

***AMMOPHILA ARENARIA* (L.) LINK (MARRAM GRASS)
IN SOUTH AFRICA
AND ITS POTENTIAL INVASIVENESS**

THESIS

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ABSTRACT

Ammophila arenaria (L.) Link is a European sand binding plant which was introduced to South Africa in the 1870's for the purpose of dune stabilisation. Because of its known invasiveness along the west coast of North America, and the problems South African ecosystems experience with alien invader plants, it was deemed necessary to study the biology and ecology of this species in South Africa. The aim of this thesis is to establish the potential invasiveness of *A. arenaria* on Cape coastal dunes and assess whether its use for dune stabilisation is still justifiable. *A. arenaria* occurs nowadays between the Langebaan area on the west coast and Gonubie in the Eastern Cape. Although widespread, the grass appears to occur only in areas where it has been planted. Its unaided spread may be prevented by adverse climatic conditions. Studies on the community biology of South African *A. arenaria* communities as compared to indigenous dune plant communities and natural *A. arenaria* communities in Europe cannot confirm the aggressive behaviour that *A. arenaria* shows in California and Oregon. In South Africa, *A. arenaria* does not exert strong floristic control over other species or outcompete and replace them, neither does it alter the topography of South African beaches and dunes. It forms weaker species associations and tends to develop communities of little species variability along the coast, thereby proving its alienness in South Africa, but this does not imply its invasiveness. Studies on succession of *A. arenaria* stabilisation areas show that monospecific *A. arenaria* plantings can be succeeded by a species-rich indigenous dune scrub or dune fynbos within a few decades. Plant-parasitic nematodes have been recorded, which may play an important role in the succession of *A. arenaria* stands in South Africa as was observed in Europe. Monitoring of *A. arenaria* communities and indigenous communities over nearly three years shows that *A. arenaria* is not spreading and replacing indigenous plants but in fact rather being replaced by the latter. *A. arenaria* profits from a superior sand burial tolerance but is affected by adverse climatic factors, mostly the lack of rainfall and strong radiation. In comparison to the indigenous dune grasses *Thinopyrum distichum* and *Ehrharta villosa*, it does not show any superior demographic traits such as an unusually high growth rate or large above-ground biomass production. Although *A. arenaria* produces viable seed in South Africa, the indigenous grasses show better germination and seedling establishment in the field. This study indicates that *A. arenaria* is not invasive in South Africa, nor likely to become an invader species in the near future. However, more research is required to confirm these results and more caution recommended regarding the further use of this alien grass for dune stabilisation.

CHAPTER SUMMARIES

CHAPTER ONE

The introductory chapter describes the immediate cause of the present work and introduces *Ammophila arenaria* (L.) Link as a sand-binding plant with potentially invasive properties. The aim of this thesis is to establish the potential invasiveness of the European dune pioneer plant *A. arenaria* on South African coastal dunes. It is a robust plant, thriving under a variety of conditions, and is with its vigorous system of both horizontal and vertical rhizomes well adapted to strong sand movement. It is one of the most capable plants for sand fixing and dune forming and used for dune stabilisation in many parts of the world. *A. arenaria* was introduced to South Africa in the 1870's and is still planted extensively along the entire Cape coast, wherever the stabilisation of dunes is deemed necessary. Since it has been observed and proven to behave aggressively in other areas outside its native range, most conspicuously along the North American west coast, concern about its further use for dune stabilisation in South Africa has been raised. In consideration of the many problems that South Africa faces with alien vegetation, the impact of *A. arenaria* on South African coastal ecosystems has to be examined. The emphasis of the present study is on the community biology of *A. arenaria* as opposed to indigenous dune plant communities in South Africa, but aspects of its population biology and reproduction biology are also addressed.

CHAPTER TWO

In this chapter the theory of biological invasions is discussed with regard to *A. arenaria* as a potential invasive species and the South African Cape coastal dunes as potential recipient ecosystem. A biological invasion can be defined as the entering of a species into a territory in which it has never before occurred, followed by the unaided extension of the range of that species and the possible ecological disturbance of the host territory. Although invasions occur naturally, humans have acted as outstanding vectors of plant distribution throughout the world, and human activity is the cause of most biological invasions of modern days. It is impossible to predict invasions, but both invasive species as well as invaded ecosystems are often characterised by certain attributes which facilitate invasions. Many of the species attributes connected with invasion appear to apply to *A. arenaria*. Above all, the grass is characterised by

a great ecological tolerance and vigorous rhizomatous reproduction. An important site attribute connected with invasion is an evolutionary history with isolation patterns, which certainly applies to the South African Cape coast. It becomes obvious that there is a potential for *A. arenaria* to become invasive on the South African Cape coast. Concern about *A. arenaria* in South Africa is enforced in view of its proven aggressiveness on Californian and Oregon dunes, which is examined in the second part of this chapter. Since its introduction to the North American west coast, *A. arenaria* has spread unaided and exerts strong floristic control over indigenous dune plant species, causing their decline or even elimination. It has also been shown to alter the dune topography and induce habitat changes which affect animal populations. Similar results, if less conspicuously, have been found in New Zealand and Australia. Therefore it appears necessary to investigate possible harmful impacts of *A. arenaria* on South African Cape coastal dunes.

CHAPTER THREE

This chapter focuses on the history of the introduction of *A. arenaria* in South Africa, its use for dune stabilisation in the past and present and its current distribution as well as the controversy over its further use. *A. arenaria* was introduced to South Africa in the 1870's, presumably as seed, which was then grown into plants in nurseries. The planting of bundles of *A. arenaria* culms became the most important stabilisation technique along the Cape coast in this century, particularly since concern about the previously favoured, but highly invasive Australian acacias was raised in the 1930's. Large-scale stabilisation areas with *A. arenaria* were created mostly in the Western and Southern Cape, but *A. arenaria* was planted all along the Cape coast between the Saldanha area on the west coast and Gonubie near East London. Although the stabilisation of dunes in itself has been questioned in South Africa since the 1980's and guidelines of the Council for the Environment suggest their avoidance wherever possible, *A. arenaria* is still planted frequently. Its modern distribution from the semi-arid west coast to the subtropical shores of the Eastern Cape extends through various climatic zones. *A. arenaria* is widespread along the Cape coast, but it occurs at most sites because of its prior planting. Although historical data is missing for some areas, there is no indication of its unaided spread. The South African climate appears to affect its vigour in most areas, being either too warm or too dry. It is the belief among many South Africans involved with dune stabilisation that *A. arenaria* is the best suitable plant for this purpose and, being a weak seeder, poses an insignificant threat as an invasive species. However, concern has been raised

since the late 1980's. While the CSIR (Council of Scientific and Industrial Research) promotes its use, CNC (Cape Nature Conservation) follows a policy that restricts the use of any alien plant, including *A. arenaria*, and requests further research about its invasive properties. Unlike many of the Australian invader plants, such as *Acacia cyclops* and *Acacia saligna*, *A. arenaria* is not known as an exotic species among South African people. A questionnaire survey shows that stabilisation sites featuring large areas of *A. arenaria* are accepted by the people of this country.

CHAPTER FOUR

In this chapter *A. arenaria* communities are compared with communities developed and dominated by indigenous dune plant species. Sampling of both types of communities was carried out along the Cape coast between Koeberg north of Cape Town and the Gulu River mouth near East London. In 82 *A. arenaria* stands and 64 indigenous stands of 100 m² respectively, twenty 1 m² quadrats were sampled for density, cover and frequency of each plant species. Soil samples were tested for pH, conductivity and organic matter content. The influence on the vegetation of other environmental factors such as ground-litter, distance from the high water mark, orientation of the stand and climate of the area were also compared. Lastly, a comparison of dune profiles was undertaken to assess whether *A. arenaria* forms steeper dunes than indigenous dune plants and thereby alters the topography of Cape coastal dunes. While species richness values in *A. arenaria* communities appear similar to those of indigenous dune plant communities, their diversity indices are significantly lower. However, importance values of individual species show that *A. arenaria* communities are of great similarity to communities formed by indigenous communities in the weighting of species. *A. arenaria* does not display any unusual tendency to dominance, which is in contrast to results from California. A conspicuous difference between *A. arenaria* and indigenous communities was found with the life-forms of their species. Because of its growth form as dense tufts, *A. arenaria* appears to encourage mostly small, soft-leaved chamaephytes and therophytes, while indigenous stands support more phanerophytes. Even more conspicuous, *A. arenaria* forms much weaker species associations with South African plants than dominant indigenous dune plant species. The alienness of *A. arenaria* in South Africa is confirmed by classification and ordination analyses with the programmes TWINSpan and CANOCO. These quantitative techniques are not able to differentiate *A. arenaria* communities according to their geographical origin as they do with indigenous communities. The number of plants that grow

well in *A. arenaria* stands seems to be restricted, and the species composition of *A. arenaria* communities along the coast does therefore not show much variety. With regard to environmental factors, *A. arenaria* was observed to be sensitive to a high organic matter content, while climatic factors do not appear to have as much influence on the vigour of *A. arenaria* as they have on some dominant indigenous dune plants. A comparison of the South African *A. arenaria* communities with *A. arenaria* communities on Sylt Island, off the German North Sea coast, reveals that in South Africa *A. arenaria* develops communities of much the same species richness, but that diversity values are lower. However, importance values of individual species are similar which confirms that South African *A. arenaria* is not outwardly dominant. Again, the most conspicuous difference was found with the species associations since *A. arenaria* plants from Sylt Island form much stronger associations with other European dune plants than *A. arenaria* plants from South Africa form with South African dune plants, thereby emphasising the species' alienness in South Africa. An analysis of profiles of *A. arenaria* dunes compared to dunes vegetated by indigenous plants cannot detect any significant impact of *A. arenaria* on dune topography as is observed along the coast of California and Oregon. Results of this chapter show that *A. arenaria* is an alien plant species in South Africa, but there is no indication of its invasiveness in present times or in the near future.

CHAPTER FIVE

The succession of a large-scale stabilisation area was examined at De Mond Nature Reserve to assess whether monospecific *A. arenaria* stands are replaced by indigenous vegetation and, if so, over what time period. The mouth of the Heuningnes River used to be periodically blocked by driftsands which caused flooding of the low-lying hinterland. Since the 1930's the sands have been stabilised with *A. arenaria*. Using aerial photos, maps and planting records, stabilisation sites of various ages were sampled for their vegetation. By means of this chronosequence of stands, there is clear evidence that succession takes place at De Mond. Six communities are distinguished as *A. arenaria* foredunes, stabilised dunes, dune scrub, dune scrub/dune fynbos, saltmarsh and indigenous foredunes. Apart from the last, these communities refer to different stages of succession. *A. arenaria* occurs in various abundances in the communities, depending on the time of stabilisation of the stands and on their topographical situation. After a period of not more than 50 years, former *A. arenaria* areas are usually covered in dense dune scrub and in some places even in specific dune fynbos. Succession is quick in sheltered, moist dune slacks, but *A. arenaria* remains vigorous on exposed, steep dune

slopes with strong sand movement. Perpendicular transects from the beach into the dune thicket confirm succession not only as a chronosequence but also as a toposequence since *A. arenaria* remains vigorous in the nearshore areas with higher sand movement and is replaced increasingly by indigenous plants at increasing distance from the shore. While the succession of *A. arenaria* stands at De Mond follows a pattern from low diversity to high diversity, on species as well as community level, the succession of *A. arenaria* stands on Sylt Island shows the opposite sequence: early successional stages with dominant *A. arenaria* were observed to be of high species- and community-diversity and to develop into species-poor heathland vegetation. With respect to a possible involvement of soil-pathogens in the succession of *A. arenaria* stands, a preliminary study on the presence of plant-parasitic nematodes was carried out with soil and root material from healthy and declining *A. arenaria* stands at three locations along the Cape coast. Numbers of plant-parasitic nematodes were found to be higher in sand from mobile dunes than from stable dunes, possibly indicating that nematodes have already moved away from declining roots to fresh roots which will in turn be affected soon. Thus, the regeneration of the plant is dependent on a continuous supply of fresh, wind-blown sand. It appears as though soil pathogens such as nematodes have a similar impact on the vigour of *A. arenaria* in South African dunes as they do in European dunes. However, more detailed experiments have to be carried out to confirm these results.

CHAPTER SIX

While Chapter 5 focused on long-term changes of *A. arenaria* communities, this chapter examines changes over shorter periods of less than a year up to a couple of years. Firstly, several *A. arenaria* and indigenous communities at Kleinemonde were sampled as described in Chapter 4 to arrive at measures of species richness, diversity and importance values. Sampling was carried out over two and a half years. In two out of six *A. arenaria* communities, *A. arenaria* is replaced by indigenous dune plant species, most conspicuously by the creeper *Cynanchum natalitium*. On the other hand, *A. arenaria* replaces *Ehrharta villosa* in one out of four indigenous communities that were studied. The *A. arenaria* population at Kleinemonde is clearly losing vigour since observations were initiated in 1994. In a second study, a driftline community at the Kleinemonde beach was observed over half a year. Species importances, relative shoot densities of various life-history stages per species and sand burial were sampled at regular intervals. In this community, *A. arenaria* is rapidly becoming the dominant species, apparently profiting mostly from its superior tolerance of sand burial, which overrides adverse

climatic impacts. Another competitive advantage is its ability to spread vegetatively: while the seedlings of indigenous dune species suffer badly from desiccation and sand burial, *A. arenaria* does not even occur in the driftline as seedling, but develops strong shoots from underground rhizomes. It is assumed that *A. arenaria* arrived in the driftline through rhizome fragments which were washed ashore. In a third study, the tiller demography of *A. arenaria* is compared with that of the indigenous dune grasses *Thinopyrum distichum* and *Ehrharta villosa* at Port Alfred over the autumn and winter growth period. The number of tillers and leaf/tiller-ratios as well as sand burial were measured at regular intervals. In this period, *A. arenaria* gains most tillers and shows the highest leaf/tiller-ratio throughout. However, tiller production and growth of *A. arenaria* suffer more from the lack of rainfall than in the case of the two indigenous dune grasses. *Ehrharta villosa*, on the other hand, was observed to react most positively to sand burial. In a fourth study, the clonal spread of *A. arenaria* was compared with that of *Thinopyrum distichum* and *Ehrharta villosa*. Clones of each species were dug out at regular intervals and their ramification, the number and length of internodes, number of buds, number and length of leafy shoots and their position of emergence were recorded. Surprisingly, *A. arenaria* showed slower rhizomatous growth than the two indigenous plants. As expected, it grows more vertically oriented. However, *Ehrharta villosa* produces most above-ground biomass of all three species. Both *A. arenaria* and *Ehrharta villosa* allocate most material to above-ground biomass, while *Thinopyrum distichum* develops extensive horizontal rhizomes. Studies on the tiller demography and clonal spread of *A. arenaria* in California have shown that *A. arenaria* outcompetes indigenous species by developing a much higher above-ground biomass. These results cannot be confirmed in the South African situation.

CHAPTER SEVEN

It is commonly believed in South Africa that *A. arenaria* does not produce viable seed and cannot establish successfully through sexual reproduction. However, no studies on the reproduction biology of *A. arenaria* in South Africa have been undertaken. In this chapter, the flowering, seed production, germination and seedling establishment of South African *A. arenaria* as well as its ability to regenerate from severed rhizome pieces are investigated. Flowering of *A. arenaria* stands along the entire Cape coast was measured as percentage of flowering shoots to all shoots. Inflorescences of these stands were examined for the number of florets and presence or absence of a fully developed caryopsis in each floret. Germination experiments were carried out both under laboratory and field conditions, while the

establishment of seedlings and the development of shoots from rhizome fragments were monitored only in the field. Results are compared both with European *A. arenaria* and indigenous dune plants. Flowering rates of South African *A. arenaria* populations appear similar to those of European populations, but seed production is significantly lower, which could be due to protandry and the consequential lack of fertilisation in isolated stands. Nevertheless, developed seed has a high germination rate under laboratory conditions, similar to European results. It is important to note though that seed viability fluctuates strongly in the various populations along the coast. Germination and seedling establishment in field experiments at Kleinemonde and the Old Woman's River mouth is extremely low. The indigenous dune plants *Thinopyrum distichum* and *Ehrharta villosa* showed much better results. Both seed and seedlings suffer most severely from desiccation and sand burial. Equally low is *A. arenaria*'s regeneration from rhizome cuttings. The reproduction biology of South African *A. arenaria* does certainly not point towards a possible vigorous spread of the grass along the South African coast.

CHAPTER EIGHT

In this concluding chapter, the results of the previous chapters are drawn together and assessed for implications about the further use of *A. arenaria* in South Africa. The information gained about *A. arenaria* in this thesis indicates that the species is not invasive in South Africa, nor likely to become an invader plant in the near future. Results do not imply a harmful impact on the Cape dune ecosystems, and the abolition of *A. arenaria* from dune stabilisation projects would be premature, since no indigenous alternative is as yet available. However, dune stabilisation as such remains a questionable practice and should be avoided wherever possible. Further research on the biology and ecology of *A. arenaria* in South Africa is required to confirm the results of this study and will be implemented in the course of the international INVASS programme on invasive grass species in sandy soils in southern Africa.

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CHAPTER ONE

Introduction

1.1 Rationale

Ammophila arenaria (L.) Link is a European dune pioneer plant known for its excellent sand binding ability. It was introduced to South Africa in the 1870's and has since been used extensively to stabilise Cape coastal dunes. Its modern distribution in South Africa extends from the semi-arid west coast to the subtropical shores of the Eastern Cape province. Concern about the further use of this grass in South Africa has been raised since the early 1990's. *A. arenaria* is an alien species in South Africa and as such potentially dangerous, considering the severe disturbance that South African ecosystems experience through the impact of alien plant species. Moreover, *A. arenaria* has been proven to be a highly invasive species along the Californian and Oregon coastline of North America, where it was similarly introduced in the last century (Wiedemann & Pickart 1996). It appears therefore as a matter of urgency to establish whether *A. arenaria* is potentially invasive along the South African Cape coast.

In his classical work on biological invasions Elton (1958) predicts that the earth's natural world will become "not more complex but simpler - and poorer. Instead of six continental realms of life, ..., there will be only one world". Humankind is an extraordinary vector of plant and animal distribution around the planet and the cause of dramatic and ever-accelerating changes in the configuration of our ecosystems. While the impact of invading species on economically important crop ecosystems is measurable in terms of a reduction in yield, information on the impact on natural ecosystems is often not readily available nor easily quantified (Mooney & Drake 1986). Invader plants may cause the replacement of diverse ecosystems with single- (or mixed) species stands of aliens; the extinction of indigenous plant species; alterations of soil chemistry, geomorphological processes and fire regimes; and they may pose a significant threat to the indigenous fauna (Cronk & Fuller 1995). An understanding of invasion processes is essential to prevent further environmental hazards. The present study contributes to the understanding of a species that is highly invasive in one continent, but still planted vastly in

another. The invasiveness of *A. arenaria* in North America has led to concern about its use in South Africa, and an examination of possible invasive patterns in South Africa is required to assess current coastal management practices.

This thesis is the first study on the ecological impact of *A. arenaria* in South Africa. Since its initiation in 1994, research on *A. arenaria* in South Africa has been linked with that of a potentially invasive grass species in the Kalahari sand dunes of Botswana (*Cenchrus bifloris*) to consolidate an extensive international research project on invasive grass species of sandy soils in southern Africa (INVASS). It constitutes a cooperation of researchers from South Africa, Botswana, the Netherlands and the United Kingdom and is supported by the European Union. The present study is aimed at giving an overview of the current status of *A. arenaria* in South Africa, primarily by focusing on its community biology. Aspects of the population and reproduction biology of *A. arenaria* in South Africa are also addressed, but future research in the course of the INVASS programme will focus in greater detail on these fields. Other research topics to be addressed by INVASS will be the population genetics of *A. arenaria* in South Africa in order to identify its origin from Europe, and interactions of the grass with soil-borne pathogens, which may provide an indication of its natural control in South Africa.

1.2 *Ammophila arenaria* - The plant and its communities

Ammophila arenaria (L.) Link (marram grass) and its American cogeneric *Ammophila breviligulata* Fern. (American beach grass) are both excellent sand binders and amongst the most important plant species used for dune stabilisation and formation throughout the world (Ranwell 1972; Boorman 1977). A taxonomic review of the genus *Ammophila* can be found in Maun & Baye (1988). The biology and ecology of *A. arenaria* have been described in detail by Huiskes (1979). A bibliography compiled by Miller (1988) demonstrates how many aspects of its biology and ecology have already been covered by research.

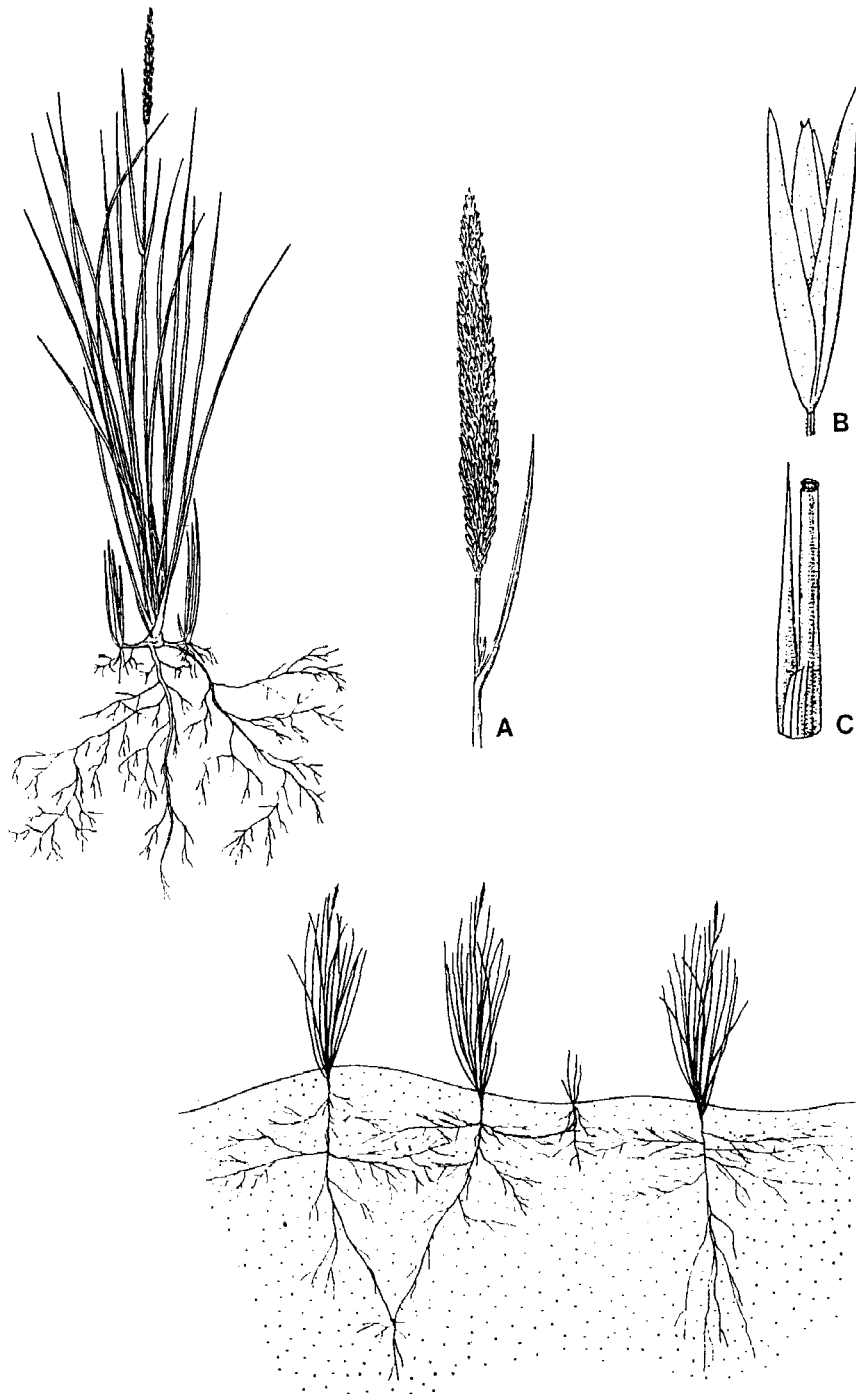
A. arenaria occurs naturally along temperate European shores between the latitudes 63°N and 30°N. The variety *genuina* grows along the Atlantic, North Sea and Baltic Sea coasts, the variety *arundinacea* grows from central Portugal southwards and along the Mediterranean and

Black Sea coasts (Huiskes 1979). Typical morphological features of the species (Fig. 1.1) are the tightly inrolled leaves with pointed tips, the dense panicles and longish spikelets containing a single floret, and the unfringed acuminate ligule (Huiskes 1979; Hubbard 1984; Gibbs Russell *et al* 1990). The southern variety *A. arenaria* var. *arundinacea* has longer and less dense panicles than the northern variety *A. arenaria* var. *genuina*. Its glumes barely exceed the lemma and palea, and the hairs surrounding the lemma are half as long as the lemma, while those of var. *genuina* are much shorter (Huiskes 1979). However, both varieties are characterised by a very vigorous system of both horizontal and vertical rhizomes (Fig. 1.1) which enables the species to bind sand so effectively (Gammel *et al* 1953). According to Ranwell (1972), *A. arenaria* can withstand sand burial of up to 1 metre per year and has therefore a great competitive advantage over most other dune plant species, e.g. *Leymus arenarius* or *Elymus farctus* (20 cm limit).

However, it is important to note that *A. arenaria* appears to be an obligate psammophyte. It declines in vigour in increasingly stable sand. The relationship between its vigour and a regular supply of fresh sand has been examined by various authors (Buchenau 1899; Benecke 1930; Tansley 1939; Salisbury 1952; Willis *et al* 1959b; Hassouna & Wareing 1964; Marshall 1965; Willis 1965; Hope-Simpson & Jefferies 1966; Lux 1969; Watkinson *et al* 1979; Abdel-Wahab & Wareing 1980; Wallén 1980; Gray 1985). Postulated reasons for the decline of *A. arenaria* in areas of low sand movement include the accumulation of organic matter and toxic substances (Buchenau 1899; Tansley 1939; Wallén 1980), increasing soil acidity (Salisbury 1952), reduction of root aeration (Tansley 1939; Salisbury 1952), increasing interspecific competition (Benecke 1930; Willis *et al* 1959b; Marshall 1965; Watkinson *et al* 1979), lack of nutrients (Willis 1965; Lux 1969), ageing of the plants (Wallén 1980) and the lack of new roots (Marshall 1965).

The possible involvement of biotic soil factors in the decline of *A. arenaria* has been put forward by van der Putten *et al* (1988). Soil sterilisation experiments have shown that soil and roots of *A. arenaria* stands contain harmful soil organisms. Nematodes, possibly interacting with fungi, deform new roots by reducing root length and root hair growth (van der Putten *et al* 1989, 1990). As long as *A. arenaria* is buried by sand regularly, it can escape this pressure and develop new roots into the fresh sand, which will in turn be infested by harmful soil organisms

after a certain time period. Hence, continuous sand burial is essential for the vigour of *A. arenaria* (van der Putten & Troelstra 1990; de Rooij-van der Goes *et al* 1995b, 1996).



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Fig. 1.1: *A. arenaria* (top) with typical features being the dense, cylindrical panicle (A), the longish spikelet with a single floret (B) and the unfringed acuminate ligule (C). Vegetative spread through mobile sand with both horizontal and vertical rhizomes (bottom). From Adriani & Terwindt (1974) and Hubbard (1984).

With regard to other habitat factors, *A. arenaria* appears extremely tolerant. It is frost and drought-resistant, it withstands high temperatures and grows well in soils of a wide-ranging chemical and nutrient status, provided their salinity level does not exceed 1% (Benecke 1930; Huiskes 1979). *A. arenaria* is found on dunes with a water-table far below the surface, e.g. up to 26 metres, while its roots do not usually extend deeper than 2 metres, the main rooting zone being the top metre (Huiskes 1979; Willis 1989). Most of the water available for *A. arenaria* comes therefore from rainfall (Salisbury 1952).

The above- and below-ground growth of *A. arenaria* has been described by Buchenau (1899), Gemmel *et al* (1953), Greig-Smith (1961), Ranwell (1972), Huiskes & Harper (1979), Watkinson *et al* (1979) and Pavlik (1983c). *A. arenaria* grows in two patterns, a tillering and a tussock forming pattern; the latter accounts mostly for the formation of high dune crests. Buds are found in the surface layers of the soil and below-ground, the grass can therefore be described both as a hemicryptophyte and a geophyte (Huiskes 1979). Vegetative reproduction appears far more important than sexual reproduction. Although *A. arenaria* produces viable seed, germination and particularly seedling establishment in the field is very low because of desiccation and sand burial (Salisbury 1952; Ranwell 1972; Huiskes 1977, 1979; van der Putten & van Gulik 1987; van der Putten 1990).

A. arenaria is the most prominent plant species on foredunes and intermediate dunes throughout Europe. It occurs in small numbers on the back-beach among more salt-tolerant species such as *Honckenya peploides* and *Salsola kali*, and becomes dominant in the next phase of dune development, the “yellow dunes” with high crests and strong sand movement, forming communities called *Ammophileta arenariae*. The species composition of the *Ammophileta arenariae* varies according to their geographical situation and has been described by many authors (e.g. Tansley 1939; Vanden Berghen 1958; Willis *et al* 1959b; Ranwell 1960; Géhu & Géhu 1969; Lux 1969; Bakker 1976; Dijkema 1983; Pedersen 1983; Westhoff & van Oosten 1991; various publications in van der Maarel 1993). *A. arenaria* loses its vigour in the later, less mobile stages of dune succession (see above) and gives way to dune heath, grassland, scrub and possibly forest depending on the area. Succession of *A. arenaria* communities in Europe has been described in detail by Willis *et al* (1959b), Ranwell (1960), Hewett (1970), Doing (1983), van Dorp *et al* (1985) Hansen & Vestergaard (1986) and van der Laan *et al* (in

press). The impact of soil-borne pathogens on plant competition and succession of European *Ammophila* dunes has been investigated by van der Putten *et al* (1993), de Rooij-van der Goes (1996) and van der Putten & Peters (1997).

1.3 The use of *Ammophila arenaria* for dune stabilisation and management implications

Dune stabilisation practices date back to the 13th century in the Netherlands (van der Meulen & van der Maarel 1989). Mention of *A. arenaria* as an agent of dune stabilisation was made as early as 1423 at Voorne in the Netherlands (van der Putten 1989). Records of the planting of *A. arenaria* in Britain and Germany are from the late fourteenth and fifteenth century (Hobbs *et al* 1983; Schulze Dieckhoff 1992). The importance of dune vegetation for coastal protection has been known to Europeans for a long time. The removal of *A. arenaria* and other plant species from dunes was prohibited in Denmark by royal decree since 1539 (Skarregaard 1989). Queen Elizabeth I. issued penalties for cutting or uprooting *A. arenaria* or disturbing recent plantings (Ranwell 1959). In the 17th century, William III. passed a law which prohibited the possession of stalks within 13 kilometres of the coast to prevent the destruction of dune vegetation and reclaimed areas (Wiedemann 1987). To this day, *A. arenaria* is the primary species used for dune stabilisation in Europe, planted usually in bundles of culms (Adriani & Terwindt 1974; Brooks 1986; Ranwell & Boar 1986; Skarregaard 1989). Van der Putten (1989) estimates that in the Netherlands some 200 hectares of dunes are annually stabilised with *A. arenaria* at a cost of 5 million Dutch guilders.

The technique of planting culms of *A. arenaria* to stabilise mobile sand was introduced by European settlers to many parts of the world. *A. arenaria* was transferred to the North American west coast (Wiedemann 1987), to Australia (Mitchell 1974), New Zealand (Wendelken 1974), Argentina (Wilhelm & Peringer 1997) and to South Africa (Stehle 1982; Reyneke 1985). Often without assessing the suitability of local dune pioneer plant species, *A. arenaria* was planted extensively in the colonies. However, its detrimental effect on the indigenous flora and fauna as well as on the dune topography is by now a proven fact in some areas, particularly in North America (Barbour *et al* 1976; van Hook 1983; Pavlik 1983a, 1983b;

Baye 1990; Pickart *et al* 1990; Buell *et al* 1995; Wiedemann & Pickart 1996), but also in New Zealand (Esler 1970; Johnson 1982, 1993; Smith *et al* 1985), and to a lesser extent in Australia (Mitchell 1974; Heyligers 1985; Sacheti & Scott 1986).

A. arenaria was introduced to South Africa in the 1870's and proved a great success in driftsand reclamation (Heywood 1894; Hutchins 1901; Dwyer 1928; Keet 1936; King 1939). The grass occurs today along some 1300 kilometres of the South African Cape coast (Plate 1.1). Several thousand hectares of dunes are covered with *A. arenaria*, and large-scale stabilisations are still undertaken in many places. The biology of *A. arenaria* in South Africa has so far been studied only in relation to its use for dune stabilisation (Stehle 1980a; Reyneke 1985; Reyneke & Theron 1991). In an examination of dune zonation and animal habitats in reclaimed foredunes in South Africa, it was shown that *A. arenaria* depresses the diversity of sand burrowing organisms (Masson & McLachlan 1990). However, no investigations have as yet been carried out specifically on the ecological impact of *A. arenaria* in South African coastal ecosystems.

South African biomes have suffered severely from biological invasions since European settlers imported plant species from all over the world. Wells *et al* (1986) list 789 alien plant species in South Africa, 47 of which are invasive "transformer species". Invasions in South Africa have been studied by many authors (e.g. Stirton 1978; Macdonald *et al* 1986; Kruger *et al* 1989; Richardson *et al* 1990, 1992, 1997; Macdonald 1991), but most work so far has focussed on the fynbos biome of the Cape region. Fynbos is characterised by a large number of endemic species and constitutes a particularly vulnerable vegetation. Of all South African biomes it has been most severely affected by alien vegetation (Richardson *et al* 1997). The planting of *A. arenaria* in large numbers on Cape coastal dunes can have hazardous impacts on specific dune fynbos vegetation. However, other vegetation types along the South African Cape coast, like the strandveld and Capensis strand vegetation of the west coast and various dune pioneer, dune scrub and dune thicket communities of the southern and eastern Cape coast (Boucher & Le Roux 1993; Taylor & Boucher 1993; Weisser & Cooper 1993; Lubke *et al* 1997), are also endangered by the possible spread of *A. arenaria*.

Concern about the use of *A. arenaria* was reinforced at the Dunes '94 international conference on the research and management of coastal dunes, held in Port Elizabeth. In consideration of the proven invasiveness of *A. arenaria* in other parts of the world, the large scale of plantings of *A. arenaria* in South Africa and the many problems faced in this country with biological invasions, it is necessary to assess the potential invasiveness of *A. arenaria* on South African Cape coastal dunes. If investigations reveal that *A. arenaria* can have a harmful impact on local coastal ecosystems, it will be imperative to suggest alternative indigenous species for dune stabilisation. Species like *Ehrharta villosa*, *Thinopyrum distichum* or *Scaevola plumieri* have been shown to have a potential for artificial dune stabilisation (Avis 1995). Finally, artificial dune stabilisation in itself is a highly questionable practice as it interferes with the natural coastal dynamics, and should only be carried out once the need therefore has been determined through careful study (Lubke 1985a; Avis 1989, 1995; Lubke *et al* 1997).

1.4 Research objectives

The aim of this thesis is to assess whether *A. arenaria* is, or has the potential to become, an invasive plant species in South African Cape coastal ecosystems. The emphasis is on community biology, but aspects of population dynamics and reproduction biology of *A. arenaria* in South Africa are also addressed. The thesis focuses on the following key objectives:

- *Where, when and to what extent was A. arenaria planted in South Africa, and what is its current distribution?*
- *How do A. arenaria and indigenous dune plant communities compare with regard to attributes of community structure, such as species composition, species diversity and species importance?*
- *Are large-scale A. arenaria stabilisation areas in South Africa succeeded by indigenous dune plant species? Or does A. arenaria remain vigorous and spread from these?*

- *How does *A. arenaria* perform in South African dunes with regard to demographic patterns such as tiller flux or clonal growth compared to indigenous dune plant species? How do *A. arenaria* communities change over time?*
- *What are the reproductive strategies of *A. arenaria* in South Africa? Is it likely to spread easily, and how does its reproduction compare to that of indigenous dune plant species?*

Results of the experimental studies are also compared with results from European *A. arenaria* populations, derived both from investigations on Sylt Island, off the German North Sea coast, and from the literature. Finally, implications of the biology of *A. arenaria* for coastal dune management in South Africa are discussed.

1.5 Outline of the thesis

In Chapter 2 the theory of biological invasions is discussed with regard to *A. arenaria* as a potential invasive species and the South African Cape coastline as potential recipient ecosystem. Current knowledge about the behaviour of *A. arenaria* in other host countries is examined, particularly its proven invasiveness along the North American west coast. Chapter 3 looks at the introduction of *A. arenaria* to South Africa and its use for dune stabilisation in the past and present. Arguments for and against its further use in South Africa are examined, and results of a survey of its modern distribution along the Cape coast presented. Chapter 4 contains a comparative vegetation analysis of *A. arenaria* communities as opposed to communities dominated by indigenous dune plant species. South African *A. arenaria* communities are also compared with *A. arenaria* communities in their European home territory. Chapter 5 examines the succession of a large-scale *A. arenaria* stabilisation area in the southwestern Cape. In Chapter 6 various aspects of the community biology and population dynamics of *A. arenaria* and indigenous dune plant species are compared with a view to assessing how species perform and how community structure changes over a period of time. Chapter 7 examines the reproduction biology of *A. arenaria* in South Africa in comparison with indigenous species and European *A. arenaria* in order to assess what reproductive

pathways it follows in South Africa, and how easily it would possibly spread along the Cape coast. Chapter 8 delivers the general conclusions of the thesis.



Plate 1.1: *A. arenaria* flowering in a stabilisation site at Hout Bay near Cape Town (top, January 1996), and trapping sand in a naturalised stand at Witsand, Cape Peninsula (bottom, January 1996).

CHAPTER TWO

Biological invasions and *Ammophila arenaria*

2.1 Theories and definitions

A plant species which enters a new environment on its own accord or is introduced by humans may find conditions so different from its home territories that it will soon die out. Alternatively, it may live inconspicuously among the indigenous species, or find an ecological niche previously unoccupied and become naturalised. Lastly, it may compete successfully with the indigenous species, grow vigorously and spread. In this case it may cause an ecological imbalance in the host community which will lead to the decline or even extinction of some or many indigenous species. Plant species that become integrated into the communities they enter may be called “immigrants”, and those that cause an ecological imbalance “invaders” (Bazzaz 1986). This chapter will focus on the latter.

The terms invader species and invasion have been dealt with extensively in the literature, nevertheless there is still much ambiguity surrounding them. Most authors agree that a plant species new to a territory can be termed invasive when it not only establishes a self-sustaining population in the host territory, but also spreads successfully from its point of arrival (e.g. Macdonald *et al* 1986). This definition leaves open the mode of transport as well as the distance covered by the species from its home territory to the new territory. Invasion can therefore be studied at many different levels of space and time (di Castri 1990): the newcomer plant can belong to the same ecosystem as the resident plants and move only a few kilometres or even metres in space. For example, it might have arrived from a different successional stage, in which case the “invasion” is merely one step in the natural succession of the ecosystem. The newcomer can also belong to a different ecosystem within the same region, or to a different region within the same biogeographical area. Lastly, it might have arrived from a different biogeographical area altogether, and covered many thousands of kilometres of travel. There are so many different perceptions of invasion possible within the above definition that Johnstone

(1986) lists nine non-successional categories and two successional categories under which biological invasion is discussed.

An attempt at making the concept of invasion more succinct is Roy's (1990) definition as "the entering of a species into a territory in which it has never before occurred, followed by the extension of the range of that species". An invader species must therefore have evolved in a different biogeographical area from the one that it invades, which excludes evolutionary developed processes such as succession or colonisation by indigenous weeds. Another restriction is put forward by Wagner (1993) who defines an invader species as "a foreign taxon that enters an established ecosystem and contaminates it". Although the term "contaminate" can refer to the harmless presence of a naturalised exotic species which has done nothing more than change the "purity" of its host system, it usually has a negative connotation: "The word contaminate can also mean that the invasive organism seriously upsets the system, ..., in that it competes with, and even smothers, its associates". Similarly, de Moor & Bruton (1988) include in their definition of an invasive species the possibility that it may be responsible for causing an imbalance in its host ecosystem. To Gouyon (1990) an invader species is one that is not at "equilibrium" from an ecological and/or demographic point of view. Bazzaz (1986) goes furthest with such negative perceptions of invasion by stating that an invader species must "enter relatively intact vegetation and strongly dominate or even displace it altogether". Like Roy (1990) he distinguishes between invaders as harmful aggressive species and the harmless colonisers, which enter unoccupied or sparsely occupied habitats and are usually early successional species. Weeds, on the other hand, are non-cultivated plants growing mainly in man-disturbed habitats (Baker 1965).

To evaluate the possible negative impacts of *Ammophila arenaria* in South Africa, this thesis will follow the more restrictive definitions of invasion. Following and expanding Roy's (1990) definition I define invasion as "the entering of a species into a territory in which it has never before occurred, followed by the unaided extension of the range of that species and the possible ecological disturbance of the host territory".

2.2 Human beings as vectors of plant distribution

In 1958 Elton predicted that, through human activities, the earth's biological world will become "not more complex but simpler - and poorer" (see Chapter 1). Twenty years later Wace (1978) wrote that "a few millennia hence, palaeontologists will perhaps view the last thousand (and certainly the last few hundred years) as the great age of stratigraphic confusion". And yet later, di Castri (1990) looks at genetic engineering and considers "a new world-wide 'anthropogenic realm' with its own peculiar characteristics and trends". It has always been part of human culture to manipulate plants and animals for its own use. For millennia they moved along with human beings, actively or passively and at increasingly greater distances. In the last few centuries especially, thousands of organisms have crossed continental barriers through human vectors and found themselves in entirely different biogeographical realms.

The numerous natural modes of travel that exist for animal and plant species are markedly outnumbered by human-induced ways, as is clearly shown by Wace (1978). The first human-induced movement of plants was an extension of range of those plants that inhabited the enriched soils of middens and other places near the campsites of stone age hunter-gatherers. In Europe common weeds such as *Plantago lanceolata*, *Ranunculus repens* and *Taraxacum officinale* are among these plants (Wace 1978). With the development of pastoralist and agricultural societies plants were transported by burring to the wool or fur of herd animals and, more directly, by humans who selected them for tillage. Another early mode of plant transport was trade. The castor oil plant (*Ricinus communis*) arrived in southern Africa in the Later Stone Age more than 2000 years ago (Deacon 1986), possibly because of trade between the local hunter-gatherers and northern tribes. Since these early days the human population has grown rapidly. Increasing urbanisation and mobility of humans furthered the range of many plant species. Through the exploration and subsequent colonisation of other continents European people in particular became outstanding vectors of plant transport across the entire planet. Today "very few ecosystems, if any, are completely 'natural' in their species composition and functioning patterns" (di Castri 1990).

When these historical implications are considered, it becomes a difficult task to estimate the number of introduced species in a given area, particularly in those parts of the earth inhabited

longest by humans, such as the tropics of Africa and Asia. Looking at numbers of species listed for areas which were isolated from the main centres of human dispersal for a fairly long time gives one an idea of the number of plants that have been moved by humans. Wace (1978) estimates that a total of 1500 flowering plant species were introduced to Australia, as were about 560 vascular plants to New Zealand. Some 22% of all vascular plants in New Zealand would therefore be exotics. A Californian estimate records 975 exotic vascular plants (Mooney *et al* 1986), which constitutes some 20 % of the local vascular flora. Wells *et al* (1986) record 789 alien vascular plant species in southern Africa, which would constitute nearly 4% of the species-rich flora of the area. Of these, 47 species are called “transformer species”, which have a severe impact on an ecosystem, changing its “character, condition, form or nature over a substantial area”. In a more recent survey, up to 368 invasive alien plant species are recorded in southern African nature reserves alone (Macdonald 1991). According to Richardson *et al* (1997) more than a third of the 47 transformer species listed by Wells *et al* (1986) are from Australia, although not more than 7.2% of all alien species in southern Africa are Australian. Of all southern African biomes, the fynbos biome is most severely affected by alien vegetation. Richardson *et al* (1997) estimate that a total area of 16% of the fynbos biome has ever been invaded (including restored areas) by predominantly Australian thicket forming scrub-species like *Acacia cyclops*, *Acacia saligna*, *Acacia longifolia*, *Eucalyptus* spp. and *Leptospermum laevigatum*.

2.3 Prerequisites of invasion

In view of such drastic changes to the biotic components of most ecosystems on earth, a global project on the “Ecology of Biological Invasions” was launched in 1982 by the Scientific Committee on Problems of the Environment (SCOPE). This was followed by a number of regional workshops held in the United States of America (Mooney & Drake 1986), Australia (Groves & Burdon 1986), South Africa (Macdonald *et al* 1986), Great Britain (Kornberg & Williamson 1987), The Netherlands (Joenje *et al* 1987) and France (di Castri *et al* 1990). Numerous other publications resulted from the project, and a global perspective is given in “SCOPE 37” (Drake *et al* 1989). The central questions of the SCOPE project were:

- 1: What are the factors that determine whether a species will be an invader or not?

- 2: What are the site properties that determine whether an ecological system will be relatively prone to, or resistant to, invasion?
- 3: How should management systems be developed using the knowledge gained from answering these questions?

Not every exotic species turns out to be invasive. According to Kowarik & Sukopp (1986) only 1-3% of all introduced species in Britain and Germany are able to establish self-sustaining populations in the new territory, and less than 1% will spread and cause problems. Sometimes, species from the same genus behave very differently in a new environment, one being highly invasive and another causing no problems (di Castri 1990): both *Ammophila arenaria* and *Ammophila breviligulata* were introduced to the North American west coast, but only the former creates an ecological imbalance (Seabloom & Wiedemann 1994; see Section 2.5). What then are the prerequisites of invasion? What features should a plant species bear to have the potential of being invasive? And what features should a host site bear to be prone to being invaded by such a plant species? Kruger *et al* (1986) suggest three barriers that a species must overcome before it can become invasive, a geographical barrier, a habitat barrier and a biotic barrier. There is an “almost inextricable mixture of biological (including evolutionary), environmental and anthropic (including historical) factors” connected to biological invasions (di Castri 1990). Not only must the species carry traits enhancing its potential invasiveness, it also has to meet an invulnerable system. Thirdly, extrinsic factors such as human actions, historical opportunity or even pure chance must be favourable.

Invasion is such a complex ecological process that pessimism regarding its predictability is prominent in most publications (Richardson *et al* 1990). In order to enhance the predictability, a number of attempts have been made at developing a mathematical model of invasion. Crawley's model (1986), for example, equates the invasiveness of a plant species with its intrinsic rate of increase in the host territory, from which functions relating to biotic barriers such as competition, enemies or the lack of mutualists must then be subtracted. An examination of the use of mathematical models in relation to the problem of biological invasions shows that they do not make reliable predictions in individual cases, but can be helpful in providing explanations of why an invasion has or has not happened (Williamson 1989).

Another approach to predicting invasions is the collection of features of proven invader species in checklist format. Baker's (1965) list of the characteristics of "the ideal weed" started this trend which was followed by many other authors. As with mathematical models, the predictive value of such lists is restricted. Wagner (1993) sees so much contingency involved among invasive organisms that he requests the study of invasion to be entirely a case-by-case analysis. Nevertheless, Tables 2.1 and 2.2 list features that facilitate biological invasions, adapted and modified from Roy (1990) and di Castri (1990) in an attempt to describe attributes of possible invader plants and of sites prone to become invaded. These could possibly be usefully applied to *A. arenaria* and the dunes of the South African Cape coast as discussed below. It is important to note that the listed features are nothing more than warning signs of the degree of either the potential invasiveness of a certain plant species (Table 2.1), or of the potential invasibility of a host site (Table 2.2).

2.4 The case of *Ammophila arenaria* in South Africa - A possible invader?

The present distribution of *A. arenaria* in South Africa and implications of its frequent use for dune stabilisation along the Cape coast to this day will be addressed in detail in Chapter 3. The use of alien plant species for dune stabilisation is a questionable practice in itself, particularly in South Africa, which faces multiple problems with a variety of alien plant species. Against the background of the North American experiences with *A. arenaria*, where the grass behaves in a clearly aggressive pattern towards natural dune plant communities (see below), it is a matter of urgency to establish whether *A. arenaria* is, or has the potential to become, an invasive plant species in South African Cape coastal dunes. However, before an observational or experimental approach to this, it is necessary to keep the matter theoretical and examine both plant and recipient land for hints that could imply a potential invasion.

Does *Ammophila arenaria* bear any of the features (Table 2.1) that would warn us of its potential invasiveness? Are the South African Cape coastal dunes prone to invasion according to the above features (Table 2.2)? Should the two listings give us a warning about the further use of *A. arenaria* for dune stabilisation in South Africa? The next sections will examine whether features of invasive plant species, or invaded sites, are applicable to *A. arenaria* and

the Cape coastal dunes respectively. The results of this examination are included in Tables 2.1 and 2.2 as a positive (+), negative (-) or unknown (?) feature.

Table 2.1: Species attributes connected with invasion. Adapted and modified from Roy (1990) and di Castri (1990). (+) applies to *A. arenaria*, (-) does not apply to *A. arenaria*, (?) not known whether applicable to *A. arenaria* (see text).

I Attributes related to ecology and physiology

1. Ecological tolerance:	<i>a) high acclimation potential and broad physiological response breadth (+)</i> <i>b) high resource allocation flexibility (+)</i> <i>c) non-specialised germination patterns (-)</i>
2. Large biomass:	<i>a) heavy seed (-) with high longevity (+)</i> <i>b) long growth period (+)</i> <i>c) high relative growth rate (?)</i>
3. Specific phenology (avoidance of competition):	<i>a) dormancy (-)</i> <i>b) unusual photosynthetic pathway (-)</i>

II Attributes related to demography

1. Sexual reproduction:	<i>a) early reproductive maturity (-)</i> <i>b) non-specialised seed production patterns (+)</i> <i>c) high resource allocation to seed production (?)</i> <i>d) long dispersal of seed in space (-)</i> <i>e) long dispersal of seed in time (+)</i>
2. Vegetative reproduction:	<i>a) rhizomatous or stoloniferous reproduction (+)</i>

III Attributes related to genetics

1. Plasticity:	<i>a) genetic variability (?)</i> <i>b) polyploidy (+)</i> <i>c) non-specialised pollination patterns (+)</i>
2. Specific mating system:	<i>a) autogamy (?)</i> <i>b) apomixis: vegetative apomixis (+) and/or agamospermy (-)</i>
-

Table 2.2: Site attributes connected with invasion. Adapted and modified from di Castri (1990). (+) applies to South African Cape coastal dunes, (-) does not apply to SA Cape coastal dunes, (?) not known whether applicable to South African Cape coastal dunes (see text).

<i>I Habitat attributes:</i>	<i>a) ecosystem subject to frequent natural or man-made disturbances (+)</i> <i>b) existence of open spaces (+)</i> <i>c) existence of spare resources (-)</i> <i>d) ecosystem homoclimatic to home territory (?)</i> <i>e) evolutionary history with isolation patterns, e.g. islands, continental endings (+)</i>
<i>II Biotic attributes:</i>	<i>a) absence of predators (?) and competitors (?)</i> <i>b) absence of pathogens (?)</i> <i>c) possibility of new mutualistic relations (?)</i>

2.4.1 Potential invasive attributes of *Ammophila arenaria* (Table 2.1)

I Attributes related to ecology and physiology

1. Ecological tolerance

a) high acclimation potential and broad physiological response breadth (+)

If *A. arenaria*'s wide natural distribution from the Faeroe Islands to the shores of the Black Sea, and its tolerance of extreme temperature fluctuations and drought (see Chapter 1) are considered, the species can be expected to have a fairly high acclimation potential. Essential for its vigour is a substratum of mobile sand with low organic matter content and a salt content of less than 1%, a condition that can be found all over the world and certainly along the South African coast. *A. arenaria* has a broad physiological response breadth: to avoid water loss, its leaves bear stomata only in furrows between the hairy ribs of their adaxial surface; furthermore, leaves are tightly inrolled under hot and dry conditions, a thermo-response that makes *A. arenaria* tolerant of droughts and high temperatures. No studies have been carried out as yet on photo-responses of the grass. However, *A. arenaria* produces taller, denser and more vertically oriented leaves than *Leymus mollis* (formerly *Elymus mollis*, an indigenous American dune grass), which permits a more efficient utilisation of direct and diffuse radiation (Barbour *et al* 1985). In response to water stress, *A. arenaria* was observed to develop stress metabolites such as proline and betaine; they enhance the heat stability of enzymes which otherwise suffer

severely from increased heat because of stomatal closure under water stress (Smirnoff & Stewart 1985).

b) high resource allocation flexibility (+)

Studies on the mechanisms of nitrate accumulation and reduction in *A. arenaria* prove that the grass responds swiftly to a change in soil water level, reducing nitrate in humid periods and storing it in dry periods (Leclerc & Robin 1983). In an American study, the comparison of resource allocation techniques of *A. arenaria* (introduced to the west coast of the United States in the last century, see Section 2.5), and the indigenous *Leymus mollis* demonstrates that *A. arenaria* partitions a larger fraction of its blade nitrogen pool into active photosynthetic enzymes than does *Leymus mollis* (Pavlik 1983a). The efficient nitrogen use in photosynthesis appears to enhance *A. arenaria*'s significantly higher long-term carbon gain. Furthermore, *A. arenaria* is found to have a higher allocation of dry matter and nitrogen to live blades than *Leymus mollis*, thus exhibiting greater above-ground productivity (Pavlik 1983b). Although there is not much more known about the physiology of *A. arenaria*, these results indicate a very efficient material allocation of the grass. Since Pavlik's experiments were carried out on Californian dunes, in an environment in which *A. arenaria* has not evolved, and since it performs so well there, it can be assumed that its mechanisms of resource allocation are indeed flexible.

c) non-specialised germination patterns (-)

Seed germination of *A. arenaria* requires a highly fluctuating temperature regime, which is usually found on mobile dunes. Furthermore, a cold period of one to several months, as is the case on European dunes in winter, enhances germination (Huiskes 1979). Germination of *A. arenaria* seed therefore appears to follow a fairly specialised pattern. However, Bencie (1990) suggests that temperature stratification under laboratory conditions does not significantly affect germination of American *A. arenaria* seed.

2. Large biomass

a) heavy seed (-) with high longevity (+)

A. arenaria seed is small in comparison to seed of other European dune grasses: its average length is recorded as 4 mm, that of *Elymus farctus* ssp. *boreali-atlanticus* as 6 mm and of *Leymus arenarius* as 10 mm (Hubbard 1984). A record of its average weight is 3.6 mg, derived from several hundred Dutch caryopses (van der Putten 1990). Seed characteristics of some important South African coastal plant species are recorded by Balarin (1996): *Arctotheca populifolia* seed is on average 5.8 mm long and weighs 0.8 mg, seed of *Ipomoea pes-caprae* ssp. *brasiliensis* reaches a length of 8.5 mm and weighs 18 mg. Even larger is *Scaevola plumieri* seed, with a length of 11.3 mm and a weight of 19 mg. Hence, in a South African context, *A. arenaria* seed is small and weighs little. Seed longevity, on the other hand, appears to be high in *A. arenaria* as it was found that storage of seed tends to improve germination (Huiskes 1979).

b) long growth period (+)

Shoots of *A. arenaria* in Europe grow mostly between April and September, but slow growth of tillers and individual leaves is still recorded in autumn and winter (Huiskes 1979). Flowers are initiated in autumn and appear the following spring. *A. arenaria* is both a hemicryptophyte and a geophyte. Buds are found all year round, and slow vegetative growth also occurs during winter. One can therefore attribute a relatively long growth period to *A. arenaria*.

c) high relative growth rate (?)

There is not much known about the components of the relative growth rate (RGR) of *A. arenaria*, namely its net assimilation rate (photosynthesis, respiration), leaf weight ratio (carbon partitioning) and specific leaf weight. Huiskes (1979) mentions a comparatively low transpiration rate. Nevertheless, Pavlik's work (1983a, 1983b; see "high resource allocation flexibility" under IIb) clearly shows not only a more efficient nitrogen use in photosynthesis of *A. arenaria* compared to *Leymus mollis*, but also a higher partitioning of carbon to its live leaves. This can explain the high biomass production that *A. arenaria* exhibits on Californian beaches (Barbour & Robichaux 1976). Comparable results from *A. arenaria*'s native European range are not available.

3. Specific phenology

a) dormancy (-)

A. arenaria is a perennial plant with a long growth period, as outlined above, and no clear pattern of dormancy except for the seed: Huiskes (1979) mentions some innate seed dormancy, although it is not likely to be very strong (see “long dispersal of seed in time” under IIIe)

b) unusual photosynthetic pathway (-)

A. arenaria is a C3 plant like most of its grassy companions on the European dunes and therefore does not use a specific photosynthetic pathway in order to avoid competition.

II Attributes related to demography

1. Sexual reproduction

a) early reproductive maturity (-)

Early reproductive maturity cannot be attributed to *A. arenaria* as it takes at least two and usually more years before inflorescences are developed (Huiskes 1979).

b) non-specialised seed production patterns (+)

From the tolerance that *A. arenaria* exhibits to various extreme habitat factors one can assume it bears a fairly non-specialised seed production pattern. Healthy clumps of *A. arenaria* can produce more than 30000 caryopses per year (Salisbury 1952). Further towards the backdune area the number of developed caryopses per floret decreases (Huiskes 1979).

c) high resource allocation to seed production (?)

The impressive number of 30000 seed per clump of *A. arenaria* that Salisbury (1952) estimated in one instance can make one believe that the grass allocates a great amount of its resources to reproduction. However, no studies have been carried out to prove this.

d) long dispersal of seed in space (-)

Seed dispersal of *A. arenaria* in space has not yet been studied in detail. The seed is small and light and is carried away by the wind easily. However, it does not bear particular structures that could facilitate the spread by wind or animals further than a few hundred meters, and it is assumed here that dispersal in space is fairly limited.

e) long dispersal of seed in time (+)

Seed dispersal in time is probably more important as *A. arenaria* seed has been shown to germinate better after a storage period (Huiskes 1979; see "dormancy" under I3a). According to van der Putten (pers. comm., January 1995) seed can be stored at about 5 °C for a couple of years without losing viability.

2. Vegetative reproduction

a) rhizomatous or stoloniferous reproduction (+)

Certainly *A. arenaria* exhibits vigorous vegetative growth. It develops an extensive system of both horizontal and vertical rhizomes which develop tussocks of the grass over a large area. The tussocks act as sand traps and trigger the formation of high and broad dunes (Greig-Smith *et al* 1947; Gemmell *et al* 1953). It is this system of strong rhizomes that makes *A. arenaria* such an excellent binder of sand. According to Ranwell (1972) no other dune species but *A. arenaria* and its American counterpart *Ammophila breviligulata* combine the potentially unlimited growth of both horizontal and vertical rhizomes.

III Attributes related to genetics

1. Plasticity

a) genetic variability (?)

No studies have yet been carried out specifically on the genetic variability of *A. arenaria*, although members of the Poaceae family do appear to be genetically very variable (Gibbs Russell *et al* 1990). There is some concern about the value of genetic variability as an indication of invasiveness, and Roy (1990) states that a high genetic diversity is not a constant

attribute of invaders. In a comparison of adaptation in *A. arenaria* with the European dune grass *Puccinellia maritima*, Gray (1985) finds that *A. arenaria* exhibits high levels of phenotypic flexibility while *Puccinellia maritima* shows both phenotypic flexibility and genetic differentiation.

b) polyploidy (+)

A. arenaria is a tetraploid species with a normal chromosome number of $2n = 28$, but even higher polyploidy levels can occur. A chromosome count of Polish *A. arenaria* arrived at $2n = 56$ (Huiskes 1979). Kubien (1968) observed polyploidisation during the development of antipodals in Polish material. It is important to note though that between 70% and 80% of all angiosperms are polyploid anyway (Gray 1986). Gray also points out that there is a great diversity of polyploidy types, and that polyploidy is frequently associated with specific life-history traits like apomixis, which are enhancing the invasive potential of a plant anyway. A generalisation about the immediate connection of polyploidy to invasiveness is therefore not possible.

c) non-specialised pollination patterns (+)

A. arenaria is wind pollinated and therefore does not exhibit any specialised pollination patterns.

2. Specific mating system

a) autogamy (?)

According to Huiskes (1979) there are records of protogyny in the Mediterranean variety *A. arenaria* var. *arundinacea*, leading to autogamy. No such records exist for the northern and western European variety *A. arenaria* var. *genuina*, whose flowers appear to be strongly protandrous. As it is assumed to be the latter variety that was introduced to South Africa (see Chapters 3 and 7), the South African strain of *A. arenaria* is unlikely to be capable of autogamy.

b) apomixis: vegetative apomixis and/or agamospermy (-)

A. arenaria's capability of vegetative apomixis has been described above. Agamospermy, on the other hand, is not evident in *A. arenaria*; the species is known to be amphimictic (Huiskes 1979).

2.4.2 Potential attributes of South African Cape coastal dunes favourable for invasion (Table 2.2)

I Habitat attributes

a) ecosystem subject to frequent natural or man-made disturbances (+)

According to di Castri (1990), coastal and urbanised environments are the two most disturbed ecosystems on earth. Coastal dunes suffer continual gross disturbances through natural causes such as wind and wave action (Wace 1978). This applies to any coastal system but in particular to extensive mobile dunefields, of which there are plenty along the South African Cape coast. The South African coastal conditions are among the most extreme in the world with average wind speeds of more than 20 km/h in windy seasons, frequent gale winds and a high energy ocean system (Tinley 1985; see also Chapter 3).

b) existence of open spaces (+)

The continuous disturbance of the coastal dune ecosystem causes frequent breaks in the natural plant cover. There is certainly plenty of open space available on South African dunes. Communities of recent origin and early successional stages, like foredune communities, are particularly prone to invasion (Pimm 1986; Rejmánek 1986).

c) existence of spare resources (-)

Soils of sand dunes are characterised by a low nutrient status and low water-holding capacity. Extreme habitat conditions plus the usual stresses of competition, predation and diseases make the dune environment one of the most hazardous to inhabit (Carter 1988). This applies strongly to the South African dunes, which certainly do not offer any substantial spare resources.

d) ecosystem homoclimatic to home territory (?)

With the South African Cape coast bearing a Mediterranean type of climate, it is homoclimatic to at least part of *A. arenaria*'s natural range in Europe. However, the entire Cape coast is characterised by extremely strong winds, certainly stronger than the strongest Mediterranean ones. Furthermore, there are no regular frost periods along the South African coast as there are in Europe, including the Mediterranean coast, which could affect germination (see "non-specialised germination patterns" under IIc). Rainfall is lower in South Africa, radiation higher, and daily temperatures subject to stronger fluctuation.

e) evolutionary history with isolation patterns, e.g. islands, continental endings (+)

The South African coastline represents the southernmost brim of the African continent. Di Castri (1990) mentions South Africa particularly as a typical southernmost ending of a continent that exhibits "insularity" conditions.

II Biotic attributes

a) absence of predators (?) and competitors (?)

A. arenaria in its natural range is exposed to predation by rabbits and insects (Huiskes 1979). Rabbit grazing has not yet been observed on South African dunes, and the impact of insects would need further investigations. Equally unknown as yet is the extent of competition that *A. arenaria* is exposed to on South Africa dunes.

b) absence of pathogens (?)

The decline of *A. arenaria* in semi-fixed and fixed dune sands with increasing organic matter content may be due to the negative impact of biotic soil factors such as fungi and nematodes (van der Putten *et al* 1988, 1990; de Rooij-van der Goes 1996). A reason for the uninhibited growth of *A. arenaria* along the west coast of North America, even in comparatively stable dunes further inland (van Hook 1983), could be the lack of such soil-borne pathogens (see Section 2.5.2). There are no records yet as to whether *A. arenaria* shows a decline of vigour in fixed dune sands in South Africa and, if it does, whether this could be connected to soil pathogens.

c) possibility of new mutualistic relations (?)

Studies of the rhizosphere in European *A. arenaria* stands indicate that nitrogen-fixing root bacteria such as *Bacillus* spp. and *Azotobacter* play a vital role in *A. arenaria*'s nitrogen nutrition (Hassouna & Wareing 1964; Abdel-Wahab 1975; Abdel-Wahab & Wareing 1980). It is also suggested that vigorous growth of *A. arenaria* is related to the development of vesicular-arbuscular mycorrhizae (Nicolson & Johnston 1979). There is not much known about similar mutualistic relationships of *A. arenaria* with microorganisms in areas other than Europe. Pavlik (1983a) mentions that no nitrogen fixing bacteria could be detected in stands of Californian *A. arenaria*. However, van Hook (1983) has found an abundance of endomycorrhizal fungi in Californian *A. arenaria* roots.

2.5 The *Ammophila arenaria* problem in North America

One of the greatest warning signs of the potential invasiveness of a certain plant species in a certain area is a record of its proven invasive behaviour elsewhere. It is the proven invasiveness of *A. arenaria* along the west coast of the United States that supports the increasing concern about *A. arenaria* in South Africa most profoundly.

2.5.1 Introduction and spread

A. arenaria (L.) Link (known to Americans as European beachgrass) was introduced to North America in 1869 to stabilise dunes in the San Francisco area (Mooney *et al* 1986). By 1890, some 200 ha of Californian coastline had been planted with *A. arenaria* (Wiedemann 1987). It spread rapidly thereafter and is today found between 34° to 54°N latitude, occurring from southern California to Queen Charlotte Island off the British Columbian coast (Buell *et al* 1995). Only very few locations along this stretch of coast are left in which *A. arenaria* has not become the dominant plant species in the foredune zone (Wiedemann 1984).

The rapid spread along the North American west coast is partly due to many repeated establishments of the grass from its founder population, aimed at the protection of waterways,

roads, railroads, water supplies, forests, recreation areas or private property (Wiedemann 1987). Numerous stabilisation projects were undertaken in the first half of this century, the largest being a 1215 ha planting by the Soil Conservation Services at the Columbia river mouth between 1935 and 1949 (Wiedemann & Pickart 1996). According to the theory that the radiation of an alien plant from many small foci accelerates its range expansion (Moody & Mack 1988), the many separate establishments of *A. arenaria* along the American west coast have surely facilitated invasion. A record of *A. arenaria*'s spread is given by Buell (1992) who found its cover at the North Spit of Humboldt Bay, northern California, to have increased from 53.5 to 196.3 ha between 1939 and 1988, an impressive increase of 574%. Buell *et al* (1995) observed two modes of spread involved at the North Spit, a steady "wave front" invasion pattern on the foredunes, characterised by exponential growth of the species, and a "broken-up fronts" pattern on inland dunes where satellite populations expand at a slower pace and fill in the space around them to finally link up. Both patterns are believed to substantiate Baker's (1986) and Hengeveld's (1989) theories of invasion dynamics.

2.5.2 Invasive properties of *Ammophila arenaria* in North America

From an American viewpoint *A. arenaria* appears well suited as a biological invader (Wiedemann & Pickart 1996). A study of its seed biology in California shows that it produces viable seed and germinates readily, both in foredunes and dune slack areas (Bencie 1990). Although there are no records as yet about seedling survival rates of American *A. arenaria*, Wiedemann (1987) assumes that successfully established seedlings account for the numerous and widely scattered hummocks found in the lower dune areas of the Oregon coast. Looking at *A. arenaria*'s vegetative reproduction, Baye (1990) records that dormant fragments of the grass can survive eight or more tidal cycles during marine transport, which implies that cold seawater does not limit long-distance dispersal of *A. arenaria*. Pavlik's (1983a, 1983b) comparative studies of nutrient and productivity relations in *A. arenaria* and the indigenous American grass *Leymus mollis* (see Section 2.4.1) demonstrate that *A. arenaria* bears a higher nitrogen use efficiency than *Leymus mollis*, enhancing its long-term carbon gain, and that it allocates more nutrients to its blades, resulting in greater above-ground productivity.

Buell *et al* (1995) attribute *A. arenaria*'s successful spread on the Humboldt Bay foredunes to "the interaction of a number of processes and conditions: optimal habitat, multiple introductions to the surrounding area, natural and human disturbance, and proximity to the strand where rhizome fragments are washed ashore by storm surf". Wiedemann & Pickart (1996) name disturbance and low cover as two major factors contributing to the susceptibility of North American dunes to invasion. According to Wiedemann (1987), *A. arenaria* is "superbly adapted for the condition of this coast". He also states that *A. arenaria* appears to be of low desirability to herbivores, furthermore that no fungal disease is known to affect its growth. *Marasmius* blight seems to be only affecting the indigenous American *Ammophila breviligulata*. Seliskar & Huettel (1993) describe several nematodes to be involved in the dieout of *Ammophila breviligulata* along the North American east coast, but no detailed examination has yet been done on the presence of such harmful microorganisms in west coast dune soils, particularly not in stands of *A. arenaria*. According to van Hook (1983) "evidence for the inland progression of this aggressive species is plentiful". The fact that *A. arenaria* thrives in California even in fixed dunes and spreads further inland than it would do in its European home range could indicate the lack of such organisms in the dune soil of the North American west coast.

2.5.3 Concern about *Ammophila arenaria* in North America

In 1976 Barbour *et al* observed that "European beachgrass not only outcompetes and replaces indigenous dune species, but alters the topography of natural beach and dune systems". According to van Hook (1983), "*A. arenaria* threatens not only foredune structure and plant species composition, but interior dune formations and plant communities as well".

As outlined by Wiedemann & Pickart (1996), concern about the successful spread of *A. arenaria* on the North American west coast has arisen in two ways. Firstly, *A. arenaria* is believed to alter the dune topography and thereby interfere markedly with the coastal geomorphology of the area. This appears to happen most dramatically along the Oregon coast where the formation of massive transverse dunes during winter storms has supposedly been inhibited by the development of sand trapping *A. arenaria* foredunes. Sand supply from the

beach is possibly cut off by *A. arenaria* rigdes, leeward dunes then 'die of sand starvation' and are soon accessible for vegetation. Thus, through the adverse action of *A. arenaria* the transverse dunes become stabilised and lose their scenic and recreation values. Secondly, *A. arenaria* appears to have a hazardous impact on the species composition of west coast dunes, outcompeting indigenous dune species and causing the loss, if not extinction, of indigenous plant communities. The aggressive behaviour of *A. arenaria* on a biotic level might alter the dune ecosystems of the North American west coast to yet unknown dimensions.

2.5.3.1 Impact on dune geomorphology

Concern about the negative impact of *A. arenaria* in America was raised as early as 1958, when Cooper stated in his work on coastal sand dunes of Oregon and Washington that "*A. arenaria* has produced in many places a prominent foredune where none existed before". Although the present high, primary foredune in Oregon has been formed only since 1910 as a result of the spread of *A. arenaria* (Cooper 1958; Wiedemann 1984, 1993), it remains questionable why no indigenous species should have formed such a foredune. Pickart & Sawyer (in press) point out the good sand trapping abilities of the indigenous *Leymus mollis*, which created a high, continuous foredune in the Lanphere-Christensen Dunes Preserve in northern California, an area where *A. arenaria* has never been present. It is also questionable whether the cut-off of sand supply accounts for the loss of the large winter transverse dunes. Wiedemann & Pickart (1996) state that no studies so far prove that continuous sand supply is a prerequisite for the maintenance of Oregon's high winter transverse dunes. Furthermore, they show that the coastal morphology of Oregon has always been characterised by cycles of stabilisation and rejuvenation, recurring in time clusters centred at 400, 1050, 1650 and 2400 years ago. Therefore, "in a historical context, *A. arenaria* may, at most, somewhat shorten the time involved in the initial events, but it is not uniquely responsible for the stabilisation process".

The impact of *A. arenaria* on large scale geomorphological events remains questionable. In regard to small scale dune topography, however, the grass does have an adverse effect as it replaces the low, rounded foredune hummocks formed by indigenous dune plants with a continuous high foredune ridge (Wiedemann 1984). Barbour & Johnson (1977) speak of an

abrupt rise of dunes that are dominated by *A. arenaria*. In a comparison with *Ammophila breviligulata*, *A. arenaria*'s cogenetic from the North American east coast which was also introduced to the west coast, *A. arenaria* develops much steeper dunes because of its superior trapping ability which in turn can be explained by a higher stem density (Seabloom & Wiedemann 1994). A higher stem density can also have adverse effects on the microclimate of the dunes: *A. arenaria* develops denser and taller tufts of leaves than the indigenous *Leymus mollis* which results in a greater extinction of direct beam radiation; low canopy plants near or within *A. arenaria* therefore face a severe disadvantage with regard to their light supply (Barbour *et al* 1985).

2.5.3.2 Impact on dune biota

However serious the impacts of *A. arenaria* on physical processes appear, the grass is believed to have a more profound impact on North American dune biota (Wiedemann & Pickart 1996). Vegetation sampling of 34 beaches between Washington State and Mexico (Barbour *et al* 1976) shows that species diversity and evenness correlate negatively with *A. arenaria*. The grass appears to exert more floristic control than any other dominant plant species, eliminating some species and depressing others. Similarly, in a description of plant communities of Pacific northwest coastal sand dunes (Wiedemann 1984), the *A. arenaria* community of the upper beach and active sand habitat is shown to have the least number of associated species. In fact, the species-rich indigenous communities of *Leymus mollis* - *Abronia latifolia* and *Poa macrantha* - *Lathyrus littoralis* are described as not occurring extensively anywhere anymore because of the spread of the *A. arenaria* community. Only two occurrences are known today of natural *Leymus mollis* - *Abronia latifolia* foredunes (Pickart *et al* 1990). On a smaller scale, Boyd (1992) carried out association analyses in small plots at Point Reyes, California, and found three out of five indigenous plant species to be negatively associated with *A. arenaria*, while the other two species were not affected. Wiedemann (1993) speaks of a "catastrophic effect" of *A. arenaria* on indigenous plant communities

Even animals may be affected, if indirectly, by *A. arenaria*. Slobodchikoff & Doyen (1977) found that *A. arenaria*-induced habitat changes resulted in a reduction of number and diversity of sand-dwelling arthropods. The higher the density of *A. arenaria*, the lower the species

diversity and number of rare species of arthropods in Californian dunes. More conspicuously, *A. arenaria* has caused a severe habitat loss to west coast snowy plover populations (*Charadrius alexandrinus*) by reducing the amount of unvegetated area above the tideline, decreasing the width of the beach, and increasing its slope. Not only have these changes led to the loss of many potential snowy plover breeding sites, but also to an increase in the number of its predators, because of the increased cover of the dunes (Miller 1993; Richardson 1995).

2.5.4 Control programmes

Faced with the rapid spread of *A. arenaria*, the massive displacement of indigenous plant communities and other biological disturbances, attempts were made to find control methods that would hinder the further growth of *A. arenaria*. One of the earliest studies on possible control methods was conducted by van Hook (1983) who tested numerous techniques like digging, burning, mowing, treatment with herbicides or rock salt, covering with black plastic or exposure of rhizomes. Out of these, digging proved to be the most effective, but also the most labour-intensive. Therefore, at the Lanphere-Christensen Dunes Preserve, visitors are asked to “incorporate into each trip 10-30 minutes of digging up of *Ammophila* either before or after the beach lunch break” (van Hook 1983). Non-systematic digging of *A. arenaria* in the Preserve throughout the 1980’s has indeed resulted in a lower density and vigour of the grass, at some places even in its eradication (Pickart *et al* 1990).

A refinement of van Hook’s method is the specific removal of both aerial and below-ground parts of *A. arenaria* clumps over a period of two growing seasons, which results in the complete eradication of the clumps and a remarkable increase of the indigenous plant cover (Pickart *et al* 1990). The cost of such manual removal is exorbitantly high: Wiedemann & Pickart (1996) mention a sum of \$20000 per hectare in 1994 alone for the efforts in the Lanphere-Christensen Dunes Preserve. The implementation of this eradication technique on a larger scale is therefore questionable, and efforts are being made to find cheaper ways of control, e.g. through the application of chemicals, burning instead of a first dig, sand deprivation or extreme seawater-drenchings (Pickart *et al* 1990; Wiedemann & Pickart 1996; Pickart & Sawyer in press). In spite of these efforts, it has to be pointed out that *A. arenaria* is

still being planted as a dune stabiliser along the United States west coast, if only in small coastal development projects and under the strict control of the California Coastal Commission (Wiedemann & Pickart 1996).

2.6 *Ammophila arenaria* in other parts of the world

2.6.1 Australia

A. arenaria was first introduced to Australia in 1883 by government botanist von Mueller, who was approached by land owners of the south coast about driftsand problems (Anonymous 1894). He imported *A. arenaria* seed from Europe which were successfully grown into plants and used for stabilisation at Port Fairy in Victoria. From there the grass was distributed to numerous localities in Victoria and New South Wales, to the Australian west coast, to Tasmania and even New Zealand; “and in no single instance has it failed to thrive” (Anonymous 1894). *A. arenaria* was first used in Western Australia in about 1900, some of the material apparently having been shipped in from South Africa (McMullan 1962). The Australian experiments with *A. arenaria* were so successful that the grass was soon known as “wonder grass” (Anonymous 1904). Not only did it appear to be “the most effective sandstay ever planted”, but also to convert driftsands into pastoral country as it was “eagerly devoured by cattle” (Anonymous 1894).

Nowadays *A. arenaria* occurs in Victoria, New South Wales, Western Australia and Tasmania. Its modern widespread distribution can be partly due to successful sexual reproduction. Mitchell (1974) records an estimated spread of at least 20 miles along the west Australian coast in 40 years through natural seeding alone. Compared to the North American situation there hasn't been much research done on possible negative impacts of *A. arenaria* on Australian coastal ecosystems. However, there has been some concern about the further use of it for a number of years now. As with the American problems, Heyligers (1985) observed a marked change of dune topography through the formation of unusually high and continuous foredunes, as well as the drastic reduction of indigenous plant habitat through *A. arenaria*'s dense and highly competitive growth. In addition to *A. arenaria*, European sea wheat *Elymus farctus* was

introduced to Australia in 1933, and a comparison of the morphology of dunes vegetated with the two European grass species with those vegetated by the indigenous Australian *Festuca littoralis* and *Spinifex hirsutus* has revealed the formation of either higher foredunes than usual, or of foredunes at localities where none would have come into existence otherwise (Heyligers 1985).

A study of the vegetation ecology of Gunnamatta Beach, Victoria, has shown that *A. arenaria* dominates the mobile dune areas and has replaced *Spinifex hirsutus* as the primary coloniser plant (Sacheti & Scott 1986). According to Kirkpatrick (1993), most beaches of southeastern Australia have been invaded by *A. arenaria*, “which forms a dense cover and tall dunes and almost totally excludes the native *Festuca littoralis* and *Spinifex hirsutus*”. *Festuca littoralis* is very rare in the provinces Victoria and South Australia and has possibly declined with the introduction of *A. arenaria*. However, according to Godfrey (1974) and Druett (1991), *A. arenaria* is the most suitable plant for dune stabilisation in Australia and because of its limited life-span of 3-8 years will have disappeared by the time stands of indigenous plant species have established. Today it is still planted along the western, southern and eastern Australian coast from north of Geraldton in Western Australia to Brisbane in Queensland (R. Whalley, pers. comm., June 1997; G. Druett, pers. comm., August 1997). Modern stabilisation techniques involve the planting and sowing of indigenous plant species among new *A. arenaria* stabilisation sites, to develop “a canopy that shades out marram growth” (G. Druett, pers. comm., August 1997). Druett states that *A. arenaria* is not invasive if used as a temporary cover in a programme which involves the re-introduction of indigenous vegetation. If it is used as a single species for dune stabilisation, it can become moderately invasive.

