *Acacia cyclops*, *Chrysanthemoides monilifera* and *Myrica cordifolia* remain on the parent plant (aerial seed bank), to be eaten and dispersed by birds (endozoochory). The seeds in the seed pod of *A. cyclops* are surrounded by a bright red and nutritious aril to attract birds, whereas for *C. monilifera* and *M. cordifolia* the diaspores are surrounded by a fruit-like structures; both are modifications for vertebrate/bird dispersal (Howe & Smallwood; Table 6.1).

Table 6.1. The major dispersal syndromes of fruits and seeds, mentioned with the dispersal agents, diaspore modification and derivation (after Howe & Smallwood 1982).

Dispersal agent and general adaptation	Modification	Derivation	Comment
Animal			
fleshy nutrient	aril, pericarp, pulp	seed coat	vertebrates
chemical attractant	elaiosome	seed integument	ants
clinging structures	hooks, viscous material	floral parts	sticks to fur
mimesis	coloured seed coat	seed coat	eaten by birds
Wind			
size reduction	dust-like seeds	seeds	hundreds per plant
high surface/volume ratio	wings, plumes	seed coat or fruit	-
Water			
resistance to sinking	hairs or slime	seed coat	submerged transport
uses surface tension	small size, unwettable	seed coat	floats until wetted
low specific gravity	air species, cork, oil	seed or fruit	floats long distance
Self dispersal			
explosive fruits	varied	fruits	secondary transport
creeping diaspores	hydroscopic bristles	fruits	-

The undispersed seeds of *A. cyclops* and *M. cordifolia* remain on the stem for months, forming an aerial seed bank, in contrast to *C. monilifera* where the undispersed seeds fall off the parent plant after a few weeks (Tinley 1985, Knight 1986, Lubke & De Moor 1998). The seeds of *Arctotheca populifolia* also stay attached to the parent plant, but in this case the seeds do not form an aerial seed bank but the flower head bends down during seed ripening, after which the wind will bury the flower head with sand. This behaviour probably is a adaptation to dispersal and protection against predators (Van der Pijl 1982). Burying diaspores near the mother plant (geocarpy) is an effective method for ensuring the avoidance of dispersal (atelochory). It will keep the seeds in the

right spot in an inhospitable environment as was observed for desert plants (Ulbriche 1928, Van der Pijl 1982). Before seed ripening and seed burial, rodents and birds often eat the soft seeds of *A. populifolia*. For the grasses *Ammophila arenaria*, *Ehrharta villosa*, *Elymus distichus* and *Sporobolus virginicus* the main dispersal will be a mixture of autochorous and anemonochorous dispersal, often combined with phase II wind dispersal. However, the foredune grasses in South Africa produce, in general, a low number of seeds, so the dispersal of rhizome fragments could also be of importance. The floating away of torn-off rhizomes and vegetative plant parts, as occurs in many beach plants, can become the main or sole mode of dispersal (Van der Pijl 1982).

Sea drift seeds

Sea drift seeds and fruits are very buoyant and survive months or even years at sea (e.g. Guppy 1907, 1917, Muir 1937, Armstrong 1998). Of all the 250,000 species of seed plants on earth, only about 0.1% are commonly collected as drift seeds; half of these species are known to produce seeds that can float in seawater for more than a month and still be viable. During their long voyages they often cross entire oceans, perhaps colonising the shores of a coral atoll or isolated volcanic island (Ridley 1930, Van der Pijl 1982, Armstrong 1998), for example the Pacific Ocean islands (Carlquist 1967). Drift seeds are often protected with thick protective shells which are impervious to salt water. In some drift fruits, such as the coconut, the seed embryo and the fleshy white "meat" (endosperm) are enclosed within a hard, bony layer (endocarp) surrounded by a thick fibrous husk. Other drift seeds have thick woody seed coats and internal air-cavities which provide their buoyancy (Ridley 1930, Van der Pijl 1982, Armstrong 1998). Part of the diaspores of the Eastern Cape coastal foredune environments have these special buoyancy-adaptations, for example *Ipomoea pes-caprae* and *Scaevola plumieri* (Ridley 1930, Tinley 1985). The stone seed of *S. plumieri* consists of two seed halves, of which one half is empty and serves as the floating compartment (Ridley 1930, Guppy 1907, Muir 1937), one of the modifications of water dispersed seeds mentioned in Table 6.1 (previous section). The hairy seeds of *I. pes-caprae* float mainly due to the same principle, but the air in this case in contained in a space between the cotyledons within the seed (Ridley 1930, Martinez *et al.* 1992). It is not known if the seeds of both species survive the sea water dispersal over time.

6.3. MATERIAL AND METHODS

For the buoyancy test, seeds of the species *Ipomoea pes-caprae*, *Myrica cordifolia*, and *Scaevola plumieri* were used as well as the rhizome fragments of the grasses *Ammophila arenaria*, *Ehrharta villosa*, and *Sporobolus virginicus* (for detailed species description see chapter 2). The seeds of *M. cordifolia*, *I. pes-caprae* and *S. plumieri* were collected in the period May-July 1998 in the Port Alfred-Fish River area, air dried and stored at room temperature in paper bags. The seeds were approximately 1.5 to 2 years old when used (see also Chapter 3.2). For *A. arenaria* and *S. virginicus* rhizomes, fragments of approximately 6 cm long containing one bud, were freshly collected in November 2000 at Kleinemonde, and in the same period at Kenton-on-Sea for *E. villosa*. All rhizomes of the three grass species were collected from vigorous mono-stands. The rhizome fragments were stored in plastic bags in a dark cold room (5°C) until used. For a detailed species description see Chapter 2.7.

6.3.1. Seed and rhizome buoyancy experiment

The buoyancy of the seeds and rhizome fragments was investigated for a maximum period of 56 days for the seeds and 168 hours for the rhizomes. Five water baths with the following volumes were used: three baths of 14 litre, one of 25 litre and one of 50 litre. The baths were equipped with a motorised stirrer and a heating device and during the entire experiment the water baths were constantly agitated by stirrers at 21°C. To avoid seeds to contact the stirrer or heater, they were both enclosed by 1 mm^2 stainless steel wire netting. The baths were filled with artificial seawater (Table 6.2), and the water level was kept at such a level that the baths were filled for 80%. It was decided to use artificial seawater so as to avoid growth of oceanic microbes (algae or bacteria) during the experiment (Ignaciuk & Lee 1980).

Table 6.2. Description of artificial seawater (Narsai 1980, Rozema *et al.* 1985).

Chemical	Gram / litre
NaCl	29.42
KCl	0.50
$MgCl_2$	3.22
NaBr	0.56
$CaSO_4$	1.36
$MgSO_4$	2.40
$CaCO_3$	0.11
Fe_2O_3	0.003

Seed buoyancy

At the start of the experiment, each water bath (n = 5) contained 60 seeds of the species *Ipomoea pes-caprae*, *Myrica cordifolia*, and *Scaevola plumieri*. Each batch of seeds of a species in a separate water bath served as a replicate.

The number of sunken seeds of each species was recorded after 0 hours (= control), 12 hours, 24 hours, 2 days, 3 days, 4 days, 7 days, 14 days, 21 days, 35 days and 56 days. After the same periods, except after twelve hours, three days and four days, ten seeds were sampled at random from each water bath. If sunken seeds were present, sunken and floating seeds were collected in a ratio of sunken to floating seeds approximately equal to the ratio that existed in the water bath at that moment. After the seeds were collected from the water baths, the seeds were rinsed with fresh water to wash away excess salt and tested for viability.

Rhizome buoyancy

The effect of dispersal by seawater on rhizome fragments was determined for the grass species *A. arenaria*, *E. villosa* and *S. virginicus*. For each species 400 single node rhizome fragments of approximately 6 cm were collected from a vigorous population. For each species 80 rhizome fragments in total were put into the water baths (n = 5), 10 fragments for each treatment and 20 fragments for the control. The different treatments consisted of six different floating times (12, 24, 48, 72, 120, 168 hours) and a control (0 hours). After each floating period the total number of fragments that were still floating was counted, and subsequently ten fragments were removed without discriminating between floating and sunken fragments (Ignaciuk & Lee 1980).

6.3.2. Post-buoyancy viability test

Seed viability test

Not all the species used were easy to germinate therefore the chemical dye Tetrazolium chloride was used to determine seed viability (Booth & Hendry 1993). The tetrazolium chloride reacts with hydrogen produced by dehydrogenase enzymes, resulting in the formation of the pink to red pigment formazan. Dehydrogenase enzymes are only present in living tissues and the tetrazolium test is therefore a good indicator to test for seed viability. No staining means no dehydrogenase is present and thus that the seed is dead, whereas purple staining indicates damaged or dying tissue (Moore 1973, Booth & Hendry 1993). After the seeds were removed from the water baths and rinsed, the seed

coat of the seeds was cut to reveal part of the embryo without damaging it. For *I. pes-caprae* the seed was cut at the point where the seed coat would break during germination. In the case of *Myrica cordifolia* approximately 2 mm^2 of the relatively thick seed coat was cut off. The seeds of *Scaevola plumieri* consist of two halves of which one is empty. At the point where both seed halves meet, part of the seed coat was cut in such a way that an area of about 2 mm^2 of the embryo became visible after which the empty seed half was removed.

After the seeds had been prepared for the tetrazolium test, all the seeds were put in petri dishes with distilled water and left to imbibe at room temperature for 48 hours (Hendry & Grime 1993). After imbibition the embryos from *Scaevola plumieri* were removed from their seed coats, and the layer of starch that enveloped the embryo was also removed to get optimal contact with the tetrazolium solution.

All seeds and embryos were then immersed in a 1% tetrazolium chloride solution and kept in the dark for 48 hours at room temperature (after Moore 1973). The tetrazolium solution was kept at a pH of 7 using a 0.2 M K_2HPO_4 buffer (Moore 1973). After the 48-hour period of immersion in tetrazolium chloride solution, embryos of the three species were examined to determine the extent and pattern of staining of the embryonic tissues using the classification from table 6.3. Purple staining caused by damage due to seed coat preparations for the staining process were not taken into account.

Table 6.3. Viability classification system of tetrazolium-chloride dyed seeds.

Viability classification	Staining (%)	
	Pink/red	Purple
0 – no viability	0	0-100
1	1-20	-
2	20-40	-
3	40-60	-
4	60-80	-
5 – viability high	80-100	-

The seeds that fell into categories 3, 4 and 5, were considered as being capable of germination. At the start of the experiment five replicates of twenty seeds of each species were tested with tetrazolium to serve as the control treatment.

Rhizome viability test

The rhizomes were tested for viability by means of a growth experiment. After the rhizome fragments were collected from the water baths, the fragments were planted 2

cm deep in pots containing 1.5 litre of beach sand (five fragments per pot) in a temperature-controlled greenhouse. The pots were covered with perforated plastic wrap to prevent excess evaporation. The plants were watered and checked at 3-4 day intervals. After 58 days the growth experiment was terminated and the length of the rhizome, the numbers of shoots and roots, and the length of the roots and shoots (longest leaf) were measured as well as the root and shoot biomass. For the biomass the roots and shoots were dried at 70°C for 48 hours (Smith 1990).

6.3.3. Data analysis

The independent variables were tested for normality and homogeneity of the variance by using the Kolmogosov-Smirnov and Levene's test, respectively. When these assumptions failed, non-parametric procedures were carried out. The data of the seed and rhizome floating experiment was analysed using an analysis-of-variance (ANOVA) and the non-parametric Kruskal-Wallis test both followed by a comparison-of-means test. The total numbers of viable seeds and the mean length of the rhizomes were tested using an ANOVA followed by a Tukey comparison of means test (Zar 1996). The total numbers of viable seeds and rhizomes was quantified as the numbers of seeds/rhizomes that germinated or grew, plus the numbers of viable ungerminated and non-growing seeds/rhizomes. The floating time of seeds and rhizomes and the effect of floating in salt water on the growth and viability of the rhizome fragments were analysed with a Kruskal-Wallis test followed by a Newman-Keuls comparison-of-means test (Zar 1996). A regression analysis was used to determine the relationships between the floating time and the number of floating seeds/rhizomes, floating times and number of total viable seeds/rhizomes, floating time and rhizome length, and between the duration and days before sprouting. For all data analyses the standard error (S.E.) and the number of replicates (*n*) was given, with the significant differences of the analysed data represented by different letters (abc, pqr, xyz) behind the values in tables or above the columns and data points in graphs. For each analysis the level of significance was specified using the following system: * = $P<0.05$, ** = $P<0.01$, and *** = $P<0.001$. The ** were placed next to the highest value of the analysed parameter. All statistical tests were performed at a 95% confidence interval using the statistical program Statistica 5.5. (Statsoft Inc.). For details of the ANOVA analysis see Appendix III.

6.4. RESULTS

The seeds of the species Ipomoea pes-caprae, Myrica cordifolia and Scaevola plumieri and the rhizome fragments of the grasses Ammophila arenaria, Ehrharta villosa and Sporobolus virginicus were floated in artificial sea water for different periods of time. The results of the seed and rhizome buoyancy tests are presented separately.

6.4.1. Seed buoyancy experiment

Floating time

The seeds of the species *I. pes-caprae*, *M. cordifolia* and *S. plumieri* were floated in artificial seawater for a maximum of 56 days (Figure 6.1). After 56 days in salt water, a mean percentage of 88 ± 11.5% of the seeds of *I. pes-caprae* and 94 ± 5.5% of *S. plumieri* were still floating. This in contrast to the *M. cordifolia* seeds, which started to sink on day 1, and after 14 days all seeds were sunken (Figure 6.1). From day one onwards significantly less *M. cordifolia* seeds were floating compared to *I. pes-caprae* and *S. plumieri* (Kruskal-Wallis, $P<0.01$, see Figure 6.1). Perhaps the seeds would have a better floating capacity without the waxy layer. There were no significant differences in floating periods between the species and within the species *I. pes-caprae* and *S. plumieri* (Figure 6.1).

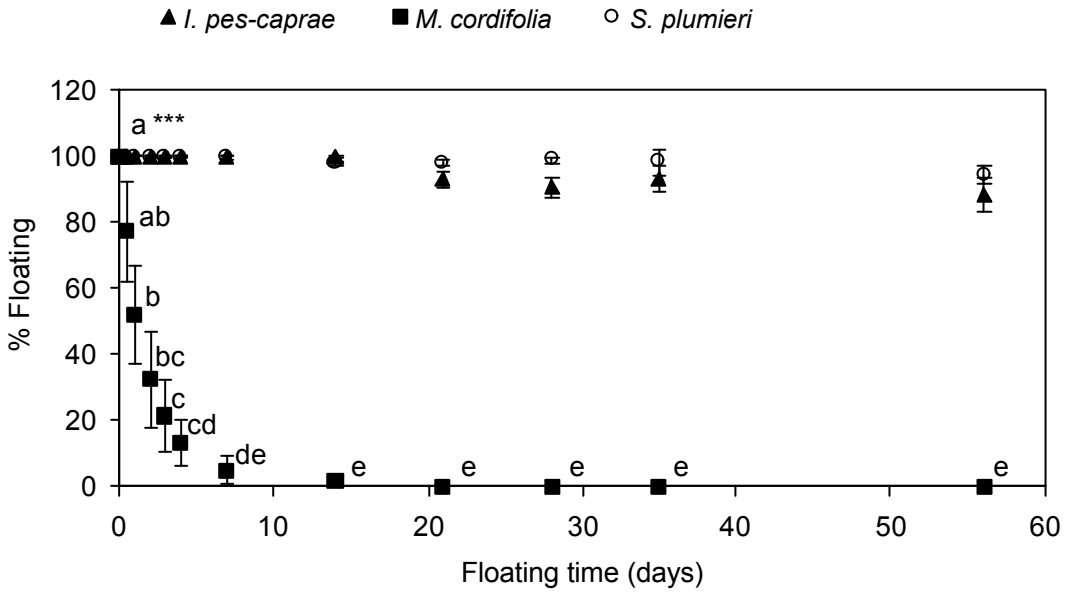


Figure 6.1. Mean percentage of seeds floating during the buoyancy experiment (n = 5) of *I. pes-caprae*, *M. cordifolia*, and *S. plumieri* (± S.E.). Any floating time within a species with the same letter does not differ significantly. Contrasts obtained by Newman-Keuls after analysis by Kruskal-Wallis. Level of significance: *** - $P<0.001$.

The spread in the number of seeds floating between the replicates was high for some species, but the downward trend was significant for all replicates (Figure 6.2). For all three species a significant negative relation between the number of seeds floating and time was found, with the order of R^2 values from high to low: *I. pes-caprae* > *M. cordifolia* > *S. plumieri* (Regression, $P<0.001$; Figure 6.2.). The decline in number of floating seeds after 56 days of floating was 18% for *I. pes-caprae* and 6% for *S. plumieri*, which was not much considering the seeds had been floating for 8 weeks.

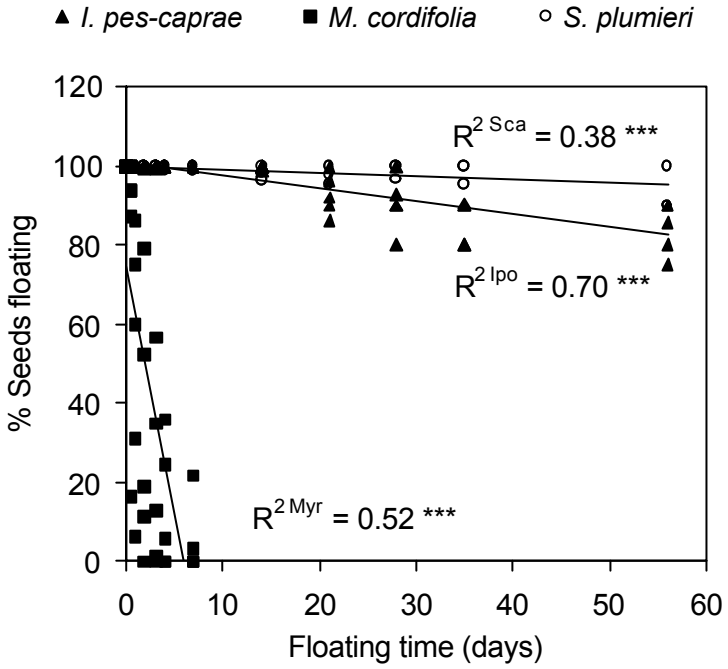


Figure 6.2. The linear relationship between the number of floating seed (in % with n = 60) and the floating time for the species *I. pes-caprae* (Ipo), *M. cordifolia* (Myr) and *S. plumieri* (Sca). Contrast obtained by regression analysis. Level of significance: *** - $P<0.001$.

6.4.2. Post-buoyancy seed viability

For *I. pes-caprae* a mean overall percentage of 55 ± 3.0% of the seeds were viable after the buoyancy test, 45 ± 2.4% for *M. cordifolia* and 69 ± 3.8% for *S. plumieri* (see Figure 6.3). Due to the high variability within and between the treatments, there were no significant differences in total number of viable seeds observed for the three species (ANOVA, $P>0.05$). For *M. cordifolia* and *S. plumieri* no differences in seed viability were observed between the control and the treatments (ANOVA, $P>0.05$; Figure 6.3). However, *I. pes-caprae* showed a significantly lower percentage of viable seeds for the

28 day floating treatment compared to the control (P<0.001; Figure 6.3). For the seeds of *I. pes-caprae,* the 14, 21, 35 and 56 day treatment showed a significantly higher viability compared to the 28 day treatment (P<0.001; Figure 6.3).

Within the treatments *S. plumieri* showed a significantly lower number of viable seeds for the seeds of the 21day period compared to the 2 day, 14 day and 56 day treatments (ANOVA, P<0.05; Figure 6.3). For both *I. pes-caprae* and *S. plumieri* the seeds of the 28 day treatment showed a significantly lower number of floating seeds, but since longer floating treatments showed a significantly higher viability, it may have been a random effect. No significant differences were observed within the treatments for *M. cordifolia* (P>0.05; Figure 6.3). This means that the viability of the seeds of all three species was not affected by floating or being submersed in artificial seawater for periods up to 56 days. Of the *M. cordifolia* seeds that were not viable, 52% were empty, and therefore did not lose their viability due to the treatments.

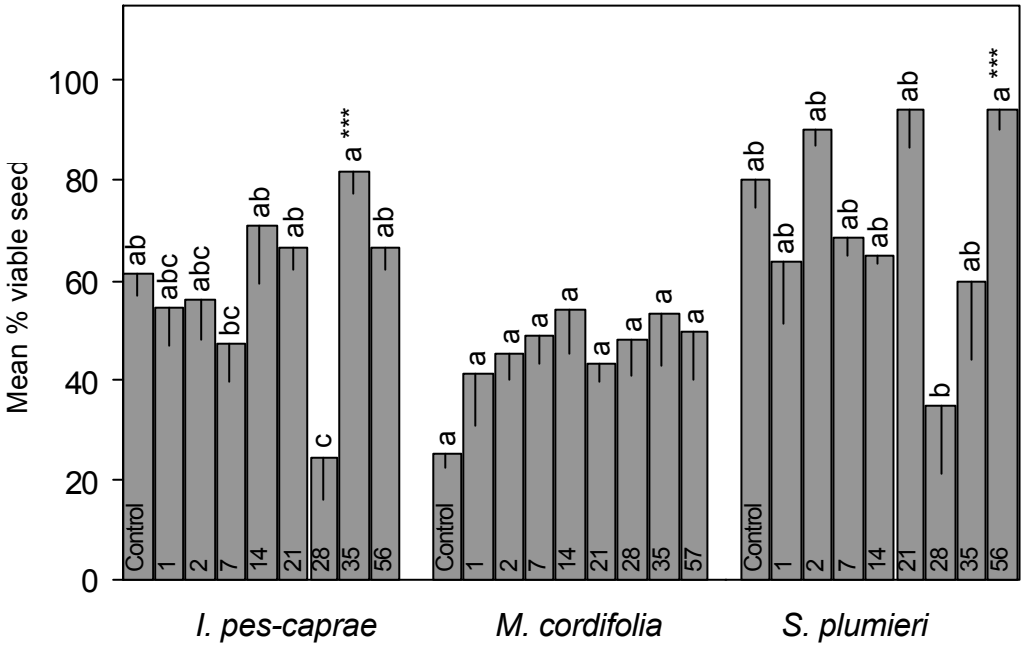


Figure 6.3. Mean percentage of viable seeds of *I. pes-caprae*, *M. cordifolia* and *S. plumieri* after different floating periods (n = 5). The floating treatments are mentioned at the base of each column. Any column within a species with the same letter does not differ significant in the percentage of viable seeds. Contrasts obtained by Tukey after analysis by ANOVA. Level of significance: *** - P<0.001.

All three species tend to have a positive relation between number of seeds viable and floating days, but none of the correlations was significant (Regression, $P>0.05$; Figure 6.4). The R^2 of all three species was observed to be near to zero which points to the fact that over time there was no change in seed viability. Hence no effect of the salt water on seed viability was observed even for the non-floating *M. cordifolia* seeds (see also Figure 6.1).

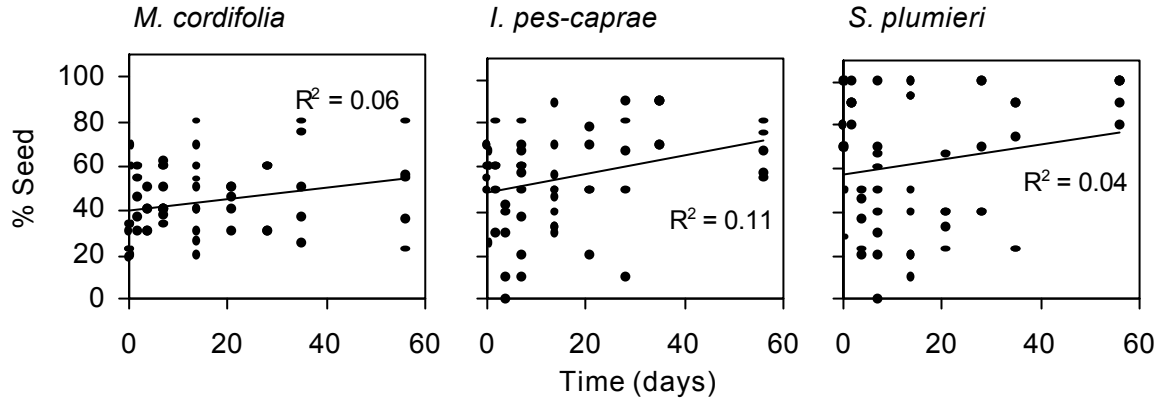


Figure 6.4. The relation between the number of viable seeds (in %) and floating time for the species *I. pes-caprae* (A), *M. cordifolia* (B) and *S. plumieri* (C). Contrast obtained by regression analysis. Level of significance: * - $P<0.05$.

