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The role of European marram grass in dune stabilization and succession near Cape Agulhas, South Africa

Lubke, R.A.[1*] **& Hertling, U.M.**[1,2]

[1]*Department of Botany, Rhodes University, 6140 Grahamstown, South Africa;*
[2]*Present address: Urban & Fischer Verlag, P. O. Box 100537, D-07705 Jena, Germany;*
E-mail u.hertling@urbanfischer.de; [*]*Corresponding author; E-mail borl@rhobot.ru.ac.za*

Abstract. The coastline near the southern tip of Africa is characterized by large mobile dunes that are driven along wide beaches by strong winds throughout the year. This results in the blockage of the river mouths causing severe flooding of the low-lying farmland of the Agulhas Plain during the rainy winter season. Large parts of the driftsands were stabilized with the European dune pioneer species Marram grass (*Ammophila arenaria*), which has proved highly invasive along the North American west coast. In order to establish the potential invasiveness of *A. arenaria* in South African coastal dune systems and its role in the succession of a large stabilization area, studies were carried out on De Mond Nature Reserve. Using aerial photos, maps and planting records, the vegetation of sites of various ages were sampled. By means of this chronosequence of stands, there is clear evidence that succession takes place at De Mond. Four communities are distinguished, varying from recent plantings of *A. arenaria* to mature dune thicket or dune fynbos (heath) vegetation. These relate to four different stages of succession, *A. arenaria* occurring in reduced abundance in the older communities. After 50 years, former *A. arenaria* areas are usually covered by dense dune scrub and in some places even in asteraceous dune fynbos. Succession is most rapid in sheltered, moist dune slacks, but *A. arenaria* remains vigorous in conditions favourable for its growth, i.e. on exposed, steep dune slopes with strong sand movement. *A. arenaria* does not appear to spread unaidedly at De Mond and has been successfully used for temporary dune stabilization.

Keywords: Biological invasion; Chronosequence; De Mond Nature Reserve; Driftsand; Dune stabilization; Fynbos: Succession.

Nomenclature: Arnold & de Wet (1993).

Introduction

Near the southern tip of Africa, Cape Agulhas, the early European settlers encountered vast, mobile dune fields, coastal fynbos, extensive flood plains fringed with salt marsh and flat fertile plains where they could graze their livestock and grow crops. Along this coastline, strong winds drive the mobile dunes along wide beaches resulting in the blockage of the river mouths. This leads to extensive flooding of the low-lying farmland during the rainy winter season. In the 1870s Marram grass (*Ammophila arenaria*) was introduced to South Africa for the purpose of artificial dune stabilization (Heywood 1894). Since the 1930s large parts of the coastline of the Agulhas Plain have been stabilized with *A. arenaria* to fix driftsands and prevent the further blockage of the river mouths.

A. arenaria has proved to be a highly invasive species along the North American west coast (Wiedemann & Pickart 1996). Research on the potential invasiveness of *A. arenaria* in South African coastal dune systems was initiated in 1995 (Lubke & Hertling 1995; Hertling 1997; Hertling & Lubke 1999a). To examine long-term changes in large stabilization areas involving *A. arenaria* and determine the succession in such initially monospecific *A. arenaria* stands, studies were carried out in a stabilization area in the vicinity of the mouth of the Heuningnes River. The mouth is part of the De Mond Nature Reserve, situated on the coast of the Agulhas Plain near Bredasdorp, and surrounded by extensive dune fields to the northwest and southeast (Fig. 1). The vegetation at De Mond has been described to some extent by Walsh (1968) and Bickerton (1984), but no account as yet has been given on succession in the De Mond dunes since they were stabilized. This study aims at establishing whether the extensive *A. arenaria* stands at De Mond have been replaced by indigenous plants or whether *A. arenaria* has spread and invaded the fynbos hinterland of the reserve.

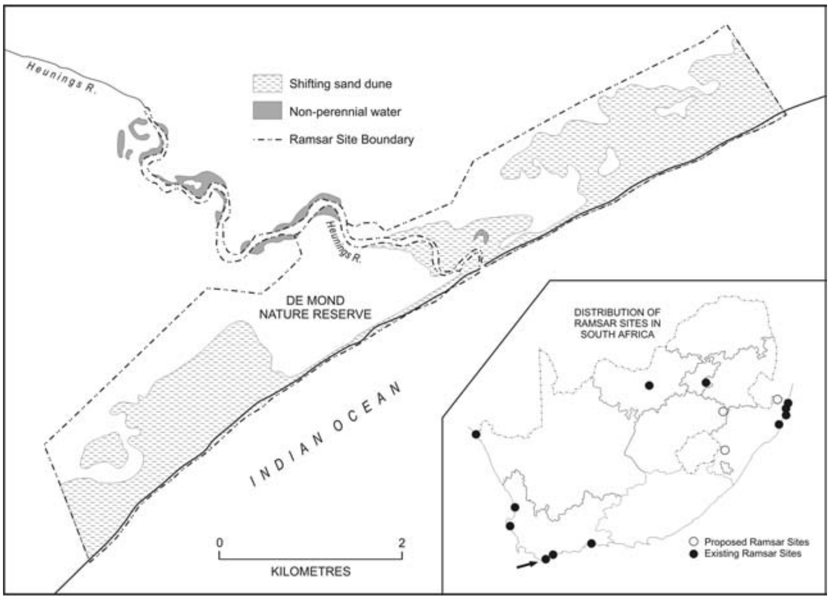


Fig. 1. Situation of the Heuningnes River mouth in the De Mond Nature Reserve, and distribution of other important Ramsar sites in South Africa (Cowan & Marneweck 1996).