2.6.2 New Zealand

Although *A. arenaria* is generally thought to have been introduced to New Zealand from Australia after 1883 (Anonymous 1894; see above), it was apparently already in use for dune stabilisation near Christchurch in the 1870's (Bradly 1993). Another early record is from 1873 of the Wellington district (Wendelken 1974). Thereafter it has been extensively used all along the New Zealand coast for dune stabilisation, since 1910 in association with the North

American tree lupin (*Lupinus arboreus*) which appears to assist in the consolidation of sand (Wendelken 1974). New Zealand has an altogether agreeable climate for *A. arenaria*, and today it occurs throughout the islands along sandy shores. According to Johnson (1982) it has spread into many areas in which it had not been planted deliberately. In a more recent review, Johnson (1993) states that *A. arenaria* has spread unaided as seed and rhizome fragments, even to remote and unmodified beaches.

Esler (1970) was one of the first to criticise the use of *A. arenaria* in New Zealand. He observed that *A. arenaria* builds dunes that are higher and steeper than dunes formed by the indigenous *Spinifex hirsutus* and that its clumped habit causes irregular deposition of unprotected sand, leading sometimes to wind channelling and blow-outs. Johnson (1993) describes dunes formed by *A. arenaria* similarly as steep and irregular, while dunes vegetated by indigenous plants have a lower and smoother shape. He also observes that *A. arenaria* replaces indigenous dune plant species such as *Desmoschoenus spiralis* (pinago) and *Spinifex hirsutus* and “has usurped the place of native sand binders on many beaches”. According to a recent webpage of the Seakeepers Charitable Trust (<http://www.hmu.com/seakeepers>), *A. arenaria* tends to stabilise the sand dunes of New Zealand to an unnatural degree, resulting in a loss of their resiliency. It is described here as a dune weed that not only “forms steep, stable dunes too close to the water” but also “pushes out pinago and spinifex, reducing the populations of these valuable plants”. Obviously the indigenous New Zealand plant communities formed by *Desmoschoenus spiralis* and *Spinifex hirsutus* are crowded out of their habitat in a similar fashion to the indigenous Californian plant communities (Smith *et al* 1985).

Measures against the further spread of *A. arenaria* were taken early. The New Zealand National Parks Act of 1980 manifests the eradication of all introduced plant species in National Parks, including *A. arenaria* (Johnson 1982). At Fiordland National Park extensive eradication efforts were undertaken, mostly with herbicides and a limited amount of digging (Wiedemann 1987).

2.6.3 Other countries

A. arenaria was used for the stabilisation of coastal driftsands both in Israel (Tsuriehl 1966) and in Egypt (Ibrahim 1969). While it is now a naturalised plant in Israel (Danin & Nukrian 1991), there is no information available about its present status in Egypt.

The introduction of *A. arenaria* to India (Anonymous 1894) is questionable as no other proof of this can be found in the literature. If *A. arenaria* was introduced, its survival would be highly unlikely because of adverse climatic conditions.

There is a record of its use in Argentina, where in 1936/1937 the land owner Carlos Gesell planted *A. arenaria* on his dunes some 400 km south of Buenos Aires in an attempt to develop a settlement on the 10 km long and up to 1.6 km broad driftsands. He succeeded, and today the village of Villa Gesell is a thriving little holiday resort (Wilhelm & Peringer 1997). Gesell's initial sowing and planting of *A. arenaria* was apparently followed by massive plantings of eucalyptus, elm trees, pine trees and acacias. It is not known whether *A. arenaria* has persisted in this environment. However, *A. arenaria* is fairly widespread in Argentina today, occurring along the coast from Buenos Aires south to Patagonia. As yet no observations of its possible invasive behaviour have been made (S.I. Curto de Casas, pers. comm., June 1997).

2.7 Conclusions

It becomes obvious from Section 2.4 that not enough is known about *A. arenaria* to indicate a clear potential to become invasive. However, as indicated in Tables 2.1 and 2.2, a larger number of the warning signs were checked positive rather than negative, both for the species *A. arenaria* as well as for the recipient South African Cape coast, although in the latter case a lot of questions remain open. So far, the examination of warning signs of invasiveness and invasibility in the case of *A. arenaria* and the South African Cape coast is based on theoretical assumptions. It is the immediate observation of how an alien species behaves in its host territory that gives the most powerful indication of whether invasion happens at present or is likely to happen in the near future. Observations of the behaviour of *A. arenaria* along the

North American west coast over several decades have led to substantiated concern about the grass and give hints of what to look for in the South African situation.

In a comparison of invasions of Mediterranean-climate regions of the world, Kruger *et al* (1989) note that many invaders of California are not recorded as invasive in South Africa, whereas some of the most notorious invaders of South Africa, the Australian *Acacia longifolia* and *Acacia cyclops*, do not appear to be invasive in California. Although there are obviously many differences in plant invasion patterns in the two regions, the American case should certainly give us enough of a warning about *A. arenaria*'s possible effects in South Africa. It appears as though South Africa is the only place, apart from Europe, where the grass is still actively planted in large amounts. Although plantings are still carried out in Australia, a stabilisation site like the Tableview site near Cape Town with kilometres of *A. arenaria* plantings (Plate 3.9) is surely unique, and possibly a very short-sighted undertaking. The past and present use of *A. arenaria* in South Africa will be discussed in greater detail in the following chapter.

From this chapter it becomes obvious that *A. arenaria* bears many physiological and demographic traits which are observed to enhance invasiveness, and that the South African Cape coast is a highly dynamic host territory dominated by early successional species and therefore prone to invasion. Against this background, concern about the further planting of *A. arenaria* in South Africa does not appear unreasonable or overreactive.

CHAPTER THREE

Ammophila arenaria in South Africa

3.1 Introduction of *Ammophila arenaria* to South Africa

3.1.1 The need for dune stabilisation

More than 80% of the South African coastline consists of sandy beaches backed by dunes (Tinley 1985) which are largely unvegetated and mobile. Coastal driftsands usually originate in dune fields where the equilibrium between open sand, the natural dune vegetation and the forces of nature have been disturbed (Stehle 1987). Such disturbance can be caused by natural agents like sea currents, storms and changes in climatic patterns, or through human activities such as the removal of vegetation for firewood or thatching, inconsiderate development and trampling of vegetation by stock animals, humans or off-road vehicles. The sandy Cape Flats to the east of Cape Town, for example, used to be vegetated and comparatively stable. However, since the first European settlement in Cape Town in the 17th century they have been devegetated rapidly and turned into an inhospitable area of shifting sands which were difficult to cross and even more difficult to develop. European settlement in South Africa led to both the further spread of driftsands as well as the need for their stabilisation (Plate 3.1). The history of stabilisation practices in South Africa has already been dealt with by several authors (Braine 1903; Keet 1936; King 1939; Walsh 1969; Shaughnessy 1980; Stehle 1982; Avis 1989). I will examine it briefly in order to explain the need for the introduction and use of *A. arenaria* as a dune stabiliser in South Africa.

The first South African record of driftsand stabilisation is from 1724 when the governing body of the Dutch East India Company, the Here Sewentien, was concerned about a possible silting up of Table Bay and initiated plantings of the adjacent driftsands (Stehle 1982). However, it took more than a hundred years before an organised, large-scale stabilisation programme was initiated in 1845 by the Central Roads Board in an attempt to protect a newly-built hard road

across the Cape Flats. Methods involved the sowing and planting of indigenous plants, such as the hottentot fig (*Carpobrotus edulis*) or pipe grass (*Ehrharta villosa*), as well as alien plants such as the Australian Port Jackson wattle, *Acacia saligna* (Shaughnessy 1980). The latter may well have been the first alien plant species used for stabilisation in South Africa. From about 1850 more alien plants were introduced for dune reclamation work; some of them were from Europe, like the Mediterranean cluster pine (*Pinus pinaster*), but the majority were Australian plants such as *Acacia longifolia*, *Acacia cyclops*, *Hakea suaveolens*, *Leptospermum laevigatum*, *Casuarina equisetifolia* and *Eucalyptus diversifolia* (Avis 1989).

The use of trees for driftsand reclamation was enforced in 1875, when dune stabilisation became a function of the Cape Forestry Department, and was seen in terms of tree harvesting, thus not only stabilising driftsands but also turning them into economically viable areas (Avis 1989). Since the trees could not be planted or sown into bare, shifting sands, the latter had to be stabilised temporarily, until the young trees became established and could then take up the long-term stabilisation process. The French method of packing brushwood onto the dunes in order to stabilise the sand and to encourage seedling establishment and growth had already been practised in South Africa since the 1850's. However, for the large-scale forestry project a new technique of temporary stabilisation was initiated in the late 1870's by forestry officer Joseph Storr Lister, by covering the sand with city refuse. The refuse consisted mostly of horse dung, thereby stabilising the sand as well as providing additional nutrients for the young trees (King 1939). Although practised in many areas, a common problem with this method was the transport of the refuse out of developed areas into the dunefields, which turned out to be very costly. Eventually, other methods of temporary stabilisation were attempted. After many trials with European marram grass (*A. arenaria*), which appeared to be such a capable sand binder in Europe and other parts of the world, it was finally agreed that the planting of this grass was the best method for temporary dune stabilisation. Since 1896 *A. arenaria* has been planted on a large scale in the Cape area (Stehle 1982).

3.1.2 *Ammophila arenaria* - A solution for the driftsand problem

It is not known when *A. arenaria* was first introduced to South Africa. Towards the end of the 1860s government botanist Peter MacOwan brought a specimen plant to the Cape Town Botanic Gardens (Heywood 1894). In 1876 Joseph Storr Lister, then superintendent of plantations at the Cape, sowed seed onto the driftsands of Durbanroad (today Bellville) near Cape Town. The seed was obtained in Lincolnshire, England, possibly from W.W. Johnson & Sons Ltd, a company that is still supplying seed for stabilisation purposes (Brooks 1986). Initially it did not do very well in South African driftsands. Lister's sowing was a failure, and he abandoned *A. arenaria* in favour of the indigenous pipe grass, *Ehrharta villosa* (Heywood 1894; Stehle 1982). Another early attempt to establish *A. arenaria* in South Africa through seed was undertaken by the Port Alfred harbour authorities in the Eastern Cape in 1883 with unknown success (McNaughton 1895).

Only in 1892 did Arthur W. Heywood, government forester at Uitvlugt near Cape Town, try again with some 45 kg of a mixture of *A. arenaria* seed and seed of other dune species, which was sown onto the Eersterivier driftsands near Cape Town. On this occasion, seed of *A. arenaria* was obtained from a French company, Vilmorin & Co in Paris. The outcome was slightly better than with Lister's experiments. Although the seed germinated only at the foot of the dunes, some 600 plants survived to grow into sand binding plants that could be transplanted to other areas when two years old (Heywood 1894). It was therefore concluded that *A. arenaria* does not germinate readily on open sand dunes and should rather be grown in nurseries to be transplanted onto the dunes at a later stage. One can wonder why the foresters had not earlier thought about planting *A. arenaria* rather than sowing, seeing that planting has been - and still is - the more common method in Europe as well (Adriani & Terwindt 1974; Brooks 1986). However, there was most certainly not much transplant material present in South Africa, if any at all, and it is understandable that the sowing of seed straight onto the sites was attempted before it was grown into plants over a lengthy period of time.

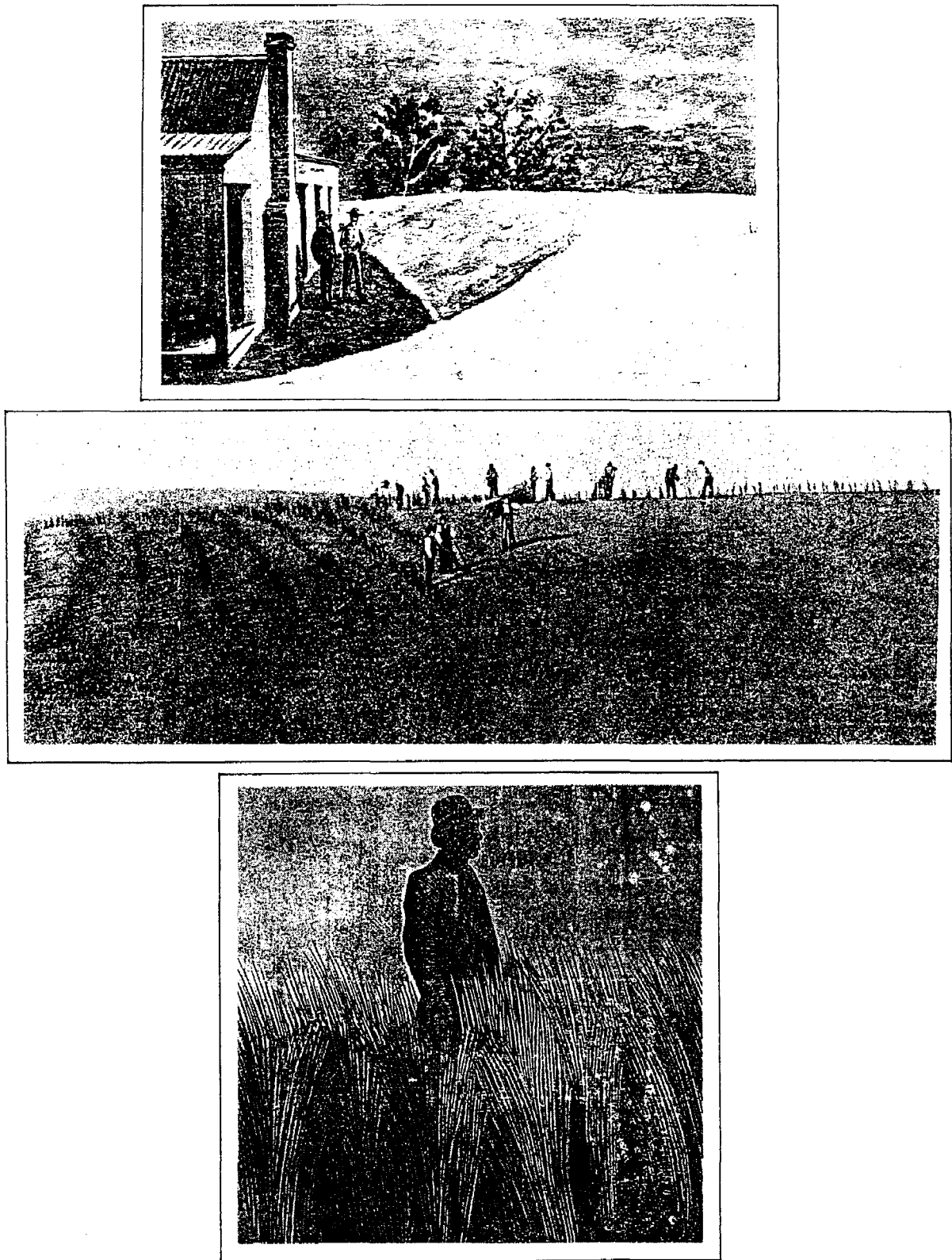


Plate 3.1: Historical illustrations from the Agricultural Journal of the Cape Colony of a building being threatened by driftsands (top, 1903), planting of *A. arenaria* (middle, 1903), and a settler amidst an *A. arenaria* stabilisation site (bottom, 1894).

In 1894, *A. arenaria* was grown successfully in nurseries in Tokai and Uitvlugt near Cape Town and subsequently used for driftsand reclamation throughout the Cape Colony (Plate 3.1). One of Heywood's supporters was government forester David E. Hutchins. He introduced a French stabilisation method to South Africa which involved the formation of a "dune littorale" by *A. arenaria* that would act as a sand catchment barrier and prevent sand from moving inland (McNaughton 1895). *A. arenaria* proved to do such a good job that enthusiasm about it in South Africa was soon comparable to that in Australia (see Chapter 2). In a 1901 article (Anonymous 1901), driftsands are referred to as "evil conditions", but it is stated happily that "nature has provided ample remedy for her own curse in the form of certain grasses that grow in sandy wastes". In one instance it was even used successfully far away from the coast to stabilise an inland driftsand near Robertson (Hutchins 1901). As in Australia, it was hoped in South Africa that *A. arenaria* would be accepted by cattle and also act as cheap fodder (Heywood 1894). At least since 1906, *A. arenaria* seed was available at the Forestry Department for distribution to farmers, who were informed that "there is no difficulty in raising marram grass from seed" as long as this is done on "a piece of dampish, sandy ground in a sheltered locality" (Anonymous 1906).

Nevertheless, driftsand stabilisation with *A. arenaria* did not succeed everywhere: the grass was reported to suffer from lack of moisture even in the winter rainfall area of False Bay near Cape Town (Hutchins 1901) or generally from unfavourable South African conditions (Braine 1903). It was found by the latter author to be less hardy for sowing than the "infinitely superior" indigenous grasses *Ehrharta villosa* and *Thinopyrum distichum* (here referred to as "*Triticum junceum*"). In spite of this, most authors agreed that *A. arenaria* was in fact the superior sand binding grass in South Africa (Hutchins 1901; Anonymous 1905; Dwyer 1928), although planting culms was indeed a preferable method to sowing seed. A 1908 planting experiment of 10000 *A. arenaria* culms resulted in a 70% success rate, i.e. a remarkable 7000 culms developed roots and became established (Stehle 1981). Although the indigenous pipe grass (*Ehrharta villosa*) proved suitable for sowing, this and other indigenous dune plants such as *Thinopyrum distichum* ("*Triticum junceum*"), *Colpoon compressum*, *Passerina ericoides* and *Myrica cordifolia* appeared to be of limited value for dune stabilisation (Stehle 1981, 1982).

3.2 Use of *Ammophila arenaria* for dune stabilisation in South Africa in past and present

Several different planting methods are recorded for the stabilisation of dunes with *A. arenaria*. Heywood (1894) suggested 3500 plants per acre, equalling roughly 1 plant per 1 m². Planting should be done in a narrower pattern according to McNaughton (1895) who recommended 4 plants per 1 m². Neither recommendation specified the size of “one plant”, which can be understood as one culm or a bunch of culms. Keet (1936) described a technique according to which 3-4 culms are planted in bundles with 60-120 cm in between them. A typical work plan of a modern, large-scale stabilisation programme is given for the De Mond area in Chapter 5 (Table 5.1).

Planting techniques have not changed much over the years, but to encourage the establishment of indigenous dune plants and quick replacement of *A. arenaria*, modern stabilisation methods involve the sowing of seed of indigenous dune plant species among the new *A. arenaria* plantings (P.G. Reyneke, pers. comm., September 1997; see also Chapter 5). Furthermore, with modern technology it is possible to maintain the sites more efficiently. A major hazard for the growth of *A. arenaria* in South Africa is the lack of rainfall (see below). Therefore, most stabilisation sites are nowadays equipped with irrigation systems. Artificial watering prevents the decline of the grass due to desiccation on the one hand but enhances the unnaturally vigorous growth of many indigenous plants on the other hand (Plate 3.2).

The use of *A. arenaria* for dune stabilisation spread rapidly from the Cape Flats area with the primary sites of Bellville and Eersterivier along the coast, both to the north and east. From 1900 dune stabilisation was carried out on such a large scale, that by 1909 an area of 3130 ha, and by 1934 one of 66886 ha had been stabilised in the Cape Colony (Stehle 1981; Avis 1989). *A. arenaria* was used in the majority of places in order to stabilise the sand temporarily before trees like the Australian acacias could be established (see above). The Bredasdorp district was particularly affected with driftsand problems (Keet 1936) and to this day is an area of frequent stabilisation efforts. The northernmost area where *A. arenaria* was ever used is Elandsbaai on the west coast. Some success in driftsand reclamation along the west coast was achieved with the indigenous grasses *Cladoraphis spinosa* and *Cladoraphis cyperoides* (Keet 1936). The

easternmost known stabilisation site involving *A. arenaria* is at Gonubie near East London. *A. arenaria* was also tried for stabilisation at Walvis Bay, then South West Africa, in the early 1970's (Le Roux 1974), but was unsuccessful.



Plate 3.2: Hout Bay stabilisation site in January 1996: The artificial watering of the site encourages the growth of indigenous dune plant species as well, in this case of *Arctotheca populifolia*.

All known stabilisation areas in South Africa are listed in Table 3.1. Obviously much data on the use of *A. arenaria* were lost. It is not known, for example, whether *A. arenaria* was repeatedly introduced to South Africa from European or even Australian or American sources, or whether the material used for the stabilisation was always derived from existing local populations. The latter could imply that all South African *A. arenaria* plants are originally derived from the French seed that was grown into plants in the nurseries of Tokai and Uitvlugt by Heywood and Hutchins in the 1890's (see above). However unlikely this is, there is no record of any later re-introductions from Europe. Today there is certainly no new *A. arenaria* stock being introduced to South Africa. The country contains large enough *A. arenaria* populations to supply its own need for stabilisation projects. For many of the recent projects the grass was obtained, for example, from the extensive Koeberg stabilisation site at the West Coast (Table 3.1).

Although concern about the unusual vigour and spread of Australian acacias such as *Acacia saligna* and *Acacia longifolia* had been raised since the 1930's (see Chapter 5), it was only in 1974 that the Forestry Department changed its policy to the effect that "the use of alien plants should be phased out and only indigenous species and the non-invasive marram grass be used" (Avis 1989). The "non-invasive" *A. arenaria* gained importance for dune stabilisation since this ban of the Australian acacias. While *A. arenaria* was until then used to "prepare" the driftsands for the planting of trees like the acacias by giving them a first temporary stability, it now became the main stabilisation agent itself. This could be another reason for the more frequent use of expensive, artificial irrigation systems in recent *A. arenaria* stabilisation sites, as the grass would now be required to grow for longer periods.

Since 1980 the stabilisation of dunes itself was questioned as extremely artificial human interference into the natural coastal dynamics, to the extent that it was only to be carried out when farmland or settlements were immediately threatened by sand encroachment. Driftsands were now looked upon as natural areas of great ecological and recreational value and to be preserved as such, rather than stabilised (Avis 1989), particularly since it was found that their stabilisation can lead to severe beach erosion as the sand supply for adjacent beaches is cut off (Lubke 1985a).

Table 3.1: Stabilisation of South African coastal driftsands with *A. arenaria* (from west to east). Data in italics before 1950's. All data obtained through questionnaires sent to municipalities, CNC (Cape Nature Conservation), CSIR (Council of Scientific and Industrial Research) and to the Department of Forestry as well as from Keet (1936), King (1939), Walsh (1968), Stehle (1980b, 1981), McLachlan *et al* (1982), Lubke (1985b), Reyneke (1985), Avis (1989, 1992), van Zyl (1989), Burns & Barwell (1989), McLachlan & Burns (1992) and P.G. Reyneke (pers. comm., September 1997). No data available (-).

site	total area planted with <i>A. arenaria</i>	time of plantings	source of <i>A. arenaria</i>	plantings carried out by
Elandsbaai	-	1975 - 1980	-	Forestry
<i>Saldanha - Danger Bay</i>	<i>0.4 ha</i>	<i>1920's - 1930's</i>	-	<i>private</i>
Langebaan - Chemfos site	-	1996	Koeberg	Top Turf
West Coast Nt. Park - Schrywershoek	-	-	-	-
Yzerfontein	-	1975 - 1980	-	Forestry
Koeberg Nuclear Power Station	400 ha	1980-1982	-	Eskom
Melkbosstrand	-	1991	Koeberg	"Water's Edge" Dev., CSIR
<i>Bloubergstrand</i>	<i>19 ha</i>	<i>until 1918</i>	-	<i>Cape Forestry</i>
- Big Bay	0.76 ha	1995-1996	Koeberg	Regional Services
Tableview	20 ha	1991-1994	Koeberg	Milnerton Municipality, CSIR
Milnerton - Zonnekus	-	-	-	"Woodbridge Island" Dev.
<i>Bellville (then Durbanroad)</i>	<i>sowing exp. (failure)</i>	<i>1876</i>	<i>seed from England</i>	<i>Cape Forestry (J. Storr Lister)</i>
<i>Bellville</i>	<i>planting</i>	<i>1904-1937</i>	-	<i>Cape Forestry</i>
<i>Robben Island</i>	<i>36 ha</i>	<i>1907-1908</i>	-	<i>Colonial Secretary</i>
<i>Cape Peninsula in general</i>	-	<i>1907-1917</i>	-	<i>Cape Forestry</i>
Hout Bay	-	1990	Koeberg	Forestry, CSIR
Kommetjie	-	1951	-	Forestry
Witsandbaai	10 ha	1996 (and earlier)	Koeberg	CNC
Glencairn	-	ca. 1988	Fishhoek	CSIR
Fishhoek	1.5 ha	1980's, 1994-1995	Fishhoek, Tableview	Local Authorities, CSIR
Muizenberg	-	1897	nurseries	Cape Forestry
<i>Muizenberg, Seekoevlei</i>	-	<i>from 1936</i>	-	<i>Forestry</i>
Muizenberg	-	1991-1992	Koeberg	Cape City Council, CSIR
<i>Strandfontein, Swartklip</i>	-	<i>1897</i>	<i>nurseries</i>	<i>Cape Forestry</i>
<i>Strandfontein</i>	<i>95 ha</i>	<i>until 1918</i>	-	<i>Cape Forestry</i>
Macassar Beach	-	1994-1995	Koeberg	Weskaap SDR
<i>Eersterivier</i>	<i>sowing exp. (± success)</i>	<i>1892</i>	<i>seed from France</i>	<i>Cape Forestry (A.W. Heywood)</i>
<i>Eersterivier</i>	<i>planting: 193 ha</i>	<i>until 1918</i>	<i>nurseries</i>	<i>Cape Forestry</i>
Strand	ca. 0.5 ha	1994-1995	Koeberg	Strand Municipality
Pringle Bay	ca. 8 ha	1970's, 1991	West Coast	Overberg District Council, CSIR
Blesberg	-	late 1970's	-	Forestry
<i>Middeelvlei (Botriviermouth)</i>	<i>137 ha</i>	<i>until 1917</i>	-	<i>Cape Forestry</i>
<i>Walker Bay State Forest</i>	<i>ca. 5 ha</i>	<i>1912-1920</i>	<i>own nurseries (2.5 ha)</i>	<i>Cape Forestry</i>
Walker Bay State Forest	ca. 750 ha	1920-1968	own material	CNC
Pearly Beach	-	1960's	-	Forestry
Uilenkraal	-	since 1950	-	Forestry
<i>Quoin Point, Buffeljags</i>	-	<i>1930's - 1950's</i>	-	<i>Forestry</i>
<i>Rietfontein</i>	-	<i>1930's</i>	-	<i>Forestry</i>
<i>Brandfontein</i>	<i>40 ha</i>	<i>1930's</i>	-	<i>Forestry</i>
<i>Cape Agulhas</i>	<i>61 ha</i>	<i>1901-1906</i>	-	<i>Public Services Dept.</i>
<i>Cape Agulhas - Papenkuilsfontein</i>	-	<i>1930's</i>	-	<i>Forestry</i>
De Mond	ca. 900 ha	1931-1996	-	Forestry

Waenhuiskrans - Struispoint	ca. 200 ha	1960's	-	Forestry
Waenhuiskrans - village	-	-	De Mond	Forestry
Ryspunt, Skipskop	-	1930's - 1960's	-	Forestry
<i>De Hoop</i>	-	<i>from 1934</i>	-	<i>Forestry</i>
De Hoop	2 ha	1994	De Mond	CNC
Witsand (S. Cape)	5 ha	1984 - 1987	De Mond	Heidelberg C.P., Forestry
Garcia State Forest	-	1970-1975	-	Forestry
Kleinjongensfontein	-	1980 - 1985	-	Forestry
<i>Stilbaai</i>	<i>4 ha</i>	<i>1901-1909</i>	-	<i>Cape Forestry</i>
<i>Stilbaai</i>	<i>ca. 450 ha</i>	<i>1932-1951</i>	-	<i>Forestry</i>
Stilbaai - Lappiesbaai	ca. 3 ha	1994	Goukamma Nat. Reserve	Local Council, CSIR, Hydromulch
Visbaai	-	1960's	-	private?
Vleesbaai	-	1960's	-	private?
Mosselbaai - Voorbaai	-	1990	Koeberg	CSIR
<i>Hartenbos</i>	<i>49 ha</i>	<i>1904-1907</i>	-	<i>Railway Dept.</i>
Hartenbos	-	1968	-	private
Klein Brakrivier	-	1966	-	Divisional Council
Groot Brakrivier	-	-	-	-
Hersham	ca. 1 ha	-	De Mond?	Searles Holdings
Bothastrand	-	-	-	-
Kleinkrantz	-	early 1980's	-	-
Swartvlei	-	-	-	-
Sedgefield	ca. 6 ha	1992-1993	Goukamma Nat. Reserve	Private Dev., CSIR
Goukamma Nature Reserve	-	1920's - 1970's	-	-
Plettenberg Bay - Keurboomsrivier	-	-	-	-
<i>Tsitsikamma River mouth</i>	<i>ca. 1 ha</i>	<i>1930's</i>	-	<i>Forestry</i>
<i>Oysterbay/St. Francis Bay</i>	<i>358 ha</i>	<i>1917-1924</i>	-	<i>Forestry</i>
Oysterbay/St. Francis Bay	-	since 1964	-	-
Sardinia Bay	-	-	-	-
<i>Port Elizabeth</i>	-	<i>1890's - 1990</i>	<i>Western Cape</i>	<i>Harbour Board, Divisional Council, Forestry</i>
Port Elizabeth - Cape Recife	-	1976-1977	own material	Port Elizabeth Municipality
Sunday's River mouth	4 ha	1960's - 1977	-	-
Alexandria Dunefield - several areas	ca. 500 ha	1981-1991	-	Forestry
Díaz Cross	-	-	-	-
<i>Port Alfred</i>	<i>sowing exp. (success?)</i>	<i>1883</i>	-	<i>Port Alfred Harbour Authorities</i>
Port Alfred	-	-	-	-
Kleinemonde	-	-	-	-
Fish River mouth - Fish Point	0.8 ha	1973	-	-
Old Woman's River mouth	-	1980	-	Forestry
Mtati River mouth	-	1978-1982	-	Forestry
Hamburg	-	-	-	-
Gulu River mouth	-	1978-1982	-	Forestry
East London - Gonubie	-	1990's	Alexandria, De Hoop	Gonubie Municipality

The following guidelines for dune stabilisation were published by the Council for the Environment in 1991:

"6. Control dune stabilisation

6.1: Unstabilised dunes do not always threaten adjacent development and they usually represent essential natural sources of sand for adjacent beaches.

6.2: The stabilisation of dunes by vegetation or other means should be avoided until a study has been undertaken to determine natural patterns of sediment movement in the areas concerned. Obtain expert advice.

6.3: The provincial conservation authority should be consulted prior to the stabilisation of driftsand areas. Where possible, indigenous and non-invasive vegetation should be used."

An argument for the reduction of dune stabilisation was certainly also the financial aspect. Stabilisation costs in the Alexandria dunefield near Port Elizabeth were estimated at R 1800 per hectare for the period 1981/82; thus the stabilisation of the entire dunefield would have added up to ca. R 32 million (McLachlan *et al* 1982). Only small scale stabilisation efforts have been undertaken in this area since the 1960's, and most of the dunefield is now a nature reserve, managed by CNC (Cape Nature Conservation). Although stabilisation efforts have obviously been reduced radically since the first half of this century, it is obvious from Table 3.1 that there is still a fair amount of it undertaken today, usually involving *A. arenaria*.

3.3 Present distribution of *Ammophila arenaria* in South Africa

The results of a detailed survey of the present distribution of *A. arenaria* in South Africa over the last three years are shown in Figure 3.1. *A. arenaria* occurs today along some 1300 km of the South African Cape coast from the semi-arid Langebaan area at the west coast to subtropical Gonubie near East London, covering several climate regions (Fig. 3.2). It is widespread in the winter rainfall area of the Western Cape (in this study referring to the coastal strip from the west coast to Cape Agulhas), but grows well enough in the drier and warmer climates of the bimodal rainfall area of the Southern Cape (Cape Agulhas to Cape St. Francis). The Eastern Cape (Cape St. Francis to East London) is also characterised by bimodal rainfalls, but the overall climate becomes increasingly subtropical, and *A. arenaria* occurs in much

smaller numbers here. Most of the Eastern Cape sites marked in Figure 3.1 consist of merely a few degenerating clumps of *A. arenaria*. In contrast, some sites in the Southern and Western Cape are covered with up to 500 ha (De Mond Nature Reserve) of *A. arenaria*.

It appears as though *A. arenaria* occurs at all sites because of its prior planting there. Clear historical data are missing in some cases, for example at Noordhoek and Witsandbaai/Cape Peninsula or for the important sites of Visbaai (ca. 20 ha of *A. arenaria*) and Vleesbaai, both near Mossel Bay. Beside the fairly well recorded stabilisation efforts of government and semi-government organisations like the Forestry Department or the CSIR (Council of Scientific and Industrial Research), *A. arenaria* has also been planted by farmers and other private land owners. Records of this use are non-existent or not obtainable, and information gained from local residents is sparse. However, historical and geographical research so far does not indicate that unaided spread of *A. arenaria* into any of the areas shown in Figure 3.1 has occurred, as is so obviously the case in California (Buell *et al* 1995; see Chapter 2). It can be concluded with acceptable certainty that all sites shown in Figure 3.1 are or were stabilisation sites, which is confirmed by their close correlation with the stabilisation sites listed in Table 3.1.

A further comparison of Table 3.1 and Figure 3.1 shows clearly the climatic constraints of *A. arenaria*'s distribution in South Africa: although planted in the Eastern Cape as well as in the Western and Southern Cape, *A. arenaria* does not last as long in this area. The sites at the mouths of the Old Woman's River and Mtati River in the Eastern Cape were stabilised in the early 1980's and today carry only a few degenerating clumps of *A. arenaria* (Plate 3.3). In contrast, the sites of Visbaai, Vleesbaai and Garcia Nature Reserve in the Southern Cape were stabilised in the 1960's and early 1970's and are still covered with vigorous *A. arenaria* (Plate 3.4). The subtropical Eastern Cape to the east of Port Elizabeth appears to be too warm for *A. arenaria*, with mean annual temperatures at East London and Great Fish Point at 18.7° and 18.0° Celsius respectively (Fig. 3.2). Equally unfavourable conditions occur along the west coast which is characterised by a long dry period from at least November until April (Fig. 3.2): at the stabilisation sites of Elandsbaai and Yzerfontein, both created in the late 1970's, no *A. arenaria* was observed in 1995. At the Koeberg site, completed in 1982 with ca. 400 ha of *A. arenaria*, some 200 ha of the grass were found in 1995, most of which appeared to be in a declining state with short tillers not extending much more than 30 cm (length of healthy tillers

ca. 1 m or more) and very few inflorescences (Plate 3.5). However, even the more favourable climatic regions of the southwestern Cape do not receive sufficient rainfall, and artificial watering remains a prerequisite for the successful long-term stabilisation of a South African dune with *A. arenaria*.

European temperature and rainfall data from both northern and southern European stations (Table 3.2) reveal an overall colder and more humid climate in *A. arenaria*'s home territories. Mean annual temperatures of the six shown stations range from 7.1°C (Bergen) to 15.6°C (Genoa), mean annual rainfalls range from 622 mm (London) to 2057 mm (Bergen). It appears as though South African areas of appropriate temperature regimes are too dry (Cape Columbine: 15.1°C mean annual temperature, but only 229 mm annually), while those of appropriate rainfall regimes are too warm (East London: 808 mm annually, but 18.7°C mean annual temperature). Interestingly, Cape Town has a higher annual precipitation than London, but one has to consider that rainfall is much more evenly distributed in London while Cape Town experiences a long drought over the summer months. In addition to unfavourable temperature and precipitation regimes, South African shores are subjected to higher radiation and stronger winds than the European ones and furthermore lack regular frost periods which have been found to enhance germination (see Chapters 2 and 7).

Table 3.2: Mean annual temperature and rainfall in several European towns in the vicinity of which *A. arenaria* occurs naturally (Kendrew 1930).

	mean annual temperature (°C)	mean annual precipitation (mm)
Bergen (Norway)	7.1	2057
Hamburg (Germany)	8.3	699
London (England)	9.9	622
Bordeaux (France)	12.4	779
Lisbon (Portugal)	15.4	754
Genoa (Italy)	15.6	1321

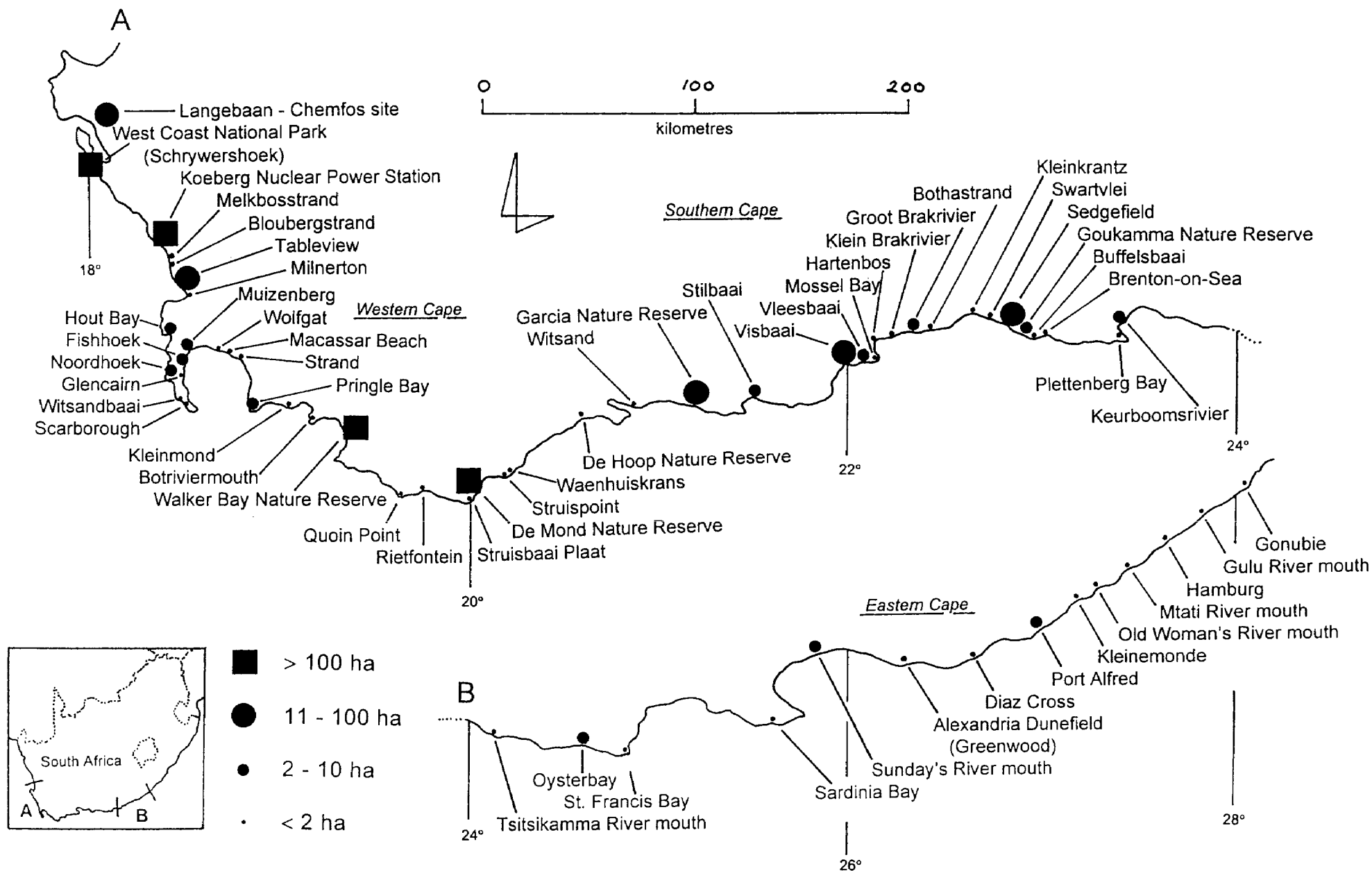


Fig. 3.1: Present distribution of *A. arenaria* along the South African coastline. Every known site of occurrence of *A. arenaria* is shown and its approximate cover with the grass illustrated (in ha).

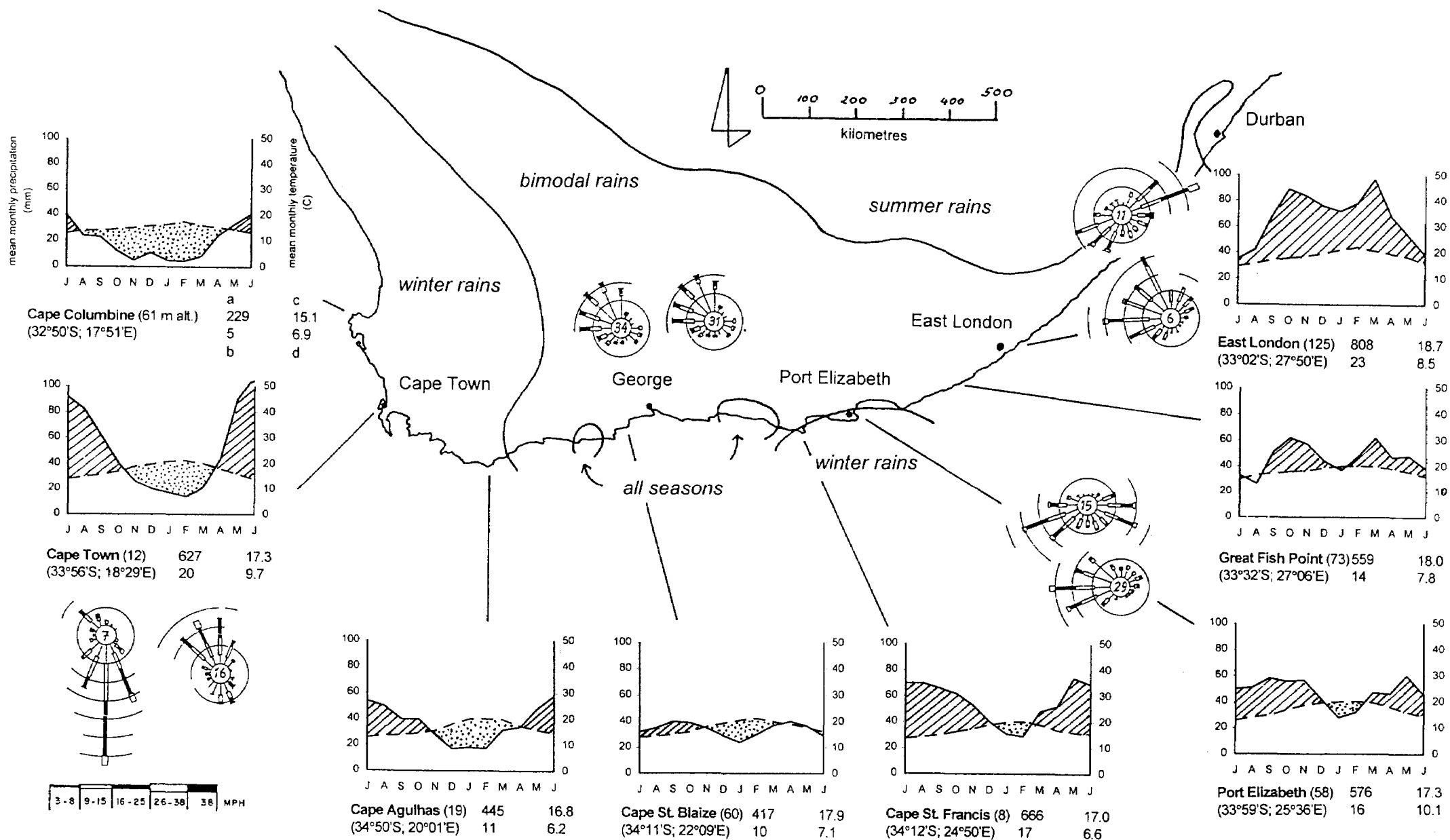


Fig. 3.2: Rainfall and coastal climographs of the South African Cape region. See Cape Columbine diagram for legend on all Walter-Lieth diagrams: The left axis reflects mean monthly precipitation (mm, thick line), the right axis mean monthly temperature (°Celsius, broken line); in brackets the altitude (m) and geographic position of the site, followed by mean total annual precipitation in mm (a), total number of days with 10 mm or more precipitation (b), mean annual temperature in °Celsius (c) and annual temperature range in °Celsius (d); dotted areas are dry periods, hatched areas humid periods. Windroses are shown for summer (S) and winter (W) for Cape Town, George, Port Elizabeth and East London. Arcs represent 5% intervals, the percentage of calms is to be found within the circle of each windrose. All data obtained from Heydorn & Tinley (1980).

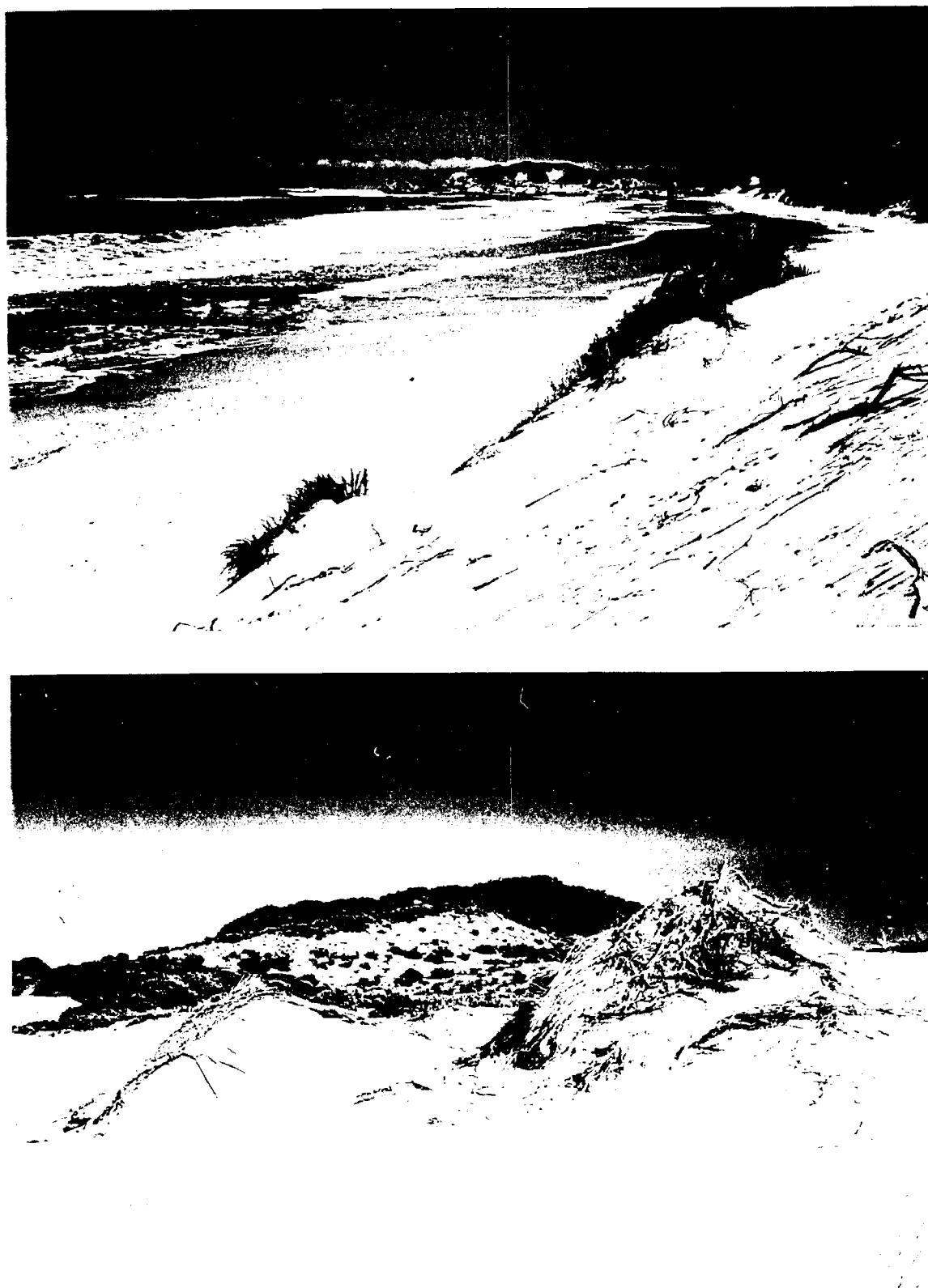


Plate 3.3: Remnants of *A. arenaria* at Old Woman's River mouth (top, February 1996) and Mtati River mouth (bottom, April 1996) in the Eastern Cape.



Plate 3.4: Vigorous *A. arenaria* at Visbaai (top, August 1995) and Vleesbaai (bottom, September 1995) in the Southern Cape.

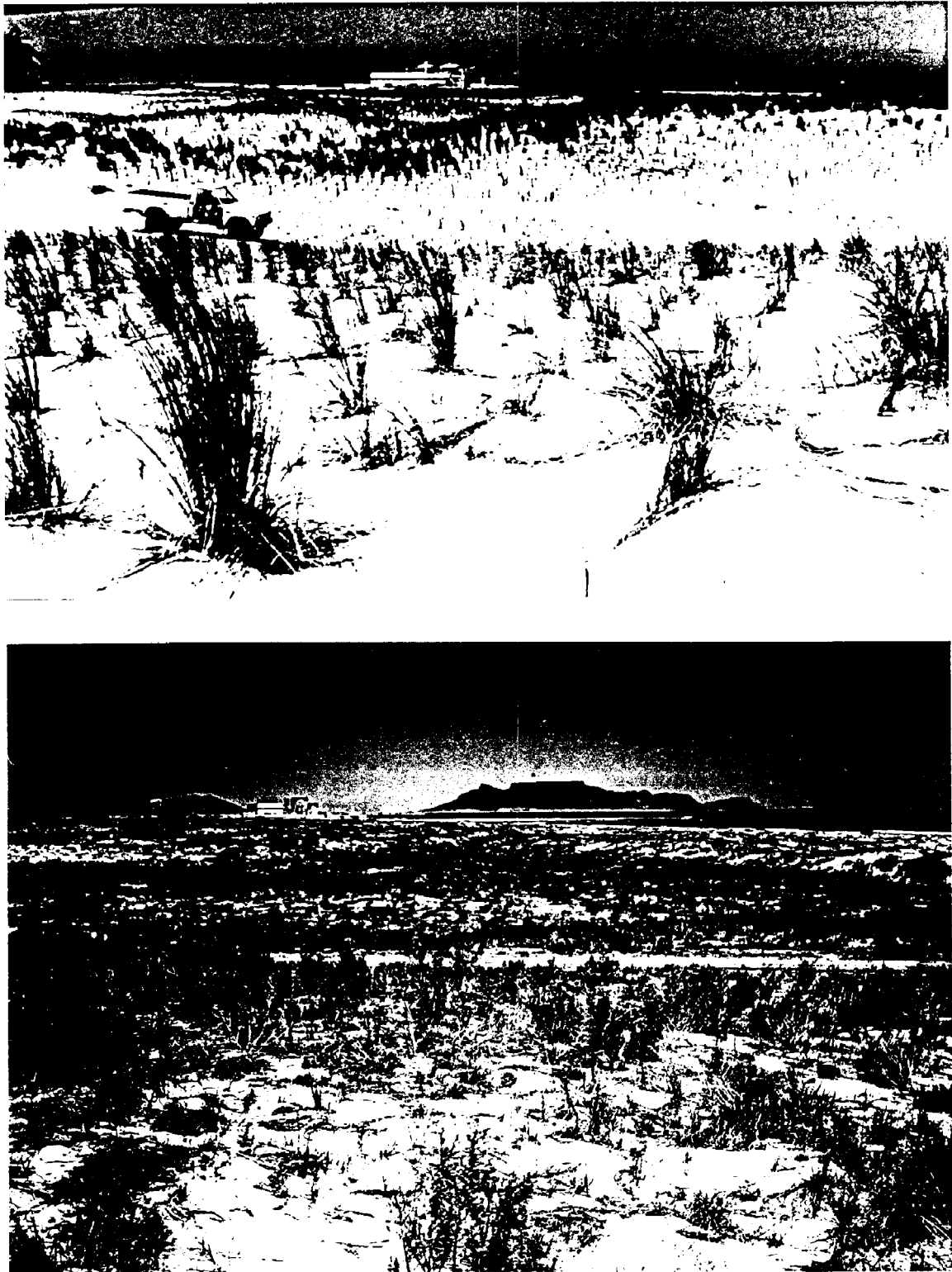


Plate 3.5: Recently completed *A. arenaria* stabilisation at Koeberg in 1982 (top) and revisited in October 1997 (bottom). The Koeberg site is not irrigated, and plants are declining in vigour. Indigenous dune scrub has become established in between *A. arenaria*.

It remains unknown which of the two varieties of *A. arenaria*, the northern and western European var. *genuina* or the Mediterranean var. *arundinacea* (see Chapters 1 and 2), are present in South Africa, or whether both of them are present. The possibility that most South African material might have been derived from French seed (see above) does not solve this problem as the seed could have been obtained both from the northern and western French shores as well as from its Mediterranean shores. It is believed by some that the parent stock of *A. arenaria* in South Africa originates from the Atlantic coast of Europe (P. Raal, pers. comm., July 1994). It would therefore be of the variety *genuina*, an assumption that can be supported by our analysis of the floral morphology of specimens from all along the Cape coast (see Chapters 1 and 7). However, no final answer can be given to this as yet, and genetic research is necessary to obtain more information about the populations present in South Africa.

3.4 The controversy over *Ammophila arenaria* in South Africa

3.4.1 *Ammophila arenaria* as “non-invasive” alien

Since 1974 *A. arenaria* has been and is still used as the main dune stabilising agent in South Africa. It is the general belief among South Africans involved with dune stabilisation that South African *A. arenaria* is a weak seeder and therefore “poses an insignificant threat as an invasive species” (P. Raal, pers. comm., July 1994). In fact, *A. arenaria* is believed to be the best suitable stabiliser in South Africa at the moment. The CSIR, which is actively involved in many recent stabilisation projects (Table 3.1), compared aerodynamic characteristics and associated sand trapping effectiveness of *A. arenaria* with those of the indigenous dune plants *Thinopyrum distichum* and *Ehrharta villosa* and found those of *A. arenaria* to be far superior (P. Raal, pers. comm., July 1994). Furthermore, *Thinopyrum distichum* is not robust enough for the task of dune stabilisation, suffering in summer even more from heat stress than *A. arenaria*, whereas *Ehrharta villosa* grows too sparsely and cannot withstand as much wind as *A. arenaria* (M. Burns, pers. comm., September 1995). However, successful trials with the indigenous *Cladoraphis cyperoides* have been undertaken by the CSIR along the west coast where this grass species occurs naturally. At Fishhoek near Cape Town, both *Cladoraphis cyperoides* and

Ehrharta villosa were used in combination with *A. arenaria* (M. Burns, pers. comm., September 1995).

Nevertheless, *A. arenaria* is the CSIR's preferred stabiliser, its use justified even more by the observation that it declines in vigour with increasing sand stability and gets replaced by indigenous plants within some 10 years, therefore "acting as a nurse plant to indigenous species" (P. Raal, pers. comm., August 1994). The same view is shared by the Department of Forestry, whose policy involves the sowing of indigenous plants amongst new *A. arenaria* plantings to ensure the quick replacement of *A. arenaria* (P.G. Reyneke, pers. comm., September 1997). Similarly, in Australian dune stabilisation projects, *A. arenaria* is nowadays used only in connection with indigenous dune plants and then observed to be replaced fairly well (Druett 1991; G. Druett, pers. comm., August 1997; see also Chapter 2).

3.4.2 Concern about its further use

Even though *A. arenaria* proves to have many positive characters and is certainly not to be put on a level with the highly invasive Australian acacias as yet, its use has been criticised by various individuals from about the late 1980's, mainly on the grounds of its foreign origin (G. Hellström, pers. comm., July 1994). During the 1980's South Africa experienced a green movement which highlighted more than ever the negative impacts that alien species can have on South African ecosystems. When CNC (Cape Nature Conservation) took over many dune areas from the Department of Forestry in 1987, no more plantings of *A. arenaria* were carried out. CNC adopted as a policy "the removal of all alien species from proclaimed nature reserves ...", and it was emphasised that "... marram is included. We now strongly believe that the use of any introduced species for the purpose of dune management should be avoided" (G. Hellström, pers. comm., July 1994).

The controversy over the use of *A. arenaria* for dune stabilisation in South Africa was enforced during the international "DUNES '94" conference held in South Africa in January 1994. American scientists like Alfred M. Wiedemann (The Evergreen State College, Washington) were surprised to find *A. arenaria* being used to such an extent in South Africa and warned

about its detrimental effects on coastal ecosystems in California and Oregon (see Chapter 2). Concern about the use of *A. arenaria* has since then not only been based on the mere “alienness” of the grass in South Africa, but also on proven facts about its invasiveness in other areas of the world. Considering that the first negative effects of *A. arenaria* in North America were only observed about a hundred years after its introduction, one can be led to the assumption that in South Africa similar negative properties of *A. arenaria* could be detected in the nearer future. In the wake of the “DUNES’94” conference, CNC therefore called for further research “into the better understanding of the invasive properties of marram as a matter of urgency” (G. Hellström, pers. comm., July 1994).

The CSIR agrees to the need for further research on *A. arenaria* and its potential invasiveness, but stresses that CNC’s concern about the use of this grass in South Africa is premature and so far based on the “incomplete understanding of the autecology of the species in South African conditions” (P. Raal, pers. comm., August 1994). While CNC promotes a policy that restricts the use of all alien plant species in South Africa, including *A. arenaria*, the CSIR requests more detailed research to be undertaken about *A. arenaria*’s potentially invasive properties before such a policy is to be adopted. Research aspects that the CSIR considers as important are outlined by P. Raal (pers. comm., July 1994) as “the ability to set seed in South Africa, and, if so, whether the seed set is viable...; the ability to become naturally established via vegetative propagation, and, if so, the range over which vegetative propagules can become established; whether the growth pattern of the species indefinitely excludes the establishment of indigenous vegetation and whether it remains persistent in the long-term”. Raal concludes: “If such investigations reveal that marram has the potential to become an invasive weed we will abide by any policy decisions made by Cape Nature Conservation and the Department of Environmental Affairs and Tourism regarding its future use. Until then it is assumed that the use of marram for current stabilisation is still acceptable practice.”



Plate 3.6: The development of the Dolphin Beach Hotel near Tableview, Cape Town, made the stabilisation of the dunes with *A. arenaria* necessary. View from the same spot to the north across the *A. arenaria* stabilisation (top) and to the south across indigenous dune plant hummocks (bottom). Both photographs were taken in September 1995.

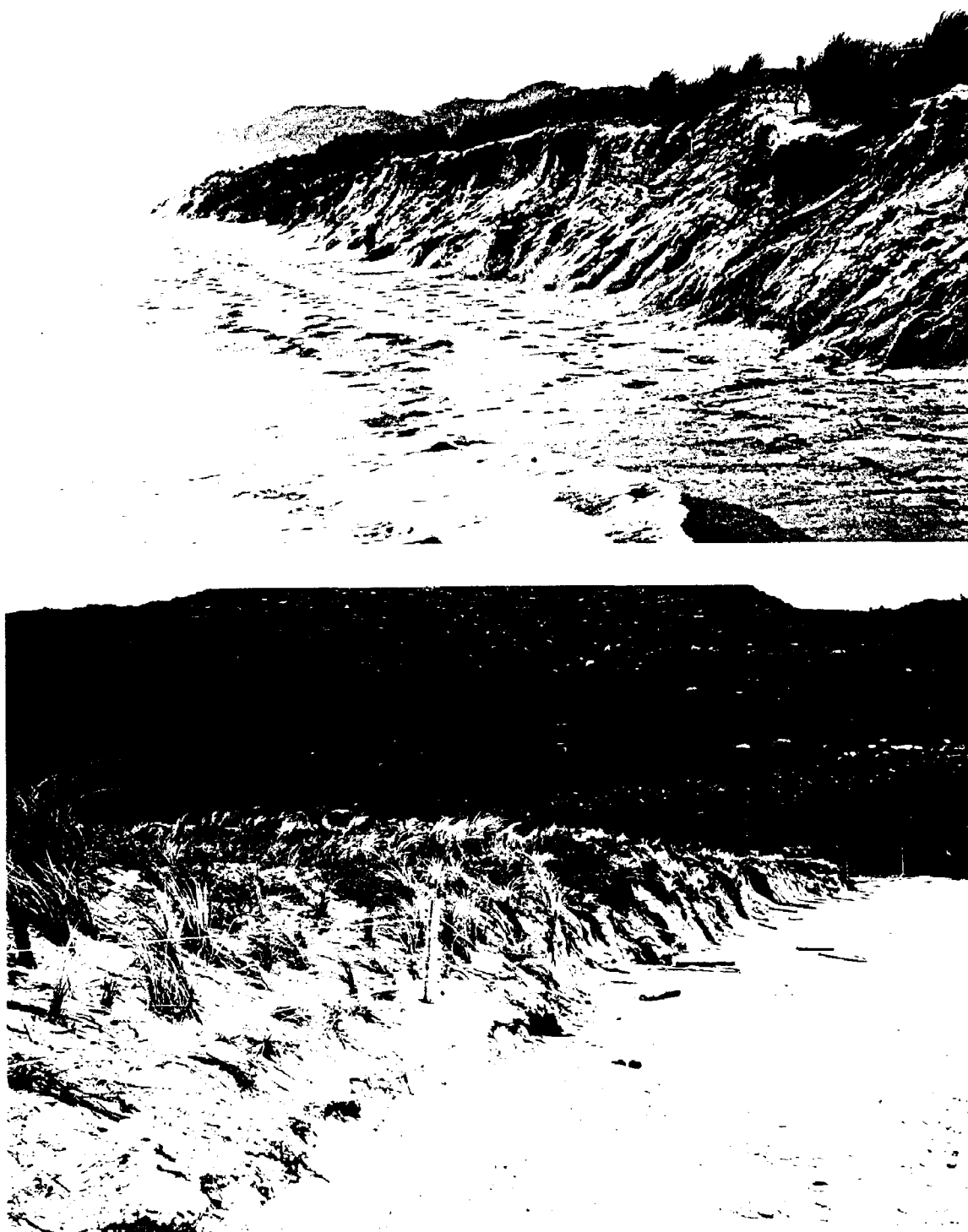


Plate 3.7: Eroded stabilisation sites too close to the high water mark at Sedgefield (top, September 1995) and at Fishhoek (bottom, January 1996). See also Plate 7.4.



Plate 3.8: Driftsands threatening inconsiderate development at Oysterbay (July 1995).



Plate 3.9: Tableview stabilisation site near Cape Town in January 1996 (top: view to southwest; bottom: view to north). Between 1991 and 1994 about 4 kilometres of this coastline were stabilised with *A. arenaria*.

The practice of artificial dune stabilisation is questionable in itself (see above). Although the policies of the Council for the Environment, aimed at keeping stabilisation efforts at an absolute minimum (see above), are followed in many instances, dune stabilisation is not always undertaken merely to prevent sand encroachment of existing development, but in some cases also in order to permit new development. The Dolphin Beach Hotel complex at the southern end of the Tableview stabilisation area is one example where dunes were stabilised to make development feasible (Plate 3.6). The development of such a large complex some 100 m away from the high water mark should not be allowed in the first instance. Development close to the tideline has often led to the stabilisation not only of dunes but of back-beach areas as well, causing frequent erosion of the stabilisation site (Plate 3.7, see also Plate 7.4). A recent survey of 26 South African dunefields (McGwynne *et al* 1993) shows that in 18 of these (69%) stabilisation efforts were in progress, mostly with the intention of combatting natural destabilisation or accommodating development. Only in one case was stabilisation undertaken in reaction to immediate sand encroachment problems. However, the development of even the smallest holiday chalet should take into account the natural sediment movements in the area in order to avoid sand encroaching problems a few years later (Plate 3.8).

3.5 Stabilisation sites in the opinion of South Africans - A questionnaire

3.5.1 Introduction

To gain information on people's perception of stabilisation sites, and of *A. arenaria* as the predominant plant in these, we conducted a survey at the large stabilisation site of Tableview near Cape Town. Between 1991 and 1994, some 4 kilometres of the Tableview coastline were stabilised with *A. arenaria* at a width of 50 m, resulting in about 20 ha of stabilised dunes (Plate 3.9). The area is fenced off, but wooden footpaths give access to the beach. Large information boards explain about dune management and the purpose of the stabilisation. In April 1997, one hundred people were interviewed at Tableview on their views about *A. arenaria* and the surrounding stabilisation site.

3.5.2 Results

The questionnaire (Appendix 3.1 I) was undertaken as random sampling, although we ensured that people of different social and racial backgrounds were interviewed. Of the 91% South African citizens interviewed, 80% were residents of Cape Town or another coastal area. Of the inlanders, 77% would visit the coast on a regular base, usually once per year (42%) or 2-3 times per year (29%). Natural beaches were generally preferred (60%) to built-up beaches (25%), although a number of people thought that their preference for either depended on the purpose of the visit (15%). Most people used the Tableview beach promenade regularly (74%), be it for work or leisure reasons, in 54% of cases even daily.

The subjects were first shown three postcards with scenic views of Table Mountain from the Tableview/Bloubergstrand coastline, featuring different plant species in the foreground (Appendix 3.1 II). When asked which of these postcards would be their preferred choice to send to friends overseas as a “typical South African scenery”, 32% voted for postcard A, which featured the *A. arenaria* stabilisation as a foreground to Table Mountain. However, even more people (46%) voted for the equally unnatural garden community of postcard B, complete with *Aloe ferox*, which does not grow naturally on southwest coast dunes. Only 22% preferred postcard C with a naturally occurring *Didelta carnososa* hummock in the foreground. However, one has to look at the reasons for this vote, and it becomes clear that the *A. arenaria* postcard was chosen in 22% of cases because it gives a “most realistic” view of the Tableview coast. Furthermore, it was often chosen (41%) because of its photographic quality and layout. Postcard B with the aloe-garden was also chosen fairly often because of its photographic quality (24%), but more so because of the “South African” plants in the foreground (35%). In contrast, people voted for postcard C almost certainly because of the plants in the foreground (82%). The indigenous *Didelta carnososa* is obviously thought of as fitting into the landscape, being a typical west coast plant.

The stabilising grass of postcard A and the surroundings was identified positively by 15% of all subjects as “marram”. The grass was in some cases thought to be part of South Africa’s indigenous and precious fynbos vegetation, or otherwise confused with “elephant grass”, “savanna grass” or even “kikuyu”. Only 6% of all people thought that it was probably not

South African, but introduced from Europe. However, of the European tourists interviewed (7%), only 57% recognised it from European beaches. *A. arenaria* appears to be largely accepted from an aesthetic viewpoint, with 63% approving of its appearance and only 27% thinking of it as unattractive or even ugly, while 10% were without an opinion (see also Table 3.3). Most people (72%) did not recognise it from any other site in South Africa and the other 28% usually recognised it from stabilisation sites in the vicinity of Cape Town, such as Muizenberg, Kleinmond or Walker Bay. Although in the majority, it is noteworthy that only 65% of subjects thought that *A. arenaria* was actually planted at Tableview, while not less than 35% were convinced of its occurring naturally there. Interestingly, and possibly in close correlation, 65% had read the information boards put up by the CSIR, while 35% had never looked at them. Of the 65% that thought *A. arenaria* to be planted, the majority (98%) also knew that this was done in order to stabilise the sands.

Table 3.3: Selected results of a questionnaire at the Tableview stabilisation site (see text for interpretation).

	of 63% who find <i>A. arenaria</i> attractive	of 37% who do not find <i>A. arenaria</i> attractive or even unattractive
believe <i>A. arenaria</i> to occur naturally at Tableview	42.9%	32.4%
are aware of problem of invasiveness of exotic plants in South Africa	65.1%	72.9%
use Tableview beach promenade regularly	73.0%	70.3%
use Tableview beach promenade daily	42.9%	35.1%
prefer natural beaches to built up beaches	55.6%	62.2%
prefer built up beaches or like both types	44.4%	37.8%

In Table 3.3, some of the above mentioned results are related to the question regarding the aesthetic impact of *A. arenaria* in South Africa. People who accept *A. arenaria* as attractive tend to believe that it occurs naturally at Tableview, while people who don't like the look of the grass seem to be more aware of the fact that it is artificially planted. The latter are also more aware of the problems of invasiveness that some exotic plants have imposed in South Africa. Furthermore, they do not use the Tableview beachfront as regularly as the people who find *A. arenaria* attractive, which can imply that they are not used to its looks to the same degree. And lastly, they tend to prefer natural beaches to built-up beaches. Their comments on the looks of

A. arenaria were as diverse as “totally unsightly” to “a bit dull” or “not enough colour”, while people that approve of its looks found it “lovely” and “wild and natural”. However, the differences between these groups are not striking (Table 3.3).

Although only 58% of the interviewed people were able to name an exotic plant species in South Africa, 64% were aware of or had heard of the problem of invasiveness of exotic plants in this country. Of the people that could name an exotic plant, 35% mentioned “Black Wattle” and “Rooikrans” respectively, 29% knew “Port Jackson”, 22% “Bluegum” or “Gumtree” and 10% “Jacaranda”. A number of garden plants such as “roses” were also mentioned. *A. arenaria* was never mentioned as an exotic plant, although two subjects, both long-time Tableview residents, were concerned about the grass and commented on its growth as “it doesn’t seem to give room for other plants” and “marram is going to be as bad as Port Jackson and will spoil our beautiful coastline”. The latter resident was disapproving of the stabilisation as being undertaken merely to give people a better view and was particularly upset about the replacement of the previously varied west coast dune plant community, composed of colourful plants like “sourvig” (*Carpobrotus edulis*) and the “beach daisy” (*Didelta carnosus*), with the “totally unsightly” *A. arenaria*.

However, concern about the grass or about invasiveness in general was unusual. A connection of *A. arenaria* as an exotic species with the detrimental effects that certain other exotic plant species have shown in South Africa is not necessarily drawn. This unsuspecting viewpoint is reflected in an investigation on perceptions of professional ecologists compared to business leaders about priorities of environmental issues in South Africa (Preston *et al* 1989): while professional ecologists give the problem of invasion of South African ecosystems by exotic plant and animal species the top priority of all environmental issues, this problem is not even mentioned by any of the business leaders. A severe lack of information on ecological issues like invasion becomes apparent among non-professionals. Environmental awareness in South Africa is closely connected to the level of education. However, some issues - like that of biological invasion - appear to be hardly known at all outside a small circle of professional ecologists.

3.6 Conclusions

Since its introduction in the second half of the 19th century, *A. arenaria* has become one of the most important plant species for the artificial stabilisation of driftsands in South Africa. It was and is planted in South Africa to such an extent that it presently occurs from the semi-arid west coast to the lush, subtropical shores of the eastern region of the Eastern Cape. However, an analysis of the use of *A. arenaria* in present and past in relation to its modern distribution does not indicate any tendency of *A. arenaria* to spread unaidedly into any areas in which it is not needed as a stabiliser. A reason can be found in the South African climate. Although *A. arenaria* has so far been looked upon as extremely tolerant towards a variety of different climatic conditions, the South African climate is possibly one important factor preventing the aggressively vigorous growth of the grass in South Africa that can be observed so clearly along the temperate shores of north California and Oregon (see Chapter 2).

Nevertheless, it is advisable to exercise more caution regarding the use of *A. arenaria* in South Africa. Considering that 69% of South African dunefields examined by McGwynne *et al* (1993) were affected by development like houses, roads, car parks, camping facilities, sewage pipelines and other human-induced structures, it becomes obvious that South African dunefields are severely threatened by human expansion. In the long run, the stabilisation of many dunes will be unavoidable. Therefore, a critical analysis of present stabilisation methods and their improvement should be tackled sooner rather than later.

Although the current practice of stabilising driftsands with *A. arenaria* appears to be widely accepted by South Africans, the grass is presently the primary and in most cases the only plant in South African stabilisation projects. A theoretical analysis of *A. arenaria* in regard to invasive species attributes and of the South African Cape coastal dunes in regard to invisable site attributes has revealed that a potential for invasion of the dunes by *A. arenaria* is indeed present (see Chapter 2). It is now necessary to examine aspects of the ecology and community biology of *A. arenaria* in South Africa in a more practical approach. If such investigations reveal that invasion is taking place, however slowly and inconspicuously, or is to be taking place in the near future, it will be imperative to suggest alternative and, preferably, indigenous plant species for dune stabilisation.

Appendix 3.1 I: Questionnaire used in the survey at the Tableview stabilisation site (postcards overleaf).**Questionnaire - beach promenade Tableview (Cape Town)**

1a) which of these three postcards do you think is most typical of S. Africa?, which one would you send to friends overseas to show them S. Africa?

A

B

C

1b) why ?

A: because of layout/composition and photographic quality of postcard
C: both A and B

B: because of plants in foreground of postcard
D: other reason:

1c) can you name any of the plants on the postcards?

Y

N

yes:

1d) do you think any of the plants on the postcards have been planted or are they natural here?

A: planted:

B: natural:

2a) do you think this grass (pointing at marram around) has been planted or is it natural here?

A: planted

B: natural

2b) if A: do you know why it has been planted?

A: beauty

B: stabilisation of beach

C: other reason:

D: don't know

2c) have you seen this grass anywhere else along the South African coast?

Y

N

2d) do you like the look of this grass?

Y

N

can't say

2e) do you know where it comes from?

Y

N

2f) have you ever read any of these signs which explain about the stabilisation?

Y

N

3a) can you name an exotic plant species in S. Africa?

3b) are you aware of the problem of invasiveness of exotic plants in S. Africa?

Y

N

4a) do you live in South Africa?

Y

N

no, in:

4b) if yes, are you from

A: the coast

B: inland

4c) if inland: do you go to the coast regularly?

Y

N

how often:

4d) do you prefer natural beaches or built up beaches like this?

A: natural beaches

B: built up beaches

C: depends on purpose of visit

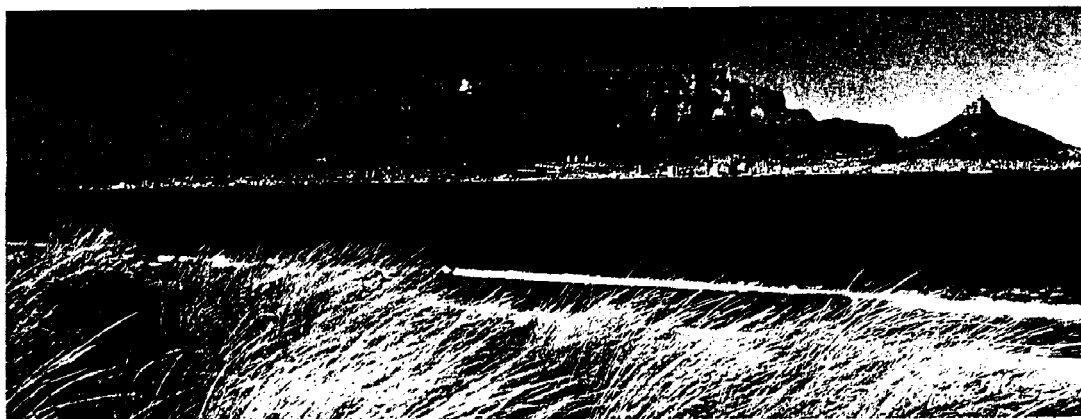
4e) do you use the Milnerton/Tableview beach promenade regularly?

Y

N

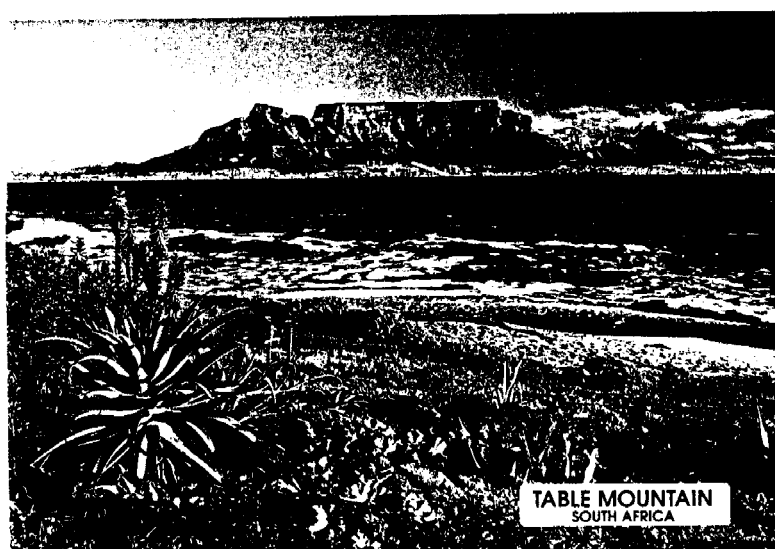
how often:

Appendix 3.1 II: Three postcards on sale in Cape Town souvenir shops, showing the view from the Tableview-Bloubergstrand coastline north of Cape Town across Table Bay with *A. arenaria* (A), various indigenous species in a garden (B) and the indigenous *Didelta carnosa* (C) in the foreground.



A

SOUTH AFRICA



B

C



CHAPTER FOUR

Ammophila arenaria communities - A comparative vegetation analysis

4.1 Introduction

Invasive plant species are often characterised by their tendency to form monospecific stands in their host country, with little opportunity for indigenous species to enter these stands. While they may be perfectly compatible in their home territories and form complex and diverse associations with other species, in a new environment they can relate in a different and often “hostile” pattern towards other species (Cronk & Fuller 1995; see also Chapter 2). The previous chapters have shown that a potential for invasion is certainly present in the case of *A. arenaria* in South African coastal dune systems. It is now necessary to gain information about the biology of *A. arenaria* in South Africa, which could indicate or even prove that biological invasion is in fact taking place. The first focus shall be on community biology. *A. arenaria* has a profoundly negative impact on dune ecosystems in California and Oregon (see Chapter 2). With respect to community biology, *A. arenaria* communities have not only proved to be of a much lower diversity than communities formed by indigenous plants species, but also to depress the formation of indigenous communities and to bear much weaker species associations than are found in indigenous communities (Barbour *et al* 1976; Wiedemann 1984; Boyd 1992; Wiedemann & Pickart 1996). In an attempt to search for similar implications of *A. arenaria*’s invasiveness in South Africa, this chapter will draw a comparison of the biology of *A. arenaria* communities in South Africa with the biology of indigenous South African dune plant communities as well as natural European *A. arenaria* communities.

The term community has been used by biologists in many different ways. Essentially it is applied to “assemblages of plants and/or animals found living together with some degree of permanence” (Greig-Smith 1986). More precisely, “there is always some degree of interaction between organisms within the community by which the occurrence and performance of a species is constrained by the other species present”. A plant community or phytocoenosis can

be described according to functional traits like life-form, phenology, spatial patterns, nutrient cycling or productivity of its plant species. It can also be described according to floristic traits such as species composition and species diversity. In this chapter, *A. arenaria* and indigenous South African dune plant communities will mostly be compared in the floristic terms of their species richness and species diversity, the cover, density and frequency of each species as well as their relative importance. A functional trait that will be looked at is the variety of life-forms of all species present in the communities.

In Europe *A. arenaria* is the most prolific foredune plant and forms a great number of different communities which have been subjected to thorough research. These communities develop from pure *Ammophila* to mixed *Ammophila* along a successional gradient (Willis 1959b; see also Chapter 1) and range from such different compositions as the *Elymo-Ammophiletum oriento-balticum* of the Baltic shores (Hundt & Tietze 1993) to the various types of the southern European *Ammophiletum mediterraneum* (e.g. Lavrentiades 1993; Pignatti 1993), depending on their geographical situation. No comparable studies have yet been carried out on South African *A. arenaria* communities. Plant communities and their composition along the South African Cape coast have been described in detail for the western section (Cape Town northwards) by Boucher & Le Roux (1993), for the southwestern and southern section (Cape Town to Port Elizabeth) by Taylor & Boucher (1993) and for the eastern section (Port Elizabeth eastwards) by Weisser & Cooper (1993). *A. arenaria* is only mentioned in the first two publications, but not as a community forming species: Boucher & Le Roux (1993) list *A. arenaria* under “differential species of the Capensis coastal dune communities”, and Taylor & Boucher (1993) under plant species “common to the *Gazania rigens* - *Heteroptilis suffruticosa* community” (now *Gazania rigens* - *Dasispermum suffruticosum*). However, the intention of above publications was to describe only natural dune plant communities as opposed to stabilisation sites. Lubke *et al* (1997) describe all dune plant communities and mention *A. arenaria* as a locally dominant plant in the southwestern and southern Cape as a consequence of stabilisation efforts, and as occurring less abundantly in the eastern Cape.