6.4.3. Rhizome buoyancy experiment

For the grass species *A. arenaria*, *E. villosa*, and *S. virginicus* the floating capacity of rhizome fragments was tested followed by a growth experiment to test viability.

Floating capability

For each species the eighty rhizome fragments (n = 5) were set to float on artificial seawater for a maximum period of 168 hours (Figure 6.5). For the control (0 hours) not all the rhizome fragments floated for the three species. For the *A. arenaria* 69 ± 1.8%, for *E. villosa* 70 ± 1.3% and for *S. virginicus* only 61 ± 0.8% of the rhizome fragments floated (Figure 6.5). Between the species, *A. arenaria* and *E. villosa* showed a significantly higher number of floating fragments when compared to *S. virginicus* at the control (Kruskal-Wallis, $P<0.001$; see Figure 6.5). After the first floating period of 12 hours the number of floating fragments declined significantly for all three species (Kruskal-Wallis, $P<0.001$; Figure 6.5). The fastest decline was observed for the species *E. villosa* (67%) and *S. virginicus* (42%), whereas the decline of the *A. arenaria* rhizome

fragments was only 11% (Figure 6.5). After 12 hours of floating the decline continued until no floating fragments were left after 24 hours for *E. villosa*, and 168 hours for *A. arenaria* and *S. virginicus* (Figure 6.5). In general the rhizome fragments of *A. arenaria* showed the best floating ability of the three species.

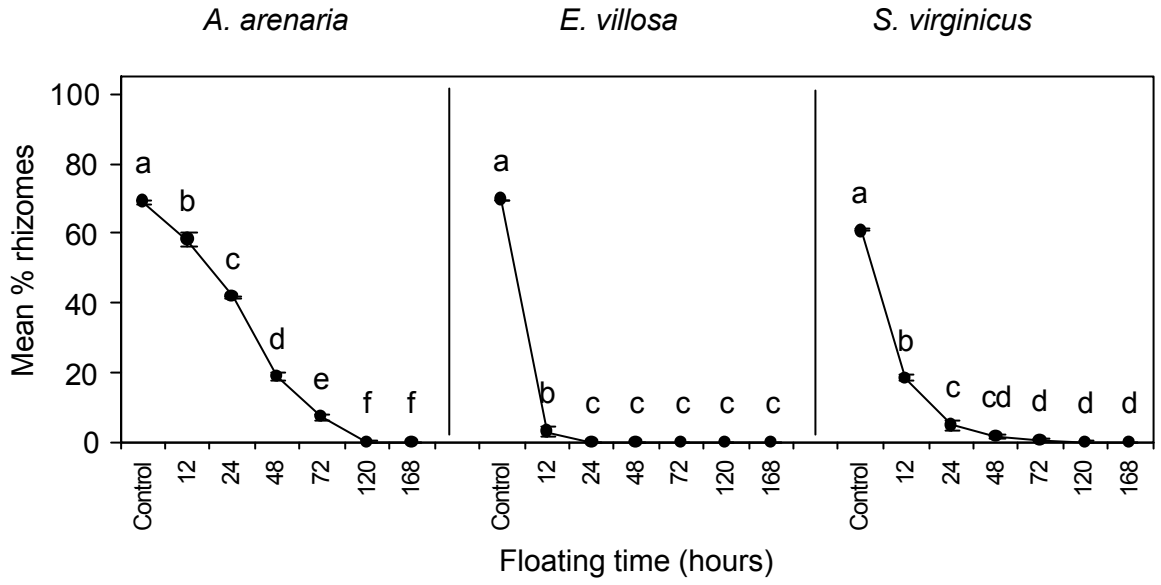


Figure 6.5. Mean percentage of floating rhizome fragments (*n* = 5) *A. arenaria*, *E. villosa* and *S. virginicus* given per floating period. Any two points within a species with the same letter do not differ significant in the percentage floating rhizomes. Contrasts obtained by Newman-Keuls after analysis by Kruskal-Wallis. Level of significance: ** - $P<0.01$, *** - $P<0.001$.

The R^2 reflects the floating capacity of the species. The species *E. villosa* showed the lowest floating capacity and lowest R^2 (0.23), whereas the better floating *A. arenaria* showed a significantly higher R^2 of 0.77 (Regression, $P<0.05$; Figure 6.5). Some of the rhizome fragments of *S. virginicus* floated for 120 days, but the percentage of fragments was much lower compared to *A. arenaria* (see Figure 6.5), hence the lower correlation coefficient (Table 6.4). In general the species that showed a lower floating capacity showed a weaker relationship between floating and time as expected.

Table 6.4. Correlation between floating capacity for the species *A. arenaria*, *E. villosa* and *S. virginicus*.

Species	Maximum floating time (days)	R^2
A. arenaria	120	0.77
E. villosa	12	0.24
S. virginicus	120	0.37

6.4.4. Post-buoyancy rhizome viability

After the floating period, the rhizome fragments were tested for viability by means of a growing experiment in the greenhouse. The rhizomes of all species produced shoots and/or roots (Table 6.5), but since only one rhizome of *A. arenaria* sprouted, the species was excluded from further analyses. *S. virginicus* showed a significantly better survival after floating in artificial seawater compared to *E. villosa* (ANOVA, $P<0.001$). For the species *E. villosa* and *S. virginicus* the number of viable rhizome fragments declined significantly with floating time (Table 6.5). For *E. villosa* no shoots and/or roots were produced after the rhizome fragments had been in the seawater for more than 48 hours, whereas *S. virginicus* rhizomes produced shoots for all the floating times (Table 6.5). For *E. villosa* after 12 hours of floating the number of viable rhizomes started to decrease significantly compared to the control (ANOVA, $P<0.001$; Table 6.5). Within the treatments, the highest number of viable *E. villosa* rhizomes were found for the 12 hour treatment compared to the 48 to 168 treatments, although the number of viable rhizomes was low with 5 ± 5.6% ($P<0.001$; Table 6.5). For *S. virginicus* the number of viable rhizomes only started to decline significantly after 168 hours compared to the control (Kruskal-Wallis, $P<0.05$; Table 6.5). Within the treatments only the 168 hour treatment showed a significant lower number of viable rhizomes (14 ± 5.1%) compared to the control ($P<0.05$; Table 6.5).

Table 6.5. Mean number of viable rhizome fragments (± S.E.) for the species *E. villosa* and *S. virginicus* given per treatment. Any two values within a species with the same letter are not significantly different. Statistics used: Kruskal Wallis followed by a Newman-Keuls test. Level of significance: *** - $P < 0.001$.

Treatment	Percentage of viable rhizome fragments					
	E. villosa			*S. virginicus*		
	n	Mean	(± S.E.)	*n*	Mean	(± S.E.)
0 (=control)	8	20.0	(3.26) a ***	10	39.4	(1.29) a ***
12	4	5.0	(2.81) b	5	32.0	(3.27) ab
24	4	2.5	(2.50) bc	5	38.0	(2.61) a
48	4	0.0	(0.00) c	5	35.0	(1.44) ab
72	4	0.0	(0.00) c	5	26.5	(1.34) ab
120	4	0.0	(0.00) c	5	31.5	(2.55) ab
168	4	0.0	(0.00) c	5	14.0	(2.30) c

Even though the rhizomes floated well, the viability of the rhizomes declined over time (Table 6.6). For *E. villosa* the growth of rhizomes was more strongly affected compared to *S. virginicus* because for three of the four parameters significant differences were found over time, whereas for *S. virginicus* only the shoot length was affected (Table 6.6). Compared to the control the number of shoots and the shoot length started to decline significantly after a 24 hour floating period, whereas the number of leaves declined after 12 hours (Kruskal-Wallis, $P<0.05$; Table 6.6). For the *E. villosa* fragments that floated for 48 hours or longer, no shoot growth was observed, whereas the leaf growth stagnated when the fragments were in the seawater for more than 12 hours ($P<0.05$; Table 6.6). For *S. virginicus* only the shoot length was affected by floating in salt water. The control treatment showed a significantly longer shoot compared to the other treatments ($P<0.05$; Table 6.6). No effect of salt water on the number of shoots, leaves and the leaf length was observed for *S. virginicus*. Apparently the species can with stand high salt concentrations.

Table 6.6. The effect of seawater on the number and length of the shoots and leaves of the species *A. arenaria*, *E. villosa*, and *S. virginicus* (n = 5). Any value within a species with the same letter does not differ significantly in number or length of shoots or leaves. Contrasts obtained by Newman-Keuls after analysis by Kruskal Wallis. Level of significance: * - $P < 0.05$, ** - $P < 0.01$, *** - $P < 0.001$.

Species	Treatment (in hours)	Parameter measured			
		Shoots		Leaves	
		Number	Length (cm)	Number	Length (cm)
E. villosa	0 (=control)	1.00 a ***	5.31 a ***	0.56 a *	1.37 a
	12	0.50 ab	1.68 ab	0.00 b	0.00 a
	24	0.25 bc	0.80 bc	0.00 b	0.00 a
	48	00.0 c	0.00 c	0.00 b	0.00 a
	72	0.00 c	0.00 c	0.00 b	0.00 a
	120	0.00 c	0.00 c	0.00 b	0.00 a
	168	0.00 c	0.00 c	0.00 b	0.00 a

Table 6.6 continued.

Species	Treatment (in hours)	Parameter measured			
		Shoots		Leaves	
		Number	Length (cm)	Number	Length (cm)
S. virginicus	0 (=control)	1.34 a	6.49 a *	3.11 a	3.60 a
	12	1.28 a	1.28 b	1.28 a	1.28 a
	24	1.83 a	1.33 b	1.58 a	1.78 a
	48	1.87 a	1.18 b	1.18 a	1.18 a
	72	1.45 a	1.65 b	1.85 a	2.05 a
	120	1.36 a	1.56 b	1.76 a	1.96 a
	168	1.25 a	1.75 b	2.25 a	2.75 a

The days till the sprouting of the buds showed a positive relation with the time spent in the salt solution for *E. villosa* and *S. virginicus* (Figure 6.6). For *A. arenaria* only one rhizome sprouted and it was therefore excluded from figure 6.6. For both species the relation between the number of pre-sprouting days and time spent in the salt solution was positive (Figure 6.6). For both *E. villosa* (R^2 = 0.33) and *S. virginicus* (R^2 = 0.46) a significant increase in sprouting days was found (Regression, P<0.01; Figure 6.6). This means that the longer the duration in the salt solution, the longer the pre-sprouting period.

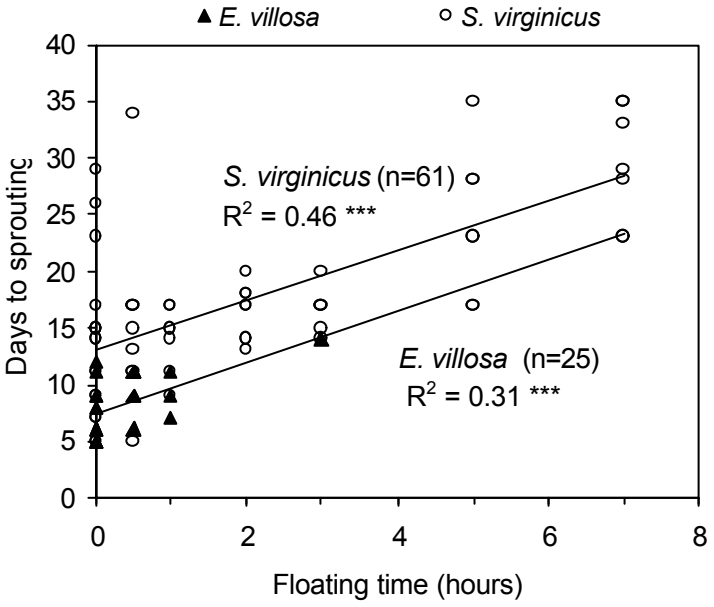


Figure 6.6. Relationship between the time spent in the salt solution (floating and non floating) and the day to sprouting for the species *E. villosa* and *S. virginicus*. Regression analysis. Level of significance: *** - P<0.001.

Not all rhizome fragments used were of the same length. The rhizomes used in the present experiment were 6.2 ± 0.9 cm long (Figure 6.7). For all three species significant differences in the length of the rhizome fragments were observed (ANOVA, P<0.05; Figure 6.7). For *A. arenaria* and *E. villosa* the 168 hours treatment showed the significantly shortest rhizome fragments (P<0.05; Figure 6.7).

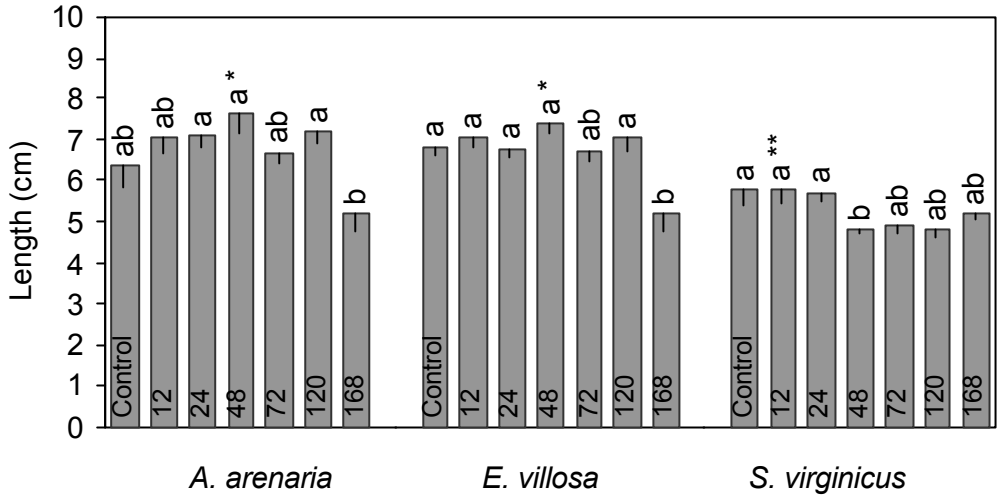


Figure 6.7. Mean length of the rhizomes (± S.E.) of *A. arenaria*, *E. villosa*, and *S. virginicus* used in the floating experiment (*n* = 10). The treatments (in hours) are mentioned at the base of each column. Any two columns within a species with the same letter do not differ significantly in rhizome length. Contrasts obtained by Tukey after analysis by ANOVA. Level of significance: * - $P < 0.05$, ** - $P < 0.01$, *** - $P < 0.001$.

The rhizome fragments where not sorted on length before start of the experiment, therefore the significance differences were not related to the treatment. No significant correlations were found between the rhizome length and the floating capacity or viability of the rhizome fragments (Table 6.7). Only for *S. virginicus* a positive correlation was found between the rhizome length and the percentage of floating rhizomes, but the correlation was not significant (Regression, $P>0.05$; Table 6.7). In general rhizome length showed no influence on floating capacity and viability for *A. arenaria*, *E. villosa*, and *S. virginicus*, even though the length differed significantly between treatments within the species.

Table 6.7. The correlations between rhizome length and the percentage of floating and viable rhizomes of the species *A. arenaria*, *E. villosa*, and *S. virginicus*. Regression coefficient R^2 obtained by regression analysis.

Species	Correlation coefficient R^2	
	Floating	Viable
A. arenaria	0.002	0.010
E. villosa	0.005	0.002
S. virginicus	0.092	0.001

5. DISCUSSION

The dispersal of seeds plays a fundamental role in the survival, migration, colonisation and succession of plants at all levels from niche to biome (Tinley 1985). In the introduction the question was asked if seawater dispersal was also of importance for the Cape coastal foredune species? To answer the question the buoyancy of the dispersal units (fruits, seeds and rhizome fragments) of strand and foredune species was tested, as well as the survival after seawater dispersal. The expectation was that only the specialised seeds of *I. pes-caprae* and *S. plumieri* would float for prolonged periods and would survive the dispersal, whereas the non-buoyant species might be able to float for a few days, but would not survive long floating periods. The seeds of *I. pes-caprae* and *S. plumieri* were very buoyant and survived a 3-month period in the seawater. As expected *M. cordifolia* seeds floated for a few days after which the seeds sank, but surprisingly the seed viability was not affected by the prolonged periods in seawater. Some of the rhizome fragments of *A. arenaria* and *S. virginicus* floated for the full 120 days, whereas the *E. villosa* fragments sank almost immediately. In the case of the grasses the viability was affected by seawater submersion

Seed buoyancy and survival

The species *Ipomoea pes-caprae* and *Scaevola plumieri* showed a high floating capacity for up to 56 days, as expected, since both species are known to be seawater dispersed (Ridley 1930). The seeds of both species showed a viability of over 40% after 56 days in seawater. Seed buoyancy was found to be a characteristic of several species of *Scaevola* (Carolin 1966, Muir 1937) and *Ipomoea* (Ridley 1930, Lonard & Judd 1999). For instance seeds of the pacific atoll species *Scaevola taccada* have been found to float on seawater for up to 120 days, after which period 46% of the seeds were still viable (Lesko & Walker 1969). The seeds of *Scaevola* species float due to the fact that one half of the seed is filled with air (Plate 6.1).

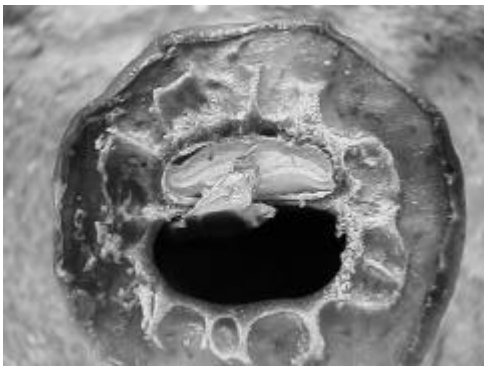


Plate 6.1. Cross-section of a *S. plumieri* drupe with one of the seed cavities filled with the embryo (top) and one filled with air (bottom). Note the corky structure of the stone seed.

For both *S. plumieri* and *S. taccada* the seed would only float without the fleshy layer (Lesko & Walker 1969). This in contrast to the results of Muir (1937) who found that the fresh drupes of *S. plumieri* would float over 63 days, whereas the bare stones floated for over 100 days. Muir (1937) found that all the sunken drupes were penetrated with water. Lonard and Judd (1999) found that apart from the seeds, the vegetative part of *Ipomoea imperati* also were buoyant in seawater.

The waxy seeds of *M. cordifolia* were not adapted to seawater dispersal. This was confirmed by the fact that after 14 days no floating seeds were left, but the sunken seeds were not showing a decline in viability, even after 56 days (42 days submerged) the viability was around 50%. The seeds of *M. cordifolia* form an aerial seed bank, and according to Huiskes (1977) one function of aerial seed banks of coastal species is that the seeds can be gathered from the stems during high water. This seems not the function of *M. cordifolia*'s aerial seed bank; although the present study showed the *M. cordifolia* seeds can survive extensive submersion in salt water, the seeds were not buoyant. The plants of *M. cordifolia* did occur in the foredune area but belonged to the backdune area, hence the selection was pointed to other dispersal mechanisms such as, for instance, bird dispersal.

Experiments with bottles from Madagascar to South Africa showed that in 161 days approximately 1,269 sea miles were travelled, in other word about 7.9 sea miles per day (see Muir 1937). Seawater dispersal in general occurred infrequently, but according to Carlquist (1967) the transport does not have to be frequent to be effective.
Muir (1937) stated that transport of seeds via seawater occurs as he found seeds of *I. pes-caprae* and *S. plumieri* on the beach at Stilbaai, but the species were not growing at the site. More evidence was found by Harman (2000) when genetic fingerprinting showed that *S. plumieri* populations of Old Woman's River were related to a population at Jeffreys Bay, a site situated more than 400 kilometres to the east.

The most likely explanation for the fact that genetically related populations was found at sites so distant from each other, was that the seeds arrived at Jeffreys Bay via seawater dispersal. The Agulhas current runs via the Mozambique Channel past the east and south coast of South Africa (Schumann 1998) and would have been able to transport seeds from Old Woman's river down to Wilderness. Another possibility is that humans

took the seeds there, but this is not very likely since the fruits and seeds did not have any ethno-botanical uses (Tinley 1985, Pooley 1998). The nearly spherical fleshy drupes of *S. plumieri* have a radius of 1.9 cm so the dispersal by birds was also unlikely, but did occasionally occur, according to Muir (1937). It is evident that for all three species the seeds survive seawater dispersal of three months (see Plate 6.2), but how long seeds stay viable after landing at a (new) site needs still to be investigated.

Plate 6.2. The seeds of *S. plumieri* among debris in the swash zone.

Rhizome buoyancy and survival

Compared to the floating ability of the seeds, the floating capacity of rhizome fragments was much poorer, but the fragments of *A. arenaria* and *S. virginicus* were able to float for up to 5 days. Only fragments of *E. villosa* did not float very well, with all fragments sunken after 12 hours. The rhizome fragments of *A. arenaria* showed the highest floating capacity. After 40 hours almost 50 % of the fragments were still floating, which agrees with the results found by Maun (1985) for *Ammophila breviligulata*. Half of the rhizome fragments of *E. villosa* had already sunk after 5 hours, for *S. virginicus* this took 9 hours. The difference in floating ability might be explained by the size of the fragments; perhaps the fragments were too small and larger fragments of rhizomes could show a higher floating capacity. Another reason could be the difference in physiology of the rhizome. Drift seeds are often in the possession of specific devices that provide buoyancy, such as air spaces within the seed (Kubitzki & Ziburski 1994). Rhizome fragments can use the same principle and 'store' air inside the fragments when they have hollow internodes. Observations of the fragments used in the present

study showed that most of the fragments of *A. arenaria* and some of *S virginicus* were hollow. This agrees with the results of Naidoo and Naidoo (1992), who found that *S. virginicus* has hollow internodes with a central air space in cross-sectional area of the rhizome that ranges from 20 to 30 %. For *E. villosa,* however, none of the fragments had hollow internodes, which ties in with the results from the literature (Lubke & Van Wijk 1998).

The fragments of *A. arenaria* showed the highest floating capacity, but the lowest viability. Aptekar and Rejmánek (2000) found that 64% of control fragments of *A. arenaria* were viable and that after 312 hours of submergence in seawater 25 % of the rhizomes still had a viable bud. In the present study the control and treatment fragments of *A. arenaria* showed a low growth. The differences between the studies could be due to many factors, including genotype of *A. arenaria*. Growth experiments of stem fragments (Chapter 7) showed that the viability of *A. arenaria* stem fragments could be very variable, as might be the case for rhizome fragments, or perhaps the buds were dormant and needed another stimulus to start growing. Since the fragments all contained a single node, there could not have been an influence of apical dominance (Greig-Smith *et al.* 1947, Kranjyk & Maun 1981, Harris & Davy 1987) that would prevent the buds from growing. This because Maun (1985) showed that the dormant buds of *Ammophila breviligulata* readily developed when apical dominance was removed as rhizomes were fragmented into smaller fragments. According to Bell (1974) this kind of response is possibly universal in plants reproducing vegetatively.

In general the rhizome fragments that have been in the seawater for the longest period take the longest times to produce a visible sprout; thus the longer the period in the saltwater, the longer the growth lag-phase. Clearly the saltwater slowed down the growth of rhizome fragments as found by Aptekar and Rejmánek (2000). The same decrease in performance was found for the viability of the fragments; the viability of the rhizome buds decreased with duration in the saltwater. In the last few treatments no shoots or roots were formed for *A. arenaria* and *E. villosa*. Rothmann (1992) found that cuttings of *E. villosa* could be propagated easily, but in this study rhizomes fragments did not propagate. Rhizome fragments could be less susceptible to propagation than stem cuttings. The fragments of *S virginicus* were producing shoots and/or root after all treatments, but only after 168 hours in saltwater a significant decline in shoot/root growth was observed.

Apart from an effect of seawater on the period before sprout emergence and on bud viability, the seawater treatment also has an effect on several growth parameters such as the number and the length of shoots and leaves. For *E. villosa* a decline in number of shoots and shoot length and number of leaves was observed, whereas for *S virginicus* only the shoot length decreased strongly. There were no differences between the different floating treatments that point to the fact that the grass could be salt tolerant. The biomass of the dune-ecotype plant even increases under saline cultivation compared to cultivation under fresh water conditions (Blits & Gallagher 1991).
In general *S virginicus* showed the best survival and growth even though the seawater treatment does affect the fragments, but not as strongly as observed for *E. villosa*.
Besides the seawater, the rhizome length could influence the pre- and post-dispersal performance because there was a significant difference within each species. However, the rhizome length was not correlated with floating time and viability, as was also found by Aptekar & Rejmánek (2000). Therefore, the main cause of reduction in viability and growth was due to the salt water.