Study area

Physiography, climate and vegetation

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. 1). The estuary is the southernmost of the African continent, not more than 15 km north of Cape Agulhas, and was designated in 1986 at the Ramsar Convention as a Wetland of International Importance (Cowan & Marneweck 1996). The lower reaches of the estuary fall within the De Mond Nature Reserve (1768 ha). From 1939 onwards the Minister of Agriculture and Forestry started buying land around the Heuningnes estuary with the intention of stabilizing the driftsands (Bickerton 1984). The area was managed by the Department of Forestry until Cape Nature Conservation took over coastal state forestry lands in the mid-1980s.

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 summers. 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. It is especially the high-velocity southeasterly winds during summer that cause shifting of the then dry and hot dune sands. 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).

A recently published field guide describes the vegetation and plant species of the region (southern Overberg), and interestingly, no mention of *A. arenaria* is made (Mustart et al. 1997). The vegetation of the reserve consists of coastal strand vegetation along the shore line, dune scrub and dune asteraceous fynbos with thicket patches (Mustart et al. 1997). Fynbos is the characteristic heath vegetation of the Cape floral region which is identified by sclerophyllous or ericoid shrubs and plant species of the *Proteaceae*, *Ericaceae*, *Restionaceae* (Cape reeds) and many endemic species and genera. The coastal fynbos types are particularly diverse in this region and protected in a number of reserves. The vegetation inland of the reserve is mostly coastal scrub or coastal fynbos or a mix of both if it is not under cultivation for wheat lands or grazing pastures.

The coastal strand vegetation (Mustart et al. 1997) consists of hummock dunes and linear dune ridges colonized by indigenous grass pioneers, *Ehrharta villosa* and *Elymus distichus*. Hummock forming asteraceous herbs include *Arctotheca populifolia* and *Didelta carnosa*. Other herbs in this fore-dune zone are *Chironia baccifera, Dasispermum suffruticosum, Senecio elegans*, *Hebenstretia cordata* and *Thesium fragile*. The succulent *Tetragonia decumbens* forms large hummock dunes and the succulent creeper *Carpobrotus acinaciformis* is common. In the scrub zone *Chrysanthemoides monilifera, Myrica cordifolia, Rhus crenata, Passerina rigida* and *Metalasia muricata* are common.

The dune asteraceous fynbos (Mustart et al. 1997) is dominant on inland sites with patches of dune thicket in

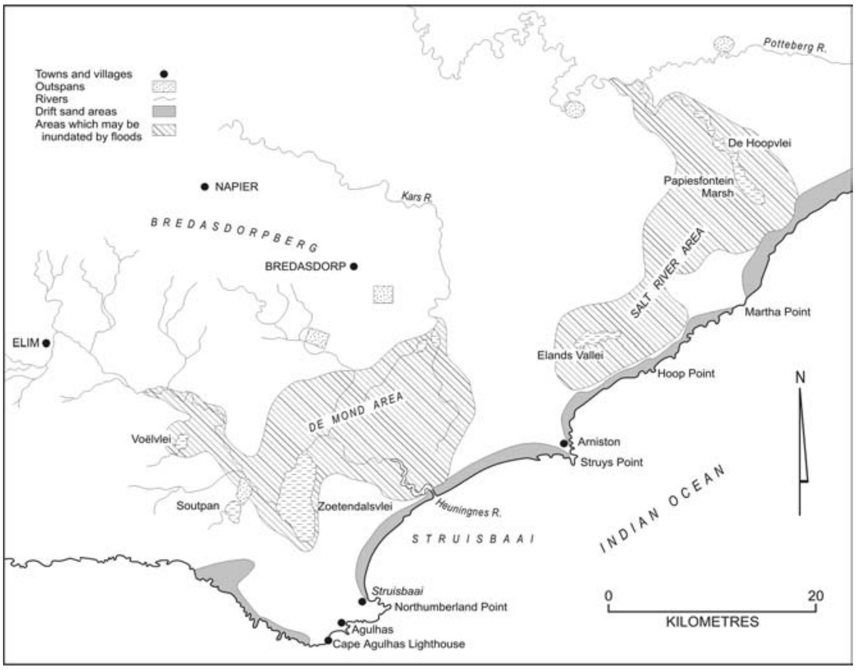


Fig. 2. Estuaries of the Heuningnes River and Salt River on the Agulhas plain, and areas that are exposed to their flooding. After the 'Divisional map of Bredasdorp 1901' (Cape Nature Conservation, De Hoop).

nutrient-rich sites. The asteraceous shrubs have ericoid leaves and include *Metalasia muricata*, *Helichrysum* spp. and *Stoebe plumosa*. Other ericoids include *Agathosma collina*, *Muraltia satureoides* and *Passerina ericoides*; *Pelargonium* spp. and *Salvia africana-lutea* are other common dune fynbos shrubs. The restioids (Cape reeds, which replace grasses in this fynbos or heath-like vegetation) include *Ischyrolepis eleocharis* and *Chondropetalum microcarpum.* Many geophytes, common Cape bulbous species, are also found in dune fynbos.