An historical investigation indicates that *A. arenaria* occurs in South Africa only in areas where it was planted for the purpose of dune stabilisation (see Chapter 3). However, some of these stabilisation efforts were undertaken many decades ago, and the grass is still present in

great numbers in the respective areas. One should therefore acknowledge the widespread occurrence of *A. arenaria* in South Africa, not only as an exotic species planted in stabilisation sites but also as a naturalised species growing independently of any recent stabilisation efforts and forming dense and vigorous communities. Nothing is known as yet about the vegetation structure and dynamics of these *A. arenaria* communities. How do they compare with South African dune plant communities made up of indigenous species? And how do they compare with European *A. arenaria* communities?

Although the focus of this chapter is on community biology in terms of vegetation structure and dynamics, one geomorphological aspect of these dune communities was also examined. Along the Oregon coast, *A. arenaria* has replaced the low, rounded foredune hummocks formed by indigenous species with a continuous, high and abruptly rising foredune ridge (Barbour & Johnson 1977; Wiedemann 1984; see Chapter 2). In New Zealand, *A. arenaria* dunes have been observed to show a more irregular pattern than indigenous dunes and cause unwanted wind-channeling and blow-outs (Esler 1970; Johnson 1993; see Chapter 2). To establish whether *A. arenaria* has a similar effect on South African dune topography, the profiles of dunes formed by South African *A. arenaria* were compared with the profiles of dunes formed by South African indigenous dune plants as well as to those of dunes formed by *A. arenaria* in Europe.

4.2 *Ammophila arenaria* communities and indigenous dune plant communities in South Africa

4.2.1 Introduction

Firstly, South African *A. arenaria* communities will be compared with South African indigenous dune plant communities. In order to establish the invasiveness of *A. arenaria* it is necessary to examine whether the grass tends to form monospecific stands and shows traits of incompatibility with South African indigenous dune plants.

The following questions are to be addressed:

- 1) How do species richness and species diversity differ in A. arenaria communities compared to communities dominated by indigenous dune plants? Do A. arenaria communities contain fewer different species? Is the diversity lower than in indigenous communities?*
- 2) How do importance values and life-forms of the individual species in the two types of communities differ from each other? Is A. arenaria of unusually high importance? Which indigenous species grow well in A. arenaria communities, i.e. have high importance values in these stands?*
- 3) Which, if any, species are significantly associated with A. arenaria? How do species associations in A. arenaria communities differ from those in indigenous dune communities?*
- 4) What trends of differentiation of stands can be detected for the two types of communities through the application of classification and ordination techniques?*
- 5) Do edaphic values like pH, conductivity and organic matter differ in the two types of communities? What influence do other environmental factors have on the structure of South African A. arenaria communities?*

6) Is there a difference between the profiles of dunes formed by *A. arenaria* and those formed by South African indigenous dune plants? Does *A. arenaria* form a steeper and more continuous dune ridge than indigenous dune plants?

4.2.2 Study area

Sampling of South African *A. arenaria* and indigenous plant communities was carried out between February 1995 and February 1997 along the Cape coast from Koeberg, north of Cape Town (33°40'S; 18°25'E), to Gonubie near East London (32°56'S; 28°02'E, see Fig. 3.1). This stretch of about 1300 kilometres of coast is situated in several different climate zones (see Fig. 3.2).

According to Tinley (1985), the overall climate of the southwest, south and east Cape coast of South Africa is warm and temperate, interrupted by a steppe climate between Cape Agulhas and Groot Brakrivier near Mossel Bay. The southwest coast is a winter rainfall area, while the south and east coast are characterised by bimodal rainfalls during spring and autumn. The whole area is affected by two major ocean 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 along the south and southeast coast (Tinley 1985). Maxima and minima of sea surface temperatures occur in February and August and influence land surface temperatures which reach their maxima and minima in the same months. The major winds along the Cape coast are all bidirectional and oblique or quasi-parallel to the coastline trend. On the west coast southerly winds alternate with northwesterly winds, on the south coast westerly with easterly winds, and on the southeast coast southwesterly with northeasterly winds (Tinley 1985). Figure 3.2 shows typical windroses at four sites along the Cape coast as well as temperature and rainfall records of four weather stations along the Cape coast.

The vegetation of *A. arenaria* and adjacent indigenous dune plant communities was sampled at 39 of the 59 sites (66%) at which *A. arenaria* is known to occur in South Africa (see Fig. 3.1). At most of these sites *A. arenaria* covered at least 2 ha of dunes. In all cases the presence of *A.*

arenaria could be explained by recent or former human planting efforts in order to stabilise the dunes (see Chapter 3). Whether artificial or naturalised, all sampled stands reflect dune communities of early successional stages and were situated on foredunes and intermediate dunes. The climax vegetation of the Cape coast varies from strandveld and coastal fynbos in the southwest, to coastal fynbos and coastal thicket in the south, to coastal thicket and coastal forest or coastal grassland in the east (Lubke *et al* 1997).

4.2.3 Methods

Stratified random sampling was applied at all sites to ensure sampling of differently aged *A. arenaria* communities and indigenous plant communities at various distances to the sea but in proximity to each other. At each site between one and seven 100 m² stands were laid out in the respective plant communities, depending on their size and occurrence at the site. Altogether 82 stands of *A. arenaria* communities and 64 stands of indigenous dune plant communities were sampled; the lower number of indigenous stands being due to the fact that there were not always indigenous stands present in the immediate vicinity of *A. arenaria* stands, especially if the latter were part of a stabilisation area. On the other hand, at some sites only indigenous stands were sampled. However, for each type of community 60 stands were sampled that were immediately adjacent to each other and therefore directly comparable.

Within each of the 100 m² stands, twenty 1 m² quadrats were placed according to random numbers (Avis 1995; Avis & Lubke 1996). The number of individuals per species was counted as number of culms or shoots, and the percentage aerial cover was estimated per species, in order to establish density, cover and frequency for each plant species (Brower *et al* 1990). The data were then used to determine species richness, species diversity and importance values for each species per stand.

1) Species richness and species diversity

A value of species richness per stand reflects the number of different species in the stand. The diversity index used is Simpson's dominance index (Simpson 1949) in its inverted form:

$$d_s = \frac{N(N-1)}{\sum n_i(n_i-1)}$$

where N is the total number of individuals in the stand (total density) and n_i the number of individuals of species i (specific density). The index d_s is “an expression of the number of times one would have to take pairs of individuals at random from the entire aggregation to find a pair from the same species” (Brower *et al* 1990).

2) Importance values and life-forms

While Simpson’s diversity index is based only on the density of each species in a stand, the importance value (IV) of a species takes into account its cover and frequency as well. A species can have a very low density in a stand, but cover a greater surface area than a more abundant species. The IV of species i gives an estimate of its influence or importance in a plant community and is calculated as the sum of its relative density, relative cover and relative frequency (Mueller-Dombois & Ellenberg 1974):

$$IV_i = Rd_i + Rc_i + Rf_i$$

One disadvantage of the concept of an importance value is that it yields “similar values for different combinations of the three relative values” (Brower *et al* 1990). It is therefore necessary to always keep in mind the three relative values separately.

The Raunkiaer plant life-forms of all species which rank amongst the first, second or third most important species in any community were noted according to the revised version of Mueller-Dombois & Ellenberg (1974).

3) Species associations

While the importance value (IV) takes into account species density, cover and frequency, it can be useful to focus only on frequencies. Inconspicuous species with low density and cover values can occur at great frequencies with other species, and therefore be associated positively

with these. Jaccard's index of species association (IA_J) is a measure of the association between two species based on their presence and absence in sample quadrats. It is calculated as follows (Mueller-Dombois & Ellenberg 1974):

$$IA_J = \frac{a}{a + b + c}$$

where a is the number of quadrats in which the two species under examination occur together, b the number of quadrats in which only one of the species occurs, and c the number of quadrats in which only the other species occurs.

The significance of species associations was tested through a χ^2 -test involving a 2x2 contingency table (a , b , c as above, and d = number of quadrats in which neither of the species occurs) and Yates' correction of continuity according to Zar (1984) and Mueller-Dombois & Ellenberg (1974).

4) Classification and ordination of stands

A first comparison of the structure of South African *A. arenaria* communities with indigenous dune plant communities was attempted by focusing on species richness, Simpson's diversity and importance values of prominent species (see above). Following this, the communities were subjected to computerised classification and ordination techniques. While classification, also termed "cluster analysis" (Jongman *et al* 1995), attempts to group similar stands into discrete entities in the form of a table, the ordination of the same stands would display them graphically along two or more axes to enhance gradients and patterns of relationships. For the classification of stands Hill's (1979) TWINSpan program was used. It classifies the stands in an ordered two-way table from a stands-by-species matrix. For the ordination of stands the program CANOCO (ter Braak 1988) was used to perform detrended correspondence analysis (DCA) with the data. The data used in both programmes were importance values per species per stand.

5) Edaphic and other environmental factors

Soil samples were taken in each stand from the upper part of the soil profile (0-20 cm) and examined for pH, conductivity and organic matter. To determine pH and conductivity, 20 g of the soil were placed in a flask with 100 ml distilled water and shaken well, then allowed to settle and shaken a second time. After the solution had settled again, pH and conductivity (μScm^{-1}) were measured. To determine the organic matter content of the soil (loss of ignition), a 10 g sample was placed in an oven and dried at 100°C for 24 hours. It was weighed (oven-dry weight), placed in a muffle furnace, burnt at 400°C for another 24 hours and then weighed again (ash-free dry weight). The percentage of organic matter (% dry weight) is the difference between the oven-dry weight and the ash-free dry weight, divided by the oven-dry weight.

The influence of the three edaphic factors and of several environmental variables on the diversity indices in each *A. arenaria* and each indigenous stand, as well as on the importance value of the respective dominant species in the stands, were examined through regression analyses. The following four environmental variables were taken into account: orientation of the stand (aspect of the shore in front of the stand), its distance from the high water mark (m), the mean total annual precipitation (mm) and the mean annual temperature (° Celsius) of the respective area. Because of the number of separate analyses, no regression lines were plotted, but r^2 -values, values of b (slope of the regression line) and the significance P are reflected for each analysis.

To interpret the composition of stands and species in the ordination results with the above edaphic and environmental variables (plus the amount of ground-litter of each stand: ordinal data ranked from 1 = bare ground to 3 = ground covered with litter), both indirect (DCA) and direct gradient analysis techniques (detrended canonical correspondence analysis: DCCA) were conducted with the vegetation and environmental data (ter Braak 1988).

6) Dune profiles

Dune profiles were measured across 38 of the above mentioned *A. arenaria* and 36 of the indigenous dune stands, all of them foredune stands. A 30 m transect was laid from the beach

perpendicular through the 10x10 m stand, starting 10 m before the stand and extending 10 m behind the stand. The elevation of every hummock along this transect was calculated through Abney level measurements. The dune profiles were examined independently of both from sea or height above high water mark: a comparison of slope and shape of each dune independent of its surroundings was sufficient to detect differences between *A. arenaria* and indigenous dunes. For such a comparison, mean dune profiles were calculated for *A. arenaria* dunes and dunes formed by common indigenous plants, namely *Thinopyrum distichum*, *Tetragonia decumbens* and *Scaevola plumieri*.

4.2.4 Results

Appendices 4.1 and 4.2 display the major floristic and edaphic properties of all 82 *A. arenaria* stands and all 64 indigenous stands sampled along the Cape coast. In each group, 60 stands were adjacent to a stand in the other group and are marked with an asterisk (*). In the following text, it is mentioned whether the analyses take all stands into account or only the 60 adjacent ones. A complete list of all species recorded in all stands is shown in Appendix 4.3.

1) Species richness and species diversity

Results of a statistical comparison of the species richness and species diversity of the 60 adjacent stands of coastal dune vegetation dominated by *A. arenaria* and indigenous plant species respectively are presented in Table 4.1. Both communities host on average between 5 to 6 different species per stand. The mean value for species richness in *A. arenaria* stands of 5.30 per stand is only marginally lower than that of 5.71 in the adjacent indigenous stands. This difference is insignificant ($P > 0.05$). The means for Simpson's diversity (d_s) appear to be slightly more distinct with 1.55 in *A. arenaria* stands and 2.39 in indigenous plant stands. Standard error of the mean and standard deviation are higher for indigenous stands, which reduces the comparability of d_s . Nevertheless, a *t*-test of the difference of the two means reveals that they are significantly different ($P < 0.05$).

In Figure 4.1 A species richness values of *A. arenaria* stands show as much of an irregular pattern along the coast as those of indigenous plant stands. The few high values in *A. arenaria* stands reflect high numbers of different species in stabilisation areas. This is obvious at Bloubergstrand and Stilbaai, where artificial watering of the vegetation encourages the vigorous growth of a great number of species, even of species that do not usually occur in dune environments (see Plate 3.2). In the *A. arenaria* stabilisation site of Bloubergstrand, where 18 different species are recorded, the introduced pasture and lawn grass *Pennisetum clandestinum* (Kikuyu) is the third most important species (not shown). The highest species richness score for indigenous plant stands is only 11 in the case of a *Myrica cordifolia* community at Hersham. Lowest score is 1 for both communities, occurring only once in each case; at Kleinemonde in a monospecific *A. arenaria* stand and at De Mond in a monospecific *Thinopyrum distichum* stand.

Values of Simpson's diversity (d_s) are generally lower in *A. arenaria* communities than in indigenous plant communities (Fig. 4.1 B). The highest d_s score for *A. arenaria* stands is 4.71 at Stilbaai, typically another well-watered stabilisation site. The three highest diversity indices are found in indigenous stands, at De Mond (5.21), at Oysterbay (5.77), and at Outeniqua Strand (5.89). The figure emphasises the overall lower diversity of *A. arenaria* stands compared to indigenous stands, and therefore confirms the result of the *t*-test of Table 4.1. Furthermore, d_s values for *A. arenaria* stands are fairly even while those of indigenous stands show a greater irregularity (Fig. 4.1 B). Consequently, standard error and standard deviation values are higher in indigenous stands (Table 4.1).

Table 4.1: Comparison of species richness and d_s values for 60 adjacent stands of coastal dune vegetation dominated by *A. arenaria* and indigenous species respectively. *P* is calculated through a *t*-test of means of two paired samples for the significance level $\alpha = 0.05$; s = significant, ns = not significant.

	species richness		Simpson's diversity (d_s)	
	<i>A. arenaria</i> stands	indigenous stands	<i>A. arenaria</i> stands	indigenous stands
mean	5.30	5.71	1.55	2.39
standard error	0.37	0.30	0.08	0.14
standard deviation	2.88	2.35	0.66	1.08
$P(t_{cal} > t_{crit})$	0.362 (ns)		9.734×10^{-7} (s)	

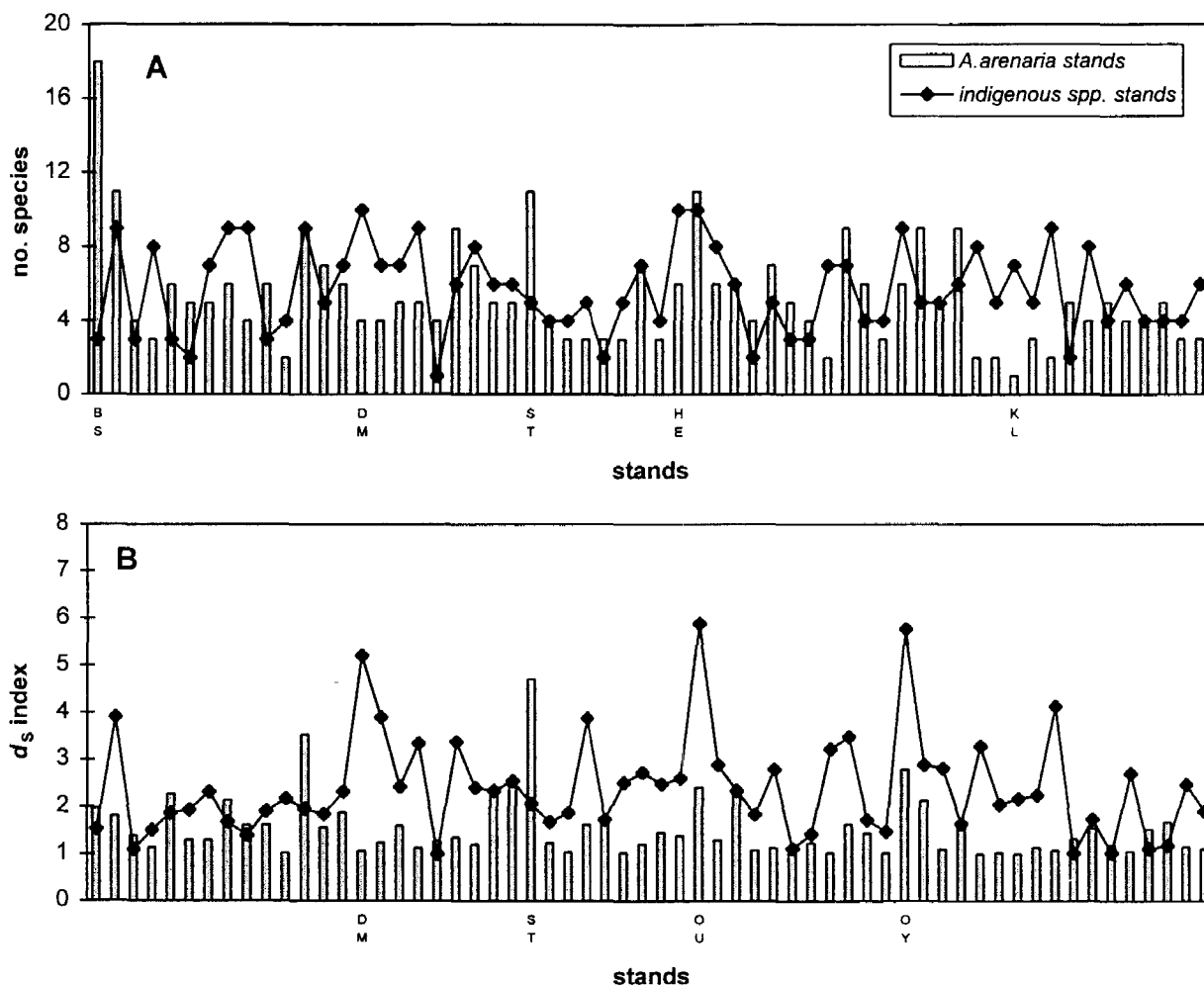


Fig. 4.1: Species richness (A) and Simpson's diversity index d_s (B) of 60 adjacent stands of coastal dune vegetation dominated by *A. arenaria* (bars) and indigenous species (line). Respective values are plotted along an axis representing the Cape coastline from west (left) to east (right). Sites mentioned in text are Bloubergstrand (BS), De Mond (DM), Stilbaai (ST), Hersham (HE), Outeniqua Strand (OU), Oysterbay (OY) and Kleinemonde (KL). Refer to Figure 3.1 for the position of these sites.

2) Importance values and life-forms

For a comparison of species' importance values (IV) in the two communities, the values of their first three most important species were summarised, averaged and then displayed, together with their Raunkiaer life-forms, in rank order in Tables 4.2 and 4.3. *Tetragonia decumbens* appears to grow most vigorously in *A. arenaria* communities, ranking highest in a list of second most important species in 60 *A. arenaria* stands with a score of 540 (Table 4.2). Next in line is *Myrica cordifolia* with a score of 266, surprisingly a phanerophyte that one

might expect to need more space than is available among the dense *A. arenaria* tufts. Less surprising is the prominence of common foredune species like *Arctotheca populifolia* and *Ipomoea pes-caprae* among *A. arenaria*. Interestingly, the above-mentioned species are also well represented among the third most important species, with the exception of *Myrica cordifolia*. It appears to be either very prominent in *A. arenaria* stands or not evident at all. The top-ranking third most important species, *Senecio elegans*, is as frequently found in *A. arenaria* stands as *Tetragonia decumbens* (each species is either second or third most important species in 13 out of 60 stands). However, its IV and therefore its overall score are much lower than those of *Tetragonia decumbens* because of its smaller and finer growth form and consequently reduced values for both density and cover.

While the most important species in *A. arenaria* stands is obviously *A. arenaria* itself (Table 4.2), a total of 18 different species were found to constitute dominant species in the 60 indigenous dune stands that were adjacent to *A. arenaria* stands (Table 4.3). Most commonly, the indigenous stands were dominated by *Thinopyrum distichum* (score of 2745), the major indigenous dune binding grass species in South Africa. *Tetragonia decumbens* follows closely (1764), and third in line is the “backdune species” *Ehrharta villosa* (1080). The fact that *Ehrharta villosa* is so frequently the dominant species in these indigenous stands of the foredune and intermediate dune zone indicates that *Ehrharta villosa* grows more commonly in proximity to the high water mark than is assumed. As with the *A. arenaria* stands (Table 4.2), *Tetragonia decumbens* is the top-ranking second most important species, and *Senecio elegans* the top-ranking third most important species (Table 4.3). *A. arenaria* itself is well represented amongst both the second and third most important species in indigenous stands. In both cases it takes fifth rank, thereby proving to be a prominent species in South African dune plant communities dominated by plants other than itself. Chapter 6 will examine whether and how easily *A. arenaria* can assume dominance in indigenous stands.

Table 4.2: Mean importance values (IV) for the three most important species and their Raunkiaer life-forms in 60 *A. arenaria* stands. The mean IV per species is calculated from the IV's of all stands (no. of stands) in which the species was first, second or third most important species. The species are ranked according to a score value by multiplying the number of stands with the mean IV. For explanations of Raunkiaer life-forms see Fig. 4.2.

most important species	life-form	no. of stands	mean IV	score (no. of stands x mean IV)
<i>Ammophila arenaria</i>	G/H	60	212	12720
2nd most important species	life-form	no. of stands	mean IV	score (no. of stands x mean IV)
<i>Tetragonia decumbens</i>	Ch	9	60	540
<i>Myrica cordifolia</i>	P	4	65	266
<i>Arctotheca populifolia</i>	Ch	3	83	249
<i>Ipomoea pes-caprae</i>	Ch	4	61	244
<i>Ehrharta villosa</i>	G/H	4	53	212
<i>Senecio elegans</i>	Ch	4	44	176
<i>Thinopyrum distichum</i>	G/H	5	33	165
<i>Dasispermum suffruticosum</i>	H	5	30	150
<i>Chrysanthemoides monilifera</i>	P	2	60	120
<i>Helichrysum asperum</i>	Ch	2	53	106
<i>Chironia baccifera</i>	Ch	2	43	86
<i>Sporobolus virginicus</i>	H	2	40	80
<i>Cynanchum natalitium</i>	Ch	2	30	60
<i>Gazania rigens</i>	Ch	2	30	60
<i>Helichrysum crispum</i>	Ch	1	49	49
<i>Psoralea repens</i>	Ch	2	22	44
<i>Silene primuliflora</i>	Ch	1	30	30
<i>Didelta carnosa</i>	T/H	1	27	27
<i>Silene crassifolia</i>	Ch	1	25	25
<i>Felicia amelloides</i>	Ch	1	10	10
<i>Passerina rigida</i>	P	1	9	9
<i>Anthospermum littoreum</i>	Ch	1	5	5
3rd most important species	life-form	no. of stands	mean IV	score (no. of stands x mean IV)
<i>Senecio elegans</i>	Ch	9	24	216
<i>Ehrharta villosa</i>	G/H	3	52	156
<i>Tetragonia decumbens</i>	Ch	4	35	140
<i>Thinopyrum distichum</i>	G/H	5	23	115
<i>Ipomoea pes-caprae</i>	Ch	3	29	87
<i>Dasispermum suffruticosum</i>	H	7	11	77
<i>Arctotheca populifolia</i>	Ch	3	25	75
<i>Cynanchum natalitium</i>	Ch	1	52	52
<i>Passerina rigida</i>	P	2	17	34
<i>Silene crassifolia</i>	Ch	1	26	26
<i>Ficinia lateralis</i>	H	1	22	22
<i>Pennisetum clandestinum</i>	H	1	20	20
<i>Didelta carnosa</i>	T/H	1	14	14
<i>Scaevola plumieri</i>	Ch	1	12	12
<i>Sutherlandia frutescens</i>	Ch	1	6	6
<i>Carpobrotus deliciosus</i>	Ch	1	5	5
<i>Chrysanthemoides monilifera</i>	P	1	5	5
<i>Silene primuliflora</i>	Ch	1	5	5

Table 4.3: Mean importance values (IV) for the three most important species and their Raunkiaer life-forms in 60 indigenous stands (for explanations see Table 4.2).

most important species	life-form	no. of stands	mean IV	score (no. of stands x mean IV)
<i>Thinopyrum distichum</i>	G/H	15	183	2745
<i>Tetragonia decumbens</i>	Ch	12	147	1764
<i>Ehrharta villosa</i>	G/H	6	180	1080
<i>Chrysanthemoides monilifera</i>	P	5	163	815
<i>Sporobolus virginicus</i>	G/H	4	184	736
<i>Scaevola plumieri</i>	Ch	3	236	708
<i>Myrica cordifolia</i>	P	3	140	420
<i>Gazania rigens</i>	Ch	2	174	348
<i>Metalasia muricata</i>	P	2	163	332
<i>Passerina rigida</i>	P	2	143	286
<i>Arctotheca populifolia</i>	Ch	1	267	267
<i>Ipomoea pes-caprae</i>	Ch	1	185	185
<i>Cynanchum natalitium</i>	Ch	1	185	184
<i>Didelta carnosia</i>	T/H	1	160	160
<i>Senecio elegans</i>	Ch	1	153	153
<i>Dasispermum suffruticosum</i>	H	1	107	107
<i>Ficinia lateralis</i>	H	1	89	89
<i>Psoralea repens</i>	Ch	1	81	81
2nd most important species	life-form	no. of stands	mean IV	score (no. of stands x mean IV)
<i>Tetragonia decumbens</i>	Ch	8	77	616
<i>Arctotheca populifolia</i>	Ch	6	91	546
<i>Thinopyrum distichum</i>	G/H	6	64	384
<i>Myrica cordifolia</i>	P	4	75	300
<i>Ammophila arenaria</i>	G/H	4	64	256
<i>Sporobolus virginicus</i>	G/H	3	84	252
<i>Passerina rigida</i>	P	4	61	244
<i>Gazania rigens</i>	Ch	3	77	231
<i>Ipomoea pes-caprae</i>	Ch	3	36	108
<i>Scaevola plumieri</i>	Ch	3	67	201
<i>Acacia cyclops</i>	P	2	47	94
<i>Cynanchum natalitium</i>	Ch	1	86	86
<i>Didelta carnosia</i>	T/H	1	81	81
<i>Metalasia muricata</i>	P	1	71	71
<i>Dasispermum suffruticosum</i>	H	1	64	64
<i>Helichrysum patulum</i>	Ch	1	54	54
<i>Chrysanthemoides monilifera</i>	P	1	45	45
<i>Mariscus congestus</i>	H	1	45	45
<i>Rhus crenata</i>	P	1	43	43
<i>Chironia baccifera</i>	Ch	1	36	36
<i>Senecio elegans</i>	Ch	1	23	23
<i>Ehrharta villosa</i>	G/H	1	12	12
<i>Gladiolus gueinzii</i>	G	1	7	7
3rd most important species	life-form	no. of stands	mean IV	score (no. of stands x mean IV)
<i>Senecio elegans</i>	Ch	12	30	360
<i>Tetragonia decumbens</i>	Ch	5	39	195
<i>Dasispermum suffruticosum</i>	H	6	30	180
<i>Myrica cordifolia</i>	P	5	35	175
<i>Ammophila arenaria</i>	G/H	3	38	114
<i>Ficinia lateralis</i>	H	2	51	102
<i>Arctotheca populifolia</i>	Ch	2	45	90
<i>Anthospermum littoreum</i>	Ch	2	45	90
<i>Chrysanthemoides monilifera</i>	P	3	30	90
<i>Gazania rigens</i>	Ch	2	39	78
<i>Ehrharta villosa</i>	G/H	2	38	76
<i>Helichrysum praecinctum</i>	H	1	52	52
<i>Thinopyrum distichum</i>	G/H	1	42	42
<i>Sporobolus virginicus</i>	G/H	2	19	38
<i>Acacia cyclops</i>	P	2	18	36
<i>Scaevola plumieri</i>	Ch	1	31	31
<i>Metalasia muricata</i>	P	1	26	26
<i>Vellereophyton vellereum</i>	H	1	29	29

In comparison, the mean importance values of the two top-ranking dominant species in *A. arenaria* and indigenous communities, *A. arenaria* and *Thinopyrum distichum* respectively (Tables 4.2 and 4.3), are surprisingly similar with 212 and 183. A *t*-test of the difference of these means (unequal variances) shows that they are only insignificantly different ($P = 0.116 > 0.05$). However, the indigenous species *Scaevola plumieri* (236) and *Arctotheca populifolia* (267) have even higher importance values than *A. arenaria*'s value of 212, when they are dominant (Table 4.3). *A. arenaria* therefore does not appear to be unusually abundant, when it is dominant. On a larger scale, it can be noted from Tables 4.2 and 4.3 that mean importance values of species in *A. arenaria* compared to indigenous dune stands are similar: mean IV's of second most important species range from 83 to 5 in *A. arenaria* stands, and from 91 to 7 in indigenous stands. Mean IV's of third most important species range from 52 to 5 in *A. arenaria* stands, and from 52 to 18 in indigenous stands.

The life-forms in the two types of stands (Tables 4.2 and 4.3) appear fairly similar, but differences are apparent in pie-charts (Fig. 4.2): not only do indigenous stands host a slightly higher variety of life-forms, but there are more phanerophytes among the second and third most important species in indigenous stands. *A. arenaria* stands, on the other hand, support more chamaephytes and slightly more therophytes/hemicryptophytes. Small, soft-leaved chamaephytes like *Senecio elegans*, *Silene primuliflora* and *Psoralea repens* are of greater importance in *A. arenaria* stands than in indigenous stands.

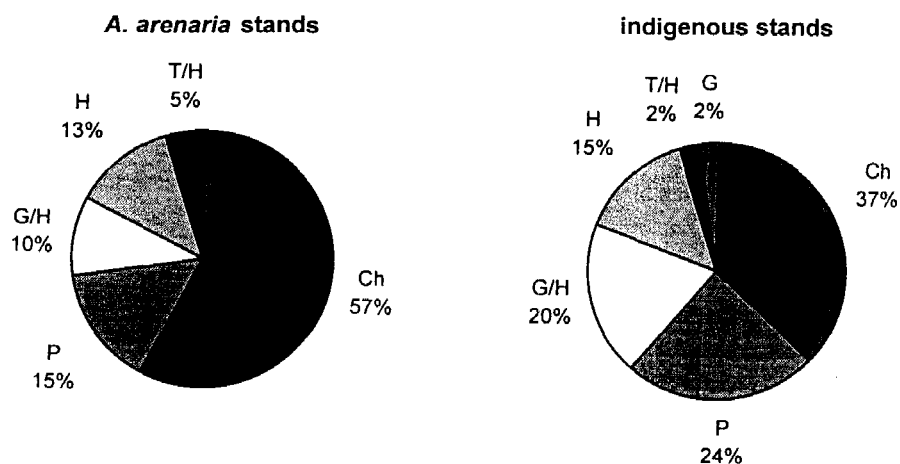


Fig. 4.2: Raunkiaer life-forms and their relative frequencies among the second and third most important species in 60 *A. arenaria* and 60 adjacent indigenous dune stands. Ch = chamaephytes, P = phanerophytes, G/H = geophytes/hemicryptophytes, H = hemicryptophytes, T/H = therophytes/hemicryptophytes, G = geophytes (Mueller-Dombois & Ellenberg 1974).

3) Species associations

While the importance value (IV) of a species in *A. arenaria* stands takes into account its density, cover and frequency, species association indices like Jaccard's index (IA_j) are based on the frequency of the species alone. Some species might not be very conspicuous in *A. arenaria* stands in terms of their density and cover, but are in fact closely associated with *A. arenaria*. This is true for *Senecio elegans*, a small and low-cover chamaephyte which ranks only sixth among the second most important species in *A. arenaria* stands (Table 4.2.), but achieves the highest index of association with *A. arenaria* of all indigenous species ($IA_j = 13.7$, Table 4.4). *Tetragonia decumbens* ranks second with a slightly lower IA_j of 13.5. Similarly to *Senecio elegans*, other low-cover species like *Ehrharta villosa*, *Dasispermum suffruticosum*, *Gazania rigens*, *Psoralea repens* and *Felicia amelloides* show increased score ranks in Table 4.4 compared to Table 4.2 because of their relatively high occurrence with *A. arenaria*.

Table 4.4: Jaccard's index of species association (IA_j) of all second most important species in *A. arenaria* stands (see Table 4.2) with *A. arenaria*. All 82 *A. arenaria* stands (1640 quadrats) are taken into account. Species are ranked according to their IA_j score.

species	no. of quadrats in which both species are present (%)	IA_j (%)
<i>Senecio elegans</i>	12.19	13.652
<i>Tetragonia decumbens</i>	12.01	13.493
<i>Ehrharta villosa</i>	6.77	7.500
<i>Arctotheca populifolia</i>	6.04	6.818
<i>Myrica cordifolia</i>	5.30	5.992
<i>Dasispermum suffruticosum</i>	5.24	5.907
<i>Thinopyrum distichum</i>	4.88	5.449
<i>Ipomoea pes-caprae</i>	3.54	3.964
<i>Cynanchum natalitium</i>	2.44	2.751
<i>Gazania rigens</i>	2.26	2.549
<i>Chrysanthemoides monilifera</i>	2.01	2.256
<i>Psoralea repens</i>	1.95	2.205
<i>Sporobolus virginicus</i>	1.95	2.202
<i>Helichrysum asperum</i>	1.52	1.718
<i>Chironia baccifera</i>	1.34	1.517
<i>Felicia amelloides</i>	1.22	1.379
<i>Silene primuliflora</i>	0.91	1.034
<i>Didelta carnosa</i>	0.79	0.897
<i>Helichrysum crispum</i>	0.73	0.828
<i>Silene crassifolia</i>	0.73	0.828
<i>Passerina rigida</i>	0.67	0.759
<i>Anthospermum littoreum</i>	0.06	0.069

In Table 4.5 the same species as in Table 4.4 were examined with regard to their association with dominant indigenous species, namely *Thinopyrum distichum*, *Tetragonia decumbens* and *Ehrharta villosa*. The smaller number of species present in these stands is due to the much lower number of quadrats taken into account than with *A. arenaria* stands. However, it is conspicuous that the highest IA_j values in Table 4.5 are much higher than those in Table 4.4. In fact, IA_j values of many species are higher in these stands than in *A. arenaria* stands (marked $\surd$), implying that they reach higher levels of association with dominant indigenous species than with *A. arenaria*. This is most clearly the case with *Thinopyrum distichum* which has an IA_j value of 27.4 in *Tetragonia decumbens* stands, compared to only 5.4 in *A. arenaria* stands. Even *Senecio elegans*, which appears well associated with *A. arenaria* according to Table 4.4 ($IA_j = 13.7$), achieves a far higher IA_j value in *Tetragonia decumbens* stands (27.7). *Tetragonia decumbens* itself is better associated with *Thinopyrum distichum* (18.5) and *Ehrharta villosa* (21.7) than with *A. arenaria* (13.5). However, *Ehrharta villosa* has lower IA_j values both in *Thinopyrum distichum* as well as *Tetragonia decumbens* stands than in *A. arenaria* stands.

A more detailed analysis of species association than Jaccard's index is achieved through a χ^2 -test which compares observed values of occurrence with expected (or hypothetical) values calculated from the observed values (Table 4.6). In many cases one or more expected values of the 2x2 contingency table were below 4, and the respective species therefore left out due to insufficient reliability of the test (Mueller-Dombois & Ellenberg (1974) suggest the limit 5). Nevertheless, the table yields some interesting results: *Senecio elegans* and *Tetragonia decumbens* are again the best associated species with *A. arenaria*, both with significantly high χ^2 values (3.2 and 2.8) to confirm positive association. However, *Senecio elegans* is highly significantly associated with *Tetragonia decumbens* ($\chi^2 = 12.3$), while *Tetragonia decumbens* itself achieves a higher χ^2 value with *Thinopyrum distichum* (4.1). Both results confirm what was shown in Table 4.5, i.e. the species that grow most readily with *A. arenaria* grow still better with dominant indigenous dune plants.

Table 4.5: Jaccard's index of species association (IA_j) of all second most important species in *A. arenaria* stands (see Table 4.4) with *Thinopyrum distichum*, *Tetragonia decumbens* and *Ehrharta villosa* respectively. These three indigenous species are dominant in 15, 12 and 6 of all 64 indigenous stands. Species of Table 4.4 that do not occur in the respective indigenous stands are not shown. The other species are ranked according to their IA_j score. Values of IA_j that are higher than the IA_j values of the same species in *A. arenaria* stands (Table 4.4) are marked (✓).

association with <i>Thinopyrum distichum</i> in 15 stands (300 quadrats) dominated by <i>Thinopyrum distichum</i>		
species	no. of quadrats in which both species are present (%)	IA_j (%)
<i>Arctotheca populifolia</i>	19.67	21.071 ✓
<i>Tetragonia decumbens</i>	17.00	18.478 ✓
<i>Myrica cordifolia</i>	7.33	7.942 ✓
<i>Dasispermum suffruticosum</i>	6.00	6.522 ✓
<i>Senecio elegans</i>	5.00	5.435
<i>Silene crassifolia</i>	2.33	2.536 ✓
<i>Didelta carnosia</i>	2.33	2.527 ✓
<i>Ehrharta villosa</i>	1.00	1.079
<i>Sporobolus virginicus</i>	1.00	1.079
<i>Felicia amelloides</i>	1.00	0.362
<i>Cynanchum natalitium</i>	1.00	0.361
association with <i>Tetragonia decumbens</i> in 12 stands (240 quadrats) dominated by <i>Tetragonia decumbens</i>		
species	no. of quadrats in which both species are present (%)	IA_j (%)
<i>Senecio elegans</i>	21.25	27.717 ✓
<i>Thinopyrum distichum</i>	21.25	27.419 ✓
<i>Gazania rigens</i>	14.17	18.085 ✓
<i>Dasispermum suffruticosum</i>	10.42	13.441 ✓
<i>Arctotheca populifolia</i>	8.75	10.714 ✓
<i>Sporobolus virginicus</i>	7.92	10.215 ✓
<i>Silene primuliflora</i>	4.17	5.495
<i>Passerina rigida</i>	2.08	2.747
<i>Ehrharta villosa</i>	0.83	1.099
<i>Myrica cordifolia</i>	0.42	0.552
association with <i>Ehrharta villosa</i> in 6 stands (120 quadrats) dominated by <i>Ehrharta villosa</i>		
species	no. of quadrats in which both species are present (%)	IA_j (%)
<i>Tetragonia decumbens</i>	20.83	21.739 ✓
<i>Myrica cordifolia</i>	12.50	13.158 ✓
<i>Senecio elegans</i>	11.67	12.069
<i>Chrysanthemoides monilifera</i>	7.50	7.895 ✓
<i>Helichrysum asperum</i>	5.00	5.263 ✓
<i>Passerina rigida</i>	3.33	3.478 ✓
<i>Chironia baccifera</i>	2.50	2.632 ✓
<i>Arctotheca populifolia</i>	1.67	1.754
<i>Cynanchum natalitium</i>	0.83	0.877
<i>Silene crassifolia</i>	0.83	0.877

Table 4.6: Results of a χ^2 -test of the association of all second most important species in *A. arenaria* stands (see Table 4.4) with *A. arenaria*, *Thinopyrum distichum*, *Tetragonia decumbens* and *Ehrharta villosa* respectively. The test is based on frequencies per species in all quadrats of all stands dominated by the respective species (presence/absence in 2x2 contingency tables, $df = 1$). Cases in which at least one expected value of the contingency table was below 4 were considered insufficiently reliable and are left out (Mueller-Dombois & Ellenberg 1974). The species are ranked according to their significance of association with the respective dominant species from very positive to very negative. Significance at $\alpha = 0.1$ (*), $\alpha = 0.01$ (**) and $\alpha = 0.001$ (***).

association with <i>A. arenaria</i> in 82 stands (1640 quadrats) dominated by <i>A. arenaria</i>			
species	trend of association	χ^2	$P(\chi^2_{cal} > \chi^2_{crit})$
<i>Senecio elegans</i>	+	3.211	0.057 *
<i>Tetragonia decumbens</i>	+	2.804	0.074 *
<i>Gazania rigens</i>	+	2.216	0.081 *
<i>Dasispermum suffruticosum</i>	+	1.944	0.118
<i>Arctotheca populifolia</i>	+	1.131	0.224
<i>Cynanchum natalitium</i>	+	0.081	0.600
<i>Myrica cordifolia</i>	+	0.016	0.776
<i>Helichrysum asperum</i>	-	0.348	0.380
<i>Ipomoea pes-caprae</i>	-	2.626	0.070 *
<i>Thinopyrum distichum</i>	-	6.256	0.008 **
<i>Chrysanthemoides monilifera</i>	-	11.228	0.0003 ***
<i>Ehrharta villosa</i>	-	13.128	0.0002 ***
association with <i>Thinopyrum distichum</i> in 15 stands (300 quadrats) dominated by <i>Thinopyrum distichum</i>			
species	trend of association	χ^2	$P(\chi^2_{cal} > \chi^2_{crit})$
<i>Tetragonia decumbens</i>	+	4.114	0.021 *
<i>Arctotheca populifolia</i>	+	0.079	0.587
association with <i>Tetragonia decumbens</i> in 12 stands (240 quadrats) dominated by <i>Tetragonia decumbens</i>			
species	trend of association	χ^2	$P(\chi^2_{cal} > \chi^2_{crit})$
<i>Senecio elegans</i>	+	12.315	0.0002 ***
<i>Thinopyrum distichum</i>	+	8.585	0.002 **
<i>Gazania rigens</i>	+	1.055	0.220
<i>Dasispermum suffruticosum</i>	+	0.722	0.282
<i>Sporobolus virginicus</i>	+	0.039	0.653
<i>Arctotheca populifolia</i>	-	5.627	0.009 **
association with <i>Ehrharta villosa</i> in 6 stands (120 quadrats) dominated by <i>Ehrharta villosa</i>			
in each case at least one expected value of the contingency tables was below 4			

A surprising result is the negative trend of association of *Ehrharta villosa* with *A. arenaria* (Table 4.6). The high χ^2 value (13.1) indicates a highly significantly negative association,

which is unexpected considering *Ehrharta villosa*'s high IA_J value in Table 4.4. This can be explained with the high number of quadrats in which *Ehrharta villosa* occurs on its own (independently of *A. arenaria*). While values of IA_J emphasise the number of joint occurrences of two species, the number of quadrats in which either of the two species occurs on its own is weighted more in a χ^2 -test. Thus the χ^2 method is considered more reliable regarding the degree of association of the two species. It reveals that the association of *Ehrharta villosa* with *A. arenaria* is weaker than was to be assumed from both IV and IA_J scores. Other species whose associations with *A. arenaria* are significantly negative according to the χ^2 -test are *Chrysanthemoides monilifera* and *Thinopyrum distichum*. Conversely, species that have higher χ^2 values in *A. arenaria* stands than in indigenous stands are *Gazania rigens* (significantly positive association), *Dasispermum suffruticosum* and *Arctotheca populifolia*, all hemicryptophytes or chamaephytes, the first two with particularly low and small growth-forms.

4) Classification and ordination of stands

Figure 4.3 displays the results of an indirect gradient analysis, CANOCO's detrended correspondence analysis (DCA), with most of the 82 *A. arenaria* (A) or 64 indigenous dune plant communities (B) respectively. In both analyses outsider-stands and species have been left out after a series of trials. However, *A. arenaria* stands are still lumped together closely and do not show any clear pattern of clustering. This was confirmed in a TWINSpan-classification of the same stands (Fig. 4.4 A), where the first division is based on stands with the primary indicator species *Ipomoea pes-caprae* and *Cynanchum natalitium* (Eastern Cape*) as opposed to stands that contain most other species (Western and Southern Cape*). Stands with the indicator species *Thinopyrum distichum* or *Ehrharta villosa* were mostly Western Cape stands, while stands containing *Tetragonia decumbens*, *Senecio elegans* or *Dasispermum suffruticosum* were mostly from the Southern Cape. However, no distinct grouping could be achieved, and since the TWINSpan clusters are indistinct, they are not clearly reflected in the correlating DCA charts. (* See Chapter 3, Section 3.3 for a definition of these areas.)

In contrast, the DCA of stands dominated by indigenous dune plants (Fig 4.3 B) clearly displays geographical clustering of the stands into those of a more Western Cape, Southern

Cape or Eastern Cape situation. A fourth cluster contains stands of both the Southern and the Western Cape. It appears as though axis 1 of the ordination corresponds well to the position of stands along the coast. The plot shows that Eastern Cape stands are more scattered than those of the Western or Southern Cape groups, which can indicate a greater variability between the stands which range from dune thicket to early pioneer communities. Similarly, the fourth cluster with stands of both Southern and Western Cape origin is scattered because of a high variability between stands ranging from low dune scrub to dune fynbos. In contrast, stands in the Southern Cape group and Western Cape group are mostly pioneer communities.

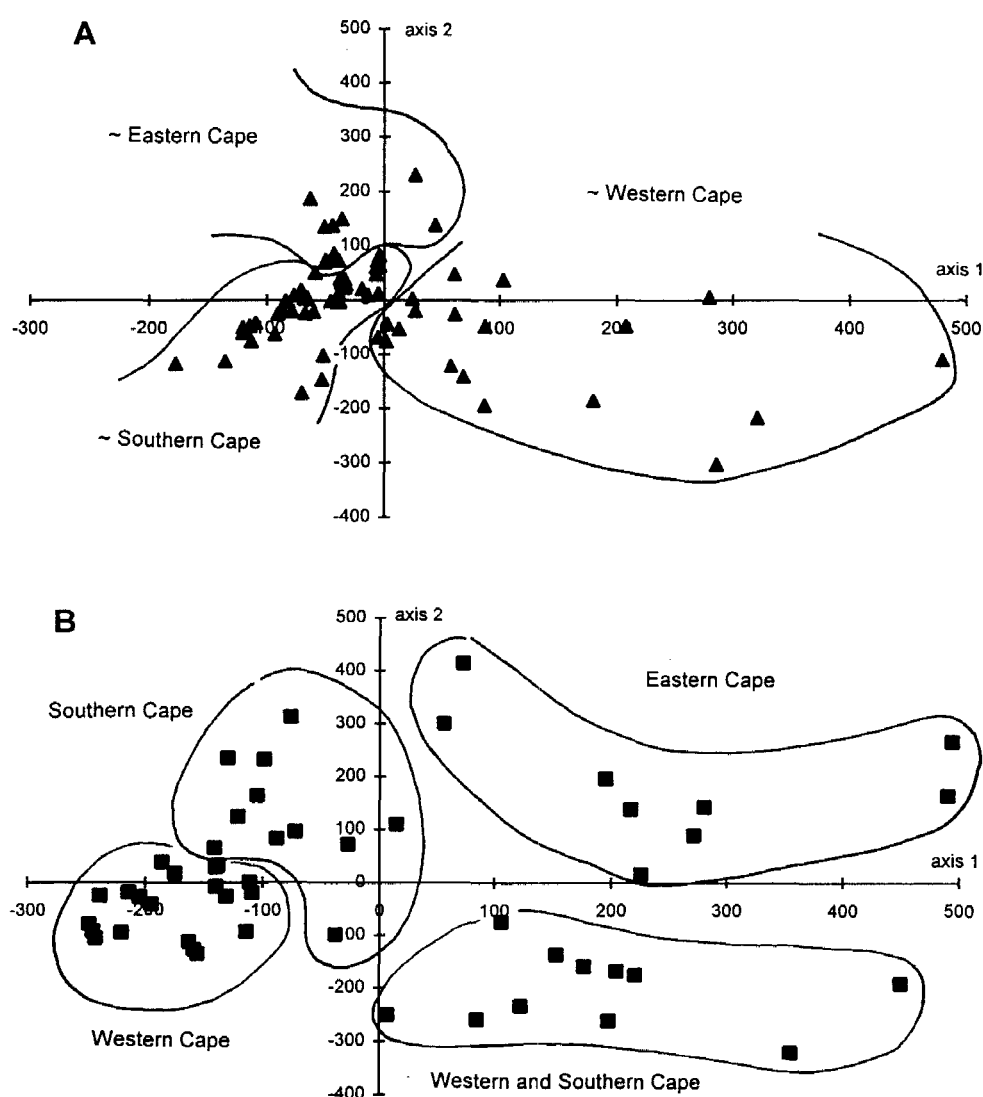


Fig. 4.3: Detrended correspondence analysis (DCA) of 82 stands dominated by *A. arenaria* (A) and 64 stands dominated by various indigenous dune plant species (B). See Fig. 4.4 A and B.

The differentiation into four groups is reflected in the TWINSpan-classification of the same stands (Fig. 4.4 B). Indicator species for the Western Cape group are *Thinopyrum distichum*, *Arctotheca populifolia* and *Didelta carnosa*. Although *Thinopyrum distichum* occurs along the entire Cape coast, it is particularly common and often the dominant species in Western Cape stands, e.g. in most stands of the Cape Peninsula. The main indicator species for the Southern Cape group is *Tetragonia decumbens*, again common throughout the coast but particularly widespread and vigorous in stands from the Mossel Bay and George areas. Other species common in Southern Cape stands are *Dasispermum suffruticosum*, *Senecio elegans* and *Gazania rigens*. The Eastern Cape group is characterised by a great number of species, most importantly *Ipomoea pes-caprae* and *Cynanchum natalitium*, which both occur only in Eastern Cape stands. Other prominent species in this group are *Chrysanthemoides monilifera*, *Gladiolus gueinzii* and *Scaevola plumieri*. This group contains most stands between Sardinia Bay and Gulu Mouth. The fourth group appears less distinct as it is characterised primarily by the widespread dune scrub species *Myrica cordifolia* and *Metalasia muricata*, both common throughout most of the Cape coast. However, this group is distinguished by several dune fynbos species that do not occur in any of the other groups. Species like *Pentaschistis eriostoma* or *Helichrysum patulum* are both common in the dune fynbos stands that were sampled in the Agulhas area and fall into this category. Other species in this group are small and inconspicuous but locally prominent species like *Ficinia lateralis*, *Psoralea repens* and *Chironia baccifera*.

A DCA of the species in all stands, both the *A. arenaria* and indigenous stands, is shown in Figure 4.5. While the indigenous species form clusters in accordance to the results of Figures 4.3 B and 4.4 B, *A. arenaria* is situated right in the centre of the plot (●) showing no particular affinity towards any of these groups. It is interesting to note that the species closest to *A. arenaria* are small, soft-leaved plants such as *Pteronia camphorata*, *Gladiolus gueinzii* or *Pelargonium capitatum*. They either occur only in *A. arenaria* stands or are more common in these than in indigenous stands, possibly profiting from their small size which allows them to grow amongst the dense *A. arenaria* tufts. This confirms the observation that small chamaephytes, therophytes or hemicryptophytes are more important in *A. arenaria* stands than in indigenous stands (Tables 4.4 and 4.5). Species such as *Ipomoea pes-caprae*, *Scaevola*

plumieri or *Passerina rigida* have greater spatial demands and are found at higher frequencies and greater vigour in indigenous stands than in *A. arenaria* stands.

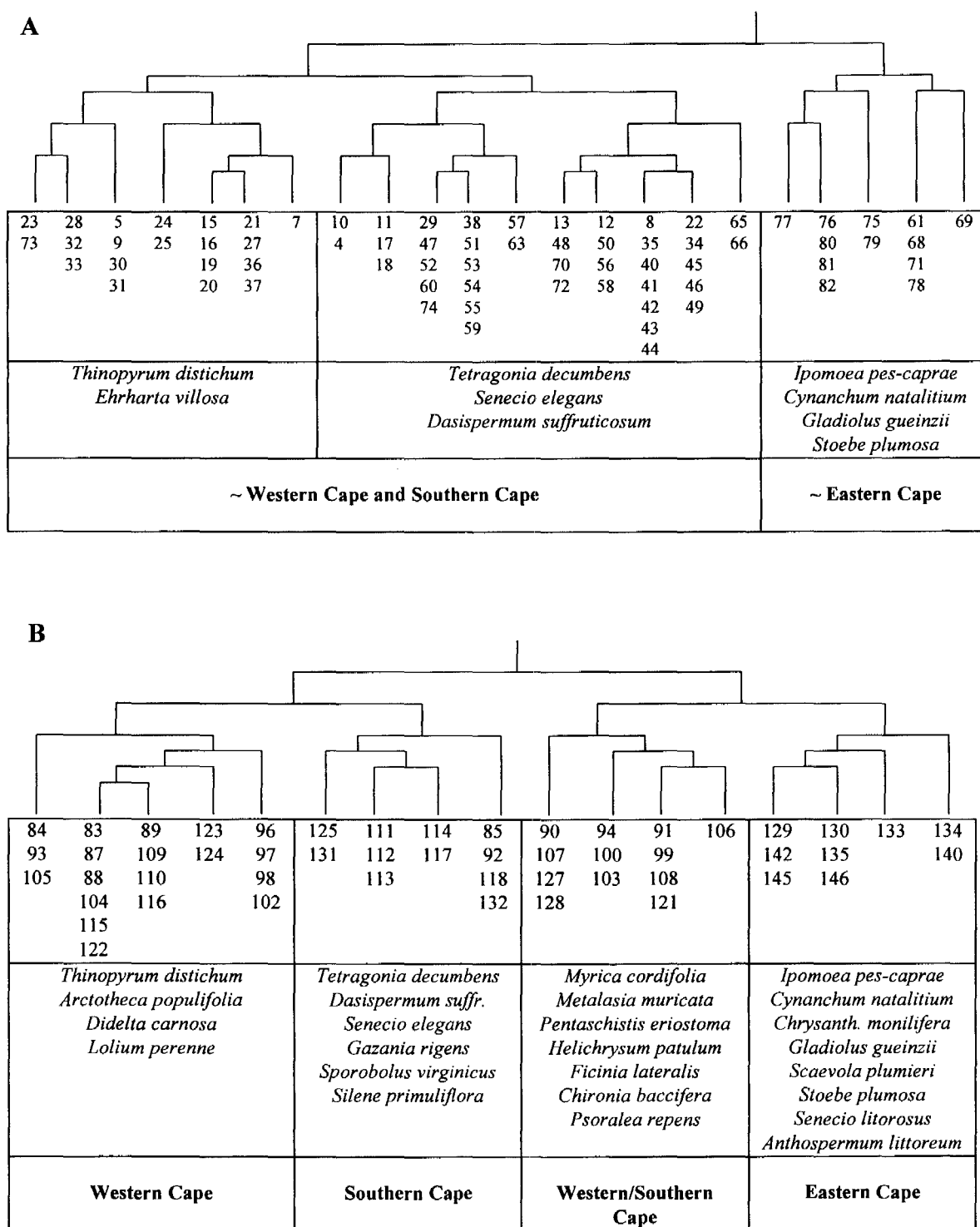


Fig. 4.4: Classification of 82 stands dominated by *A. arenaria* (A) and of 64 stands dominated by indigenous plant species (B) according to TWINSpan (related to Figure 4.3 A and B respectively).

Other species that do not associate well with *A. arenaria* (Figure 4.5) are indigenous species that have strong tendencies towards dominance themselves. Good examples are *Arctotheca populifolia*, *Thinopyrum distichum* or *Sporobolus virginicus*, all of which tend to form monospecific stands. Finally, species that are well presented in both *A. arenaria* and indigenous dune communities are *Senecio elegans*, *Dasispermum suffruticosum*, *Myrica cordifolia*, *Tetragonia decumbens* and *Ehrharta villosa*, all common species and sometimes dominant themselves but still compatible with *A. arenaria*. Although *Senecio elegans* and *Tetragonia decumbens* are extremely well associated with *A. arenaria* according to the previous studies, they also occur commonly in indigenous stands independently of *A. arenaria* and are therefore further removed from *A. arenaria* in Figure 4.5 than the uncommon *Pteronia camphorata* or *Pelargonium capitatum*.

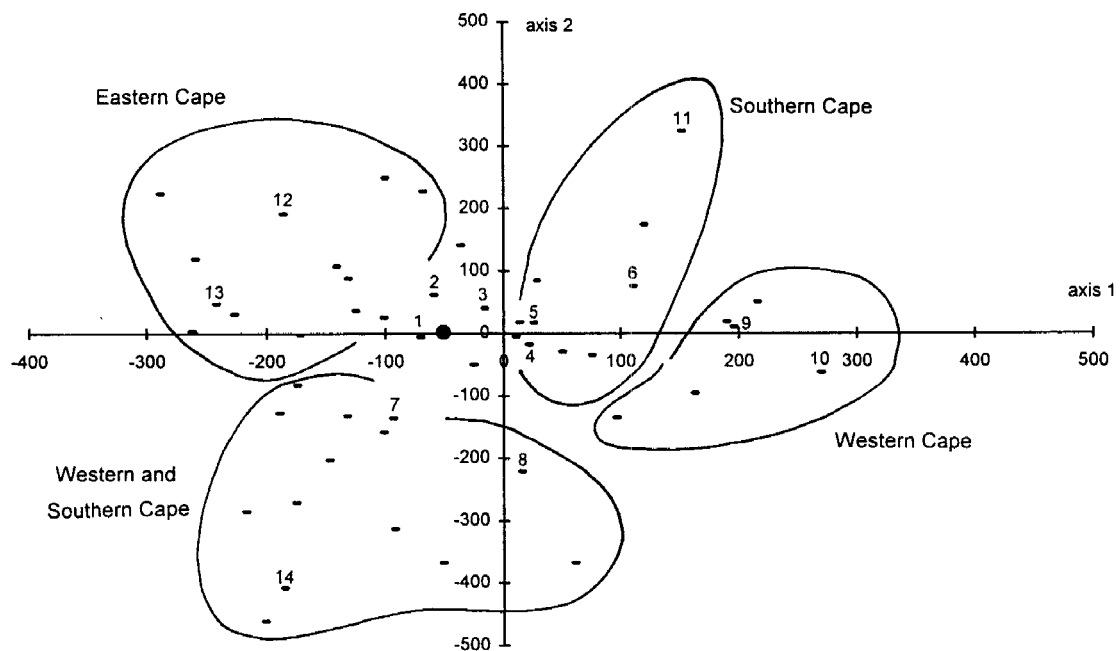


Fig. 4.5: Detrended correspondence analysis (DCA) of the species in all *A. arenaria* stands and all indigenous stands. *A. arenaria* is marked (•). Other species mentioned in the text are numbered as follows: 1 *Pteronia camphorata*, 2 *Gladiolus gueinzii*, 3 *Pelargonium capitatum*, 4 *Senecio elegans*, 5 *Dasispermum suffruticosum*, 6 *Tetragonia decumbens*, 7 *Ehrharta villosa*, 8 *Myrica cordifolia*, 9 *Arctotheca populifolia*, 10 *Thinopyrum distichum*, 11 *Sporobolus virginicus*, 12 *Ipomoea pes-caprae*, 13 *Scaevola plumieri*, 14 *Passerina rigida*.

5) Edaphic and other environmental factors

The results for pH, conductivity and organic matter of the soil samples taken in *A. arenaria* and indigenous plant communities provide evidence of a great similarity of both communities in respect of their edaphic factors (Table 4.7). A *t*-test shows no significant differences at the confidence level $\alpha = 0.05$. At $\alpha = 0.1$ only the organic matter content would be significantly different with 0.44% (of dry weight) for *A. arenaria* compared to 0.48% for indigenous dune stands ($P = 0.085$).

Table 4.7: Comparison of pH, conductivity and organic matter content of the soil in 60 adjacent stands of coastal dune vegetation dominated by *A. arenaria* and indigenous species respectively. *P* is calculated through a *t*-test of means of two paired samples for the significance level $\alpha = 0.05$; s = significant, ns = not significant.

	pH		conductivity (μScm^{-1})		organic matter (% dry weight)	
	<i>A. arenaria</i> stands	indigenous stands	<i>A. arenaria</i> stands	indigenous stands	<i>A. arenaria</i> stands	indigenous stands
mean	8.23	8.19	146.23	158.53	0.44	0.48
standard error	0.05	0.05	21.55	20.15	0.04	0.04
standard deviation	0.39	0.38	166.89	158.53	0.27	0.33
$P (t_{\text{cal}} > t_{\text{crit}})$	0.132 (ns)		0.635 (ns)		0.085 (ns)	

There is little variability among the pH values in the soils from both *A. arenaria* and indigenous communities, their means being high in either case, with low standard errors and deviations (Table 4.7). This is not surprising as the Cape coast is rich in carbonates throughout and high pH values are to be expected along the entire coastline (Tinley 1985). Nevertheless, the stability of pH values along the coast is noteworthy in view of the high variability of conductivity values for the same stands, bearing in mind that a high pH is usually associated with a high content of free ions present in saline soils. The standard deviation of the mean conductivity is very high in both communities, in *A. arenaria* communities even higher than the calculated mean, which reduces its significance substantially. The plotting of all values along an axis representing the South African coastline from west to east was therefore

necessary (Fig. 4.6 A). This confirms the strong fluctuation of soil conductivity values, indicating highly variable salinity levels in both communities. With a few exceptions at Witsand/Cape Peninsula, De Mond, Groot Brakrivier and Kleinemonde these fluctuations are fairly similar in the *A. arenaria* and indigenous dune plant stands.

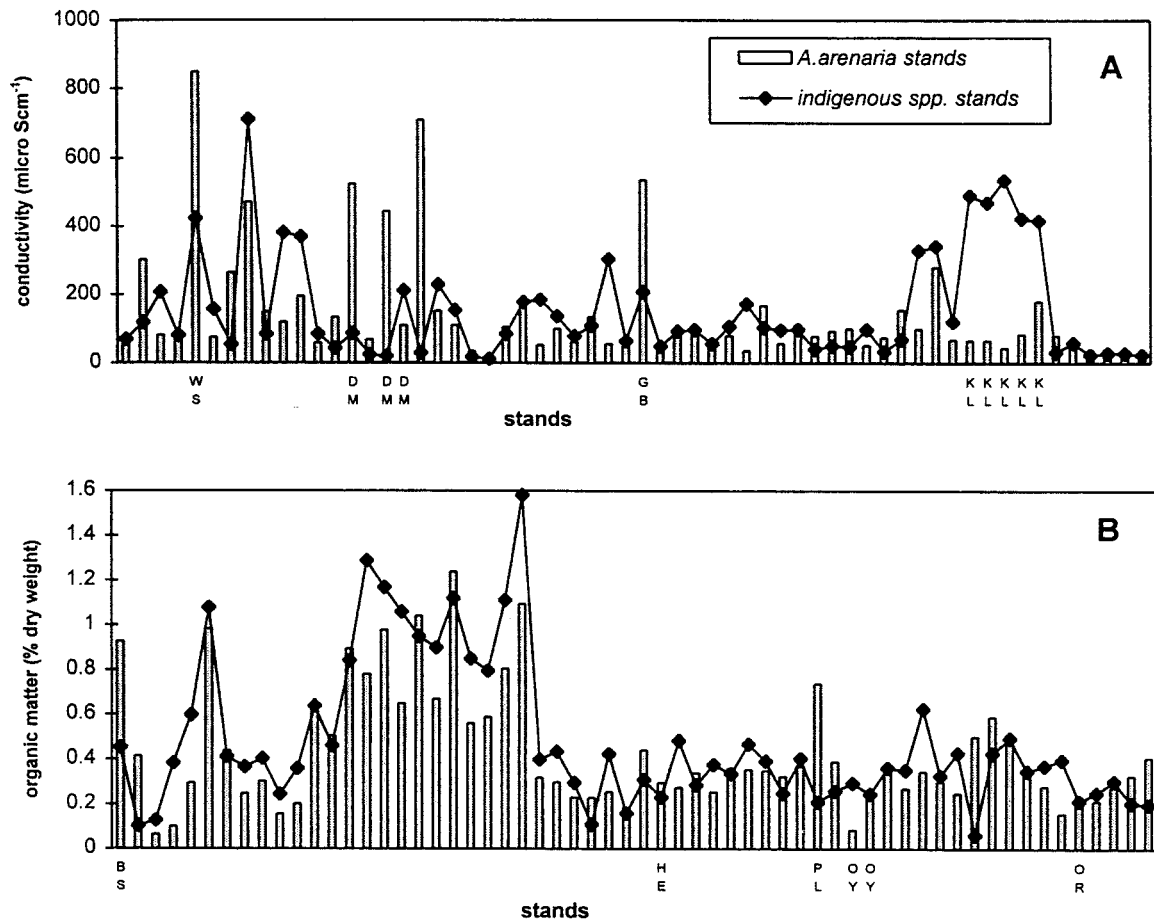


Fig. 4.6: Soil conductivity (A) and organic matter content (B) of 60 adjacent stands of coastal dune vegetation dominated by *A. arenaria* (bars) and indigenous species (line). Respective values are plotted along an axis representing the Cape coastline from west (left) to east (right). Sites mentioned in text are Bloubergstrand (BS), Witsand/Cape Peninsula (WS), De Mond (DM), Groot Brakrivier (GB), Hersham (HE), Plettenberg Bay (PL), Oysterbay (OY), Kleinemonde (KL) and Old Woman's River Mouth (OR). Refer to Figure 3.1 for the position of these sites.

The means of organic matter content also show fairly high standard deviations (Table 4.7) in both communities. However, their plotting along an axis shows that the organic matter content of soil in indigenous stands is usually greater than that of *A. arenaria* stands (Fig. 4.6 B). The two most obvious exceptions are the *A. arenaria* stands at Bloubergstrand, a stabilisation site,

and at Plettenberg Bay, hosting an old *A. arenaria* community on the lagoon site of the Keurboomsrivier mouth. Apart from these exceptions the content of organic matter is slightly higher in indigenous stands throughout the coast. However, several indigenous stands bear surprisingly low values of organic matter content. For example the two Oyster Bay stands (Fig. 4.6 B), sampled in *Chrysanthemoides monilifera* communities, have organic matter contents that are, with 0.29% and 0.25%, among the lower values sampled. Low amounts of organic matter content are also found in dune scrub communities at Hersham near Groot Brakrivier (dominated by *Myrica cordifolia*), Old Woman's River mouth (*Passerina rigida*) and at Plettenberg Bay (*Metasia muricata*).

In a regression analysis of the dependence of Simpson's diversity (d_s) and importance values (IV of the respective dominant species) in all sampled stands on various environmental variables (Table 4.8), it becomes obvious that environmental factors have little influence on these measures either in *A. arenaria* stands or in indigenous stands. All r^2 -values are low, and the significance of some is mainly due to the high number of samples. No significant dependence of d_s and IV was detected for pH and conductivity of the soil, orientation of the stands and their distance from the high water mark, as well as the air temperature of the sites in either of two types of stands. In *A. arenaria* stands, both d_s and IV are significantly dependent on the organic matter content of the soil; the higher the organic matter content, the greater is d_s in *A. arenaria* stands ($P = 0.003$) and the lower the IV of *A. arenaria* as dominant species ($P = 0.018$). In comparison, the IV of dominant indigenous species is not affected to the same extent by an increased organic matter content. However, dominant indigenous species appear to be more affected by rainfall: the higher the rainfall (mean total annual precipitation) of a site, the higher the IV of the dominant species in indigenous stands ($P = 0.007$). In contrast, the IV of *A. arenaria* does not depend significantly on rainfall.

Table 4.8: Regression analysis of the dependence of Simpson's diversity (d_s) and the importance value (IV) of the respective dominant species in all *A. arenaria* and indigenous stands on various environmental factors. A positive regression coefficient b (slope of the regression line) indicates positive association, a negative b negative association. The higher r^2 , the higher the dependence. Significance (**bold**) at $\alpha = 0.05$ (*) and $\alpha = 0.005$ (**).

		stands dominated by <i>A. arenaria</i> (n = 82)		stands dominated by indigenous dune plants (n = 64)	
		d_s	IV	d_s	IV
soil pH	r^2	0.006	0.002	0.004	0.001
	b	+ 0.006	- 0.254	- 0.185	+ 4.308
	P	0.506	0.687	0.602	0.802
soil conductivity	r^2	0.001	4.5×10^{-5}	0.015	0.015
	b	+ 1.3×10^{-4}	- 0.002	- 8.4×10^{-4}	+ 0.040
	P	0.757	0.952	0.332	0.338
organic matter content of soil	r^2	0.105	0.067	0.020	0.052
	b	+ 0.799	- 47.260	+ 0.414	- 31.964
	P	0.003 **	0.018 *	0.260	0.071
orientation	r^2	0.021	0.024	0.003	0.029
	b	+ 0.002	- 0.167	- 0.001	+ 0.183
	P	0.192	0.168	0.672	0.182
distance from high water mark	r^2	0.009	0.029	0.001	0.081
	b	+ 2.3×10^{-4}	- 0.029	+ 1.0×10^{-4}	- 0.020
	P	0.382	0.126	0.808	0.329
rainfall	r^2	0.001	1.5×10^{-7}	0.052	0.113
	b	- 1.6×10^{-4}	+ 1.8×10^{-4}	- 0.002	+ 0.149
	P	0.814	0.997	0.069	0.007 *
temperature	r^2	0.035	0.012	0.032	0.036
	b	- 0.268	+ 11.552	- 0.350	+ 17.879
	P	0.093	0.327	0.156	0.136

To examine the influence of environmental variables on the differentiation of stands in CANOCO, the ordination axes of Figures 4.3 A and B were subsequently related to the variables. The result of this detrended correspondence analysis (DCA) with unconstrained ordination axes (related only indirectly to environmental variables) is shown in Figure 4.7 for *A. arenaria* (A) and indigenous stands (B). Very similar results (not shown) were achieved by a detrended canonical correspondence analysis (DCCA), in which case the ordination axes are constrained to be linear combinations of the environmental variables and therefore directly related to the latter. In any case, it can be observed that indigenous stands correspond more closely to environmental factors than do *A. arenaria* stands. Table 4.9 shows that the ordination

of *A. arenaria* stands can be related significantly to several environmental variables, particularly to temperature, distance from high water mark and orientation. However, the regression coefficients show overall higher values for the indigenous stands. Interestingly, both climatic variables, temperature and rainfall (mean annual values), appear to be more important for the ordination of indigenous stands than for *A. arenaria* stands.

The clustering of indigenous stands (Figures 4.3 B and 4.4 B) can therefore be explained to a certain extent by climatic constraints (Fig. 4.7 B): Eastern Cape stands are different from the other stands due to distinct temperature and rainfall patterns. Indeed, the area is characterised by high temperatures coupled with high rainfall (see Fig. 3.2). Southern Cape stands are characterised by similarly high temperatures but less rainfall. Western Cape stands are distinguished from the other stands mostly by their bare, unlittered ground. Finally, the fourth cluster of both Western and Southern Cape stands, distinguished floristically by the presence of some dune fynbos species (see above), appears to be influenced by the distance of the stands from the high water mark. In fact, several of the stands in this group are from the De Mond site and situated at a great distance from the sea. The latter variable, the distance from the high water mark, is the only environmental variable that appears to have some influence on the ordination of *A. arenaria* stands (Fig. 4.7 B).

Table 4.9: Regression coefficients (multiplied by 100) of various environmental variables with the first two axes resulting from indirect gradient analyses (DCA) with *A. arenaria* and indigenous stands respectively (see Fig. 4.7). Significance at $\alpha = 0.05$ (*) as indicated through *t*-values supplied by the same analyses.

	<i>A. arenaria</i> stands (df = 62)		indigenous stands (df = 41)	
	axis 1	axis 2	axis 1	axis 2
soil pH	- 2	- 15	+ 60 *	- 8
soil conductivity	- 33 *	- 35 *	- 20	- 16
organic matter content of soil	+ 9	- 26	- 61	- 23
orientation	+ 11	- 46 *	- 57 *	- 43
distance from high water mark	+ 33 *	- 33 *	+ 4	- 26
litter on ground (leaves etc.)	- 13	+ 15	- 110 *	- 5
rainfall	+ 31 *	+ 36 *	+ 85 *	+ 22
temperature	- 50 *	- 6	- 4	+ 64 *

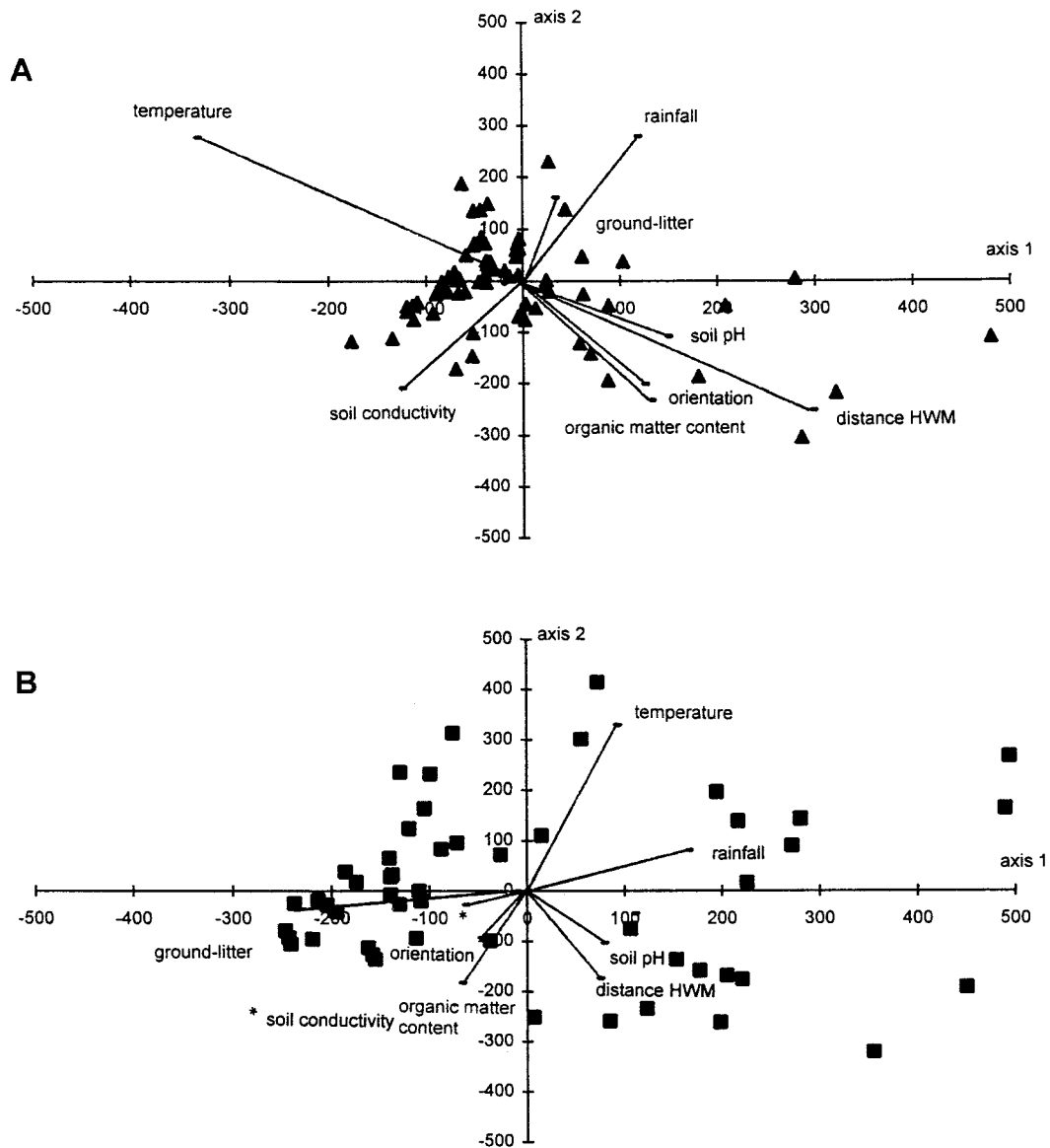


Fig. 4.7: DCA of all *A. arenaria* stands (A) and all indigenous stands (B) with ordination axes related indirectly to environmental variables (HWM = high water mark). The plots are the same as in Figure 4.3 A and B. See Table 4.9 for corresponding regression coefficients.

6) Dune profiles

Mean dune profiles of *A. arenaria* communities and communities formed by various indigenous foredune plants are shown in Figure 4.8. *A. arenaria* dunes do not appear distinctly higher or steeper than dunes formed by indigenous plants. Dunes formed by *Thinopyrum distichum* and even more so by *Tetragonia decumbens* show a more irregular profile with a

higher number of small hummocks within the dune. In contrast, *A. arenaria* dunes seem to be more evenly shaped, quite similar to dunes formed by the indigenous *Scaevola plumieri*, although the latter often have a steeper leeward side. A continuous foredune ridge of *A. arenaria* was found only in stabilisation areas (Plate 3.6). Naturalised *A. arenaria* communities in South Africa tend to reflect the rounded hummock pattern of indigenous dune communities.

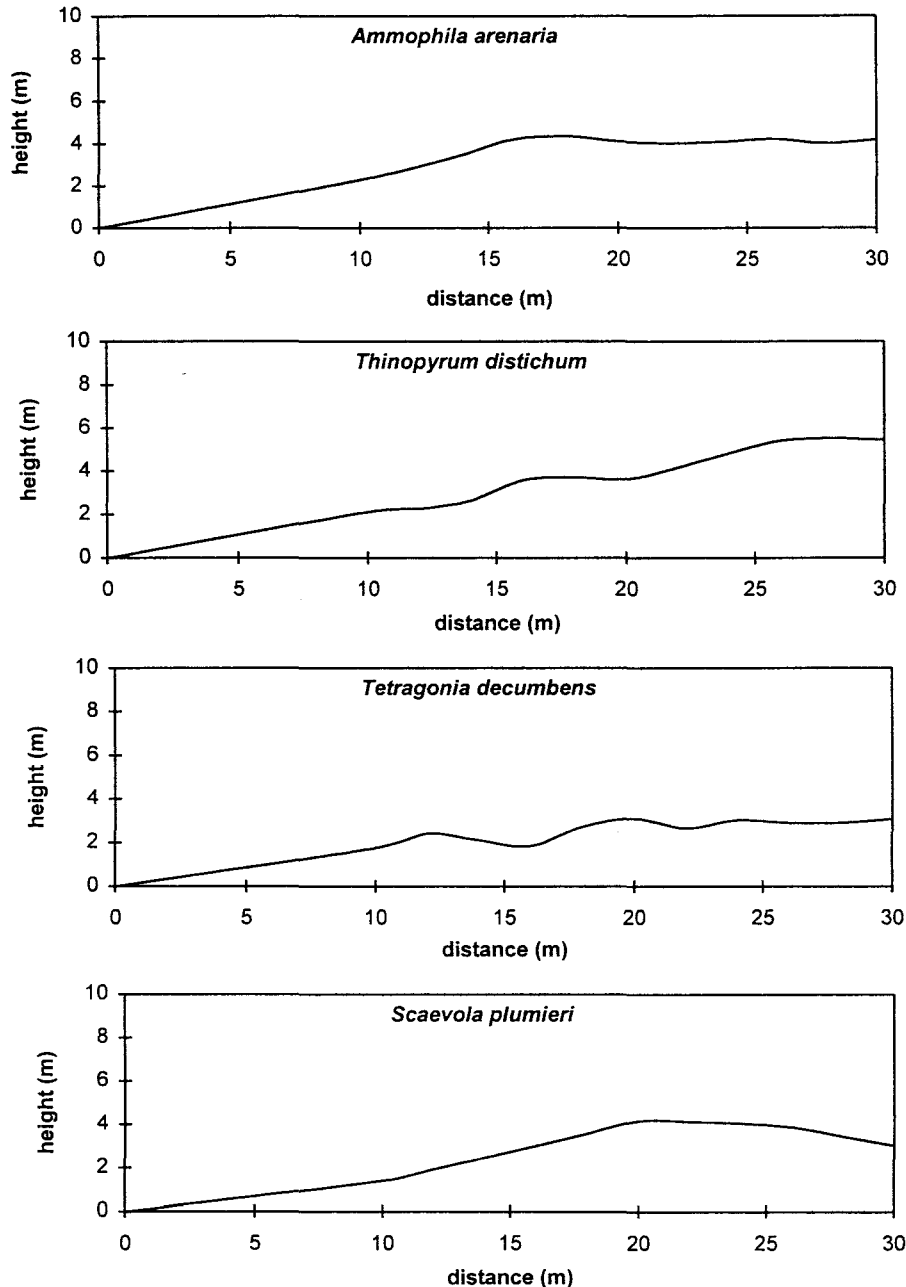


Fig. 4.8: Mean dune profiles of dunes formed by *A. arenaria* ($n = 38$), *Thinopyrum distichum* ($n = 10$), *Tetragonia decumbens* ($n = 9$) and *Scaevola plumieri* ($n = 6$). The axes represent distance (m) and height (m) from the beginning of the transect, which was laid out perpendicular through a 10x10 m stand from the shore (left), starting 10 m before the stand and extending 10 m behind the stand.