Concluding remarks

Knowledge of the movements and fates of coastal seeds is essential for ecosystem restoration and conservation efforts and is thus an important feature in the life history of plants. The dispersal of seeds and rhizomes via seawater is a way to colonise new habitats, and is an important aspect of the coastal dune environment. In the present study not all foredune species were able to be dispersed via seawater, as expected, but the some of the non-buoyant dispersal units from, for instance, *S. virginicus*, surprisingly survived prolonged seawater submergence. Even the bird dispersed seeds of the thicket species *M. cordifolia*, living away form the sea, was buoyant for 7 days and survived seawater immersion for up to 3 months. Thus the hypothesis that only the specialised seeds of *I. pes-caprae* and *S. plumieri* will float for prolonged periods, and survive dispersal was proven to be partly true.

CHAPTER 7

THE ROLE OF SOIL-BORNE PATHOGENS IN SOUTH AFRICAN COASTAL FOREDUNE VEGETATION

If all the matter in the universe except nematodes were swept away, our world would still be recognisable. We should find mountains, hills, rivers, oceans, the location of plants, animals and cities represented by a film of certain nematodes.

Cobb (1915)

7.1. INTRODUCTION

Plant life histories represent compromises among many conflicting demands; pathogens represent one of those demands. The potential importance of soil-borne pathogens for the ecology of plant populations will depend upon both the frequency of infection and the nature of pathogen effects on the host(s), relative to other biotic and abiotic features of the local environment (Clay & Van der Putten 1999). Pathogens can alter particular life-history characteristics by inducing morphological and/or physiological changes in host plants, for instance the fecundity and viability of individual plants and hence whole communities (Louda *et al.* 1990, Dobson & Crawley 1994, Jaroz & Davelos 1995, Clay & Van der Putten 1999). Soil-borne pathogens can have both direct and indirect impacts on the structure of plant communities, but only occasionally received attention as agents of ecosystem function and change, despite their apparent ability to alter the diversity and species composition of ecological communities (Van der Putten & Troestra 1990, Seliskar & Huettel 1993, Bever 1994, Dobson & Crawley 1994, Van der Veen 2000). In Europe the occurrence of plant-specific soil-borne disease complexes in the coastal environment is one of the factors that play an important role in natural succession (Van der Putten *et al.* 1993). The presence of these soil pathogens in a successional sequence of plant species in the coastal dunes has consequences for competitive interactions among species growing in the same area (Crawley 1993, Van der Putten & Peters, 1997).

The succession in the Eastern Cape coastal area is not clearly represented in zones as found in Europe and KwaZulu-Natal, South Africa but often features multispecies communities (Doing 1985, Avis & Lubke 1996). Van der Putten and Peters (1997) found that soil-borne plant pathogens affect foredune plant competition and zonation. The main question of the present study is do soil-borne pathogens also play a role in the Eastern Cape foredune vegetation as found in Europe? To answer this question a study was carried out with the objective to assess (1) to what extend plant specific soil organisms (plant-parasitic nematodes in particular) are present in the coastal foredunes of the Eastern Cape and (2) the possible consequences of the soil pathogens present in the rhizosphere of the foredune plants.

Even though the pioneer foredune vegetation of the Cape coast shows a multiple species succession (Tinley 1985), the endoparasitic plant-parasitic nematodes associated with coastal plants are usually host specific (Van der Putten & Van der Stoel

1998, Van der Stoel 2000). Therefore, the first hypothesis of the present study is: There will be a specific plant-parasitic nematode composition around each individual plant species. In Europe the foredune species would perform well on soil of succession predecessors, but not good on the soil of succeeding species. Since the foredunes show multispecies foredune communities, the succession pattern is usually not very clear. Therefore the second hypothesis is: Foredune plants perform better on foreign soil due to escape from their own pathogen fauna.

The work on soil pathogens will include a field survey on nematodes in the root zone of the foredune species *Arctotheca populifolia, Ipomoea pes-caprae, Scaevola plumieri, Ehrharta villosa, Sporobolus virginicus*, and *Ammophila arenaria*. A transplantation experiment was carried out with the same species, to determine the effect of the soil organisms on the growth of plants.

7.2. COASTAL FOREDUNES AND SOIL-BORNE PATHOGENS

Soil-borne pathogens are known to be important for a range of crop species (Garrett 1970) it is, therefore, likely that soil-borne pathogens also play an important role in natural communities (Jarosz & Davelos 1995). The potential importance of pathogens for the ecology and evolution of plant populations will depend upon both the frequency of infection and the nature of the pathogens (Clay & Van der Putten 1999). There are a few examples where soil pathogens have been shown to affect spatio-temporal patterns in natural vegetation (Jarosz & Davelos 1995). One example is the dynamics of *Trifolium repens* in pastures (Yeates *et al.* 1985), although not a natural ecosystem, the plant-parasitic nematodes were involved in the development of the vegetation. Oremus and Otten (1981) first suggested the possible contribution of plant-parasitic nematodes to the degradation of sand dune plants. In 1993 Van der Putten *et al.* found that the root zones of sequentional foredune plant species apparently contain pathogens that are specific for their host and pre-successional plant species, and play a role in plant competition (Van der Putten & Peters 1997). Thus, plant roots are associated with many harmful soil organisms that could be beneficial or harmful to the plant. In the present study the mean focus will be on the nematodes.

7.2.1. Soil-borne pathogens: The nematodes

What are nematodes?

Nematodes are the most numerous multicellular animals on earth and they represent two-thirds of the total fauna. Nematodes (Phylum Nematoda) are abundant, and a hand full of soil will contain thousands of the microscopic worms (400 μm to 5 mm long). They are structurally simple organisms, characterised as a tube within a tube and many of them are parasites of insects, animals or plants (Zacheo 1993).

The plant-parasitic nematodes feed from outside the plant (ectoparasitic) or from inside the plant tissue (endoparasitic) and are either sedentary or migratory (free living).

Plant-parasitic nematodes puncture the plant cell with the use of an oral stylet or prickle, and once open the nematode empties the contents of the cell. The nematode feeding reduces the flow of water and nutrients into the plant, increasing the plant susceptibility to other stress factors such as heat, water, and nutritional deficiency. Thus soil pathogens may reduce host productivity at different stages of the life cycle and can affect both the density and the genetic composition of plant populations in space and time (Harper 1977, Burdon 1987, Agrios 1997, Clay & Van der Putten 1999).

7.2.2. The role of nematodes in vegetation dynamics

Ecological succession is said to take place when the vegetation, associated fauna and micro-organism population in a particular place change with time. One unstable community progressively gives way to another until a stable climax community becomes established. The intermediate communities modify the environment in such a way as to create the conditions necessary for the establishment of the next community, thus plant communities are not static but are ever changing, especially in coastal dune systems which are extremely dynamic (Chapman 1976, Barbour 1992, Lubke & De Moor 1998). The vegetation of coastal foredunes is characterised by sequentional stages of vegetation types or zones often dominated by single plants species (Oosting & Billing 1942, Maun 1993). Therefore, often the vegetation history of a site is roughly mirrored by the sequence of the pre-successional stages backwards to the initial colonisation stage (Willis 1989).

In the vegetation of European coastal foredunes soil-borne diseases appear to be common (Maas *et al.* 1983, Zoon *et al.* 1993) and are supposed to have a high degree of specificity (Van der Putten *et al.* 1993). Van der Putten *et al.* (1993) found a zonation linked to the coastal vegetation in the root zones for the nematode fauna as found by other authors (saprotrophic fungi (Brown 1958), arbuscular mycorrhizal fungi (Foster & Nicloson 1981, Ernst *et al.* 1984), soil micro-arthropods (Koehler *et al.* 1995), and (free-living) nematodes (Yeates *et al.* 1968, Bussau 1991).
The root zones of sequentional foredune plant species apparently contain pathogens that are specific for their host and pre-successional plant species, but that affect the next species in the successional sequence to a much lesser extent (Van der Putten *et al.* 1993; Figure 7.1).

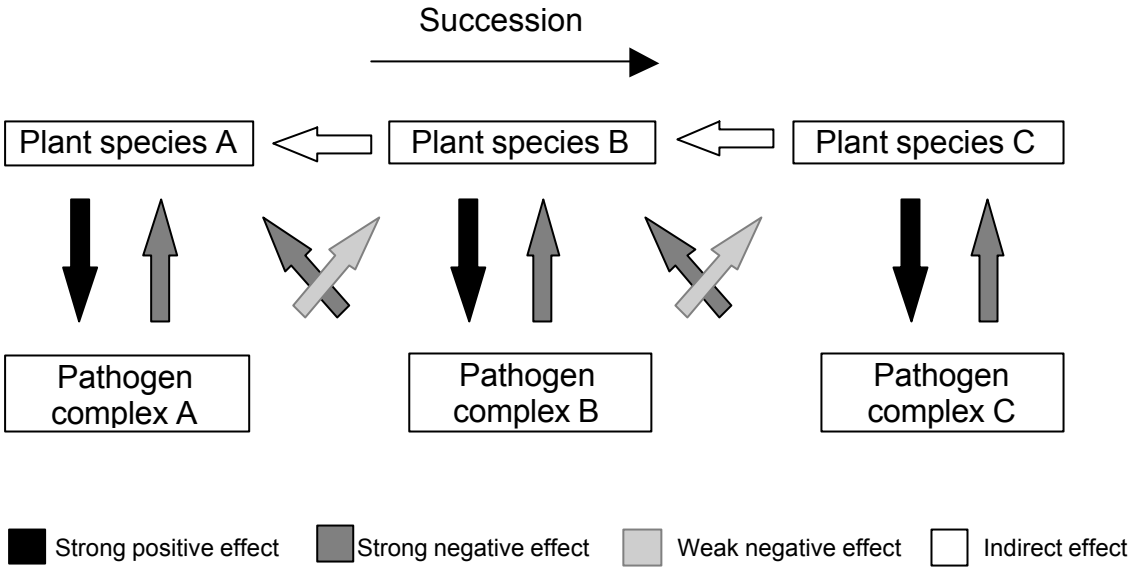


Figure 7.1. Theoretical design of the role of soil pathogen complexes in the succession of coastal foredune plant species in Europe (After Van der Putten & Van der Stoel 1998).

In other words late successional species tolerate soil pathogens of prior successional species more than their own and following successional species. Chemical exclusion of nematodes by the application of nematicides resulted in enhanced growth of test plants in the research of Van der Putten and Troelstra (1990), and Zoon (1991). Further chemical tests with fungicides and nematicides strongly suggest that plant-parasitic nematodes play a role in the pathogen complexes (De Rooij-Van der Goes *et al.* 1995, Zoon 1995). Later Van der Putten and Peters (1997) found that soil-borne plant pathogens occurring in coastal dunes were also affecting plant competition.

7.3. MATERIAL AND METHODS

To investigate the nematodes of the foredune plant community a field survey and a transplantation experiment will be conducted involving the indigenous species *Arctotheca populifolia*, *Ipomoea pes-caprae*, *Scaevola plumieri*, *Ehrharta villosa*, *Sporobolus virginicus*, and the alien sand binding grass *Ammophila arenaria*. The rhizosphere of the species *Scaevola plumieri* were impossible to reach without destroying the dune therefore the species is excluded from the field survey.

7.3.1. Field survey

To investigate the nematodes of the foredunes plant community a field survey and a transplantation experiment has been conducted involving the indigenous plant species *A. populifolia*, *I. pes-caprae*, *S. plumieri*, *E. villosa* and *S. virginicus* and the alien sand binding grass *A. arenaria* (see table 7.1).

Table 7.1. The sampled species with sample site, date and distance to high water mark (HWM) in metres.

Species	Site	Distance to HWM (m)
Ammophila arenaria	Kleinemonde	23
Ehrharta villosa	Kenton-On-Sea	97
Scaevola plumieri	Old Woman's River	55
Sporobolus virginicus	Kleinemonde	47
Ipomoea pes-caprae	Fish River	150
Arctotheca populifolia	Old Woman's River	36

The soil sampling was conducted by laying out a single plot of 320m^2 in a monostand (Van der Putten & Peters 1997) for each of the plant species (160 m^2 for *A. populifolia*). The plot was subsequently divided into ten subplots of 8x4m (4x4m for *A. populifolia*). In each subplot two random soil samples of approximately 1kg were taken. For the root sampling the top 10 cm of the sand (wind-deposited layer) was removed to reach the upper root zone. In each plot three bulk root samples of minimal 20 gram were taken divided over the ten subplots. The soil of the rhizosphere and roots of the selected species were put into plastic bags and placed in a cooler box, and transported to the laboratory. The soil and roots were kept in a dark cold room (5°C) until identification.

Vegetation recording sample plots

Not all the sites provided a monostand of the sampled plant species, therefore, plant species cover and abundance was recorded for each subplot. The importance value

(IV) was calculated for all plant species present for each of the sample plots. The IV provides an overall estimate of the influence or importance of a species in a community. The importance value takes into account the cover and frequency of the species. It is based on the fact that most species do not normally reach a high level of importance in the community, but those that do serve as an index, or guiding species (Smith 1990). Importance Value *IV* is the sum of relative density *rD*, relative cover *rC*, and relative frequency *rF* for each species *i* involved (Smith 1990):

Importance value - $IV_i = rD_i + rC_i + rF_i$

The IV is expressed within a range of 0 to 3, with the maximum value 3 for species in a monostand (Smith 1990).

7.3.2. Nematode extraction and identification

The ecto-parasitic nematodes (free-living in the soil) were isolated from a sub-sample of 400ml soil from each subplot sample taken, using the decanting and sieving method (Cobb 1918). The soil sub-sample was placed in a bucket of 10 litre. Water was added and the soil was brought in suspension by vigorously stirring the soil for 10 seconds. The soil was left for 30 seconds before being poured over a series of sieves (mesh size: 1000µm, 500µm, 365µm, 160µm, 100µm, 45µm). By means of a gentle jet of water applied to the back of the sieves the residue of nematodes was rinsed of the sieve into a glass beaker. This process was repeated a three times for each sample. After that the nematode residue was poured into an extraction filter made from a thick plastic tube (19 cm by 5 cm) with a coarse mesh bottom (plastic mosquito netting) which supported a cotton filter (milk filter) upon which the residue was poured. The extraction filter was placed in a tray, and the tray was subsequently filled with tap water up to the bottom of the filter. The nematodes will crawl down the filter into the tap water after which they could be collected. An extraction period of 48 hours was used for each sample. The nematode extractions were collected in glass bottles and placed in a dark cold room at 5°C until identification.

Endoparasitic nematodes (spending part of their life in the root) were isolated by cutting the collected roots into 1 cm pieces and putting the roots into the funnels of the mistifier (funnel-spray method) for six days (after Oosterbrink 1960, Van Bezooijen 1997). A fine

mist of water was sprayed onto the chopped roots which made that the emerging nematodes were washed into the funnel, after which water in the funnel which contained the nematodes was collected in glass bottles, and placed in a dark cold room (5°C) until identification. After the nematode extraction of the roots, the dry weight of the roots was measured after a period of 48 hours at 70°C (Smith 1990).

After soil and root extraction the nematodes were counted and identified to at least genus level following Van den Berg and Heyns (1973), Van den Berg (1982, 1986), Bongers (1988) and Kleynhans *et al.* (1996). Identification focused on phytophagous or plant-parasitic nematodes. Species in the saprophagous and omniphagous (Dorylaimids) groups were not identified individually. After counting, the nematodes were fixated in formaline (Seinhorst 1966) and glycerine (Bongers 1993).

Three different indices were calculated for the plant-parasitic nematodes present, namely the plant-parasitic index (PPI), the Margalef species richness index and the Shannon-Weaver species diversity index. The plant-parasitic index (PPI) of the plant feeding nematode fauna was calculated for each sample following Bongers (1990) and De Goede and Bongers (2001). The different plant-feeding nematodes have different PPI values ranging from 1 to 5. Each individual present is allocated a PPI value (see Appendix II). Using the abundance information, the PPI is calculated as follows:

$$PPI = \Sigma (v_i * a_i) / \Sigma (a_i)$$

where v_i is the PPI value assigned to nematode taxon *i* and a_i is the abundance of taxon *i* in sample *a*.

Margalef's (1951) species richness index relates the number of specimens *n* and taxa *s* in each sample according to the formula: $R = (s - 1) / \ln(n)$.
For the Shannon index (*H'*) the proportion (p_i) of species *i* relative to the total number of species is calculated and then multiplied by the natural logarithm of this proportion. The resulting product is summed across species and multiplied by -1:

$$\text{Shannon index } H' = -\sum_{i=1}^{S} p_i \ln p_i$$

The range of the Shannon index is without limit (≥ 0) and increases as the number of species increases and/or the proportional distribution of species become more equitable. The Shannon index assumes that the habitat contains an infinite number of individuals (Shannon & Weaver 1949).

7.3.3. Soil analysis

For soil analysis approximately 60 grams of soil was collected (n = 3) in a randomly chosen subplot for each plant species. The soil was air dried, sieved (2 mm mesh) before the following parameters were measured: pH (H_2O), concentration of chloride ions, conductivity (salinity), and organic matter content (Mackereth *et al.* 1978, Van Vliet *et al.* 1988):

pH: To determine the pH (H_2O), 20 grams of fresh soil was placed in a 250ml flask with 100ml distilled water. The solution was shaken for one minute, allowed to settle, after that the shaking was repeated for three more times. The pH was measured at 18°C with a Cyberscan 100 pH meter.

Conductivity (or salinity): After the pH measurement the soil solutions was filtered over a Whatman no 1 filter paper to prepare the soil solution for the conductivity measurement. The filtered solution was placed in a plastic beaker and the conductivity was measured in µS/cm at 25°C with a digital bench-top conductivity meter (HI 8820 Hanna Instruments). The calibration was done using a 0.01 mol/l KCl).

Chloride: Because chloride contributes greatly to salinity, this anion is determined separately (Brower *et al.* 1990). For the chloride ion measurement 100 ml of the soil solution was placed in a beaker on a magnetic stirrer and the chloride concentration measured in mV with a Eutech chloride ion electrode (EC-CLO-03) at 20°C (Eutech 2000).

Organic matter: To determine the moisture content of the soil 10 grams of soil was placed in a 70°C oven for 48 hours, weighed (oven-dry weight) after which the soil was placed in a muffle furnace to be burned at 400°C for 24 hours (ash-free dry weight). The percentage organic matter (loss on ignition) is the difference between the oven-dry weight and the ash-free-dry weight, divided by the oven-dry weight.

7.3.4. Transplantation experiment

In this experiment *A. populifolia, I. pes-caprae*, *E. villosa*, *S. virginicus* and the alien grass *A. arenaria*, were grown in their own sterilised and unsterilised rhizosphere soils, as well as in the soil of the other species (n = 5). *S. plumieri* was excluded from the experiment for the reason mentioned for the field survey.

For each plant species, five sub-samples of 20 kg each were collected at the same sites where the samples for nematode identification were taken (See Table 7.1). After careful homogenising the sub-samples, the sand was sieved (5 mm mesh) to remove coarse material and separate the roots from the soil. The roots were cut into pieces of approximately 1 cm and re-introduced into the homogenised sand. After finishing one soil type, the sieve and equipment were sterilised with 96% alcohol, left to dry and rinsed with water before continuing with the next soil type. Half of the homogenised soil was sterilised using a pressure cooker (16 minutes at 254°C), after which the sterilised soil was aired by spreading the sand out on sterile plastic sheets. This to avoid possible sterilisation effects on the plants due to toxic compounds that appeared after sterilisation. After six days of aeration, two litre pots each were filled with 1.5 litre of sand containing 10% moisture (Van der Putten & Peters 1997).

Growth of plants

Plants of *A. arenaria*, *E. villosa* and *S. virginicus* were grown from stem pieces collected from the sampled site. After 24 hours in the mistifier, the stem pieces were put in dishes (∅ 20 cm) containing sterile beach sand, and subsequently covered with a 1cm layer of sand. The dishes were covert with a perforated plastic sheet to prevent excess water loss. *A. populifolia* and *I. pes-caprae* plants were grown in the conviron from seeds collected in 1998 at Port Alfred and Fish River, respectively.

For germination in the conviron, 50 seeds per species were placed on filter paper saturated with distilled water in 9 cm plastic petri dishes. Under a 25°C day and 15°C night temperature with a light regime of 16 hours light and 8 hours dark (Fenner 1985, Hertling 1997) the seeds were set to germinate for 35 days. The petri dishes were randomised for position every 2-3 days when checked for moisture status and germination. The germinated seeds were counted and removed from the petri dish, and subsequently planted in trays filled with sterilised beach sand and placed at room temperature.

After termination of the germination test the ungerminated seeds where tested on viability by either squeezing the seeds upon a hard surface or cutting the seeds in half to check the embryo. The soft and easy to squeeze seeds with brown embryos were considered dead, whereas the hard seeds with white embryos were considered viable (Baskin & Baskin 1998, Bekker *et al.* 1998a).

For the seeds that germinated the coefficient of the rate of germination was calculated per species (Scott *et al.* 1984):

$$\text{Coefficient Rate Germination: } CRG = \frac{\Sigma (n_i)}{\Sigma (n_i * t_i)} X\ 100$$

with *n* the number of germinated seeds at time *i*, and *t* the number of germination days at time *i*. The coefficient of rate of germination (CRG) gives an indication of how uniform the seeds have germinated.

When the plants from the stem pieces and the seedlings were approximately two weeks old they were planted. Four plants were planted per pot after which the soil in the pots was covered with tin foil to protect the sand from desiccation and placed in the greenhouse in randomised blocks. A mean temperature of 20°C and a photoperiod of 12 hours were maintained during the experiment. When necessary, shade cloth was hung above the pots to prevent the plants from burning. Every week the growth of the plants was measured. The number of leaves of each plant were counted and the length of the longest leaf (grasses) or stem length (dicots) measured. All the pots were weighed and then watered with de-mineralised water one to three times a week to reset the moisture of the soil at 10%. A full strength Hoagland nutrient solution was added on day 1 and subsequently once every week to counteract the effect of sterilisation. The strength was doubled every two weeks starting with 12.5ml (after Van der Putten 1993). After six weeks, the plants were harvested and the root separated from the shoot. The total end stem/leaf length, fresh and dry weight (48 hours at 70°C) of the roots and shoots were measured. From the dry weight data the relative production (RP) of the total biomass was calculated. This is the total biomass in unsterilised soil divided by the total biomass in sterilised soil: RP = total biomass NS / total biomass S. The RP gives an indication of the effect of the sterilisation of the soil.

7.3.5. Data analysis

The independent variables were tested for normality and homogeneity of the variance by using the Kolmogosov-Smirnov and Levene's test, respectively. When these assumptions failed, non-parametric procedures were carried out. All nematode field survey data were analysed using an analysis-of-variance (ANOVA) and a Tukey's multiple comparison test was applied to compare the means. For the transplantation test a ANOVA, followed by a Tukey comparison-of-means test was conducted in the case of the germination data, growth of stem pieces, between species survival, stem length and growth rate between the different soil origins (treatments), total biomass within species, root and shoot biomass, and root:shoot ratio comparisons between treatments. Some of the data did not show a normal distribution, and therefore a Kruskal-Wallis ANOVA was used followed by the Newman-Keuls test (Zar 1996). Kruskal-Wallis was used for the soil parameters and parameters within plant species survival, leaf production, growth stem rate per week, total biomass between species, root and shoot biomass between species and relative production between treatments.

To test the relation between the chloride content of the soil and the distance to the high water mark, a regression analysis was used. To investigate the possible effect of sterilisation on the release of organic matter or ions like chloride, a correlation test was conducted. For all data analyses the standard error (S.E.) and number of replicates (*n*) is given and the differences between the analysed data was indicated by different letters (abc, pqr, xyz) behind the values in tables or above the columns and data points in graphs. For each analysis the level of significance was specified using the following system: * = $P<0.05$, ** = $P<0.01$, and *** = $P<0.001$. The ** were placed next to the highest value of the analysed parameter. All statistical tests are performed at a 95% confidence interval using the statistical program Statistica 5.5. (Statsoft Inc.). For details of the ANOVA analysis see Appendix III.

7.4. RESULTS

7.4.1. Field survey

For the species *Ammophila arenaria*, *Arctotheca populifolia*, *Ipomoea pes-caprae*, *Sporobolus virginicus*, and *Ehrharta villosa* root and rhizosphere soil samples were collected to determine the nematodes density and species richness associated with the plant species.