Thicket patches are characterized by shrubs of *Rhus glauca*, *R. crenata*, *Euclea racemosa*, *Olea exasparata*, *Cassine maritima*, *Maytenus procumbens* and vines and climbers such as *Cynanchum obtusifolium*, *Solanum quadrangulare* and *Asparagus asparagoides.* In some patches small trees of *Sideroxylon inerme*, *Pterocelastrus tricuspidatus* and *Tarchonanthus camphoratus* may be found.

History of the area

In the past, driftsands used to block the mouth of the Heuningnes River in summer, when sand movement is highest and the flow of the river low. This would cause extensive 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 twentieth century "a rise of 20 feet in water level at the river mouth would cause flooding of about 90 square miles of inland farms" (Walsh 1968). Fig. 2 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. Because of the known invasibility of alien *Acacia* spp. they requested that these plants not be used in the dune stabilization (Hertling 1997). From the late 1930s the stabilization of driftsands at De Mond with *A. arenaria* has been continued until present times. Between 1942 and 1958 alone a total of 283 ha were stabilized (Walsh 1968), today (1996) the stabilized area extends over some 900 ha.

Stabilization techniques at De Mond Nature Reserve

Since the first efforts in the 1930s until the present day, the same stabilization technique has been applied at De Mond with only slight variations. In view of other stabilization practices of the time, particularly the planting of invasive Australian acacias in many other areas, this method was very advanced for the 1930s: between the planted clumps of *A. arenaria* (Fig. 3), 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

Fig. 3. Government Forester Hendrik O. Swart among fresh *A. arenaria* plantings at De Mond in the mid-1980s (courtesy of Cape Nature Conservation, De Hoop).

created in the stabilization 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*.

Fig. 4 illustrates the stabilization efforts at De Mond in the 1930s and 1940s The foredunes were stabilized with *A. arenaria* in three continuous rows between 1940 and 1944, while the stabilization of the larger and more inland part of the dune field is patchier and focuses mostly on the more exposed areas of higher elevation. It is noteworthy that the indigenous dune grass species *Elymus distichus* 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.

Aerial photographs from 1938 and 1981 (Fig. 5) show clearly the change from completely mobile driftsands (Fig. 5A) to densely vegetated dunes on either side of the now open river mouth (Fig. 5B). The positions of the plantings of dune stabilizing species in Fig. 4 can be related to the aerial photos (Fig. 5). The opening of the river mouth is, according to Bickerton (1984), primarily due to an artificial littoral dune being established between the estuary and the sea (Fig. 4). 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. The asteraceous indigenous pioneers of the foredunes, *Didelta carnosa* and *Arctotheca populifolia* as well as the grasses *Elymus distichus* and *Ehrharta villosa* (more common in rear dunes at this site) are unable to stabilize the sands at the mouth of the river due to excessive sand movement. The large scale stabilization of driftsands in the vicinity of the river mouth is preventing any further blockage of the mouth, but it is the artificial littoral dune to the front of the mouth which keeps it open in the first place. It must therefore be constantly maintained using brushwood and *A. arenaria* plantings.

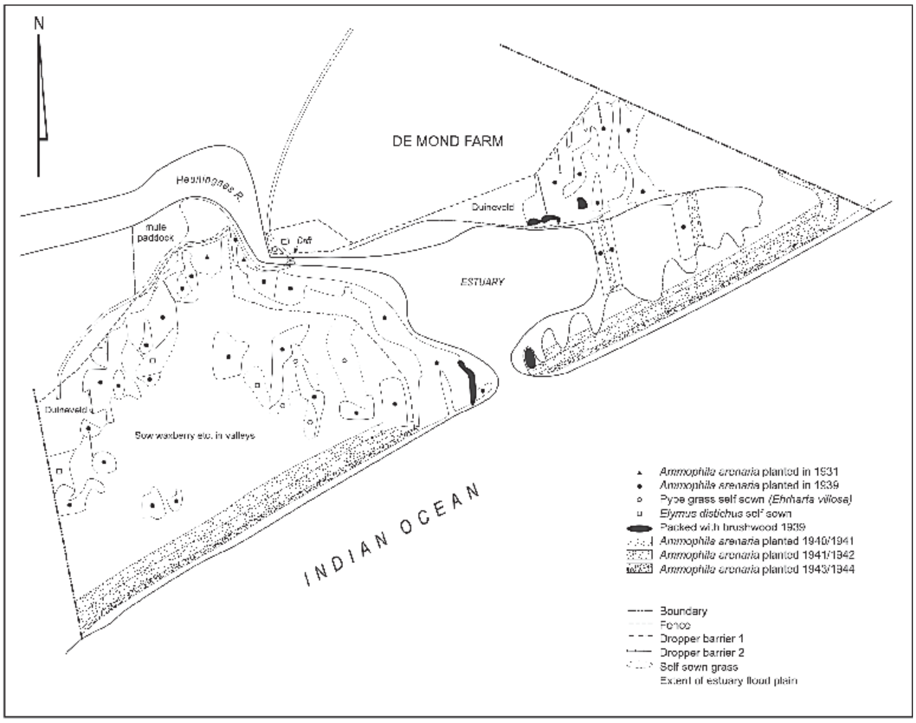
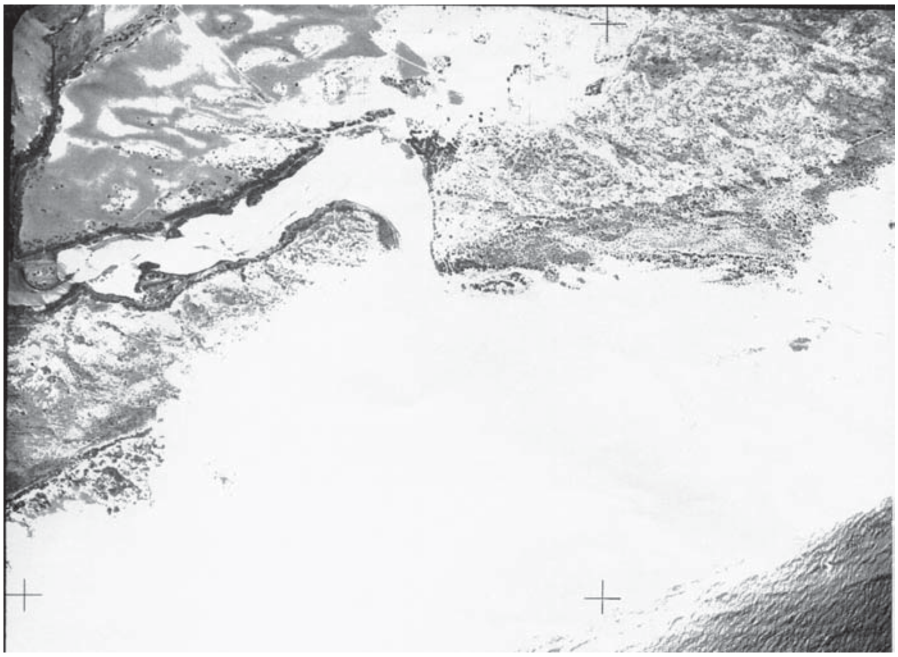