4.2.5 Discussion

Unlike invader plants such as *Acacia* spp., *Hakea* spp. or *Pinus* spp., which have been shown to suppress indigenous species and to cause the replacement of diverse systems with single- (or mixed) species stands of aliens (Macdonald & Richardson 1986; Richardson *et al* 1992, 1997), *A. arenaria* does not show traits of any outwardly aggressive behaviour in South African ecosystems. It forms plant communities with similar species richness values and only slightly lower diversity indices than communities dominated by indigenous dune plant species. Data in the literature show that indigenous dune pioneer communities can have lower diversity indices than the index of 2.39 found in this survey (Table 4.1). Avis & Lubke (1996) sampled indigenous communities at Kleinemonde, Eastern Cape, with diversity indices as low as 1.59. Avis (1992) found pioneer communities in Natal with diversity indices of not more than 1.41. These values are similar to the one found for South African *A. arenaria* communities (1.55, Table 4.1).

A comparison of importance values proves that, in regard to species composition as well as the weighting of species, *A. arenaria* communities are very similar to communities formed by indigenous dune plant species. Although *A. arenaria* bears high importance values throughout the stands in which it is dominant (mean IV: 212, Table 4.2), some indigenous species like *Scaevola plumieri* and *Arctotheca populifolia* have even higher importance values when they are dominant (e.g. *Scaevola plumieri* with a mean IV of 236, Table 4.3). High importance values for dominant indigenous species are also found by Avis & Lubke (1996), e.g. a mean IV of 255 for *Scaevola plumieri* in a study at Kleinemonde, Eastern Cape. Since the importance values of *A. arenaria* as dominant species are well within the range of those of dominant indigenous species, and since its accompanying species grow at much the same vigour as they do in indigenous stands, it can be concluded that *A. arenaria* does not display any unusual tendency to dominance and to developing monospecific stands in South Africa.

These results are in contrast to findings from California and Oregon where *A. arenaria* has a proven record of exerting great floristic control over other species in that it is overly dominant and thus depresses or even eliminates indigenous species (see Chapter 2). Barbour *et al* (1976) found that both species richness and species diversity of *A. arenaria* communities along the

North American west coast were significantly lower than in indigenous dune plant communities; indigenous communities at Point Reyes (California), dominated by *Elymus mollis*, contained twice as many different species as *A. arenaria* communities. The mean Shannon-Weaver diversity index of *A. arenaria* communities along the whole west coast was 0.26, while it was on average twice as much or more in indigenous communities. Wiedemann (1984) and Pickart *et al* (1990) observe that *A. arenaria* depresses valuable indigenous plant communities to such an extent that these are not found commonly anymore in the vicinity of *A. arenaria* communities. In contrast, no data on South African *A. arenaria* communities so far imply the depression of indigenous communities by *A. arenaria*. Unless the examined *A. arenaria* stands were part of large stabilisation areas, species-rich and diverse indigenous dune stands were always found in their vicinity.

However, a conspicuous difference between the two communities is found with the life-forms of their accompanying species (Fig. 4.2). *A. arenaria* communities appear to encourage the growth of small, soft-leaved plant species, mostly chamaephytes, but also therophytes and hemicryptophytes. They seem to be well equipped to grow amongst the dense grass tufts that are typically formed by a healthy stand of *A. arenaria* (Plate 4.1). A maximum of 338 shoots per 1 m² was found in a stand of *A. arenaria* at Old Woman's River (Eastern Cape), while a vigorous stand of the indigenous dune grass *Thinopyrum distichum* would not consist of more than 70 shoots per 1 m². Phanerophytes with greater spatial demands are therefore found more frequently in indigenous communities. The only phanerophyte that can obviously grow well amongst *A. arenaria* tufts is *Myrica cordifolia*. It can be an erect shrub of up to 2 m in height (Lubke & van Wijk 1988), but in *A. arenaria* communities usually displays a smaller, scrambling growth-form. Comparative studies on life-forms have not yet been undertaken in North American *A. arenaria* and indigenous stands, but a similar difference in growth forms was observed between *A. arenaria* and the indigenous *Elymus mollis* in California (Barbour & Johnson 1977).

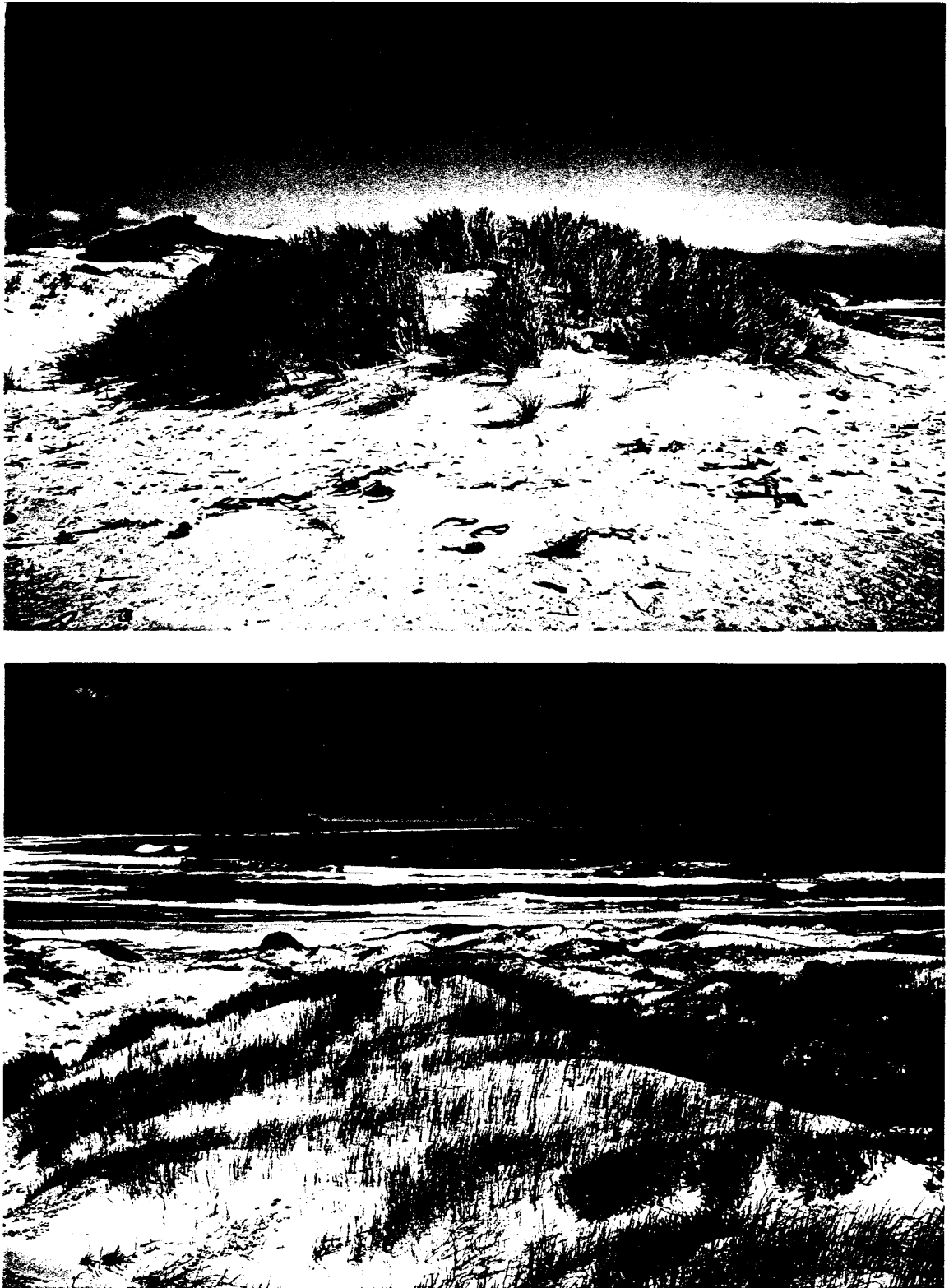


Plate 4.1: Stands of *A. arenaria* (top, at Noordhoek/Cape Peninsula) show much denser growth than those of the indigenous dune grass *Thinopyrum distichum* (bottom, at Witsand/Cape Peninsula). Both photographs taken in January 1996.

The most prolific species in *A. arenaria* communities with respect to importance values is *Tetragonia decumbens*. If analyses of species association are taken into account, *Senecio elegans* appears to be even more closely associated with *A. arenaria*. An analysis of Jaccard's index of species association (IA_J) as well as a χ^2 -test show that these two species form the strongest associations with *A. arenaria* (Tables 4.4 and 4.6). However, both species exhibit even higher values of IA_J and χ^2 with indigenous species (Tables 4.5 and 4.6): *Senecio elegans* is always more closely associated with *Tetragonia decumbens*, while the latter shows stronger associations with *Thinopyrum distichum*. In fact, the results show that the associations of the majority of species that are common in *A. arenaria* communities are weaker with *A. arenaria* than they are with dominant indigenous dune plants. At this point it cannot be denied that a certain "alienness" of *A. arenaria* in South Africa becomes obvious.

The association analyses also reveal different kinds of association of the indigenous species with *A. arenaria*. Plants like *Thinopyrum distichum* and *Ehrharta villosa* that grow well in *A. arenaria* communities, considering their high importance values in *A. arenaria* stands, are in fact fairly independent of *A. arenaria*. They are frequently found on their own and tend to become dominant themselves. A χ^2 -test proves that they are more negatively associated with *A. arenaria*, while several small hemicryptophytes and chamaephytes like *Gazania rigens* and *Dasispermum suffruticosum* are clearly positively associated with *A. arenaria* in spite of their comparatively low importance values (Table 4.6). In a species association analysis in Californian *A. arenaria* communities at Point Reyes (Boyd 1992), it was shown that out of five indigenous species, three species were negatively associated with *A. arenaria* while the other two were not affected by *A. arenaria* (see Chapter 2). In contrast, out of twelve South African indigenous species investigated in this study, seven species were positively associated with *A. arenaria*, and only five negatively. Although only three of the seven positive associations were significant, while four out of the five negative associations were significant, *A. arenaria* appears to form species associations with indigenous species more easily in South Africa than in California.

The above comparison of importance values points towards a considerable floristic similarity between South African *A. arenaria* communities and those formed by indigenous species. However, the same importance values yield different results if used for the computerised

classification and ordination of the stands. With programs like TWINSpan and CANOCO one can detect more hidden aspects of community structure (Jongman *et al* 1995), and in the present study these techniques point strongly towards the alienness of *A. arenaria* in South Africa. Neither technique is able to group the South African *A. arenaria* stands according to their floristic composition (Fig. 4.3 A and 4.4 A), while stands dominated by indigenous dune plants clearly form clusters of different floristic compositions corresponding to different geographical situations (Fig. 4.3 B and 4.4 B).

Similar to the present phytogeographical differentiation of indigenous stands, an ordination of Eastern Cape dune stands (Avis 1995) also results in a clustering of the stands in correspondence to their geographical position. On a larger scale, and in better comparison with the South African coastline under examination in this chapter (1300 km), Barbour *et al* (1987) detected three distinct phytogeographical areas in a study of the dune vegetation along the American Gulf coast (2500 km). Moreno-Casasola (1988) describes three phytogeographical areas along part (1500 km) of the Mexican Gulf coast. Both studies used detrended correspondence analyses (DCA) as was done in the present study. They confirm the grouping of indigenous stands in South Africa according to their geographical positions and make the “lumping” of *A. arenaria* stands appear highly conspicuous.

Certainly *A. arenaria* stands are all dominated by *A. arenaria*, while the indigenous stands are dominated by a variety of different species. However, since importance values of all species are taken into account, and since the dominant species’ value is not necessarily much higher than that of the accompanying species, it is not weighted more heavily in the ordination of stands. One would assume that the accompanying indigenous species in *A. arenaria* stands would vary according to the geographical situation of the respective stands as they do in indigenous stands, but it appears as though this effect is masked by the alien *A. arenaria*, resulting in a greater uniformity of *A. arenaria* communities.

As was mentioned before, plants with little spatial demands are having an advantage in *A. arenaria* communities. The variety of such species is small in South African dune ecosystems, hence the number of different species accompanying *A. arenaria* along the coast cannot be as high as in the case of indigenous dune stands. This could account for the fairly monotonous

floristic structure of *A. arenaria* communities in South Africa. Although mean species richness and diversity in South African *A. arenaria* communities are hardly lower than in indigenous communities, there is not as much variability along the coast with respect to the species that are found with *A. arenaria*. Mean species diversity values are similar in both types of communities, but the diversity index of indigenous communities fluctuates strongly along the coast whereas the index of *A. arenaria* stays much the same in the various stands (Fig. 4.1).

The ordination of species in all stands confirms that *A. arenaria* is not a natural component of South African dune plant communities. The indigenous species form clusters reflecting much the same pattern as formed by indigenous dune stands, while *A. arenaria* is found right in the middle of the ordination plot with no affinity to any of these clusters (Fig. 4.5). Although *A. arenaria* appears frequently and fairly vigorously as an accompanying species in indigenous dune stands, it is clearly lacking the evolutionary history to develop close affinities with any of the South African plants. It has already been shown that many common South African dune plants form weaker associations with *A. arenaria* than with their indigenous “fellow species”. This result is confirmed by the TWINSPLAN and CANOCO results, and a certain incompatibility of *A. arenaria* with South African dune plants must be acknowledged. The ordination of species also confirms that small soft-leaved plant species are at an advantage in *A. arenaria* stands.

Fluctuations of soil pH and soil conductivity appear to reflect the natural variation of soil pH and salinity along the South African coast (Tinley 1985), no matter in which community they were sampled (Fig. 4.6 A). There is a slight difference between *A. arenaria* and indigenous communities with regard to organic matter contents of the soil (Fig. 4.6 B). In a few cases *A. arenaria* stands have high organic matter values, most obviously in some of the stabilisation sites like Bloubergstrand or Stilbaai where artificial watering is also the cause of high species richness and diversity values (see Plate 3.2). At most sites, however, the organic matter content is higher in the indigenous stands. Nevertheless, one could have expected a stronger digression of the organic matter content, considering that *A. arenaria* prefers fresh sand with very low organic matter to avoid harmful microorganisms (van der Putten *et al* 1988; see Chapters 1, 2 and 5).

A reason for the high organic matter contents in all Western Cape stands, particularly in the De Mond area (Fig. 4.6 B) was proposed to be a higher carbonate content of the sand. However, soil samples were burned below 550°C (see Methods), which ensures that CaCO_3 is not converted to CaO and the ash-free dry weight not biased (Brower *et al* 1990). The amount of organic matter does not only appear to be fairly high in *A. arenaria* stands but also to be surprisingly low in some of the indigenous stands. A low organic matter content is particularly conspicuous in stands that are dominated by indigenous dune scrub species like *Chrysanthemoides monilifera* or *Metalsia muricata*, usually secondary plants on dunes (Lubke & van Wijk 1988) giving preference to soils that are less saline and richer in organic matter than those of the foredunes.

Although organic matter values appear so similar in the two communities, an examination of the dependence of species diversity and importance values of the dominant species on various environmental factors clearly reveals the higher sensitivity of *A. arenaria* to the level of organic matter in the soil (Table 4.8): the higher the organic matter content, the lower is *A. arenaria*'s importance value which in turn increases the diversity of the community. In contrast, dominant indigenous species are not affected by the organic matter content to the same effect, and the diversity in indigenous stands does not gain as much from an increased organic matter content. On the other hand, the vigour of *A. arenaria* along the South African coastline is apparently not influenced by climatic constraints such as rainfall and temperature, while indigenous species gain vigour with increasing rainfall. More detailed examinations on this are necessary though, since in the present study only annual means of eight greater climatic areas (Fig. 3.2) are taken into account.

Nevertheless, the relative independence of climatic constraints that *A. arenaria* appears to exhibit along the Cape coast is confirmed by both indirect and direct analyses of the influence that environmental variables have on the ordination of *A. arenaria* and indigenous stands respectively (Fig. 4.7): the regression coefficients that rainfall and temperature have with the ordination axes are higher for the ordination of indigenous stands. Since the regression coefficients of most environmental variables are higher for indigenous stands than for *A. arenaria* stands (Fig. 4.7), it becomes obvious that *A. arenaria* did not evolve in South African

coastal conditions, and that its communities do not respond to climatic and other environmental barriers to the same extent that indigenous dune plant communities do.

Lastly, an analysis of dune profiles (Fig. 4.8) cannot confirm the North American result that *A. arenaria* forms steeper, higher and more continuous foredunes, thereby affecting the dune geomorphology of Californian and Oregon shores (Barbour & Johnson 1977; Wiedemann 1984). Nor do South African *A. arenaria* dunes show a highly irregular pattern causing wind channelling or blow-outs as observed in New Zealand (Esler 1970, Johnson 1993). In a comparative study of the three-dimensional shape of Eastern Cape dunes, Blood (1995) found that *A. arenaria* dunes are steeper and more angularly shaped than indigenous dunes. However, only four *A. arenaria* dunes were taken into account. The present study indicates that dunes formed by *A. arenaria* repeat the pattern of rounded hummock formation that indigenous dune plants show. Although more detailed studies are required, it appears as though *A. arenaria* has little impact on the dune morphology in South Africa, both from a purely geomorphological as well as an aesthetic point of view.

4.3 *Ammophila arenaria* communities in South African and Europe

4.3.1 Introduction

In this chapter, South African *A. arenaria* communities are compared with *A. arenaria* communities in their native Europe. It is important to establish if South African communities are significantly different from European communities in vegetation structure and dynamics. As with the comparison of South African *A. arenaria* stands with indigenous dune stands (see Section 4.2.1), the following key questions are addressed for a comparison of South African and European *A. arenaria* stands:

- 1) How do species richness and species diversity differ in South African A. arenaria communities compared to European ones? Do South African A. arenaria communities contain fewer different species? Is their diversity lower than in European communities?*
- 2) How do importance values and life-forms of the various species in the two types of communities differ from each other? Is A. arenaria of greater importance in South African communities than in European communities? What life-forms are common in South African communities compared to European communities?*
- 3) How do species associations in South African A. arenaria communities differ from those in European communities? Does A. arenaria in South Africa associate less readily with other species than in Europe?*
- 4) What trends of differentiation of stands can be detected in European communities through the application of classification and ordination techniques? Are they different from results found for South African communities?*
- 5) Do edaphic values like pH, conductivity and organic matter differ in South African compared to European A. arenaria communities? What influence do other environmental factors have on the structure of European communities?*

6) Is there a difference between the profiles of dunes formed by *A. arenaria* in South Africa and in Europe?

4.3.2 Study area

Sampling of European *A. arenaria* communities was undertaken on the German barrier island of Sylt, situated in the North Sea offshore the province of Schleswig-Holstein (Fig. 4.9). The island is the northernmost of the North Frisian group of Wadden Sea islands and extends from 55°01'N; 08°25'E to 54°44'N; 08°18'E. Its total length from north to south is about 38 kilometres, but from west to east it rarely extends more than a few kilometres. The island is narrowest and in acute danger of being torn apart at its northern end, the "Ellenbogen", where at one place it is only a few hundred metres wide. Sylt has always been exposed to strong westerly currents of the North Sea and has suffered from severe erosion for many centuries. The main impact of wind and sea currents confronts the island perpendicularly from the west, and sediment is carried away alongshore both north- and southward elongating the spits at its northern and southern ends. Since 1950 the shore has withdrawn about 1.5 m per year, involving an annual sediment loss of 1.4 million m³ (Pott 1995). In an ongoing attempt to protect the island, large stabilisation efforts are undertaken with *A. arenaria*, and beaches are being replenished artificially by pumping sand from the sea floor ashore (Plate 4.2).

Sylt is unique among the Wadden Sea islands with its extensive natural driftsands, some of them up to 35 m high, 400 m broad and 1300 m long, moving between 2 and 10 m eastward per year (Pedersen 1983; Pott 1995). The island consists of 40% dunes, 30% sandy heath-land ("Geest") and 30% marsh land ("Marsch"). The climate is temperate, with rainfall throughout the year and frost periods during winter. Sampling was undertaken throughout the island, but concentrated on the "Ellenbogen" section at the northern end. The sampled stands were from various successional stages and from either natural *A. arenaria* communities or communities that were created by humans in order to stabilise the dunes. The vegetation of the island area varies from the pioneer communities of the beach and back-beach, consisting mainly of salt tolerant species like *Cakile maritima* and *Honckenya peploides*, to yellow dunes dominated by *Elymus farctus* ssp. *borealis-atlanticus* and *A. arenaria*, to grey dunes in which grassland

species like *Agrostis tenuis* and *Corynephorus canescens* become more important, and finally to dune heath communities with *Empetrum nigrum* and *Calluna vulgaris*. In some areas a dune scrub can develop with the dominant species *Sambucus nigra* or *Hippophaë rhamnoides* (Dijkema 1983; Pedersen 1983; Westhoff & van Oosten 1991).

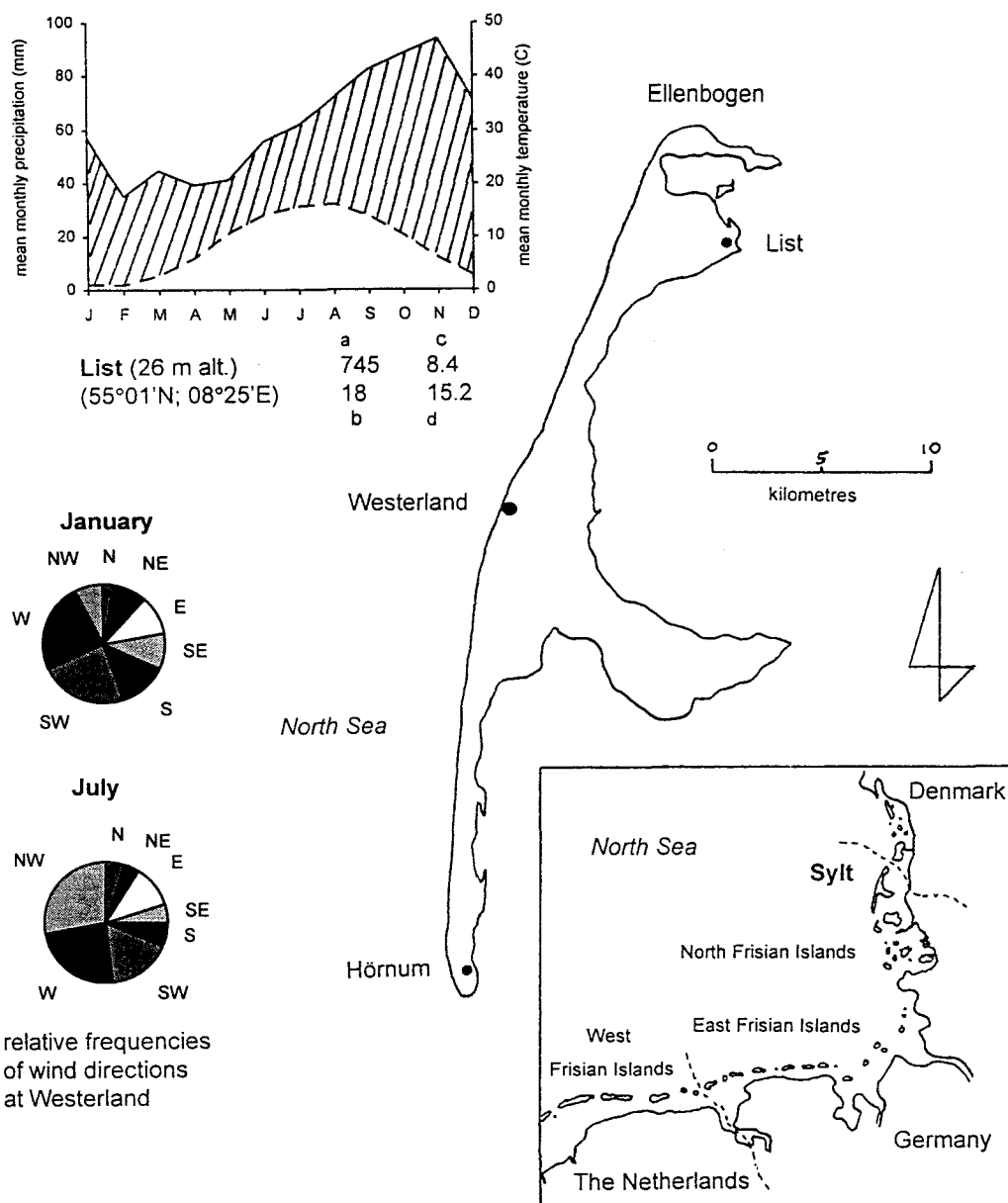


Fig. 4.9: Location and climate of the German barrier island Sylt, the northernmost of the North Frisian Wadden Sea islands. Walter-Lieth climograph for List with mean monthly precipitation (mm, thick line), mean monthly temperature (°Celsius, broken line), mean total annual precipitation in mm (a), total number of days with 10 mm or more precipitation (b), mean annual temperature in °Celsius (c) and annual temperature range in °Celsius (d). Data obtained from Müller-Westermeier (1996) and Umweltbundesamt (1997).



Plate 4.2: Coastal protection on Sylt Island through *A. arenaria* plantings (top), brushwood paddocks establishing a temporary foredune (middle) and beach replenishment with sand from the sea floor (bottom). All photographs taken in August 1996.

4.3.3 Methods

A. arenaria communities on Sylt Island were sampled in August 1996 during the European summer. The methods of sampling vegetation and soil data, of their interpretation and of the dune profile measurements were described in Section 4.2.3. It has to be emphasised that, for this case study on Sylt Island, only 17 *A. arenaria* stands were sampled because of the spatial restriction of the sampling area. Within the island of Sylt there would not be enough variability in *A. arenaria* communities to compare them with the 82 South African *A. arenaria* stands sampled along the entire Cape coast through various climatic zones. Such a comparison would need sampling of European *A. arenaria* communities throughout the continent, from Scandinavia to Portugal and along the Mediterranean coast. However, this would be beyond the scope of the thesis and was not intended. To obtain a more complete picture of the properties of European *A. arenaria* communities, publications on European dune vegetation were reviewed for comparable information.

Apart from the 17 *A. arenaria* stands, two stands were sampled in early and mature dune heath communities and were therefore dominated by plants other than *A. arenaria*. Dune profiles were measured across 12 foredune stands dominated by *A. arenaria*. The results of the 17 Sylt *A. arenaria* stands were compared with the 60 South African *A. arenaria* stands that were also compared with indigenous South African dune stands (see above). A comparison of data obtained from 17 and 60 stands respectively has to be viewed with care as will become obvious in the high standard errors and standard deviations of Sylt values compared to South African values. However, it offers a first approximation of differences and similarities of *A. arenaria* communities in the two continents.

4.3.4 Results

Floristic and edaphic properties of all 19 Sylt stands are shown in Appendix 4.3. Of these, 17 stands were dominated by *A. arenaria* (see above). A complete list of all species recorded in all Sylt stands is shown in Appendix 4.5.

1) Species richness and species diversity

Table 4.10 displays the surprising similarity of South African *A. arenaria* communities with those in their European “home territory” in terms of species richness and diversity: South African *A. arenaria* stands carry on average a slightly lower number of different species than Sylt *A. arenaria* stands, although the difference is not significant ($P > 0.05$). The index for Simpson’s diversity (d_s) is also lower in South African *A. arenaria* stands, and in this case fairly significantly so ($P < 0.05$).

Table 4.10: Comparison of species richness and d_s values of 60 South African and all (17) Sylt *A. arenaria* stands. P is calculated through a Mann-Whitney U -test for the significance level $\alpha = 0.05$; s = significant, ns = not significant.

	species richness		Simpson’s diversity (d_s)	
	South Africa	Sylt	South Africa	Sylt
mean	5.30	6.18	1.55	2.11
standard error	0.37	0.86	0.08	0.29
standard deviation	2.88	3.56	0.66	1.18
$P (U_{cal} > U_{crit})$	0.560 (ns)		0.047 (s)	

2) Importance values and life forms

The importance values (IV’s) of the first, second and third most important species in the 17 Sylt *A. arenaria* stands are listed in ranking order in Table 4.11, together with their Raunkiaer life-forms, as was done with South African stands in Table 4.2. The IV range of second most important species in European stands (96 to 19) is similar to that of the second most important

species in South African stands (from 83 to 5). *Elymus farctus* (in this text always of the subspecies *borealis-atlanticus*), the European sea wheat or couch grass, is on top of the rank with a mean IV of 96, followed by the very frequent *Leymus arenarius* (44). The third most important species in both communities also attain IV values of similar ranges, in Sylt from 53 to 5, in South Africa from 52 to 5. It appears as though *A. arenaria* in South Africa seems to enable the growth of accompanying species to much the same extent as it does in Sylt. The IV of *A. arenaria* itself is slightly lower in Sylt stands with 191 as opposed to 212 in South African stands, although a *t*-test of the difference of these means (unequal variances) proves it to be insignificant ($P = 0.193 > 0.05$). It is noteworthy though, how similar the Sylt IV of *A. arenaria* (191) is to the IV of *Thinopyrum distichum* (183) when it was dominant in South African indigenous dune stands.

The second most important species in Sylt *A. arenaria* stands are all grasses with the exception of one sedge (*Carex arenaria*), their life-forms being only hemicryptophytes or a combination of geophytes and hemicryptophytes (Table 4.11 and Fig. 4.10). There are no chamaephytes or phanerophytes even among the third most important species in Sylt stands, whereas these plants are so common in South African *A. arenaria* stands (Fig. 4.2). Apart from the *Poaceae* and *Cyperaceae* species, only herbaceous geophytes and hemicryptophytes were found in the European stands.

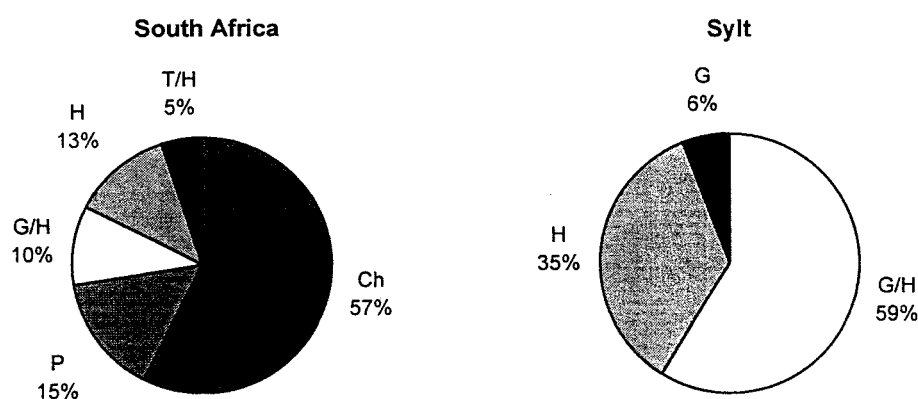


Fig. 4.10: Raunkiaer life-forms and their relative frequencies among the second and third most important species in 60 South African and 17 Sylt *A. arenaria* stands (for explanation see Fig. 4.2).

Table 4.11: Mean importance values (IV) for the first, second and third most important species and their Raunkiaer life-forms in 17 *A. arenaria* stands on Sylt Island (for explanation see Table 4.2). For Raunkiaer life-forms see also Figure 4.10.

most important species	life-form	no. of stands	mean IV	score (no. of stands x mean IV)
<i>Ammophila arenaria</i>	G/H	17	191	3247
2nd most important species	life-form	no. of stands	mean IV	score (no. of stands x mean IV)
<i>Elymus farctus</i>	G/H	4	96	384
<i>Leymus arenarius</i>	G/H	5	44	220
<i>Corynephorus canescens</i>	H	3	53	159
<i>Festuca ovina</i>	G/H	3	53	159
<i>Carex arenaria</i>	G/H	1	29	29
<i>Koeleria glauca</i>	G/H	1	19	19
3rd most important species	life-form	no. of stands	mean IV	score (no. of stands x mean IV)
<i>Jasione montana</i>	H	2	35	70
<i>Elymus farctus</i>	G/H	1	53	53
<i>Corynephorus canescens</i>	H	1	42	42
<i>Hypochoeris radicata</i>	H	3	14	42
<i>Lathyrus maritimus</i>	G	1	41	41
<i>Carex arenaria</i>	G/H	1	39	39
<i>Galium verum</i>	H	1	34	34
<i>Festuca rubra</i> ssp. <i>arenaria</i>	G/H	2	12	24
<i>Festuca ovina</i>	G/H	1	22	22
<i>Leymus arenarius</i>	G/H	1	15	15
<i>Honckenya peploides</i>	H	1	5	5

Table 4.12 reflects important species in *A. arenaria* communities in various parts of western and northern Europe. It confirms the high number of hemicryptophytes and combined geophytes/hemicryptophytes that was found in the Sylt stands. It also shows that European *A. arenaria* communities are characterised by a fairly large number of therophytes. Although by chance no annual plant was present in any of the Sylt stands, therophytes like *Senecio vulgaris*, *Cerastium diffusum* or *Oenothera parviflora* are important species in European *A. arenaria* communities. In contrast, only two therophytes are recorded in dune communities of the western section of the South African Cape coast, *Mesembryanthemum* sp. and *Pentzia sabulosa* (Boucher & Le Roux 1993). *Didelta carnosus* is mentioned by the same authors as a therophyte/hemicryptophyte. No therophytes are recorded in dune communities of the southwestern and southern section (Taylor & Boucher 1993) or of the eastern section (Weisser & Cooper 1993) of the Cape coast.

Table 4.12: Important species and their life-forms in western European *A. arenaria* communities (Atlantic shore). The list is not complete, but reflects typical species observations recorded in the literature (**Britain:** Tansley 1939; Hepburn 1945; Willis *et al* 1959b; Ranwell 1960; Huiskes 1979; Boorman 1993. **Denmark:** Böcher 1945; Pedersen 1983; Jensen 1993. **Belgium, The Netherlands and Germany:** Lux 1969; Bakker 1976; Dijkema 1983; Pedersen 1983; Westhoff & van Oosten 1991; Dijkema *et al* 1993; van der Meulen & van der Maarel 1993. **France:** Vanden Berghen 1958; Géhu & Géhu 1969; Bakker 1976).

species	life-form	Britain	Belgium, The Netherlands, Germany, Denmark	France
<i>Elymus farctus</i>	G/H	x	x	x
<i>Carex arenaria</i>	G/H	x	x	x
<i>Euphorbia paralias</i>	Ch	x	x	x
<i>Eryngium maritimum</i>	H	x	x	x
<i>Senecio vulgaris</i>	T	x	x	x
<i>Cakile maritima</i>	H	x	x	x
<i>Leymus arenarius</i>	G/H	x	x	
<i>Festuca rubra</i>	G/H	x	x	
<i>Cerastium diffusum</i>	T	x	x	
<i>Hypochoeris radicata</i>	H	x	x	
<i>Hieracium umbellatum</i>	H	x	x	
<i>Viola tricolor</i>	H	x	x	
<i>Sedum acre</i>	Ch	x	x	
<i>Jasione montana</i>	H	x	x	
<i>Hippophaë rhamnoides</i>	P	x	x	
<i>Oenothera parviflora</i>	T	x	x	
<i>Ononis repens</i>	G/H	x		x
<i>Cynodon dactylon</i>	H	x		x
<i>Matthiola sinuata</i>	H	x		x
<i>Lathyrus maritimus</i>	G		x	x
<i>Erodium cicutarium</i>	T	x		
<i>Crepis capillaris</i>	T	x		
<i>Hieracium pilosella</i>	T	x		
<i>Tussilago farfara</i>	H	x		
<i>Anagallis arvensis</i>	T	x		
<i>Sonchus arvensis</i>	G		x	
<i>Silene otites</i>	H		x	
<i>Viola canina</i>	H		x	
<i>Corynephorus canescens</i>	H		x	
<i>Vicia cracca</i>	H		x	
<i>Galium arenarium</i>	H			x
<i>Silene thorei</i>	H			x
<i>Artemisia lloydii</i>	Ch/H			x
<i>Medicago marina</i>	H			x
<i>Atriplex sabulosa</i>	T			x
<i>Astragalus bayonnensis</i>	H			x
<i>Diotis candidissima</i>	H			x
<i>Linaria thymifolia</i>	T/H			x
<i>Hieracium eriophorum</i>	H			x

3) Species associations

A comparison of association indices of *A. arenaria* with the respective second most important species in South Africa (Table 4.4) and Sylt (Table 4.13) reveals that the associations in the latter communities are in fact much stronger. With one exception (*Koeleria glauca*), all IA_J values in Sylt are higher than the highest South African values. They range from 17.2 to 22.8, while the maximum IA_J of any species with *A. arenaria* in South Africa is a mere 13.7. In fact, the association indices with *A. arenaria* found on Sylt are very similar to those that South African species form with dominant indigenous dune plants (Table 4.5): *A. arenaria* appears to form species associations in Europe at much the same strength that dominant indigenous species form association in South Africa.

Table 4.13: Jaccard's index of species association (IA_J) of all 2nd most important species in European *A. arenaria* stands (see Table 4.11) with *A. arenaria*. All 17 *A. arenaria* stands (340 quadrats) are taken into account. Species are ranked according to their IA_J score. A χ^2 -test was not conducted as in most cases at least one value of the 4x4 contingency table was below 4 and the test therefore regarded as insufficiently reliable (Mueller-Dombois & Ellenberg 1974).

species	no. of quadrats in which both species present (%)	IA_J (%)
<i>Festuca ovina</i>	20.88	22.756
<i>Corynephorus canescens</i>	20.00	21.795
<i>Elymus farctus</i>	17.94	19.243
<i>Carex arenaria</i>	16.76	18.269
<i>Leymus arenarius</i>	15.88	17.197
<i>Koeleria glauca</i>	0.59	0.671

4) Classification and ordination of stands

All 19 Sylt stands were subjected to a detrended correspondence analysis (DCA) which reveals a clear pattern of succession (Fig. 4.11). The six distinct clusters detected by TWINSpan analysis (not shown) each relate to a certain stage in the succession typical of western European dune vegetation: embryonal and early yellow dunes with *Elymus farctus*; yellow dunes with *Leymus arenarius*; older yellow dunes with a higher number of different species and typical grey dune species like *Carex arenaria* and *Corynephorus canescens* making their first appearance; grey dunes with large amounts of the latter two species, also typical here is *Lathyrus maritimus*; older grey dunes with first occurrences of heath species like *Empetrum*

nigrum; and lastly, the mature dune heath stage with little or no *A. arenaria* left and *Empetrum nigrum* or *Calluna vulgaris* being the dominant species. Four of these stages are illustrated in Plate 4.3.

In comparison with this result, the “lumping effect” of South African *A. arenaria* stands (Fig. 4.3 A) is conspicuous. However, unlike in Europe, stands in South Africa were sampled mostly in early successional stages, i.e. foredunes and intermediate dunes (see Section 4.2.2). The clustering of indigenous South African stands does therefore not follow a successional gradient either, but rather geographical differences, i.e. particularly climatic constraints (see above). The sampling area of Sylt Island appears spatially and thus climatically restricted enough to allow for a more sensitive successional differentiation. It is therefore necessary to compare the Sylt findings with those of South African *A. arenaria* stands sampled in one area only and in distinctly different vegetation zones. This will be done in the study of succession in a stabilisation area at De Mond Nature Reserve (see Chapter 5).

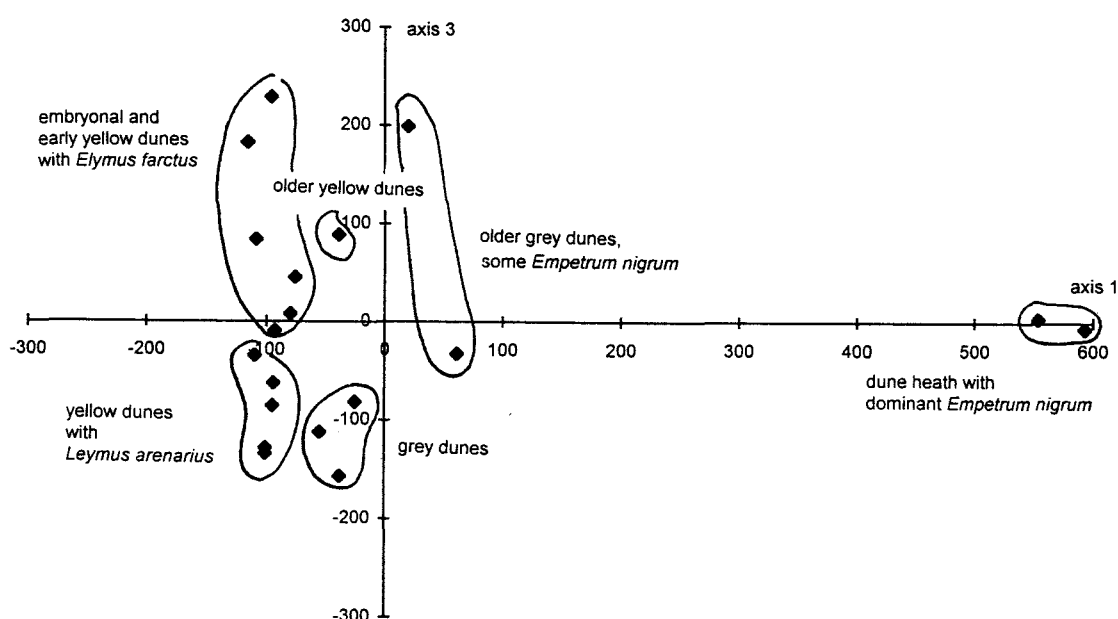


Fig. 4.11: Detrended correspondence analysis (DCA) of all 19 Sylt stands. The stands are clustered according to their successional stage from early yellow dunes (left) to the dune heath stage (right). A TWINSPLAN analysis of the same data (not shown) confirms these groupings.

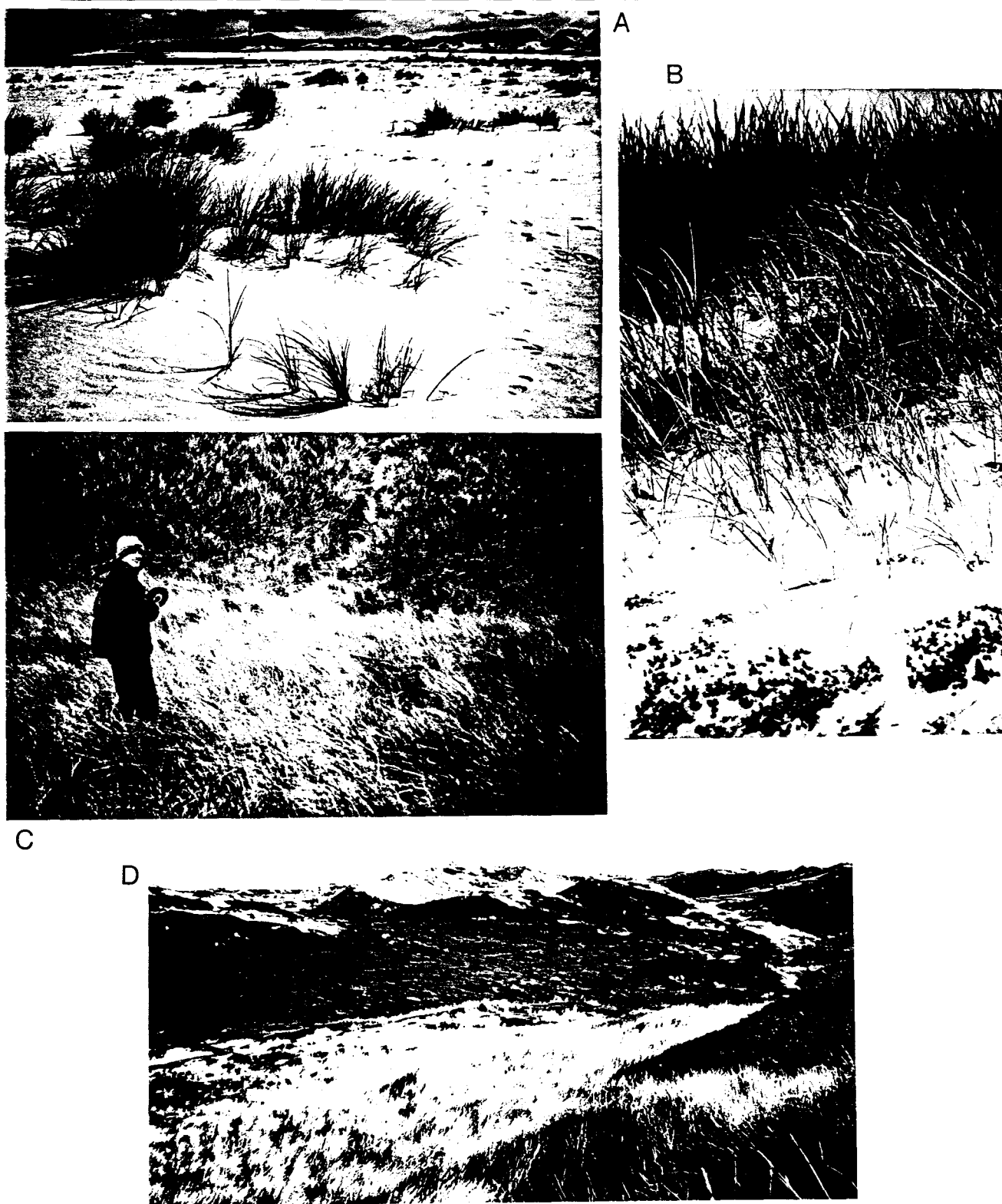


Plate 4.3: Successional stages of dune vegetation on Sylt Island. A. Mixed *A. arenaria* - *Elymus farctus* embryonal dunes. B. Yellow dune community consisting of *A. arenaria* and *Leymus arenarius*, in foreground *Honckenya peploides*. C: Species-rich grey dune community with a variety of different species among the dominant *A. arenaria*. D. Transition zone between species-rich grey dunes and species-poor dune heathland, consisting mostly of *Empetrum nigrum* and *Calluna vulgaris*. All photographs taken in August 1996.

At this stage, the DCA result of all South African *A. arenaria* stands (Fig. 4.3 A) are compared with information on the species composition of *A. arenaria* communities in a larger part of Europe, thus ensuring the comparison with an area similar in its geographical diversity to the South African Cape coast. Table 4.12 shows how, even for a small part of Europe, many of the species accompanying *A. arenaria* are restricted to either the British Isles, or to the western European mainland of Denmark, Germany, the Netherlands or Belgium, or to the French Atlantic coast. Similarly, no fewer than four types of *Ammophileta* are reflected in Table 4.14 for the French, Belgian, Dutch and German Atlantic coast alone. In addition to these communities, there are further types of *Ammophileta* along the Baltic and Mediterranean coasts as well as along the Black Sea. The most prominent of these, the *Ammophiletum mediterraneum*, can again be divided into at least three subgroups (Lavrentiades 1993; Lovric 1993; Pignatti 1993; Randall 1993).

Table 4.14: Four *Ammophileta* distinguished along the French, Belgian, Dutch and German Atlantic coast (Géhu & Géhu 1969; Bakker 1976).

community	indicator species beside <i>A. arenaria</i>	geographical range
Sileno- <i>Ammophiletum</i>	<i>Silene thorei</i> <i>Astragalus bayonnensis</i> <i>Linaria thymifolia</i> <i>Hieracium eriophorum</i> <i>Euphorbia polygonifolia</i>	southwestern France: Spanish border to Gironde River mouth
Galio- <i>Ammophiletum</i>	<i>Galium arenarium</i> <i>Crithmum maritimum</i> <i>Matthiola sinuata</i> <i>Medicago marina</i> <i>Diotis candidissima</i> <i>Artemisia lloydii</i> <i>Pancratium maritimum</i>	western France: Gironde River mouth to southern Brittany
Euphorbio- <i>Ammophiletum</i>	<i>Euphorbia paralias</i> <i>Calystegia soldanella</i> <i>Eryngium maritimum</i>	northwestern France: Brittany to Belgian border
Elymo- <i>Ammophiletum</i>	<i>Leymus arenarius</i> and many more (see Table 4.12)	western Europe: Brittany to Denmark

This information reveals the lack of differentiation of South African *A. arenaria* communities through classification and ordination techniques in spite of their diverse geographical situations (Fig. 4.3 A). A comparable differentiation of stands into at least three geographical groups can

be achieved with South African indigenous dune plant communities (Fig. 4.3 B), but not with South African *A. arenaria* communities.

5) Edaphic and other environmental factors

While mean results of community structure were insignificantly (species richness) or fairly significantly (species diversity) different in South African stands from Sylt stands (Table 4.10), the differences of their edaphic properties, pH, conductivity and organic matter of the soil, are highly significant (Table 4.15). In each case, P is far below the significance level $\alpha = 0.001$. The higher mean pH in South African *A. arenaria* communities could indicate a higher concentration of free ions in the soil, which would therefore enhance its conductivity. In fact, the mean conductivity of soil from South African *A. arenaria* stands is much higher than that of soil from Sylt stands. Although Sylt stands have a lower pH (usually connected with high organic matter values), their mean organic matter content is also significantly lower (0.11% dry weight) than that of South African stands (0.44%). A reason for Sylt sands having such unusually low pH and conductivity values in spite of a low organic matter content could be the method of sand replenishment on some Sylt beaches with sand from the sea floor (Plate 4.2), which contains a lower proportion of carbonates and salines than naturally evolved beach sand.

Table 4.15: Comparison of pH, conductivity and organic matter content of soil in 60 South African and all Sylt *A. arenaria* stands. P is calculated through a Mann-Whitney U -test for the significance level $\alpha = 0.001$; s = significant, ns = not significant.

	pH		conductivity (μScm^{-1})		organic matter (% dry weight)	
	South Africa	Sylt	South Africa	Sylt	South Africa	Sylt
mean	8.23	6.72	146.23	23.09	0.44	0.11
standard error	0.05	0.22	21.55	5.59	0.04	0.03
standard deviation	0.39	0.87	166.89	23.04	0.27	0.11
$P(U_{\text{cal}} > U_{\text{crit}})$	1.050×10^{-6} (s)		2.651×10^{-8} (s)		1.163×10^{-7} (s)	

A more complete picture of soil factors in European *A. arenaria* communities is found in the literature (Table 4.16). Interestingly, the pH values that Lux (1969) published for an *A. arenaria* foredune on the German North Sea coast are again on the acidic side ranging between 5.5 and 6.5. Although some British values tend to be equally low, most *A. arenaria* stands in Britain thrive in sands of more alkaline pH's with values between 8.0 and 9.1. The South African value of 8.23 fits well into this scheme. As for conductivity and organic matter values, it is obvious again that the Sylt values are comparatively low, while the South African values do not deviate much from other typical European values.

Table 4.16: Range of soil values in European *A. arenaria* communities recorded in the literature (- no data available).

area (author)	pH	conductivity (μScm^{-1})	organic matter content (% dry weight)
North Cornwall, UK (Hepburn 1945)	8.0 - 8.3	-	0.25 - 0.85
Blakeney Point, UK (Gorham 1958)	5.7 - 8.2	50 - 110	0.2 - 6.3
Newborough Warren, UK (Ranwell 1959)	8.4 - 8.7	-	0 - 0.2
Braunton Burrows, UK (Willis <i>et al</i> 1959a)	8.8 - 9.1	-	0.19 - 0.94
various areas, UK (Huiskes 1979)	4.6 - 9.1	-	0.31 - 1.4
German North Sea coast, (Lux 1969)	5.5 - 6.5	-	-

An attempt to relate the two ordination axes of Figure 4.11 to environmental variables (Fig. 4.12) confirms the ordination of Sylt *A. arenaria* stands along a successional gradient: dune heath stands on the far right of the plot bear a higher content of organic matter of the soil and are at considerable distance from the sea. In contrast, yellow dune stands to the left of the second axis show higher values for pH and conductivity of the soil. The orientation appears to influence the ordination of stands that are characterised by both *A. arenaria* and *Leymus arenarius*, since most of these stands were situated at the northfacing tip of the "Ellenbogen" spit.

The importance of organic matter content, distance from high water mark and pH for the ordination of Sylt stands is reflected in their high regression coefficients (Table 4.17). In comparison, the regression coefficients of the South African ordination do not reach the same high values. Although more of the latter are significant according to a *t*-test, they do not have the same influence on the ordination of stands as do the respective variables in Sylt stands. A reason for the lower significances of the European coefficients could be the lower value of degrees of freedom (df), resulting from fewer samples and fewer environmental variables under examination.

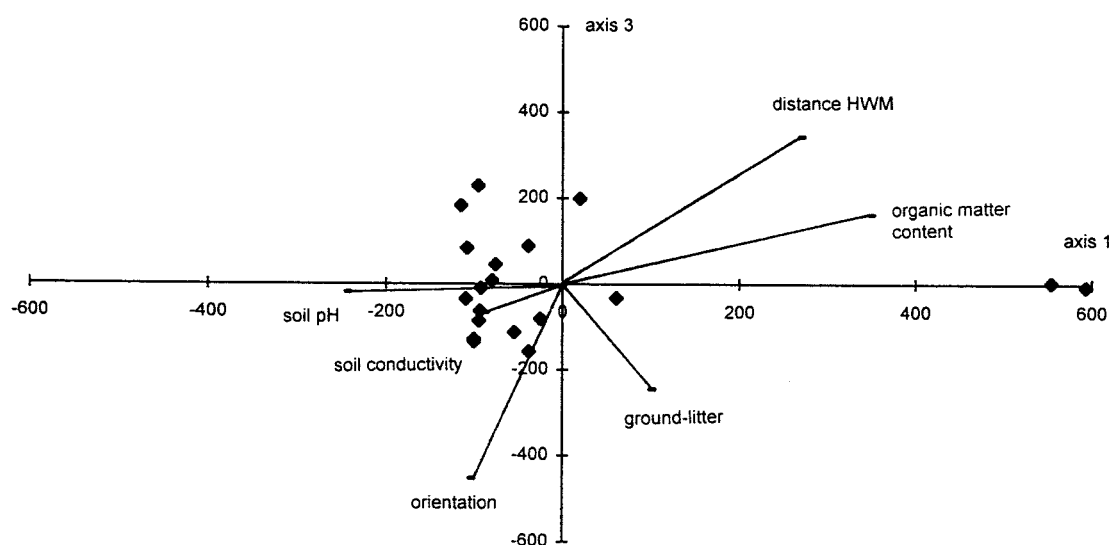


Fig. 4.12: DCA of all 19 Sylt stands with ordination axes related indirectly to environmental variables (HWM = high water mark). The plot is the same as in Figure 4.11. See Table 4.17 for corresponding regression coefficients.

Table 4.17: Regression coefficients (multiplied by 100) of various environmental variables with the respective two axes resulting from indirect gradient analyses (DCA) with South African and Sylt *A. arenaria* stands (see Fig. 4.12). Significance at $\alpha = 0.05$ (*) as indicated through *t*-values supplied by the same analyses.

	South African stands (df = 62)		Sylt stands (df = 12)	
	axis 1	axis 2	axis 1	axis 3
soil pH	- 2	- 15	- 46	+ 63
soil conductivity	- 33 *	- 35 *	- 15	- 49
organic matter content of soil	+ 9	- 26	+ 237 *	- 24
orientation	+ 11	- 46 *	- 35	- 59
distance from high water mark	+ 33 *	- 33 *	- 147	+ 67
litter on ground (leaves etc.)	- 13	+ 15	+ 16	- 46

6) Dune profiles

It appears as though *A. arenaria* forms a higher and steeper foredune in Europe than in South Africa (Fig. 4.13). The mean profile of Sylt dunes reaches a height of more than 6 m, while South African *A. arenaria* dunes are not much higher than 4 m. A reason for this difference could be the fact that Sylt Island is exposed to very strong winds from west and northwest (Fig. 4.9) throughout the year, while in South Africa wind directions change frequently (Fig. 3.2). Therefore, sand would be blown against *A. arenaria* tufts on Sylt Island continuously from one side, which accounts for the formation of higher foredunes. The sand supply of South African *A. arenaria* communities as well as indigenous dune plant communities is more irregular, hence dunes are not only smaller, but also more irregularly shaped.

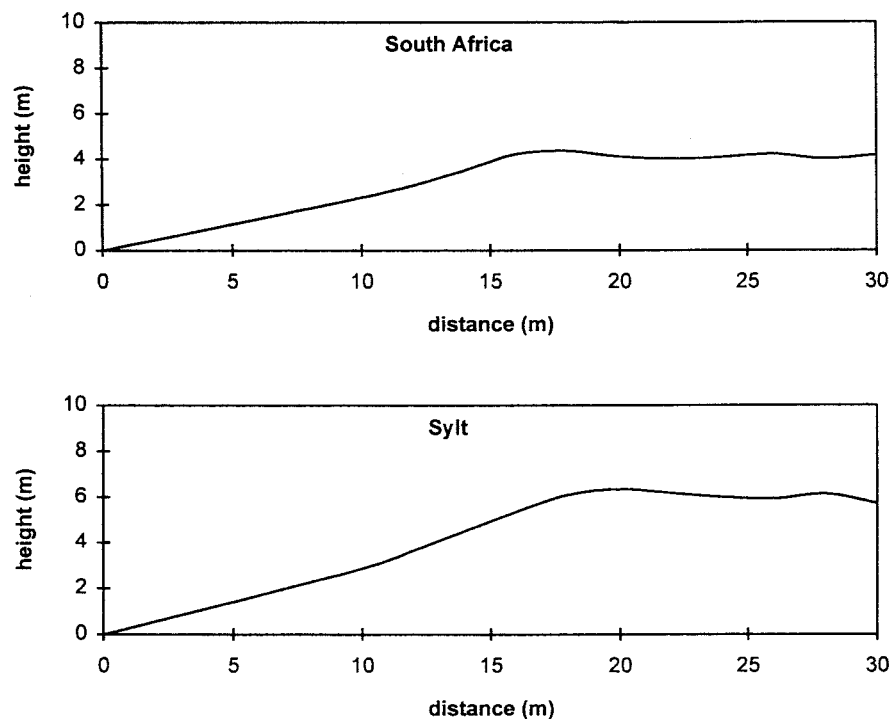


Fig. 4.13: Mean dune profiles of dunes formed by *A. arenaria* in South Africa ($n = 38$) and on Sylt Island ($n = 12$). The axes are representing distance (m) and height (m) from the beginning of the transect, which was laid out perpendicular through a 10x10 m stand from the shore (left), starting 10 m before the stand and extending 10 m behind the stand.

4.3.5 Discussion

Sylt and South African *A. arenaria* communities are similar in regard to a number of factors. Their species richness and diversity indices are similar, although the latter are overall slightly higher in Sylt *A. arenaria* communities (Table 4.10). The same applies to importance values of species in the two communities (Table 4.11). The importance value of *A. arenaria* as dominant species is only insignificantly higher in South African stands, while other species in the *A. arenaria* communities are represented at much the same importance on both continents.

A difference is found in life-forms of the accompanying species, considering the much higher percentage of geophytes and hemicryptophytes in Sylt *A. arenaria* communities and the complete lack of chamaephytes or phanerophytes (Fig. 4.10). This is certainly due to the different climate as the regular frost periods of northwest Europe support a higher number of plants with perennial organs under or close to the ground (Sitte *et al* 1991). However, even along the Mediterranean shores, which are less exposed to harsh frost periods and have in fact a climate closely related to that of the western Cape coast, we find a much higher number of hemicryptophytes and therophytes in *A. arenaria* communities (Corre 1993; Lavrentiades 1993; Lovric 1993; Pignatti 1993). This could confirm the niche-advantage of soft-leaved plants in *A. arenaria* stands (see above). The number of plants with small, soft growth-forms is not very high along the Cape coast (Boucher & Le Roux 1993; Taylor & Boucher 1993), and the place of the European hemicryptophytes and therophytes (Table 4.12) seems to be taken by a few soft-leaved chamaephytes like *Senecio elegans* and *Dasispermum suffruticosum*, or even by less common species like *Pelargonium capitatum* or *Pteronia camphorata*. The presence of *A. arenaria* in South Africa may provide species that are not common on South African dunes with a substantial advantage and thus might slowly lead to changes in the floristic structure of South African dune plant communities.

It is again through the analysis of species associations that the most distinct differences in community structure become obvious (Table 4.13): *A. arenaria* forms much weaker associations with South African species than with its European “fellow species”. In fact, the associations that *A. arenaria* forms with species on Sylt Island have very similar IA_j scores to the associations that dominant indigenous dune species form in South Africa with other South

African species. This result highlights that *A. arenaria* is not indigenous in South Africa. It has evolved in Europe and developed associations with European species whose strength cannot be matched by the associations *A. arenaria* has developed with South African species within a period of roughly a hundred years.

The TWINSpan and CANOCO analyses of Sylt stands reflect the succession of European dunes from an early yellow dune stage with vigorous *A. arenaria* populations to a dune heath vegetation with little or no *A. arenaria* (Fig. 4.11, Plate 4.3). Such a sensitive differentiation was possible because of the spatial restriction of the Sylt stands, and their ordination has to be compared rather with an ordination of South African *A. arenaria* stands of an equally restricted area (see Chapter 5). But if one compares the lumping of South African *A. arenaria* stands (Fig. 4.3 A) with results in the European literature (e.g. Vanden Berghen 1958; Willis *et al* 1959b; Ranwell 1960; Géhu & Géhu 1969; Lux 1969; Bakker 1976; Dijkema 1983; Pedersen 1983; various publications in van der Maarel 1993), the great variety of *Ammophila* that occur in Europe (Table 4.14) makes the lack of differentiation of South African *A. arenaria* communities - in spite of their diverse geographical situations all along the Cape coast - appear very conspicuous.

One reason for the great variety of *A. arenaria* communities in Europe is certainly the European climate (Table 3.2), which is much more variable than the Cape coastal climate. Some areas experience harsh frost periods, while others have mild and mostly wet winters. The climate of the South African Cape coastal strip does not vary as excessively (Fig. 3.2). While in South Africa “eastern” species such as *Scaevola plumieri* occur in stands as far west as Buffelsbaai near Knysna - Taylor and Boucher (1993) even record it at Cape Agulhas -, and the South African coastal zone has a “comparatively simple and homogenous flora” (Taylor & Boucher 1993), the flora of the European coastal zone is more heterogeneous because of a more diverse range of geological and climatological factors (Bakker 1976). Nevertheless, it must be considered that the ordination of South African dune plant communities dominated by indigenous species does indeed reflect at least three to four distinct groups of coastal vegetation: South African indigenous dune plant communities can be differentiated to about the same level as *A. arenaria* communities along the northwestern European shores, while South African *A. arenaria* communities appear to be of great uniformity.

A comparison of edaphic and environmental factors in European and South African *A. arenaria* communities shows how similar the South African values are to European values recorded in the literature, whereas the edaphic values of Sylt Island are rather low (Tables 4.15 and 4.16). The pH values of dune soils in South Africa are comparatively high, but the growth of *A. arenaria* is found to be little affected by the pH as long as it is above 5 (Huiskes 1979). Neither does the South African dune soil bear any adversely negative values of conductivity or organic matter that could affect *A. arenaria*'s growth and survival in South Africa. While these physical soil factors seem to have little or no impact on the vigour of *A. arenaria*, an analysis of possibly harmful soil microorganisms in South African dune soils is presented later (see Chapter 5). Secondly, the ordination axes of a DCA of our Sylt stands can be related very well to environmental variables, especially to organic matter and pH, which is in accordance with the successional pattern the stands show in a gradient analysis (Fig. 4.12 and Table 4.17). As expected, the regression coefficients are always higher than with South African *A. arenaria* stands. *A. arenaria* communities apparently do not respond to environmental factors in South Africa as they do in their native European range. This corresponds well to the result that South African *A. arenaria* communities do not respond to environmental factors as easily as South African indigenous dune plant communities.

It is interesting to note that the profiles of dunes formed by *A. arenaria* on Sylt Island are steep and abruptly rising (Fig. 4.13) as was described for *A. arenaria* dunes along the North American west coast (Barbour & Johnson 1977; Wiedemann 1984). *A. arenaria* does not form such high dunes in South Africa, but similarly to indigenous dune plants forms smaller, more rounded hummocks, probably because of the irregular wind patterns along the Cape coast. However, along the North American west coast, the indigenous dune plants also form smaller, rounder hummocks, hence factors other than the wind regimes must account for the difference in dune profiles here. One such factor is possibly the growth-form of the various plant species; *A. arenaria* has a higher stem density than the American indigenous dune plants and can therefore trap sand more efficiently (Seabloom & Wiedemann 1994; see Chapter 2). Although the South African *A. arenaria* also bears a higher stem density than any of the indigenous dune plants (Plate 4.1) and therefore grows in thicker tufts trapping more sand, this difference in growth-forms is presumably not as profound in South Africa as it is in North America.

Moreover, the extreme South African wind regimes may override any such effect and ensure that *A. arenaria* builds dunes of much the same morphology as indigenous dune plants do.

4.4 Conclusions

The aggressive behaviour of *A. arenaria* along Californian and Oregon beaches is not reflected along the Cape coast. In South Africa, *A. arenaria* forms dune plant communities of much the same species richness and species diversity as those of communities formed by indigenous dune plant species. Importance values of species in *A. arenaria* and in indigenous dune plant communities are also of similar ranges. It can therefore be concluded that *A. arenaria* communities are of a considerable floristic variety, and that *A. arenaria* does not exert any abnormal dominance over other species. Nor does *A. arenaria* tend to develop higher and steeper foredunes than indigenous dune plants as it does along the North American west coast. No negative impact on the morphology of South African beaches and dunefields can be reported from the Cape coast.

However, the floristic variety of South African *A. arenaria* communities is a valid argument only on a local scale; i.e. species richness and diversity of *A. arenaria* stands are similar to those in indigenous stands only at one particular site at a time. In respect of the Cape coastline as a whole, *A. arenaria* communities appear fairly monotonous compared to indigenous dune plant communities. Their accompanying species do not differ as much according to their geographical situation, and it is always the same species that occur in the *A. arenaria* stands. Small, soft-leaved chamaephytes, hemicryptophytes and therophytes with small spatial demands have a considerable advantage among the dense tufts of *A. arenaria*. As their variety is limited along the Cape coast, the number of plants that grow well with *A. arenaria* appears somewhat restricted. This could account for the repetitive pattern of species composition in *A. arenaria* communities along the Cape coast, and it could also lead to a shift of the general vegetation structure of South African Cape dune ecosystems as *A. arenaria* encourages the growth - and expands the range - of less common plants.

The alienness of *A. arenaria* in South Africa becomes obvious from species association analyses. The associations that *A. arenaria* forms with indigenous species in South Africa are weaker than those formed by dominant indigenous species with other indigenous plants. They are also weaker than those formed by *A. arenaria* with European plants in Europe. The lack of a common evolutionary history accounts for the fair incompatibility of *A. arenaria* with South African indigenous species. Although *A. arenaria* is, in South Africa, as sensitive to a rise in organic matter content of the soil as it is in Europe, it does not respond well otherwise to different environmental variables. This again demonstrates that it did not evolve under South African coastal conditions.

Appendix 4.1: Floristic and edaphic properties of 82 stands dominated by *A. arenaria*. Of these, 60 stands are adjacent to indigenous stand (see Appendix 4.2) and are marked (*).

stand no.	stand name	species richness	Simpson's diversity (d_s)	IV <i>Ammophila arenaria</i>	pH	conductivity (μScm^{-1})	org. matter (% dry weight)
1	koeberg 1	13	2.708	134	7.9	68.7	0.24
2	koeberg 2	5	1.711	185	8.2	77.2	0.71
3	koeberg 3	5	1.742	174	8.1	76.9	0.37
4*	bloubergstrand 1	18	1.979	156	7.9	56.2	0.93
5*	tableview 1	11	1.817	180	7.7	303.1	0.42
6	houtbay 1	10	2.060	168	8.5	244.0	0.37
7	houtbay 2	3	1.067	270	8.5	282.0	0.28
8*	noordhoek 1	4	1.385	231	8.5	82.3	0.07
9*	noordhoek 2	3	1.137	258	8.4	72.6	0.10
10*	witsand (w.cape) 1	6	2.270	159	8.2	851.0	0.30
11*	schuster's kraal 1	5	1.301	223	8.4	75.3	1.00
12	fishhoek 1	8	1.291	223	8.1	364.0	0.48
13	fishhoek 2	1	1.000	300	8.1	152.0	0.09
14	fishhoek 3	5	2.322	140	8.0	827.0	0.03
15*	muizenberg 1	5	1.297	237	8.2	266.0	0.44
16	muizenberg 2	8	1.388	214	8.0	801.0	1.09
17	muizenberg 3	6	3.008	120	8.1	367.0	1.09
18*	wolfgat 1	6	2.139	181	8.2	473.0	0.25
19*	pringle bay 1	4	1.612	186	7.8	151.1	0.30
20	pringle bay 2	4	1.489	213	7.8	93.2	0.33
21	kleinmond 1	8	2.539	132	7.9	68.3	0.52
22*	meerensee 1	6	1.620	185	8.0	120.1	0.16
23*	meerensee 2	2	1.026	288	7.9	196.1	0.20
24*	walker bay 1	9	3.528	109	8.3	59.9	0.65
25*	walker bay 2	7	1.568	207	8.3	134.0	0.51
26*	walker bay 3	7	2.140	182	91.1	91.1	0.75
27*	struisbaai plaat 1	6	1.887	189	8.4	526.0	0.89
28*	de mond 1	4	1.068	280	9.0	69.1	0.78
29*	de mond 2	4	1.239	248	8.7	446.3	1.00
30*	de mond 3	5	1.596	218	8.8	111.3	0.65
31	de mond 3b	11	3.113	117	8.9	48.9	1.03
32*	de mond 4	5	1.125	243	8.8	710.3	1.04
33*	de mond 5	4	1.271	241	9.0	153.3	0.67
34*	waenhuiskrans 1	9	1.355	206	7.8	111.1	1.24
35	waenhuiskrans 2	8	2.747	138	8.2	66.8	1.00
36*	de hoop 1	7	1.198	220	9.2	34.1	0.56
37*	de hoop 2	5	2.263	128	9.1	13.8	0.59
38*	stilbaai 1	5	2.438	130	8.1	105.1	0.81
39*	stilbaai 2	11	4.713	85	8.2	168.1	1.10
40*	vleesbaai 1	4	1.242	223	7.9	53.3	0.32
41*	vleesbaai 2	3	1.041	284	7.8	101.1	0.30
42*	vleesbaai 3	3	1.627	188	8.1	62.2	0.23
43	vleesbaai 4	4	1.213	221	8.2	71.7	0.33
44*	hartenbos 1	3	1.769	182	8.2	135.1	0.23

45*	hartenbos 2	3	1.029	272	7.6	56.7	0.26
46*	klein brakrivier 1	7	1.209	231	7.6	50.7	0.19
47*	groot brakrivier 1	3	1.454	228	7.6	537.1	0.44
48*	hershams 1	6	1.390	232	8.0	52.6	0.29
49*	outeniqua strand 1	11	2.405	151	8.0	100.7	0.28
50*	swartvlei 1	6	1.295	230	7.3	81.7	0.34
51*	sedgefield 1	6	2.326	131	8.2	54.3	0.26
52*	sedgefield 2	4	1.088	201	8.2	79.9	0.36
53*	sedgefield 3	7	1.132	228	8.1	36.6	0.36
54	sedgefield 4	8	3.395	108	8.2	55.9	0.49
55	sedgefield 5	4	1.138	224	8.2	98.5	0.47
56*	goukamma 1	5	1.149	245	8.0	168.1	0.35
57*	goukamma 2	4	1.224	232	7.9	58.0	0.33
58	goukamma 3	7	1.788	183	7.9	86.8	0.32
59	goukamma 4	4	2.247	158	7.9	138.1	0.35
60	goukamma 5	3	1.216	210	7.9	325.1	0.39
61*	buffelsbaai 1	2	1.018	290	8.0	113.1	0.37
62*	plettenberg bay 1	9	1.630	180	7.9	78.5	0.74
63*	plettenberg bay 2	6	1.436	188	8.8	94.6	0.39
64	plettenberg bay 3	9	2.222	141	8.0	51.7	0.47
65*	oysterbay 1	3	1.017	285	7.7	100.5	0.09
66*	oysterbay 2	6	2.788	124	7.6	52.0	0.26
67*	sardinia bay 1	9	2.125	153	8.5	74.8	0.36
68*	port alfred (west) 1	2	1.001	295	8.5	155.4	0.27
69*	port alfred (west) 2	2	1.029	272	8.4	100.0	0.35
70*	port alfred (east) 1	5	1.104	251	8.3	281.4	0.30
71*	port alfred (east) 2	9	1.700	184	8.3	68.1	0.25
72*	kleinemonde 1	1	1.000	300	8.4	66.3	0.50
73*	kleinemonde2	3	1.140	254	8.4	66.5	0.59
74*	kleinemonde 3	2	1.070	242	8.4	45.1	0.48
75*	kleinemonde 4	5	1.311	207	8.3	85.3	0.34
76*	kleinemonde 5	4	1.545	216	8.3	181.1	0.28
77*	old woman's river 1	5	1.186	204	8.5	81.3	0.16
78*	old woman's river 2	4	1.056	243	8.4	72.1	0.23
79*	hamburg 1	4	1.524	169	8.4	38.3	0.21
80*	hamburg 2	5	1.680	184	8.4	42.9	0.28
81*	gulu mouth 1	3	1.151	229	8.4	38.7	0.33
82*	gulu mouth 2	3	1.111	225	8.5	20.3	0.41

Appendix 4.2: Floristic and edaphic properties of 64 stands dominated by various indigenous species. Of these, 60 stands are adjacent to *A. arenaria* stands (see Appendix 4.1) and are marked (*).

stand no.	stand name	species richness	Simpson's diversity (d_s)	dominant species	IV	pH	conductivity (μScm^{-1})	org. matter (% dry weight)
83*	bloubergstrand 1n	3	1.529	<i>Thinopyrum distichum</i>	215	7.7	70.2	0.45
84*	tableview 1n	9	3.906	<i>Thinopyrum distichum</i>	91	8.0	119.1	0.10
85*	noordhoek 1n	3	1.097	<i>Thinopyrum distichum</i>	279	8.4	208.0	0.13
86*	noordhoek 2n	8	1.511	<i>Sporobolus virginicus</i>	189	8.4	81.4	0.39
87*	witsand (w.cape) 1n	3	1.868	<i>Thinopyrum distichum</i>	164	8.2	424.0	0.60
88*	schuster's kraal 1n	2	1.941	<i>Thinopyrum distichum</i>	181	8.2	158.0	1.08
89*	muizenberg 1n	7	2.312	<i>Tetragonia decumbens</i>	163	8.2	55.1	0.41
90*	wolfgat 1n	9	1.684	<i>Metalasia muricata</i>	205	8.2	713.0	0.37
91*	pringle bay 1n	9	1.393	<i>Ehrharta villosa</i>	214	7.9	84.7	0.41
92*	meerensee 1n	3	1.908	<i>Thinopyrum distichum</i>	209	7.8	383.1	0.25
93*	meerensee 2n	4	2.174	<i>Thinopyrum distichum</i>	178	7.8	371.1	0.36
94*	walker bay 1n	9	1.958	<i>Ehrharta villosa</i>	177	8.2	85.4	0.64
95*	walker bay 2n	5	1.852	<i>Thinopyrum distichum</i>	199	8.1	43.9	0.46
96	struisbaai 1n *	4	1.702	<i>Thinopyrum distichum</i>	180	7.8	122.1	1.01
97	struisbaai 2n *	7	2.488	<i>Thinopyrum distichum</i>	133	7.8	361.1	1.33
98	struisbaai 3n *	5	2.598	<i>Chrysanthemoides monilifera</i>	136	7.8	64.2	1.47
99*	struisbaai plaat 1n	7	2.323	<i>Myrica cordifolia</i>	162	8.3	88.0	0.84
100*	de mond 1n	10	5.210	<i>Psoralea repens</i>	81	8.8	25.4	1.29
101*	de mond 2n	7	3.897	<i>Myrica cordifolia</i>	102	9.0	20.7	1.17
102*	de mond 3n	7	2.418	<i>Didelta carnosa</i>	160	8.6	212.3	1.06
103*	de mond 4n	9	3.339	<i>Ficinia lateralis</i>	89	9.1	30.2	0.95
104*	de mond 5n	1	1.000	<i>Thinopyrum distichum</i>	300	8.6	230.3	0.90
105*	waenhuiskrans 1n	6	3.369	<i>Dasispermum suffruticosum</i>	107	7.6	155.1	1.12
106*	de hoop 1n	8	2.401	<i>Ehrharta villosa</i>	146	9.2	18.9	0.85
107*	de hoop 2n	6	2.343	<i>Ehrharta villosa</i>	132	9.0	12.9	0.80
108	witsand (s.cape) 1n *	9	1.959	<i>Psoralea repens</i>	144	8.1	124.1	0.77
109*	stilbaai 1n	6	2.554	<i>Tetragonia decumbens</i>	150	8.3	85.5	1.11
110*	stilbaai 2n	5	2.063	<i>Senecio elegans</i>	153	8.0	179.1	1.58
111*	vleesbaai 1n	4	1.680	<i>Tetragonia decumbens</i>	193	8.2	186.1	0.40
112*	vleesbaai 2n	4	1.879	<i>Tetragonia decumbens</i>	187	8.3	138.1	0.44
113*	vleesbaai 3n	5	3.879	<i>Tetragonia decumbens</i>	119	8.2	79.2	0.30
114*	hartenbos 1n	2	1.732	<i>Sporobolus virginicus</i>	160	8.1	110.1	0.11
115*	hartenbos 2n	5	2.506	<i>Thinopyrum distichum</i>	147	7.9	305.1	0.42
116*	klein brakrivier 1n	7	2.721	<i>Thinopyrum distichum</i>	131	7.7	65.7	0.16
117*	groot brakrivier 1n	4	2.480	<i>Tetragonia decumbens</i>	170	8.1	209.1	0.31
118*	hershams 1n	10	2.600	<i>Myrica cordifolia</i>	154	8.0	49.7	0.23
119*	outeniqua strand 1n	10	5.890	<i>Tetragonia decumbens</i>	89	7.9	94.4	0.49
120*	swartvlei 1n	8	2.880	<i>Tetragonia decumbens</i>	114	7.3	98.3	0.29
121*	sedgfield 1n	6	2.343	<i>Tetragonia decumbens</i>	150	8.0	56.7	0.38
122*	sedgfield 2n	2	1.840	<i>Tetragonia decumbens</i>	159	8.3	107.1	0.34
123*	sedgfield 3n	5	2.788	<i>Tetragonia decumbens</i>	129	8.1	173.1	0.47
124*	goukamma 1n	3	1.158	<i>Arctotheca populifolia</i>	267	8.0	104.1	0.39

125*	goukamma 2n	3	1.422	<i>Gazania rigens</i>	219	8.1	96.7	0.25
126*	buffelsbaai 1n	7	3.220	<i>Tetragonia decumbens</i>	136	8.2	99.3	0.41
127*	plettenberg bay 1n	7	3.483	<i>Metalsia muricata</i>	127	8.1	41.0	0.21
128*	plettenberg bay 2n	4	1.724	<i>Ehrharta villosa</i>	168	8.1	51.5	0.26
129*	oysterbay 1n	4	1.477	<i>Chrysanthemoides monilifera</i>	238	7.4	48.8	0.29
130*	oysterbay 2n	9	5.771	<i>Chrysanthemoides monilifera</i>	66	7.3	99.0	0.25
131*	sardinia bay 1n	5	2.884	<i>Gazania rigens</i>	129	8.7	34.9	0.36
132*	port alfred (west) 1n	8	3.279	<i>Chrysanthemoides monilifera</i>	142	8.2	70.1	0.35
133*	port alfred (west) 2n	5	2.055	<i>Chrysanthemoides monilifera</i>	175	8.1	330.4	0.63
134*	port alfred (east) 1n	5	2.819	<i>Thinopyrum distichum</i>	157	8.1	343.4	0.33
135*	port alfred (east) 2n	6	1.643	<i>Sporobolus virginicus</i>	167	8.2	121.4	0.43
136*	kleinemonde 1n	7	2.164	<i>Scaevola plumieri</i>	132	8.2	492.0	0.06
137*	kleinemonde 2n	5	2.239	<i>Thinopyrum distichum</i>	134	8.0	471.0	0.43
138*	kleinemonde 3n	9	4.133	<i>Passerina rigida</i>	136	8.0	537.0	0.49
139*	kleinemonde 4n	2	1.015	<i>Scaevola plumieri</i>	293	8.2	424.0	0.35
140*	kleinemonde 5n	8	1.740	<i>Cynanchum natalitium</i>	184	8.1	418.0	0.37
141*	old woman's river 1n	4	1.026	<i>Scaevola plumieri</i>	283	8.4	32.2	0.40
142*	old woman's river 2n	6	2.703	<i>Passerina rigida</i>	150	8.4	59.3	0.22
143*	hamburg 1n	4	1.115	<i>Ehrharta villosa</i>	242	8.4	24.9	0.25
144*	hamburg 2n	4	1.177	<i>Sporobolus virginicus</i>	220	8.6	30.1	0.30
145*	gulu mouth 1n	4	2.470	<i>Ipomoea pes-caprae</i>	185	8.3	29.9	0.21
146*	gulu mouth 2n	6	1.907	<i>Chrysanthemoides monilifera</i>	192	8.3	24.9	0.20

Appendix 4.3: Plant species recorded in 82 *A. arenaria* stands and 64 indigenous dune stands along the South African Cape coast between Koeberg (Western Cape) and Gonubie (Eastern Cape). A total of 75 species was recorded. The stands were from the foredune and intermediate dune zone.