7.4.1.1. Nematodes associated with foredune species in South Africa

In total twelve genera of plant-parasitic nematodes have been found (Table 7.2). The Saprophague and omnivorous nematodes were the most common nematodes found, and were present in the soil and the roots of most plant species, with the exception of the omniphague nematodes, which were absent from the roots (Table 7.2). These nematodes do not parasitise plants, as do the phytophagues nematodes.

Phytophague or plant-parasitic nematodes were found in all species, but the phytophagues nematode species richness for *E. villosa* was the highest with 7 species, of which only 1 species occurred in the roots. The *I. pes-caprae* and *A. arenaria* samples were the second highest with 6 species each, of which 3 species occurred in the roots of both species. For *S. virginicus* 2 of the 5 species found occurred in the roots, and 2 of the 4 species for *A. populifolia* (Table 7.2B).

The phytophague *Filenchus* sp. was the only plant-parasitic nematode that occurred in the root samples of all species, as well as in the root samples of *A. arenaria* and *A. populifolia* (Table 7.2).

Pratylenchus sp. and *Meloidogyne* sp. were the only endoparasitic nematodes found, so the other phytophague species found were all ectoparasites. Although, nematodes of the genus *Aphelenchus* were mainly a fungi eating nematode, they were frequently found in the soil of *E. villosa, A. populifolia* and *I. pes-caprae*, as well as the soil of *A. populifolia* and *I. pes-caprae* (Table 7.2). Nematodes of the genus *Meloidogyne* (sedentary endoparasites) were found in the roots of *S. virginicus* and *I. pes-caprae*. Whereas *Pratylenchus*, a migratory endoparasitic capable of moving through the root, was found only in *E. villosa* roots. For *A. populifolia* no endoparasitic nematodes found in the roots (Table 7.2B). The semi-endoparasitic nematodes of the genera *Rotylenchus* were found only in *A. arenaria*, and the semi-endoparasitic *Scutellonema* was found only in *I. pes-caprae* (Table 7.2). Nematodes of the genus *Tylenchorhynchus*

(ectoparasitic) were found in soil of *A. arenaria* and *E. villosa*, whereas the epidermis cell/root hair eating *Tylenchus* sp. were found in *A. arenaria*, *A. populifolia* and *I. pes-caprae* (Table 7.2). The order found for the highest density of total plant-parasitic nematodes (soil + root) was from high to low; *I. pes-caprae, E. villosa, S. virginicus, A. populifolia, A. arenaria* (Table 7.2). Thus the lowest number of total plant-parasitic nematodes was found for the alien grass *A. arenaria*, whereas the highest density in the soil and roots was found for the indigenous pioneer *I. pes-caprae* (Table 7.2).

Table 7.2. Mean densities (± S.E.) of associated nematode genera and their feeding types found for the plant species *A. arenaria*, *E. villosa*, *S. virginicus*, *A. populifolia*, and *I. pes-caprae* in the soil (A; number per 400 ml soil; *n* = 10) and roots (B; number per g dry root; *n* = 3). For statistics of nematode density see figure 7.2B.

A)

Nematode genera with feeding type [1]	*A. arenaria*		*E. villosa*		*S. virginicus*		*A. populifolia*		*I. pes-caprae*	
	Mean	(S.E.)	Mean	(S.E.)	Mean	(S.E.)	Mean	(S.E.)	Mean	(S.E.)
Soil:										
Phytophagues										
Aphelenchus ecto			9.2	(3.2)			53.3	(14.9)	185.8	(16.5)
Filenchus ecto	53.3	(33.9)	23.3	(4.3)	46.7	(16.9)	17.5	(8.3)	29.2	(14.1)
Hemicycliophora ecto			46.7	(13.2)			12.5	(8.1)		
Longidorus endo			1.7	(1.1)						
Meloidogyne juv. endo					3.3	(1.8)			5.8	(2.5)
Meloidogyne male endo					2.5	(1.8)			4.2	(4.2)
Paralongidorus ecto					0.8	(0.8)				
Paratylenchus ecto	0.8	(0.8)								
Pratylenchus endo	1.7	(1.7)	97.5	(15.3)						
Rotylenchus semi	10.0	(5.2)	2.5	(1.3)	2.5	(1.8)				
Scutellonema semi									104.2	(41.7)
Tylenchorhynchus ecto	5.8	(3.1)	2.5	(1.3)						
Tylenchus ecto			3.3	(1.8)			2.5	(1.8)	5.8	(2.2)
Omnivores	40.0	(9.1)	35.0	(7.0)	59.1	(12.6)	36.7	(12.5)	82.5	(21.8)
Saprophagues	383.3	(49.8)	366.7	(37.5)	392.9	(59.6)	666.7	(114.4)	929.2	(130.6)

Table 7.2 continued.

B)

Nematode genera with feeding type [1]	*A. arenaria*		*E. villosa*		*S. virginicus*		*A. populifolia*		*I. pes-caprae*	
	Mean	(S.E.)	Mean	(S.E.)	Mean	(S.E.)	Mean	(S.E.)	Mean	(S.E.)
Roots:										
Phytophagues										
Aphelenchus ecto			0.0				14.0	(7.7)	19.3	(15.8)
Filenchus ecto	43.3	(8.1)	0.0		0.0		35.3	(24.9)		
Hemicycliophora ecto			0.0							
Longidorus endo			0.0							
Meloidogyne juv. endo					745.9	(428.7)				
Meloidogyne male endo					201.0	(129.0)			409.3	(86.5)
Paralongidorus ecto										
Paratylenchus ecto										
Pratylenchus endo	0.0		842.2	(206.0)						
Rotylenchus semi	2.2	(2.2)	0.0		0.0					
Scutellonema semi									683.6	(324.4)
Tylenchorhynchus ecto	0.0		0.0							
Tylenchus ecto	6.1	(3.7)			0.0					
Omniphagues	0.0		0.0		x [2]		0.0		0.0	
Saprophagues	518.0	(102.2)	237.3	(137.6)	x		547.8	(132.1)	188.4	(26.3)

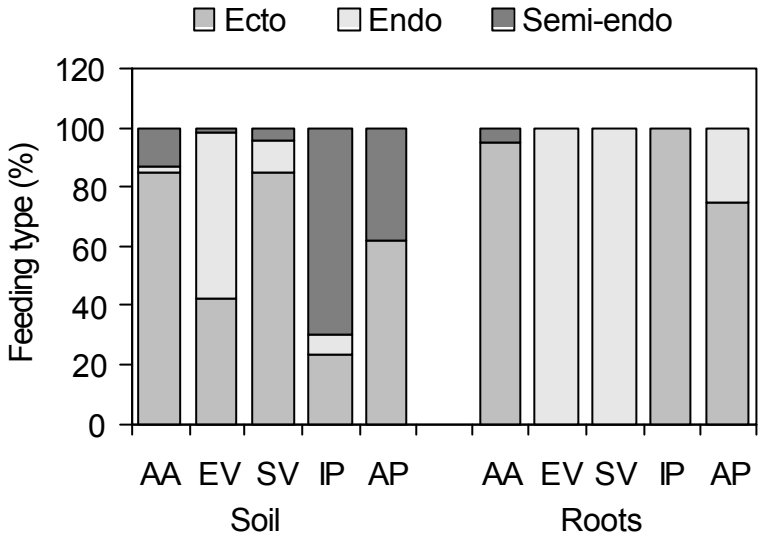
[1] Feeding type: ecto - ectoparasitic nematodes, endo - endoparasitic nematodes, semi - semi-endoparasitic nematodes.
[2] x: Missing data.

7.4.1.2. Plant-parasitic nematodes: Feeding types in root and soil

The distribution of the different feeding types and the total number of plant-parasitic nematodes found in the roots and the soil for the plant species was different for each plant species. In general, the ectoparasites are the most abundant feeding type found in the soil and are found in the soil samples. Semi-endoparasites were found in the soil and the roots of all the species, except *A. populifolia* (Figure 7.2A). Endoparasites were not often found in the soil, since they spend most of their lifecycle in the roots. *E. villosa* showed a high percentage (50%) of endoparasitic nematodes in the soil, whereas for *S. virginicus*, *I. pes-caprae*, and *A. arenaria* less than 15% of the nematodes found were endoparasitic nematodes. For *A. populifolia* no endoparasitic nematodes were found in the soil (Figure 7.2A). In the roots of *A. arenaria* and *A. populifolia* no endoparasitic nematodes were found. For *A. arenaria* a few semi-endoparasitic nematodes, whereas for *E. villosa* and *S. virginicus* only endoparasitic nematodes were found (Figure 7.2A).
In the soil and roots of *I. pes-caprae* the highest number of plant-parasitic nematodes was found, with the lowest number found for in the soil for *A. populifolia*, and in the roots for *A. arenaria* and *A. populifolia* (ANOVA, $P<0.001$; Figure 7.2B). The soil of the species *I. pes-caprae* showed significant higher numbers of plant-parasitic nematodes

in the roots when compared to the other species, with the exception of *A. arenaria* (*P*<0.001; Figure 7.2.B). Since there were no endoparasitic nematodes found for the species *A. arenaria* and *A. populifolia,* the nematodes found in the roots must be semi-endoparasitic or ectoparasitic nematodes that were still attached to the root when put in the mistifier.

A)



B)

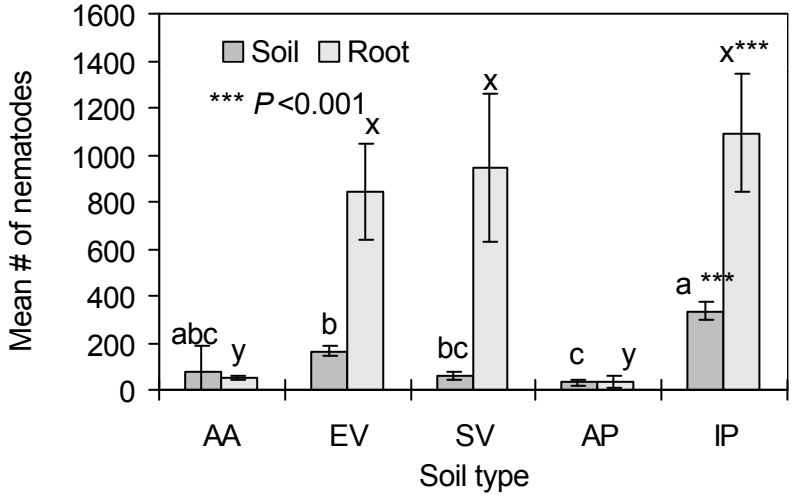


Figure 7.2. The distribution of feeding types (A) and the mean total number (± S.E.) (B) of plant-parasitic nematodes in the soil (*n* = 10) and root (*n* = 3). Any column with the same letter does not differ significantly for the number of nematodes in root or soil. Contrast obtained by Tukey after analysis by ANOVA. Level of significance: *** - *P*<0.001. Species/soil type: AA - *Ammophila arenaria*, EV - *Ehrharta villosa*, SV - *Sporobolus virginicus*, AP - *Arctotheca populifolia*, IP - *Ipomoea pes-caprae*.

7.4.1.3. Nematode species composition around each dune pioneer

To compare the nematode fauna at genus level around each plant species, the richness (Margalef), the diversity (Shannon-Weaver) and the plant-parasitic (PPI) indices were calculated for each species (Table 7.3). The species richness (Margalef) and diversity (Shannon-Weaver) of *A. arenaria* and *E. villosa* are the highest when compared to the other species. This similarity between the species diversity and richness of *A. arenaria* and *E. villosa* may support the suggestion that *E. villosa* provides the origin of most plant-parasitic nematodes of *A. arenaria* (Table 7.3). The PPI's of *I. pes-caprae* and *E. villosa* were higher compared to the other species. The plant-parasitic index (PPI) gives an indication of conditions related to the herbivore subsystem. The PPI in table 7.3 is calculated only with the plant-parasitic nematodes because all the non-plant-feeding nematodes were not identified and thus excluded from the PPI calculations. Although the nematodes were only identified up to genus level, the data in table 7.3 suggests that each plant species had a different plant-parasitic nematode fauna in its rhizosphere.

Table 7.3. The nematode species richness (Margalef), species diversity (Shannon-Weaver) and the plant-parasitic (PPI) indices of the nematode fauna at genus level, associated with the five plant species.

Plant species	Richness (Margalef index)	Diversity (Shannon-Weaver index)	PPI
A. arenaria	1.2	1.0	2.2
E. villosa	1.0	1.1	2.7
S. virginicus	0.7	0.6	2.2
I. pes-caprae	0.6	0.9	2.8
A. populifolia	0.6	0.9	2.4

7.4.1.4. Similarities nematode fauna of alien and indigenous foredune plants

The plant-parasitic nematode genera found for the alien *A. arenaria* showed the highest genera similarity when compared to the indigenous species *E. villosa*, *S. virginicus*, *A. populifolia*, and *I. pes-caprae* (Table 7.4).

For *A. arenaria* the highest similarity was found with *E. villosa*, sharing 5 of the 9 genera (55.6%), but with the other species, *A. arenaria* only shared one or two genera (Table 7.6). The nematode genera *Filenchus* was present in all of the plant species and was the only species that *A. arenaria* had in common with *I. pes-caprae* (Table 7.4).

Table 7.4. Comparison of the nematode genera found for the alien *A. arenaria* and the indigenous dune pioneers *A. populifolia*, *I. pes-caprae*, and *S. virginicus*.

Nematode genera	Plant species				
	A. arenaria	*E. villosa*	*S. virginicus*	*A. populifolia*	*I. pes-caprae*
Aphelenchus		+		+	+
Ditylenchus	+				
Filenchus	+	+	+	+	+
Hemicycliophora	+	+		+	
Meloidogyne juveniles			+		+
Meloidogyne males			+		+
Longidorus		+			
Paralongidorus			+		
Paratylenchus	+				
Pratylenchus	+	+			
Rotylenchus	+	+	+		
Scutellonema					+
Tylenchorhynchus	+	+			
Tylenchus				+	+

7.4.1.5. Vegetation composition sampled plots

The cover and abundance of the plant species growing in the sample plots were recorded and the importance value (IV) calculated to determine if the nematodes were sampled in pure mono-stands (Table 7.5). The species all showed a low cover percentage (35% or less; Table 7.4). The soil and roots of the species *S. virginicus* and *A. populifolia* were not found in a pure mono-stand ($IV \neq 3.0$; Table 7.5). The importance value of *A. populifolia* was not much below 3.0, but the *S. virginicus* plot showed a relatively low importance value of 1.3. This because of the presence predominantly of *Scaevola plumieri* and *Dasispermum suffructicosum* in some of the sub-plots.

Table 7.5. The cover values (in %) and importance values (IV) of the sampled plots for the five different plant species.

Plant species	Cover (%)	IV
Ammophila arenaria	19.0	3.0
Ehrharta villosa	21.4	3.0
Sporobolus virginicus	18.1	1.3
Arctotheca populifolia	31.8	2.6
Ipomoea pes-caprae	15.4	3.0

Although *S. virginicus* was not sampled in a complete monostand, this does not seem to have any effect on the species richness of the plant-parasitic nematodes associated with this plant (Figure 7.3). An increase in plant species (as in sub-plots E, F and G)

does not result in an increase in the number of nematode species. The nematode species richness fluctuates in the whole sampled area between one and three per sub-plot (Figure 7.3). The plant diversity in the sampled area does not seem to have an effect on the diversity of the plant-parasitic nematode diversity.

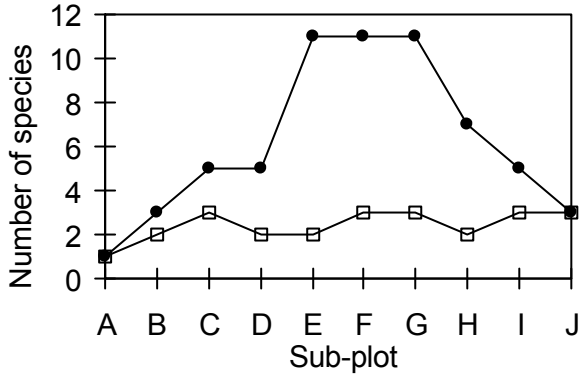


Figure 7.3. Species richness in rhizosphere soil for the different sub-plots of *S. virginicus*, with number of plant species (•) and number of plant-parasitic nematode genera (□).

7.4.1.6. Soil analysis

The chemical characteristics of the soil types originating from the rhizosphere of *A. arenaria*, *E. villosa*, *S. virginicus*, *A. populifolia*, and *I. pes-caprae* show only slight differences (Table 7.6). The pH (H_2O) values for all the soil types were around 9.0, and were not significantly different from each other. The organic matter, conductivity and chloride contents differ significantly among the soil types (Kruskal-Wallis, $P<0.05$; Table 7.6). The soils of *E. villosa* and *S. virginicus* showed the significantly highest organic matter content, whereas the *A. arenaria* soil showed the lowest (Table 7.6). The conductivity of the *A. populifolia* soil is significantly the highest, whereas it showed the lowest chloride content together with *I. pes-caprae* ($P<0.05$; Table 7.6, see also Figure 7.4).

Table 7.6. Mean parameters (± S.E.) of the rhizosphere soil (n = 3) for the species *A. arenaria*, *E. villosa*, *S. virginicus*, *A. populifolia* and *I. pes-caprae*. Any value with the same letter does not differ significantly per soil parameter within the soil type. Contrasts

obtained by Newman-Keuls after analysis by Kruskal-Wallis. Level of significance: * - $P<0.05$.

Soil type	Soil parameters (Mean ± S.E.)			
	pH (H_2O)	Organic Matter (%)	Conductivity (μScm^{-1})	Chloride (mg per 100 g)
A. arenaria	9.0 (0.07) a	0.3 (0.13) b	80 (4.54) ab	0.7 (0.03) a *
E. villosa	9.0 (0.05) a	0.9 (0.06) a *	57 (1.86) c	0.6 (0.05) a
S. virginicus	9.0 (0.06) a	0.8 (0.09) a	65 (4.76) bc	0.6 (0.05) a
A. populifolia	9.1 (0.10) a	0.7 (0.13) ab	83 (1.85) a *	0.4 (0.05) b
I. pes-caprae	8.8 (0.10) a	0.6 (0.14) ab	64 (4.32) c	0.2 (0.07) b

The effect of salt spray showed a significant correlation with the high water mark (HWM) with an R^2 of 0.48 (Regression analysis, $P<0.001$; Figure 7.4). Only the *A. populifolia* showed a lower chloride content than expected, since it was situated close to the HWM (36m). But the site was cut off from the sea by a high mobile dune which might account for a reduction in salt spray and hence in chloride content of the soil.

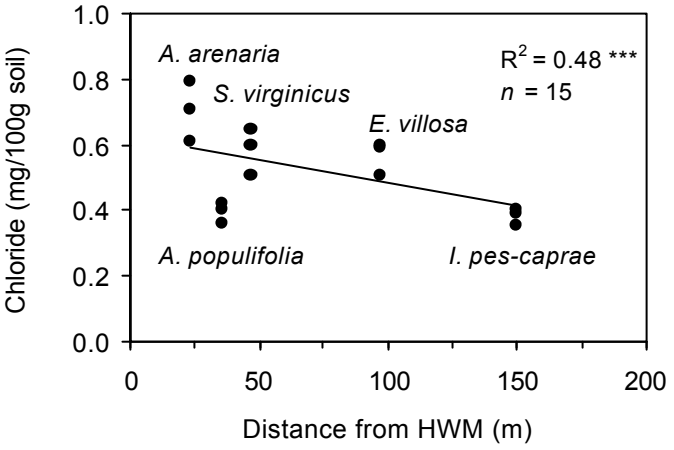


Figure 7.4. The negative correlation between the chloride content (mg/100g soil) and the distance to the high water mark (HWM) in metres for the species *A. arenaria* (AA), *E. villosa* (EV), *S. virginicus* (SV), *I. pes-caprae*, (IP) and *A. populifolia* (AP). Regression analysis with a significance level of: *** - $P<0.001$.

7.4.2. Transplantation experiment

In the transplantation experiment the grass species *A. arenaria*, *E. villosa*, and *S. virginicus* were used as well as the dicots *A. populifolia*, *I. pes-caprae* and *Scaevola plumieri*.

7.4.2.1. Growth of plants before the transplantation experiment

Germination of seeds

The seeds of *A. populifolia* and *I. pes-caprae* germinated well. *I. pes-caprae* showed a higher germination percentage when compared to *A. populifolia* (ANOVA, $P<0.001$; Figure 7.5). The seeds of S. plumieri showed no germination at all, whereas from the *A. populifolia* seeds that did not germinate 17.5 ± 7.1% were viable and 9.5 ± 4.7%

were non-viable or dead. All the non-viable seeds of *A. populifolia* were soft and infected by fungi. For the seeds of *I. pes-caprae* most seeds germinated. The ungerminated seeds of *I. pes-caprae* were viable (5.0 ± 3.3%, Figure 7.5)

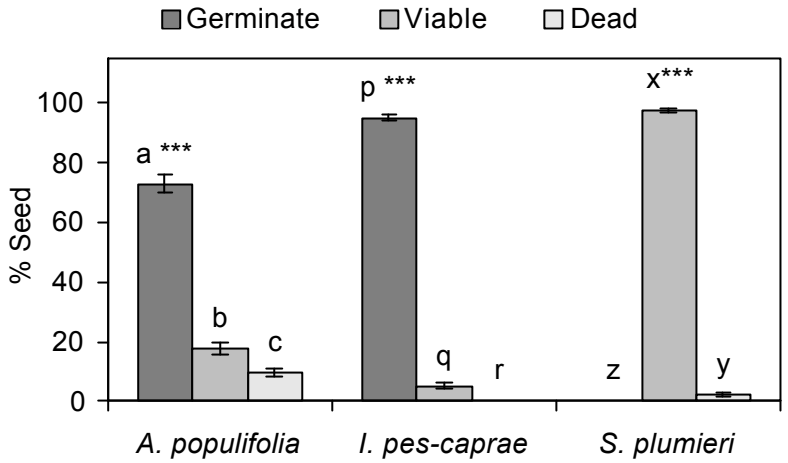
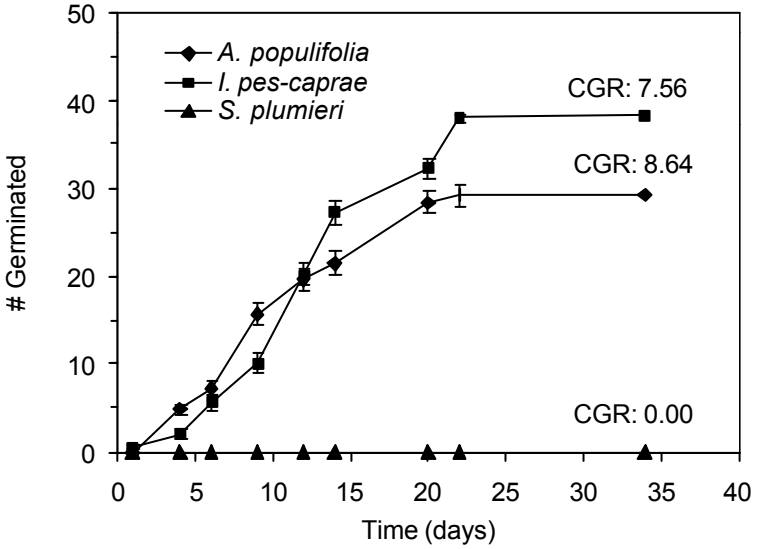


Figure 7.5. Mean number (± S.E.) of germinated, non-germinated viable and non-viable or dead seeds of the species *A. populifolia*, *I. pes-caprae* and *S. plumieri* (*n* = 10). Contrast obtained by Tukey after analysis by ANOVA. Any column with the same letter does not differ significantly per species for the categories germinate, viable and dead. Level of significance: *** - *P*<0.001.

In the germination period of 34 days, 54% of the seeds of *A. populifolia* and 68% of *I. pes-caprae* germinated within the first 15 days (Figure 7.6). The coefficient of germination rate (CGR) for the germination of *A. populifolia* (8.6) is higher than of *I. pes-caprae* (7.6), in other words the seeds of *A. populifolia* had a shorter germination lag-phase, and were the fastest to start germinating (see Figure 7.6).

Figure 7.6. Mean number (± S.E) of germinated seeds (of a total of 40 per replicate) given per day with the coefficient germination rate (CGR) for the species *A. populifolia*, *I. pes-caprae* and *S. plumieri* (*n* = 10).



Growth of stem pieces

The stem pieces of *E. villosa* and *S. virginicus* showed hardly any growth, only 3% of the stem pieces developed a shoot and/or root for both species. Therefore, only the plants of *A. arenaria* were used in the transplantation experiment.