Fig. 4. Stabilization efforts at De Mond Nature Reserve (then De Mond State Forest) in the 1930s and 1940s. After the 'Stock map of De Mond Forest Reserve 1940' by J. De Genis (Cape Nature Conservation, De Hoop).

A



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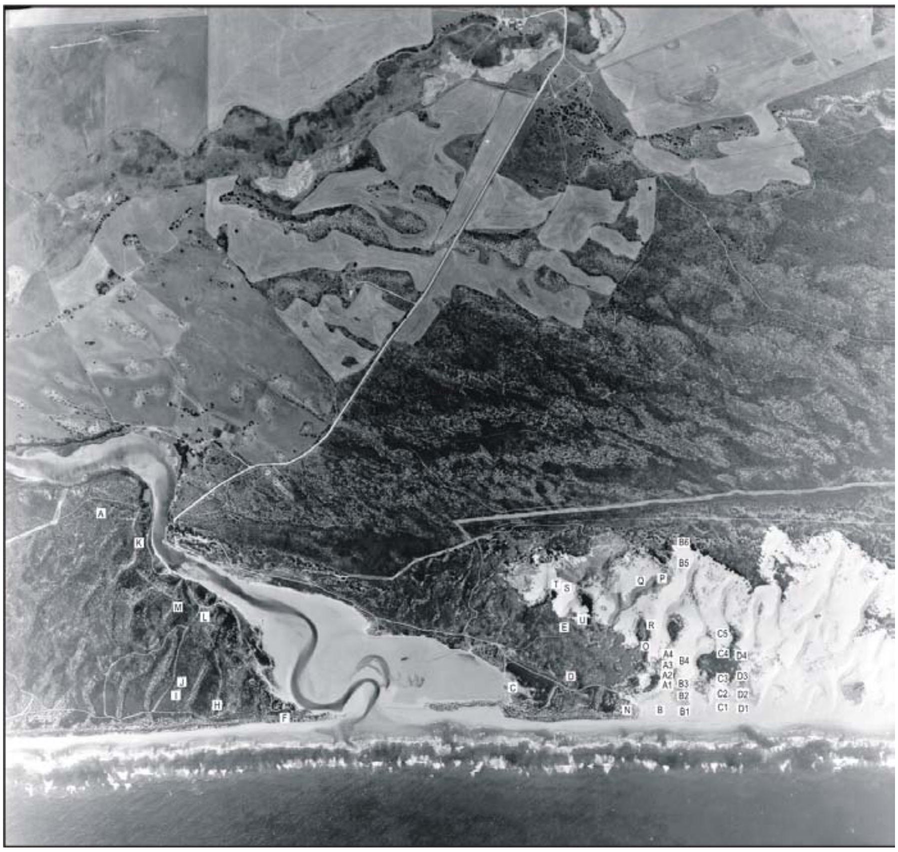


Fig. 5. Aerial photographs of the De Mond Estuary and Nature Reserve from 1938 (A: bare driftsands, river mouth blocked) and 1981 (B: a large proportion of the mobile sands has been stabilised, the river mouth is open). The letters and numbers marked on Fig. 5B are the sample sites and transects for this study.

Methods

Sampling

Sampling was carried out in February and June 1996, some 65 years since the original planting of A. arenaria in the region. Vegetation and soil were sampled in 42 stands of 10 m × 10 m throughout the reserve. Within each of the 100-m^2 stands, 20 1-m^2 quadrats were placed according to random numbers (Avis 1995; Avis & Lubke 1996). For each plant species the percentage aerial cover was estimated and the number of individuals counted (number of culms or shoots) in order to establish cover, density and frequency of each species. The data were then used to determine species richness and species diversity for each stand as well as importance values of species for each stand (Brower et al. 1990). Soil samples were tested for pH, organic matter content (% of dry weight) and conductivity (mS cm^{-1}) according to standard methods (Brower et al. 1990).