Monocotyledonae	Dicotyledonae		
Poaceae <i>Ammophila arenaria</i> <i>Cladoraphis cyperoides</i> <i>Cynodon dactylon</i> <i>Ehrharta villosa</i> <i>Lolium perenne</i> <i>Pennisetum clandestinum</i> <i>Pentaschistis eriostoma</i> <i>Thinopyrum distichum</i> <i>Sporobolus virginicus</i>	Myricaceae <i>Myrica cordifolia</i>	Polygalaceae <i>Nylandtia spinosa</i>	Goodeniaceae <i>Scaevola plumieri</i>
Cyperaceae <i>Cyperus</i> sp. <i>Ficinia lateralis</i> <i>Mariscus congestus</i> <i>Scirpus nodosus</i>	Chenopodiaceae <i>Atriplex nummularia</i>	Anacardiaceae <i>Rhus crenata</i>	Asteraceae <i>Arctotheca populifolia</i> <i>Arctotis elongata</i> <i>Chrysanthemoides monilifera</i> <i>Cineraria geifolia</i> <i>Conyza canadensis</i> <i>Didelta carnosus</i> <i>Felicia amelloides</i> <i>Felicia</i> sp. <i>Gazania rigens</i> <i>Helichrysum asperum</i> <i>Helichrysum crispum</i> <i>Helichrysum cymosum</i> <i>Helichrysum patulum</i> <i>Helichrysum praecinctum</i> <i>Metalasia muricata</i> <i>Osteospermum ecklonis</i> <i>Osteospermum fruticosum</i> <i>Pteronia camphorata</i> var. <i>longifolia</i> <i>Senecio elegans</i> <i>Senecio litorosus</i> <i>Senecio</i> sp. <i>Stoebe plumosa</i> <i>Taraxacum officinale</i> <i>Ursinia chrysanthemoides</i> <i>Vellereophyton vellereum</i>
Restionaceae <i>Ischyrolepis eleocharis</i>	Aizoaceae <i>Tetragonia decumbens</i>	Thymelaeaceae <i>Passerina ericoides</i> <i>Passerina rigida</i>	
Asphodelaceae <i>Trachyandra divaricata</i>	Mesembryanthemaceae <i>Carpobrotus deliciosus</i> <i>Carpobrotus edulis</i> <i>Drosanthemum candens</i> <i>Malephora lutea</i> <i>Malephora mollis</i>	Apiaceae <i>Dasispermum suffruticosum</i>	
Iridaceae <i>Gladiolus gueinzii</i> <i>Moraea fugax</i>	Caryophyllaceae <i>Silene primuliflora</i> <i>Silene crassifolia</i>	Gentianaceae <i>Chironia baccifera</i>	
	Fabaceae <i>Acacia cyclops</i> <i>Acacia saligna</i> <i>Psoralea repens</i> <i>Sutherlandia tomentosa</i> <i>Sutherlandia frutescens</i>	Asclepiadaceae <i>Cynanchum natalitium</i>	
	Geraniaceae <i>Geranium incanum</i> <i>Pelargonium capitatum</i>	Convolvulaceae <i>Ipomoea pes-caprae</i> ssp. <i>brasiliensis</i>	
	Oxalidaceae <i>Oxalis hirta</i>	Lamiaceae <i>Salvia africana-lutea</i>	
		Solanaceae <i>Solanum americanum</i> <i>Solanum nigrum</i>	
		Scrophulariaceae <i>Manulea obovata</i>	
		Rubiaceae <i>Anthospermum littoreum</i>	
			spec. indet.

Appendix 4.4: Floristic and edaphic properties of all 19 Sylt stands.

stand no.	stand name	species richness	Simpson's diversity (d_s)	dominant species	IV	pH	conductivity (μScm^{-1})	org. matter (% dry weight)
1	ellenbogen süd	10	2.619	<i>A.arenaria</i>	158	6.3	9.5	0.09
2	ellenbogen süd	11	1.641	<i>A.arenaria</i>	199	6.7	9.7	0.03
3	ellenbogen süd	11	5.072	<i>A.arenaria</i>	74	6.5	10.7	0.29
4	ellenbogen mitte	3	1.061	<i>A.arenaria</i>	270	7.2	36.6	0.10
5	ellenbogen mitte	4	1.807	<i>A.arenaria</i>	186	8.9	38.8	0.07
6	ellenbogen mitte	11	1.385	<i>A.arenaria</i>	221	8.6	105.2	0.08
7	ellenbogen mitte	5	2.028	<i>A.arenaria</i>	183	6.2	23.2	0.03
8	hörnum	11	2.204	<i>A.arenaria</i>	165	5.9	9.4	0.06
9	hörnum	6	2.436	<i>A.arenaria</i>	137	7.6	12.8	0.21
10	hörnum	3	2.042	<i>A.arenaria</i>	151	6.6	11.4	0.03
11	puan klent	4	1.227	<i>A.arenaria</i>	234	6.1	16.8	0.07
12	puan klent	7	3.105	<i>A.arenaria</i>	133	6.4	12.3	0.07
13	hörnum-rantum	5	1.092	<i>Empetrum nigrum</i>	237	6.2	10.1	0.12
14	ellenbogen spitze	3	1.281	<i>A.arenaria</i>	231	6.5	14.5	0.07
15	ellenbogen spitze	2	1.241	<i>A.arenaria</i>	237	6.6	28.4	0.04
16	ellenbogen spitze	2	1.004	<i>A.arenaria</i>	290	6.5	21.0	0.07
17	ellenbogen spitze	3	1.169	<i>A.arenaria</i>	263	6.4	18.5	0.07
18	listland	8	2.649	<i>Empetrum nigrum</i>	121	4.3	24.2	3.16
19	listland	9	4.500	<i>A.arenaria</i>	120	5.8	13.7	0.44

Appendix 4.5: Plant species recorded in all 19 dune stands sampled on Sylt Island, Germany. Of these, 17 stands were dominated by *A. arenaria*, and 2 stands were dominated by *Empetrum nigrum*. A total of 25 species was recorded. The stands were of the foredune, intermediate dune and backdune zone.

Monocotyledonae	Dicotyledonae	
Poaceae <i>Agrostis tenuis</i> <i>Ammophila arenaria</i> <i>Corynephorus canescens</i> <i>Elymus farctus</i> ssp. <i>borealis-atlanticus</i> <i>Festuca ovina</i> <i>Festuca rubra</i> ssp. <i>arenaria</i> <i>Koeleria glauca</i> <i>Leymus arenarius</i> Cyperaceae <i>Carex arenaria</i> <i>Carex</i> cf. <i>ericetorum</i>	Fabaceae <i>Lathyrus maritima</i> Violaceae <i>Viola canina</i> <i>Viola tricolor</i> Ericaceae <i>Calluna vulgaris</i> <i>Vaccinium uliginosum</i> Empetraceae <i>Empetrum nigrum</i> Caryophyllaceae <i>Honckenia peploides</i>	Polygonaceae <i>Polygonum neglectum</i> <i>Rumex acetosella</i> Rubiaceae <i>Galium verum</i> Campanulaceae <i>Jasione montana</i> Asteraceae <i>Hieracium umbellatum</i> <i>Hypochoeris glabra</i> <i>Hypochoeris radicata</i> <i>Sonchus arvensis</i>

CHAPTER FIVE

Succession of *Ammophila arenaria* communities in South Africa

5.1 Introduction

The succession of *A. arenaria* communities along the European coast has been well documented by various authors (e.g. Willis *et al* 1959b; Ranwell 1972; Huiskes 1979; see Chapter 1). *A. arenaria* occurs in small numbers at the back-beach, forming embryonal dunes, and becomes the dominant plant in the yellow dune phase. Increasing sand stability causes its decline and subsequent replacement by other species. This pattern of succession can be disturbed if erosion occurs in the stable backdune zone which encourages the re-establishment of *A. arenaria* and a repetition of the succession at spatially restricted patches.

Succession in artificial coastal dunes appears to follow the same pattern as in natural dune systems. Studies of the colonisation of man-made *A. arenaria* dunes in Great Britain (Hewett 1970), the Netherlands (van Dorp *et al* 1985), and Denmark (Hansen & Vestergaard 1986) show how young *A. arenaria* plantings develop into dense, vigorous stands of *A. arenaria* and, with increasing sand stability, decline to make room for secondary species. The *A. arenaria* plantings develop into grey dunes and possibly dune woodland of similar species composition to those derived from natural *A. arenaria* foredunes, but over a much shorter time period. *A. arenaria* remains dominant only in plantings close to the shore.

Comprehensive studies of succession in South African coastal systems have been carried out by Lubke & Avis (1988), Avis (1992) and Avis & Lubke (1996) on dunes of the Eastern Cape and KwaZulu-Natal. These studies were undertaken in natural dune systems where no *A. arenaria* was present. No information is as yet available on the possible succession of *A. arenaria* dunes in South Africa. The only South African study that focuses on the succession of artificial dunes has been carried out on Eastern Cape dunes that were stabilised with indigenous species (Avis 1995). North American studies indicate that *A. arenaria* is not necessarily affected by increasing stability of the substrate and can grow inland (van Hook 1983), thereby

disturbing the natural pattern of succession along Californian and Oregon shores. In view of *A. arenaria*'s potential invasiveness in South Africa, it is essential to investigate whether South African *A. arenaria* declines in stable sand and is replaced by indigenous species.

In this chapter, the development of a large-scale *A. arenaria* stabilisation area in South Africa over several decades is examined. Furthermore, a preliminary study of the possible impact of plant-parasitic nematodes on the die-back of *A. arenaria* in South Africa was undertaken. The harmful effects that soil-borne pathogens have on *A. arenaria* in increasingly stable sand and their impact on the succession of dunes have been investigated in Dutch dune systems (van der Putten *et al* 1988, 1990, 1993). The uninhibited growth of *A. arenaria* along the North American West coast even in stable sand can be due to a lack of such soil-borne pathogens. Absence of pathogens is often attributed to biological invasion (di Castri; see Chapter 2), and it is to be examined whether the possible die-back of South African *A. arenaria* in stable sand can be related to the presence of harmful soil organisms.

5.2 Succession of a large-scale stabilisation site at De Mond Nature Reserve, southwestern Cape

5.2.1 Introduction

To examine long-term changes in large stabilisation areas involving *A. arenaria* and determine the potential of succession in such initially monospecific *A. arenaria* stands, studies were carried out in a large stabilisation area in the vicinity of the mouth of the Heuningnes River. The mouth is part of the De Mond Nature Reserve (formerly De Mond State Forest), situated on the coast of the Agulhas Plain near Bredasdorp, and surrounded by extensive dunefields to the northwest and southeast (Fig. 5.1). These mobile dunes used to block the river mouth in the dry summer months during strongest sand movement, which would cause flooding of the low-lying hinterland during the rainy winter season. To prevent further flooding events, large scale stabilisations of the driftsands with *A. arenaria* were started in the 1930's and continued in succeeding years to various degrees. To this day *A. arenaria* is planted at De Mond on a smaller, patchier scale.

The present study will focus on the change over time that this large stabilisation area has undergone and analyse possible successional patterns. The vegetation at De Mond has been described to some extent by Walsh (1968) and Bickerton (1984), but no account has yet been given on succession in the De Mond dunes since they were reclaimed. With regard to the potentially negative impact that *A. arenaria* can have on South African coastal ecosystems, the De Mond Nature Reserve is an ideal site for investigations of long-term vegetation changes in areas of large-scale planting of the grass. It will be of great importance for this project to assess whether the extensive *A. arenaria* stands at De Mond have been succeeded by indigenous plants or whether *A. arenaria* has spread and invaded the fynbos hinterland of the reserve.

The following key questions are addressed:

- 1) Has the stabilisation site at De Mond been succeeded by indigenous dune plants? If yes, how quickly does succession take place? At what locations does A. arenaria persist longest?*
- 2) What is the species composition of the various stages of succession? What indigenous plants get established first in the stabilisation site, and what plants get established later?*
- 3) How do edaphic factors of the soil and other environmental factors influence the succession?*

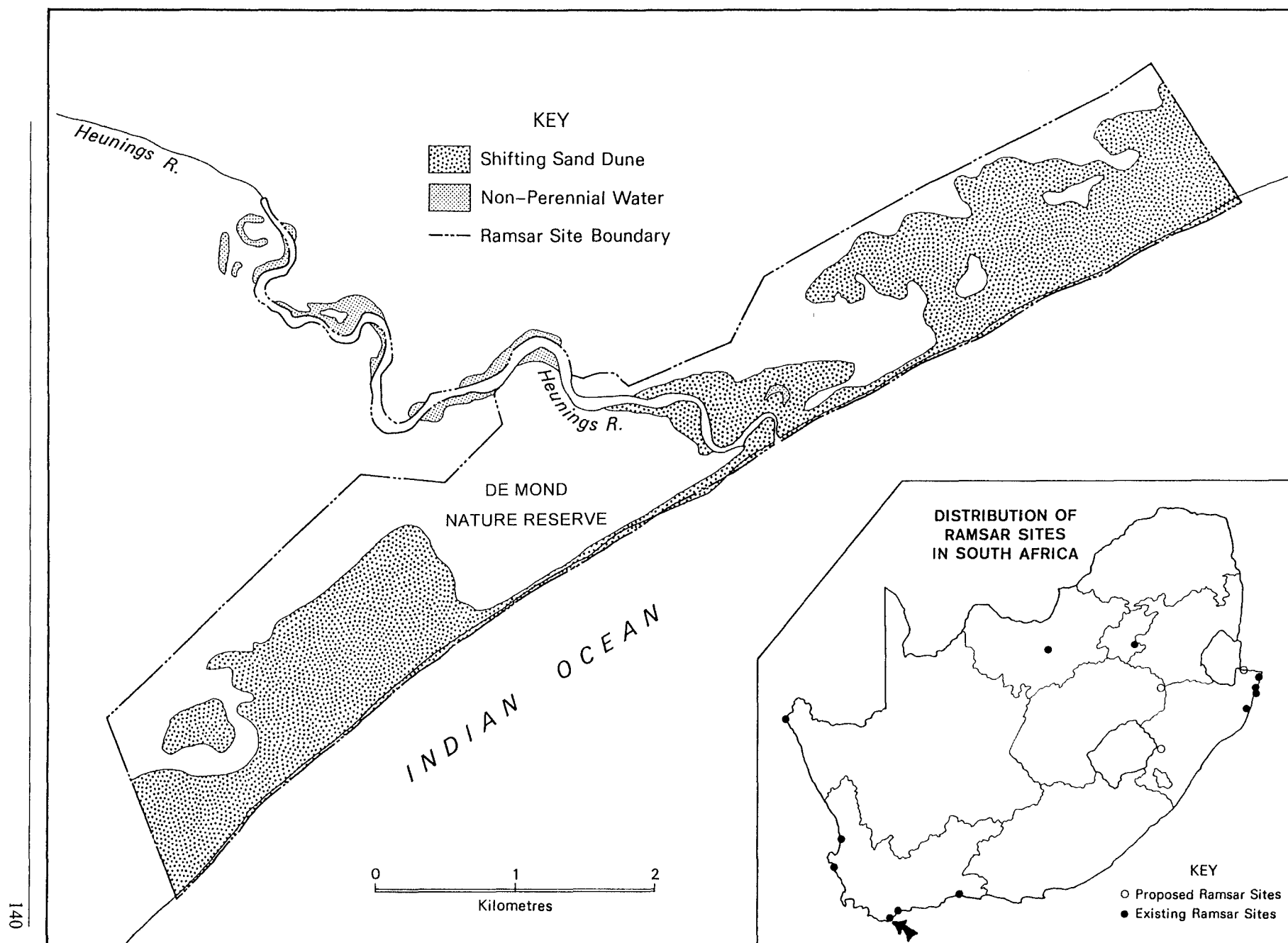


Fig. 5.1: Situation of the Heuningnes River mouth in the De Mond Nature Reserve, and distribution of other important Ramsar sites in South Africa (Cowan & Marneweck 1996).

5.2.2 Study area

5.2.2.1 Physiography and climate

The mouth of the Heuningnes River is situated at 34°43'S; 20°07'E in the Bredasdorp district of the Western Cape province of South Africa (Fig. 5.1). The estuary is the southernmost of the African continent, not more than 15 kilometres north of Cape Agulhas, and was designated at the Ramsar Convention as a Wetland of International Importance in 1986 (Cowan & Marneweck 1996). The lower reaches of the estuary fall within the De Mond Nature Reserve (1768 ha). From 1939 the Minister of Agriculture and Forestry started buying land around the Heuningnes estuary with the intention of stabilising the driftsands (Bickerton 1984). The land was managed by the Department of Forestry until Cape Nature Conservation took over in the mid 1980's

The soil is sandy with limestone outcrops (Day 1981). De Mond Nature Reserve falls within South Africa's winter rainfall area, with wet winters and mostly hot and dry summer (Fig. 3.2). The mean annual precipitation for the Heuningnes drainage system is around 400 mm, maximum daily temperature means are 28°C for January and 17°C for July, winds are mainly from the west in winter and from the southwest and southeast in summer (Fig. 5.2). It is especially the high-velocity southeasterly winds during summer that cause shifting of the then dry and hot dune sands (Bickerton 1984). Long-term observations of deep sea waves for the coast off Struisbaai near De Mond Nature Reserve have shown that the predominant direction of deep sea waves is from the southwest. Nevertheless, sediment transport along the De Mond shore is only slightly higher to the northeast than to the southwest. (Bickerton 1984). The vegetation inland of the reserve is mostly coastal scrub or coastal fynbos or a mix of both if it is not under cultivation. A recently published field guide describes the vegetation of the broader area, and interestingly, no mention of *A. arenaria* is made (Mustart *et al* 1997).

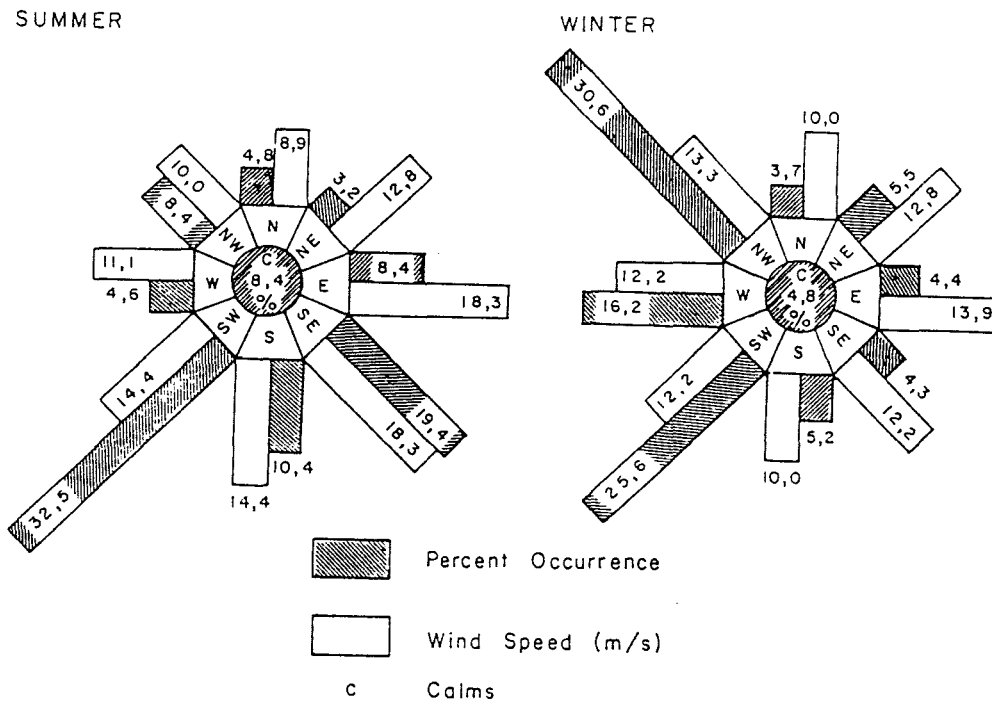


Fig. 5.2: Wind distribution and speed at Cape St. Blaize near Mossel Bay in winter and summer (Bickerton 1984).

5.2.2.2 History of the area

In the past, driftsands used to block the mouth of the Heuningnes River in summer, when sand movement is highest (see above) and the flow of the river low. This would cause severe floodings of the low-lying farmland behind the reserve during the rainy winter season. Farmers were severely afflicted by the frequent blocking of the Heuningnes River mouth. At the beginning of the century “a rise of 20 feet in waterlevel at the river mouth would cause flooding of about 90 square miles of inland farms” (Walsh 1968). Keet states in his report on driftsands (1936) that “the condition of the Bredasdorp coast is really a desperate one, ... unless reclamation work is taken in hand”. Figure 5.3 illustrates the extension of farmland of the Agulhas plain that was so low-lying as to be prone to inundation. Severe floodings occurred in 1871, 1880, 1902, 1903, 1906 and 1920 (Bickerton 1984). In 1937 the Minister of Agriculture and Forestry was approached by farmers of the district who requested the reclamation of the driftsands. Interestingly, the Minister had to assure the farmers that no use of Australian rooikrans (*Acacia cyclops*) would be made (Bickerton 1984). *Acacia cyclops* had been used for

driftsand reclamation in South Africa since the mid 1850's (Shaughnessy 1980; see also Chapter 3). The above 1937 record is probably the first of a public concern about its aggressiveness (Stehle 1987). Instead of rooikrans, the European dune grass *A. arenaria* was used at De Mond.

Although, according to Walsh (1968), the reclamation work at De Mond was only started in 1942, a 1940 "stock map of the De Mond Forest Reserve" by forester J. De Genis (Cape Nature Conservation, De Hoop) displays many patches of dunes along the Heuningnes estuary that were stabilised with *A. arenaria* in 1939, two patches opposite the Forestry Station even in 1931 (Fig. 5.4). From the late 1930's the stabilisation of driftsands at De Mond has been continued until present times. Between 1942 and 1958 alone a total of 283 ha were stabilised (Walsh 1968), today the stabilised area extends over some 900 ha.

Aerial photographs from 1938 to 1989 (Plate 5.1 I and II) show clearly the change from completely mobile driftsands to densely vegetated dunes on either side of the river mouth. All photos except the ones from 1938 and 1976 show an open river mouth, which is, according to Bickerton (1984), primarily due to an artificial littoral dune between the estuary and the sea. It was built parallel to the coast by erecting droppers and palings along the beach to support brushwood which trapped sand that was then artificially vegetated. While the large scale stabilisation of driftsands in the vicinity of the river mouth is preventing any further blockage of the mouth, it is the artificial littoral dune to the front of the mouth which keeps it open in the first place, and must therefore be constantly maintained. In spite of all efforts, the mouth was closed from 1973 to 1976 (see Plate 5.1 II: 1976 photo). Hence, while Stehle (1987) speaks of the "successes at De Mond" concerning the reclamation work, Bickerton (1984) sees a problem: "The Heuningnes is a good example of how the solution of one estuarine problem, that is the inundation of the agricultural hinterland, has created another one, namely the expensive continuous maintenance of an artificial mouth."

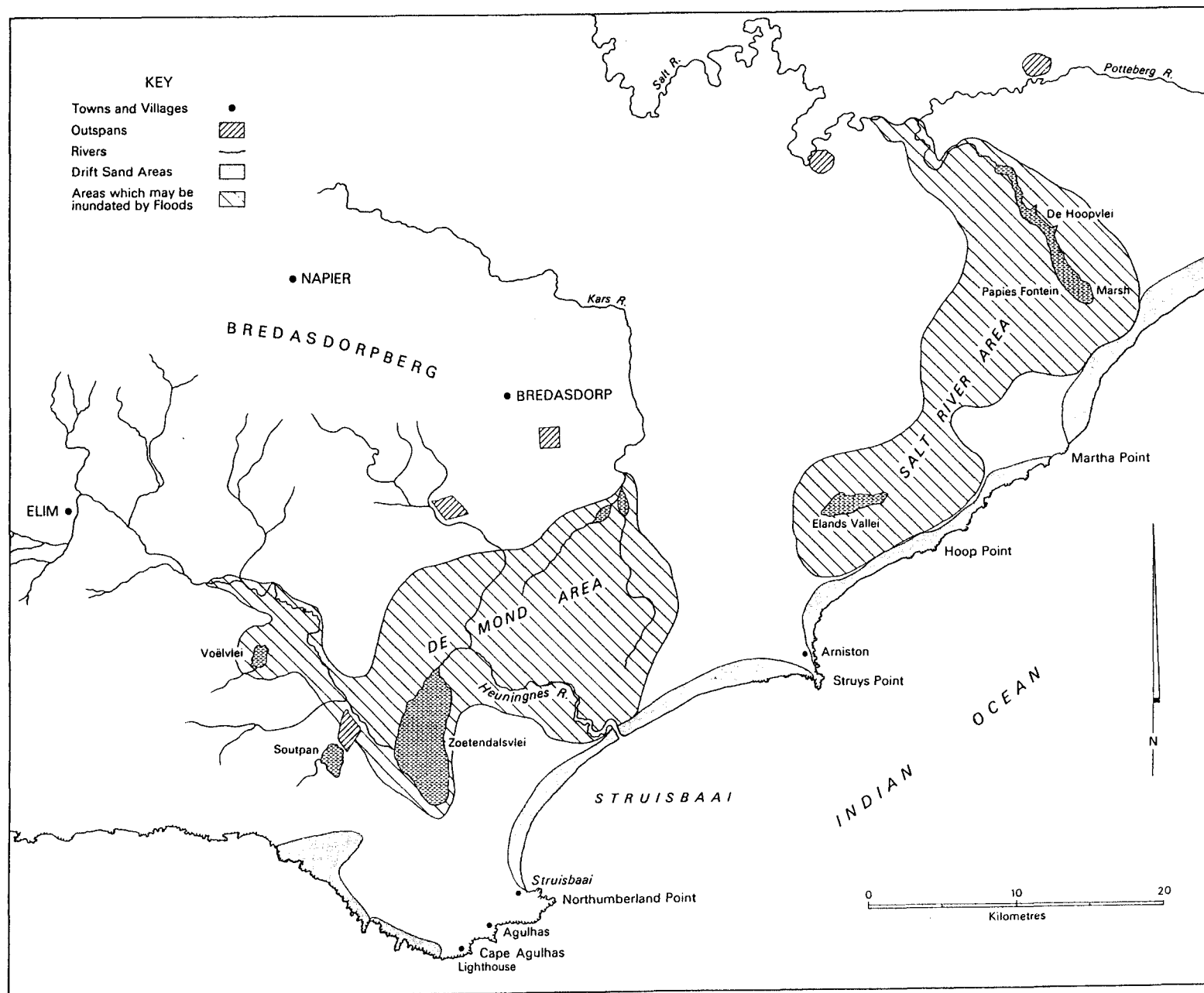


Fig. 5.3: Estuaries of the Heuningnes River and Salt River on the Agulhas plain, and areas that are exposed to their flooding. After "Divisional map of Bredasdorp 1901" (Cape Nature Conservation, De Hoop).

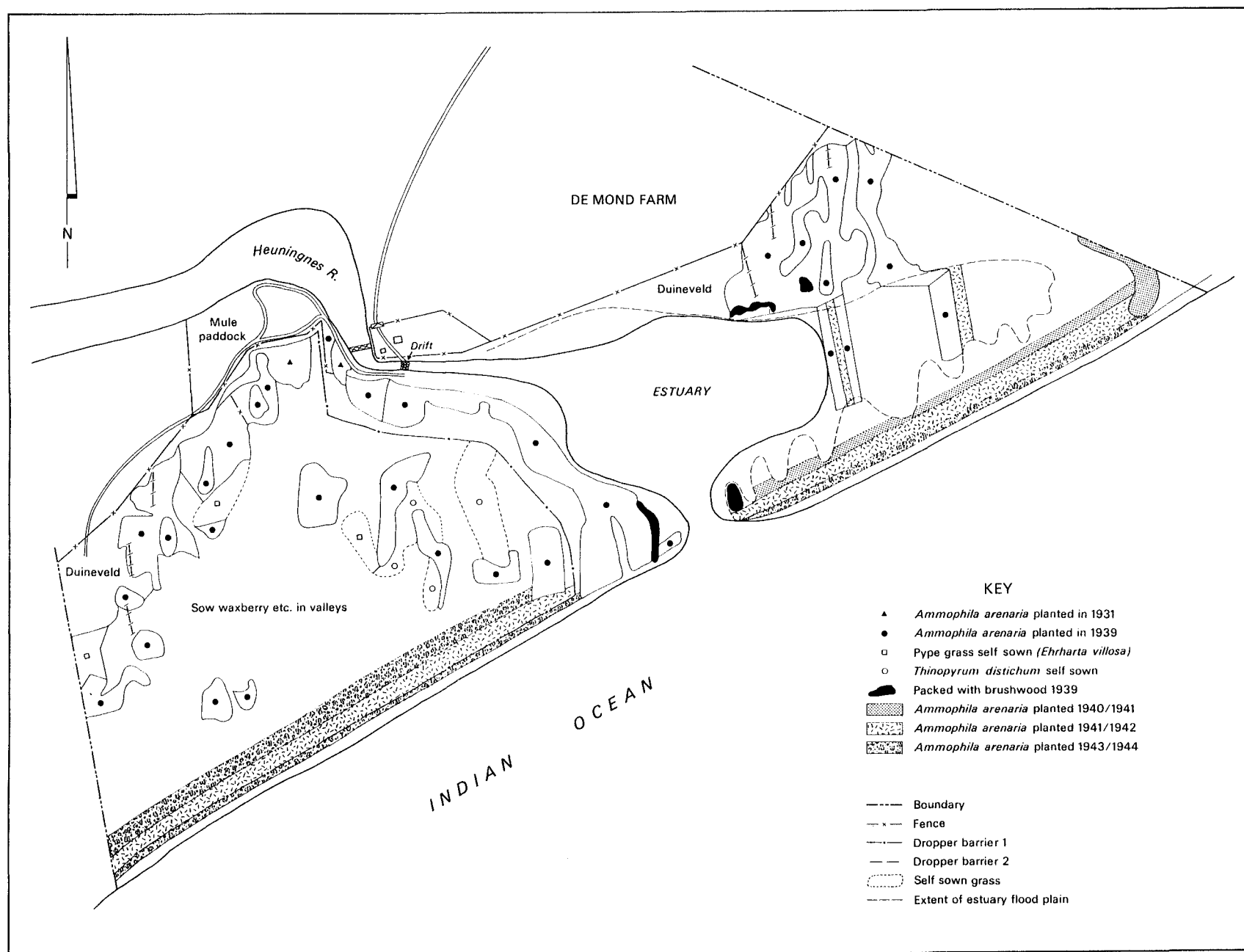


Fig. 5.4: Stabilisation efforts at De Mond Nature Reserve (then De Mond State Forest) in the 1930's and 1940's. After "Stock map of De Mond Forest Reserve 1940" by J. De Genis (Cape Nature Conservation, De Hoop).

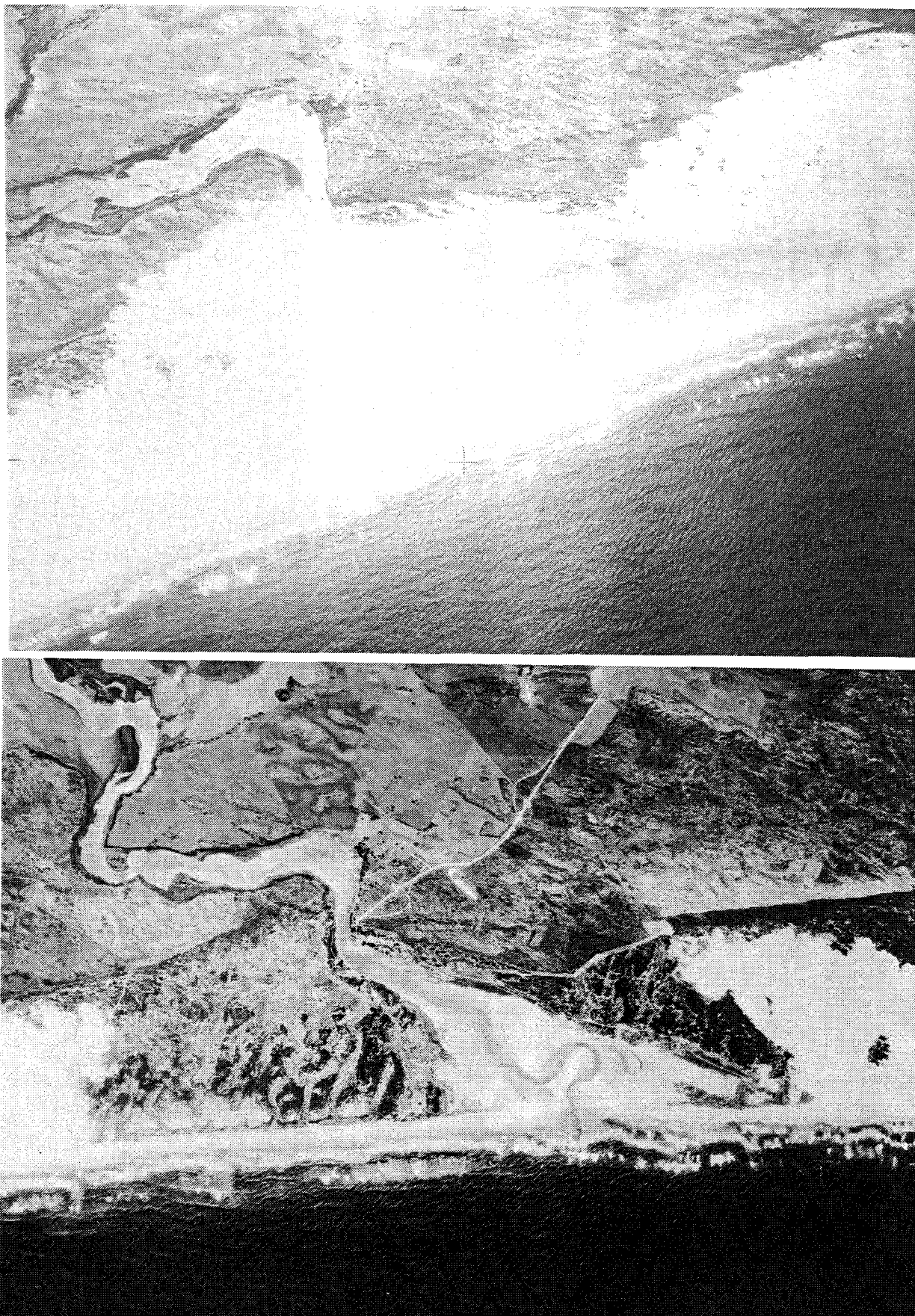


Plate 5.1 I: Aerial photographs of the De Mond Estuary and Nature Reserve from 1938 (top; bare driftsands, river mouth blocked) and 1961 (bottom; driftsands have been stabilised partially, river mouth open).

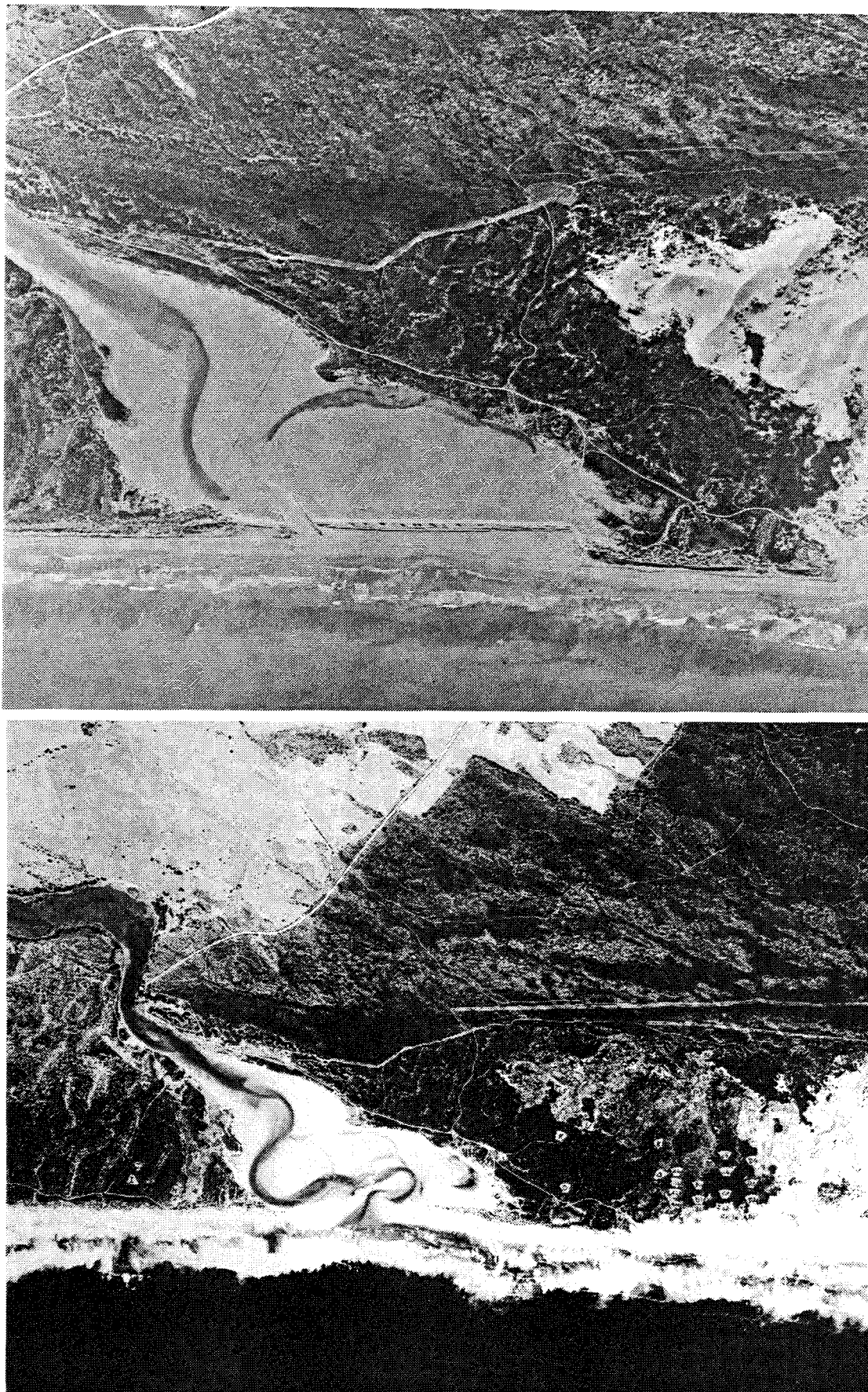


Plate 5.1 II: Aerial photographs of the De Mond Estuary and Nature Reserve from 1976 (top; river mouth blocked again) and 1989 (bottom; river mouth open, stands that were sampled in this study are marked).

5.2.2.3 Methods of stabilisation at De Mond Nature Reserve

Since the first efforts in the 1930's until the present day, the same stabilisation technique has been applied at De Mond with only slight variations. In view of other stabilisation practices of the time, particularly the planting of Australian acacias in many other areas, this technique was very advanced for the 1930's: between the planted clumps of *A. arenaria*, seed of indigenous dune plants was sown, mostly of shrub species like *Metalasia muricata* and *Chrysanthemoides monilifera*. Therefore a seed bank of indigenous species was created in the stabilisation area which would encourage the succession of the mostly monospecific *A. arenaria* stands by indigenous dune plants. Once the driftsands were fixed to a certain extent by *A. arenaria*, seedlings of indigenous dune plants would establish successfully and "take over" the area from *A. arenaria*.

A typical record of present day dune reclamation work at De Mond is shown in Table 5.1. A total area of 41.3 ha was stabilised with *A. arenaria*, an area of 7.38 ha packed with brushwood, and 6.9 kilometres of brushwood fence built between May 1987 and August 1991. The original source of *A. arenaria* for the first plantings in 1931 are unknown (see Chapter 3), but for all later plantings vigorous local *A. arenaria* stands were made use of, both at De Mond and the nearby site of Waenhuiskrans. Table 5.1 shows the effort of sowing indigenous dune plants among the recently planted *A. arenaria* sites, particularly the dune scrub species *Myrica cordifolia* and *Chrysanthemoides monilifera*. Although such sowing is mentioned only for the years 1987 and 1988, it is assumed that similar efforts were undertaken in the other years, whenever *A. arenaria* was planted. It is also interesting to note that fertiliser has been added to the *A. arenaria* plantings at several times and that invader plants (presumably *Acacia* spp.) have been removed in the reserve.

Figure 5.4 illustrates the stabilisation efforts at De Mond in the 1930's and 1940's. The foredunes were stabilised with *A. arenaria* in three continuous rows between 1940 and 1944, while the stabilisation of the larger and more inland part of the dunefield is patchier and focuses mostly on the more exposed areas of higher elevation. It is noteworthy that the indigenous dune grass species *Thinopyrum distichum* and *Ehrharta villosa* occurred naturally at several spots, which were consequently spared *A. arenaria* plantings. Dune scrub species like

waxberry (*Myrica cordifolia*) were sown mostly in the dune valleys. Stabilisation efforts of the 1980's and 1990's are shown in Plate 5.2.



Plate 5.2: Government Forester Hendrik O. Swart among fresh *A. arenaria* plantings at De Mond in the mid 1980's (top; courtesy of Cape Nature Conservation, De Hoop); the most eastward extent of *A. arenaria* plantings cover the windward side of a large driftsand at De Mond in 1996 (middle); brushwood barrier at the Heuningnes River mouth in 1995 (bottom).

Table 5.1: Records of dune reclamation work at De Mond from May 1987 to December 1991 (courtesy of De Mond Nature Reserve).

month/ year	marram pulled out for planting (no. of clumps)	marram planted (ha)	seed sown amongst marram plantings (kg)	brushwood fence built (m), * = at mouth	area packed with brushwood (m ²)	other activities
6/1987	605	3.1	<i>Myrica cordifolia</i> (70), <i>Chrysanthemoides monilifera</i> (65), <i>Sutherlandia frutescens</i> (20), <i>Stoebe plumosa</i> (12)	350		"collect <i>Carpobrotus</i> seed and sow 2015 m ² "
7/1987	334	1.8		260	0.9	
8/1987	210	1.5	<i>Chrysanthemoides monilifera</i> (35), <i>Myrica cordifolia</i> (35), <i>Sutherlandia frutescens</i> (5), <i>Stoebe plumosa</i> (17), <i>Arctotis acaulis</i> (5), <i>Chironia baccifera</i> (8), <i>Metalasia muricata</i> (8), <i>Thinopyrum distichum</i> (10)	190	0.6	
9/1987				240		"sow fertiliser among marram":
5/1988	295	2.2	<i>Myrica cordifolia</i> (41), <i>Chrysanthemoides monilifera</i> (41), <i>Sutherlandia frutescens</i> (20), <i>Metalasia muricata</i> (12)	0		
6/1988	927	6.1	<i>Myrica cordifolia</i> (180), <i>Stoebe plumosa</i> (24), <i>Metalasia muricata</i> (32), <i>Chrysanthemoides monilifera</i> (80)	130		
7/1988	191	1.2	<i>Myrica cordifolia</i> (100), <i>Chrysanthemoides monilifera</i> (62), <i>Stoebe plumosa</i> (15), <i>Metalasia muricata</i> (26), <i>Arctotis acaulis</i> (18), <i>Chironia baccifera</i> (10)	213	0.9	
8/1988			<i>Myrica cordifolia</i> (25), <i>Chrysanthemoides monilifera</i> (25), <i>Arctotis acaulis</i> (5), <i>Stoebe plumosa</i> (11), <i>Metalasia muricata</i> (11)	130	1.1	
3/1989				?		"sow fertiliser among marram"
6/1989	673	4.6				
7/1989	216	2.2	?			
8/1989	104			210		"cut and remove invader plants"
9/1989				200 *		
10/1989				240		
11/1989				200		"sow fertiliser"
5/1990	186	1.6		230 *		
6/1990	300	2.2		35		
7/1990	71	6.9		370	0.7	
2,3/1991				905	1.08	"tear out invader plants"
4,5/1991			<i>Myrica cordifolia</i> (amount?)	600	2.0	
6,7/1991	493	7.9		1000	0.3	
8,9/1991				450		
10/1991				570 *		
11,12/1991				377 *		"tear out invader plants"

5.2.3 Methods

The vegetation and soil were sampled in 100 m² stands following the same method as in Chapter 4 (Section 4.2.3). Twenty three stands (A, B, C, D, ..., W) were laid out in a stratified random fashion throughout the reserve to ensure sampling of the various habitats, on the foredunes as well as in dense dune scrub, on steep slopes and hilltops as well as at the edge of the saltmarsh. More importantly, the stands were chosen according to J. De Genis' 1940 "stock map of De Mond Forest Reserve" (Fig. 5.4) and according to aerial photographs no.22406/job130 (1938), 8662/461 (1961), 1857/719 (1973), 0285/498-148 (1980), 325-3/391 (1981) and 2043/931 (1989) to represent differently aged stabilisation sites. They are situated in patches that were stabilised in 1931, 1939, between 1942 and 1961, between 1962 and 1973, between 1974 and 1981, between 1982 and 1989, and in the 1990's.

Nineteen other stands were laid out along 4 transects (a, b, c, d) perpendicular to the coastline, about 1330 to 2000 m to the northeast of the mouth of the Heuningnes River, extending between 52 m and 850 m from the high water mark. The time of their stabilisation was noted from the above mentioned maps and aerial photos. In addition, a 150 m transect was laid out at the same site as transect a. The vegetation along this transect was sampled continuously in 1m² stands for density, cover and frequency of each species. Soil samples were taken every 5 meters and tested for pH, conductivity and organic matter as described in Chapter 4.

All 42 stands (marked in 1989 photo of Plate 5.1 II) were combined for interpretation and subjected to comparisons of species richness, Simpson's diversity index, importance values of each species and edaphic factors. The dependence of these values on the age of the stands was examined in regression analyses. To detect patterns of succession the stands were subjected to the computerised classification and ordination techniques TWINSpan (Hill 1979) and CANOCO (ter Braak 1988) as was done in Chapter 4. The data used in both programmes were importance values per species per stand (for calculation of importance values see Chapter 4, Section 4.2.3).

In an indirect gradient analysis the ordination of stands was then interpreted with the environmental variables soil pH, soil conductivity (μScm^{-1}), organic matter content of soil (%)

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dry weight), time of stabilisation of the stands (ordinal data ranked from 1 to 9: 1 = 1931, 2 = 1939, 3 = before 1961, 4 = 1961-1973, 5 = 1974-1979, 6 = 1980/1981, 7 = 1982-1989, 8 = early 1990's, 9 = never stabilised), and topographical situation of the stands (ordinal data ranked from 1 to 6: 1 = within 150 m from high water mark, 2 = dry dune slack, 3 = backdune with level surface, 4 = top of backdune, 5 = slope of backdune, 6 = moist dune slack). A dune slack is here understood as a hollow between dune ridges which is often influenced by salt in the early stages of formation, generally influenced by moderate accretion and subject to the opposing influences of submergence or drought seasonally or at different stages of its development (Ranwell 1972).

5.2.4 Results

1) Evidence for succession

Table 5.2 reflects all 42 stands that were sampled at De Mond in chronological order. First, second and third most important species are recorded for each stand, and noteworthy characters of their respective topographical situation mentioned. Stand V has possibly never been stabilised with *A. arenaria*. The stabilisation of stand d4 is also questionable since aerial photos imply that this stand was part of a natural bushpocket amidst the former driftsands. In all others stands *A. arenaria* has been replaced by indigenous dune plant species to various degrees. The table shows clearly how dune fynbos species like *Ischyrolepis eleocharis* are often dominant in the older stands, while *Myrica cordifolia* is very common in medium-aged stands and *A. arenaria* in recently stabilised stands. A list of all species found in the De Mond stands is given in Appendix 5.1.

Table 5.2: List of characters of all 42 sampled stands at De Mond. Stands are listed in chronological order (HWM = high water mark).

stand	period stabilised	most important species	second most imp. sp.	third most imp. sp.	location	aspect (if slope)
A	1931	<i>Ischyrolepis eleocharis</i>	<i>Passerina paleacea</i>	<i>Otholobium bracteolatum</i>	margin of fynbos, behind <i>Sideroxylon inerme</i>	-
K	1931	<i>Rhus crenata</i>	<i>Metalasia muricata</i>	<i>Helichrysum patulum</i>	bottom of duneslope, 30 m from river	E
B	1939	<i>Ischyrolepis eleocharis</i>	<i>Passerina paleacea</i>	<i>Thamnochortus insignis</i>	fynbos, near old <i>Euclea racemosa</i> tree	-
C	1939	<i>Psoralea repens</i>	<i>Thesidium fragile</i>	<i>Ficinia indica</i>	margin of inner saltmarsh, 3 m from HWM	-
D	1939	<i>Ischyrolepis eleocharis</i>	<i>Metalasia muricata</i>	<i>Ficinia lateralis</i>	east end of salt marsh, 2nd transverse dune	-
F	1939	<i>Thinopyrum distichum</i>	<i>Didelta carnosa</i>	<i>Tetragonia decumbens</i>	front top of foredune west of mouth, ca. 30 m HWM	SE
G	1939	<i>Didelta carnosa</i>	<i>Tetragonia decumbens</i>	<i>Thesidium fragile</i>	top of foredune west of mouth, 10 m high, 40 m HWM	SE
H	1939	<i>Metalasia muricata</i>	<i>Chironia baccifera</i>	<i>Helichrysum patulum</i>	slope of old dune ridge	E
J	1939	<i>Ischyrolepis eleocharis</i>	<i>Myrica cordifolia</i>	<i>Pentaschistis eriostoma</i>	small dune in centre of slack, slightly more elevated	-
M	1939	<i>Ischyrolepis eleocharis</i>	<i>Thamnochortus insignis</i>	<i>Pentaschistis eriostoma</i>	upper slope of high transverse dune ridge	E
E	before 1961	<i>Ischyrolepis eleocharis</i>	<i>Rhus crenata</i>	<i>Ficinia ramosissima</i>	margin of fynbos, flat area near junction of 2 tracks	-
L	before 1961	<i>Limonium scabrum</i>	<i>Sarcocornia decumbens</i>	<i>Plantago crassifolia</i>	saltmarsh 70 m away from river, next to track within HWM	-
N	before 1961	<i>A. arenaria</i>	<i>Chironia baccifera</i>	<i>Thesidium fragile</i>	top of 3rd transverse dune behind extreme end of saltmarsh	-
b4	before 1961	<i>Myrica cordifolia</i>	<i>Metalasia muricata</i>	<i>Ficinia lateralis</i>	slack with dune scrub	-
b6	before 1961	<i>Ischyrolepis eleocharis</i>	<i>Passerina paleacea</i>	<i>Ficinia ramosissima</i>	top of high dune ridge far inland, many fynbos plants	-
c5	before 1961	<i>Myrica cordifolia</i>	<i>Ficinia lateralis</i>	<i>Chrysanthemoides monilifera</i>	dune slack area	-
I	1961-1973	<i>Myrica quercifolia</i>	<i>Myrica cordifolia</i>	<i>Chrysanthemoides monilifera</i>	slack behind transverse dune ridge away from river	-
U	1961-1973	<i>Rhus crenata</i>	<i>Myrica quercifolia</i>	<i>Ischyrolepis eleocharis</i>	slack with tall dune scrub, some fynbos plants	-
O	1973-1980	<i>Myrica cordifolia</i>	<i>Otholobium bracteolatum</i>	<i>Helichrysum patulum</i>	slack between transverse dune ridges, dead <i>A.a.</i> groundcover	WSW
R	1973-1980	<i>Ficinia lateralis</i>	<i>Helichrysum patulum</i>	<i>Ischyrolepis eleocharis</i>	dune slack with pebbles	-
a3	1973-1980	<i>Psoralea repens</i>	<i>Helichrysum patulum</i>	<i>Ficinia lateralis</i>	slack with loose dune scrub	-
a4	1973-1980	<i>Myrica cordifolia</i>	<i>Chrysanthemoides monilifera</i>	<i>Helichrysum patulum</i>	slack with tall dune scrub	-
S	1980-1981	<i>A. arenaria</i>	<i>Ficinia lateralis</i>	<i>Helichrysum patulum</i>	sandy, exposed, steep slope	SE
T	1980-1981	<i>Ischyrolepis eleocharis</i>	<i>Ficinia lateralis</i>	<i>Otholobium bracteolatum</i>	next to stand S, on top of same dune ridge	-
P	1980-1989	<i>Myrica cordifolia</i>	<i>Ficinia lateralis</i>	<i>Pentaschistis eriostoma</i>	upper slope of highest transverse dune ridge in area	SSW
Q	1980-1989	<i>Myrica cordifolia</i>	<i>Ficinia lateralis</i>	<i>Pentaschistis eriostoma</i>	slack beneath highest dune ridge of stand P	-
a1	1980-1989	<i>A. arenaria</i>	<i>Psoralea repens</i>	<i>Thinopyrum distichum</i>	top of high foredune, 130 m HWM	S

a2	1980-1989	<i>Psoralea repens</i>	<i>A. arenaria</i>	<i>Chironia baccifera</i>	slack behind dune, transition from <i>A. a</i> foredune to dune scrub	-
b2	1980-1989	<i>A. arenaria</i>	<i>Chironia baccifera</i>	<i>Psoralea repens</i>	<i>A.a.</i> foredune with medium aged-old plants, 121 m HWM	S
b3	1980-1989	<i>Psoralea repens</i>	<i>A. arenaria</i>	<i>Myrica cordifolia</i>	<i>A.a.</i> on slope	N
b5	1980-1989	<i>Myrica cordifolia</i>	<i>Ficinia lateralis</i>	<i>Pentstemon eriostoma</i>	slope on high dune ridge far inland	SE
c2	1980-1989	<i>A. arenaria</i>	<i>Chironia baccifera</i>	<i>Myrica cordifolia</i>	medium-old <i>A.a.</i> dune, dead stuff on ground, 130 m HWM	S
c3	1980-1989	<i>Sutherlandia frutescens</i>	<i>Myrica cordifolia</i>	<i>A. arenaria</i>	dune slack area, <i>Passerina rigida</i> invading	-
c4	1980-1989	<i>Ficinia lateralis</i>	<i>Psoralea repens</i>	<i>Metalasia muricata</i>	dune slack area, surrounded by <i>A.a.</i> dunes	-
d2	1980-1989	<i>Ficinia lateralis</i>	<i>Myrica cordifolia</i>	<i>Helichrysum praecinctum</i>	dune slack with pebbles and stones, <i>A.a.</i> & <i>Myrica cordifolia</i> invading?	-
d3	1980-1989	<i>Psoralea repens</i>	<i>A. arenaria</i>	<i>Myrica cordifolia</i>	gentle dune slope	SE
d4	1980-1989 (?)	<i>Myrica cordifolia</i>	<i>Ficinia lateralis</i>	<i>Chrysanthemoides monilifera</i>	slack with dune scrub (former bushpocket?)	-
W	early 1990's	<i>A. arenaria</i>	<i>Thinopyrum distichum</i>	<i>Senecio elegans</i>	vigorous <i>A. a.</i> stabilisation, high dune ridge, 102 m HWM	S
b1	early 1990's	<i>A. arenaria</i>	<i>Senecio elegans</i>	<i>Didelta carnosa</i>	little <i>A.a.</i> hummock, 4 m tall, 52 m HWM	S
c1	early 1990's	<i>Didelta carnosa</i>	<i>Thinopyrum distichum</i>	<i>Chrysanthemoides monilifera</i>	young, low foredune, 110 m HWM	S
d1	early 1990's	<i>A. arenaria</i>	<i>Didelta carnosa</i>	<i>Thinopyrum distichum</i>	<i>A.a.</i> hummock, 96 m HWM	S
V	never (?)	<i>Thinopyrum distichum</i>	-	-	vigorous <i>Thinopyrum distichum</i> community on foredune, 80 m HWM	S

Table 5.2 indicates that succession is taking place at De Mond. This is confirmed by a detrended correspondence analysis (DCA) of all 42 stands (Fig. 5.5). The stands are split into six distinct communities, as identified by TWINSpan (not shown), namely *A. arenaria* foredunes or recent plantings, stable dunes with some foredune elements, dune scrub, dune scrub/dune fynbos, saltmarsh and indigenous foredunes. Plate 5.3 illustrates some of these communities. While the first four communities are lined up along a gradient (axis 2) and represent sequential successional stages, the communities “saltmarsh” and “indigenous foredunes” cannot be placed within this line. The species composition of these stands shows no resemblance to that of the other stands because of their specific habitats: stands C and L have completely changed into saltmarsh communities, while in stands F, G and c1 *A. arenaria* has been replaced by indigenous foredune species.

A second DCA was therefore carried out without these stands and is shown in Figure 5.6, its related TWINSpan output in Figure 5.7. The four remaining communities can thus be distinguished more clearly, and it is possible to attribute their times of stabilisation to them. Stands of the early stage of foredunes dominated by *A. arenaria* were all stabilised in the 1980's and 1990's. Stands of the second community, the more stable dunes with few foredune elements, were mostly stabilised in the 1980's. Next are stands vegetated with dune scrub, many dominated by *Myrica cordifolia*, which is not surprising considering the amount of *Myrica cordifolia* seed that was sown among the *A. arenaria* plantings (Table 5.1). Although most stands in this community were also stabilised in the 1980's, several were stabilised in the 1960's and 1970's, one stand even in 1939. The last community contains stands of an advanced dune vegetation, leading either to a species-rich scrub vegetation characterised by *Rhus crenata* or *Myrica quercifolia*, or to dune fynbos with a clear dominance of the restio *Ischyrolepis eleocharis*. These were stabilised long ago, namely in 1931, 1939 or in the 1950's and 1960's.

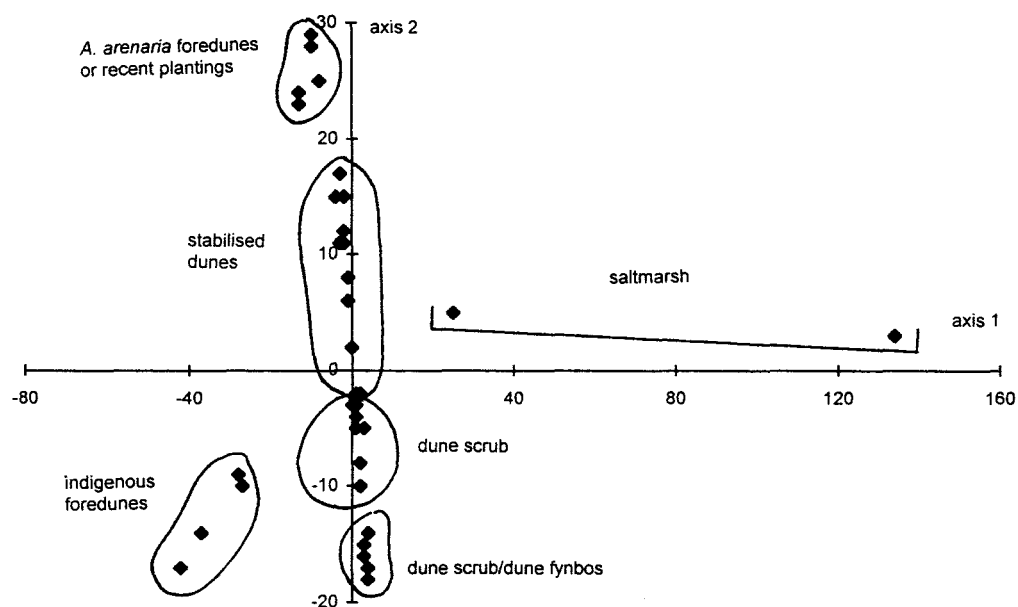


Fig. 5.5: A detrended correspondence analysis (DCA) of all 42 stands sampled in De Mond Nature Reserve shows six distinct communities as identified by TWINSpan (not shown).

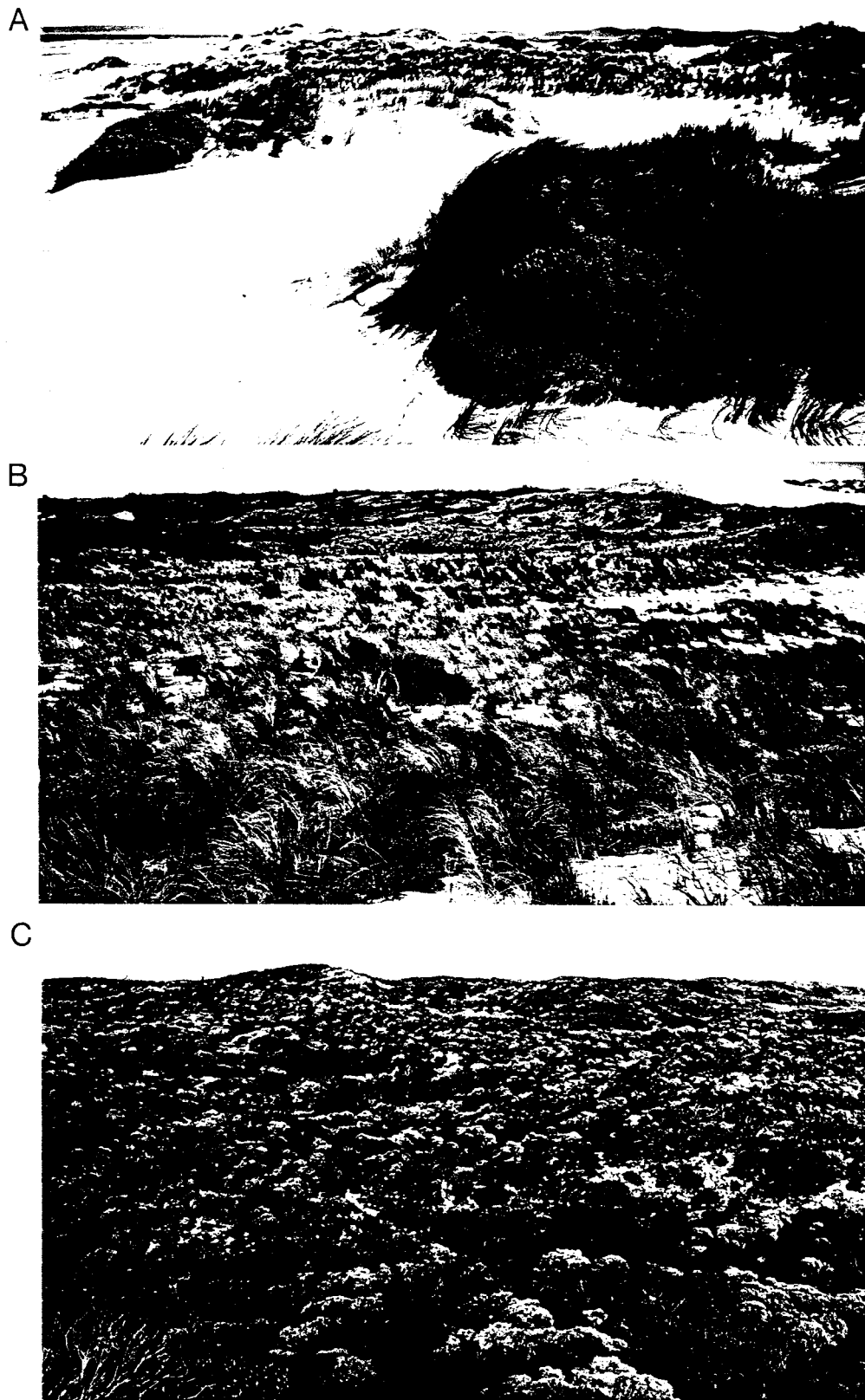


Plate 5.3: Illustrations of different communities found at De Mond (see Fig. 5.5): A. *A. arenaria* dominated foredunes or recent plantings (with *Didelta carnosa*). B. Increasingly stable dunes. C. Dune scrub and enriched dune scrub or dune fynbos. Photographs A and B taken in February 1996, photograph C in June 1996.

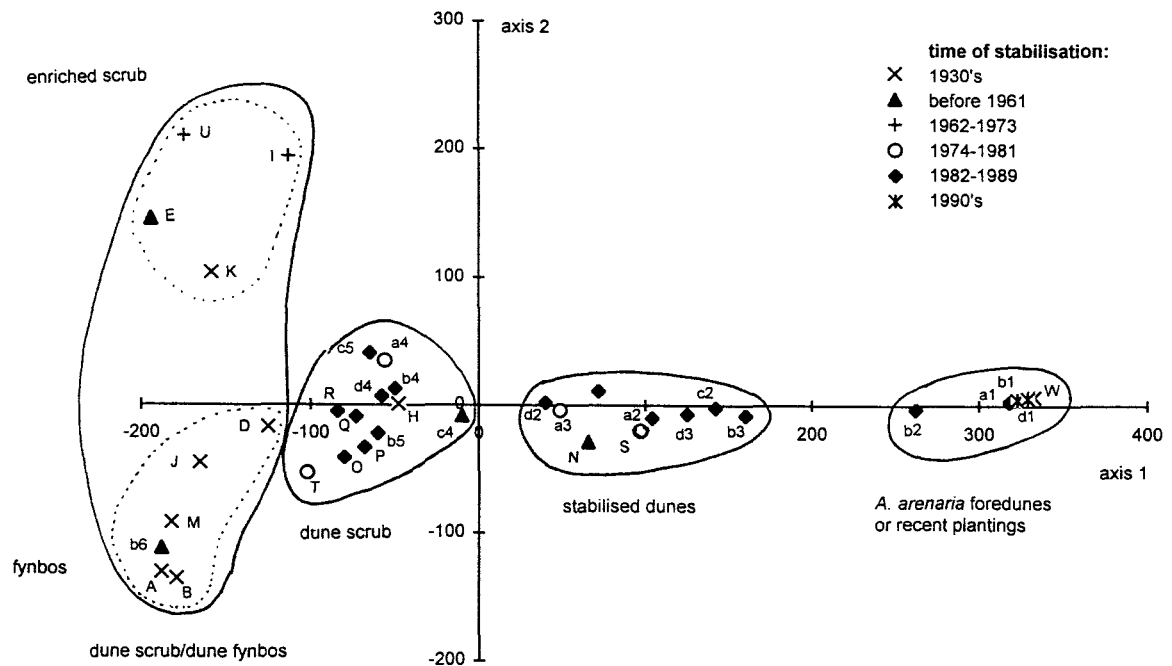


Fig. 5.6: A DCA without stands from saltmarsh and indigenous foredunes (see Fig. 5.5) allows for clearer differentiation of successional stages at De Mond Nature Reserve. The four stages relate well to the stabilisation times of their respective stands. See Fig. 5.7 for related TWINSpan results.

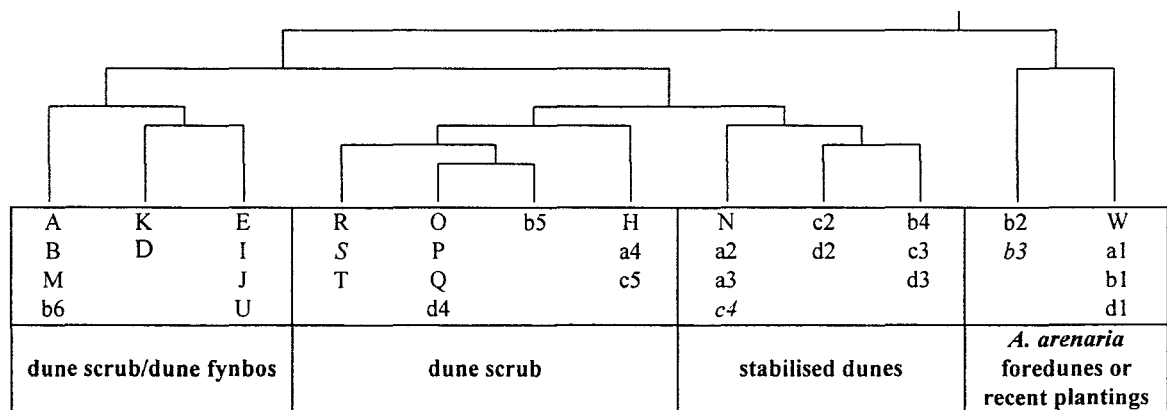


Fig. 5.7: Classification of 42 stands of vegetation sampled in De Mond Nature Reserve according to TWINSpan. See Fig. 5.6 for related DCA results (stands in *italics* appear in different groups according to the DCA results).

Figure 5.6 provides an idea about the time involved in the process of succession at De Mond. Stands that were stabilised between the 1930's and 1960's are today well vegetated with dense dune scrub. The older a stand, the more fynbos plant species are present. More information about the pace of the replacement of *A. arenaria* at De Mond is given in Figure 5.8. The vigour of *A. arenaria* in all sampled stands was grouped into six categories and plotted along an axis of the stands in chronological order. It is obvious that *A. arenaria* is more vigorous in sites of a younger stabilisation time. Most stands that were stabilised between the 1930's and 1970's carry few, thin culms or some clumps of *A. arenaria* (categories 1 and 2), while stands from the 1980's and 1990's contain vigorous, strong and often dominant *A. arenaria*.

In combination with Table 5.2 one can explain the unexpected high or low vigour of *A. arenaria* in some stands with very exposed dune top or very sheltered dune slack locations respectively. For example, stand N was stabilised before 1961, yet *A. arenaria* is the dominant plant, if mostly medium-aged (Fig. 5.8). This can be explained by the fact that stand N is situated on top of a transverse dune in relative closeness to the beach and thus exposed to harsh winds as well as frequent sand burial. Similarly, stand S was stabilised around the year 1980, but it still contains fairly vigorous *A. arenaria* (Plate 5.4 B). Again, this stand is found on a very steep slope facing SE, hence directed towards harsh southeasterly winds during summer. Stand Q, on the other hand, was only stabilised in the 1980's, yet no *A. arenaria* is left today (Plate 5.4 C). In this case, the stand is situated in a sheltered and moist dune slack, in which indigenous plant species less tolerant of sand burial can establish easily. The same reasoning can be applied to stand d4, another recently stabilised dune slack stand with little *A. arenaria* left. However, it is also possible that this stand was part of a natural bushpocket amidst the former driftsands and has never been subjected to stabilisation at all (see above).

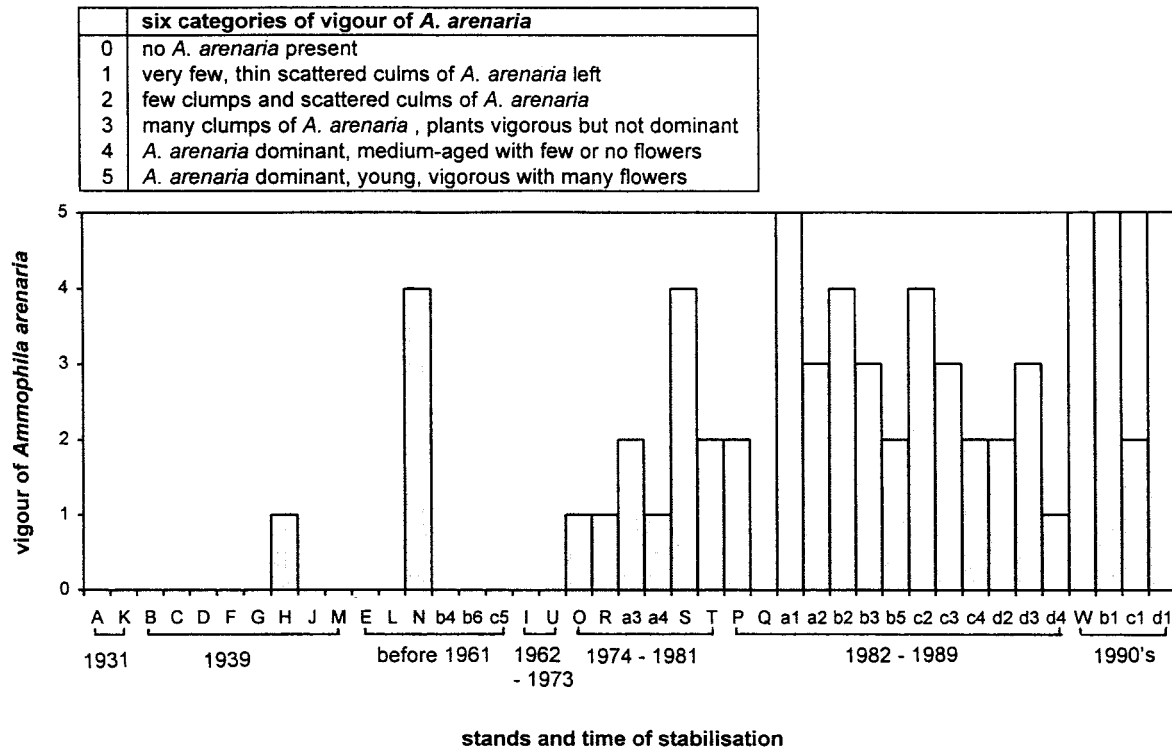


Fig. 5.8: Vigour of *A. arenaria* in all De Mond stands (in chronological order, excluding stand V) according to six categories from 0 (no *A. arenaria*) to 5 (very vigorous).

Values for species richness and Simpson's diversity of each stand are plotted along a chronological stands-axis in Figure 5.9. Although the graphs are irregular for all three values, a regression analysis shows that their general trend is downwards to the right, i.e. the values drop with decreasing age of the stands as would be expected: both species richness and species diversity are higher in stands that were stabilised in the 1930's than in stands that were stabilised only in the 1990's. However, the trend is more conspicuous for species richness ($r^2 = 0.23$) than for species diversity ($r^2 = 0.17$). The topographical situation of several stands (Table 5.2) offers explanations for unexpected high or low values in Figure 5.9: the low species richness in stands F and G, both stabilised in 1939, can be explained by the fact that they are foredune stands. The high level in Simpson's diversity of stand c3, which was only stabilised in the 1980's, is due to its sheltered and moist location in a dune slack.

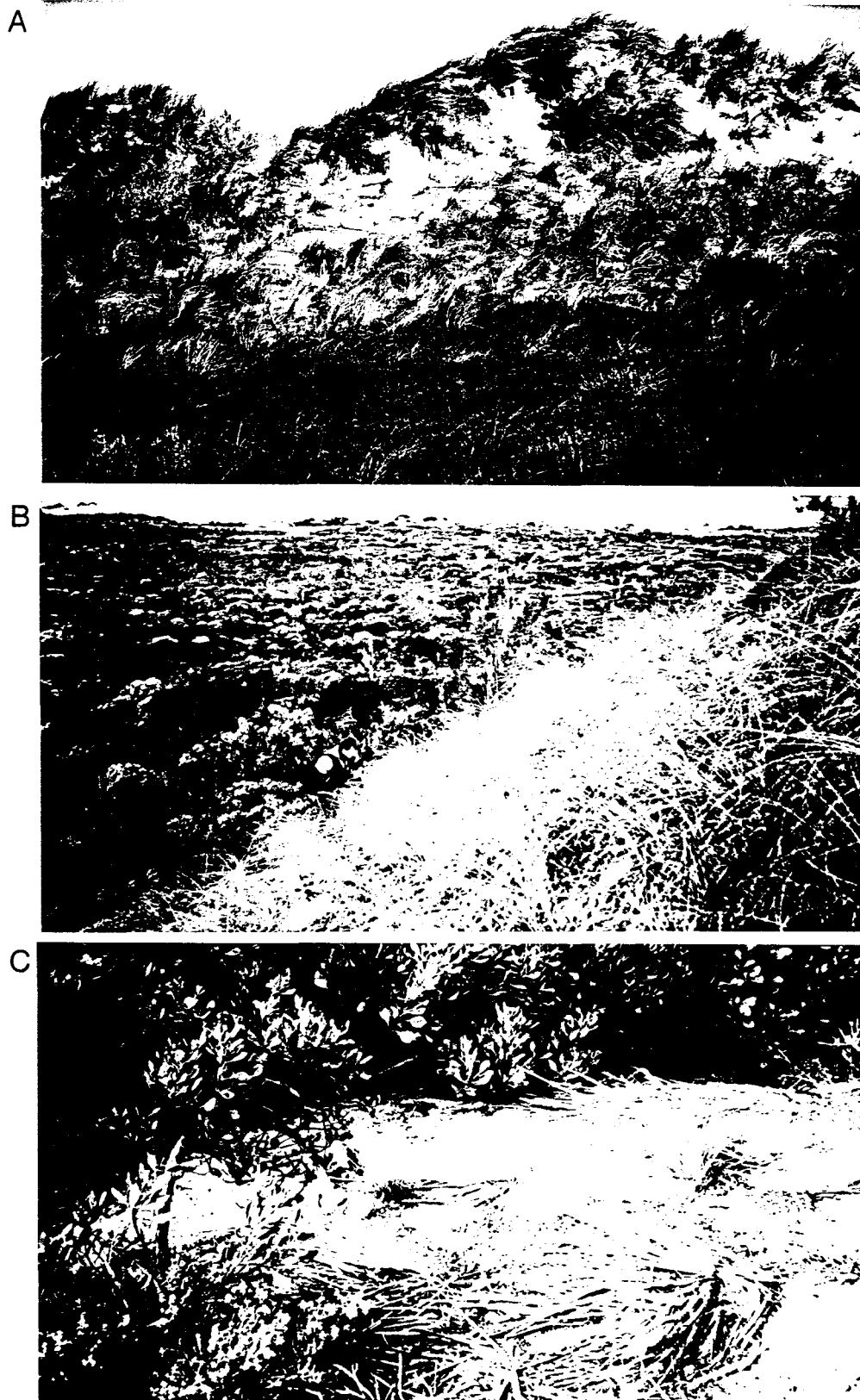


Plate 5.4: A. *A. arenaria* remains vigorous on exposed dune slopes among dense dune scrub. B. Medium-aged but dominant *A. arenaria* on a steep dune slope, in the background enriched dune scrub/fynbos (stand S). C. Dead culms of *A. arenaria* covering the ground of a sheltered and moist dune slack (stand Q).