From the 30 stem pieces per dish (n = 25), not all stem pieces developed a root and a shoot, with the highest percentage (56 ± 9.6%) of the stems developed into a shoot with a root (ANOVA, P<0.001; Figure 7.7). Significantly more stem pieces developed only a root when compared to the pieces that developed only a shoot (P<0.001; Figure 7.7). From the remaining 20% of the stems, 3 ± 4.0% showed re-growth of the old shoot, whereas 17 ± 7.5% showed no growth at all (Figure 7.7). Only the stem pieces that developed a shoot and a root were used for the transplantation experiment.

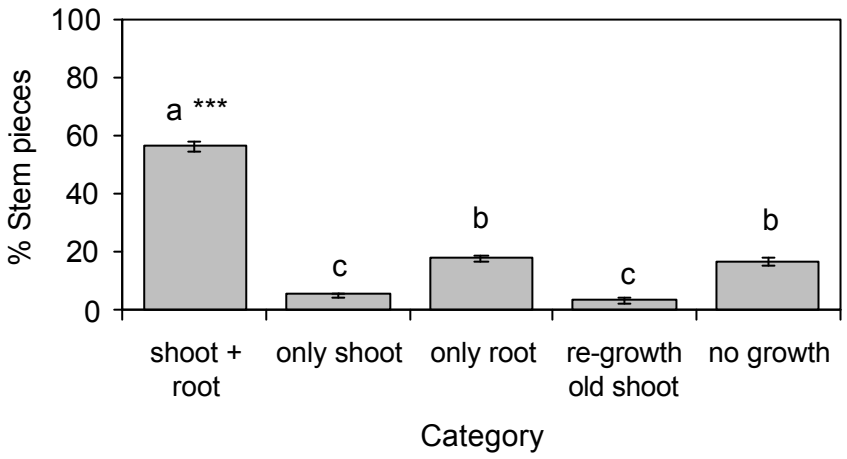


Figure 7.7. The mean percentage (± S.E.) of *A. arenaria* stem pieces (n = 25) that developed a shoot and/or root, plotted per category of shoot and/or root development. Any column with the same letter does not differ significantly in percentage of pieces per category. Contrasts obtained by Tukey after analysis by ANOVA. Level of significance: *** - P<0.001.

7.4.2.2. Plant growth during the transplantation experiment

Even though the stem pieces of *S. virginicus* and *E. villosa* were excluded from the experiment, the soil of these species was used in the transplantation experiment.

Plant survival

Not all plants survived during the experiment. The plants grown in the sterile soil of *A. arenaria* (AA S), especially, showed low survival. For each treatment 4 plants were planted per pot (n = 5) at the start of the experiment. After 43 days of growth only *I. pes-caprae* plants showed a 100% survival for the different treatments, except for treatments AA NS and AA S (Kruskal-Wallis, P<0.001; Figure 7.8). On the other hand, *A. arenaria* and *A. populifolia* showed loss of plants during the experiment for the treatments EV NS/S and SV S for both *A. arenaria* and *A. populifolia*, and for the treatments SV NS and AP S for only *A. arenaria* (Figure 7.8, Table 7.7).

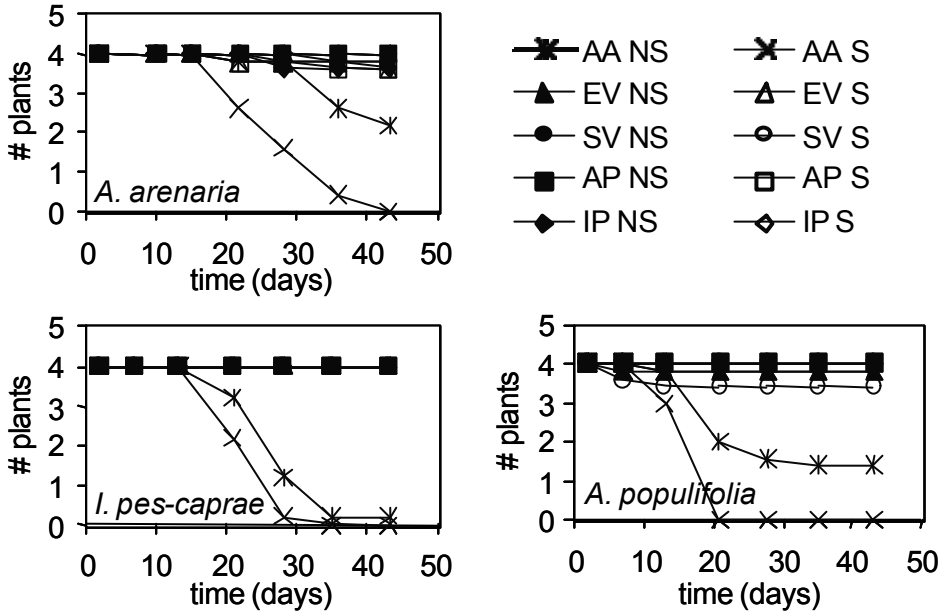


Figure 7.8. Survival of *A. arenaria*, *A. populifolia* and *I. pes-caprae* plants during the transplantation experiment. The plants were grown in non-sterile (NS) and sterile (S) rhizosphere soil originating from *A. arenaria* (AA), *E. villosa* (EV), *S. virginicus* (SP), *I. pes-caprae*, (IP), and *A. populifolia* (AP). Per treatment 5 replicas of 4 plants per pot were used.

For *I. pes-caprae* all plants survived, with the exception of the AA NS treatment form which all plants died (Table 7.7). In general the survival of all three species growing on the AA NS soil was significantly the lowest compared to the other soil treatment (Kruskal-Wallis, P<0.001; Table 7.7). Besides the AA NS treatment the species *A. arenaria* showed no significant plant loss for the other treatments, whereas there was significant plant loss observed for *A. populifolia* plants growing on the SV S soil

(*P*<0.001, Table 7.7). When comparing within the treatments for the different plant species, the survival of *A. arenaria* plants of the AA NS treatment was significantly higher when compared to the survival of the *I. pes-caprae* plants (ANOVA *P*<0.001).

Table 7.7. Mean number of plants per pot (± S.E.) after termination of the experiment for the species *A. arenaria*, *I. pes-caprae*, and *A. populifolia* grown in sterile (S) and non-sterile (NS) soil (*n* = 5). Any value with the same letter does not differ significantly in the number of plants per pot within a species. Contrasts obtained by Newman-Keuls test after analysis by Kruskal-Wallis. Level of significance: *** - *P*<0.001.

Soil type and treatment [1]		Plant species					
		A. arenaria		*A. populifolia*		*I. pes-caprae*	
		Mean	(± S.E.)	Mean	± S.E.	Mean	± S.E.
AA	NS	2.20	(0.49) b	1.40	(0.43) b	0.20	(0.17) b
	S	- [2]		- [2]		- [2]	
EV	NS	4.00	(0.00) a ***	3.80	(0.17) ab	4.00	(0.00) a ***
	S	3.60	(0.21) ab	3.80	(0.17) ab	4.00	(0.00) a
SV	NS	3.80	(0.17) ab	4.00	(0.00) a ***	4.00	(0.00) a
	S	3.80	(0.17) ab	3.40	(0.21) b	4.00	(0.00) a
IP	NS	3.60	(0.21) a	4.00	(0.00) a	4.00	(0.00) a
	S	4.00	(0.00) ab	4.00	(0.00) a	4.00	(0.00) a
AP	NS	4.00	(0.00) a	4.00	(0.00) a	4.00	(0.00) a
	S	3.60	(0.21) ab	4.00	(0.00) a	4.00	(0.00) a

[1] Soil type: AA - *Ammophila arenaria*, EV - *Ehrharta villosa*, SV - *Sporobolus virginicus*, AP - *Arctotheca populifolia*, IP - *Ipomoea pes-caprae*, and Treatment: NS - Non-sterile soil, S - Sterile soil.

[2] No plants survived.

Leaf production

The plants of *A. populifolia* of the IP S treatment showed the significant highest leaf production on day 43 compared to all the NS treatments, except IP NS (Kruskal-Wallis, *P*<0.001, Figure 7.9). For *I. pes-caprae* the AP S treatment showed the significant highest leaf production when compared to AP NS and AA NS (*P*<0.001; Figure 7.9). The species *A. arenaria* showed no significant differences between the soil treatments for the number of leaves (*P*>0.05, Figure 7.9). After 6 weeks of growth the *A. populifolia* plants have produced significantly more leaves when compared to the dicot *I. pes-caprae* and the grass *A. arenaria* (Kruskal-Wallis, *P*<0.001; see Figure 7.9).

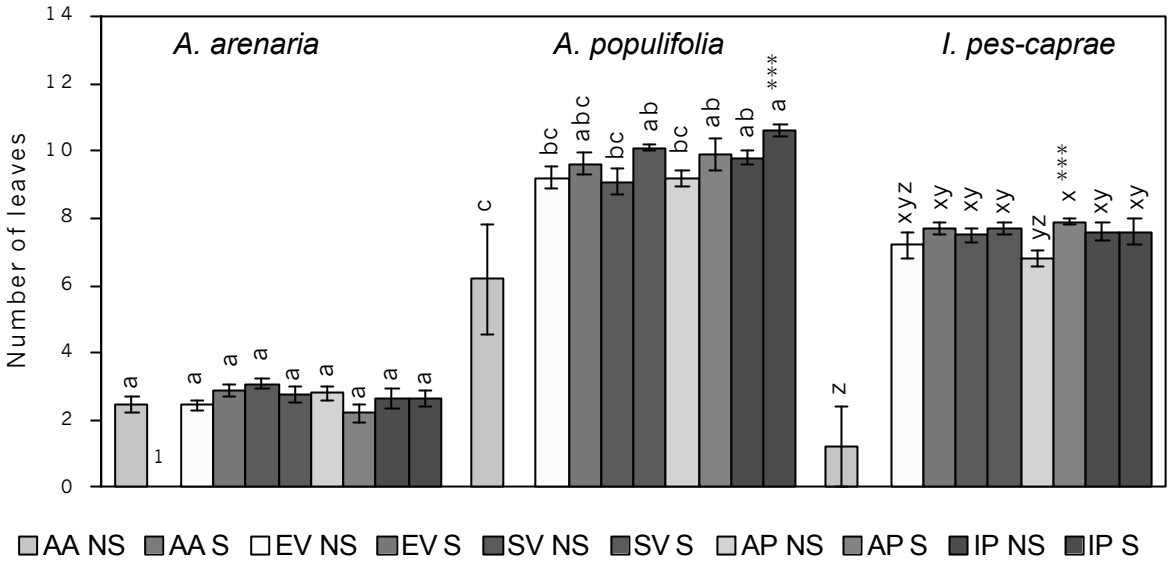


Figure 7.9. Mean number of leaves (± S.E.) of the species *A. arenaria*, *I. pes-caprae* and *A. populifolia* on day 43 by soil treatment (*n* = 5). Any column within a plant species with the same letter does not differ significantly in the number of leaves. Contrasts obtained Newman-Keuls test after analysis by Kruskal-Wallis. Level of significance: *** - *P*<0.001. Soil treatment: NS - Non-sterile soil; S - Sterile soil of AA - *A. arenaria*, EV - *E. villosa*, SV - *S. virginicus*, AP - *A. populifolia*, IP - *I. pes-caprae,* 1 - All plants died.

Stem growth

The stem length was measured after exhumation (total end length), as well as on a weekly base during the experiment. Note that for *A. arenaria* the longest leaf is measured (Table 7.8). All three species showed significant differences in total end length of the stem (longest leaf for *A. arenaria*) between the treatments (ANOVA, *P*<0.05; Table 7.8). For the species *A. arenaria* and *A. populifolia* the Tukey test for comparisons of means could not find any significant pair-wise differences among the means of the treatments, even though the ANOVA test was significant for both species (*P*<0.05;Table 7.8). For *I. pes-caprae* the plants grown on EV NS, EV S and AP S soil were significantly higher in total end length of the stem than these grown on AA NS and IP NS (*P*<0.01; Table 7.8). This might point to growth inhibiting pathogens in the soil for the species *I. pes-caprae* since it shows the lowest total stem length when grown on its own non-sterile soil.

Table 7.8. The mean end length (± S.E., in cm) of the longest leaf of *A. arenaria*, and of the stems of *I. pes-caprae* and *A. populifolia* after 43 days of growth on different soil treatments (n = 5). Any value within a species with the same letter does not differ significantly for stem/leaf length. Contrast obtained by Tukey after analysis by ANOVA. Level of significance: * - P<0.05, ** - P<0.01.

Soil treatment [1]	Mean length per plant species (in cm)					
	A. arenaria		*A. populifolia*		*I. pes-caprae*	
	Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
AA NS	264.9	(14.7) a	82.8	(4.9) a	116.0	(0.0) b
AA S	- [2]		- [2]		- [2]	
EV NS	304.4	(24.6) a	107.2	(6.6) a	144.6	(5.3) a
EV S	331.3	(35.4) a	95.5	(9.9) a	148.4	(3.1) a **
SV NS	359.5	(38.4) a	102.3	(6.3) a	140.9	(6.3) ab
SV S	355.2	(30.2) a	85.4	(7.7) a	141.6	(4.7) ab
AP NS	350.5	(24.7) a	114.1	(1.3) a *[3]	142.9	(4.9) ab
AP S	255.2	(31.8) a	106.3	(5.0) a	145.7	(3.7) a
IP NS	277.4	(35.7) a	112.3	(6.5) a	120.2	(5.7) b
IP S	394.7	(30.4) a *[3]	102.7	(9.2) a	138.5	(3.8) ab

[1] Soil treatments: non-sterile (NS) and sterile (S) rhizosphere soil of the species *Ammophila arenaria* (AA), *E. villosa* (EV), *S. virginicus* (SV), *A. populifolia* (AP), *I. pes-caprae* (IP).

[2] All plants died.

[3] No pair wise differences among the means.

Stem growth rate

The growth rate of the longest leaf of *A. arenaria* was fluctuating strongly over time, but the mean growth rate (over all treatments) showed a significant increase with time (Kruskal-Wallis, P<0.001; Table 7.9). Week 5 showed a significant higher growth rate when compared to the other weeks, with the exception of week 6 (P<0.001; Table 7.9). The plants growing in the AA NS soil showed a significant lower mean growth rate when compared to EV S, AP S, SV NS, and SV S (ANOVA, P<0.001; Table 7.9). For *I. pes-caprae* the growth rate of the stem was not as strongly linked with time as for *A. arenaria*. In week 3 the stem showed significantly the highest mean growth rate compared to week 1, 4, 5, and 6 (Kruskal-Wallis, P<0.001;Table 7.9).

Table 7.9. The mean growth rate per week in cm over all treatments (± S.E.) of the longest leaf for *A. arenaria*, and of the stem for *I. pes-caprae* and *A. populifolia* (n = 50). Any length values within a species with the same letter do not differ significantly. Contrast obtained by Newman-Keuls test after analysis by Kruskal-Wallis. Level of Significance: *** - P<0.001.

Week	Mean growth per week per plant species (in cm)					
	A. arenaria		*A. populifolia*		*I. pes-caprae*	
	Mean	(± S.E.)	Mean	± S.E.)	Mean	± S.E.)
1	3.47	(0.52) d	0.31	(0.05) e	0.44	(0.07) c
2	5.70	(0.85) c	0.68	(0.10) d	1.58	(0.24) a
3	7.62	(1.14) bc	1.64	(0.24) c	1.75	(0.26) a ***
4	5.98	(0.89) bc	2.18	(0.32) b	1.20	(0.18) b
5	9.59	(1.43) a ***	1.95	(0.29) bc	1.04	(0.16) b
6	7.66	(1.14) abc	3.78	(0.56) a ***	0.63	(0.09) c

When compared per treatment the AA NS showed the lowest stem growth for *A. arenaria* and *I. pes-caprae* (ANOVA, *P*<0.001), but for *I. pes-caprae* only the pants of the AA NS treatment showed a lower stem length. For *A. populifolia* no significant differences in stem length were between the soil types (P>0.05; Table 7.10).

Table 7.10. The mean stem (longest leaf for *A. arenaria*) growth rates (± S.E.) over all weeks. Any value within a species with the same letter does not differ significantly for the mean stem (leaf) length. Contrasts obtained by Tukey after analysis with ANOVA. Level of significance: *** - *P*<0.001.

Soil type and treatment [1]	Mean length per plant species (in cm)					
	A. arenaria		*A. populifolia*		*I. pes-caprae*	
	Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
AA NS	4.40	(0.66) b	1.18	(0.18) a	0.43	(0.06) b
AA S	- [2]		- [2]		- [2]	
EV NS	6.16	(0.92) ab	1.79	(0.27) a	0.99	(0.15) a
EV S	7.55	(1.13) a	1.69	(0.25) a	1.13	(0.17) a
SV NS	7.51	(1.12) a	1.82	(0.27) a	1.22	(0.18) a
SV S	7.84	(1.17) a	1.68	(0.25) a	1.36	(0.20) a
IP NS	6.14	(0.91) ab	1.96	(0.29) a	1.32	(0.20) a
IP S	7.85	(1.17) a ***	1.70	(0.25) a	1.37	(0.20) a ***
AP NS	6.74	(1.00) ab	1.95	(0.29) a	0.93	(0.14) a
AP S	5.83	(0.87) ab	1.87	(0.28) a	1.05	(0.16) a

[1] Soil treatment: non-sterile (NS) and sterile (S) of the species *A. arenaria* (AA), *E. villosa* (EV), *S. virginicus* (SV), *A. populifolia* (AP) and *I. pes-caprae*, (IP).

[2] All plants died.

7.4.2.3. Biomass, root:shoot ratio, and relative production

Biomass production

On day 43 the plants were harvested and the dry weight of the root and shoots was determined (Figure 7.10). For the species *A. arenaria* the a significant higher total biomass at day 43 was found for the SV S treatment when compared to the other

treatments, whereas the lowest was found for the AA NS treatment (ANOVA, $P<0.001$; Figure 7.10). For *A. arenaria* a significant difference between the SV S and SV NS treatment was found which might indicate that there was a growth-reducing factor in the SV NS soil, since after the sterilisation of the SV soil the biomass almost doubled.

For *A. populifolia* the total biomass produced in the AA NS soil was significant lower compared to the other treatments ($P<0.01$), whereas between the other treatments no significant differences in biomass production were observed (Figure 7.10). The plants of *I. pes-caprae* showed the significantly highest total biomass when grown on its own sterile soil (IP S) compared to AP NS, SV NS and AA NS soil, with the lowest biomass produced at AA NS ($P<0.01$; Figure 7.10). These are all NS treatments, so they indicate at a possible growth-reducing factor in the soil of SV and AP because the total biomass was significantly higher after soil sterilisation. The comparison between the AA NS and AA S treatment was impossible due to the fact that no plants survived of the AA S treatment.

For the species *A. populifolia* and *I. pes-caprae* no differences in biomass production were observed between the NS and S soil types for any of the soil origins (Figure 7.10). Overall, figure 7.10 suggests that soil originated from *I. pes-caprae* provided the most suitable growing properties for all the three plant species. They all show high production on soil originating from *I. pes-caprae*.

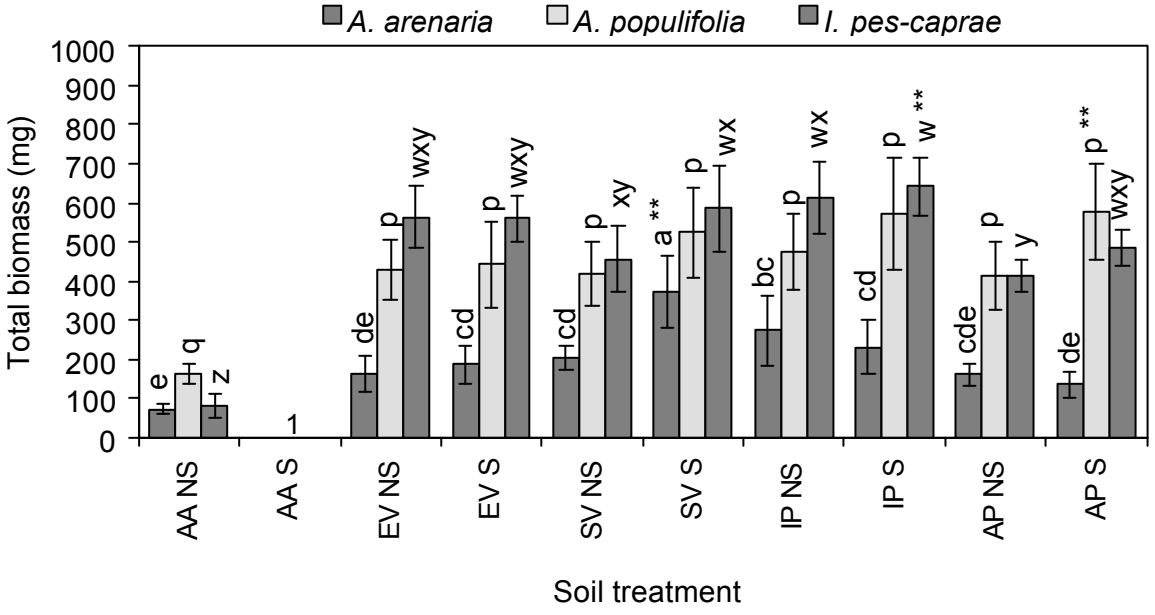


Figure 7.10. Mean total biomass (± S.E.) as dry weight in mg per pot , for *A. arenaria*, *I. pes-caprae* and *A. populifolia* grown in rhizosphere soil from their own and alien root zones. Any column with the same letter does not differ significantly for total biomass within a species. Contrast obtained by Tukey after analysis with ANOVA. Level of

significance: ** - $P<0.01$. Soil treatments: non-sterile (NS) and sterile (S) soil of the species *A. arenaria* (AA), *E. villosa* (EV), *S. virginicus* (SV), *I. pes-caprae*, (IP), and *A. populifolia* (AP), 1 - All plants died.

The mean total biomass of the species *A. populifolia* and *I. pes-caprae* was considerably higher when compared to *A. arenaria* (Table 7.11). The plants of A. *arenaria* produced a higher root biomass, whereas for *A. populifolia* and *I. pes-caprae* a higher shoot biomass was produced (Table 7.11). When the shoot biomass was compared between the species, *A. populifolia* and *I. pes-caprae* showed a significantly higher mean shoot biomass. The highest root biomass was produced by *I. pes-caprae* compared to the other two species, however the root biomasses of *A. arenaria* and *A. populifolia* were not significantly different (Table 7.11).

Table 7.11. Mean total, shoot and root biomasses (± S.E; dry weight in mg) over all treatments for the species *A. arenaria*, *I. pes-caprae* and *A. populifolia*. Different letters indicate significant differences in total, shoot or root biomass tested between species using Kruskal-Wallis followed by Newman-Keuls test. Level of significance: *** - $P<0.001$.

Species	Biomass (dry weight in mg)					
	Total biomass		Shoot biomass		Root biomass	
	Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
A. arenaria	218.2	(11.0) c	84.8	(3.5) q	133.4	(8.9) y
A. populifolia	446.1	(13.8) b	322.2	(10.9) p	123.9	(21.6) y
I. pes-caprae	528.5	(12.8) a ***	341.3	(9.4) p ***	187.3	(16.1) x ***

The biomass was also determined per treatment for the shoot and the root (Table 7.12). For *A. arenaria* the treatment SV S gives a significantly higher shoot and root production compared to AA NS and EV NS (ANOVA, $P<0.001$; Table 7.12). Within the soil types there were no significant differences between the treatments for the shoot biomass, but the root biomass of *A. arenaria* doubles after sterilisation of the SV soil (Table 7.12). This might indicate that the soil biota in the SV Soil inhibited the growth of *A. arenaria* roots.

The shoot and root biomass of *I. pes-caprae* was significantly higher when compared to *A. arenaria* (Kruskal-Wallis, $P<0.001$; see Table 7.12). Within the species a significantly higher shoot biomass for *I. pes-caprae* was found for the IP S treatments when compared to the other treatments, except for IP NS, EV S and SV S (ANOVA $P<0.001$; Table 7.12). For the root biomass IP NS and EV NS gave a significantly higher biomass

when compared to AA NS, SV NS, AP NS and AP S (P<0.001; Table 7.12). Within the soil types there were significant differences in the shoot biomass for AP soil, but none were found for the root biomass (Table 7.11). The plants of the AP NS treatment showed a significantly higher biomass when compared to the S treatment, in other words the biomass decreases after sterilisation. In general *I. pes-caprae* plants showed the best performance on their own soil.