We laid out 23 stands (A, B, C, D, ..., W) 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 dune summits as well as at the edge of the salt marsh (Fig. 5B). Another 19 stands were laid out along four transects (A1 to A4, B1 to B6, C1 to C5, D1 to D4) perpendicular to the coastline, about 1330 to 2000 m to the northeast of the mouth of the Heuningnes River, extending from 52 m to 850 m from the high-water mark. According to old planting records and aerial photos, the stabilization times of all stands are known. They are situated in patches that were stabilized in 1931, 1939, between 1942 and 1961, between 1962 and 1973, between 1974 and 1981, between 1982 and 1989, and in the 1990s. 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 1-m^2 stands for density, cover and frequency of each species.

Data analysis

All 42 stands 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 classification and ordination techniques TWINSPAN (Hill 1979) and CANOCO (ter Braak 1988). The data used in both programmes were importance values of species for each stand. In an indirect gradient analysis the ordination of stands was then interpreted with the environmental variables soil pH, soil conductivity, organic matter content of soil, time of stabilization 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 1990s; 9 = never stabilized.

As to the topographical situation of the stands the ordinal data were ranked from 1 to 6:

1 = within 150 m from the 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).

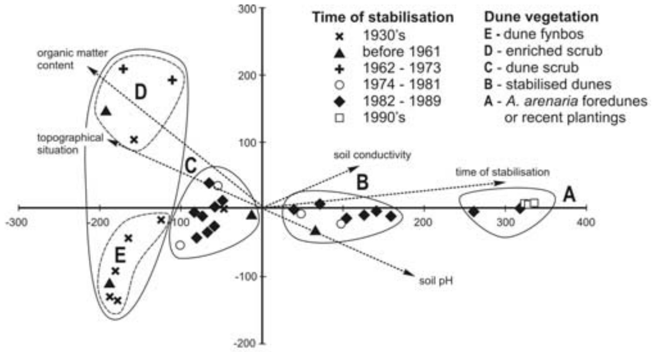
Results

Evidence of succession

Evidence of succession was reflected by Detrended Correspondence Analysis (DCA) of all 42 stands. The stands were split into six distinct communities, as identified by TWINSPAN, namely *A. arenaria* foredunes or recent plantings, stable dunes with some foredune elements, dune scrub, dune scrub/dune fynbos, saltmarsh and indigenous foredunes. While the first four communities were lined along a gradient representing sequential successional stages, the communities 'saltmarsh' and 'indigenous foredunes' cannot be placed within this line. A second DCA was therefore carried out without these stands (Fig. 6). The four remaining communities can be distinguished more clearly, and it is possible to attribute their times of stabilization to them. Stands of the early stage of foredunes dominated by *A. arenaria* were all stabilized in the 1980s and 1990s (3 - 10 yr old). Stands of the more stable dunes with only few foredune elements were mostly stabilized in the 1980s (6 - 20 yr old). Dune scrub stands were stabilized in the 1980s or earlier, in the 1960s and 1970s or even in 1939 (mostly 13 - 35 yr). The last community contains stands of an advanced dune vegetation, leading either to a species-rich scrub vegetation, or to dune fynbos. These were stabilized in 1931, 1939 or in the 1950s and 1960s (mostly 22 - 60 yr).

Vigour of A. arenaria related to age of the stabilized area and dune form

More information about the pace of the replacement of *A. arenaria* at De Mond is given in Fig. 7. The vigour of *A. arenaria* in all sampled stands was grouped into six categories and plotted along an axis of the stands in



Dune fynbos / enriched dune scrub				
E. dune fynbos 22 - 60 years	**D.** *enriched scrub* 35 - 60 years	**C.** dune scrub 13 - 35 years	**B.** stabilised dunes 6 - 20 years	**A.** *A. arenaria* foredunes or recent plantings 3 - 10 years
Ischyrolepis eleocharis *Thamnochotus insignis* *Phylica ericoides* *Euclea racemosa* *Agathosma collina* *Passerina paleacea* *Rhus glauca* *Helichrysum dasyanthum* *Felicia zeyheri*	*Rhus crenata* *Rhus laevigata* *Myrica quercifolia* *Knowltonia capensis* *Chasmanthe aethiopica*	*Myrica cordifolia* *Metalasia muricata* *Ficinia lateralis* *Passerina rigida* *Helichysum patulum* *Pentaschistis eriostoma* *Nylandtia spinosa* *Otholobium bracteolatum* *Ehrharta villosa*	*Psoralea repens* *Chironia baccifera* *Dasispermum suffruticosum* *Ammophila arenaria* *Helchysum praecinctum* *Trachyandra divaricata* *Sutherlandia frutescens*	*Ammophila arenaria* *Elymus distichus* *Arctotheca populifolia* *Didelta carnosa* *Senecio elegans*

Fig. 6. DCA of all De Mond stands (except saltmarsh and indigenous foredunes) results in the clear differentiation of successional stages at De Mond Nature Reserve. The important characteristic species are listed for the related communities. The ordination axes were also related indirectly to five environmental variables. The four stages relate well to the stabilisation times of respective stands. See Table 1 for corresponding regression coefficients.