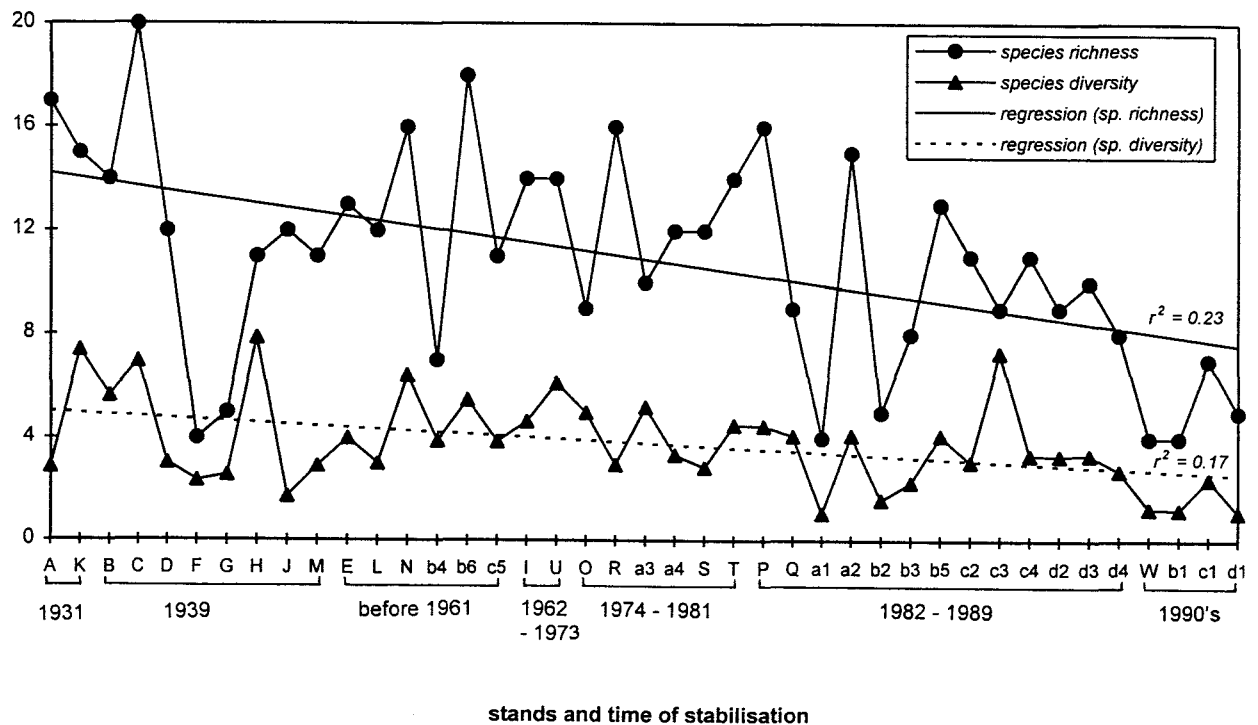
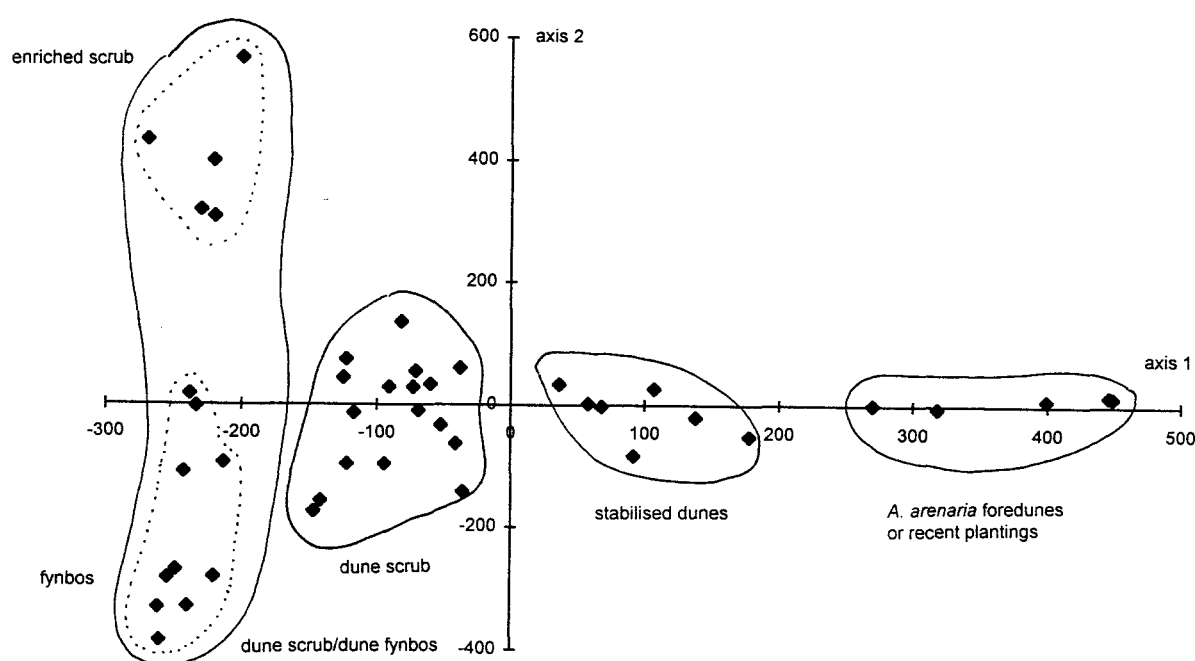


Fig. 5.9: Species richness and Simpson's diversity (d_s) in all De Mond stands (excluding stand V) in chronological order. Regression lines of the respective graphs and r^2 -values show that both values decrease with decreasing age of the stands.

2) Vegetation of the different successional stages

All species recorded in the various successional stages are reflected in Appendix 5.1. Figure 5.10 displays the species values of the same DCA that was shown in Figure 5.6: four groups of species can be recognised and related to the four successional stages of Figure 5.6. The foredunes dominated by *A. arenaria* contain very few different species, namely the typical foredune plants *Didelta carnosus*, *Thinopyrum distichum* and *Arctotheca populifolia*. More variety of species is found in the second community: the stands still show a high frequency of *A. arenaria*, but species common on more stable substrate such as *Chironia baccifera*, *Senecio elegans*, *Psoralea repens* and *Ficinia lateralis* become frequent. The third stage is characterised by proper dune scrub vegetation. *Myrica cordifolia* is certainly the most important plant here, but *Metalsia muricata*, *Chrysanthemoides monilifera* and *Helichrysum*

patulum are also very common. Interestingly, the indigenous dune grass *Ehrharta villosa* is also found in this community. The more advanced stages of succession at De Mond diverge towards a dense and species-rich dune scrub vegetation, characterised by *Rhus crenata*, but also bearing less common scrub species such as *Myrica quercifolia*, *Rhus laevigata* and the only Iridaceae species recorded in this survey, *Chasmanthe aethiopica*. Another direction of the succession leads towards a dune fynbos characterised mostly by the small but abundant *Ischyrolepis eleocharis*. Other fynbos elements are *Thamnochortus insignis*, *Euclea racemosa*, *Ficinia ramosissima* and *Phylica ericoides*.



enriched dune scrub/dune fynbos		dune scrub	stabilised dunes	<i>A. arenaria</i> foredunes
fynbos	scrub			
<i>Ischyrolepis eleocharis</i>	<i>Rhus crenata</i>	<i>Myrica cordifolia</i>	<i>Psoralea repens</i>	<i>A. arenaria</i>
<i>Thamnochortus insignis</i>	<i>Rhus laevigata</i>	<i>Metalasia muricata</i>	<i>Chironia baccifera</i>	<i>Thinopyrum distichum</i>
<i>Phylica ericoides</i>	<i>Myrica quercifolia</i>	<i>Ficinia lateralis</i>	<i>Dasispermum suffruticosum</i>	<i>Arctotheca populifolia</i>
<i>Euclea racemosa</i>	<i>Knowltonia capensis</i>	<i>Passerina rigida</i>	<i>Ammophila arenaria</i>	<i>Didelta carnosia</i>
<i>Agathosma collina</i>	<i>Chasmanthe aethiopica</i>	<i>Helichrysum patulum</i>	<i>Helichrysum praecinctum</i>	<i>Senecio elegans</i>
<i>Passerina paleacea</i>		<i>Pentaschistis eriostoma</i>	<i>Trachyandra divaricata</i>	
<i>Rhus glauca</i>		<i>Nylandtia spinosa</i>	<i>Sutherlandia frutescens</i>	
<i>Helichrysum dasyanthum</i>		<i>Otholobium bracteolatum</i>		
<i>Felicia zeyheri</i>		<i>Ehrharta villosa</i>		

Fig. 5.10: Detrended correspondence analysis (DCA) of species in all De Mond stands (except saltmarsh and indigenous foredunes). Only important, characteristic species are mentioned for the related communities (see Fig. 5.6). For a complete species list in the different stages see Appendix 5.1.

Figures 5.11 (a-d) reflect species richness, Simpson's diversity, dominant species and organic matter content of all transect stands (a-d) in their sequence from the high water mark to the backdune area. Transect b shows most clearly the change from an *A. arenaria* dominated foredune, close to the sea and with a low diversity index, to stands of increasing diversity indices with species such as *Psoralea repens* and *Myrica cordifolia* dominant, to finally dune scrub or dune fynbos stands nearly 1000 m to the sea, their vegetation dominated by *Myrica cordifolia* or *Ischyrolepis eleocharis*.

The results of a continuous vegetation analysis along one transect is given in Figure 5.12. The profile of a 150 m transect is shown in combination with the cover values of all species for each metre of the transect and with the respective values of soil conductivity and organic matter content for every five metres. pH values were also measured but are not presented in the graph because of their uniformity (ranging between 8.5 and 9.1). The first species on the beach is *Arctotheca populifolia*. After a sandy, unvegetated zone on the back-beach large amounts of *A. arenaria* occur with very few *Thinopyrum distichum* in the beginning. *A. arenaria* is a prominent plant throughout the transect, occurring up to a distance of 210 m from the high water mark. An important plant in the middle part of the transect is *Psoralea repens*. *Chironia baccifera* is not quite as prominent, but extends further to the back than *Psoralea repens*. Similarly common throughout the greater part of the transect are *Ficinia lateralis* and *Helichrysum patulum*. Of the shrub species, *Metalsia muricata* and *Chrysanthemoides monilifera* appear only sporadically, while *Myrica cordifolia* is very common, occurring vigorously especially in the back parts of the transect. Although this transect seems to extend only through the first three communities of Figure 5.6, *Ischyrolepis eleocharis* was recorded from 214 m. It is one of the first fynbos plants to appear in the advanced dune scrub vegetation at De Mond. The soil values show an increase of organic matter to the back of the transect while the values of conductivity stay much the same and are only marginally higher in the front part of the transect because of higher salinity levels of the beach.

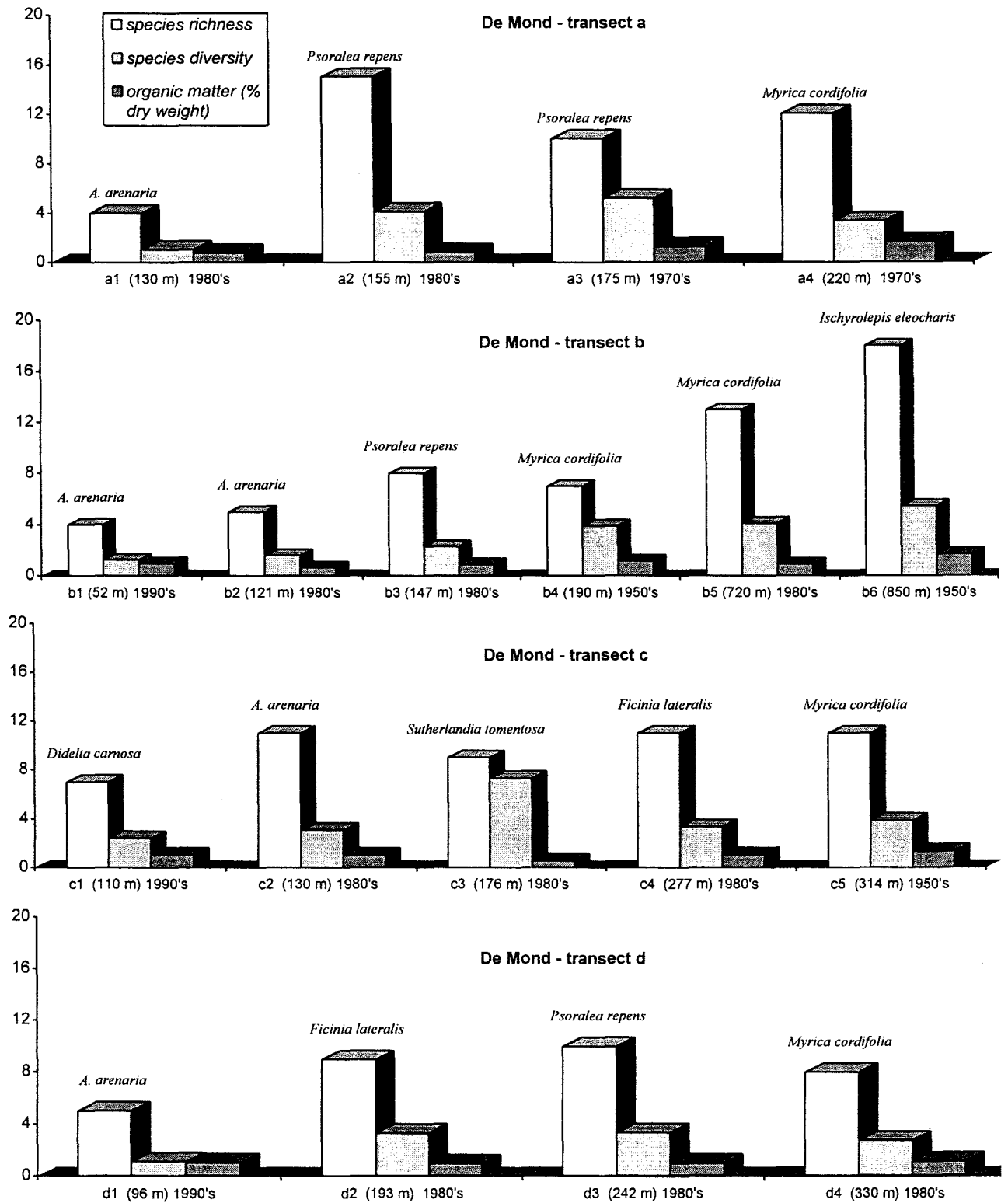


Fig. 5.11: Four transects (a-d) from the beach into the backdune area at De Mond Nature Reserve, reflecting dominant species in each stand and respective values of species richness, Simpson's diversity (d_s) and organic matter. Distance from the high water mark and times of stabilisation of each stand are noted next to its number.

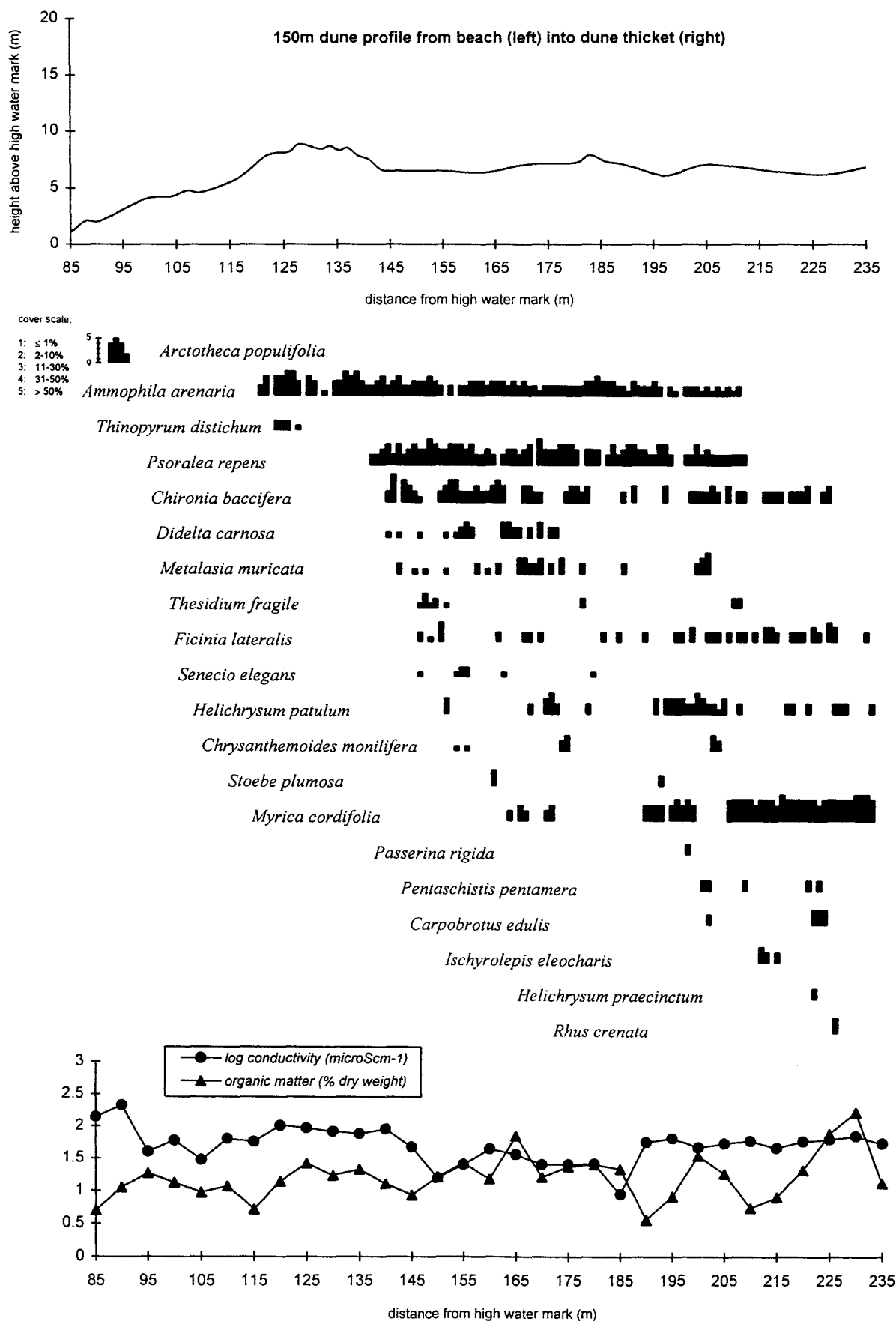


Fig. 5.12: Profile of a 150 m dune transect at De Mond Nature Reserve with values of species cover for every metre and values of soil conductivity and organic matter content for every five metres.

3) Edaphic and other environmental factors

Figure 5.13 displays values of soil conductivity and organic matter plotted along an axis of stands in chronological order. The pH values were found to be too uniform (ranging between 8.1 and 9.2) and are not included in the graph. Conductivity values are uniform in the differently aged stands, a regression line shows hardly any trend ($r^2 = 0.05$). Fairly high values in some of the younger stands are explained with higher salinity levels due to their proximity to the high water mark. Although the organic matter content is slightly higher in older stands and shows a clear downward trend ($r^2 = 0.23$) of values to the right of the axis towards more recently stabilised stands, a greater difference of organic matter content in differently aged stands was expected. Low organic matter values in old stands (e.g. A, H, M) can often be explained with an exposed slope situation where soil erosion prevents the accumulation of organic matter (Table 5.2). Unusually high organic matter contents are found in stands (e.g. K, U) that are situated in moist, sheltered dune slacks (Table 5.2).

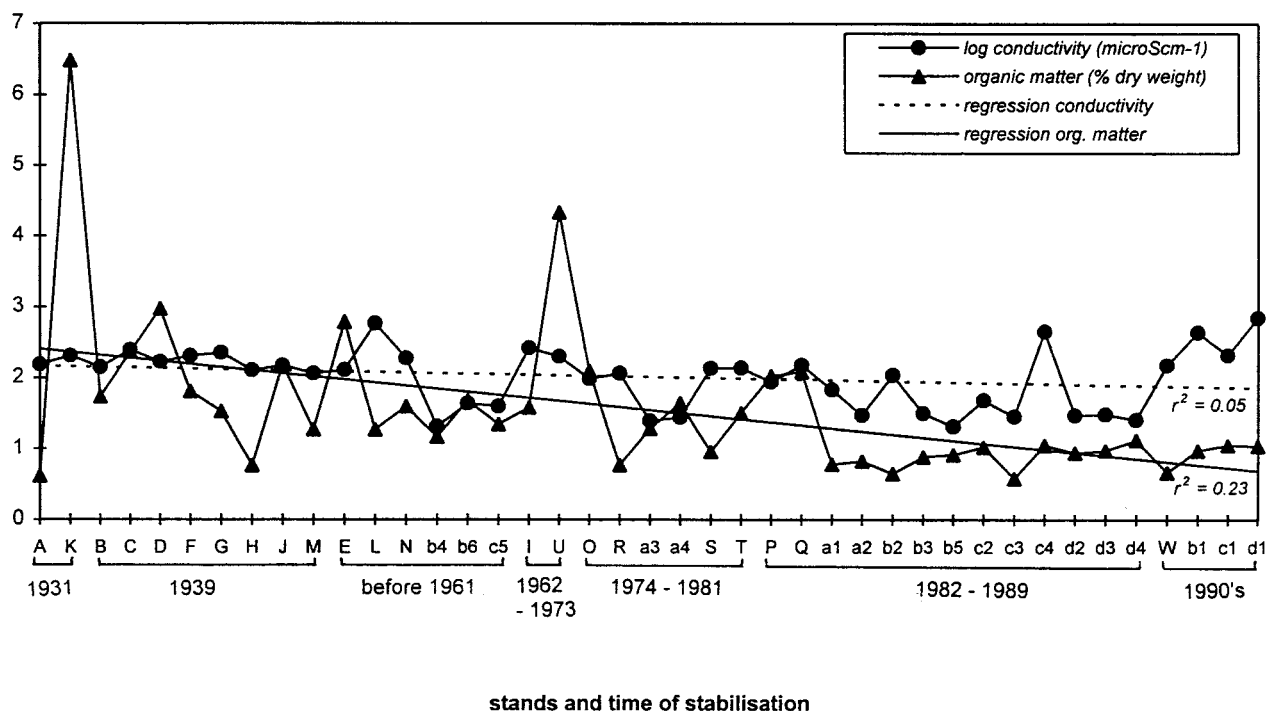


Fig. 5.13: Soil conductivity and organic matter of all De Mond stands (excluding stand V) in chronological order. Regression lines and r^2 -values show decreasing organic matter values with decreasing age of stands, while conductivity values are hardly changing.

To examine the influence of edaphic soil factors (pH, conductivity and organic matter content), of the time of stabilisation and of the topographical situation per stand on the differentiation of De Mond stands in CANOCO, the ordination axes of Figure 5.6 were subsequently related to these five variables (Fig. 5.14). The environmental variables correspond particularly well to the ordination axis 1, along which a succession was detected according to Figure 5.6. Therefore, the four communities described above and their sequence are confirmed by an environmental gradient: the more recently the stands were stabilised (variable “time of stabilisation”), the further to the right are these stands found in the plot; in contrast, stands to the left of axis 2, vegetated by dune scrub and dune fynbos, are characterised by a high organic matter content and more sheltered and moist locations. However, the organic matter is not equally well related to these stands: the dune fynbos stands appear to have a lower organic matter content than stands from the advanced dune scrub stage. This is confirmed by the highly significant ($P < 0.01$) regression of the organic matter content with axis 2 (Table 5.3), which therefore accounts mostly for the divergence of vegetation in later successional stages.

Of the five environmental variables examined, the conductivity and pH values appear to have the least influence on the stands ordination. This is confirmed by their low regression coefficients (Table 5.3). The strongest influence on the ordination of De Mond stands is shown by their stabilisation time and topographical situation, both variables bear highly significant ($P < 0.01$) regression coefficients. This confirms the decline in vigour and replacement of *A. arenaria* at De Mond with indigenous dune plant species as dependent on time and habitat.

Table 5.3: Regression coefficients (multiplied by 100) of five environmental variables with the first and third axis resulting from indirect gradient analysis (DCA) of all De Mond stands ($df = 30$). See Fig. 5.14 for the plot. Significance at $\alpha = 0.01$ (*) as indicated through t -values supplied by the same analysis. No values were significant at $\alpha = 0.05$ or $\alpha = 0.1$.

	axis 1	axis 2
soil pH	+ 136	+ 240
soil conductivity	+ 226	+ 139
organic matter content of soil	- 240	+ 546 *
stabilisation time	+ 907 *	+ 161
topographical situation	- 627 *	+ 118

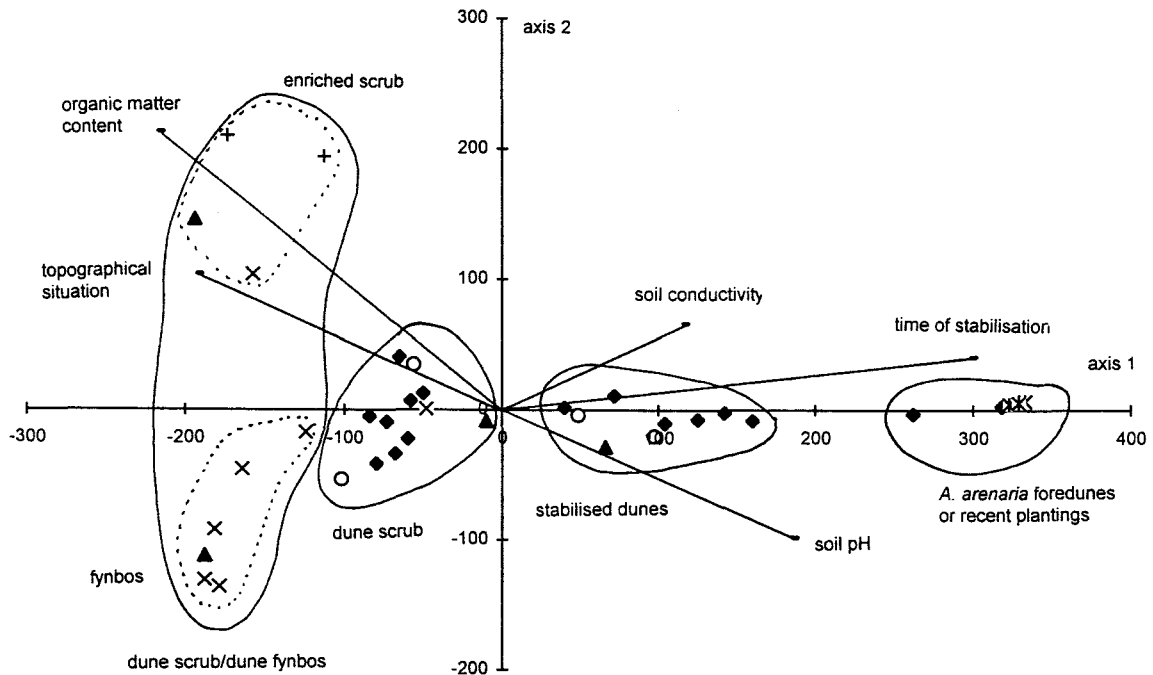


Fig. 5.14: DCA of all De Mond stands (except saltmarsh and indigenous foredunes) with ordination axes related indirectly to five environmental variables. The plot is the same as in Figure 5.6. See Table 5.3 for corresponding regression coefficients.

5.2.5 Discussion

The results of the vegetation analysis at De Mond Nature Reserve prove that succession is taking place in this large-scale stabilisation site. Monospecific *A. arenaria* stands can be transformed into dense dune scrub/dune fynbos within 50-60 years. Six communities were identified at De Mond: young, vigorous *A. arenaria* communities on foredunes or as recent plantings further inland, mixed *A. arenaria* communities on stabilised dunes, dune scrub, dune scrub with fynbos elements, saltmarsh and indigenous foredunes (Fig. 5.5). The first four stages show an increase of species richness and species diversity and can be lined up along a successional gradient. In the latter two cases, saltmarsh and indigenous foredunes, the initial *A. arenaria* plantings have not been replaced via an increasingly dense dune scrub vegetation but developed immediately into species-poor saltmarsh or indigenous foredune vegetation.

The succession at De Mond can be related to a chronosequence (Fig. 5.6). Most areas at De Mond that were stabilised in the 1930's and 1940's are today vegetated by a dense, species-rich dune scrub with many elements of area-specific fynbos. Stands that were stabilised from the 1950's to 1970's are mostly vegetated by dense dune scrub. More recently stabilised stands are often still dominated by *A. arenaria*. However, even stands that were stabilised only in the 1980's can carry a rich and dense dune scrub vegetation. This would be due to facilitating habitat features such as a sheltered dune slack location with a higher organic matter accumulation and greater moisture. On the other hand, sites of an early stabilisation date can bear persistently vigorous *A. arenaria* populations if they are situated on exposed dune slopes and therefore characterised by a higher sand movement. *A. arenaria* profits at such sites from its superior sand burial tolerance. In sheltered dune slack locations, *A. arenaria* does not have this niche advantage and is outcompeted by other species (Plate 5.4).

An analysis of the colonisation of a British stabilisation site involving *A. arenaria* confirms these results (Hewett 1970): within 14 years of planting, the frequency of *A. arenaria* had decreased from more than 70% to less than 20%, while that of other grass species like *Festuca rubra* and *Phleum arenarium* increased from 0% to 100%. *A. arenaria* remained vigorous only on the seaward plantations and in small areas of mobile sand. On Sylt Island off the German North Sea coast (see Chapter 4), the grass was observed to grow vigorously at a distance of up to 2 kilometres inland in areas of active driftsands and around blow-outs caused by human or animal trampling. The niche advantage that moist, sheltered dune slack locations offer colonising species in *A. arenaria* stabilisation sites is reflected in a Dutch study: Van Dorp *et al* (1985) report that *Alnus glutinosa* woodland can succeed *A. arenaria* plantings if it develops in adjacent lower-lying slacks from which it would extend into the *A. arenaria* zone. Sowing of woody indigenous species in the De Mond stabilisation area was carried out preferentially in moist dune valleys (Fig. 5.4), in which similar initial spots of successor species were developed. The colonisation of *A. arenaria* dunes at De Mond has possibly proceeded out of these dune slack locations.

One of the commonest indigenous species at De Mond is the waxberry, *Myrica cordifolia*. Although generally very common along the South African coast, its high frequency at De Mond is certainly due to its sowing amongst new *A. arenaria* plantings (Table 5.1). While

other sown species like *Chrysanthemoides monilifera*, *Metalsia muricata* and *Chironia baccifera* also occur throughout the reserve today, the sowing of *Sutherlandia frutescens* appears to be less successful since this species was recorded only once. However, the sowing of indigenous species can only account for the occurrence of a fraction of species. The early establishment of the above dune scrub species amongst the *A. arenaria* plantings has facilitated the process of succession by enriching the soil with organic matter and providing shelter and shade for other, less hardy indigenous species. Most species that occur in the reserve today have established in the stabilisation areas after such microhabitats were provided. It is assumed that, without sowing indigenous seed, succession would have been insignificantly slower though.

The succession of species at De Mond in the above described chronosequence is reflected in a related toposequence. Transects from the shore into the backdune area confirm the transformation of vegetation from *A. arenaria* foredunes to dense dune scrub along a spatial gradient (Figs. 5.11 and 5.12). *Psoralea repens* and *Chironia baccifera* are common species among stands of *A. arenaria*, while *Ficinia lateral*is and *Helichrysum patulum* become more frequent as the cover of *Myrica cordifolia* increases. The restio *Ischyrolepis eleocharis* is the first fynbos species to appear in the stabilisation sites at De Mond. Because of the recent origin of the vegetated De Mond dunes, *A. arenaria* occurs generally further back than is observed in European dune series. The greater part of a 235 m transect sampled from the high water mark is covered with *A. arenaria* (Fig. 5.12), while in Europe *A. arenaria* grows at high cover values only in the nearshore foredune and yellow dune stages (Willis *et al* 1959b; Dijkema *et al* 1993), unless patches of backdunes are subjected to severe disturbance such as trampling (see above).

The pattern of succession along a chronological gradient found for the *A. arenaria* plantings at De Mond is comparable to that recorded on the Mtunzini dunes in Natal, South Africa (Avis 1992): both α -diversity (species diversity) and β -diversity (community diversity) increase with the age of the dunes. In the Mtunzini study an ordination of the sampled stands resulted in a pattern of a unilinear sequence of young and medium-aged communities (pioneer, enriched pioneer, open dune scrub, closed dune scrub) which then diverged like a fork into a variety of older, more advanced communities (bushclumps, forest margin, forest). The divergence of

community types into at least two different directions is even more distinct at De Mond, where the oldest dunes can carry either an enriched dune scrub vegetation or a very differently composed dune fynbos vegetation (Fig. 5.6). In both studies, the increase in α -diversity of the communities is therefore correlated with an increase in their β -diversity.

The succession at Sylt shows the opposite pattern (see Chapter 4, Fig. 4.11, Plate 4.3). In this case the β -diversity decreases with the age of the area, there is a greater variety of species associations among the younger pioneer communities. At least three different vigorous *A. arenaria* associations were observed on Sylt foredunes, characterised by different accompanying species. The α -diversity of these pioneer communities is low, but increases towards the grey dune stage. However, it decreases clearly after the grey dune stage, and the climax community is a species-poor heathland vegetation. In this case, both α - and β -diversity are lowest in the oldest dune communities.

While the ordination of Sylt stands is strongly influenced by levels of organic matter and pH of the soil (Fig. 4.12), these values appear of less importance for the ordination of De Mond stands (Fig. 5.14). Even old stands at De Mond show comparatively low values of organic matter. Dense dune thicket in South Africa has been observed to bear up to 6.7% (Avis 1992) or 4.2% (La Cock 1986) organic matter. Soils of dense dune scrub vegetation in Europe were recorded to have an organic matter content of up to 12.6 % (Willis *et al* 1959a) or 9.5% (Ranwell 1959). In contrast, only two stands at De Mond have organic matter values of more than 4%. Most stands, even those stabilised early and vegetated densely today, do not bear higher values than 2% (Fig. 5.13). This can be explained by the young age of the De Mond dunes. Time has been too short for the accumulation of organic matter.

With a range between 8 and 9, pH values in the advanced stages of the De Mond succession are similar to values measured for dune scrub both in Europe (e.g. Willis *et al* 1959a) and South Africa (e.g. Avis 1992). The restioid and asteraceous dune fynbos of the Bredasdorp area thrives on a calcareous substrate (Mustart *et al* 1997). Therefore, even in the fynbos stage of the De Mond succession comparatively high pH values were recorded. The low levels of pH in the later stages of the Sylt succession, and thus the significant influence that pH values have in the ordination of Sylt stands, is mainly due to the acid dune heath soils. Heath species like

Calluna vulgaris and *Empetrum nigris* accelerate the leaching of the soil by disposal of humic as well as carbonic acids (Ranwell 1972).

Of much greater influence in the ordination of De Mond stands than edaphic factors are the topographical position of the stands and their stabilisation times. This confirms that the replacement of *A. arenaria* is dependent on the time and the habitat of the site. The longer a site has been stabilised and the more sheltered its location, the sooner indigenous dune plant species colonise the *A. arenaria* plantings and the faster *A. arenaria* degenerates. The De Mond Nature Reserve offers one of the most significant examples of succession in a stabilisation area involving *A. arenaria* in South Africa. On a smaller scale, the succession of *A. arenaria* by indigenous plant species has been observed at several other sites along the coast, such as Kleinkrantz near Wilderness (Plate 5.5) or in the Alexandria dunefield.



Plate 5.5: Staircase leading to the beach at Kleinkrantz (Southern Cape) across a recently completed stabilisation site using *A. arenaria* in 1986 (top, from La Cock 1986) and, revisited, leading across dense dune scrub in 1995 (bottom).

5.3 The involvement of nematodes in the die-back of *A. arenaria* in South Africa - A preliminary study

5.3.1 Introduction

The De Mond study confirms the competitive advantage that *A. arenaria* has over other species in places of high sand movement. Its superior tolerance of sand burial enables it to survive on exposed dune slopes amongst otherwise dense dune scrub vegetation. Reduced sand movement is correlated with reduced vigour of *A. arenaria*. This phenomenon, well-known in Europe, cannot be attributed only to an increase of competitors, but also to changes in biotic soil properties (see Chapter 1). The possible role that harmful soil microorganisms like fungi and nematodes play in the decline of *A. arenaria* in stable sand has been studied extensively in Dutch dune systems (authors see below). Their involvement in the decline of *Ammophila breviligulata* is receiving increasing attention in North American east coast dune systems (Seliskar & Huettel 1993).

Soil organisms, congregating in fixed dunes, can have a negative impact on *A. arenaria* by reducing both root length and root hair formation (van der Putten *et al* 1988, 1989). Treatment of sand with fungicides and nematicides has shown that the most harmful impact was done by plant-parasitic nematodes, but that interaction with fungi cannot be excluded (van der Putten *et al* 1990). Further investigations have shown that a regular supply of fresh sand enables *A. arenaria* to escape this pressure and develop fresh roots which will in turn be infested by harmful soil organisms after a certain time period. Hence, continuous sand movement is essential for the vigour of *A. arenaria* (van der Putten & Troelstra 1990, Rooij-van der Goes *et al* 1995b; Rooij-van der Goes 1996).

A preliminary study on the presence of plant-parasitic nematodes in South African *A. arenaria* communities of different ages was conducted in consideration of the importance that such harmful soil microorganisms may have on the succession of *A. arenaria* plantings (van der Putten *et al* 1993). This study will provide a first indication of numbers and kinds of nematodes in soils and roots of vigorous *A. arenaria* stands as compared with declining *A. arenaria* stands. For a wider comparison, soils and roots of the three indigenous dune plant species

Thinopyrum distichum, *Tetragonia decumbens* and *Scaevola plumieri* were also examined for nematode presence.

The following questions are addressed:

- 1) Do differently aged stands of *A. arenaria* carry different abundances of nematodes?
- 2) Are similar species or genera of plant-parasitic nematodes present in South African and European *A. arenaria* stands?
- 3) How many and which nematodes are present in the soil and roots of the indigenous dune plants *Thinopyrum distichum*, *Tetragonia decumbens* and *Scaevola plumieri*?

5.3.2 Methods

Soil and roots of *A. arenaria* stands were sampled at three sites along the South African Cape coast: at Noordhoek on the Cape Peninsula, Western Cape (34°07'S; 18°22'E), Klein Brakrivier in the Southern Cape (34°06'S; 22°08'E) and Kleinemonde in the Eastern Cape (33°33'S; 27°08'E). At each site the following sampling was undertaken:

- * 3 replicas (100 ml each) of soil from the root zone of young, vigorous *A. arenaria*. For each replica, 3 10x10x10 cm³ samples were taken from an area of 1 m² and mixed gently on a plastic sheet.
- * 1 replica of roots from young, vigorous *A. arenaria*. The roots were taken from the same spots as the three soil replicas but combined as one replica.
- * 3 replicas of soil from the root zone of old, declining *A. arenaria*, as above.
- * 1 replica of roots from old, declining *A. arenaria*, as above.
- * 1 replica of soil from the root zone of one common, medium-aged indigenous dune plant species, as above.
- * 1 replica of roots from one common, medium-aged indigenous dune plant species, as above.

The respective indigenous plant species were *Thinopyrum distichum* (Noordhoek), *Tetragonia decumbens* (Klein Brakrivier) and *Scaevola plumieri* (Kleinemonde).

The samples were kept cold at 7°C and then transferred to the Centre for Terrestrial Ecology of the Netherlands Institute of Ecology in Heteren, The Netherlands, for analysis of nematode presence. Nematodes were isolated from soil and roots by elutriation according to Oostenbrink (1960) and counted and identified according to Bongers (1988).

5.3.3 Results

1) Nematodes in differently aged stands of *A. arenaria*:

Nematode numbers were generally higher in soils of vigorous *A. arenaria* stands than in soils of degenerating stands (Table 5.4). Only at Noordhoek were the roots of degenerating *A. arenaria* strongly infested with plant-parasitic nematodes, mostly *Filenchus* sp. and *Ditylenchus* sp.. Interestingly, the *A. arenaria* stand at this site was the least declined. Conversely, the *A. arenaria* stand in the most advanced stage of degeneration, at Klein Brakrivier, showed the least infestation with nematodes. At all three sites the roots of vigorous *A. arenaria* carried a lot of *Pratylenchus* sp., while the soils of vigorous *A. arenaria* were infested mostly with *Pratylenchus* sp., *Rotylenchus* sp. and *Filenchus* sp.. The strongest infestation with phytophagous nematodes was found in soils and roots of vigorous *A. arenaria* at Klein Brakrivier.

Table 5.4: Number of nematodes in soil (per 100 ml soil) and roots (per g fresh weight) of *A. arenaria* of two different ages and of a common indigenous dune plant of medium age at Noordhoek, Klein Brakrivier and Kleinemonde respectively (values for soil of *A. arenaria* are means of 3 replicates with lowest-highest numbers in parentheses). The first nematodes of each list are phytophagous, i.e. parasitising plants, and their total number is given underneath their names. The other nematodes listed are unknown, omniphagous (the group of Dorylaimidae) or saprophagous. One sample was lost (-).

Noordhoek						
	<i>A. arenaria</i> vigorous		<i>A. arenaria</i> declining		<i>Thinopyrum distichum</i>	
	soil	roots	soil	roots	soil	roots
<i>Pratylenchus</i> sp.	0.7 (0-1)	15	0	1	-	125
<i>Rotylenchus</i> sp.	1.7 (0-3)	0	5.3 (2-11)	0	-	0
<i>Filenchus</i> sp.	2 (1-3)	6	3.3 (2-5)	20	-	0
<i>Hemicycliophora</i> sp.	0	0	0.3 (0-1)	0	-	0
<i>Aphelenchus</i> sp.	0.3 (0-1)	0	0.7 (0-1)	0	-	0
<i>Aphelenchoides</i>	1 (0-2)	3	1.3 (0-3)	1	-	0
<i>Ditylenchus</i> sp.	0.3 (0-1)	0	6.3 (3-10)	25	-	0
total phytophagous	6	24	17.2	47	-	125
sp. indet.	0.7 (0-1)	0	0	0	-	0
Dorylaimidae	7 (5-8)	0	5.7 (1-13)	0	-	0
saprophagous	112.7 (106-121)	270	92.3 (9-196)	82	-	1055
Klein Brakrivier						
	<i>A. arenaria</i> vigorous		<i>A. arenaria</i> declining		<i>Tetragonia decumbens</i>	
	soil	roots	soil	roots	soil	roots
<i>Pratylenchus</i> sp.	20.3 (1-54)	80	0.3 (0-1)	1	87	521
<i>Rotylenchus</i> sp.	7.3 (1-16)	1	3.3 (3-4)	0	6	1
<i>Tylenchorhynchus</i> sp.	0.3 (0-1)	8	0	0	0	0
<i>Filenchus</i> sp.	28 (7-11)	0	3.3 (3-4)	0	1	0
<i>Telotylenchus</i> sp.	5.3 (0-13)	0	0.3 (0-1)	0	0	0
<i>Aphelenchus</i> sp.	2 (1-3)	0	0.7 (0-1)	0	7	0
<i>Aphelenchoides</i>	9.3 (0-28)	3	1.3 (0-3)	1	0	8
<i>Ditylenchus</i> sp.	0	0	0	0	0	1
total phytophagous	72.5	92	9.2	2	101	531
sp. indet.	2.7 (2-3)	0	0.7 (0-1)	0	1	0
Dorylaimidae	2.7 (2-4)	0	3.3 (0-8)	0	3	0
saprophagous	99.3 (46-203)	940	88 (66-125)	21	117	61
Kleinemonde						
	<i>A. arenaria</i> vigorous		<i>A. arenaria</i> declining		<i>Scaevola plumieri</i>	
	soil	roots	soil	roots	soil	roots
<i>Pratylenchus</i> sp.	4 (0-8)	24	1.7 (0-5)	0	0	8
<i>Rotylenchus</i> sp.	15 (7-28)	15	12.3 (0-35)	0	0	0
<i>Tylenchorhynchus</i> sp.	0.7 (0-2)	0	0.3 (0-1)	0	0	0
<i>Filenchus</i> sp.	32 (6-79)	17	8.3 (5-15)	5	0	0
<i>Telotylenchus</i> sp.	0.3 (0-1)	0	1 (0-3)	0	0	0
<i>Hemicycliophora</i> sp.	0	0	0.7 (0-1)	0	0	0
<i>Aphelenchus</i> sp.	5 (2-10)	0	0	2.3 (0-4)	4	0
<i>Aphelenchoides</i>	0.3 (0-1)	1	4.3 (1-8)	4	0	0
<i>Ditylenchus</i> sp.	0	1	0.3 (0-1)	0	0	0
total phytophagous	57.3	58	28.9	6.3	4	8
Dorylaimidae	5 (1-8)	0	134.7 (6-385)	0	3	0
saprophagous	309.3 (352-255)	1017	120 (1-208)	165	69	4

2) Identification of nematodes

The nematodes were identified only to genus level (Table 5.4). Saprophagous nematodes were the most commonly found nematodes, but these do not parasitise plants. Of more interest in this study are the phytophagous nematodes. The only endoparasite of these was *Pratylenchus* sp., all others were ectoparasites. One kind of nematode was unidentified, but otherwise, both the genera and the densities of the nematodes were similar to those found for soils and roots of European *A. arenaria* (van der Putten & Troelstra 1990; de Rooij-van der Goes *et al* 1995a). However, no cyst and root knot nematodes are recorded for South African stands, which are common in European stands.

3) Nematodes in stands of indigenous dune plants

Although the soil of *A. arenaria* stands contained generally more different nematodes than did the soil of indigenous dune plants, the total number of nematodes was higher in the case of *Thinopyrum distichum* and *Tetragonia decumbens*. Both were heavily infested with the endoparasitic *Pratylenchus* sp., while *Scaevola plumieri* was least infested with nematodes of any plant. However, numbers for indigenous samples were from only one replicate and are of reduced significance, if one considers the high variability of values for the three replicates of *A. arenaria* soils.

5.3.4 Discussion

Similar results have been found in several studies of Dutch *A. arenaria* stands. Nematode numbers were found to be higher in sand from mobile dunes than from stable dunes (van der Putten & Troelstra 1990). In ordination and classification analyses, no relation could be found between groups of microorganisms and the vigour of *A. arenaria* (de Rooij-van der Goes *et al* 1995a). Although this appears to contradict the theory that phytophagous nematodes have a negative impact on the vigour of *A. arenaria*, it is not necessarily so. Vigorous *A. arenaria* plants develop many new roots, which in turn provide fresh substrate for soil microorganisms.

An increased vigour of *A. arenaria* therefore causes increased numbers of plant-parasitic nematodes. However, in places of high sand movement, *A. arenaria* is able to escape this increase in pathogens by the continuous formation of new roots and an upward rejuvenation of the plant: roots of *A. arenaria* colonise windblown sand before they are colonised by harmful soil organisms (van der Putten & Troelstra 1990). The vertical migration of nematodes towards newly formed roots and their rapid infection has been examined and confirmed by de Rooij-van der Goes (1996). Regular sand accretion provides the plant with new rooting space and prevents the increase of phytophagous nematodes to damaging thresholds. The vigour of *A. arenaria* plants is therefore primarily determined by the presence of healthy uninfested roots which in turn depends on a continuous supply of fresh, windblown sand (de Rooij-van der Goes *et al* 1995b).

In South African dunes as in Dutch dunes, higher numbers of plant-parasitic nematodes were found in healthy stands of *A. arenaria* than in declining stands. They are harmless provided the plant can continuously escape this pressure and develop new roots in freshly blown sand. Although at the time of sampling these stands were still healthy, their vigour depends strongly on the supply of windblown sand. In stands that are less exposed to sand movement, the number of nematodes will reach damaging levels and cause the decline of *A. arenaria*. The more *A. arenaria* declines, the fewer nematodes will be present in and around it, which accounts for the low numbers found in old stands. While the decline of *A. arenaria* in the Noordhoek stand was still in progress, and a relatively high number of nematodes counted, the plants at Klein Brakrivier were already nearly dead, and nematodes had moved away to fresher material. Similarly, nematode numbers are also small in the vigorous Noordhoek stand which is exposed to the severest sand movement, while the Klein Brakrivier stand of vigorous *A. arenaria* has already been colonised by many nematodes.

From the above, the South African results appear to “fit” well with the findings of numerous Dutch investigations. However, the present South African study is greatly simplified and only intended as a preliminary view towards the numbers and kinds of nematodes in local *A. arenaria* stands. Much more detailed experiments have to be carried out to confirm the above presumptions. Most importantly, plant-parasitic nematodes interact synergistically with fungi (van der Putten *et al* 1990; van der Putten & Troelstra 1990), and studies on the effect of fungi

on *A. arenaria* have to be undertaken in close relation with the nematode studies. With a view towards *A. arenaria*'s possibly harmful effects in South Africa, similar studies must focus on indigenous dune plants. The strong infestation of *Tetragonia decumbens* at Klein Brakrivier with *Pratylenchus* sp. could indicate a higher tolerance of the plant to this endoparasite. The extremely low numbers of any nematodes in *Scaevola plumieri* stands at Kleinemonde could indicate that this plant is not sought after by these parasites. However, more detailed research is necessary.

5.4 Conclusions

The case study at De Mond Nature Reserve proves that succession of monospecific *A. arenaria* stabilisation areas by indigenous dune plant species can take place in South Africa. Six communities were identified at De Mond, which relate to successional stages and constitute a clear chronosequence. Areas at De Mond that were stabilised in the 1930's and 1940's are today vegetated by species-rich dune scrub or dune fynbos. Stands that were stabilised from the 1950's to 1970's are mostly vegetated by dune scrub. More recently stabilised stands are often still dominated by *A. arenaria*. However, even stands that were only stabilised in the 1980's can carry a diverse dune scrub vegetation, if they are situated in sheltered, moist dune slacks. On the other hand, sites of an early stabilisation date can bear persistently vigorous *A. arenaria* populations if they are situated on exposed dune slopes. *A. arenaria* profits at such sites from its superior sand burial tolerance.

Vegetation sampling along transects from the shore into the backdune area confirms the transformation of vegetation from *A. arenaria* foredunes to dense dune scrub along a spatial gradient. A detrended correspondence analysis (DCA) of all stands at De Mond shows that their topographical situation has more influence on their ordination along an environmental gradient than edaphic factors. This confirms that the replacement of *A. arenaria* is dependent on the time and the habitat of the site. The longer a site has been stabilised and the more sheltered its location, the sooner indigenous dune plant species colonise the *A. arenaria* plantings and the faster *A. arenaria* degenerates.

Biological soil properties have probably more impact than physical properties on the vigour of *A. arenaria*. Soil and root sampling of differently aged *A. arenaria* stands for the number of plant-parasitic nematodes indicates that *A. arenaria* is in South Africa as in Europe affected negatively by the presence of soil organisms. To escape the pressure of root damaging endo- and ectoparasitic nematodes, *A. arenaria* needs a regular supply of fresh sand into which new roots can develop. In stands that are less exposed to sand movement, the number of nematodes will reach damaging levels and cause the decline of *A. arenaria*. Soil-borne pathogens possibly contribute substantially to the succession of *A. arenaria* stabilisation areas in South Africa.

Appendix 5.1: List of all species recorded in all 42 stands sampled at De Mond Nature Reserve and their association with six successional stages according to DCA (see Fig. 5.5) and TWINSpan. A total of 57 species was recorded.

<i>A. arenaria</i> foredunes or recent plantings	indigenous foredunes
<i>A. arenaria</i> <i>Arctotheca populifolia</i> <i>Senecio elegans</i>	<i>Didelta carnosa</i> <i>Tetragonia decumbens</i> <i>Thinopyrum distichum</i>
stabilised dunes	saltmarsh
<i>Astephanus triflorus</i> <i>Chironia baccifera</i> <i>Dasispermum suffruticosum</i> <i>Ehrharta villosa</i> <i>Helichrysum praecinctum</i> <i>Passerina rigida</i> <i>Psoralea repens</i> <i>Stoebe plumosa</i> <i>Sutherlandia frutescens</i> <i>Thesidium fragile</i>	<i>Chenolea diffusa</i> <i>Cynodon dactylon</i> <i>Ficinia indica</i> <i>Limonium scabrum</i> <i>Plantago crassifolia</i> <i>Sarcocornia decumbens</i> <i>Spergularia media</i> <i>Sporobolus virginicus</i> <i>Trachyandra divaricata</i>
dune scrub	
<i>Agathosma collina</i> <i>Carpobrotus edulis</i> <i>Chrysanthemoides monilifera</i> <i>Ficinia lateralis</i> <i>Helichrysum patulum</i> <i>Metalsia muricata</i> <i>Myrica cordifolia</i> <i>Nylandtia spinosa</i> <i>Olea exasperata</i> <i>Otholobium bracteolatum</i> <i>Pentaschistis eriostoma</i> <i>Scirpus nodosus</i> <i>Solanum americanum</i>	
dune scrub/dune fynbos	
<i>Chasmanthe aethiopica</i> <i>Cuscuta cassytoides</i> <i>Euclea racemosa</i> <i>Felicia zeyheri</i> <i>Ficinia ramosissima</i> <i>Helichrysum dasyanthum</i> <i>Ischyrolepis eleocharis</i> <i>Knowltonia capensis</i> <i>Myrica quercifolia</i> <i>Othonna filicaulis</i> <i>Passerina paleacea</i> <i>Phyllica ericoides</i> <i>Portulaca sp.</i> <i>Protasparagus africanus</i> <i>Rhus crenata</i> <i>Rhus glauca</i> <i>Rhus laevigata</i> <i>Thamnochortus insignis</i> <i>Viscum capense</i>	

CHAPTER SIX

Ammophila arenaria communities in South Africa - Short-term changes

6.1 Introduction

While the vegetation analysis of *A. arenaria* and indigenous South African dune communities (Chapter 4) reflects the present status of these communities, it is desirable to examine and evaluate the behaviour of *A. arenaria* in South Africa over time. In the following studies, *A. arenaria* and indigenous dune plant communities were monitored over periods of half a year to a few years, and changes in their floristic as well as functional traits compared. The focus is on short-term changes of community traits such as species richness, species diversity and the importance value of species, as well as elements of population biology of the respective species, such as their demography and growth patterns.

Various aspects of the population biology of *A. arenaria* have been studied in its natural European range. Greig-Smith *et al* (1947) examined the growth of *A. arenaria* with particular regard to its tussock formation, while Gemmell *et al* (1953) described in detail the impact of the growth of *A. arenaria* on the formation of sand dunes. Two growth patterns, a tillering and a tussock forming pattern, are distinguished by Greig-Smith (1961). Huiskes & Harper (1979) studied the demography of leaves and tillers along a successional gradient from the foredunes to the backdune area.

However, comparative studies of *A. arenaria* with other dune species in regard to their population biology are scarce. A comparison of demographic traits of *Carex arenaria*, another European dune perennial with extensive vegetative growth, with those of *A. arenaria* (Watkinson *et al* 1979) shows that only few *A. arenaria* tillers flower, whereas tillers of *Carex arenaria* which last into their second year will usually develop flowers and then die. Tillers of *A. arenaria* therefore appear to have a longer life. *A. arenaria* does not develop as many buds as *Carex arenaria*. There are generally more buds on vertical rhizomes, and even buds of

horizontal rhizomes usually give rise to aerial shoots. In contrast, *Carex arenaria* develops only horizontal rhizomes, but these bear extensive bud banks. Considering the higher shoot longevity, the quick elongation of vertical rhizomes and the development of vertically oriented buds, *A. arenaria* appears to be not only better equipped to withstand extreme sand burial, but also to develop much more above-ground biomass than *Carex arenaria*. Very similar results were obtained by Pavlik (1983c) in an American comparison of the clonal expansion of *A. arenaria* and the indigenous Californian dune species *Leymus mollis*. While *A. arenaria* carries buds preferentially on vertical rhizomes which form dense clumps of aerial shoots, *Leymus mollis* distributes buds more evenly between vertical and horizontal rhizomes. *A. arenaria* develops an above-ground biomass about two or three times the size of *Leymus mollis*. Hence, it appears as though *A. arenaria* is oriented more towards gaining a higher photosynthetic surface area, while *Leymus mollis* allocates more material to its extensive horizontal growth.

Such comparative studies on the population biology of *A. arenaria* with other dune plants are particularly important in order to gain information about its possible invasive behaviour. Barbour & Robichaux (1976) have recorded unusually high values of above-ground biomass for *A. arenaria* on Californian beaches. Pavlik's study (1983c) shows that this has led to a marked change of the microenvironment of Californian dunes, which is connected to the decreasing vigour of indigenous dune communities. On the other hand, the indigenous species *Leymus mollis* has a lower above-ground density and grows in relative rich assemblages with other coastal plants.

In this chapter four experiments are described which aim at comparing the change of floristic community traits as well as elements of population biology, namely the demography and growth patterns, of *A. arenaria* with those of various indigenous South African dune plants over a certain time period. The key objectives are to assess whether *A. arenaria* populations increase in abundance over a period of a couple of years, and if they do, whether it has a negative impact on indigenous species; furthermore, whether *A. arenaria* has a competitive advantage over indigenous dune plants through a favourable demography, e.g. a higher growth rate, higher regeneration rate, higher above-ground biomass. Each section describes the study area, methods and results of the respective experiments. A discussion of all sections together is presented at the end.

6.2 Floristic changes in *Ammophila arenaria* and indigenous dune plant communities at Kleinemonde, Eastern Cape

6.2.1 Introduction

This study aimed at comparing floristic changes in *A. arenaria* communities with indigenous South African dune plant communities over a period of two and a half years. Dominant indigenous plants used in this comparison were *Scaevola plumieri*, *Thinopyrum distichum* and *Ehrharta villosa*. While *Scaevola plumieri* and *Thinopyrum distichum* thrive particularly in the foredune area and are important hummock builders, *Ehrharta villosa* is found both on fore- and backdunes. No information is available on the biology of *Thinopyrum distichum*, whereas *Scaevola plumieri* and *Ehrharta villosa* have been subjected to various physiological analyses (Pammenter 1983, 1985; Hoare 1994 respectively). However, no studies have so far focused on any of these species' population biology, apart from an examination of *Ehrharta villosa* in regard to possibilities for its propagation and use for dune stabilisation (Rothman 1992).

The following key questions are posed:

- 1) *How do species richness and species diversity of A. arenaria communities change over a period of 2.5 years compared to indigenous dune plant communities?*
- 2) *How do the species develop in the various communities over the study period? Is there an increase or decrease in abundance, and do changes of different species correlate, i.e. do species show negative or positive associations with one another?*

6.2.2 Study area

Kleinemonde is a small holiday resort about 12 km east of Port Alfred (33°33'S; 27°08'E), situated at the mouths of two rivers, the Kleinemonde West and the Kleinemonde East River (Fig. 6.1). A detailed description of the area is given by Avis (1992). The area is influenced by the warm south-flowing Mocambique-Agulhas current and has a subtropical climate with an average annual temperature of 18°C (max. 22°C in December and January, min. 14°C in July).

Average annual precipitation is 559 mm with most rainfall, usually as maritime showers, occurring in spring (October) and autumn (March). Frost does not occur, but fog is fairly common (Schultz 1985). Winds are predominantly southwesterly and northeasterly in summer and westerly in winter. They blow usually parallel to the coast and sometimes reach gale forces, their net result being a 2-3 m easterly movement of sand per year (Avis 1992). The net longshore drift in the area is in an eastward direction, thus sea sand collects on the eastern side of all bays. The coastline is generally characterised by a very dynamic surf zone, productive sandy beaches and large mobile dunefields consisting predominantly of parabolic dunes (Lubke & Sudgen 1990).

The study site is a field of mobile and semi-stable dunes west of the mouth of the Kleinemonde West River and a strip of narrow dunes stretching from this field along the sea about 1 km further to the west (Fig. 6.1). The dune field is interspersed with dune hummocks and frequently inundated dune slacks. In the late 1970's an attempt was made at stabilising the area to protect chalets from the drifting sand. For this purpose *Acacia cyclops* and *A. arenaria* were planted in considerable amounts, but unfortunately no records of the plantings were made. Today the dunes are dominated by *A. arenaria* or by the indigenous plants *Scaevola plumieri*, *Sporobolus virginicus*, *Arctotheca populifolia* or *Thinopyrum distichum* (foredunes and intermediate dunes), or by *Ehrharta villosa* or *Ipomoea pes-caprae* (intermediate and backdunes). The Australian *Acacia cyclops* is still common in dune scrub further back, but has been purposefully destroyed by fire in the 1980's when concern about the species was increasing. Important dune slack species are *Scirpus nodosus* and *Juncus kraussii*. Behind the dune field is a zone of dune scrub vegetated mostly with *Chrysanthemoides monilifera*, *Myrica cordifolia*, *Passerina rigida*, *Metalasia muricata*, *Stoebe plumosa* and *Acacia cyclops*. Behind the scrub zone grows thick coastal forest dominated by *Sideroxylon inerme*, *Mimusops caffra* and *Brachylaena discolor*.

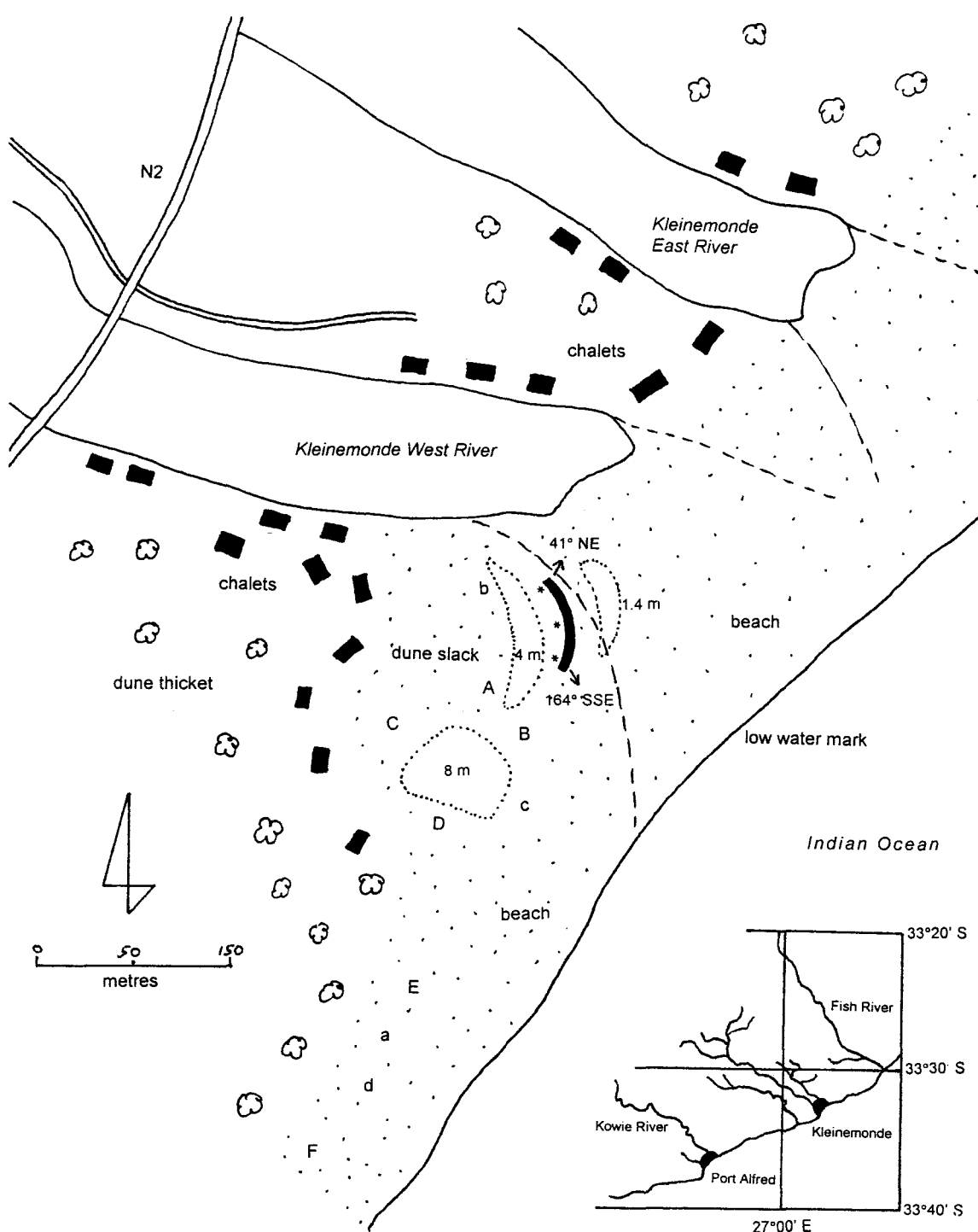


Fig. 6.1: The Kleinemonde dunefield. The sampled six *A. arenaria* and four indigenous communities are marked (A, B, C, D, E, F, a, b, c, d). Dotted lines indicate major shifting sands (height in metres). The two river mouths are usually closed, but can break open during rainy periods (perforated lines). The driftline examined in the next section (Section 6.3) is marked as a black sickle between two shifting sands (* = position of sand burial markers).

6.2.3 Methods

Six *A. arenaria* communities (A, B, C, D, E, F) and four indigenous dune plant communities (a, b, c, d) were sampled in 100 m² stands for density and cover of each species to arrive at measurements of species richness, species diversity (Simpson's diversity index, d_s) and species importance values as described in Chapter 4. The communities are situated at various distances from the sea and are exposed to the wind and major driftsands to various degrees (Fig. 6.1). Two of the four indigenous communities are dominated by *Scaevola plumieri*, one by *Thinopyrum distichum* and one by *Ehrharta villosa*. These pioneer species were chosen because by observation all three species appear to be replaced at Kleinemonde by *A. arenaria* to a certain extent. Sampling was carried out five times approximately every eight months over a period of 2.5 years (from 10 February 1995 to 18 September 1997). To ensure sampling of exactly the same stands, a metal pole of 1 m length with a red tip was left in the middle of each stand as a permanent marker, and orientations of the stand were recorded with a compass.

The change in abundance of each species in the Kleinemonde communities is best reflected in their densities. Importance values provide a thorough picture of a species' abundance, but only in relation to other species of the stand. If only one species occurs in a stand, that species has at any time the maximum importance value of 300, no matter how much its abundance increases or decreases. A species' density (number of shoots per unit area), on the other hand, is independent of the occurrence of other species in the same stand and therefore better suited for the Kleinemonde study, where some stands contain very few or only one species.

To reveal the degree of species correlations in the Kleinemonde communities, correlation analyses for all species pairs in *A. arenaria* and indigenous dune communities respectively were undertaken (5 data sets over the study period: $n = 5$ for each analysis). For these analyses, mean importance values per species were used rather than their mean densities in order to take into account the cover and frequencies of the species as well.

6.2.4 Results

1) Change of species richness and species diversity

Mean values of species richness and species diversity over the study period are shown for *A. arenaria* and indigenous dune plant communities in Figure 6.2. The values do not fluctuate much and show only little digression between the two types of communities at any one time. Both species richness as well as species diversity values were initially lower for *A. arenaria* communities, but increased above the values of indigenous communities towards the end of the observation period. Although this rise could indicate that *A. arenaria* associates well with other species, a closer look at the development of each community (see next section: Table 6.1) reveals the opposite: In two of the *A. arenaria* communities indigenous dune species increased in abundance over the study period; in one of them the indigenous creeper *Cynanchum natalitium* became the dominant species. It is therefore the increasing presence of indigenous dune species and consequential loss of vigour of *A. arenaria* that leads to increased species richness and diversity values in the Kleinemonde *A. arenaria* communities. The decline of species richness and diversity values in indigenous communities cannot conversely be explained with a rise of *A. arenaria* in these communities.

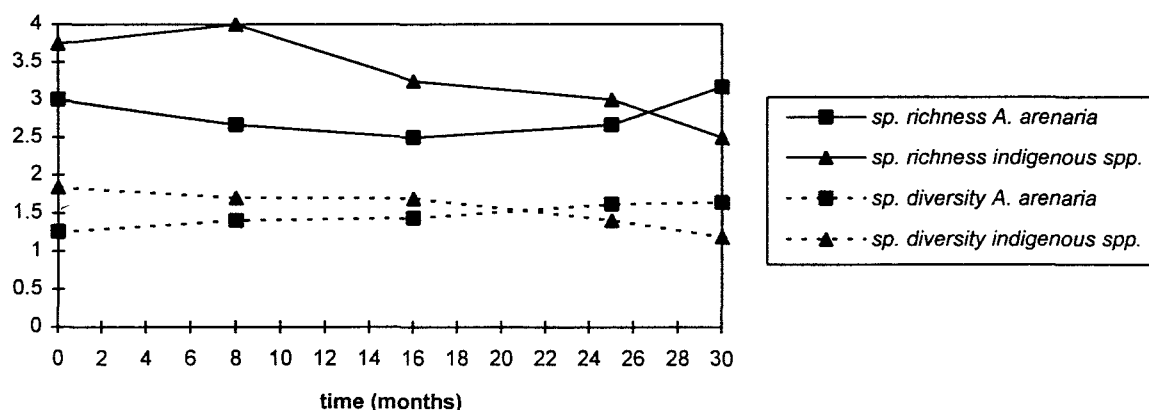


Figure 6.2: Change of mean values of species richness and Simpson's diversity (d_s) of Kleinemonde dune plant communities dominated by *A. arenaria* and indigenous dune plants respectively over a period of 30 months.

2) Change of abundance of species

The change of species densities over time in six *A. arenaria* communities at Kleinemonde is reflected in Table 6.1. Community A is a monospecific *A. arenaria* stand that continuously lost vigour from the first observation. This may be due to severe sand burial in combination with a flooding event in November 1996, when the dune slack surrounding community A was inundated to about 1.6 metres with saline sea water and only dried out in April 1997 (Plate 6.1). Communities B and C are relatively stable communities, but community D suffered extreme sand burial which only *A. arenaria* survived (Table 6.1). While indigenous species like *Senecio litorosus* and *Ipomoea pes-caprae* could not withstand the sand burial, *A. arenaria* initially declined in vigour but recovered to grow even more vigorously, thereby demonstrating its superior adaptation to strong sand movement. Plates 6.2 and 6.3 illustrate the impact of excessive sand burial on this community.

A. arenaria was replaced rapidly in community E and to a lesser extent in community F (Table 6.1). Both communities are situated closer to the high water mark than the others (15.2 m and 23.7 m). Less sand movement encourages the growth of indigenous dune pioneer species. In community E, the indigenous creeper *Cynanchum natalitium* had become the dominant plant at 25 months of observation, with 197 shoots per 100 m² compared to 68 shoots of *A. arenaria*. *Senecio elegans* had also become more numerous than *A. arenaria*, with a density of 72 shoots per 100 m², while other indigenous species like *Dasispermum suffruticosum* and *Passerina rigida* had markedly gained abundance. Interestingly, the indigenous dune grass *Ehrharta villosa* was not as affected by this increase of species as *A. arenaria* was and remained at much the same abundance throughout the study period. In community F, slightly further removed from the high water mark, the decline of vigour of *A. arenaria* and increase of *Cynanchum natalitium* and other indigenous species was less extreme but equally notable. It becomes obvious that the changes in these two communities accounts for the increase of species richness and diversity in *A. arenaria* communities towards the end of observation (see above).

Table 6.1: Density (per 100 m²) of all species in six *A. arenaria* communities (A - F) at Kleinemonde at five sampling dates. In brackets behind the stands their distance from the high water mark (m).

species	time (months)				
	0 (10-3-1995)	8 (18-11-1995)	16 (24-7-1996)	25 (12-4-1997)	30 (18-9-1997)
community A (55.5 m)					
<i>A. arenaria</i>	285	136	119	94	87
community B (35.5 m)					
<i>A. arenaria</i>	116	56	82	97	162
<i>Thinopyrum distichum</i>	7	12	10	8	14
<i>Scaevola plumieri</i>	1	4	35	29	54
<i>Gladiolus gueinzii</i>	0	0	0	3	0
<i>Arctotheca populifolia</i>	0	0	0	0	1
community C (79.1 m)					
<i>A. arenaria</i>	570	521	450	509	532
<i>Arctotheca populifolia</i>	20	0	0	5	10
<i>Dasispermum suffruticosum</i>	0	8	0	0	0
community D (66.7 m)					
<i>A. arenaria</i>	504	122	178	211	542
<i>Senecio litorosus</i>	38	0	0	0	0
<i>Ipomoea pes-caprae</i>	35	0	0	0	0
<i>Passerina rigida</i>	2	0	0	0	0
<i>Acacia cyclops</i>	1	0	0	0	0
community E (15.2 m)					
<i>A. arenaria</i>	532	190	164	113	68
<i>Ehrharta villosa</i>	103	87	61	103	101
<i>Cynanchum natalitium</i>	39	64	94	163	197
<i>Dasispermum suffruticosum</i>	0	9	10	12	15
<i>Senecio elegans</i>	0	36	0	49	72
<i>Passerina rigida</i>	0	0	0	20	26
<i>Stoebe plumosa</i>	0	0	0	0	2
community F (23.7 m)					
<i>A. arenaria</i>	108	157	136	145	88
<i>Cynanchum natalitium</i>	12	10	17	28	36
<i>Dasispermum suffruticosum</i>	12	3	0	0	0
<i>Passerina rigida</i>	0	0	0	4	16
<i>Carpobrotus deliciosus</i>	0	0	0	1	2



Plate 6.1: *A. arenaria* community A in May 1996 (top), surrounded by sea water in January 1997 (middle), and nearly disappeared in May 1997 (bottom).



Plate 6.2: *A. arenaria* community D (view towards north) flowering vigorously in November 1995 (top) and suffering severe sand burial in May 1996 (middle). *A. arenaria* recovers slowly in January 1997 (bottom), all other species cannot withstand the sand burial. See also Plate 6.3.

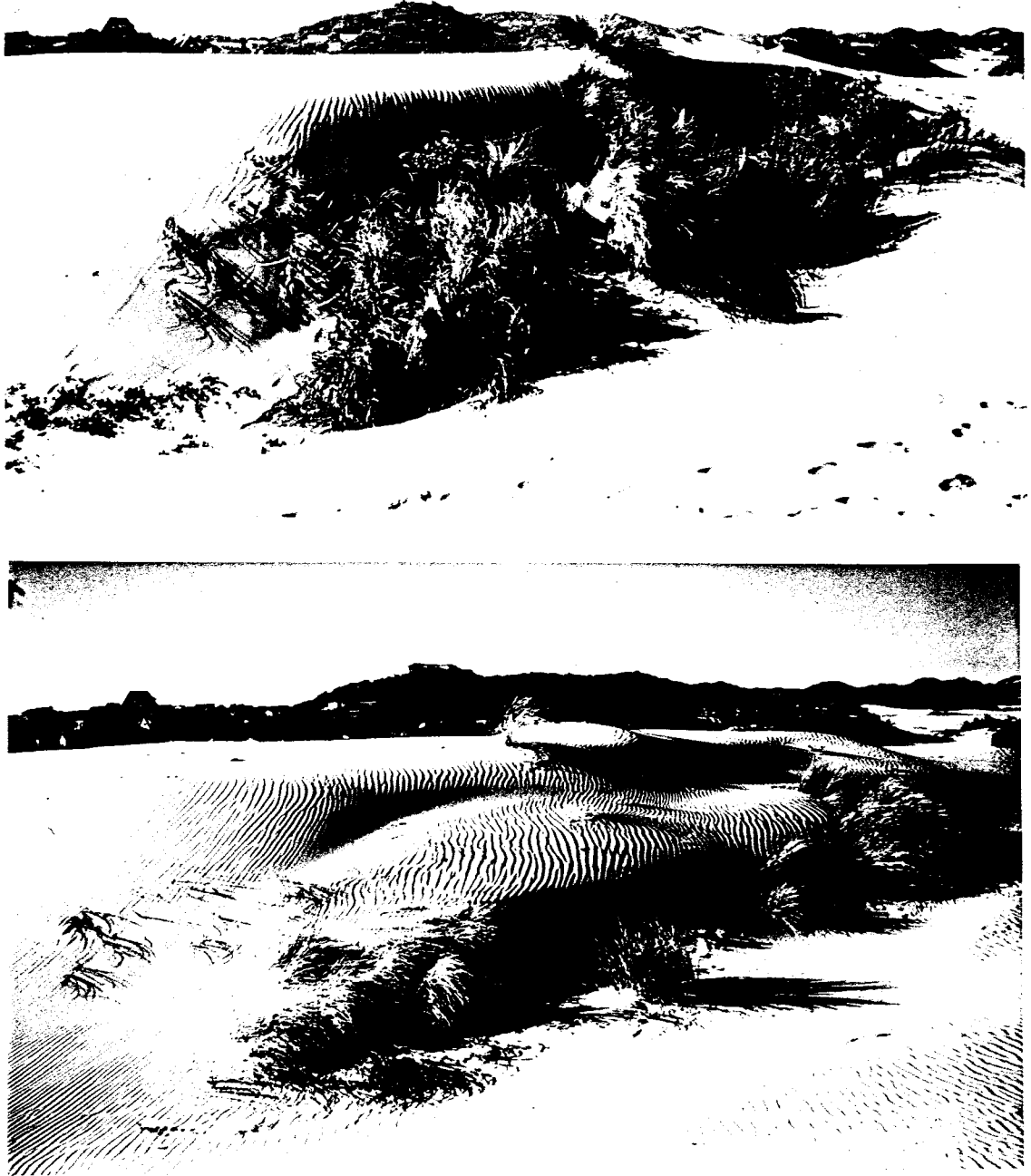


Plate 6.3: *A. arenaria* community D (view towards east) being buried by sand. In May 1996, indigenous species like *Senecio litorosus* and *Ipomoea pes-caprae* are still present (top), in July 1996 only *A. arenaria* has survived the sand burial (bottom). See also Plate 6.2.

A. arenaria was replaced in two of its Kleinemonde communities by indigenous dune plants, but it also replaced an indigenous dune plant (Table 6.2): The density of *Ehrharta villosa* in community a was reduced from 308 per 100 m² to only 15 over the observation period, while *A. arenaria*'s density in the same community increased from 150 to 380. A reason could be the vicinity of the community to the sea (15.2 m from the high water mark). *Ehrharta villosa* is usually found in the intermediate or backdune area and is possibly less tolerant of adverse factors of the foredunes like salt spray than *A. arenaria*. However, the other observed indigenous communities were not affected by *A. arenaria*. In community b, only *Thinopyrum distichum* and *Scaevola plumieri* survived. Since this community is situated immediately behind a mobile dune, a possible reason could again be the amount of sand burial which only the two hardiest of the species in this community could withstand. Communities c and d are dominated by increasingly healthy *Scaevola plumieri*. This appears to coincide with a reduction of shoot numbers of *Sporobolus virginicus* in community d. Other species grow well within the vigorous *Scaevola plumieri* though.

Tables 6.1 and 6.2 reflect clearly the changes of species abundance in the various communities. However, the only significant species correlation is found for *A. arenaria* communities in the case of *A. arenaria* and *Cynanchum natalitium* (Table 6.3). In confirmation of Table 6.1, which reflects the replacement of *A. arenaria* by *Cynanchum natalitium*, the two species are significantly ($P = 0.047$) negatively correlated. The strongest correlation in indigenous dune communities is found for *Ehrharta villosa* and *A. arenaria* (Table 6.3), again negative and also confirming the replacement of *Ehrharta villosa* by *A. arenaria* in community a as shown in Table 6.2. However, this correlation is not significant ($P = 0.117$). All other species correlations have even lower significance values and are not shown.