The *A. populifolia* plants produce the significantly highest shoot biomass in AP S soil when compared to SV NS and AA NS (ANOVA, P<0.001; Table 7.12). For the root biomass there were no significant differences between the treatments, except for AA NS which produced a significant lower root biomass than EV NS, SV NS, IP NS and AP S (P<0.001; Table 7.12). There were differences found within the different soil types (NS versus S) for the shoot and root biomass of *A. populifolia*.

When compared between the species, *I. pes-caprae* and *A. populifolia* produced a significantly higher shoot biomass when compared to *A. arenaria* (Kruskal-Wallis, P<0.001; Table 7.12). A significantly higher root biomass was produced by *I. pes-caprae* plants compared to *A. populifolia* and *A. arenaria* (P<0.001; Table 7.12). In general the *I. pes-caprae* showed the best growth on the different soil treatments.

Table 7.12. The mean (± S.E.) shoot biomass (A) and root biomass (B) given by soil treatment and by plant species (mean dry weight in mg). Any biomass value within a species with the same letter does not differ significantly in shoot ^{abc} or root ^{xyz} biomass between the soil treatments. Contrasts obtained by Tukey after analysis by ANOVA. Level of significance: *** - P<0.001.

A)

Soil type and Treatment[1]	Shoot biomass per lant species (in mg)					
	A. arenaria		*A. populifolia*		*I. pes-caprae*	
	Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
AA NS	42.9	(4.7) c	111.6	(12.6) c	49.0	(0.0) d
AA S	- [2]		- [2]		- [2]	
EV NS	60.8	(5.2) bc	281.0	(22.5) ab	314.9	(19.2) bc
EV S	91.3	(9.2) abc	309.8	(35.9) ab	383.8	(18.1) ab
SV NS	98.4	(7.7) ab	275.0	(28.5) b	322.6	(28.1) bc
SV S	119.3	(12.2) a ***	374.8	(47.7) ab	364.2	(28.3) abc
IP NS	83.7	(11.3) abc	361.7	(34.4) ab	341.9	(26.5) abc
IP S	100.5	(11.9) ab	413.6	(45.6) ab	437.9	(24.5) a ***
AP NS	97.7	(10.1) ab	311.4	(33.3) ab	278.0	(12.5) c
AP S	68.7	(7.8) abc	418.5	(43.6) a ***	344.9	(19.6) d

Table 7.12 continued.

B)

Soil type and Treatment[1]	Root biomass per lant species (in mg)					
	A. arenaria		*A. populifolia*		*I. pes-caprae*	
	Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
AA NS	25.5	(4.2) d	39.4	(5.5) b	32.0	(0.0) c
AA S	- [2]		- [2]		- [2]	
EV NS	97.5	(20.5) cd	152.6	(19.6) a ***	247.1	(25.4) a
EV S	93.6	(17.9) cd	110.4	(25.3) ab	176.3	(13.6) abc
SV NS	105.8	(10.5) bcd	143.5	(17.0) a	133.7	(15.3) bc
SV S	252.5	(36.2) a ***	121.5	(16.7) ab	221.7	(31.6) ab
IP NS	188.0	(37.0) ab	113.1	(15.2) ab	271.0	(26.4) a ***
IP S	130.7	(28.1) bc	157.7	(28.3) a	204.6	(18.4) abc
AP NS	62.2	(9.6) cd	101.6	(14.6) ab	135.2	(9.6) bc
AP S	69.1	(11.5) cd	158.6	(20.3) a	139.4	(13.3) bc

[1] Soil treatments: non-sterile (NS) and sterile (S) *A. arenaria* (AA), *E. villosa* (EV), *S. virginicus* (SV), *I. pes-caprae*, (IP), and *A. populifolia* (AP).

[2] All plants died.

Root:shoot ratio

The mean total root:shoot ratio of *A. arenaria* (1.33) was significantly higher when compared to *I. pes-caprae* (0.51) and *A. populifolia* (0.41: ANOVA, $P<0.05$). This means that the plants of *A. arenaria* have invested more in root growth than *A. populifolia* and *I. pes-caprae*, but all three species showed variation in root:shoot ratios for the different soil treatments (Table 7.13).

When examining effects within the species, the *A. arenaria* plants that were growing in the SV S soil showed a significant higher root:shoot ratio when compared to AA NS, EV S, AP NS and AP S (ANOVA, $P<0.001$; Table 7.13). There were no significant differences between *A. arenaria* plants growing on the NS and S treatment of any of the soil types (Table 7.13). The plants of *I. pes-caprae* seem to have the highest root:shoot ratio when growing on their own soil (IP NS), which was significantly higher compared to the other treatments, with the exception of AA NS, EV NS and SV NS ($P<0.001$; Table 7.13). For the soil type EV and IP there were significant differences found between the NS and S treatment for the *I. pes-caprae* plants growing on that soil. For both soil types the NS treatment gave a significantly higher root:shoot ratio when compared to the S treatment ($P<0.001$; Table 7.13). In other words sterilisation of the soil of EV and IP reduces root production of the *I. pes-caprae* plants. *A. populifolia* showed no significant differences between the root:shoot ratios for the different soil treatments ($P>0.05$; Table 7.13).

Table 7.13. The mean (± S.E.) root:shoot ratios of *A. arenaria*, *I. pes-caprae*, *A. populifolia* given by soil treatment (*n* = 5). Contrasts obtained by Tukey after analysis by ANOVA. Any ratio value with the same letter does not differ significantly in root:shoot ratio for soil types within a species. Level of significance: *** - *P*<0.001.

Soil type and treatment[1]	Mean root:shoot ratio per plant species					
	A. arenaria		*I. pes-caprae*		*A. populifolia*	
	Mean	(± S.E.)	Mean	(± S.E.)	Mean	(± S.E.)
AA NS	0.70	(0.10) c	0.13	(0.07) d	0.48 a	(0.09) a
AA S	- [2]		-		-	
EV NS	1.66	(0.23) abc	0.79	(0.05) ab	0.56 a	(0.03) a
EV S	1.02	(0.10) bc	0.46	(0.02) c	0.35 a	(0.03) a
SV NS	1.09	(0.06) abc	0.42	(0.01) c	0.55 a	(0.05) a
SV S	2.17	(0.09) a ***	0.61	(0.06) abc	0.32 a	(0.02) a
IP NS	1.87	(0.32) ab	0.80	(0.03) a ***	0.31 a	(0.01) a
IP S	1.43	(0.13) abc	0.47	(0.03) c	0.40 a	(0.03) a
AP NS	0.69	(0.07) c	0.49	(0.01)bc	0.32 a	(0.02) a
AP S	1.06	(0.07) bc	0.41	(0.02) c	0.38 a	(0.02) a

[1] Soil treatments: non-sterile (NS) and sterile (S) soil of *A. arenaria* (AA), *E. villosa* (EV), *S. virginicus* (SV), *I. pes-caprae*, (IP), and *A. populifolia* (AP).

[2] All plants died.

Relative production

The relative production of *A. arenaria*, *A. populifolia*, and *I. pes-caprae* was calculated by dividing for each species the non-sterile biomass of a certain soil type by the sterile biomass production of that soil type (Figure 7.11). The biomass produced on AA soil was excluded since there were no data available for the AA S treatment. Significant differences in relative production between the different soil origins were found only for *A. arenaria* (Kruskal-Wallis, *P*<0.05; Figure 7.11). The significantly lowest relative production was observed for the SV soil type (P<0.05; Figure 7.11). This decrease in relative production on SV soil could be due to soil-borne pathogens, since the soil originating from *S. virginicus* contained many (endo)parasitic nematodes (See Figure 7.1). Both *A. populifolia* and *I. pes-caprae* showed no significant increase or decrease when grown in different soil origins, and thus do not seem to have problems in non-sterile soil.

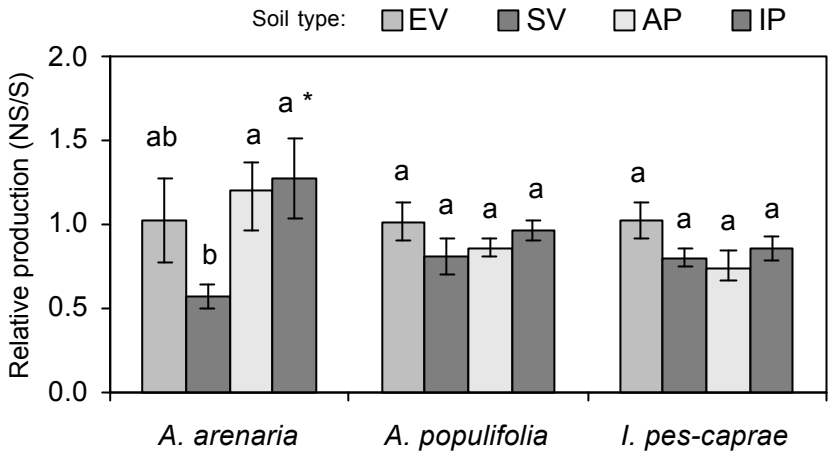


Figure 7.11. The mean relative production (non-sterile/sterile, ± S.E.) of *A. arenaria*, *A. populifolia*, and *I. pes-caprae* grown in soil from different origins (n = 5). Contrast obtained by Newman-Keuls test after analysis by Kruskal-Wallis. Level of significance: * - P<0.05. Soil type: EV - *E. villosa*, SV - *S. virginicus*, IP - *I. pes-caprae*, AP - *A. populifolia*

7.4.2.4. Effects of sterilisation on organic matter and chloride in the soil

A sudden increase in nutrients after sterilisation could result in a high relative production, since more nutrients were available than with unsterilised soil, thus masking a possible effect of soil-borne pathogens present in unsterilised soil. To test this the correlation between relative production (non-sterile biomass/sterile biomass) with the organic matter and chloride ions found in the soil was calculated (Table 7.14).

None of the correlations were significant (P>0.05; Table 7.14), so that there does not seem to be any correlation between the relative production of the three plant species and the amount of organic matter or chloride ions in the soil. Therefore, a possible sterilisation effect, based on a sudden increase of nutrients (organic matter or Chloride ions), was not very likely.

Table 7.14. Pearson's correlation coefficient for the correlation between the relative production (NS/S) and the organic matter and the chloride (Cl) concentration for the different soils and plant species.

Plant species	r –value	
	% Organic Matter	Cl concentration (mg per 100 g)
Ammophila arenaria	- 0.252	- 0.371
Ipomoea pes-caprae	0.062	- 0.079
Arctotheca populifolia	0.339	0.290

7.4.3. Summary

The performance of *A. arenaria*, *A. populifolia*, and *I. pes-caprae* on the different soil types is summarised in table 7.15. For some of the parameters not all soil types were mentioned. This because these soil types showed a lower performance, but were not significantly different when compared to the soil type showing the best performance. For *A. arenaria* and *A. populifolia* the length of the stem/leaf showed significant differences but no differences among the means within the species were observed by the Tukey test (Table 7.15).

Table 7.15. The performance of the species on the different soil types per parameter. The performance: the best (++), worse (-), or worst (--).

Parameter (with level of significance)	Performance of plant species on different soil types [1]					
	A. arenaria		*A. populifolia*		*I. pes-caprae*	
Plant survival ***	Rest AA NS AA S	++ - --	Rest AA NS AA S	++ - --	Rest AA NS AA S	++ - --
Leaf production **	Not significant		IPS EV NS, SV NS, AP NS, AA NS	++ --	AP S AP NS, AA NS	++ --
Stem (Leaf):						
Length *	No differences among means		No differences among means		EV NS, EV S, AP S IP NS, AA NS	++ --
Growth rate/week ***	week 5 week 1	++ --	week 6 week 1	++ --	week 3 week 1, week 6	++ --
Growth rate/treatment ***	EV S, SV NS, SV S, IP S AA NS	++ --	Not significant		Rest AA NS	++ --
Biomass / treatment:						
Total ***	SV S IP NS EV NS, AP S, AA NS	++ - --	Rest AA NS	++ --	IP S AP NS AA NS	++ - --
Shoots only ***	SV S EV NS AA NS	++ - --	AP S SV NS AA NS	++ - --	IP S EV NS, SV NS, AP NS AA NS, AP S	++ - --
Roots only ***	SV S Rest AA NS	++ - --	AP S AA NS	++ --	IP NS, EV NS AA NS, SV NS, AP NS, AP S	++ --
Shoot: root ratio ***	SV S AA NS, EVS, AP NS, AP S	++ --	Not significant		IP NS EV S, SV NS, IP S, AP NS, AP S AA NS	++ - --
Relative production *	AP, IP SV	++ --	Not significant		Not significant	

[1] Soil treatments: non-sterile (NS) and sterile (S) rhizosphere soil of the species *Ammophila arenaria* (AA), *Ehrharta villosa* (EV), and *Sporobolus virginicus* (SV), *Arctotheca populifolia* (AP), *Ipomoea pes-caprae* (IP) - Rest = all not mentioned soil types - Significance: * $P<0.05$, ** $P<0.01$, *** $P<0.001$

7.5. DISCUSSION

The pioneer zone of South Africa dunes does not show distinct vegetation zones as in Europe, but features a multi-species zonation. Burdon (1987) suggested that even in mixed vegetation the plant species could have different threshold values for successive soil pathogen communities, and according to Van der Putten *et al.* (1993) and Van der Stoel (2000) these soil-borne diseases probably have a high degree of specificity. The field surveys of the soil and roots of the plant species sampled showed distinct differences in number and genera of nematodes, which supports the hypothesis that around each species, a specific plant-parasitic nematode composition can be found.

7.4.1. Nematodes associated with foredune species in South Africa

For all the plant species Omnivorous, Saprophagues and Phytophagues nematodes were found in the soil and/or roots, but only the last group was identified up to genus level. Among the plant-parasitic nematodes, the endoparasitic nematodes are supposed to be the most destructive (Mortimer *et al.* 1999), although recent results show that this assumption should be regarded with caution (Van der Stoel 2001). In the samples, the endoparasitic nematode genera *Longidorus*, *Meloidogyne* and *Pratylenchus* were found, but never more than one endo-parasite in the same sample, which points in the same direction as the statement from Van der Putten *et al.* (1993) that endoparasitic nematodes are host specific. All the other nematode species found were generalist ectoparasitic nematodes that often feed on more than one plant species (Mortimer *et al.* 1999, Van der Putten 2000) and often feed on the network of fine roots close to the soil surface (D'Arcy-Burt & Blackshaw 1991).

Density and species richness

In general the plant species that showed the highest density of plant-parasitic nematodes, also showed the highest number of nematodes species, with the exception of *A. arenaria*, which showed a low density but a high number of species. The species richness of nematodes is for the plant species (from high to low): *A. arenaria* > *E. villosa* > *I. pes-caprae* > *S. virginicus* > *A. populifolia*. Whereas, the order for nematode density, from high to low is: *I. pes-caprae* > *S. virginicus* > *E. villosa* > *A. arenaria* > *A. populifolia*.

Not for all the sampled plant species endoparasitic nematode species were found, which resulted in a low plant-parasitic index for *A. arenaria* and *A*. *populifolia*. The plant

parasitic index (PPI) gives an indication of conditions related to the herbivore system (Bongers 1990). For both nematode density and species richness, *A. populifolia* showed the lowest values, as well as a low PPI value.

In the roots of *S. virginicus* a high number of endoparasitic nematodes were found, but the PPI was low. *S. virginicus* was the only species not sampled from a complete monostand, and this might influence the herbivory system and thus the PPI. However, the plant diversity in that particular area did not seem to have an effect on the plant-parasitic nematode diversity. Note that similarities at genus level might not be a guarantee of similarities at species level, but it gives a good indication.

Nematode genera found

The plant species *I. pes-caprae* showed the significantly highest total number of plant-parasitic nematodes in soil and root; *Scutellonema* sp. especially showed a high abundance. Although members of this group were generally regarded as semi-endoparasites, high numbers of nematodes (683 per g dry root) have been found in the roots. Similar observations of *Scutellonema* sp. acting as migratory endoparasites have been reported in South Africa (Van den Berg 1982). An explanation for this could be that the nematodes were still attached to the root when put in the mistifier, or some soil was still attached to the roots. Although the roots were washed thoroughly, this could have been a source of the semi-endoparasitic nematode species.

In total few plant-parasitic nematodes were found for *A. populifolia*. This opportunistic pioneer species lives in unstable sites right at the edge of beach and dune (Heyligers 1983, Lubke & De Moor 1998). These areas experience regular flooding events, high sand movement, and salt spray (Hesp 1991). Consequently, the habitat or soil conditions of *A. populifolia* could affect the density and richness of nematodes in the rhizosphere. The conductivity of the *A. populifolia* soil was the highest with 83 µS/cm, which fits in with the results from Avis (1992) and Hertling (1997). However, Goralcyk (1998) found that the pH was one of the key factors in the structure of nematode communities, but no soil pH differences were found for the soil types of the present study.

The plant species *E. villosa* and *S. virginicus* have to deal with the same environment as *A. populifolia*, but the number of nematodes found for these species was a 100-fold higher, whereas the conductivity was lower. According to Little and Maun (1996) high colonisation by Arbuscular Mycorrhizal fungi (AM fungi) would mitigate the negative

effects of plant-parasitic nematodes. Mycorrhizae are mutually beneficial associations between soil fungi and the roots of plants (Schoenbeek 1980, Schenk 1981, Schoenbeek & Dehne 1981, Puppi & Reiss 1987, Francl 1993). The AM fungi might compete for the same root space (De Rooij-Van der Goes 1995) or alter and/or reduce the root exudates responsible for the chemotactic attraction of nematodes (Hussey & Roncadori 1982, Francl 1993, Corkide 1997). Haller (2000) sampled *A. populifolia* plants and found a significant low percentage of colonisation of the roots of *A. populifolia* with AM fungi compared to other dune pioneers. Perhaps the rhizosphere is just not suitable for nematodes due to, for instance, chemical excretion of the root (e.g. Kasasian 1971, Fenner 1985, Haller 2000). Even though the nematode abundance and diversity was low, nematodes were found in the *A. populifolia* population. How did the nematodes get there? Since the *A. populifolia* population was growing at the edge of the beach, near the high water mark, it was far removed (70 metre) from other foredune vegetation. Mortimer *et al.* (1999) stated that nematodes have local dispersal through the water film in the soil and passive long distance dispersal by wind and water. Since the population was too far away for local dispersal (max. 1m/year; Van der Putten *et al.* 1989), the nematodes might have been dispersed by wind, water or via soil attached to for instance the seed blown over the sand surface.

The low number of total plant-parasitic nematodes in the soil and roots of *A. arenaria* might have a different cause since the species is an alien grass. *A. arenaria* often builds the first foredune ridge, and basically has to deal with the same conditions as *A. populifolia*, *E. villosa* and *S. virginicus.* Only the endoparasitic genera *Pratylenchus* was observed in the *A. arenaria* samples, but it was found in the soil instead of the root and with a very low abundance of 1.7 nematode genera per 400 g soil, and was therefore considered incidental. The other nematode genera found in *A. arenaria* were mainly ectoparasitic nematodes, all low in abundance, with the exception of *Filenchus* sp., a general ecto-parasitic nematode found in all plant species sampled. The organic matter content of the *A. arenaria* soil was the lowest with 0.3%, which falls in the same range as found by Avis (1992 and Hertling (1997). The organic matter content of the other soils was at least twice as high. According to Goralcyk (1998) the existence of an organic layer was a key factor in the structure of the nematode communities.

Origin nematode fauna Ammophila arenaria

In South Africa *A. arenaria* was imported in the 1890s, so a possible explanation for the lack of endoparasitic nematodes could be that the time since the introduction is still too short for "present" endoparasitic nematodes to adapt to the alien *A. arenaria*. Another explanation can be that since *A. arenaria* is not invasive in South Africa, as found in North America, Australia and New Zealand (Hertling & Lubke 1999), there was no selection pressure for the specialist nematodes but to have to feed on *A. arenaria* roots. If the plant had been invasive, there would be no other choice for the specialist nematodes to feed on the *A. arenaria* roots, because *A. arenaria* would have pushed out their host plant species. The nematode composition of *A. arenaria* found in the present research have much in common with the fauna found in Europe (e.g. the Netherlands), the area of origin. Of the 16 genera of nematodes found, 50% occurred in both areas, 31% only in South Africa and 19% only in the Netherlands. An important difference between the two was the absence of the (sedentary) endoparasitic genera *Heterodera* and *Meloidogyne* in South Africa.

The lack of endoparasites could also be explained by the wide spread of *A. arenaria* along the Eastern Cape Coast. Since *A. arenaria* is not regarded an invasive in South Africa (Hertling 1997, Hertling & Lubke, 1999) as it does not spread naturally along the Cape Coast. This implies that the chance of picking up new pathogens is much smaller. A third explanation could be that, instead of the north-western European type (studied in the Netherlands), the Mediterranean ecotype of *A. arenaria* was planted in South Africa (see Van der Putten 2000). The Mediterranean ecotype might be less sensitive to endoparasitic nematodes than the north-west European ecotype. Little is known about the nematode fauna of the Mediterranean ecotype.

Although the nematode density was low, the species richness was high for *A. arenaria*. If the species was introduced as seed (Hertling 1997), then the question is where did those nematodes come from?

The similarity between the nematode fauna associated with *A. arenaria* and *E. villosa* suggests that the latter might have provided the origin for most plant-parasitic nematodes found on *A. arenaria*. This is supported by the diversity indices, which show similarities between the two dune pioneers. But the *A. arenaria* and *E. villosa* sampled were from different sites, and no *E. villosa* was found in the vicinity of the sampled *A. arenaria*. The plants of *A. arenaria* were grown in nurseries before they were planted at the sites, and new plants for stabilisation were obtained by dividing the plants (with

the roots) and transplanting them at other stabilisation sites (Stehle 1987). Thus at the same time that the plants were transplanted, the nematode fauna may have been transplanted from other stabilisation sites. Perhaps the nematode fauna of *A. arenaria* originated from the nursery, although the question is if these nematodes would survive in dune sand. Another possibility is that the nematodes associated with *A. arenaria* in South Africa were generalist species that were not very specific about their host (e.g. Mortimer *et al.* 1999). Since the plants are not spreading naturally this might be an explanation why the different populations show such similar nematode communities. Hertling (1997) and Van der Putten (2000) sampled *A. arenaria* at different sites in South Africa. When compared to the samples of the present study the similarity was strong with a 90%and 62% nematode genera similarity with both studies, respectively.

7.5.2. Transplantation experiment

Plants of *A. arenaria*, *A. populifolia* and *I. pes-caprae* were grown on their own and foreign non-sterile, and sterile soil. Even though the plant species often grow in a multispecies community, it was expected that the plants would have their own specific nematode fauna, as has been proven in the present study. Because of the specific nematode fauna the expectation was that there would be a negative effect on the growth of the plant species when grown on their own soil. When grown on foreign (or sterile) soil the plants 'escape' their nematode fauna and its effect on the plant. The results of the present research were not as clear as found in Europe. Some plant species showed a better plant performance when grown on foreign soil, as expected, whereas other species showed a better performance when grown on their own soil.

In Europe succeeding plants grew well on the soil of pre-successional plant species compared to growth on soil of succeeding species. Since the succession in South African dunes is not as clear as in Europe and the species grow all in mixed multiple-plant communities at the foredune, this was difficult to measure for the South Africa foredunes.

Survival of plants during the transplantation experiment

Not all the plants survived throughout the experiment. The survival of the three plant species growing on the sterile *A. arenaria* (AA S) soil was significantly the lowest as no plants survived. For the other treatments the plants did survive, with the plants growing on AA NS soil showing the lowest survival. It is not clear why the three plant species,

including *A. arenaria*, were able to survive on sterile AA soil. The other soils do not show this phenomenon. It is possible that the sterilisation process initiated the formation of toxic compounds for the plants. However, all sterile soils were treated equally and the dune pioneers seem also to have problems to establish themselves in not sterilised soils from *A. arenaria*; therefore a possible sterilisation effect can be excluded. The *A. populifolia* and *I. pes-caprae* seedlings planted on AA NS/S soil showed symptoms similar to damping-off symptoms caused by pathogenic fungi like *Pythium*, *Rhizoctonia* and *Phytophthora* (Agrios, 1997; Plate 7.1). High moisture is the dominant factor in the development of the pathogenic fungi diseases (Agrios 1997). It could be that the pots, containing soil originating from *A. arenaria* were watered too extensively due to an error in the calculation for the 10 % moisture weight or to different water capacity properties of this soil. By overwatering those pots an ideal niche for these fungi, whether present already or not, was created. Without any antagonist present, damping-off diseases can cause serious damage. In non-sterile soil the presence of a natural antagonist to a certain extent inhibits the development of the damping-off diseases, and might therefore explain the survival of more plants in those pots (Agrios 1997).