chronological order. It is obvious that *A. arenaria* is more vigorous in sites of a younger stabilization time. Most stands that were stabilized between the 1930s and 1970s carry few, thin culms or some clumps of *A. arenaria* (categories 1 and 2), while stands from the 1980s and 1990s contain vigorous, strong and often dominant *A. arenaria*. The unexpected high or low vigour of *A. arenaria* in some stands, e.g. stands N and Q, can be explained with very exposed dune summit (Fig. 8A) or very sheltered dune slack locations respectively (Fig. 8B). Stand N was stabilized before 1961, yet *A. arenaria* is the dominant plant, if mostly medium-aged. The stand is situated on top of a transverse dune in relative closeness to the beach and thus exposed to strong winds as well as frequent sand burial. Stand Q, on the other hand, was only stabilized in the 1980s, yet no *A. arenaria* is left today. 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 easily be established.

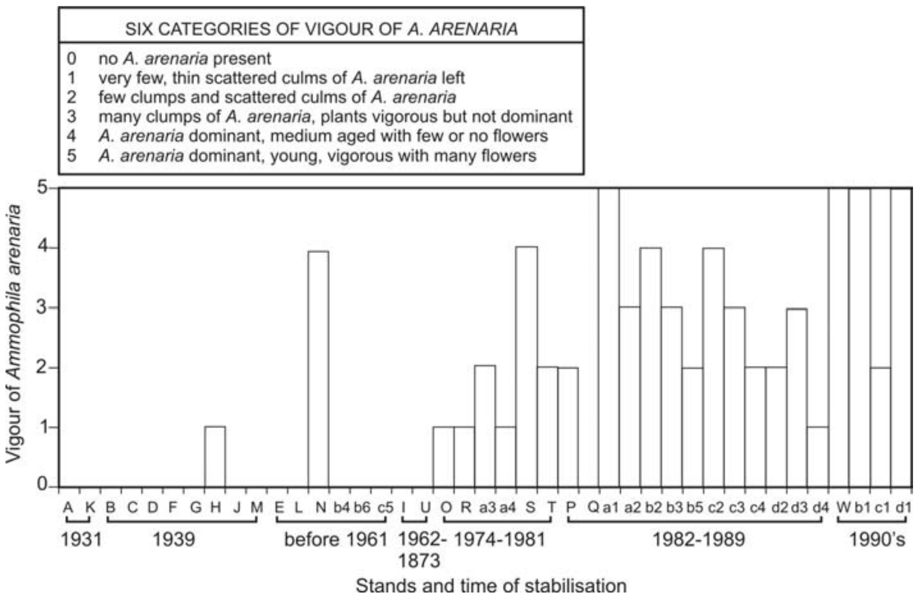


Fig. 7. Vigour of *Ammophila arenaria* in all De Mond stands (in chronological order, excluding stand V) according to six categories from 0 (no *A. arenaria*) to 5 (very vigorous).

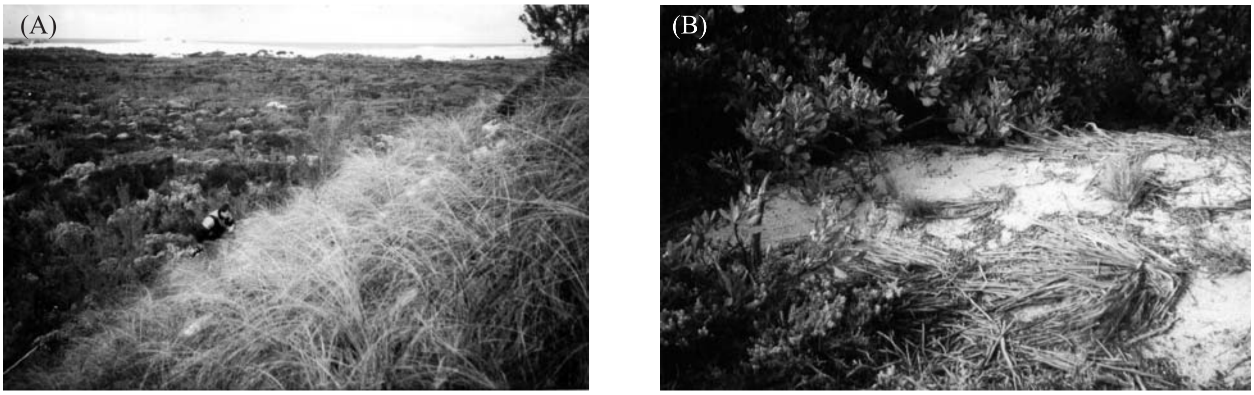


Fig. 8. A. Medium-aged but dominant *A. arenaria* (Vigour category 4) on a steep dune slope, in the background enriched dune scrub/ fynbos. **B.** Dead culms of *A. arenaria* (Vigour category 2) covering the ground of a sheltered and moist dune slack.

Vegetation of the different successional stages

A typical toposequence of the vegetation at De Mond is reflected in Fig. 9 along a 150-m transect (transect A, Fig. 5B) perpendicular to the coastline. 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 *Elymus distichus* on the fore dunes. *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, *Metalasia muricata* and *Chrysanthemoides monilifera* appear only sporadically, while *Myrica cordifolia* is very common, occurring vigorously especially in the back parts of the transect. The restio *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. Fynbos elements found along other transects are *Thamnochortus insignis*, *Euclea racemosa, Ficinia ramosissima* and *Phylica ericoides*. These species are the characteristic or diagnostic species of the various communities identified by TWINSPAN and are listed in Fig. 6.