Table 6.2: Density (per 100 m²) of all species in four indigenous communities (a - d) at Kleinemonde at five sampling dates. In brackets behind the stands their distance from the high water mark (m).

species	time (months)				
	0 (10-3-1995)	8 (18-11-1995)	16 (24-7-1996)	25 (12-4-1997)	30 (18-9-1997)
community a (14.4 m)					
<i>Ehrharta villosa</i>	308	195	52	36	15
<i>A. arenaria</i>	150	181	209	273	380
community b (26.2 m)					
<i>Thinopyrum distichum</i>	112	133	79	183	271
<i>Scaevola plumieri</i>	41	37	3	3	6
<i>Senecio elegans</i>	12	13	0	0	0
<i>Dasispermum suffruticosum</i>	0	3	0	0	0
<i>Vellereophyton vellereum</i>	22	24	17	0	0
community c (23.4 m)					
<i>Scaevola plumieri</i>	134	137	142	210	236
<i>Gladiolus gueinzii</i>	2	1	0	0	0
<i>Thinopyrum distichum</i>	0	0	0	15	20
<i>Hebenstreitia cordata</i>	0	0	0	3	11
community d (9.0 m)					
<i>Scaevola plumieri</i>	143	151	136	248	346
<i>Sporobolus virginicus</i>	235	260	93	14	0
<i>Senecio elegans</i>	81	52	36	0	0
<i>Vellereophyton vellereum</i>	7	8	0	0	0
<i>Myrica cordifolia</i>	3	5	7	0	0
<i>Thinopyrum distichum</i>	0	2	13	8	4
<i>Gladiolus gueinzii</i>	0	1	0	0	14
<i>Ehrharta villosa</i>	0	0	0	0	48

Table 6.3: The two strongest species correlations in Kleinemonde communities dominated by *A. arenaria* or indigenous dune pioneer species respectively. Weaker correlations are not shown. Results are based on mean importance value per species of all communities in which the species occurred and over the whole study period (n = 5). Significance at $\alpha = 0.05$ (*).

<i>A. arenaria</i> communities:		Indigenous dune plant communities:	
<i>A. arenaria</i> and <i>Cynanchum natalitium</i>		<i>A. arenaria</i> and <i>Ehrharta villosa</i>	
<i>r</i>	- 0.883	<i>r</i>	- 0.783
<i>P</i>	0.047 *	<i>P</i>	0.117

6.3 Floristic and demographic changes in a driftline community of *Ammophila arenaria* and various indigenous dune plants at Kleinemonde, Eastern Cape

6.3.1 Introduction

The driftline community under study is a ca. 35 m long and not more than 2.5 m broad strip of pioneer vegetation on the Kleinemonde beach. It is formed mainly by four species, *A. arenaria* and the indigenous *Scaevola plumieri*, *Arctotheca populifolia* and *Gladiolus gueinzii*, with very few *Thinopyrum distichum* and *Ipomoea pes-caprae* in between. Although the first plants must have established themselves at the end of 1996, they were first observed in mid January 1997 as a thin line of vegetation on the otherwise bare beach (Plate 6.4). From March 1997, the vegetation was sampled at regular intervals over half a year with the overall aim of monitoring how *A. arenaria* copes in the harsh conditions of an Eastern Cape beach habitat in comparison to various indigenous dune plants.

Key questions that are to be addressed in this study are:

- 1) *How do dominance and importance of each plant species change over a period of half a year? Which plants appear to be most vigorous?*
- 2) *How do life history stages of the plant species change over the period? Which plants establish themselves successfully, and which plant species do not reach maturity?*

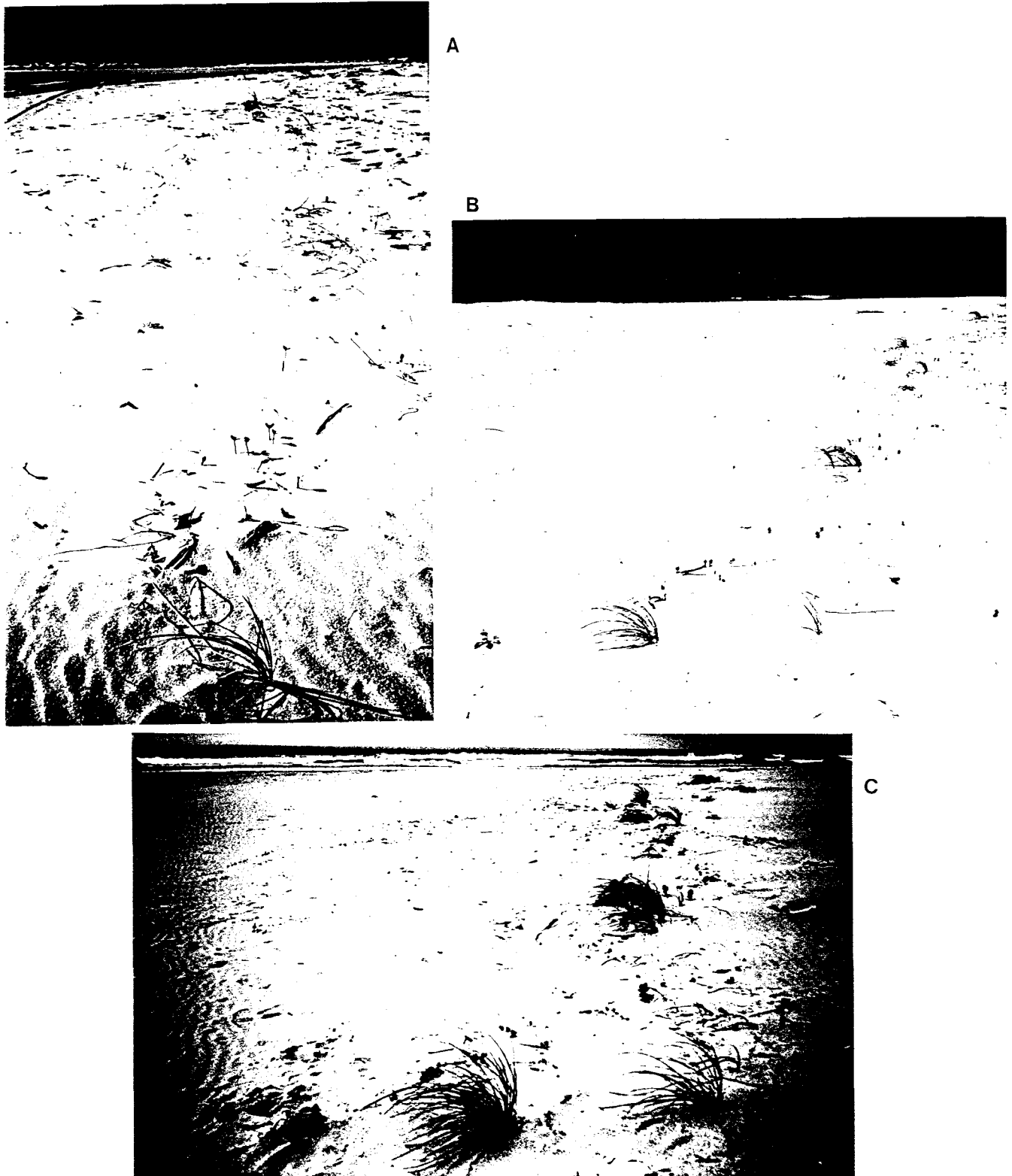


Plate 6.4: Driftline community at Kleinemonde in January 1997 (A), March 1997 (B) and May 1997 (C). In January the thin line of vegetation contains a few juvenile *A. arenaria* plants and *Scaevola plumieri* seedlings. By May *A. arenaria* has developed several healthy tussocks.

6.3.2 Study area

The area of the study, Kleinemonde, is described above (Section 6.2.2). The driftline is situated between 60 and 100 m west of the mouth of the Kleinemonde West River, depending on the water level of the river and its flow (Fig. 6.1). It developed after strong rainfalls in November 1996, which opened the river mouth, thereby accounting for high tides almost perpendicular to the shore. The driftline is sickle-shaped, the one end facing the river at 41° NE, the other end facing the sea at 164° SSE. The sea-facing end is ca. 40 m, the other end ca. 80 m away from the high water mark. The driftline stretches along the river mouth to the sea in between, and parallel to, two barchan mobile dunes. The smaller of these dunes, to the sea/river-side of the driftline, had a height of ca. 1.4 m above sea level and was 20 m away from the driftline at the beginning of sampling in March 1997. The landward dune was ca. 4 m high and situated 38 m away from the driftline. By the end of the sampling in September 1997, the smaller dune had moved ca. 40 cm towards the driftline, and the larger dune ca. 2 m away from it.

6.3.3 Methods

Along the length of the driftline a 35 x 2 m belt transect was laid out, i.e. sampling was undertaken at a breadth of two 1m² quadrats along the 35 m transect. To ensure sampling of exactly the same quadrats three metal poles of 50 cm length were used as permanent markers at the two ends and in the middle of the line. Furthermore, three of the larger *Arctotheca populifolia* plants were tagged, and their situation in relation to the tape was recorded. Vegetation was sampled for density and cover of each species to calculate their importance values as described in Chapter 4.

The shoot density per species per life-history stage was recorded to arrive at a measure of relative shoot density, calculated as % shoot density of all shoots of all life-history stages of all species in the driftline. The following five life history stages were distinguished for all species: Seedling, juvenile plant, mature plant, mature and flowering plant, and senescent plant. Sand burial was measured at the three marker poles. Sampling was carried out five times every six weeks between 26 March 1997 and 10 September 1997. Climate data, i.e. total daily rainfall

(mm) and daily mean temperatures ($^{\circ}$ C), were obtained for the same period from Fish Point Lighthouse, ca. 8 kilometres west of Kleinemonde.

The dependence of species importance values on the amount of sand burial in the whole driftline community was examined in regression analyses (4 data sets over the whole study period: $n = 4$ respectively) for each species except *Ipomoea pes-caprae*, which only occurred at one sampling date. No regression lines were plotted, but r^2 -values, values of b (slope of the regression line) and the significance P are reflected for each analysis.

6.3.4 Results

1) Importance values

Figure 6.3 displays the change of the importance value of each species over six months. *Gladiolus gueinzii* started off as the dominant species in the driftline, but declined steadily during the period of observation. Similarly, *Scaevola plumieri* was well represented in the driftline in the beginning, but then declined in importance. In contrast, *A. arenaria* grew rapidly within the first six weeks of observation and had high importance values at the end of the period. A higher importance value was reached by *Arctotheca populifolia* after twelve weeks, but thereafter *A. arenaria* became the overall dominant species of the driftline. *Arctotheca populifolia* declined but was still well represented in the community at the end of observation. *Scaevola plumieri* appeared to recover slightly towards the end, but remained one of the weaker plants in the driftline. There was some *Ipomoea pes-caprae* present in the driftline at the beginning of the observation, but it died off within the first six weeks and was not recorded again. In contrast, *Thinopyrum distichum* was only recorded in the second sampling set and slowly increased in abundance, although its importance values were much lower throughout than any of the above four species.

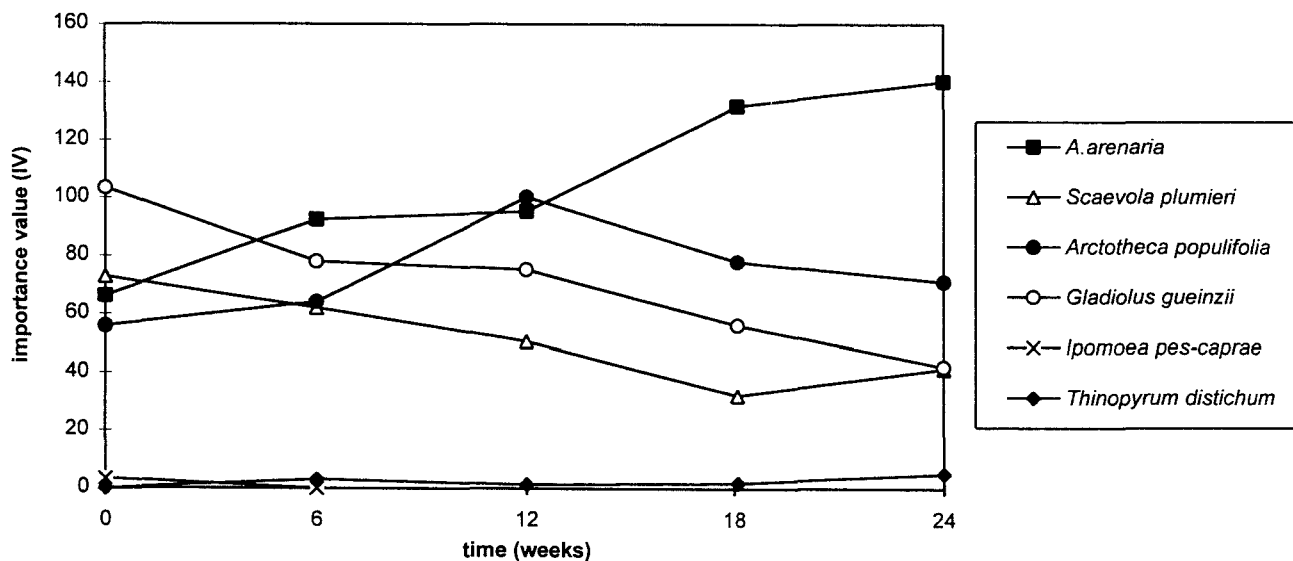


Fig. 6.3: Importance values (IV) of all six species that were recorded in a driftline community at Kleinemonde over a period of six months.

2) Life history stages

The demographic development of the respective species in the driftline over six months is reflected in Figure 6.4. A first look at the different graphs for the life history stages, especially the scaling of their y-axis, reveals that most plants were of the seedling or juvenile stage with density values of up to 20% or even 80% in the case of juvenile *A. arenaria*. In contrast, mature plants, mature and flowering plants and senescent plants were rare, their density values never extending 4%. This is to be expected as driftline communities are pioneer communities exposed to such harsh environmental conditions that the survival of individuals is always low. In the following, changes in relative shoot densities per species (Fig. 6.4) are described and possible correlations with the amount of sand burial discussed (Tables 6.4 and 6.5).

A. arenaria did not occur in the seedling stage, but was numerous as a juvenile plant with the overall record of relative density of 79% at the end of sampling (Fig. 6.4). The constant rise of the juvenile *A. arenaria*'s density without any occurrence in the seedling stage implies that *A. arenaria* reproduced in this driftline community only vegetatively through the production of culms from rhizomes, which were counted as juvenile plants. Only a few of the juvenile plants

reached maturity during the time of observation, and no flowering was recorded, which is not surprising since tillers of *A. arenaria* develop inflorescences only in their second or third year. However, after 12 weeks some of the plants declined in vigour rapidly and were recorded as senescent. The increase of juvenile *A. arenaria* plants can be related well to sand burial measurements along the same driftline (Table 6.4): a rapid increase was recorded over the first 6 weeks and after 12 weeks. During these periods, sand burial was high. The lack in increase of juvenile plants between 6 and 12 weeks correlates with the lowest measurement of sand burial during the same period. These observations are confirmed by the results of a regression analysis (Table 6.5) which prove that a high importance value of *A. arenaria* is significantly ($P = 0.043$) positively correlated to high sand burial.

Scaevola plumieri produced numerous seedlings in the driftline, but their survival rate was extremely low. The relative seedling density varied between 19% and 5%, but juvenile plant density did not extend 0.8% (Fig. 6.4). Consequently, *Scaevola plumieri* did not occur in any later life history stage. A reason for the low seedling survival rate could be sand burial: between weeks 12 and 18 of the observation, sand burial was between 6.6 cm and 8.4 cm (Table 6.4), possibly fluctuating a lot during these 6 weeks and reaching higher levels at some times. During the same period, the most rapid decrease of seedlings was recorded. A *Scaevola* seedling is not usually more than 6 cm tall, and most seedlings were possibly buried by sand during this period. Although the regression analysis (Table 6.5) shows no significant relation between the importance value of *Scaevola plumieri* and the amount of sand burial, the regression coefficient is negative ($b = -2.379$), confirming a negative impact of sand burial on the plant. After the sand burial event, hardly any new *Scaevola* seedlings emerged, probably because of increased sand burial (Table 6.4) in combination with a simple lack of further seed.

In contrast, the decrease of seedling numbers of *Gladiolus gueinzii* can be related to an increase in the number of juvenile and mature plants (Fig. 6.4). *Gladiolus* seedlings more frequently reached the juvenile stage than *Scaevola* seedlings. Although they appear to be less affected by sand burial, the sand burial increase after 12 weeks is notable even here as a marked decline of *Gladiolus* juveniles. A regression analysis reveals a fairly significant ($P = 0.059$) negative relation between the importance values of *Gladiolus gueinzii* and sand burial (Table 6.5). Nevertheless, maturity was reached frequently by *Gladiolus gueinzii*, and this species showed

the greatest density of mature plants. However, one has to consider that densities in the older stages of life history were low for all species. In the case of *Gladiolus gueinzii*, the maximum densities of seedling and juvenile plants were 18% and 17%, but the maximum density of mature *Gladiolus* plants was just above 3%.

Arctotheca populifolia was never numerous in the driftline at any of the life stages, but it stands out as the only plant that appeared in all of them (Fig. 6.4). It reached its highest density as a juvenile plant with nearly 6% and was as numerous as a mature plant as it was in its seedling stage (2%). *Arctotheca populifolia* was the only flowering plant in the driftline, thus apparently capable of developing flowers within the first life-cycle. Flowering was low (0.7% at maximum) over this autumn and winter period, but the increase of mature plants towards the end of the period will give rise to more flowering plants in the coming spring.

Ipomoea pes-caprae was present only in the beginning of sampling as one small seedling (0.3%), which soon died, presumably from sand burial.

Thinopyrum distichum appeared after 6 weeks, already in the juvenile stage. Although the *Thinopyrum distichum* population at Kleinemonde is not very large, frequent seeding and numerous vigorous seedlings and juveniles were observed during the 6 month period, and it is assumed here that within the first 6 weeks of the experiment seedlings emerged which had grown into juvenile plants before the next sampling was undertaken. Only at the last sampling date were two seedlings counted (0.5%). However, the juvenile *Thinopyrum* plants did not gain in abundance over the period, no vegetative reproduction was recorded, none of the plants reached maturity, and their density was never more than 0.9% at maximum.

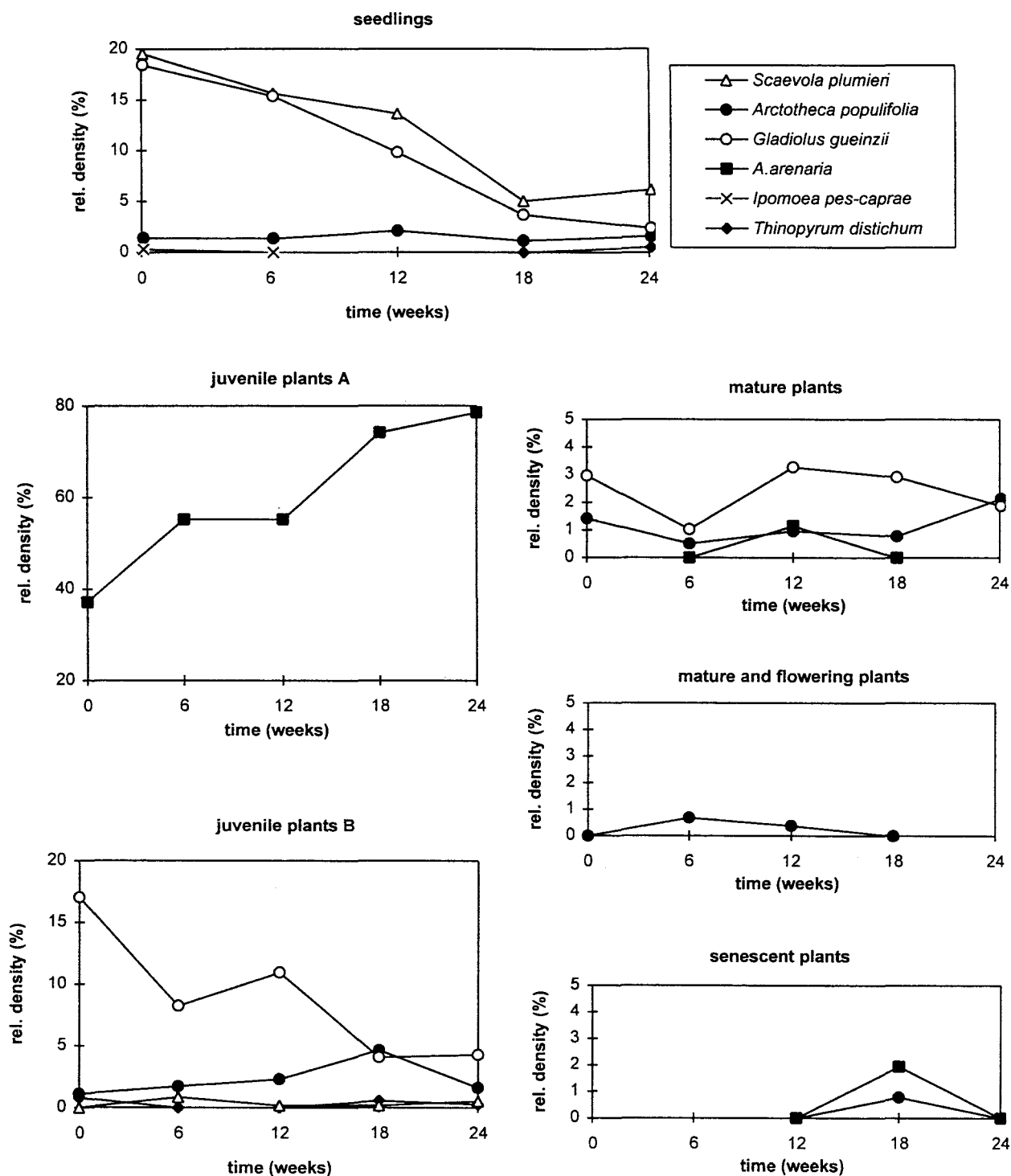


Fig. 6.4: Relative shoot densities (%) per species in five life history stages in a driftline community at Kleinemonde over a period of six months. The graph for the juvenile plant stage had to be divided into two parts (A and B) because of the discrepancy of density values from just above 0% to nearly 80%. Relative shoot densities are calculated as % of all shoots of all life history stages of all species. Note the different scaling of the y-axes.

Table 6.4: Sand burial (cm) measured at three poles (a, b, and c) along a Kleinemonde driftline community over a period of six months.

pole	time (weeks)			
	6 (7-5-1997)	12 (17-6-1997)	18 (30-7-1997)	24 (6-9-1997)
a	+ 5.2	- 0.5	+ 7.9	+ 10.2
b	+ 1.7	+2.4	+ 8.4	+ 6.4
c	+ 3.5	+ 1.9	+ 6.6	+ 11.5

Table 6.5: Regression analyses of the dependence of species importance values on the amount of sand burial in a driftline community at Kleinemonde over six months ($n = 4$ in each case). A positive regression coefficient b (slope of the regression line) indicates positive association, a negative b negative association. The higher r^2 , the higher the dependence. Significance (**bold**) at $\alpha = 0.1$ (*) and $\alpha = 0.05$ (**).

	<i>A. arenaria</i>	<i>Scaevola plumieri</i>	<i>Gladiolus gueinzii</i>	<i>Arctotheca populifolia</i>	<i>Thinopyrum distichum</i>
r^2	0.916	0.482	0.885	0.278	0.459
b	+ 6.319	- 2.379	- 4.305	- 2.213	+ 0.304
P	0.043 **	0.306	0.059 *	0.473	0.323

The influence of rainfall and temperature on shoot densities is less obvious than that of sand burial. Temperatures during South African autumn and winter are neither high nor excessively low, therefore only the rainfall would be expected to have any substantial impact on plant vigour. Climatic changes over the observation period from the end of March to September 1997 are shown in Figure 6.5. If one considers the rapid decrease of *Scaevola plumieri* seedlings during the wettest period of observation, i.e. the first three weeks, it appears as though the negative impact of sand burial overrides a positive climatic influence. Similarly, the density of juvenile *A. arenaria* shoots increased remarkably after 12 weeks, i.e. during the driest period of observation (Fig. 6.5). Its higher tolerance of sand burial gives *A. arenaria* an advantage over the other species, which results in higher importance values and shoot densities in spite of the lack of rainfall.

Considering the high number of mature plants at the beginning of sampling in March 1997 of both *Arctotheca populifolia* and *Gladiolus gueinzii*, it can be assumed that these plants were the

first to establish along the driftline from December 1996. *A. arenaria* must have followed soon, since it had developed a fair number of juveniles by March. The origin of each plant species in the driftline is obvious for *Scaevola plumieri*, *Arctotheca populifolia*, *Ipomoea pes-caprae*, *Gladiolus gueinzii* and *Thinopyrum distichum*, which have all arrived as seed, or bulb in the case of *Gladiolus*. All of these species have large enough populations at Kleinemonde to account for their fruit being transferred to the beach, either rolling down, being picked up and dropped by birds or being removed by the wind. The fruits were then washed up along the beach by a high tide in December 1996 and deposited in one line, which together with debris formed the driftline. The case of *A. arenaria* is more difficult. Although there are several healthy *A. arenaria* communities at Kleinemonde which develop flowers and a fair amount of viable seed (see Chapter 7), it did not occur at all in the seedling stage along the driftline. Neither are any of the Kleinemonde *A. arenaria* communities close enough to the driftline to account for the culms, which must have developed from rhizomes. It is therefore assumed that rhizome pieces washed ashore or transported by the wind have shooted and thus initiated the *A. arenaria* population on the driftline.

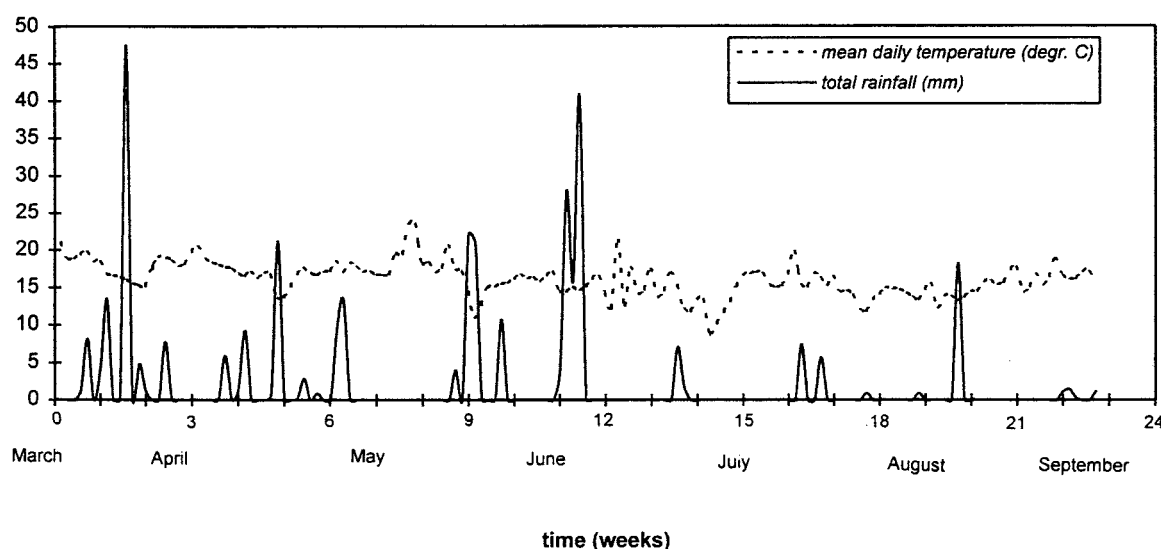


Fig. 6.5: Mean daily temperature and total daily rainfall at Fish Point lighthouse over the 24 weeks of observation from 26 March 1997.

6.4 The demography of leaves and tillers of *Ammophila arenaria* and indigenous dune plants at Port Alfred, Eastern Cape

6.4.1 Introduction

While Huiskes & Harper (1979) compared the flux of leaves and tillers of *A. arenaria* communities in different successional stages, it is more interesting for this study to draw such a comparison on a species level, namely between *A. arenaria* and indigenous South African dune plants. A large biomass is an important indication of potential invasiveness of any alien plant species. It was shown that *A. arenaria* develops a much larger above-ground biomass in California than the indigenous *Leymus mollis*, thereby changing the dune microenvironment and causing adverse conditions for indigenous plants and animals (Barbour & Robichaux 1976; Pavlik 1983c; see Chapter 2). A large biomass can be achieved by a long growth period and a high relative growth rate. The production of leaves and tillers, their growth and decline over time, was monitored over one growth period of half a year for populations of *A. arenaria* and the two indigenous dune grasses *Thinopyrum distichum* and *Ehrharta villosa*.

The following questions are posed:

- 1) *How does the flux of tillers of A. arenaria compare with that of indigenous dune plants?*
- 2) *What is the leaf/tiller-ratio of A. arenaria and how does it change during this period compared to that of indigenous dune plants? How do leaf lengths of the three grasses compare?*

6.4.2 Study area

The small coastal town of Port Alfred is situated at the mouth of the Kowie River about half way between Port Elizabeth and East London (33°26'S; 26°53'E). Climate and maritime conditions are closely related to those of Kleinemonde and are described above (Section 6.2.2). The studies were undertaken at Port Alfred West Beach, where the mobile dune area is reported to reach a width of 250 m at low tide, with dunes as high as 40 m above sea level (Lubke &

Sudgen 1990). However, this work was carried out in three dune communities at a much narrower stretch of beach. The three communities are dominated by *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* respectively and are situated only 6 m (*A. arenaria*), 8.5 m (*Thinopyrum distichum*) and 32 m (*Ehrharta villosa*) away from the high water mark. Conspicuous dune plants in the vicinity are *Arctotheca populifolia*, *Gazania rigens* and *Senecio elegans*.

6.4.3 Methods

In each of the three communities, dominated by *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* respectively, 5 separate clusters of tillers were chosen at random and permanently marked with tags and 50 cm long metal poles. Each cluster was treated as a subpopulation of the respective plant species and at regular intervals measured for number of live tillers, number of live leaves per tiller and length of each leaf. Sand burial at each cluster was measured as burial of the marker pole. Distances of each cluster from the high water mark were recorded in the beginning.

Sampling was carried out from 26 March 1997 to 10 September 1997, the same period during which work was carried out on the Kleinemonde driftline community (see above). Measurements of number of tillers and leaves and of sand burial were taken six times approximately every five weeks (after 0, 5, 9, 14, 19 and 24 weeks), leaf lengths were measured four times after 0, 9, 19 and 24 weeks. The leaves of *Ehrharta villosa* at Port Alfred were found to be mostly deciduous and broken off, therefore comparable data of leaf lengths of *Ehrharta villosa* were obtained from an unpublished study (R.A. Lubke, pers comm., October 1997) of *Ehrharta* populations at Kenton-on-Sea, 15 kilometres west of Port Alfred, carried out between March and September 1990.

To detect dependences of tiller numbers and leaf/tiller-ratios on sand burial, regression analyses were carried out for each cluster of each species for five data sets over the study period ($n = 5$ respectively). Because of the number of individual analyses, no regression lines

were plotted, but r^2 -values, values of b (slope of the regression line) and the significance P are reflected for each analysis.

6.4.4 Results

1) Gain and loss of tillers

Figure 6.6 displays the change in tiller numbers for the three grass species over 24 weeks. *A. arenaria* gained tillers over the first 15 weeks, but after that lost tillers. This could be due to the dry climate recorded for the same period (Fig. 6.5). Only after some rainfall around the twentieth week of observation did tiller numbers rise again. The constant rise of tiller numbers during the first half of the observation period can conversely be explained by the frequent rainfall during that time, especially in April and June. In contrast to *A. arenaria*, the number of tillers did not fluctuate as much with *Thinopyrum distichum* or *Ehrharta villosa*. In both cases, the few fluctuations do not appear to correspond with the rainfall, and it can be assumed that rainfall patterns do not have as much influence on the growth of the two indigenous grasses as they do in the case of *A. arenaria*. Temperature fluctuations appear to have no effect on any of the three species. As was mentioned in the driftline study (see above), since temperatures do not reach any particularly high or low values during South African autumn and winter, their influence on plant growth would be limited. The total gain/loss of tillers over the whole period of observation was + 1.15 for *A. arenaria* and + 0.60 for *Ehrharta villosa*, but - 0.40 in the case of *Thinopyrum distichum*. However, no significant differences can be detected between any of the values through a t -test.

Measurements of sand burial are shown in Table 6.6, and the influence of sand burial on the number of tillers is reflected in Table 6.7. While the number of tillers of *A. arenaria* and even more so of *Thinopyrum distichum* show hardly any correspondence to the amount of sand burial, there are significantly positive associations in the case of *Ehrharta villosa*: three out of the five examined clusters show a significant gain of tillers with increasing sand burial. It was expected that *A. arenaria* would show a similar positive association, but sand burial of the *A. arenaria* clusters was lower than that of the *Ehrharta villosa* clusters, and therefore its effect

on tiller production is less detectable. With regard to Table 6.6, it appears as though the higher sand burial of *Ehrharta villosa* clusters is due to their situation further back on the beach (between 19.2 and 27.5 m). They are more exposed to sand movement than the *A. arenaria* and *Thinopyrum distichum* clusters, which are closer to the high water mark (between 6.0 and 11.0 m and between 8.5 and 9.7 m respectively). This in turn had a markedly positive effect on the tiller production of *Ehrharta villosa*.

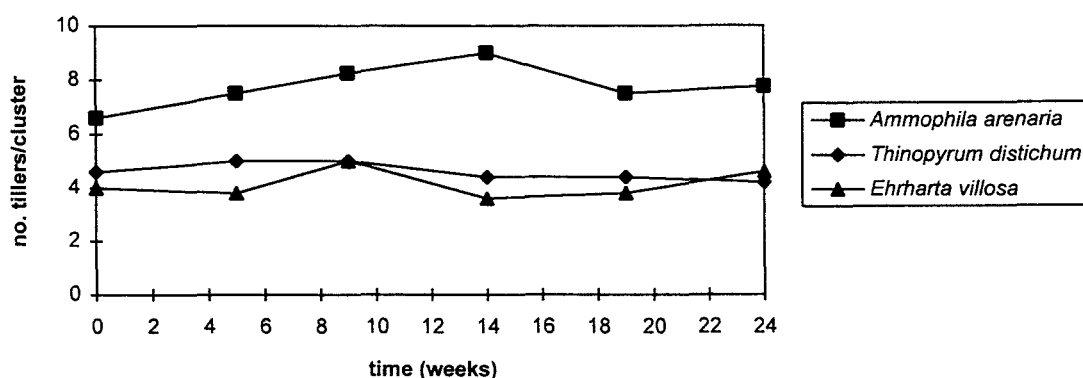


Fig. 6.6: Change of number of tillers per cluster (means of 5 clusters respectively) of *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* at Port Alfred West over a period of 24 weeks.

Table 6.6: Sand burial (cm) measured at 5 clusters respectively (a, b, c, d, e) of *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* at Port Alfred over a period of six months (- = no data available, pole was lost and cluster not retrieved). The distance from the high water mark (HWM) of each cluster is noted in metres.

species	cluster	dist. HWM (m)	time (weeks)				
			5 (28-4-1997)	9 (31-5-1997)	14 (4-7-1997)	19 (6-8-1997)	24 (10-9-1997)
<i>Ammophila arenaria</i>	a	7.5	-	-	-	-	-
	b	7.8	+ 11.7	+ 0.5	+ 0.5	+ 4.0	- 1.2
	c	8.2	+ 1.0	- 3.0	0	+ 6.4	- 0.6
	d	6.0	+ 3.0	+ 3.5	- 1.8	+ 3.8	+ 0.5
	e	11.0	+ 4.0	+ 8.1	+ 3.3	- 1.0	+ 1.7
<i>Thinopyrum distichum</i>	a	9.7	+ 7.0	+ 0.5	+ 1.5	+ 0.8	+ 1.7
	b	8.5	+ 3.4	+ 2.5	+ 1.7	- 0.4	0
	c	8.5	+ 2.5	- 0.1	- 0.7	+ 1.2	+ 2.2
	d	8.8	- 0.1	- 1.8	+ 1.7	- 1.5	+ 1.6
	e	9.5	- 1.8	+ 2.0	+ 0.5	+ 0.6	+ 4.1
<i>Ehrharta villosa</i>	a	23.0	+ 15.0	+ 2.6	+ 0.8	+ 5.0	+ 3.0
	b	24.2	+ 6.8	+ 2.1	+ 0.5	- 3.5	0
	c	19.2	+ 3.6	+ 5.7	+ 3.3	+ 4.0	- 2.3
	d	22.8	+ 2.9	+ 3.4	0	- 1.5	+ 3.0
	e	27.5	+ 11.9	+ 2.9	+ 2.1	+ 1.0	+ 3.5

Table 6.7: Regression analysis of the dependence of number of tillers on sand burial for each cluster of *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* respectively at Port Alfred West (n = 5 in each case). Significance (**bold**) at $\alpha = 0.1$ (*) and $\alpha = 0.05$ (**). x = number of tillers did not change, - = no data available, pole was lost and cluster not retrieved. See Table 6.5 for more explanations.

		cluster				
		a	b	c	d	e
<i>A. arenaria</i>	r^2	-	0.149	0.191	0.136	x
	b		- 0.097	- 0.218	+ 0.109	
	P		0.521	0.461	0.541	
<i>Thinopyrum distichum</i>	r^2	0.399	x	x	0.362	x
	b	+ 0.388			- 0.163	
	P	0.253			0.283	
<i>Ehrharta villosa</i>	r^2	0.781	0.849	0.078	0.688	0.448
	b	+ 0.192	+ 0.321	+0.065	+ 0.318	- 0.200
	P	0.047 **	0.026 **	0.648	0.082 *	0.217

2) Leaf/tiller-ratio and leaf lengths

Figure 6.7 shows that the number of leaves per tiller was always higher for *A. arenaria* than for the two indigenous dune grasses. According to a *t*-test of the five data sets, there is a significant difference between the leaf/tiller-ratio of all three grasses: *A. arenaria* carried more leaves per tiller than *Thinopyrum distichum* ($P = 0.009$) and *Ehrharta villosa* ($P = 3.0 \times 10^{-6}$), and *Thinopyrum distichum* carried more leaves per tiller than *Ehrharta villosa* ($P = 0.014$). Leaf production of *A. arenaria* appears to be as much dependent on rainfall as is tiller production, since the number of leaves decreased during the first weeks of observation with decreasing rainfall and increased after heavy rainfall around the ninth and eleventh week (Fig. 6.5). The leaf/tiller-ratio of *Thinopyrum distichum* decreased throughout the study period, and no correspondence with climatic data can be found. Neither does the number of leaves per tiller appear to be influenced by the climate in the case of *Ehrharta villosa*. The total gain/loss of leaves per tiller over the period of observation was positive only in the case of *A. arenaria* with + 0.26, which is significantly higher ($P = 0.042$) than the loss of *Thinopyrum distichum* (- 1.57), but not significantly different ($P = 0.428$) from *Ehrharta villosa*'s loss of - 0.65. No significant difference is detected between the values of *Thinopyrum distichum* and *Ehrharta villosa*.

An examination of the effects of sand burial on the production of leaves of all three grasses is unsuccessful (Table 6.8). Only one fairly significant ($P = 0.090$) negative association can be detected for *Thinopyrum distichum*: the number of leaves per tiller appears to decrease with increasing sand burial. Although without strong significance, the regression coefficients of *Ehrharta villosa* tend to be more positive compared to those of *Thinopyrum distichum*. Again, *Ehrharta villosa* appears to be well adapted to high amounts of sand burial. The case of *A. arenaria* remains unclear as hardly any sand burial could be measured around the clusters (see above), and regression coefficients are both negative and positive. In confirmation of these results, a regression between the number of leaves per tiller and the distance from the high water mark of each cluster (not shown) reveals a significantly negative dependence only in the case of *Thinopyrum distichum* ($P = 0.011$). The further removed from the high water mark - hence the more exposed to sand movement -, the fewer leaves does *Thinopyrum distichum* carry per tiller. No such correspondence can be found for *A. arenaria* or *Ehrharta villosa*.

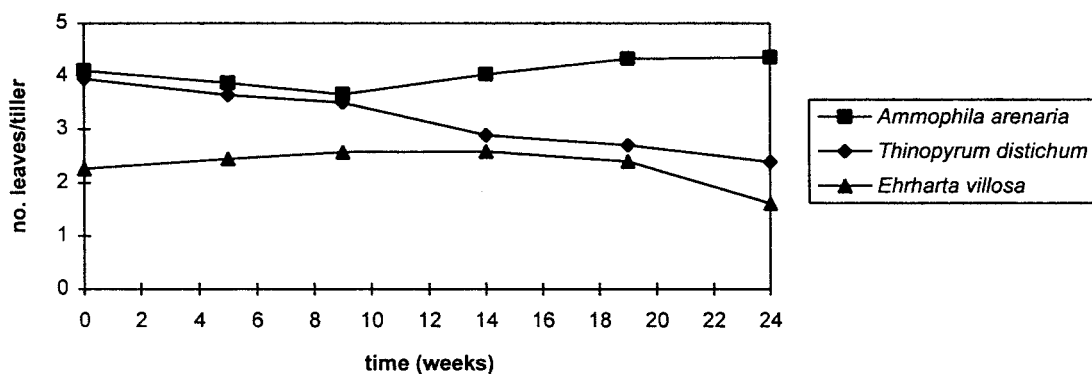


Fig. 6.7: Change of number of leaves per tiller (means of 5 clusters respectively) of *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* at Port Alfred West over a period of 24 weeks

Table 6.8: Regression analysis of the dependence of number of leaves per tiller on sand burial for each cluster of *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* respectively at Port Alfred West (n = 5 in each case). Significance (**bold**) at $\alpha = 0.1$ (*) (- = no data available, pole was lost and cluster not retrieved). See Table 6.5 for more explanations.

		cluster				
		a	b	c	d	e
<i>A. arenaria</i>	r^2	-	0.339	0.429	0.284	0.481
	b		- 0.379	+ 0.167	+ 0.191	- 0.060
	P		0.604	0.545	0.642	0.512
<i>Thinopyrum distichum</i>	r^2	0.980	0.443	0.449	0.091	0.234
	b	- 2.570	+ 0.261	- 0.220	- 0.052	- 0.135
	P	0.090 *	0.536	0.532	0.805	0.679
<i>Ehrharta villosa</i>	r^2	0.934	0.948	0.416	0.636	0.874
	b	+ 0.558	+ 1.025	+ 0.138	- 0.179	+ 0.528
	P	0.345	0.146	0.554	0.413	0.231

A. arenaria produced the longest leaves of the three grasses, but they appeared to lose vigour most conspicuously, their mean lengths dropping from 65.1 cm to 56.2 cm over the time of observation (Table 6.9). In contrast, leaves of *Thinopyrum distichum*, although much shorter, kept their lengths of around 34 cm throughout the period. A possible reason for the decreasing leaf lengths of *A. arenaria* could again be the overall decreasing rainfall over the period, since *A. arenaria* leaves were observed to dry out at the tips and then break. However, the *Ehrharta villosa* population at Port Alfred showed these symptoms even more so, to such an extent, that leaf length could not be measured at all (see Methods). In the case of *A. arenaria* and *Thinopyrum distichum*, no significant relationship of the leaf length to the amount of sand burial or distance from the high water mark can be detected, while comparable data is not available for the *Ehrharta villosa* populations at Kenton-on-Sea. The total gain/loss of leaf lengths was - 8.93 for *A. arenaria*, but only - 1.03 for *Ehrharta villosa* and - 0.24 for *Thinopyrum distichum*. However, these differences are insignificant.

Table 6.9: Mean leaf lengths of all leaves of all tillers of all 5 clusters per grass species at four sampling dates at Port Alfred (* data for *Ehrharta villosa* are obtained from a population at Kenton-on-Sea, see Methods).

			time (weeks)			
			0 (26-3-1997)	9 (31-5-1997)	19 (6-8-1997)	24 (10-9-1997)
leaf length (cm)	<i>A. arenaria</i>	mean	65.1	61.7	60.7	56.2
		standard error	4.6	8.3	7.4	6.4
	<i>Thinopyrum distichum</i>	mean	34.5	34.9	33.9	34.3
		standard error	6.0	5.6	4.4	5.8
	<i>Ehrharta villosa</i> *	mean	16.2	17.4	14.6	15.1
		standard error	1.9	3.0	1.8	1.3

6.5 Clonal spread of *A. arenaria* and indigenous dune plants at Port Alfred, Eastern Cape

6.5.1 Introduction

While the previous study on leaf and tiller demography described the above-ground plant growth, the following section will focus on the below-ground spread of *A. arenaria* and indigenous dune grasses. Comparisons of rhizomatous growth of *A. arenaria* with that of other dune plants have shown that *A. arenaria* is predominantly oriented towards vertical growth, resulting in a high above-ground biomass, whereas associated species like *Carex arenaria* (Europe) or *Leymus mollis* (California) allocate more material to horizontal growth (Watkinson *et al* 1979; Pavlik 1983c). As yet there is not much known about the rhizomatous growth of South African dune grasses, most of which do however appear to be capable of extensive vegetative growth. In this study the clonal spread of *A. arenaria* was compared with that of *Thinopyrum distichum* and *Ehrharta villosa*.

The following key questions are posed:

- 1) How fast do clones of *A. arenaria* grow and spread compared to those of indigenous dune plants?

2) *What ramification pattern does A. arenaria exhibit compared to indigenous dune grasses? Does A. arenaria allocate more energy to vertical growth than horizontal growth?*

3) *Does A. arenaria produce more above-ground biomass than indigenous dune grasses?*

6.5.2 Study area

Studies were carried out at Port Alfred West Beach at the same site as the demographic study (see Section 6.4.2).

6.5.3 Methods

For each of the three species, *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa*, three clones (A, B, and C) were randomly chosen and marked by tagging their most peripheral ramet. The term clone refers here to a group of ramets originating by vegetative propagation from a single parent (Krajnyk & Maun 1981), and a ramet is a subunit of a clone consisting of a leafy shoot and roots and capable of independent existence if severed (Maun 1985). Every eight weeks each clone was excavated to a length of 1 m from the tagged ramet towards the mother plant. This was done manually and late in the afternoon to prevent damage to any part of the plant or drying of the rhizomes. The ramification of the rhizomes, number and length of internodes, number of buds per node, number and length of leafy shoots and their position of emergence on the rhizome (Krajnyk & Maun 1981; Maun 1985) were recorded four times (26-3-1997, 21-5-1997, 16-7-1997, 10-9-1997). After the last sampling the examined units were excavated in quadrats of 0.25 m² (0.5 m x 0.5 m) around the tagged ramet and removed from the site. The above- and below-ground parts were clipped, washed and dried at 70°C to constant weight. Above-ground parts, vertical rhizomes and horizontal rhizomes were weighed separately.

6.5.4 Results

1) Growth

Measurements of rhizome growth and spread are reflected in Table 6.10 and reveal some surprising results. Primary rhizomes appear to grow at a faster rate in the cases of *Thinopyrum distichum* and *Ehrharta villosa* than *A. arenaria*. The maximum growth of an *A. arenaria* rhizome was from 34.8 cm to 42.3 cm within 24 weeks (clone C), which is equivalent to a rate of 0.31 cm week⁻¹. In comparison, the maximum rate of *Thinopyrum distichum* was 0.94 cm week⁻¹ (clone A), and in the case of *Ehrharta villosa* even 1.30 cm week⁻¹ (clone A). *Ehrharta villosa* also showed the most vigorous growth of secondary rhizomes and the highest increase of leafy shoots (clones A and C) of all three grasses. *Thinopyrum distichum* gained most internodes during the observation period (clones A and C). However, the decline of clones could also be observed most clearly for *Ehrharta villosa* (clone B) and *Thinopyrum distichum* (clone B). In comparison, the weakest clone of *A. arenaria* (clone B) lost vigour only marginally.

The quantitative measurements of Table 6.10 are less fluctuating in the case of *A. arenaria*, thereby implying that *A. arenaria* grows slower, but more steadily than the two indigenous dune grasses. Although all three grasses show higher growth rates during the high rainfall period (Fig. 6.5) of the first half of observation than during the drier second half, this difference is more conspicuous in the cases of the indigenous grasses. The production of buds was similar in all three grasses, the lower values for *A. arenaria* being due to the lower total rhizome lengths. Finally, the height of shoots fluctuated in all three cases independently of the vigour of the clone, their mean values being of course reduced when new young shoots were included in the calculation. *Ehrharta villosa* developed the longest shoots, with a maximum of 95.0 cm (clone A). Maximum heights of *A. arenaria* and *Thinopyrum distichum* shoots were only 75.5 cm (clone B) and 65.7 cm (clone B) respectively.

Table 6.10: Quantitative characters over 24 weeks of three clones of *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* respectively. Total numbers refer to all rhizomes of the clone (- = no value calculable; x = no data available, clone died off).

clone	time (weeks)	length of primary rhizome (cm)	no. of secondary rhizomes	mean length of secondary rhizomes (cm) $\pm$ SE	total no. of inter-nodes	total no. of buds	total no. of leafy shoots	mean shoot height (cm) $\pm$ SE
<i>A. arenaria</i>								
A	0	40.5	1	8.5	6	9	4	50.7 $\pm$ 7.2
	8	40.7	1	8.5	6	9	5	50.9 $\pm$ 3.9
	16	40.8	1	8.5	7	7	2	52.0 $\pm$ 1.3
	24	47.1	1	8.7	7	4	2	59.9 $\pm$ 0.5
B	0	33.0	3	4.4 $\pm$ 1.2	8	11	12	51.3 $\pm$ 5.3
	8	31.9	3	4.8 $\pm$ 1.5	9	13	12	71.9 $\pm$ 2.4
	16	31.0	2	5.5 $\pm$ 2.5	7	6	9	75.7 $\pm$ 1.5
	24	31.5	2	4.8 $\pm$ 0.8	7	4	9	69.1 $\pm$ 2.1
C	0	34.8	1	5	5	6	3	32.3 $\pm$ 5.5
	8	41.6	1	7	6	8	4	22.7 $\pm$ 8.7
	16	41.8	1	7	6	7	4	21.3 $\pm$ 7.7
	24	42.3	0	-	7	6	5	60.6 $\pm$ 4.4
<i>Thinopyrum distichum</i>								
A	0	47.0	1	1.0	11	14	1	34.0
	8	52.7	1	1.2	13	18	1	45.0
	16	66.1	2	7.5 $\pm$ 2.4	25	19	2	41.0 $\pm$ 1.0
	24	69.5	2	8.2 $\pm$ 3.1	27	11	3	35.2 $\pm$ 0.8
B	0	73.5	1	3.1	17	18	5	50.6 $\pm$ 3.2
	8	76.4	3	1.9 $\pm$ 0.4	21	20	5	42.2 $\pm$ 1.8
	16	47.6	1	2.5	14	13	7	65.7 $\pm$ 2.2
	24	32.5	2	2.4 $\pm$ 0.8	12	11	4	42.6 $\pm$ 5.4
C	0	28.5	1	0.9	8	5	1	43.2
	8	30.2	1	1.0	9	6	1	49.0
	16	31.3	1	1.0	13	7	3	40.0 $\pm$ 16.0
	24	34.5	2	1.5 $\pm$ 0.5	16	9	3	43.0 $\pm$ 12.5
<i>Ehrharta villosa</i>								
A	0	36.0	4	8.3 $\pm$ 2.1	9	14	11	95.0 $\pm$ 9.3
	8	64.3	6	10.4 $\pm$ 2.4	15	21	17	88.5 $\pm$ 9.3
	16	66.0	4	7.6 $\pm$ 2.0	10	11	10	82.5 $\pm$ 15.5
	24	67.2	4	10.8 $\pm$ 1.9	17	8	13	56.5 $\pm$ 6.2
B	0	46.5	2	19.8 $\pm$ 2.8	14	10	2	39.5 $\pm$ 9.5
	8	39.6	2	10.7 $\pm$ 7.7	10	12	0	-
	16	x	x	x	x	x	x	x
	24	x	x	x	x	x	x	x
C	0	56.5	3	5.0 $\pm$ 1.7	13	4	3	25.7 $\pm$ 8.3
	8	71.1	4	4.4 $\pm$ 1.3	15	15	6	36.9 $\pm$ 11.4
	16	72.5	4	4.8 $\pm$ 0.9	16	16	7	59.3 $\pm$ 6.9
	24	73.8	5	10.1 $\pm$ 2.2	19	14	6	62.0 $\pm$ 6.6

2) Orientation of rhizomatous growth

All three grasses developed secondary rhizomes preferentially in the vertical direction (Table 6.11). Only clone B of *A. arenaria* bore horizontal secondary rhizomes (Plate 6.5). Although internodes of vertical rhizomes were much shorter than internodes of horizontal rhizomes in all three grasses, they grew faster, particularly in the case of *Ehrharta villosa*, where the mean internode length of vertical rhizomes increased in one instance (clone C) from 2.3 cm to 5.5 cm over the period of observation. In comparison, the maximum internode elongation of vertical rhizomes was for *A. arenaria* only from 5.2 cm to 6.5 cm (clone C). A conspicuous difference between *A. arenaria* and the indigenous dune grasses is the distribution of buds. While all grasses had more buds on their horizontal rhizomes, *A. arenaria* carried a large number of buds on vertical rhizomes: clone A carried up to 44.4% of all buds on vertical rhizomes, clone B up to 66.7%. In contrast, *Thinopyrum distichum* had a maximum of 25% of buds on vertical rhizomes (clone B), and *Ehrharta villosa* one of 37.5% (clone A). Another clear difference between *A. arenaria* and the indigenous grasses is that horizontal rhizomes can give rise to aerial shoots frequently: up to 100% of nodes with leafy shoots were found on horizontal rhizomes in the case of clone C, up to 50% in the case of clone B, and up to 33.3% in the case of clone A. Shooting of horizontal rhizomes was observed less frequently for *Thinopyrum distichum* (clones A and B: 50%) and for *Ehrharta villosa* (clone A: 25%).

Table 6.11: Rhizomatous orientation of three clones of *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* respectively (h = horizontal, v = vertical; - = no value calculable; x = no data available, clone died off).

clone	time (weeks)	mean length of internodes of all rhizomes (cm) ±SE				buds (all rhizomes)		nodes bearing leafy shoots (all rhizomes)	
		secondary rhizomes							
		% h	% v	h	v	% h	% v	% h	% v
<i>A. arenaria</i>									
A	0	0	100	11.6 ±1.9	4.3 ±2.8	55.6	44.4	33.3	66.7
	8	0	100	12.3 ±0.9	4.3 ±1.7	55.6	44.4	0	100
	16	0	100	12.3 ±1.2	4.4 ±2.8	57.1	42.9	0	100
	24	0	100	12.7 ±0.7	4.4 ±2.4	75	25	0	100
B	0	33.7	66.7	8.8 ±2.5	3.7 ±1.4	72.7	27.3	50	50
	8	33.3	66.7	6.8 ±2.4	3.7 ±1.4	69.2	30.8	50	50
	16	50	50	7.2 ±2.2	4.0 ±2.0	33.3	66.7	0	0
	24	50	50	7.9 ±2.2	4.3 ±1.3	75	25	0	0
C	0	0	100	8.7 ±2.8	5.2	100	0	66.7	33.3
	8	0	100	10.5 ±2.8	6.4	100	0	66.7	33.3
	16	0	100	10.3 ±2.8	6.5	71.43	28.6	66.7	33.3
	24	-	-	8.5 ±2.6	-	100	0	100	0
<i>Thinopyrum distichum</i>									
A	0	0	100	3.3 ±0.5	1.0	85.7	14.3	0	100
	8	0	100	3.6 ±0.4	1.2	88.9	11.1	0	100
	16	0	100	3.9 ±0.5	1.3 ±0.3	94.7	5.3	50	50
	24	-	-	-	-	-	-	-	-
B	0	0	100	4.6 ±0.5	0.8 ±0.1	99.4	5.6	0	100
	8	0	100	4.3 ±0.4	0.9 ±0.1	95	5	0	100
	16	0	100	4.8 ±0.5	2.4 ±0.9	75	25	0	100
	24	0	100	3.6 ±0.8	1.6 ±0.2	90.9	9.1	0	100
C	0	0	100	1.8 ±0.3	0.9	100	0	0	100
	8	0	100	1.9 ±0.4	1	100	0	0	100
	16	0	100	2.1 ±0.3	1	100	0	50	50
	24	0	100	2.2 ±0.3	1.5	88.9	11.1	0	100
<i>Ehrharta villosa</i>									
A	0	0	100	7.2 ±0.9	8.3 ±2.1	75	25	25	75
	8	0	100	8.9 ±1.4	8.9 ±1.7	71.4	28.6	16.7	83.3
	16	0	100	7.7 ±1.5	6.1 ±2.1	63.6	36.4	0	100
	24	0	100	6.7 ±1.5	9.3 ±2.2	62.5	37.5	0	100
B	0	0	100	7.8 ±0.7	4.9 ±0.7	80	20	0	100
	8	0	100	7.9 ±0.6	4.2 ±0.4	91.7	8.3	-	-
	16	x	x	x	x	x	x	x	x
	24	x	x	x	x	x	x	x	x
C	0	0	100	8.1 ±0.3	2.3 ±0.2	100	0	0	100
	8	0	100	7.9 ±1.2	2.9 ±0.3	80	20	0	100
	16	0	100	7.8 ±1.3	2.7 ±0.3	68.8	31.3	0	100
	24	0	100	8.2 ±1.3	5.5 ±1.1	78.6	21.4	0	100

3) Biomass allocation

With regard to biomass allocation, *A. arenaria* and *Ehrharta villosa* show similarities, while *Thinopyrum distichum* appears to grow in a very different pattern (Fig. 6.8). Mean total dry weight per quadrat was 14.6 g for *A. arenaria* and 14.2 g for *Ehrharta villosa*. Surprisingly, *Ehrharta villosa* produced more above-ground biomass (66%) than *A. arenaria* (58%), apparently due to the development of long and much-branched tillers. The highest production of both vertical and horizontal rhizomes, and therefore the least above-ground biomass (30%), was exhibited by *Thinopyrum distichum*. It developed extensive horizontal rhizomes, making up 48% of its total biomass, compared to 24% of *A. arenaria* and only 17% of *Ehrharta villosa* (Plate 6.5). Horizontal rhizomes strongly outweighed vertical rhizomes in the case of *Thinopyrum distichum*, but were only marginally better developed in the case of *A. arenaria* and *Ehrharta villosa*. Interestingly, *Thinopyrum distichum* also produced the highest relative number of vertical rhizomes, with 22% vertical rhizomes as opposed to 19% of *A. arenaria* and 16% of *Ehrharta villosa*.

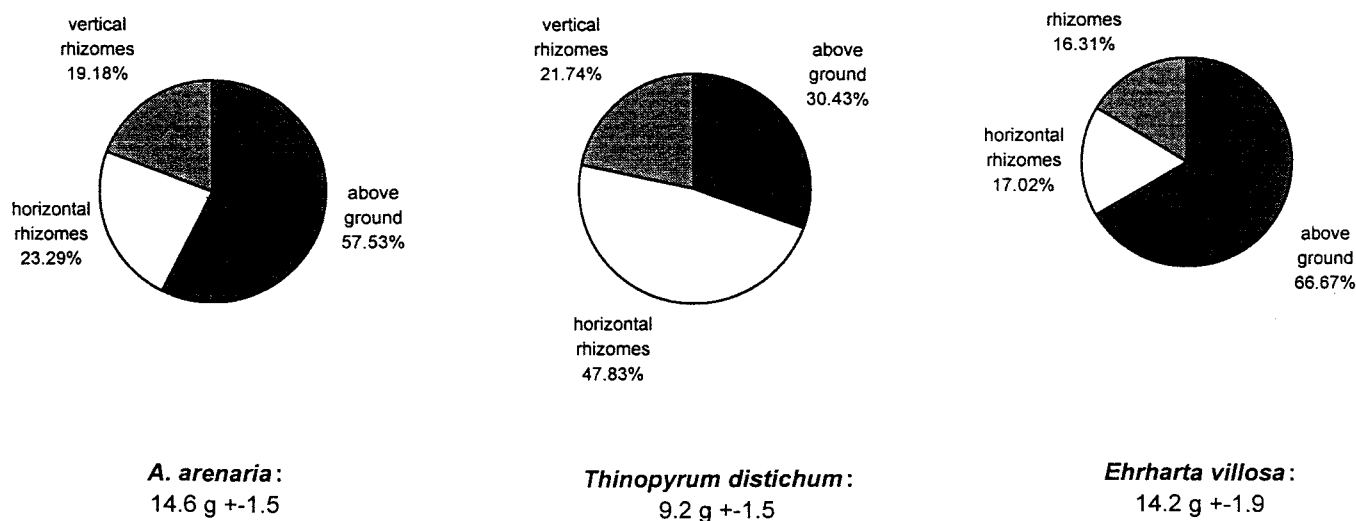


Fig. 6.8: Mean total dry weight $\pm$ standard error per quadrat (0.25 m^2) per species and its allocation to above-ground biomass and vertical or horizontal rhizomes (%). Means were calculated from three clones (A, B, C) of each species. In the case of *Ehrharta villosa*, a new clone had to be excavated in place of clone B, which had died off.

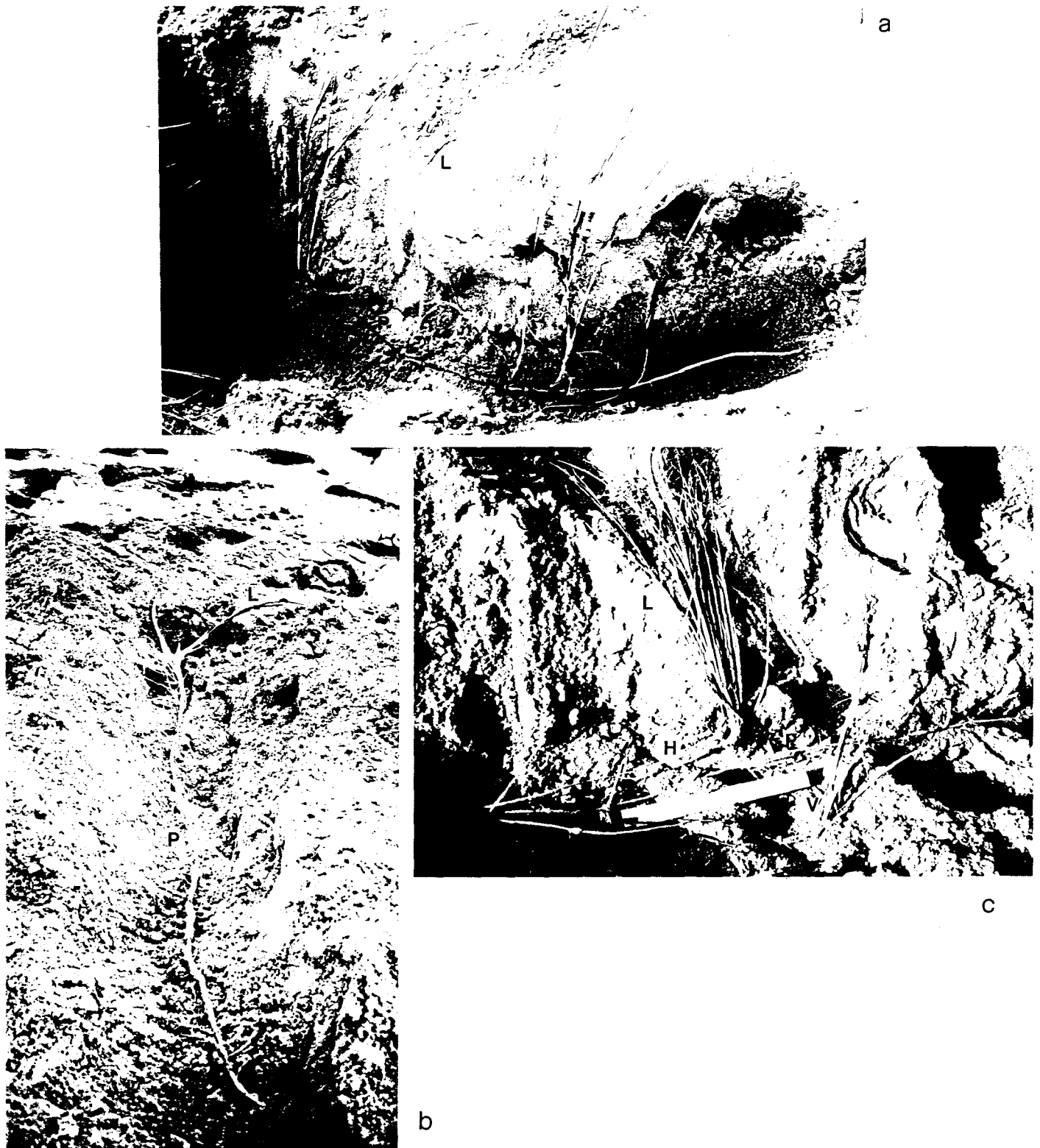


Plate 6.5: Excavated clones (10-9-1997) of *Ehrharta villosa* (a, clone A), *Thinopyrum distichum* (b, clone A) and *A. arenaria* (c, clone B). *A. arenaria* and *Ehrharta villosa* produce a higher above-ground biomass while *Thinopyrum distichum* allocates most energy to an extensive system of horizontal rhizomes (P = primary rhizome, V = vertical secondary rhizome, H = horizontal secondary rhizome, L = leafy shoots). The ruler is 30 cm long.

6.6 Discussion

It was shown in Chapter 4 that species richness and diversity values in South African *A. arenaria* communities do not differ much from those in communities dominated by indigenous dune plant species. Monitoring of communities at Kleinemonde appears to confirm this for a time period of two and a half years. The Kleinemonde *A. arenaria* communities showed consistent values for species richness and species diversity throughout the period similarly to the indigenous communities (Fig. 6.2). As expected, the values were marginally lower in *A. arenaria* communities, and their increase towards the end of the observation period was due to a shifting of the species composition in favour of indigenous species, coincident with a decline of *A. arenaria*. The mild fluctuations in species diversity at Kleinemonde over a period of two and a half years (from 1.3 to 1.6 in *A. arenaria* communities and from 1.8 to 1.2 in indigenous communities) contrast with changes of diversity values measured for Kleinemonde foredunes over five years (Lubke & Avis 1988): along a 90 m transect the species diversity changed from 2.8 in 1980 to 4.3 in 1985. Changes in species diversity can apparently be much more marked than was found in the present study, indicating that *A. arenaria* does not disturb the natural patterns of community dynamics at Kleinemonde.

A. arenaria appears to have a competitive advantage over the South African indigenous species in places of excessive sand movement. Severe sand burial was in one community survived by only *A. arenaria*. However, where the supply of fresh sand was low, *A. arenaria* was replaced by indigenous dune plants. These results confirm observations from Europe about *A. arenaria*'s superior tolerance of sand burial, as well as its dependence on a regular supply of fresh sand (Willis *et al* 1959b; Ranwell 1972; Huiskes 1979; see Chapters 1 and 5). Vigorous indigenous dune plants at Kleinemonde were *Cynanchum natalitium* and *Scaevola plumieri*. Although one of the indigenous communities at Kleinemonde was invaded by *A. arenaria*, the opposite process was more common (Tables 6.1 and 6.2). *A. arenaria* exhibits no unusual vigour or tendency to spread across the dunes at Kleinemonde. Its communities are subject to fluctuations of species composition and vigour, similar to indigenous communities.

It is surprising how well *A. arenaria* coped in the driftline community at Kleinemonde, replacing *Gladiolus gueinzii* and *Scaevola plumieri* as dominant species within the first six

weeks of observation (Fig. 6.3). Again, *A. arenaria* appears to profit from its tolerance of severe sand movement to which this driftline community is exposed (Table 6.5). The driftline study proves that one of the reasons for its heightened tolerance of sand burial is its capability of vigorous vegetative reproduction (Gemmell *et al* 1953; Ranwell 1972). While plants like *Scaevola plumieri* and *Gladiolus gueinzii* produced numerous vulnerable seedlings in the driftline, *A. arenaria* developed strong, hardy culms from a system of underground rhizomes (Fig. 6.4).

The effect of sand accretion on seedling establishment has been examined by various authors (van der Valk 1974; Maun & Lapierre 1986; Zhang & Maun 1990; Martinez *et al* 1992). Studies by Moreno-Casasola (1986) indicate that there is a close correlation between sand movement and species composition, cover and density. Sand accretion eliminates intolerant species, reduces the abundance of less tolerant species and increases the abundance of tolerant species (Maun 1994). Although the climatic conditions at Kleinemonde during the study period would favour indigenous plants, which are adapted to long periods of drought, the sand burial was so severe that it overshadowed these factors. In consequence, *A. arenaria* became the dominant plant species in the driftline. The most vigorous indigenous species in the Kleinemonde driftline was *Arctotheca populifolia*, which was also the only one flowering and reaching maturity frequently. It has to be noted though that none of the plants in the driftline community were of remarkable vigour. Therefore, the dominance of *A. arenaria* has to be viewed only relatively.

It is not so much the dominance of *A. arenaria* in this driftline community that would indicate its potential for spread, but rather the fact that *A. arenaria* must have arrived in the driftline from rhizome fragments: no seedlings of *A. arenaria* were recorded in the community, the tussocks had all developed from underground rhizomes. Since no *A. arenaria* communities are in close vicinity to the driftline, rhizomes must have been either washed ashore or transported along the beach with the wind. Rhizome fragments of *A. arenaria* have been observed on several occasions in driftline communities along the Cape coast (see Chapter 7, Plate 7.4). According to an American study (Baye 1990), dormant fragments of *A. arenaria* can survive marine transport over at least eight tidal cycles (see Chapter 2). Maun (1985) found that the American *Ammophila breviligulata* established on Lake Huron beaches rarely from seedlings,

but that most new plants along the beach originated from clonal fragments cast on the driftline by high waves. The dispersal of rhizomes by sea and their deposition along driftlines is a considerable possibility also in South Africa.

Over the growth period of South African autumn and winter, *A. arenaria* showed the best gain of tillers and leaves per tiller in the Port Alfred study (Figures 6.6 and 6.7). Furthermore, both values showed the strongest correlation with rain patterns. In contrast to European studies (Gemmell *et al* 1953) and experiments with the American *Ammophila breviligulata* (Disraeli 1984), there is no significant correlation of tiller and leaf numbers with sand burial measurements (Tables 6.7 and 6.8). However, this is probably due to the vicinity of the examined *A. arenaria* clusters to the high water mark and the resulting lack of sand movement which makes a detection of such a correlation difficult. *Ehrharta villosa* showed a significantly positive correlation with sand burial, while *Thinopyrum distichum* was more negatively affected by sand movement. Although leaf/tiller-ratios were higher for *A. arenaria* than for the two indigenous dune grasses throughout the study period, and with values above 4 also higher than the European summer average of 3 (Huiskes 1979), leaves of *A. arenaria* also appear to suffer most from drought (Table 6.9). Altogether, there were only few significant differences detected between *A. arenaria* and the indigenous dune grasses in regard to their tiller and leaf demography. It is necessary though to carry out similar studies over a longer period of time.

While the above-ground parts of *A. arenaria* grew more vigorously than those of indigenous dune grasses, its rhizomatous growth was slower (Table 6.10). Growth rates of rhizomes in South African autumn and winter were generally higher for *Ehrharta villosa* and *Thinopyrum distichum*. Nor did *A. arenaria* develop more buds than the indigenous dune grasses. However, the Port Alfred study reveals a clearly different orientation of rhizomatous growth of the species (Table 6.11): *A. arenaria* carried not only more buds on its vertical rhizomes, but buds on horizontal rhizomes also gave rise to aerial shoots. In comparison, the majority of buds of *Ehrharta villosa* and *Thinopyrum distichum* were on horizontal rhizomes. Only a few of them gave rise to aerial shoots though.

Although *Ehrharta villosa* does not exhibit a strong vertical orientation of its bud distribution as *A. arenaria* does, and no dense tiller clusters are produced, the development of very long and

much branched tillers gives it an overall higher above-ground biomass than *A. arenaria* (Fig. 6.8). Both species showed a greater material allocation to above-ground parts than *Thinopyrum distichum*, which in turn allocated more material to the production of an extensive, and preferentially horizontal, system of rhizomes (Plate 6.5). In this respect, *Thinopyrum distichum* is comparable to the European *Carex arenaria* (Watkinson *et al* 1979) or the American *Leymus mollis* (Pavlik 1983c), which also allocate much more material to the growth of horizontal rhizomes. It can be concluded that the clonal spread of the Port Alfred population of *A. arenaria* is not more vigorous than that of populations of indigenous dune grasses. Although *A. arenaria* shows a stronger vertical orientation of its rhizomatous growth, *Ehrharta villosa* has a higher above-ground biomass.

6.7 Conclusions

A comparison of *A. arenaria* communities and communities dominated by indigenous South African dune plant species at Kleinemonde over nearly three years does not reveal any tendency of *A. arenaria* to spread and replace indigenous plants. It does replace *Ehrharta villosa* in one instance, but is in turn replaced by *Cynanchum natalitium* in two other cases. However, species richness and diversity values are always slightly lower in *A. arenaria* communities and rise only when indigenous plants become more dominant. *A. arenaria* has a competitive advantage over South African dune plants through its tolerance of severe sand burial. Sand movement along Eastern Cape beaches can be extreme, and *A. arenaria* appears better equipped to withstand this pressure than any of the indigenous dune plants at Kleinemonde. Although it suffers more from drought, negative climatic factors are overridden by favourable sand burial levels.

A. arenaria possibly arrived in a driftline community at Kleinemonde via marine transport of rhizome fragments. It exhibits healthy vegetative growth in the driftline, resulting in its overall dominance. However, studies on the flux of leaves and tillers of Port Alfred populations do not reveal any superior vigour of *A. arenaria* in terms of growth rate and biomass production. Although *A. arenaria* exhibits a clearly vertical orientation of its rhizomatous growth, the indigenous *Ehrharta villosa* develops a higher above-ground biomass. It is important to note

that these demographic studies are preliminary studies. Similar observations and comparisons of *A. arenaria* and indigenous South African dune pioneer plants have to be carried out over a longer time period. Results so far indicate that *A. arenaria* does not have a tendency to spread unaidedly over Eastern Cape dunes, nor does it exhibit favourable demographic traits which would give it an advantage over indigenous dune plant species.

CHAPTER SEVEN

7. Reproduction biology of *Ammophila arenaria* in South Africa

7.1 Introduction

Flowering and seed production have been studied in detail for the American *Ammophila breviligulata* (Laing 1958; Eldred & Maun 1982; Maun 1985), but not many studies have focused on these aspects for the European *A. arenaria*. Greig-Smith (1961) found the density of flowering tillers to be higher in mobile foredunes than in the more stable backdunes. Huiskes (1979) observed that although the number of spikelets per inflorescence did not differ significantly in the different successional stages of the dunes, the number of fully developed caryopses was much lower in the older dunes.

More is known about *A. arenaria*'s germination and seedling establishment. The grass appears to germinate readily but to have a low rate of seedling establishment (Huiskes 1977, 1979). Germination occurs preferably in strongly-fluctuating temperature regimes, as can be found in mobile dunes, and after a period of cold treatment (Huiskes 1979; van der Putten 1990): Pizzey (1975) found the maximum germination capacity of *A. arenaria* at constant laboratory temperatures and without a cold pre-treatment to be only 15%, but Huiskes (1979) records a 90% germination success under fluctuating temperature regimes and after storing the seed at 5°C for two months. Cold pre-treatment appears to stimulate germination, which explains the high germination success of *A. arenaria* seed after winter in Europe (van der Putten & van Gulik 1987). Within weeks after germination though, seedlings usually die because of desiccation, excessive sand burial and small scale sand erosion. Successful seedling establishment on a large scale has in Europe so far only been observed in damp dune slacks (Huiskes 1977).

It appears as though reproduction of *A. arenaria* by seed takes second place to its vigorous and extensive clonal spread through both horizontal and vertical rhizomes (see Chapter 6). Van der Putten (1990) compared three methods of establishing *A. arenaria* with a view to its use for

dune stabilisation, namely the planting of bundles of culms, sowing of seed, and disc-harrowing of rhizomes. Sowing of seed always resulted in the lowest biomass, even after a considerable period of time and the application of fertiliser.

Bencie (1990) examined aspects of seed biology of *A. arenaria* in California and found that the grass germinates well and seedlings establish both on fore- and backdunes, which certainly contributes to its invasiveness there. Nothing is known about the reproduction biology of South African *A. arenaria*. In this chapter, the fertility of South African *A. arenaria* populations will be examined in terms of their flowering and seed production. Another focus will be on germination and seedling establishment. Aspects of *A. arenaria*'s clonal spread have been dealt with in Chapter 6, but the establishment of the grass from severed rhizome pieces will be examined in this chapter. Rhizomes can be removed from a foredune by erosion and distributed by the wind or sea (Maun 1984, 1985; see Plates 3.7 and 7.4). The monitoring of a driftline community at Kleinemonde indicates that *A. arenaria* can establish from such rhizome fragments (see Chapter 6). In this chapter, a more detailed examination will be made to see whether *A. arenaria* can develop healthy shoots from fragmented rhizomes in South Africa. The reproduction biology of South African *A. arenaria* will be compared both with that of European populations as well as with that of the South African dune grasses *Thinopyrum distichum* and *Ehrharta villosa*.

Key questions of this chapter are:

- 1) *What is the percentage flowering of South African A. arenaria populations? How much viable seed does South African A. arenaria produce? How do both aspects compare with findings from Europe?*
- 2) *Does A. arenaria germinate well in South Africa, and do seedlings establish easily? How does it perform compared to European A. arenaria and with indigenous South African dune plant species?*
- 3) *How well can South African A. arenaria develop shoots from severed rhizome pieces compared to Thinopyrum distichum and Ehrharta villosa?*

7.2 Study areas

Sampling for flowering and seed production was carried out in *A. arenaria* populations along the entire Cape coast between Koeberg and Gonubie as well as on the German North Sea island of Sylt. Both areas are described in Chapter 4.

Germination experiments were carried out in the laboratory and in the field. Seedling establishment experiments were carried out only in the field. Field experiments were conducted both at Kleinemonde and at the mouth of the Old Woman's River. The coastal resort of Kleinemonde is described in Chapter 6. The Old Woman's River is a small river with a usually closed mouth about 1 km east of the Great Fish River mouth and 12 km east of Kleinemonde (27°08'E; 33°01'S). Climate, physiography and maritime conditions are similar to those of Kleinemonde. Because of its situation east of the rocky outcrops of the Great Fish River mouth, the beach at the Old Woman's River mouth is comparatively sheltered and not as exposed to strong westerly and southwesterly winds as the Kleinemonde beach. The foredunes are mostly vegetated with *Scaevola plumieri* and subject to frequent erosion by the sea. One foredune is dominated by *A. arenaria* and several small ones by *Sporobolus virginicus*. The zones of dune scrub and dune forest have a similar species composition to those at Kleinemonde (see Chapter 6).

Experiments on vegetative reproduction were also carried out at Kleinemonde and Old Woman's River mouth.

7.3 Methods

1) Flowering and seed production

The same *A. arenaria* communities along the South African and Sylt coast were sampled as for the vegetation analysis of Chapter 4. During vegetation sampling in each of the twenty 1 m² quadrats per 100 m² stand (Chapter 4), the density of flowering *A. arenaria* shoots was recorded and is expressed as percentage of total *A. arenaria* shoots. Obviously not all stands

contained flowering plants. Flowering was recorded in 43 of the 82 South African *A. arenaria* stands and in 13 of the 19 Sylt *A. arenaria* stands. In 31 South African and 4 Sylt stands up to 20 inflorescences were then collected at random and examined for seed production. The 4 batches of seed from Sylt were supplemented with Dutch inflorescences obtained from Dr. van der Putten (Centre for Terrestrial Ecology, Heteren) in January 1995.