The symptoms of *A. arenaria* were less clear. Problems occurred especially in the first weeks after planting. The basal parts of the stems changed in colour and became thinner, and eventually the plants fell over and desiccated completely. The below-ground damage of plant-parasitic nematodes often resembles the effect of reduced water availability (Agrios 1997), but that would not explain the even poorer survival on the sterile AA soil.

Plate 7.1. Seedlings of *I. pes-caprae* after growth of one week on *A. arenaria* soil (left) and *I. pes-caprae soil* (right), note the yellowish and smaller leaves on the left picture.

Only *A. populifolia* showed significant plant loss for the plants growing on other than AA soil, namely AP S soil. The symptoms were the same as observed for the plants growing on the AA soil, but not all plants died. Since the plants from *A. arenaria* and *I. pes-caprae* survived on AP soil, the theory about high moisture and damping off diseases might not relevant in this case.

Growth during the experiment

The A. arenaria plants grown on the different soil types showed no differences in leaf production between the soil treatments, whereas an increase in growth rate of the longest leaf over time was observed. In general the A. arenaria plants seem to perform best on the SV S soil. The root:shoot ratio, total biomass, and the shoot and root biomasses were the highest for A. arenaria when grown on SV S soil.

An explanation of the biomass increase after sterilisation might be found in the nematode fauna, since SV soil contains large numbers of endoparasites (*Meloidogyne* sp.). Although *A. arenaria* does not seem to be a suitable host for endoparasites that are native to South African dunes, it could still be sensitive to these nematodes in their pre-multiplication stage. Experiments with sedentary endoparasites and dune pioneers in Europe showed a complex relationship between plant and nematodes (Mortimer *et al.* 1999). On some dune plants endoparasitic nematodes were not able to multiply, but nevertheless caused severe damage. However, on some dune pioneers the nematodes completed their lifecycle, but higher numbers did not cause more damage. A certain threshold was reached which hardly caused damage to the plant (Mortimer *et al.* 1999). A second explanation could be that besides nematodes, other soil-borne pathogens (e.g. pathogenic fungi) in the rhizosphere soil might have caused a growth reduction of *A. arenaria* (Mortimer *et al.* 1999, Khan 1993) because nematodes could be vectors for viruses and (pathogenic) fungi (Khan 1993).

The plants growing on AA NS, EV S, AP NS and AP S soil showed lower root:shoot ratios, as well as the lowest root biomass for AA NS. This might be due to below-ground herbivory of plant-parasitic nematodes, which often results in root reduction, hence a lower root biomass (Mortimer *et al.* 1999). The relative production of the *A. arenaria* plants on the different soil origins showed a significantly lower relative production for the SV soil, a sterilisation effect was observed for the plants growing on the *S. virginicus* soil. This fits in with the result that the highest total, shoot, and root biomasses were produced on the SV S soil.

The plants of *A. populifolia* showed the least effect when grown on foreign soil as there were no differences between the soil treatments for the leaf growth rate, the relative production and the root:shoot ratio. Since *A. populifolia* was known to thrive in unstable habitats (Lubke & De Moor 1998), not demanding specific soil properties, this is no surprise. The roots did not seem to have problems with soil-borne pathogens. Perhaps the plant was either not a good host, or the plants strategy was not to invest most of its biomass in the roots, which is supported by the lower root:shoot ratio compared to the other species. In general the *A. populifolia* plants produce more leaves on the sterilised foreign soils. This might be due to the fact that these soils contain certain factors that reduce the growth and number of leaves and which these factors were removed by sterilisation, which points to a biotic factor.

The shoot biomass also showed a reduction in biomass for AA NS and SV NS soils. In the soil and roots of *S. virginicus* a large number of endoparasitic plant-parasitic nematodes (*Meloidogyne* sp.) were found that do not occur in the *A. populifolia* samples. However, the shoot biomass production of the SV NS and S treatment was not significantly different and therefore the reduction might not be due to these plant-parasitic nematodes. Is this difference due to a sterilisation effect? Sterilisation can cause an enormous increase in nutrients, which were released by dead organisms during the sterilisation process (Powlson & Jenkinson 1976, De Nooij *et al.* 1986, Thompson 1990). Especially in the poorer nutrient sandy soils from the dunes (D'Arcy-Burt & Blackshaw 1991) or under drought conditions (Mortimer *et al.* 1999) this difference can be crucial. This effect could mask a possible effect of soil-borne pathogens present in unsterilised soil. Therefore the growth differences due to nutrient flushes after sterilisation were avoided by adding nutrients. The compensation for this nutrient release, by adding nutrients to both sterilised and unsterilised treatments may also bias results because nutrient addition decreases the colonisation rate of mycorrhizal fungi (West *et al.* 1993, Johnson 1993). However, in the present study sterilisation does not have any significant effect on the organic matter and the chloride concentration, which was a measure for the availability of nutrients. The relative production on all the different rhizosphere soils is uncorrelated to either of these factors. This means that the observation regarding the increase in biomass after sterilisation can most likely be ascribed to the effect of soil-borne pathogens present in non-sterilised soil. Perhaps a synergetic effect with other soil organisms in the NS soil may be responsible for the shoot biomass reduction.

The reaction *I. pes-caprae* plants on foreign soil was more complicated than *A. populifolia*. In general the stem growth rate was highest on the EV NS, EV S and AP S and lowest on IP NS and AA NS soils, whereas the leaf production was highest on the AP S soil and lowest on AP NS and AA NS. Again, sterilisation enhances production, as seen for *A. arenaria*. The highest stem growth rates were observed at the first stages of the experiment, as the *I. pes-caprae* plants stopped growing after week 4. This could be an effect of the soil pathogens but also a natural process that, after a number of weeks investing in the above-ground parts, the energy will be put into the development of a root system. Harvesting during the experiment (Van der Putten 1989) could have given information about that. In general the mean stem growth rate of *I. pes-caprae* plants was not affected by the soil treatment. Only the AA NS treatment gave a much lower growth rate, but this might be due to other factors than purely (plant-parasitic) nematodes. The plants of *I. pes-caprae* produced the highest biomass for the IP S treatment, and the lowest on the non-sterile soils of AA, SV and AP, but no differences were observed within the soil types between NS and S treatment. Perhaps the soil pathogens in these soils give a reduction of biomass, but not one great enough to enhance the biomass growth significantly after sterilisation. The nematodes found for *I. pes-caprae* and *S. virginicus* were almost identical, with both a high number of the endoparasitic *Meloidogyne* sp. in root and soil. The SV soil showed a significant higher chloride content when compared to the soil of *I. pes-caprae*. If this should have come of influence, the plants growing on the SV S soil should also have shown a reduction in biomass growth, which was not the case. However, the soil chemical composition might have changed after sterilisation. When looked at the shoot and root biomass production there were some more differences between the treatments. The shoot biomass production was highest for the IP S treatment compared to all NS treatments and the AP S treatment, with the exception of *I. pes-caprae*'s own soil (IP NS).

For the AP soil the shoot biomass of *I. pes-caprae* was significantly reduced after sterilisation, thus the non-sterile soil produced a higher biomass. This might be due to the fact that beneficial, arbuscular mycorrhizae fungi (AM fungi) also died due to the sterilisation process, thus taking away the positive effect that AM fungi might have on the plants (Schoenbeek 1980, Schenk 1981, Schoenbeek & Dehne 1981, Dehne 1982, Francl 1993). Even though in the soil of *A. populifolia* not many AM fungi were observed (Haller 2000), the fungi present in the non-sterile soil might have been enough to keep the *I. pes-caprae* plants going. In general the root:shoot ratio was higher for the IP NS

treatment when compared to that of the plants grown on sterile soil types, including its own sterile soil and SV NS, AP NS and AA NS. This means that the plants growing in these treatments put more into the shoot than the root production, pointing towards root herbivory (Mortimer *et al.* 1999).

The plant-parasitic nematodes found in SV soil were compatible with those in the IP soil, so a reduction in root growth (lower root:shoot ratio) was found, as expected. For the AP soil no endoparasitic nematodes were found, the result was somewhat surprising, but the effect of plant-parasitic nematodes is complex, and will depend on the feeding type, population density, interaction with other soil biota, as well as the interaction with abiotic factors (Mortimer *et al.* 1999). In the soil and especially the roots of *E. villosa,* a high number of *Pratylenchus* sp. were found which were absent for *I. pes-caprae*. These nematodes are migratory endoparasites capable of moving throughout the root and may affect the plant not only by damaging tissue as a result of their movement, but also by photosynthetase withdrawal (e.g. Little & Maun 1996). The damage in the roots may in this case be reflected in a shoot growth reduction (Hussey & Roncadori 19982, Mortimer *et al.* 1999). No differences in relative production were observed for *I. pes-caprae* for the different soil origins.

7.5.3. Concluding remarks

In general only the plants of *A. arenaria* showed a strong negative effect when grown foreign soil, especially *S. virginicus* soil. For *S. virginicus* soil a high number of endoparasitic nematodes were found, which probably had a strong effect on the growth of *A. arenaria* since the biomass production nearly doubled after sterilisation of the *S. virginicus* soil. No endoparasitic nematodes were found in the roots of *A. arenaria* during the field survey, but when growing in non-sterile *S. virginicus* soil the endoparasitic nematodes had no choice but to infect the roots of *A. arenaria* to be able to survive. In the field there was no pressure on the endoparasitic nematode to feed on the *A. arenaria* roots since the roots of other plant species were around to feed on. Unfortunately most plants showed a very low performance on the *A. arenaria* soil, therefore no comparison could be made between results of the non-sterile and sterile soils.

The species *I. pes-caprae* showed the best performance on its own sterile and non-sterile soils. For *I. pes-caprae* the highest number of nematodes were found in the root and the soil compared to the other species. It seems that the performance of *I. pes-*

caprae was not much affected by soil of especially *A. populifolia,* but the sterilisation of the soil did not improve the performance. Hence, there must have been another soil factor decreasing the plant performance of *I. pes-caprae*. Perhaps the high conductivity of the soil of *A. populifolia* was responsible for the lower performance.

Plants of *A. populifolia* showed the least effect on plant performance when grown on foreign or its own soil with no significant differences for many parameters. For *A. populifolia* only few nematodes were found in the root and the rhizosphere soil. The population of *A. populifolia* sampled was very unstable caused by high sand movement and being situated close to the sea, hence showing a high conductivity. This might account for the lack of nematodes, but when grown in soil of lower conductivity with plant-parasitic nematodes, *A. populifolia* showed hardly any effect of on the plant performance. It seems that the roots are protected in some way so that plant-parasitic nematodes do not affect the plant.

7.6. ACKNOWLEDGEMENTS

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CHAPTER 8

GENERAL DICUSSION

That sand will move and dunes will change is certain.

What form that change should take will never be under our control…

Elfont and Elfont (1997)

8.1. Research topics: concluding remarks

In 1974 the South African Forestry Department changed its policy with respect to dune stabilisation so that 'the use of alien plants (e.g. *Acacia cyclops*) should be phased out and only indigenous species and the non-invasive *A. arenaria* should be used' (Avis 1989, Hertling & Lubke 1999). Since 1980 dune stabilisation itself has been questioned, and since 1980 drift sands have been looked upon as natural areas of great ecological and recreational value and should be preserved as such, rather than stabilised (Council for the Environment 1991). The stabilisation of mobile sands is not always desirable. Firstly, they are part of a natural landscape; secondly, the activity alters aeolian processes, and thirdly, it is costly. A stabilisation programme should only be initiated once its need has been identified through careful study, and the objective should rather be the creation of a functional, aesthetic ecosystem (Van der Meulen *et al.* 1989).
In this view the use of indigenous species for drift sand stabilisation, instead of the alien grass *Ammophila arenaria*, is important. Even though the grass was not considered to be invasive (Hertling 1997), the impact on the dune ecosystem is considerable (see Plate 1.1, Chapter 1). Avis (1995) and Nichols (1996) showed that indigenous species can be used successfully along the South Africa coast, but hardly any research on the life history of the dune pioneers used was performed. To have a maximum stabilisation success with indigenous species, information on life-history processes such as reproduction is essential. The present study fills part of the big gap in the life-history processes of several coastal pioneer plant species which are thought to be suitable candidates for replacing *A. arenaria* as drift sand stabiliser.

In the following paragraph each of the main research questions posed in the general introduction is reconsidered. The applicability of the actual knowledge of the life history of the pioneer species and further research perspectives will be discussed in the next paragraphs.

When and how rapidly do the foredune pioneer species grow?

To stabilise drift sand of a mobile dune, the plant has to grow fast and withstand severe sand burial. *Scaevola plumieri* is one of the most common primary colonisers, and probably a key species of the foredune area of the Eastern and Southern Cape coast (Ward 1960, Steinke & Lambert 1986). But the plants of *S. plumieri* seemed to be slow growers, producing less than two leaves per month per stem.

Leaf phenology gives information about the fact that the stems of *S. plumieri* show the highest growth in spring and summer, but does not give enough information on the total growth of the stems. Apart from leaf production the stems have to deal with factors such as sand accretion. The stems of *S. plumieri* that were growing in a prograding system with sand accretion showed more and bigger leaves and a more elongated stem, suggesting that *S. plumieri* belongs to the small group of plant species that flourish under sand accreting situations. The vigorous growth due to sand accretion was probably due to altered soil temperatures, increased space for root development, and higher moisture/nutrient availability in the root zone (e.g. Olson 1958, Marshall 1965, Zhang & Maun 1992).

No differences in sand accretion between the landward and seaward plots were observed during the study. The leaf production of *S. plumieri* stems of the more protected landward-facing stems performed much better compared to the seaward-facing stems, hence the leaf production was significantly influenced by the position of the stems on the foredune (Chapter 3). The dunes of *S. plumieri* are often formed by one individual plant (Pammenter 1986, Harman 2000). The *S. plumieri* plots A and C used for leaf and reproduction phenology studies (see chapter 3) were situated on the landward face and the seaward face, respectively, of an isolated dune. Of this dune it was known that it was formed by one plant, as Harman (2000) sampled the dune and analysed its genetics. When the leaf production of the plots A and C were compared, the landward plot C showed a significant higher leaf production. Thus the dune position of the stems has a significant effect on leaf growth even within an individual plant with the same genetic background (Chapter 3).

Do soil-borne pathogens influence the growth and vegetation dynamics of South African pioneer plant species?

It is apparent that dune plants play a vital role in stabilising dunes, hence determining the size, shape and stability of the coastal foredunes. By binding the drift sand with their root structures the plants are providing the first terrestrial habitat for animals and soil micro-organisms. Dealing with soil micro-organisms such as soil-borne pathogens represents one of the many conflicting demands in the life history of plants (Clay & Van der Putten 1999). Soil organisms are of great importance and play an major role in the vegetation dynamics of European dunes, and in the Netherlands in particular (Van der

Putten *et al.* 1993). In South Africa this seemed not to be the case. Most of the species sampled in the European foredune environment showed infection of the roots by the destructive plant-parasitic nematodes. Plant-parasitic nematodes are the main factor in the vegetation dynamics in European dunes. In South Africa, the nematodes only showed an effect on the growth of the main foredune pioneers *A. populifolia* and *I. pes-caprae* in the transplantation experiment. The effect was not as strong as that observed by Van der Putten *et al.* (1993) for European species.

In South Africa foredunes, multiple-species succession occurs, compared to single-species succession in Europe, which may have influenced the effect of the nematodes on the growth of the plants, as well as the growth form of the plants. The foredune vegetation of the Eastern Cape is much more open than that of European dunes, as grasses dominate the vegetation forming a closed vegetation. Thus plant-plant competition is probably a more important factor (Mack & Harper 1977, Grace & Tilman 1990). The dominant dune pioneers *A. populifolia*, *I. pes-caprae*, and *S. plumieri* form an open vegetation with a low cover percentage, even the grasses *S. virginicus, E. villosa* and *A. arenaria* show a low cover percentage (see Table 7.4, Chapter 7). Hence, direct plant-plant competition for e.g. light does not seem to be of importance. Even though the effect of the plant parasitic nematodes on the growth of the plants was low, in times of nutrient or water stress it might be of influence because of root damage.

What is the reproduction phenology of foredune pioneers?

The timing and duration of the reproduction is an important in the life history of a plant species. In the coastal environment flowering plants must overcome many problems for successful reproduction to take place. These include fluctuations in moisture, nutrients and temperature, salt spray, sand movement, and wind and sand abrasion (e.g. Tinley 1985, Fitter & Hay 1992, Molau 1992, Carter 1993). These environmental conditions can affect reproductive success through their effect on flowering and fruiting phenology, which could influence seed size and maturation (Primack 1987, Totland & Birks 1996). Reproduction by seed, consequently, has limited success because of the difficulties of establishing seedlings under such conditions (Fenner 1985, 1987, Jones & Gliddon 1999). Many perennials overcome these difficulties through vegetative reproduction. However, a strategy of combining vegetative reproduction with sexual reproduction is important in a dynamic habitat such as coastal dunes, as a heavy reliance on clonal

growth, rather than sexual reproduction, can reduce intra-specific genetic diversity enough to threaten long-term survival in a changing environment (Jones & Gliddon 1999).

In the present study many seeds were observed for many of the foredune species, but only *S. plumieri* was studied in detail. Many fruiting structures or peduncles were produced per stem, each supporting multiple buds. Once again, the stems situated on the landward face of the foredune showed the highest performance and produced higher numbers of buds, unripe and ripe seeds (Chapter 3). The potential reproductive output (number of buds) was 15 times higher compared to the released output (number of ripe seeds). This proves that sexual reproduction is by no means insignificant compared to vegetative reproduction (Eriksson 1997). This was also proven by the fact that *S. plumieri* allocates up to 36% of its primary production into seed production (Pammenter 1989). The reason that the realised production was so much lower than the potential output due to the fact that, of the many flowers produced, only a few developed into ripe seeds because many flowers were unfertilised and many unripe seeds aborted due to seed predation (Chapter 3). This is not an uncommon situation as in many studies the number of flowers produced exceeds seed set, even if all flowers are pollinated by hand (Stephenson 1981). The low ovule maturation found for *S. plumieri* could have been caused by resource limitation (Stephenson 1981), but was probably due to inadequate pollination due low pollinator abundance (Schaal 1980, Bierzychudek 1981).

The flowers of *S. plumieri* showed traits of animal pollination, i.e. large, visible, sturdy white flowers with a nectar supply, all factors which generally indicate pollination by moths or butterflies. However, many close relatives of *S. plumieri* have dark blue to purple flowers, implying a Hymenopteran pollinator (Faegri & Van der Pijl 1979). Trevelyan (1995) found that birds pollinate the flowers of *Scaevola taccada*, but observations during the present study have failed to produce a pollinator for *S. plumieri*. Only small bees and other insects were observed on the flowers, but they were robbing the flower of nectar without touching the reproductive structures of the flower. Hence the low seed set could have been due to the low number or flowers pollinated, but besides the pollination of flowers the resources might also have been of influence on the number of seeds produced (Stephenson 1981, Nakamura 1988).

What is the fate of dispersal units in the coastal foredune environment?

The long-distance dispersal of South African foredune species is usually via seeds, but also rhizome and stolon pieces have been found floating at sea (Muir 1937). Most of the seeds produced roll down the dune after shedding and germinate (Chapter 4) or get buried and incorporated in the soil seed bank (Chapter 5). Many seeds, however, will be secondary dispersed by wind to depressions at the base of the dunes or the drift line and swept away into the sea for long-distance dispersal.

It is known from the literature that some foredune pioneer seeds can float for months, but most of the dune species possess non-buoyant seeds (Guppy 1917, Ridley 1930, Muir 1937, Thieret & Brandenburg 1986). In the present study the seeds of *I. pes-caprae* and *S. plumieri* floated for over three months (experiment terminated after three months). Approximately 50% of the seeds were still viable after a three-month period in seawater (Chapter 6). The seeds of *M. cordifolia* floated for a maximum of seven days. Even though the seeds sank, their viability after those prolonged periods in salt water was not affected. The seeds were probably impervious to seawater leakage because of the thick wax coat that surrounds the seed. This short floating time for non-buoyant seeds was also observed for other non-buoyant seeds such as *Hebenstreitia cordata* and *Passerina rigida* (Muir 1937). The small seeds of other dune species such as *Senecio elegans* and *Dasispermum suffructicosum* were found to 'hitchhike' in the crevices of wood logs to germinate in the drift line of the new sites (Muir 1937).

That seeds of *S. plumieri* do end up at different sites via seawater dispersal was supported by the fact that at several sites *S. plumieri* seeds were found in the soil seed bank in bays where no plants were growing at all. Harman (2000) proved that seawater dispersal must occur, as at Old Woman's River, Port Alfred, and Jeffreys Bay plants of the same genet were found. Port Alfred and Jeffreys Bay are situated down the coast from Old Woman's River, suggesting that the latter would be site of origin of the genet.
Besides seeds, Muir (1937) often found stolons, bulbs, corms, and pieces of rhizomes of many dune species in the drift line of sites where the plant species were absent, for instance the pioneer grass *S. virginicus*. In this study of the rhizome pieces of three pioneer grasses, only those of *S. virginicus* floated for over seven days. The viability of *S. virginicus* rhizomes was affected by salt water, but only the time till sprouting showed a positive correlation with floating time.

Do the dispersal units germinate and establish seedlings in the field?

Under controlled conditions, the seeds of the species *A. populifolia, I. pes-caprae, M. cordifolia* and *S. plumieri* showed an intermediate to good germination and good growth in the greenhouse after germination. The same was found for the growth of buds from the rhizomes and stem pieces of the grasses *Ammophila arenaria* and *Sporobolus virginicus*.

For the air-dried fresh seeds of *S. plumieri* and *I. pes-caprae* scarification or stratification techniques were needed to break the dormancy. For *I. pes-caprae* the dormancy was seed coat induced, as with just a nick out of the seed coat, the seeds germinated well. The seeds of *S. plumieri* showed no response to any scarification test, but a slight decrease in time to germination when placed under heat stratification. From literature (e.g. Wrigley & Fagg 1988, Bhalla & Xu 1999) it is known that the seeds of *S. plumieri* are difficult to germinate, but what dormancy is imposed on the seeds in unknown.

The present research showed that once the seeds germinate, the germination success is reasonable, only it will take weeks instead of days as observed for other species. The seeds do germinate readily in the field, so obviously there must be a trigger to break dormancy that was not detected by stratification and scarification experiments but was observed in the field. Both times seeds germinated in the greenhouse, it was synchronous with germination in the field, which might have been a coincidence, or maybe the day length is of importance together with the increase in temperature. The survival of seedlings in the field of *S. plumieri* (Chapter 4) and *A. populifolia* (personal observation) was good, considering the environmental conditions they have to face, but again was better on the landward side of the foredunes compared to the seaward side. The growth of the *S. plumieri* seedlings (leaf production) was lower compared to the adult stems, but the seedlings must invest more in root growth, as the roots must rapidly reach a water supply in the ground water. The *S. plumieri* seedlings experienced a few large seas with high tides during the sample period, resulting in the death of the younger and smaller seedlings. In general older seedlings in general survived this ordeal, although a standstill in leaf production was observed after seawater inundation.

Do foredune pioneer species form a soil seed bank?

The few available reports suggest that persistent (survival of > 1 year) seed banks may not be present in dune systems (Barbour 1972, Watkinson 1978b, Boorman & Fuller 1984, Planisek & Pippen 1984), but the present study proved otherwise. In the dunes secondary dispersal or post-dispersal movement of seeds causes the seeds to become aggregated in an irregular spatial distribution (Major & Pyott 1966, Graber & Thompson 1978). The seeds usually accumulate in depressions at the base of the dunes, as found by Harper (1977) and Danin (1991). Therefore, the seed bank was sampled in depressions in front and behind the foredunes as a first step in proving that the foredune species do form a seed bank.

According to the present study the foredune species form at least a short-term persistent seed bank in which the seeds will remain viable and capable of germination for 1 to 5 years. Examples are *I. pes-caprae* and *T. decumbens*, both equipped very hard and tough diaspores. Moreover, the seeds of *I. pes-caprae* of more than four years old were still showing a high germination success, suggesting that the seed is long-lived (Chapter 3). Therefore, the both species were thought to be able to form a long-term persistent seeds bank (> 5 years).