Edaphic and other environmental factors

To examine the influence of edaphic soil factors (pH, conductivity and organic matter content), of the time of stabilization and of the topographical situation per stand on the differentiation of De Mond stands in CANOCO, the ordination axes of the original plot were subsequently related to these five variables (Fig. 6). The environmental variables correspond particularly well to the ordination axis 1, along which a succession was detected: the more recent stands were stabilized (variable 'time of stabilization'), 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 characterized 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 1), 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 stand ordination. This is confirmed by their low regression coefficients (Table 1). The strongest influence on the ordination of De Mond stands is shown by their stabilization 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 1. 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. 10 for the plot. Significance at a = 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 *
Stabilization time	+ 907*	+ 161
Topographical situation	– 627*	+ 118

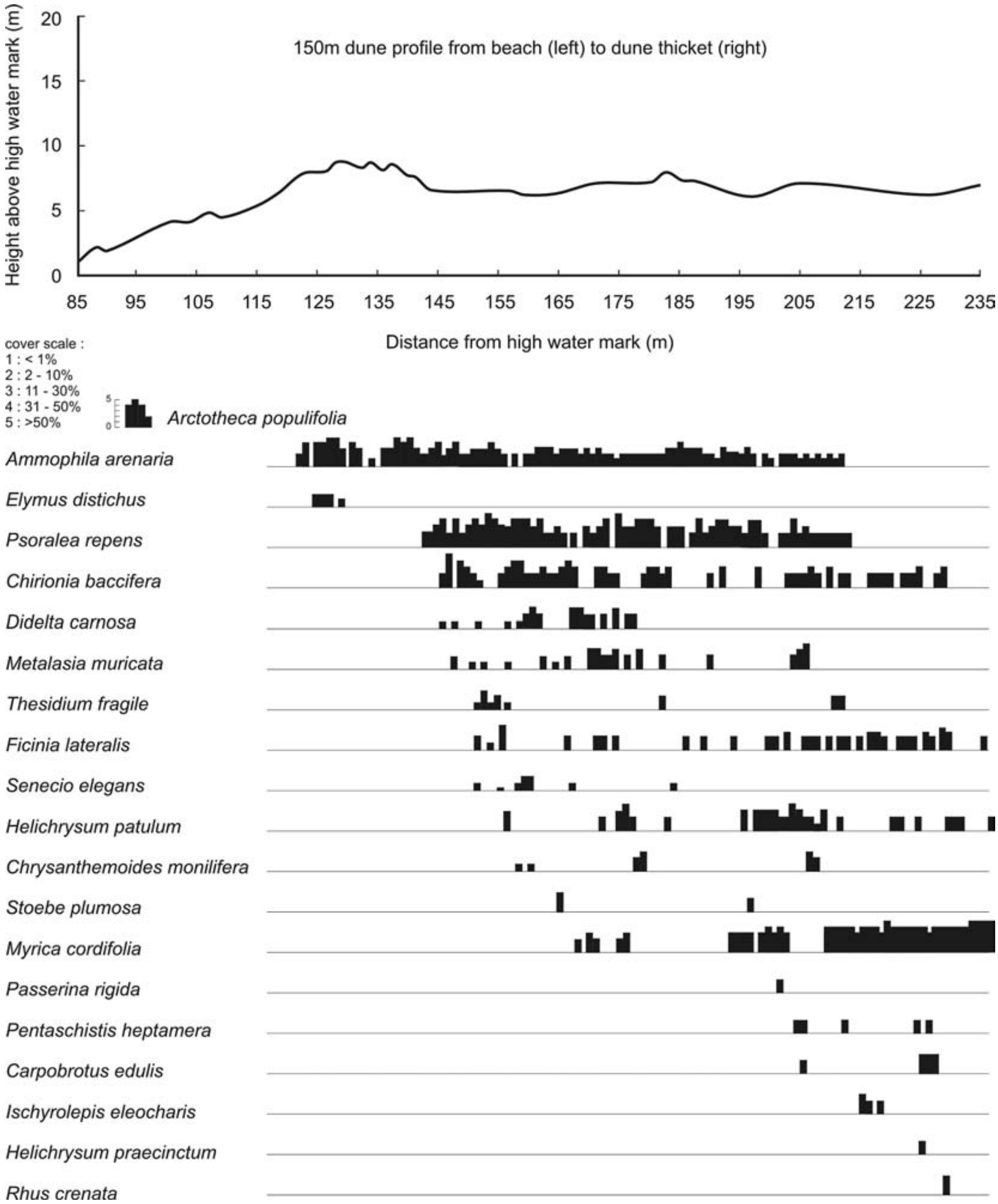


Fig. 9. Profile of a 150-m dune transect (A in Fig. 5B) at De Mond Nature Reserve with values of species cover for every m.