The length of each panicle was measured from the base of the lowest floret on the rachis to the tip of the uppermost floret. Florets of each panicle were then removed, counted and examined for fungal infection. Finally each floret was opened manually, and presence or absence of a caryopsis was recorded. 20 caryopses or the maximum available number per batch were weighed (weight after dry storage for 2-5 months). Results of all measurements were expressed in means per batch (collection area). To compare seed production with South African indigenous dune grasses, 15 inflorescences of *Thinopyrum distichum*, collected at Port Alfred, and 15 inflorescences of *Ehrharta villosa*, collected at Kenton-on-Sea, were examined in the same way.

Sampling and collecting were carried out between February 1995 and February 1997 and mostly in months of greatest flowering (spring and summer) or greatest maturity of seed (late summer and autumn). The few stands, in which percentage flowering could be measured only in winter, were examined carefully for old or loosened panicles. However, panicles were found to last well into the next flowering season. All stands in which percentage of flowering was measured were vigorous stands of the foredune or intermediate dune zone. It was also assured that all panicles examined for seed production were of full maturity, so that "empty florets" were not merely immature.

2) Germination and seedling establishment

Before germination experiments were started, several different methods of seed disinfection were tested to avoid fungal growth on the seed. Of these, the treatment of seed with 3.5% NaHCl (70% "JIK") for 5 minutes gave best results.

Germination under different environmental conditions

To determine optimal germination conditions, 3 batches of 180 fully developed caryopses of *A. arenaria*, a mixture from Tableview and Sedgefield stands, were given a cold pre-treatment of 0 days, 20 days and 40 days at 5°C respectively. One further batch of 60 seed was incised by cutting into the seed coat without damaging the embryo, following van der Putten's (1990) observation that incised seed can have significantly higher germination rates. This batch was also given a cold pre-treatment of 20 days at 5°C. Seed were then disinfected with 3.5% NaHCl for 5 min and placed on filter paper in Petri dishes in groups of 30 into 2 different environments: the "window sill" environment had a natural diurnal pattern of about 15 hrs dark / 9 hrs daylight (June) at fluctuating temperatures between 14°C and 26°C on average; the controlled "growth chamber" environment had an artificial diurnal thermoperiod of 16 hrs dark / 8 hrs light (40W/33RS neon bulb) between 23°C and 29°C. In each environment 3 replicates of the 3 differently pre-treated batches respectively were tested for germination (2x3x3). The seed was kept wet with de-ionised water and examined for germination (radicle visible) and fungal growth every 8th day over a period of 46 days.

Germination of different batches of seed

In this experiment seed batches from along the South African coast and Europe were tested for germination success. In total 25 South African, 4 Sylt and 1 Dutch *A. arenaria* seed batches, plus 2 batches of *Thinopyrum distichum* and 2 batches of *Ehrharta villosa*, were examined. For each of the seed batches, 2 replicates of a maximum of 30 fully developed seed each, or otherwise the maximum available amount of seed, were sterilised for 5 min in 3.5% NaHCl. Each replicate of seed was then placed on filter papers in Petri dishes and into a growth chamber with the above described light and temperature regime. Seed was kept wet with de-ionised water and examined for germination (radicle visible) every 3rd day over a period of 50 days.

Germination and seedling establishment in the field

KLEINEMONDE

A mixture of South African seed from Kleinemonde and De Mond, both collected in February 1996, with the mean of 8% developed caryopses was subjected to 3 different cold pre-treatments of 0 days, 25 days and 45 days at 5°C respectively. The batches were then sown

onto the Kleinemonde dunes at the following 5 successional stages along a transect perpendicular to the coast: the top of a foredune, its leeward slope, a dune slack in the intermediate dune zone, the leeward side of an intermediate dune and a backdune in the scrub zone. At each stage 3 replicates of 1 handful of seed (seed from 10 inflorescences) per cold pre-treatment were sown onto round 0.1 m² plot (Ø 35 cm) respectively (5x3x3). The seed was covered with a thin layer of wet sand to prevent it from being blown away too easily. Metal poles of 1.5 m length served as markers and to measure sand burial at each site. The distance from the high water mark of each site was recorded. Approximately every 2 months the number of newly emerged seedlings was counted and their shoot lengths measured. Experiments were started on 23 June 1996 and intended to be carried out over a year. Due to heavy rainfalls in November and December 1996 a large number of seedlings was either washed away or inundated with water, and the experiments had to be terminated on 13 February 1997. Plots were also exposed to human trampling, and marker poles were removed over the holiday season in December 1996 in spite of signposting and explanations. Therefore the much less frequented area around the mouth of the Old Woman's River was chosen for the next set of experiments.

OLD WOMAN'S RIVER

Seed was sown along transects perpendicular to the coast at 5 different successional stages, namely the back beach, the top of a foredune, its leeward slope, the leeward side of an intermediate dune and a backdune in the scrub zone. Three transects were used with slightly different micro-environments (see below: Table 7.5). At each of the 5 sites of each transect the same seed of South African *A. arenaria* batches with different cold pre-treatments (0 days, 25 days and 45 days at 5° C) was sown as described for the Kleinemonde experiment (5x3x3). Furthermore, 1 handful of Kleinemonde *A. arenaria* seed (10 inflorescences / 11% developed caryopses), 1 handful of Port Alfred *Thinopyrum distichum* seed (8 infl. / 29% dev.) and 1 handful of Kenton-on-Sea *Ehrharta villosa* seed (10 infl. / 2% dev.) was sown at each site of each transect (5x3 respectively). In addition, 1 handful of Sylt *A. arenaria* seed (10 infl. / 44% dev.) was sown at the 5 sites of the first transect (5x). All sites were marked with permanent metal poles of 1 m length which also served to measure sand burial. The distance from the high water mark of each site was recorded. Sand samples were taken at each site and examined for pH, conductivity and organic matter content as described in Chapter 4. Between 22 February

1997 and 18 September 1997 the number of seedlings, their shoot lengths and sand burial were measured every 2 weeks.

3) Vegetative reproduction

KLEINEMONDE

In June 1996, *A. arenaria* rhizomes were dug out underneath a vigorous stand at Kleinemonde and cut into 450 pieces of ca. 15 cm length with 2-3 viable buds and 1-2 roots each (Maun 1984; van der Putten 1990). The rhizome pieces were kept in wet plastic bags to prevent drying before being “sown” in 3 replicates of 30 pieces onto round 1 m² plots at the same 5 sites along the above described Kleinemonde dune transect (5x3). The pieces were then covered with a sand layer of ca. 10 cm. On the same days that seedling emergence was examined in the adjacent germination plots, the development of shoots from the rhizome pieces was examined, the length of each shoot measured and its position in the plot recorded (every 2 months between 23 June 1996 and 13 February 1997).

OLD WOMAN’S RIVER

In February 1997, rhizomes of *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* were dug out and cut in the above manner into 300 pieces respectively at Port Alfred (*A. arenaria* and *Thinopyrum distichum*) and Kenton-on-Sea (*Ehrharta villosa*). They were then “sown” in 3 replicates of 20 pieces onto round 1 m² plots at the 5 sites along each of the 3 Old Woman’s River transects described above (5x3x3). On the same days that seedling emergence was examined in the adjacent germination plots, the development of shoots from the rhizome pieces was examined, the length of each shoot measured and its position in the plot recorded (every 2 weeks between 22 February 1997 and 18 September 1997).

7.4 Results

1) Flowering and seed production

South African *A. arenaria* populations appear to have on average a slightly higher flowering percentage than Sylt populations, with maxima of 22% against 14% and means of 5.2% against

3.9% respectively (Table 7.1). However, a Mann-Whitney *U*-test of the two means of the populations proves the difference to be insignificant at $\alpha = 0.05$ ($P = 0.267$). High flowering was recorded in the Bredasdorp district at Struisbaai, De Mond (maximum of 21.6%) and De Hoop, but also in Eastern Cape populations at Port Alfred and Kleinemonde (Table 7.1 and Fig. 7.1).

The highest number of florets per panicle of South African *A. arenaria* populations was found at False Bay with 461 florets panicle⁻¹, the lowest number with 72 florets panicle⁻¹ at Plettenberg Bay (Table 7.2). The South African mean is slightly lower (203 florets panicle⁻¹) than that of European populations (231 florets panicle⁻¹), but the difference is insignificant according to a Mann-Whitney *U*-test for $\alpha = 0.05$ ($P = 0.410$). However, South African populations produced highly significantly less seed ($P = 6.016 \times 10^{-4}$): in European populations about 29 out of 100 florets contained a fully developed caryopsis, but in South African populations only 1 out of 100 (Table 7.2). The maximum seed production of South African *A. arenaria* was found in Kleinemonde with 11%, but populations at Tableview, Noordhoek and Sedgefield also had high values in a South African comparison (Table 7.2 and Fig. 7.1). However, considering the seed production on Sylt Island of up to 44% (52% for Dutch seed), South African values appear extremely low.

On the other hand, South African seed was less afflicted by fungus than European seed, the difference of the respective means (0.19% against 1% infected caryopses) is significant ($P = 0.027$) at $\alpha = 0.05$ (Mann-Whitney *U*-test). The weight difference of caryopses of European or South African origin is insignificant ($P = 0.200$), but panicles of South African *A. arenaria* were significantly ($P = 2.176 \times 10^{-3}$) longer than European ones, with an average length of 19.7 cm compared to 15.3 cm of European panicles (Table 7.2). The longer panicles and lower floret density makes the South African *A. arenaria* populations appear similar to the Mediterranean variety *A. arenaria* var. *arundinacea*. However, subsequent examination of the floral morphology disproves this as glumes easily exceed the lemma and palea, and the hair around the lemma is shorter than half the length of the lemma (Huiskes 1979; see Chapters 1 and 3).

Table 7.1: Flowering of 43 South African (left) and 13 European (right) *A. arenaria* stands.

stand	date sampled	flowering (% flowering shoots / all shoots)	stand	date sampled	flowering (% flowering shoots / all shoots)
tableview 1	24/1/96	3.11	sylt 1	30/8/96	0.71
noordhoek 2	22/1/96	4.75	sylt 2	30/8/96	6.39
witsand (w.cape) 1	24/1/96	8.00	sylt 4	31/8/96	9.42
schuster's kraal 1	24/1/96	2.98	sylt 5	31/8/96	2.19
fishhoek 1	23/1/96	1.91	sylt 6	31/8/96	0.82
fishhoek 2	23/1/96	4.64	sylt 7	31/8/96	13.52
muizenberg 1	23/1/96	1.49	sylt 8	1/9/96	0.44
pringle bay 1	17/9/95	4.35	sylt 9	1/9/96	4.84
pringle bay 2	17/9/95	1.06	sylt 10	1/9/96	0.62
meerensee 2	17/9/95	1.87	sylt 11	1/9/96	0.87
walker bay 1	13/2/96	7.56	sylt 14	2/9/96	0.18
walker bay 2	13/2/96	12.95	sylt 15	2/9/96	1.22
struisbaai plaat 1	15/2/96	15.73	sylt 17	2/9/96	9.78
de mond a2	17/2/96	0.37	mean		3.92
de mond b1	17/2/96	8.39	standard error		1.24
de mond b2	17/2/96	2.67	standard deviation		4.47
de mond d1	18/2/96	4.11			
de mond 3	15/2/96	21.64			
wacnhuiskrans 1	14/9/95	2.55			
wacnhuiskrans 2	14/9/95	2.31			
de hoop 1	19/2/96	14.25			
de hoop 2	19/2/96	3.98			
hartenbos 1	30/7/95	0.89			
groot brakrivier 1	31/7/95	1.89			
hershams 1	31/7/95	2.38			
sedgefield 1	24/5/95	2.08			
sedgefield 3	24/5/95	2.03			
sedgefield 4	28/5/95	0.87			
goukamma 1	4/8/95	0.74			
goukamma 3	5/8/95	4.33			
plettenberg bay 2	28/7/95	2.67			
port alfred (west) 1	13/2/97	10.58			
port alfred (west) 2	13/2/97	3.93			
port alfred (east) 1	6/2/97	0.55			
port alfred (east) 2	6/2/97	7.11			
kleinemonde 2	24/11/96	1.47			
kleinemonde 3	24/11/96	5.36			
kleinemonde 4	24/11/96	13.22			
kleinemonde 5	12/3/95	18.16			
kleinemonde 7	12/3/95	1.97			
old woman's river 1	5/4/96	0.38			
hamburg 2	6/4/96	1.29			
gulu mouth 2	8/4/96	10.00			
mean		5.18			
standard error		0.79			
standard deviation		5.19			

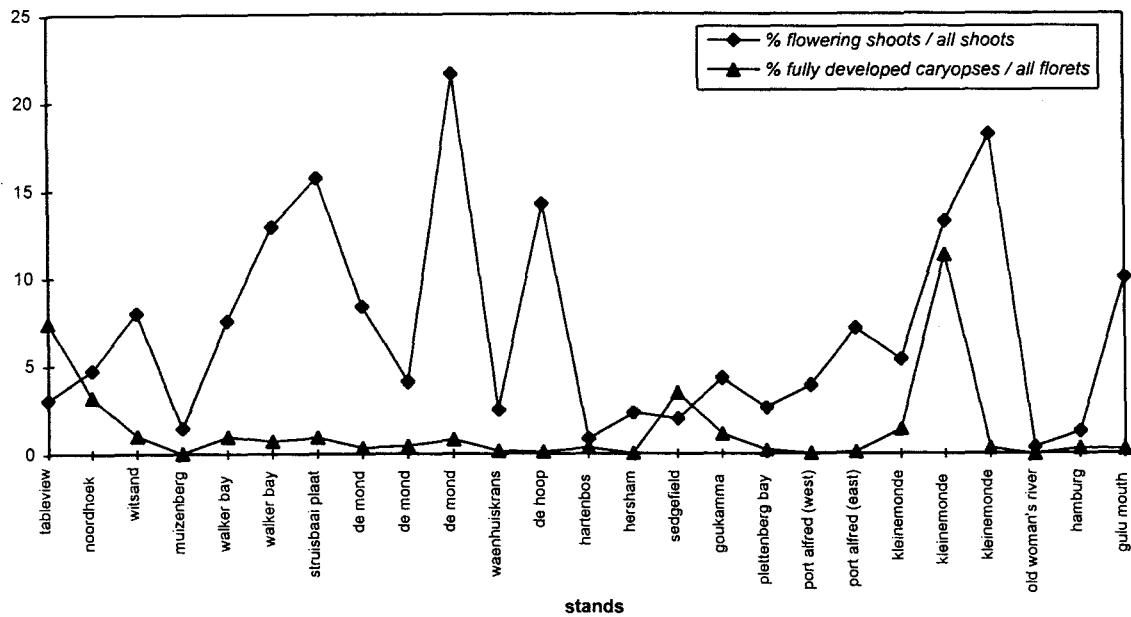


Fig. 7.1: Flowering and seed production of 25 South African *A. arenaria* populations along the Cape coast from west (left) to east (right). Although the data is discrete rather than continuous, it was plotted as lines and not as histograms to display changes along the Cape coast with more clarity.

The South African indigenous grass *Ehrharta villosa* carried only few florets (58/panicle; Table 7.2) with very few developed caryopses (1.5%). It possibly allocates more energy to vegetative reproduction than reproduction by seed. *Thinopyrum distichum*, on the other hand, produced a high number of caryopses (29%), although its panicles carry less florets than *A. arenaria*'s (113/panicle). Caryopses of these two indigenous dune grasses weighed much more than those of both the South African and the European *A. arenaria*.

Both for South African as well as European *A. arenaria* populations no significant correlation can be detected between the number of florets per panicle and the number of developed caryopses, but correlation coefficients are slightly positive ($r = 0.105$) for South African, and slightly negative ($r = -0.194$) for European populations. A comparison of flowering and seed production of South African *A. arenaria* stands along the coast (Fig. 7.1) shows a great discrepancy between the two measures, especially in the southwest around Cape Agulhas (Walker Bay, Struisbaai, De Mond), where flowering rates were very high but hardly any seed was developed. In confirmation of this, no significant correlation can be detected between the two factors ($r = 0.095$, $P = 0.659$).

Table 7.2: Seed production of 31 South African and 5 European *A. arenaria* stands and of one South African stand of *Thinopyrum distichum* and *Ehrharta villosa* respectively.

stand	date collected	mean length of panicles (cm)	mean no. of florets per panicle	% fully developed caryopses	% florets infected with fungus	mean weight of developed caryopses (g)
South African <i>A. arenaria</i>						
tableview 1	24/1/96	20.10	283.40	7.45	0	3.71
noordhoek 2	22/1/96	16.90	140.90	3.26	0.04	4.82
witsand (w.cape) 1	24/1/96	21.23	176.13	1.06	0.3	3.36
muizenberg 1	23/1/96	17.67	235.13	0.05	0.19	3.50
false bay y	21/1/96	27.58	460.87	0.13	0.01	2.17
walker bay 1	13/2/96	20.60	277.50	1.01	0.22	4.55
walker bay 2	13/2/96	19.90	284.20	0.77	0.18	4.71
struisbaai plaat 1	15/2/96	22.15	300.30	0.98	0.07	3.72
de mond b1	18/2/96	26.68	181.20	0.39	0.39	4.86
de mond d1	15/2/96	22.70	241.00	0.49	0.17	4.24
de mond 3	15/2/96	22.70	258.20	0.85	0.58	3.98
waenuiskrans 1	14/9/95	19.20	247.30	0.20	0.20	5.62
de hoop 1	19/2/96	17.57	137.67	0.15	1.65	2.77
witsand (s.cape) 1	2/8/95	18.40	136.13	0.92	0.28	3.32
visbaai	3/8/95	24.78	101.75	2.16	0.15	2.14
vleesbaai	3/8/95	21.80	161.04	0.02	0.03	3.21
hartenbos 1	30/7/95	17.50	92.36	0.39	0.39	5.90
hershams 1	31/7/95	13.86	91.29	0.08	0	4.20
bothastrand	31/7/95	14.78	106.09	0.94	0	3.35
sedgefield 3	12/2/96	21.20	262.70	3.53	0.11	3.85
goukamma 3	5/8/95	18.73	132.55	1.17	0	6.03
plettenberg bay 2	28/7/95	15.13	71.94	0.26	0.35	4.63
st. francis bay	25/5/96	19.18	211.40	0.09	0	4.60
port alfred (west) 2	13/2/97	21.78	335.80	0.06	0.06	4.60
port alfred (east) 2	6/2/97	20.60	343.60	0.12	0.15	3.35
kleinemonde 3	22/1/97	17.84	247.40	1.46	0	5.27
kleinemonde 4	3/12/96	19.58	229.58	11.32	0	4.27
kleinemonde 5	29/2/96	19.40	118.20	0.34	0.34	4.08
old woman's river 1	29/2/96	17.99	131.37	0	0.23	2.2
hamburg 2	6/4/96	18.89	206.93	0.32	0	3.98
gulu mouth 2	6/2/95	19.475	101.15	0.27	0	3.875
mean		19.70	203.39	1.29	0.19	4.03
standard error		0.55	16.41	0.43	0.06	0.18
standard deviation		3.09	91.39	2.38	0.31	0.99
European <i>A. arenaria</i>						
sylt 2	30/8/96	14.32	241.70	7.28	1.16	4.67
sylt 4	30/8/96	14.36	218.10	17.29	0.73	5.27
sylt 7	31/8/96	14.58	253.60	22.44	0.28	4.54
sylt 9	1/9/96	17.18	192.00	44.38	2.81	6.19
dutch seed	?	15.92	251.00	51.55	0.04	2.45
mean		15.27	231.28	28.59	1.00	4.621
standard error		0.56	11.65	8.35	0.49	0.62
standard deviation		1.25	26.04	18.68	1.09	1.38
South African <i>Thinopyrum distichum</i> (Port Alfred) and <i>Ehrharta villosa</i> (Kenton-on-Sea)						
<i>T. distichum</i>	13/2/1997	14.22	112.50	28.89	3.78	15.51
<i>E. villosa</i>	13/2/1997	16.85	58.42	1.54	0	12.59

2) Germination and seedling establishment

Germination under different environmental conditons

Germination of South African *A. arenaria* seed was higher and more rapid in the growth chamber environment than in the window sill environment (Fig. 7.2). Batches of all cold pre-treatments germinated quickly in the warmer temperature regime of the growth chamber and differed only slightly in germination percentages between a maximum of 65% of seed which had not been exposed to cold pre-treatment, and a minimum of 58% of seed that had been pre-treated at 5°C for 40 days. In the window sill environment with much stronger fluctuating temperatures and an overall cooler climate, a greater variation of germination between the different cold pre-treatments was observed. Maximum germination was reached by the incised seed with 47%, and the lowest germination of only 29% by seed that had not been exposed to a cold period. Separate one-factor analyses of variance (ANOVA) for each environment (factor: different cold pre-treatment) confirm that the difference of the four treatments with regard to germination results is significant only in the window-sill environment (Table 7.3). It becomes obvious that cold pre-treatment of South African *A. arenaria* seed as well as the incision of its seed coat appears to enhance germination only in fluctuating, colder temperature regimes.

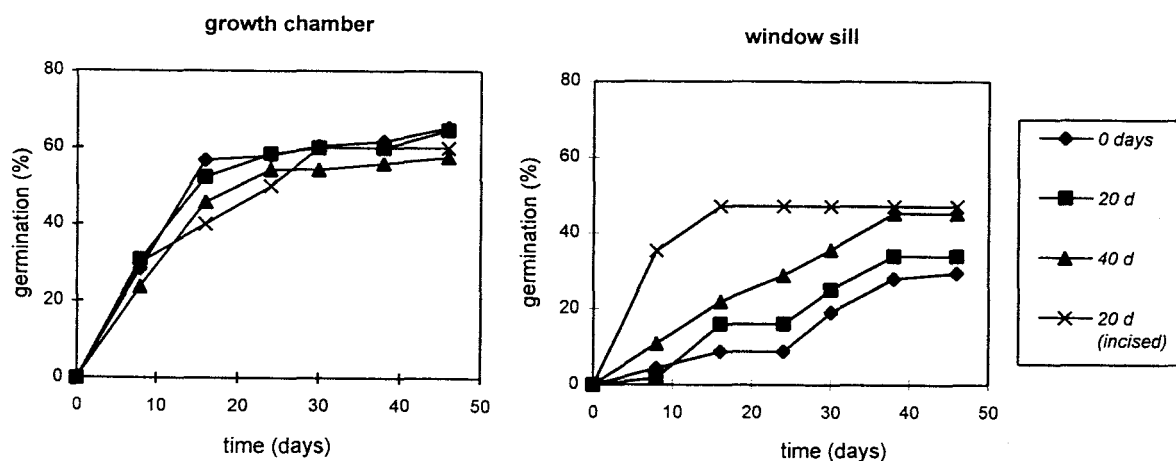


Fig. 7.2: Germination rates in the growth chamber and window sill environments for *A. arenaria* seed batches after different cold pre-treatments (means of 3 replicates).

Table 7.3: One-factor ANOVA results of the effect of four different cold pre-treatments of South African *A. arenaria* seed on germination in the growth chamber and window sill environment. Significance at $\alpha = 0.001$ (***).

	growth chamber	window sill
df	3	3
F	0.379	8.175
P	0.769	9.51×10^{-4} ***

Germination of different batches of seed

According to Table 7.4, South African seed had a higher germination maximum with 84.6% (at Kleinemonde) compared to 63.3% of Sylt seed. But it also showed a stronger fluctuation of germination success with seed of several batches not having germinated at all or only at low percentages and high values for both standard deviation and variance (Table 7.4). Its mean percentage germination was only 38% compared to 51% of European seed. However, a Mann-Whitney *U*-test does not detect a significant difference ($P = 0.181$).

Seed from the indigenous dune grasses *Thinopyrum distichum* and *Ehrharta villosa* appeared to germinate fairly well, but less readily than *A. arenaria* seed, with a mean percentage germination of 34% and 33% respectively (not shown). A comparison of South African *A. arenaria* seed production and germination (Fig. 7.3) along the coast shows a strong discrepancy between the two measures. High seed productivity does not appear to be related to high seed viability or vice versa: the correlation coefficient is clearly positive ($r = 0.263$), but not significant ($P = 0.262$).

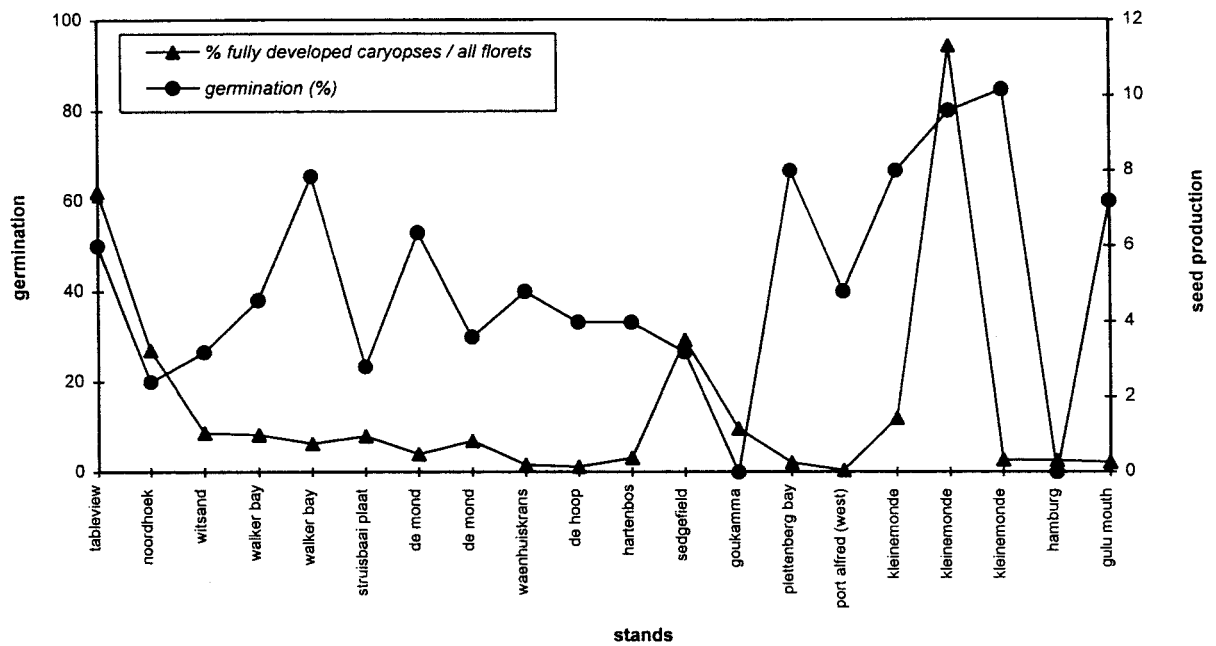


Fig. 7.3: Seed production and germination of 20 South African *A. arenaria* populations along the Cape coast from west (left) to east (right).

Table 7.4: Percentage germination of 25 South African (left) and 5 European (right) *A. arenaria* batches.

stand	date sampled	germination (%)	stand	date sampled	germination (%)
tableview 1	24/1/96	50.00	sylt 2	30/8/96	33.33
noordhoek 2	22/1/96	20.00	sylt 4	31/8/96	63.33
witsand (w.cape) 1	24/1/96	26.67	sylt 7	31/8/96	60.00
false Bay	21/1/96	28.57	sylt 9	1/9/96	60.00
walker bay 1	13/2/96	38.09	dutch seed	?	36.67
walker bay 2	13/2/96	65.52	mean (%)		50.67
struisbaai plaat 1	15/2/96	23.33	standard error (%)		6.45
de mond d1	18/2/96	52.94	standard deviation (%)		14.41
de mond 3	15/2/96	30.00	variance		207.78
waenhuiskrans 1	14/9/95	40.00			
de hoop 1	19/2/96	33.33			
visbaai	3/8/95	25.00			
vleesbaai	3/8/95	13.33			
hartenbos 1	30/7/95	33.33			
bothastrand	31/7/95	0			
sedgefield 3	12/2/96	26.67			
goukamma 3	5/8/95	0			
plettenberg bay 2	28/7/95	66.67			
port alfred (west) 1	13/2/97	40.00			
kleinemonde 3	24/11/96	66.67			
kleinemonde 4	3/12/96	80.00			
kleinemonde 5	12/3/95	84.62			
hamburg 2	6/4/96	0			
gulu mouth 2	8/4/96	60.00			
mean (%)		38.19			
standard error (%)		4.73			
standard deviation (%)		23.67			
variance		560.08			

Germination and seedling establishment in the field

KLEINEMONDE

Germination and seedling establishment in all five stages of the Kleinemonde dune transect was very low, and results are not reflected. No seedlings emerged on top of the foredune or on its leeward side, where sand movement was extreme. Maximum sand burial occurred in early October 1996 when howling southwesterly winds deposited nearly half a meter (43.6 cm) of sand on the two sites (Plate 7.1). In the dune slack, seedling growth could only be monitored over four months because of a major flooding event in November 1996. However, maximum germination was observed at this site with 3% emerged seedlings (percentage of developed seed sown) in one replicate of the 0 day cold pre-treatment. Most seedlings in the dune slack emerged from the 0 day cold pre-treatment, but the 25 day cold pre-treatment showed better growth results with seedlings reaching up to 8.2 cm in height. Unexpectedly, no seedlings emerged on the leeward side of a supposedly sheltered intermediate dune. It appears as though the slope of this dune was too steep (43°), and seed got washed down with the rain and then blown away. 1 seedling (0.7%) emerged amongst the dune scrub. After quick growth this seedling died of desiccation.

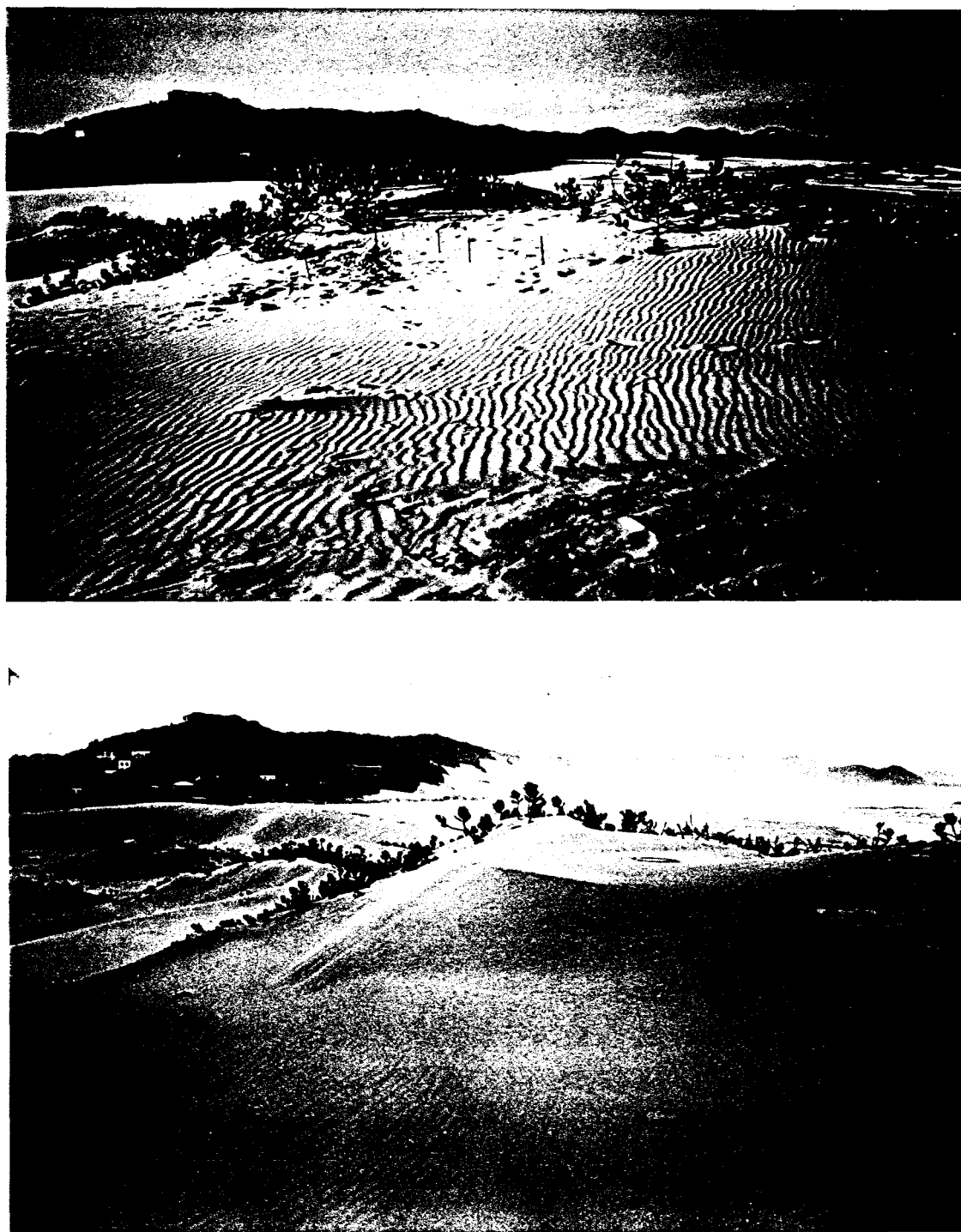


Plate 7.1: Sand burial of the first two sites of the Kleinemonde transect (top of a foredune and its leeward side) between mid June 1996 (top) and mid October 1996 (bottom). No seedlings or shoots emerged at these sites.

OLD WOMAN'S RIVER

A description of all five sites of the three transects is given in Table 7.5. The first two transects were laid through steep *Scaevola plumieri* foredunes and intermediate dunes of an open *Metalasia muricata* and *Passerina rigida* scrub vegetation. The third transect reached from a small, rounded *Sporobolus virginicus* foredune through intermediate dunes covered with dense *Ipomoea pes-caprae* and remnant *Scaevola plumieri*. pH values do not fluctuate much along any of the transects, but the soil conductivity is generally higher in sites closer to the shore, indicating higher salinity levels. Site 3 of transect 3, the windward side of the *Sporobolus* foredune, is exposed to frequent southwesterly winds, which could account for its conductivity level to be higher than that of sites 1 and 2 of the same transect. Along all three transects organic matter values increase from the front to the back with increasing density of the vegetation.

Germination of South African *A. arenaria* seed of different cold pre-treatments was extremely low and is not shown. The maximum germination rate was only 2 seedlings (1.4%) for the 45 days treatment in the dune scrub (site 5) of transect 1. None of the few seedlings became established.

Figure 7.4 I, II and III reflects the number of emerged seedlings (% of developed seed sown) of the three dune grasses *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* for the three transects at Old Woman's River. The highest percentages of germinated seed for all three species was found in transect 2 (Fig. 7.4 II) with the overall maximum of 34% for *Thinopyrum distichum* (site 2), 23% for *Ehrharta villosa* (site 5) and 11% for *A. arenaria* (site 5). In all three transects, the indigenous species *Thinopyrum distichum* and *Ehrharta villosa* appeared to germinate more readily than *A. arenaria*. The germination of European *A. arenaria* seed, monitored only along transect 1 (Fig. 7.5), was even lower than that of South African *A. arenaria* seed with a maximum of only 5%. *Ehrharta villosa* showed highest germination success at the back dune sites of all transects, while *A. arenaria* and especially *Thinopyrum distichum* germinated well at sites closer to the shore. *Thinopyrum distichum* is the only species that developed seedlings on the back beach (Fig. 7.4 III: transect 3, site 1), and it reached its maximum germination on top of an exposed *Scaevola plumieri* foredune (Fig. 7.4 II: transect 2, site 2).

Table 7.5: Characteristics of sites 1-5 of three transects at the Old Woman's River mouth along which reproduction experiments were carried out (HWM = high water mark).

site	distance from HWM (m)	situation	plant species in vicinity	pH	conductivity (μScm^{-1})	organic matter (% dry weight)
transect 1 (200 m west of mouth)						
site 1	24	back beach	no vegetation	7.8	305	0.18
site 2	27	top of steep foredune	<i>Scaevola plumieri</i>	8.0	154	0.22
site 3	33	leeward side of foredune	<i>Scaevola plumieri</i>	7.8	213	0.33
site 4	54	top of intermediate dune	<i>Metalasia muricata</i> <i>Passerina rigida</i> <i>Ipomoea pes-caprae</i>	7.9	174	0.34
site 5	71	back dune	<i>Metalasia muricata</i> <i>Passerina rigida</i> <i>Rhus crenata</i> <i>Cynanchum natalitium</i>	7.8	216	0.34
transect 2 (280 m west of mouth)						
site 1	22	leeward back beach	no vegetation	7.6	307	0.20
site 2	24	top of steep foredune	<i>Scaevola plumieri</i> <i>Ipomoea pes-caprae</i>	7.8	199	0.29
site 3	27	leeward side of foredune	<i>Scaevola plumieri</i>	7.8	146	0.37
site 4	63	intermediate dune swale	<i>Metalasia muricata</i> <i>Passerina rigida</i> <i>Myrica cordifolia</i> <i>Ficinia lateralis</i>	7.9	143	0.36
site 5	75	back dune	<i>Metalasia muricata</i> <i>Ficinia lateralis</i> <i>Chrysanthemoides monilifera</i> <i>Stoebe plumosa</i>	8.0	142	0.39
transect 3 (400 m west of mouth)						
site 1	16	back beach	no vegetation	7.8	229	0.16
site 2	23	top of small, rounded foredune	<i>Sporobolus virginicus</i> <i>Ipomoea pes-caprae</i>	7.8	200	0.18
site 3	25	windward side of foredune	<i>Sporobolus virginicus</i> <i>Ipomoea pes-caprae</i>	7.6	364	0.29
site 4	36	intermediate dune swale	<i>Ipomoea pes-caprae</i> <i>Scaevola plumieri</i> <i>Passerina rigida</i>	7.8	153	0.26
site 5	53	back dune	<i>Passerina rigida</i> <i>Myrica cordifolia</i> <i>Ficinia lateralis</i> <i>Chrysanthemoides monilifera</i>	7.8	163	0.40

The influence of sand burial (results not shown) at each site was not as significant as expected. However, no seedlings emerged on the beach sites of the first two transects, which were exposed to the most severe sand movement. The maximum sand burial was measured at site 1 of transect 1 with 29 cm between weeks 2 and 5 of observation. One clear impact of sand burial on germination and seedling survival was observed at sites 3 and 4 of transect 1 (Fig. 7.4 I): Between weeks 8 and 12, more than 12 cm of sand burial was measured, possibly with greater fluctuations in between. The percentage of *Thinopyrum distichum* seedlings dropped in this period from 3% to 0% at site 3 and from 13% to 4% at site 4. Both sand burial and sand removal affected the germination and seedling establishment at Old Woman's River. Very often seed was found uncovered and would either get blown away or dry out because of the strong radiation. Seedlings were often found exposed to their roots and desiccated. Seed and seedlings were in one instance (Fig. 7.4 III: transect 3, site 5) severely affected by animal trampling, which destroyed *Ehrharta villosa* seedlings and exposed most seed. Another effect was observed through the climate: heavy rainfalls in June (see Fig. 6.5) washed away most *Thinopyrum distichum* seed and seedlings at site 3 of transect 2 (Fig. 7.4 II) from weeks 12 to 16 of observation.

The only beach site of all transects that supported seedlings (Fig. 7.4 III: *Thinopyrum distichum* seedlings at site 1 of transect 3) is the most sheltered of the three beach sites with the lowest conductivity value (Table 7.5), therefore the least salinity level. However, it is also the closest to the high water mark, and the seedlings were lost between week 14 and 16 of observation because of a flooding event. The back dune sites amongst dune scrub vegetation supported the highest seedling numbers in all three transects. In particular *Ehrharta villosa*, known as a back dune species, thrived well at these sites. Surprisingly, even the "foredune species" *A. arenaria* showed highest germination amongst the dune scrub. However, one has to note that organic matter values of all back dune sites are comparatively low, with a maximum of only 0.40% in transect 3 (Table 7.5). The advantage of these sites is clearly the shade offered by surrounding scrub species like *Metalsia muricata* or *Passerina rigida*. Both seed and seedlings were not as exposed to strong radiation as they were at the other sites and show higher germination or survival rates.

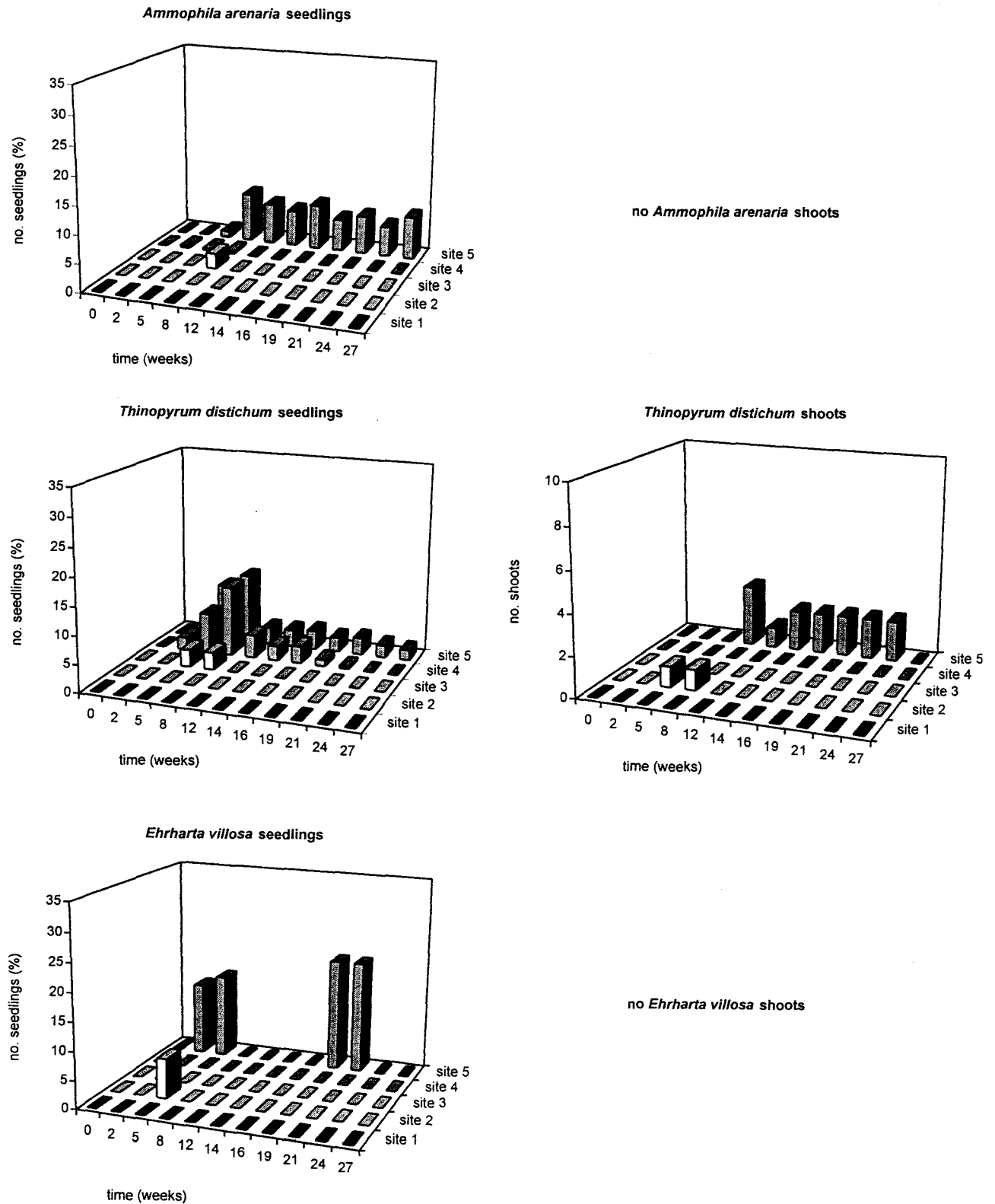


Fig. 7.4 I: Number of seedlings (as percentage of developed seed sown), left side, and total number of shoots developed from rhizome fragments, right side, of *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* along 5 sites of transect 1 at Old Woman's River mouth.

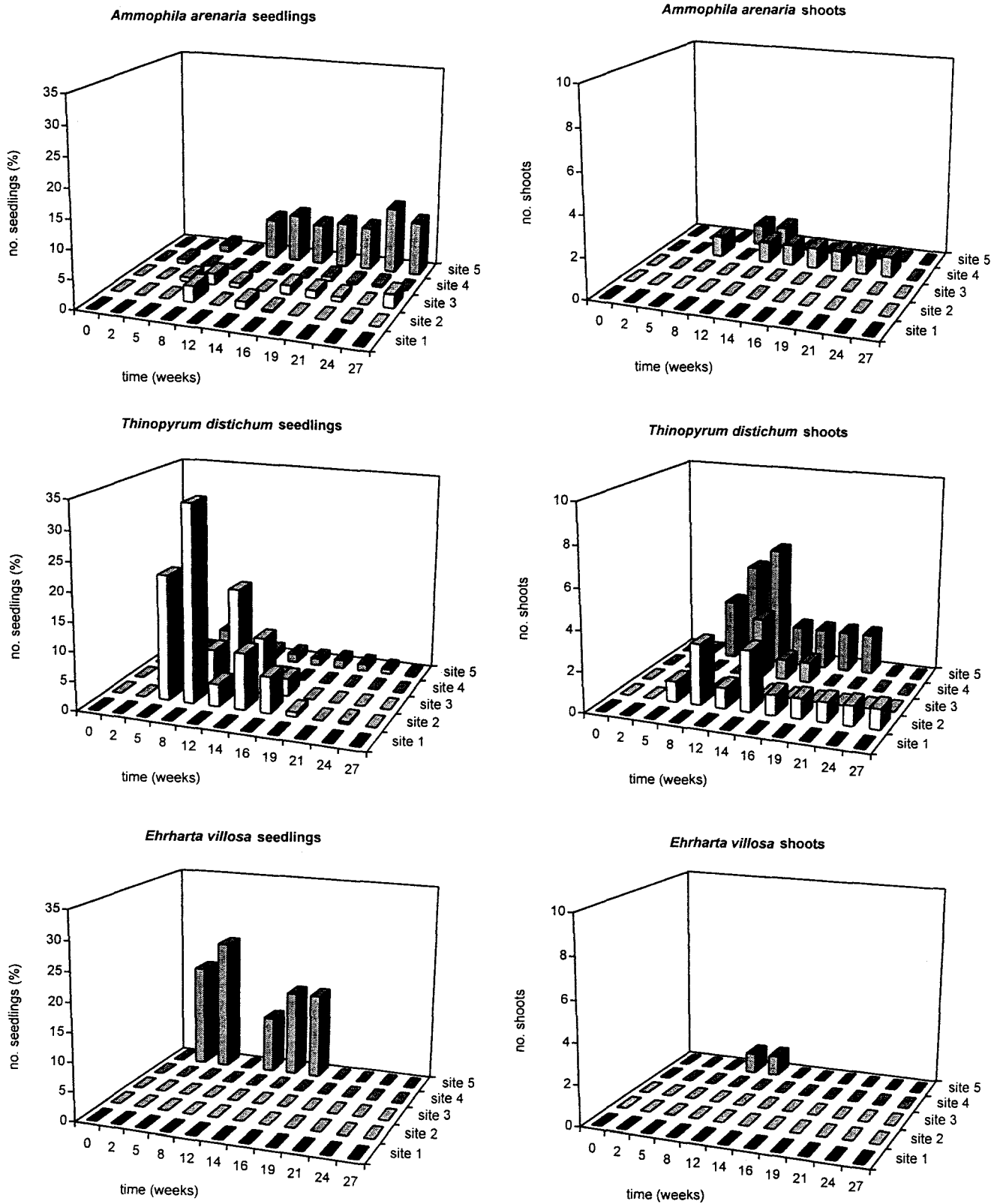


Fig. 7.4 II: Number of seedlings (as percentage of developed seed sown), left side, and total number of shoots developed from rhizome fragments, right side, of *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* along 5 sites of transect 2 at Old Woman's River mouth.

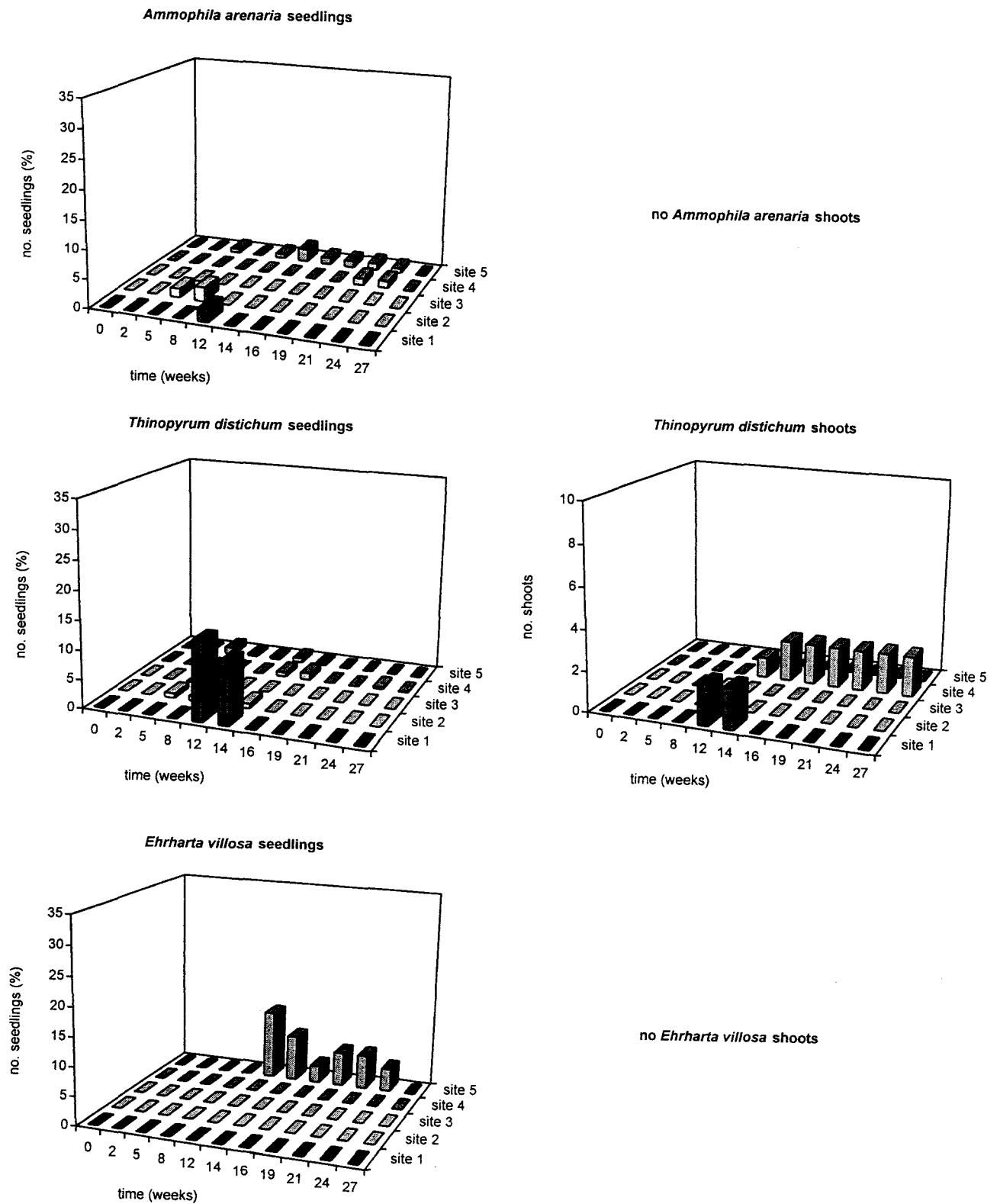


Fig. 7.4 III: Number of seedlings (as percentage of developed seed sown), left side, and total number of shoots developed from rhizome fragments, right side, of *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* along 5 sites of transect 3 at Old Woman's River mouth.

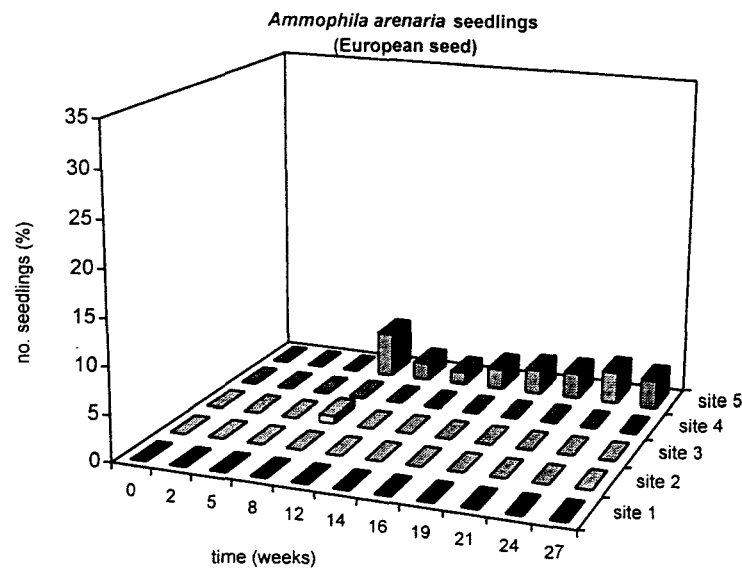


Fig. 7.5: Number of seedlings (as percentage of developed seed sown) of European *A. arenaria* seed (from Sylt Island) along 5 sites of transect 1 at Old Woman's River mouth.

Heights of seedlings were measured at all sites, but are reflected in Figure 7.6 only for the back dune sites of the three transects (sites 5), where large numbers of seedlings were recorded for all three species. Not only did *Ehrharta villosa* show the maximum mean seedling height of 19.2 cm, but also the highest growth rate with 3.4 cm week⁻¹ (both in transect 3). Seedlings of *A. arenaria* and *Thinopyrum distichum* never reached more than the average height of 7.6 cm and 6.9 cm respectively (both in transect 3). Their growth rates were also lower than those of *Ehrharta villosa*: *A. arenaria* seedlings had a maximum growth rate of 1.6 cm week⁻¹ (transect 2), and *Thinopyrum distichum* one of 1.3 cm week⁻¹ (transect 2).

While the sudden decrease of seedling heights in Figure 7.6 to zero is due to the total die-back of the respective seedlings, the decrease to lower values can be explained by drying of the tips and even more so by animal grazing. Seedlings of all three species had neatly bitten-off tips at all sites in all transects (Plate 7.2). It is assumed that the damage is due to insects, since surrounding plants, especially *Ipomoea pes-caprae*, were severely affected by insects feeding on their leaves.

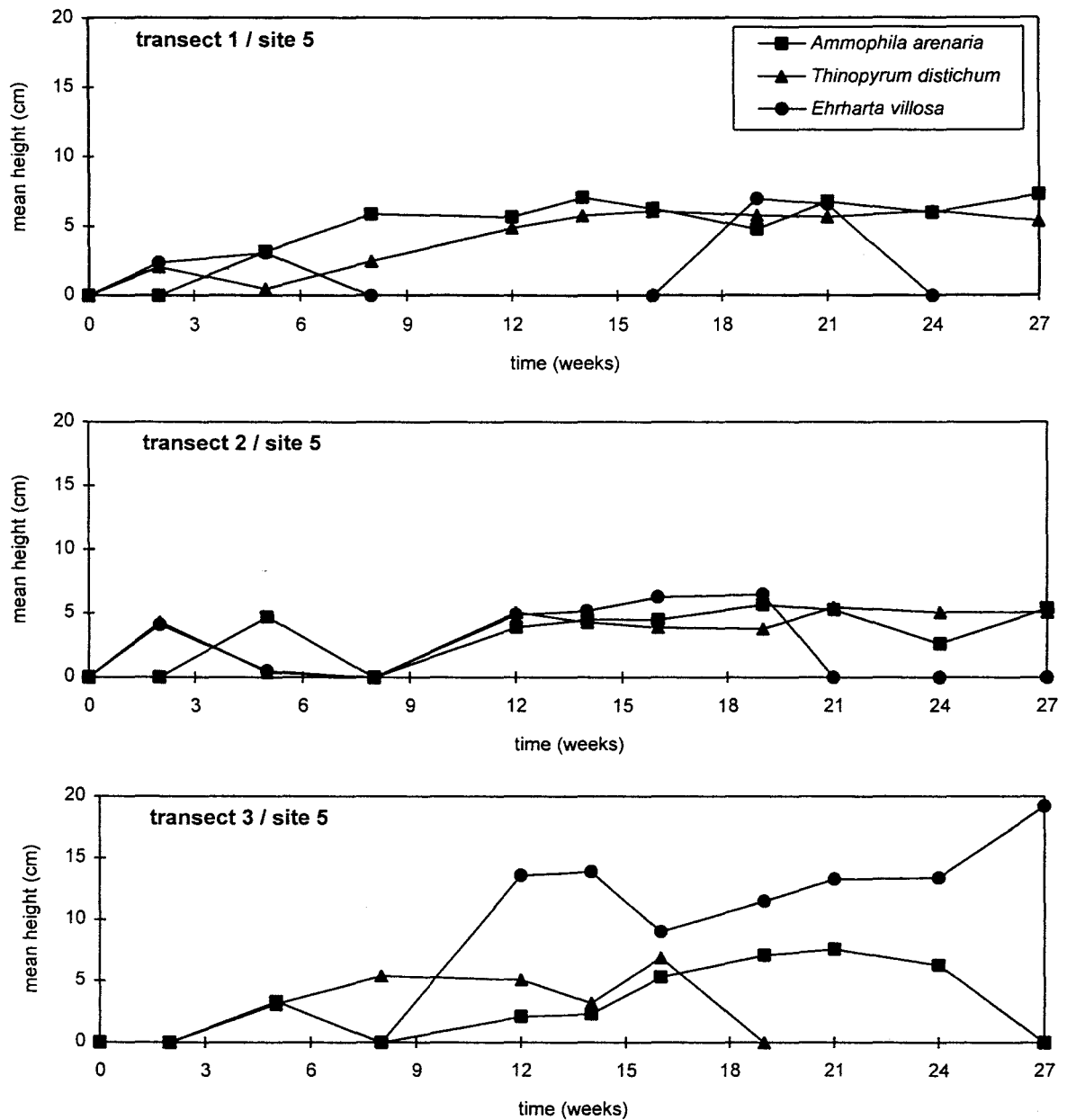


Fig. 7.6: Mean height of all seedlings of *A. arenaria*, *Thinopyrum distichum* and *Ehrharta villosa* at the back dune sites of all 3 transects at Old Woman's River mouth.

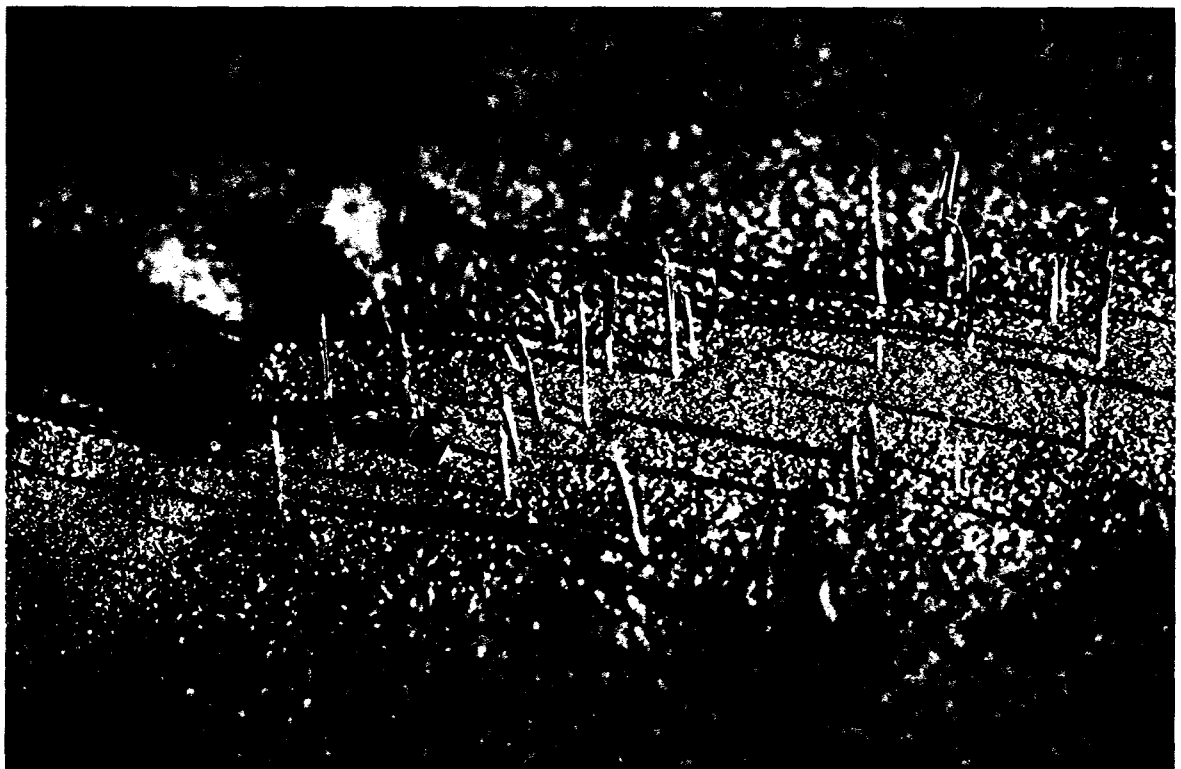


Plate 7.2: Healthy (top) and damaged (bottom) seedlings of *A. arenaria* at Old Woman's River mouth. The damage is possibly due to insect grazing.

3) Vegetative reproduction

KLEINEMONDE

As with the germination results, shoot development from rhizome fragments was equally low at Kleinemonde and is not presented. No shoots developed on top of the foredune or on its leeward side. Sand movement was far too high here, and rhizomes were either buried too deeply or blown free and exposed to strong radiation so that buds would dry out. There was a fairly high emergence of shoots in the moist dune slack environment with 7 shoots on average (in one replicate a maximum number of 12 shoots emerged). Mean shoot emergence was only 0.7 at the leeward side of an intermediate dune, and 1.3 amongst the dune scrub. At the latter site, shoots decreased in vigour rapidly because of desiccation and died off; only one shoot was capable of growing into a reasonably strong tiller with three leaves and a maximum height of 21 cm.

OLD WOMAN'S RIVER

Shoot development from rhizome fragments at the Old Woman's River mouth was highest for *Thinopyrum distichum* (Figure 7.4 I, II and III). It developed shoots in all three transects, while *A. arenaria* and *Ehrharta villosa* developed shoots only in transect 2. Rhizome fragments of *Thinopyrum distichum* gave rise to shoots most frequently in transect 2, where the overall maximum number of 6 shoots emerged at site 5 (Fig. 7.4 II). The decrease of shoots from 6 to 2 at the next sampling date is due to insect grazing, since four of the shoots were found with bitten-off tips. The sudden decrease of *Thinopyrum* shoot numbers at site 4 (transect 2) has a different explanation: at this site, the shoots were covered with stolons of the scrub species *Myrica cordifolia*, which had completely overgrown the site by week 14 of the observation period. Shoots of *Thinopyrum distichum* also emerged on the beach, at site 1 of transect 3 (Fig. 7.4 III), but died off after the flooding event similarly to the seedlings at the same site (see above). However, at this site, *Thinopyrum distichum* developed the overall longest shoots with an average of 17.6 cm. In comparison, maximum length of *A. arenaria* shoots was 6.2 cm and of *Ehrharta villosa* shoots only 3.2 cm.

7.5 Discussion

Percentage flowering was higher in South African *A. arenaria* populations (max. 18.2%) than in populations on Sylt Island (max. 13.5%, see Table 7.1). Even lower values are found in the literature for *A. arenaria* (Greig-Smith 1961: max. 0.68% in a healthy yellow-dune stand) or the American *Ammophila breviligulata* (Laing 1958: max. 0.13%). However, seed production of South African *A. arenaria* populations stands was significantly lower than that of Sylt populations (Table 7.2). Although South African *A. arenaria* produced similar amounts of florets per inflorescence as European populations, the maximum rate of developed caryopses was only 11% for South African stands compared to 44% for Sylt stands. Huiskes (1979) recorded between 60% and 100% developed seed in British *A. arenaria* stands. However, in some supposedly healthy stands no developed caryopses were recorded, which can be due to the strong protandry observed for *A. arenaria* var. *genuina* (Huiskes 1979). Anthers are ripe before the pistils, and flowers of isolated stands are not fertilised. It is possible that this phenomenon accounts for the low numbers of fully developed caryopses in South African *A. arenaria* stands.

Cold pre-treatment of the seed as well as the incision of the seed coat appears to enhance germination only in strongly fluctuating, colder temperature regimes, an observation also made for European seed by van der Putten (1990). Similarly to his findings, South African *A. arenaria* seed showed highest germination rates in a warm environment of temperatures ranging between 20 and 30°C, irrespective of their cold pre-treatment (Fig. 7.2). Although the examined South African seed batches did not reach the maximum germination percentages of 80% or 90% that European seed has been shown to reach under optimal conditions (Huiskes 1979; van der Putten 1990), a germination success of up to 65% is high and proves that South African *A. arenaria* certainly produces viable seed. Californian *A. arenaria* seed was shown to have a similar germination success of up to 66% (Bencie 1990).

However, stands of South African *A. arenaria* do not always produce such viable seed. The above germination experiments were carried out with particularly healthy seed from young populations at Tableview and Sedgfield. An examination of seed from various *A. arenaria* stands along the South African Cape coast shows that the average germination under optimal

conditions is only 38% (Table 7.4). Sylt seed are on average much more viable under the same conditions with a germination success of 51%. Furthermore, the percentage germination of South African *A. arenaria* seed fluctuates strongly in the various populations along the coast, ranging between 0% and the maximum of 84% (at Kleinemonde, Fig. 7.3). Nevertheless, seedlings of *A. arenaria* were observed at many sites along the Cape coast (Plate 7.3).

Seed production of the indigenous dune grass *Thinopyrum distichum* at Port Alfred was, with 29%, comparatively high (Table 7.2). In contrast, the Kenton-on-Sea population of the indigenous *Ehrharta villosa* produced only few developed caryopses (1.5%). Both species germinated less readily under laboratory conditions than *A. arenaria*, with germination percentages of 34% and 33% respectively. These results are only preliminary though and based on too small a number of samples to be reliable.

Germination of *A. arenaria* seed of different cold pre-treatments in the field, both at Kleinemonde and at Old Woman's River mouth, was extremely low. Out of an estimate of 146 developed caryopses per replicate, a maximum of only 5 seedlings (3%) emerged. It is in accord with records by Huiskes (1977) on the germination of British *A. arenaria* that the highest germination was achieved in the dune slack with little sand movement and a moist substratum.

Field experiments on germination and seedling establishment of untreated seed were generally more successful at Old Woman's River. The area is less exposed to harsh southwesterly winds than Kleinemonde and does not suffer sand burial to the same extent. In comparison with the indigenous dune grasses *Thinopyrum distichum* and *Ehrharta villosa*, the germination of both South African and European *A. arenaria* seed along all transects was low (Fig. 7.4 I, II, III). This is noteworthy, since the germination rates of *A. arenaria* were higher under laboratory conditions (see above), and could point towards a better adaptation of the indigenous dune plants to the field conditions. *Thinopyrum distichum* achieved the highest germination with 34%, and *Ehrharta villosa* germinated more successfully (23%) than South African *A. arenaria* (11%) or *A. arenaria* seed transferred to South Africa from Sylt Island (5%, Fig. 7.5). Germination of *Ehrharta villosa* was best in the back dune areas of the transects, while *A. arenaria* and especially *Thinopyrum distichum* were able to germinate in sites closer to the

shore. Of the three compared grasses, *Ehrharta villosa* showed the highest growth rate and developed the tallest seedlings during the period of observation (Fig. 7.6).



Plate 7.3: *A. arenaria* seedlings at De Mond (top, February 1996) and Vleesbaai (bottom, September 1995).

Germination was prevented mostly by sand burial, desiccation and wind (seed was blown away). Seedlings suffered even greater pressure: although all three grasses developed a fair amount of seedlings, their establishment was severely endangered by sand burial, desiccation, rainwater flushing, animal trampling and, possibly most importantly, by insect grazing. Similar impacts of environmental factors on germination and seedling establishment of dune plant species have been observed in other studies (Laing 1958; van der Valk 1974; Huiskes 1977; Maun 1981; Maun 1985; Maun & Lapierre 1986; Zhang & Maun 1990; Martinez *et al* 1992; Maun 1994; Balarin 1996).

The particularly low rates of germination and seedling emergence of *A. arenaria* in comparison with the two indigenous dune grasses at Old Woman's River are reflected in a study by Maun & Lapierre (1986). They compared the effects of sand burial on the American dune species *Ammophila breviligulata*, *Cakile edentula*, *Elymus canadensis* and *Corispermum hyssopifolium*. Of these, *Ammophila breviligulata* showed the lowest rates of emergence, which could be explained by its small and light seed. Large seeded species emerged more easily and were more abundant in sites of high sand accretion. Since the seed of *A. arenaria* is much smaller and lighter than that of *Thinopyrum distichum* and *Ehrharta villosa* (Table 7.2, see also Chapter 2), this may be one reason for its low germination and emergence in the Old Woman's River sites.

South African *A. arenaria* proves to have similar difficulties in germinating and establishing its seed in the field as it does in Europe (Salisbury 1952; Ranwell 1972; Huiskes 1977, 1979; van der Putten & van Gulik 1987; van der Putten 1990). Reasons listed by these authors are above all desiccation, sand burial and wind. With stronger winds and a much higher radiation, environmental conditions for germination and seedling survival are even less favourable in South Africa than in Europe. In consideration of these factors, it is understandable that *A. arenaria* germinated most successfully in the shadowy back dune areas at Old Woman's River. While germination of *A. arenaria* in stable dune areas along the North American west coast (Bencie 1990) can point towards its invasiveness there, the results from Old Woman's River do not imply any invasive behaviour of *A. arenaria* in South Africa. Quite to the contrary, the indigenous dune grasses *Thinopyrum distichum* and *Ehrharta villosa* show superior qualities of both germination and seedling establishment than *A. arenaria*.

Shoot development of *A. arenaria* from rhizomes fragments was low at Kleinemonde, where the maximum amount of emerged shoots was only 12 in one replicate, typically in the moist dune slack environment. One has to consider that per replicate 30 rhizomes with 1-2 viable buds each were sown, hence a maximum of 30 - 60 potential shoots could be expected under optimal conditions. Altogether shoots were found to be much stronger than seedlings and to grow more quickly (maximum seedling height at Kleinemonde was 8.2 cm against maximum shoot height of 21 cm). Nevertheless, shoots were similarly affected by sand movement, especially by removal of sand and desiccation following exposure of the roots.

Shoot development of *A. arenaria* was less successful at Old Woman's River with not more than 1 shoot at a time, mostly in the back dune stages. While *Ehrharta villosa* did not yield better results, *Thinopyrum distichum* showed a maximum of 6 developed shoots (Fig. 7.4 I, II, III). However, considering that up to 40 viable buds were present per species in each replicate (20 rhizome pieces with 2 viable buds each), even this number is low. None of the three dune grasses appears to spread easily from severed rhizomes. A reason could be the desiccation of buds because of strong sand movement and consequential exposure. Rhizomes were dug up from at least 30 cm underground and then sown onto the study sites and covered with not more than 10 cm of sand. This might have been insufficient, since the sand had possibly been blown away in many cases. The rhizome fragments were then either also blown away or left exposed.

Sowing of rhizome fragments of *A. arenaria* in Europe resulted in high establishment rates in combination with sand stabilisation by straw (van der Putten & van Gulik 1987; van der Putten 1990). It is therefore not possible to exclude the spread of *A. arenaria* in South Africa via rhizome cuttings. Stabilisation sites along the Cape coast were frequently found eroded by high tides, and rhizome cuttings observed to be washed ashore (Plate 7.4, see also Chapters 3 and 6). The American *Ammophila breviligulata* has been shown to be distributed easily by erosion and fragmentation of rhizomes by the sea (Maun 1984, 1985). The presence of *A. arenaria* in a driftline community at Kleinemonde (see Chapter 6) is most probably due to this vector, but more experimentation is required to confirm this.



Plate 7.4: Erosion of the Sedgefield stabilisation site (top). Fragments of tillers and rhizomes of *A. arenaria* were washed ashore further along the same beach (bottom). Both photographs were taken in September 1995. See also Plate 3.7.

7.6 Conclusions

South African *A. arenaria* populations flower vigorously, but produce fewer caryopses than European populations, which is possibly due to strong protandry in combination with geographical isolation: *A. arenaria* has been planted along the Cape coast at many isolated sites (see Chapter 3), and there is hardly any continuity (yet) between existent *A. arenaria* communities. Synchronous flowering within isolated stands can prevent successful fertilisation.

Seed viability fluctuates strongly along the coast, but at several sites high germination percentages were recorded under optimal conditions. South African *A. arenaria* is certainly able to produce viable seed. However, germination in the field as well as seedling establishment and establishment from severed rhizomes appears to be very low for *A. arenaria*. The indigenous dune grasses *Thinopyrum distichum* and *Ehrharta villosa* show better results and appear better equipped to withstand the harsh conditions of South African dunes.

CHAPTER EIGHT

Conclusions

The objective of this thesis was to establish the potential invasiveness of *A. arenaria* along the South African Cape coast with a view to assessing whether its use for dune stabilisation is still justifiable. The grass bears many physiological as well as demographic traits which are observed to enhance invasiveness. Furthermore, it has been known as an aggressive invader along the North American west coast for several decades, and also to cause problems in New Zealand and Australia. Apart from Europe, South Africa appears to be the only place where *A. arenaria* is still actively planted in large stabilisation programmes. Prior to this study there was a conspicuous lack of knowledge about the biology of *A. arenaria* in South African dune systems.

In a survey of the current distribution of *A. arenaria* in South Africa, the grass was found from the dry west coast to the subtropical shores of the Eastern Cape province. However, in combination with historical records of its use for dune stabilisation, it appears as though *A. arenaria* occurs only at sites where it has previously been planted. There is no proof so far of its unaided spread along the South African Cape coast. Quite the contrary, *A. arenaria* has declined at many sites since its initial establishment by humans. This may be due to adverse climatic conditions, since the climate of the South African Cape coast does not appear to offer the right combination of temperature and rainfall. The Western Cape has a favourable temperature regime for *A. arenaria*, but is too dry in summer, while the Eastern Cape receives plenty of rainfall, but is generally too warm. Some areas of the Southern Cape, situated between these two extremes, may bear the best conditions for *A. arenaria*. This would explain why Southern Cape sites like Vleesbaai and Visbaai (near Mossel Bay) have supported healthy, naturalised *A. arenaria* populations for several decades.

Studies on the structure of *A. arenaria* communities show that they are of a considerable floristic diversity and do not differ substantially from communities developed and dominated by indigenous dune plant species. Unlike on the shores of California and Oregon, *A. arenaria*

does not exhibit a strong tendency to dominance over indigenous species on Cape coastal dunes, nor does it invade open, unvegetated dune systems. However, in comparison with the variability of indigenous dune plant communities along the entire Cape coast, *A. arenaria* communities appear monotonous in terms of their species composition. The amount of species growing well in *A. arenaria* stands is restricted to small, soft-leafed plants, thereby reducing the variability and physiognomy of *A. arenaria* communities along the coast. The presence of *A. arenaria* on Cape dunes is thus reducing species variation along the coast and could lead to a shift in the vegetation structure of Cape coastal ecosystems.

Species association analyses reveal the alienness of *A. arenaria* in South Africa, since most indigenous plant species are much better associated with other indigenous species than with *A. arenaria*. It lacks the common evolutionary history to form strong bonds with South African species, a conclusion that is confirmed by comparisons with European *A. arenaria* communities, where *A. arenaria* forms very strong species associations. However obvious *A. arenaria*'s alienness in South Africa is, this does not imply its invasiveness. The comparison of South African *A. arenaria* communities with indigenous communities, as well as with natural *A. arenaria* communities in Europe, cannot confirm any of the alarming North American experiences with the grass. *A. arenaria* is visibly alien in South Africa, but neither aggressively spreading and outcompeting indigenous dune plants, nor altering the topography of South African natural beaches and dunes.

A study of the development of a large-scale *A. arenaria* stabilisation area shows that *A. arenaria* can be succeeded by a species-rich indigenous dune scrub, or by dune fynbos, within not more than 40-50 years. It fixes loose sand, thus providing a habitat for indigenous plants less tolerant of sand movement, and dies back with increasing sand stability. Succession is mainly dependent on the time of stabilisation, but also on the topographical situation of the stand, since stands in sheltered dune slacks are replaced by indigenous species more rapidly than those on exposed tops or slopes of dunes. A first examination of the presence of nematodes in differently aged *A. arenaria* stands shows that, as in European dunes, *A. arenaria* may be affected by plant-parasitic nematodes in Cape dune sands which prevent normal root development. Only a regular supply of windblown sand enables *A. arenaria* to develop new

roots and escape this pressure. Soil-borne pathogens may therefore play an important role in the succession of *A. arenaria* stands in South Africa.

Monitoring *A. arenaria* and indigenous dune plant communities on Eastern Cape dunes over several years disproves a tendency of *A. arenaria* to spread and replace indigenous plant species. It profits from its superior tolerance of sand burial, which appears to override adverse climatic factors and enables it to compete with the indigenous dune plants. Nevertheless, the *A. arenaria* communities at Kleinemonde appear to decline in vigour. Comparative studies on *A. arenaria* populations and populations of the two indigenous dune grasses *Thinopyrum distichum* and *Ehrharta villosa* reveal that *A. arenaria* bears no superior demographic traits such as a high growth rate and large biomass production. Although its rhizomatous growth is clearly more above-ground oriented than that of the two indigenous species, *Ehrharta villosa* produces a higher above-ground biomass.

Contrary to the general belief, *A. arenaria* produces viable seed in South Africa. However, seed production is lower than in European populations, which may be due to protandry in combination with the geographical isolation of South African *A. arenaria* populations. While caryopses germinate readily under laboratory conditions, germination and seedling establishment are low in the field. Seedlings suffer mostly from desiccation and severe sand burial. The indigenous dune grasses *Thinopyrum distichum* and *Ehrharta villosa* appear to cope better in the harsh conditions of the South African dunes. None of the three grasses develop shoots easily from severed rhizome pieces, but experimental conditions were unfavourable, and the spread of *A. arenaria* via rhizome fragments transported by the sea cannot be excluded.

From the results presented in this thesis it is evident that *A. arenaria* is not invasive in South Africa and unlikely to become an invasive species in the near future. Its impact on Cape coastal ecosystems is too small to suggest its abolition from dune stabilisation practices. It is, however, advisable to exercise more caution regarding the use of *A. arenaria* in South Africa. Long-term effects of *A. arenaria* cannot be predicted and examples of its detrimental impact in other continents are too plentiful to be ignored. The practice of artificial dune stabilisation in itself is a highly questionable interference in the natural dynamics of the coastal ecosystem and should only be carried out once the need therefore has been determined through careful study.

However, South African dunes are severely threatened by human expansion, and in the long run, the stabilisation of many dunes will be unavoidable. For this, the planting of *A. arenaria* appears to be still the best available method, if done in combination with the sowing of indigenous plant seed and in consideration of local sediment movements and tides. Although indigenous dune plants appear to have many qualities which put them at an advantage over *A. arenaria*, especially with regard to climatic factors, they are not as tolerant to sand burial as *A. arenaria* is and do not bind sand as effectively. However, more research is required to assess specific sand fixation capabilities of indigenous dune plant species.

This thesis is the first study on the biology of *A. arenaria* in South Africa and its impact on Cape coastal ecosystems. More research is required to confirm the above results and complement the information gained so far. Research areas such as the demography of South African *A. arenaria* populations or the possible interactions of *A. arenaria* with soil-borne pathogens in Cape dunes have only received preliminary analyses in this work. Nothing as yet is known about the population genetics of the species in South Africa. Building on the information gathered in the present work, these themes will be focused on in future research in the course of the international INVASS programme.

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