The shape and weight of the seed is important in the seed bank behaviour of a species in most habitats. For instance in temperate grasslands small and round seeds enter the seed bank more readily when compared to elongated or flattened seeds (Thompson *et al.* 1993, Bakker *et al.* 1996a). This was not the case in the foredune habitat due to the highly mobile substrate where seeds get buried more easily due to shifting sand, compared to other habitats where the seeds have to 'work' their way into the soil seed bank (Hodgson & Grime 1990, Thompson *et al.* 1993). In habitats such as temperate grasslands the seed shape and weight is related to longevity and to the fact that deeper buried seeds are older (Thompson *et al.* 1998). The seed shape seems to be of minor importance in the soil seed bank behaviour in the dune environment as far as the burial process is concerned. The seed weight, however, may be of importance.

As mentioned the seeds of *S. plumieri* are heavy and are more likely to end up in depressions and get buried; this also applies for the seeds of *Ipomoea pes-caprae, Myrica cordifolia* and *Tetragonia decumbens*. Hence many viable and nonviable seeds of these species were found in the upper and deeper layers of the soil. Besides these species, many hard and soft, small and big, round or elongated/flattened seeds were

found in the deeper layers such as *Elymus distichus*, *Chrysanthemoides monilifera*, *Arctotheca populifolia* and *Hebenstreitia cordata.* Thus seeds of all kinds were found in the deeper layer, supporting the theory that sand movement is of more importance than seed shape in seed bank behaviour of seeds. Hence, the general rule of deeper buried seeds are older than shallow buried seeds can not be applied to the foredune environment, because depth is related to sand movement and not to seed shape in the foredune habitat. For the seeds of more temperate regions a combination of seed shape and weight in one parameter showed a strong correlation with seed longevity and could be used to predict persistence in the soil seed bank (Bekker *et al.* 1998b). For the pioneer species measured in the present study, the combinations between weight, shape or volume did not show any correlation with persistence. The seeds of maritime and arid habitats are often bigger (Fenner 1985, Funes *et al.* 1999). This could account for the fact that seed shape and weight were not good predictors for seed longevity in the South African foredune environment, as was also found for Australian species by Leishman and Westoby (1998). Another reason could be the fact that in the foredune environment many shrubs were growing, as the other studies many used herbaceous species. However, even the herbaceous South African foredune species did not show any relationship between seed parameters and seed longevity.

8.2. Implications of results: The use of indigenous dune stabilisers

Vegetation can be established best on temporally stabilised dunes by either seeding or planting. It is crucial that species common to the region should be selected so as to form the most natural dune system possible.

Sowing seed and planting seedlings and saplings

Stabilisation is often necessary over vast areas. The essential requirement to establish vegetation on mobile sand is preventing sand movement while seedlings and young plants become established, and also creating a habitat favourable for germination. On mobile dunes this requires the construction of structures to restrict sand movement, and often brushwood is used to cover the sand. Brushwood moderates temperature fluctuations of the sand, halts sand drift and increases humidity and water content of the soil, thus providing a better environment for seed germination and seedling growth (Lubke & Avis 1986).

The planting of seedlings and young plants is more labour intensive, but bound to have a better result than the sowing of seed, as natural seedling establishment is low. After the vegetation is established seeds of various pioneer species could be sown in between the plants to form a diverse indigenous flora (Avis 1985, 1986). Seeds of the indigenous species are not commercially available and have to be collected in the field, this can be done in late summer and autumn for most species (see Chapter 2 and Chapter 3).

The low and often erratic rainfall, as observed in the present research, is a major limiting factor for seedling and plant growth in the Eastern Cape. The low rainfall often results in poor field germination, whereas extensive sand movement, due to the persistent all-year-round winds, results in seedling burial. Due to these factors the dune stabilisation with indigenous species is a slow process in the drier Eastern Cape, compared to higher rainfall areas (Lubke & Avis 1986). Therefore, the period of planting of seedling or young plants should, especially in the drier areas, coincide with the rainy season, which is during spring and autumn for the east, and in autumn for the southern Cape coast.

To get species to germinate under field conditions possibly requires prolonged cooler and wetter periods. According to Lubke and Avis (1986), the problem in using indigenous species for stabilisation, is their low germination capacity. From the results of the present research it is apparent that the seeds of the species *A. populifolia*, *I. pes-caprae* and *M. cordifolia* germinate readily under controlled conditions, with a reasonable to high germination success. In the field only seedlings *A. populifolia* and *S. plumieri* seemed to be able to survive.

Although no seedlings of *M. cordifolia* were observed in the field, the seedlings grew well under controlled conditions. The seeds of *S. plumieri* took along time to germinate, but once the seeds germinated the seedling growth and survival was good. The grass species *Ehrharta villosa* and *A. arenaria* do not produce much seed (Tinley 1985), or in the case of *Sporobolus virginicus,* which produces many seed, they are difficult to germinate (Avis & Lubke 1985). Grasses can also been grown from pieces of rhizomes, or even stem pieces containing dormant buds as demonstrated in chapter 4 and chapter 7. Unfortunately seeds of indigenous dune species were often not commercially available, and thus had to be collected at the right time in the field. For species of the present study the seeds could be collected in late summer to autumn and than planted

in the field in the spring rain season. This would leave the winter months for germinating seeds and growing plants of, for instance, *A. populifolia, Myrica cordifolia* and *I. pes-caprae*. Seeds of *S. plumieri* are difficult to germinate in a short time, but the seeds could be collected and stored in paper bags at room temperature for at least a year and still be viable. In that way the seeds that need several months to germinate, have enough time to grow. The present study showed that *S. plumieri* is a slow-growing species and that plant performance was much influenced by the position on the dune, and that the stems thrived in sand-accretion situations. Therefore, the species would be a good secondary stabiliser and the seedlings of *S. plumieri* could be planted in between the primary stabilisers such as *A. populifolia* and *Sporobolus virginicus*.

8.3. Concluding remarks: Is there a need for drift sand stabilisation in South Africa?

Since the Eastern Cape coastline is relatively sparsely populated, it is expected that the pressures of development will increase with time (Fabricius *et al.* 1991, Moffett 1994). Rapid population growth as well as changing political and socio-economic conditions have resulted in an increased demand on coastal land for the development of holiday housing, recreation resorts and retirement purposes (Heydorn & Tinley 1980, Moffett 1994). This is supported by the fact that in 1993 about 69% of the South African dune fields were affected by development of houses, roads, car parks, camping facilities, sewage pipelines and other artificial structures (McGwynne *et al.* 1993, Moffett 1994). Thus, the South African dune fields are severely threatened by human expansion and in the long run the stabilisation of many dunes would be unavoidable.

Poor and incorrect management can lead to the loss of vegetation, resulting in dune erosion, and ideally, no development should take place on the beach, foredune, primary and rear dune regions of sandy shorelines (see Figure 1.1, Chapter 1). Although the use of indigenous species is desirable, dune stabilisation is not always necessary and a suitable management tool since many problems may arise from its use (Avis 1989).
The foredunes are generally regarded as a high-risk area, due to the natural processes that occur in the active zone of the dunes environment. Foredunes are sensitive due to the inherent instability of the substratum, which only appears to be stable because of the covering vegetation (Heydorn 1986). Therefore, it follows that any form of utilisation or development in this region is subject to risk and should be avoided, but if unavoidable indigenous species should be used for sand stabilisation. Since coastal areas are in

close dynamic equilibrium with the wave and wind regime, they are prone to mismanagement. Any serious human interference will be reflected in the structure of the coastal area, for instance the beach profile (Rust & Illenberger 1996).

The present thesis is a start in filling the big gap in the knowledge of the life history processes of coastal foredune species. But besides knowledge on the plant ecology of coastal dunes, a clear understanding of the controlling environmental factors is imperative for correct management.

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APPENDICES

Appendix I Sites visited for the soil seed bank with the abbreviation, degrees, dominant plant species, other species found in the vegetation and some site comments.

Appendix II Plant parasitic index values for plant feeding nematode families sensu Bongers.

Appendix III Details of ANOVA analysis.

Appendix I. Sites visited for the soil seed bank with the abbreviation, degrees, dominant plant species, other species found in the vegetation with some site comments.

Site	Degrees		Dominant species			**Other species**	**Comments**
	East	South					
Struisbaai	20° 03'	35° 00'	*Tetragonia Decumbens*	*Elymus distichus*	*Arctotheca populifolia*	*Chrysanthemoides monilifera* *Acacia cyclops*	Foredune ridge
Arniston and Waenhuiskrans	20° 13'	34° 50'					No real foredunes
De Hoop - Koppie Alleen	20° 45'	34° 32'				*Acacia cyclops* *Myrica cordifolia* *Elymus distichus*	Koppie alleen – very mobile - no vegetation only some pockets of vegetation - a lot of *Acacia cyclops* in thicket
Witsand	21° 03'	34° 30'	*Scaevola plumieri*	*Elymus distichus*	*Chrysanthemoides monilifera*	*Arctotheca populifolia* *Dasispermum suffructicosum* *Tetragonia decumbens* *Acacia cyclops seaweed*	-
Jongensfontein	21° 21'	34° 32'	*Scaevola plumieri*	*Dasispermum suffructicosum*	*Chrysanthemoides monilifera*	*Passerina rigida* *Elymus distichus Hebenstreitia cordata* *Silene primuliflora* *Acacia cyclops*	-
Stilbaai - Shellybeach	21° 28'	34° 30'	*Scaevola plumieri*	*Gladiolus gueinzii*	*Hebenstreitia cordata*		-
Stilbaai - Lappiesbaai	21° 28'	34° 30'	*Ammophila arenaria*	*Tetragonia decumbens*	*Hebenstreitia cordata*	*Arctotheca populifolia* *Elymus distichus* *Acacia cyclops*	Lappiesbaai (near restaurant)
Vleesbaai	21° 55'	34° 20'					No foredunes
Dana Bay - Second beach	22° 00'	34° 13'	*Tetragonia decumbens*	*Arctotheca populifolia*	*Elymus distichus*	*Dasispermum suffructicosum* *Gazania rigens* *Silene primuliflora*	Second beach – no foredunes, but some remnants of species

Appendix I. Continued.

Site	Degrees		Dominant species			Other species	Comments
	East	South					
Paradise Beach - Parking lot before big wooden tower	22° 00'	34° 08'	*Scaevola plumieri*	*Elymus distichus*	*Tetragonia decumbens*	*Arctotheca populifolia* *Sporobolus virginicus* *Dasispermum suffructicosum* *Stoeb e plumosa* *Silene primuliflora* *Acacia cyclops*	Near the parking lot – a lot of hummock dunes with high species diversity
Danabay - First Beach	22° 04'	34° 12'	no dominant species			*Pentachustis heptamera* *Tetragonia decumbens* *Acacia cyclops* *Dasispermum suffructicosum*	First beach - small beach in rocky area - some hummocks starting to appear
Hartenbos	22° 07'	34° 07'	*Acacia cyclops*				Steep dune to beach - no foredune communities
Mosselbaai	22° 10'	34° 10'	no dominant species				No beach
Klein Brak	22° 10'	34° 05'	no dominant species			*Some Elymus distichus* *Tetragonia decumbens* *Arctotheca populifolia* *Ammophila arenaria*	No foredunes - 1 row of dunes - not very natural
Glentana	22° 15'	34° 03'	*Scaevola plumieri*	*Tetragonia decumbens*	*Elymus distichus*	*Passerina rigida* *Gladiolus gueinzii* *Dasispermum suffructicosum.* *Acacia cyclops* *Gazania rigens*	Middle beach (old sewage pipe)
Glentana - left beach	22° 20'	34° 03'	no dominant species			*Arctotheca populifolia and Sporobolus virginicus mix at bottom thicket*	Left beach - thicket up to beach - no foredunes
Wilderness	22° 39'	34° 00'	no dominant species				Some beach but fenced off Nature reserve - no foredunes
Sedgefield	22° 48'	34° 02'	*Ammophila arenaria*			*Arctotheca populifolia* *Tetragonia decumbens*	North from Lagoon - no foredunes - some *A. arenaria* remains

Appendix I. Continued.

Site	Degrees		Dominant species			Other species	Comments
	East	South					
Plettenberg bay	23° 23'	34° 04'	*Arctotheca populifolia*	*Tetragonia decumbens*	*Ammophila arenaria*	*Dasispermum suffructicosum* *Sporobolus virginicus*	Beacon Island – no dunes, but the start of little hummocks on the beach
Keurboom	23° 25'	34° 02'	no dominant species				Holiday resort - unreachable beach
Natures Valley	23° 34'	34° 00'	*Arctotheca populifolia*	*Tetragonia decumbens*	*Elymus distichus*	*Metalasia muricata* *Passerina rigida* *Gladiolus gueinzii*	West from River
St Frances	24° 51'	34° 10'	*Tetragonia decumbens*				Steep dunes with thicket, no foredunes
Aston Bay	24° 54'	34° 06'	*Arctotheca populifolia*	*Ehrharta villosa*	*Tetragonia decumbens*	-	Mobile dunes - Seekoei river mouth - other side some degrading *S. plumieri*
Jeffreys Bay	24° 55'	34° 04'	*Scaevola plumieri*	*Elymus distichus*	*Chrysanthemoides monilifera*	-	Ferreira Town/Pellrus
Seaview	25° 21'	34° 01'	*Chrysanthemoides monilifera*	*Tetragonia decumbens*	*Gazania rigens*	*Sporobolus virginicus* *Metalasia muricata* *Acacia cyclops* *Gladiolus gueinzii*	Rocky shore with some beach, but no dunes
Bluewater Bay - Port Elizabeth	25° 38'	33° 51'	*Tetragonia decumbens*	*Arctotheca populifolia*	*Sporobolus virginicus*	*Acacia cyclops* *Passerina rigida* *Gazania rigens* *Metalasia muricata* *Scaevola plumieri* *Elymus distichus* *Scirpus nodosus*	-
Alexandria - Sundays River	25° 52'	33° 44'	*Ipomoea pes-caprae*	*Arctotheca populifolia*	*Ammophila arenaria*	-	Some buried *A. cyclops* brush wood, not much vegetation
Kenton on Sea	26° 43'	33° 41'	no dominant species				Middle beach - no foredunes
Port Alfred	26° 53'	33° 37'	*Scaevola plumieri*	*Tetragonia decumbens*	*Ammophila arenaria*	*Gazania rigens* *Passerina rigida* *Gladiolus gueinzii*	-

Appendix I. Continued.

Site	Degrees		**Dominant species**			**Other species**	**Comments**
	East	**South**					
Kleinemonde	27° 03'	33° 34'	*Scaevola plumieri*	*Chrysanthemoides monilifera*	*Sporobolus virginicus*	*Ipomoea pes-caprae* *Acacia cyclops* *Passerina rigida* *Cynanchum natalitium* *Silene primuliflora*	-
Fish River	27° 08'	33° 30'	*Ehrharta villosa*	*Ipomoea pes-caprae*	*Chrysanthemoides monilifera*	*Arctotheca populifolia* *Passerina rigida* *Acacia cyclops* *Metalasia muricata* *Elymus distichus*	-
Old Woman's River	27° 03'	33° 28'	*Scaevola plumieri*	*Ipomoea pes-caprae*	*Arctotheca populifolia*	*Myrica cordifolia* *Passerina rigida* *Chrysanthemoides monilifera* *Metalasia muricata* *Cynanchum natalitium*	-

Appendix II. Plant parasitic index values for plant feeding nematode families' sensu Bongers (De Goede & Bongers 2001).

Nematode family	PP value	Nematode family	PP value
Anguinidae	2	Longidoridae	5
Criconematidae	3	Meloidogynidae	2
Dolichodoridae	3	Paratylenchidae	3
Ecphyadophoridae	2	Pratylenchidae	2
Hemicycliophoridae	3	Trichodoridae	4
Heteroderidae	3	Tylenchidae	2
Hoploaimidae	3		

Appendix III. Detailed ANOVA results given by reference (figure or table), with the test performed, the factor test, interactions, the degrees of freedom (Df), F- and *P*-value and information on data transformation.

Reference	Parameter	Test used	Factor		Df	F	*P*-value	Comments
CHAPTER 3								
Table 3.2	Stems per plot	One-way ANOVA	Plot		9	7.27	0.0001	
		Two-way ANOVA	Position		1	1.00	0.327	
		Two-way ANOVA	Year		2	0.29	0.745	
			Interactions	Position x Year	2	0.15	0.860	
Figure 3.4	Leaves/stem	One-way ANOVA	Plot		8	15.94	0.0001	√ transformation
		Two-way ANOVA	Position		1	11.80	0.001	√ transformation
		Two-way ANOVA	Year		2	154.2	0.0001	√ transformation
			Interactions	Position x Year	2	1.00	0.352	√ transformation
Figure 3.5	Leaves/stem	One-way ANOVA	Season		3	13.20	0.0001	
Figure 3.9	Peduncles	One-way ANOVA	Plot		8	9.24	0.0001	
		Two-way ANOVA	Position		1	24.57	0.000	
		Two-way ANOVA	Year		2	0.73	0.482	
			Interactions	Position x Year	2	2.04	0.133	
Table 3.6	Unfertilised flowers/stem	One-way ANOVA	Plot		8	14.08	0.0001	
		Two-way ANOVA	Position		1	3.42	0.066	
		Two-way ANOVA	Year		2	3.82	0.024	
			Interactions	Position x Year	2	2.91	0.057	
	Aborted seeds/stem	One-way ANOVA	Plot		8	4.50	0.011	
		Two-way ANOVA	Position		1	0.009	0.925	
		Two-way ANOVA	Year		2	5.67	0.004	
			Interactions	Position x Year	2	2.82	0.062	
Table 3.8	Duration bud stage	One-way ANOVA	Plot		8	1.87	0.129	
	Duration bud stage	Two-way ANOVA	Position		1	1.8	0.187	
	Duration bud stage	Two-way ANOVA	Year		2	6.29	0.007	
			Interactions	Position x Year	2	0.236	0.792	
	Duration flower stage	One-way ANOVA	per plot		8	1.57	0.203	
	Duration flower stage	Two-way ANOVA	per position		1	0.229	0.637	
		Two-way ANOVA	per year		2	3.91	0.0036	
			Interactions	Position x Year	2	0.19	0.828	

Appendix III. Continued.

Reference	Parameter	Test used	Factor	Df	F	*P*-value	Comments
	Duration unripe seed stage	One-way ANOVA	per plot	8	1.27	0.316	
	Duration unripe seed stage	Two-way ANOVA	per position	1	1.52	0.231	
	Duration unripe seed stage	Two-way ANOVA	per year	2	5.12	0.015	
			Interactions Position x Year	2	0.17	0.842	
	Duration ripe seed stage	One-way ANOVA	per plot	8	4.54	0.004	
	Duration ripe seed stage	Two-way ANOVA	per position	1	0.97	0.336	
	Duration ripe seed stage	Two-way ANOVA	per year	2	0.45	0.641	
			Interactions Position x Year	2	0.04	0.957	
Table 3.11	Moisture	One-way ANOVA	Plot	9	1.84	0.123	
		One-way ANOVA	Position	1	2.79	0.106	
	pH	One-way ANOVA	Plot	9	4.30	0.003	
		One-way ANOVA	Position	1	4.62	0.04	
	Chloride	One-way ANOVA	Plot	9	2.54	0.04	
		One-way ANOVA	Position	1	0.30	0.587	
	Organic matter	One-way ANOVA	Plot	9	8.76	0.0001	
		One-way ANOVA	Position	1	0.88	0.357	
	Conductivity	One-way ANOVA	Plot	9	13.09	0.001	
		One-way ANOVA	Position	1	8.88	0.006	
Figure 3.13	Seed weight	One-way ANOVA	Site OWR	1	1.94	0.182	
			Site KL	1	1.52	0.234	
Figure 3.15	Reproduction stages	One-way ANOVA	-	3	8.62	0.0001	
CHAPTER 4							
Figure 4.1	Seed germination	One-way ANOVA	*A. populifolia*	1	37.27	0.0001	
			I. pes-caprae	1	271.9	0.0001	
			M. cordifolia	1	1.96	0.192	
			S. plumieri	2	-	-	No germination
Table 4.1	Germination rate (CRG)	One-way ANOVA	*A. populifolia*	1	0.06	0.809	
			I. pes-caprae	1	0.06	0.811	
			M. cordifolia	1	3.21	0.103	
			S. plumieri	2	-	-	No germination
			Between species	2	20.12	0.0001	*S. plumieri* excluded

Appendix III. Continued.

Reference	Parameter	Test used	Factor	Df	F	*P*-value	Comments
Figure 4.5	Mechanical scarification	One-way ANOVA	*I. pes-caprae*	1	131.1	0.0001	
Figure 4.6	Stratification germination	One-way ANOVA	*A. populifolia*	1	0.99	0.351	
			I. pes-caprae	2	0.75	0.495	
			M. cordifolia	1	0.06	0.814	
			S. plumieri	2	155.5	0.0001	
CHAPTER 6							
Figure 6.3	Viable seeds	One-way ANOVA	*I. pes-caprae*	9	1.22	0.306	Arcsine transformation
			M. cordifolia	9	3.89	0.005	Arcsine transformation
			S. plumieri	9	3.00	0.006	Arcsine transformation
Figure 6.7	Rhizome length	One-way ANOVA	*A. arenaria*	6	4.60	0.001	
			E. villosa	6	2.90	0.016	
			S. virginicus	6	2.64	0.024	
CHAPTER 7							
Figure 7.2b	Number of nematodes	One-way ANOVA	In the soil	4	5.34	0.001	
			In the roots	4	6.02	0.020	
Figure 7.5	Seed germination	One-way ANOVA	*A. populifolia*	2	134.4	0.0001	Arcsine transformation
			I. pes-caprae	2	1340	0.0001	Arcsine transformation
			S. plumieri	2	993.5	0.0001	Arcsine transformation
Figure 7.5	Seed germination	One-way ANOVA	*A. populifolia*	2	134.4	0.0001	Arcsine transformation
			I. pes-caprae	2	1340	0.0001	Arcsine transformation
			S. plumieri	2	993.5	0.0001	Arcsine transformation
Figure 7.7	*A. arenaria* stem pieces	One-way ANOVA	-	4	264.0	0.001	
Table 7.8	End length plants	One-way ANOVA	*A. arenaria*	8	2.54	0.026	
			A. populifolia	8	2.40	0.035	
			S. plumieri	8	3.57	0.035	

Appendix III. Continued

Reference	Parameter	Test used	Factor	Df	F	*P*-value	Comments
Table 7.10	Stem growth rates	One-way ANOVA	*A. arenaria*	8	3.82	0.0001	√ transformation
			A. populifolia	8	1.05	0.402	√ transformation
			S. plumieri	8	6.92	0.001	√ transformation
Figure 7.10	Total biomass	One-way ANOVA	*A. arenaria*	8	12.88	0.0001	
			A. populifolia	8	8.77	0.0001	
			S. plumieri	8	8.90	0.0001	
Table 7.12	Shoot biomass	One-way ANOVA	*A. arenaria*	8	4.04	0.002	
			A. populifolia	8	8.25	0.0001	
			S. plumieri	8	9.36	0.0001	
	Root biomass	One-way ANOVA	*A. arenaria*	8	14.11	0.0001	
			A. populifolia	8	3.77	0.003	
			S. plumieri	8	6.38	0.0001	
Table 7.13	Root:shoot ration	One-way ANOVA	*A. arenaria*	8	4.77	0.0001	
			A. populifolia	8	1.55	0.176	
			S. plumieri	8	5.45	0.0001	

CURRICULUM VITAE

I was born on the 6th of September 1968 in Ermelo, the Netherlands. In 1980 I started the first level of Agricultural Technical College. After graduation In 1984, I started the second level of Agricultural College that was specialised in animal care. In 1987 I graduated as a veterinarian assistant, after which I worked for a year in the animal care sector. In 1988 I started a two-year study at the third level of Agricultural College as a stepping-stone to study Biology at the University of Groningen, with the specialisation of ecology. In this field I conducted two master subjects each of approximately one year long. The first masters subject started in 1994 with the Population Genetics Department of Groningen University on the genetic variability of ground beetle populations from fragmented habitats. After finishing this, I started my second masters subject on the soil nutrient input effects on seed longevity of fen-meadow species in 1995 with the Laboratory of Plant Ecology at the University of Groningen. The work was carried out at the Institute of Grassland and Environmental Research in England and was part of an EC project on extensive management of grasslands (see Publications). Both master subjects leaded to a publication and the data of the second subject was also used in the final report of the EC project (see Publications).

After graduation I went in 1997 to Germany to work for five months at the Centre for Environmental Research in Halle-Leipzig, where I examined the role of different seed attributes in predicting seed longevity. In March 1998 I set off to South Africa to start the work on my PhD thesis in Grahamstown at the Botany Department of Rhodes University, from which the results are presented in this thesis.

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