Discussion

Succession at De Mond

The results of the vegetation analysis at De Mond Nature Reserve prove that succession is taking place in this large-scale stabilization site. Monospecific *A. arenaria* stands can be transformed into dense dune scrub/dune fynbos within 50 - 60 yr. Six communities were identified at De Mond: (1) young, vigorous *Ammophila arenaria* communities on foredunes or as recent plantings further inland, (2) mixed *Ammophila arenaria* communities on stabilized dunes, (3) dune scrub, (4) dune scrub with fynbos elements, (5) saltmarsh and (6) indigenous foredunes. The first four stages show an increase of species richness and species diversity and can be lined up along a successional gradient related to a chronosequence (Fig. 6). Most areas at De Mond that were stabilized in the 1930s and 1940s are today vegetated by a dense, species-rich dune scrub with many elements of area-specific fynbos. Stands that were stabilized from the 1950s to 1970s are mostly vegetated by dense dune scrub. More recently stabilized stands are often still dominated by *A. arenaria*.

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 (Fig. 9). *Psoralea repens* and *Chironia baccifera* are common species among stands of *A. arenaria*, while *Ficinia lateralis* 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 stabilization sites at De Mond. The succession of the species in the identified communities does not relate as clearly to a toposequence as do other successional gradients in South African dune fields, for example at Mtunzini in KwaZulu-Natal (see below, Avis 1992).

Location of stands on dunes and rate of succession

Even stands that were stabilized only in the 1980s 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 stabilization date can bear persistently vigorous *A. arenaria* populations if they are situated on exposed dune slopes and therefore characterized by a greater 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 (Figs. 7 and 8). The interpretation of the ordination of all De Mond stands with environmental factors confirms that, beside the time of stabilization, the topographical position of the stands has the strongest influence on their vegetation (Fig. 6).

A comparison with succession of A. arenaria stands in Europe

An analysis of the colonization of a British stabilization site at Braunton Burrows, North Devon, involving *A. arenaria* confirms the De Mond 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, the grass was observed to grow vigorously at a distance of up to 2 km inland in areas of active driftsands and around blowouts caused by human or animal trampling (Hertling 1997; Knevel 2001). The niche advantage that moist, sheltered dune slack locations offer colonizing species in *A. arenaria* stabilization 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, such as the waxberry *Myrica cordifolia*, in the De Mond stabilization area was carried out preferentially in moist dune valleys, in which similar initial spots of successor species were developed. The colonization of *A. arenaria* dunes at De Mond has possibly proceeded out of these dune slack locations.

Along transects perpendicular to the sea, *A. arenaria* occurs generally further back than is observed in other situations on the Cape Coast (Hertling 1997; Hertling & Lubke 1999b). Due to the recent origin of the vegetated De Mond dunes, the greater part of a 235-m transect sampled from the high water mark is covered with *A. arenaria* (Fig. 9). This is similar to the situation in Europe where *A. arenaria* covers vast areas of the yellow dune, for example, at Braunton Burrows (Willis et al. 1959) and on the North-Sea coastline at Meijendel in The Netherlands (Lubke pers. obs.). More often on the Cape coast where *A. arenaria* has been planted, it forms a 50 - 100 m maximum belt along the foredunes (Hertling & Lubke 1999b).

Studies on the vegetation of European coastal foredunes show that soil-borne diseases, especially nematode parasites, are closely linked to the succession of species on the dunes. The root zones of sequential foredune plant species contain nematode species that are specific for their host and pre-successional plant species, but affect the next species in the succession to a much lesser extent (van der Putten et al. 1993). The potential importance of these pathogens in the successional process has not been overlooked in this study and both field trials and growth studies have been carried out in the South African situation (Hertling 1997; Knevel 2001). *A. arenaria* was introduced as seed to South Africa (Heywood 1984) presumably without the nematode parasites, and those now found on the roots of *A. arenaria* have possibly come from other grasses such as *Ehrharta villosa* which shared ca. 36% of the approximately 12 species of nematodes found in five dune pioneer species. The impact of these pathogens, which exclude endoparasites, have been analysed from a growth experiment (Knevel 2001).

A comparison with succession of vegetation in other South African dune fields

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 KwaZulu-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 (bush clumps, 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. 8). In both studies, the increase in α-diversity of the communities is therefore correlated with an increase in their β-diversity.

The mosaic of dune thicket (enriched dune scrub) and dune fynbos has been described by Cowling (1984) further to the east in the Humansdorp district and by Hoare (1994) in Goukamma Nature Reserve near Knysna. The shrubs and trees are favoured with the development of organically enriched soil patches in the dunes, whereas fynbos species are more commonly found in nutrient-poor soils (Cowling 1992).

Conclusions

The case study at De Mond Nature Reserve proves that succession of monospecific *A. arenaria* stabilization areas by indigenous dune plant species can take place in South Africa. Six communities were identified at De Mond, which relate to six successional stages and constitute a clear chronosequence. Areas at De Mond that were stabilized in the 1930s and 1940s are today vegetated by species-rich dune scrub or dune fynbos. Stands that were stabilized from the 1950s to 1970s are mostly vegetated by dune scrub. More recently stabilized stands are often still dominated by *A. arenaria*. However, even stands that were only stabilized in the 1980s can carry a diverse dune scrub vegetation, if they are situated in sheltered, moist dune slacks. On the other hand, sites of an early stabilization 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 and at sites of known planting dates confirms the transformation of vegetation from *A. arenaria* foredunes to dense dune scrub along both a spatial and temporal 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 stabilized and the more sheltered its location, the sooner indigenous dune plant species colonize the *A. arenaria* plantings and the faster the grass degenerates.

The De Mond Nature Reserve offers one of the most significant examples of succession in a stabilization area involving *A. arenaria* in South Africa. It appears as though *A. arenaria* has been successfully used at De Mond, providing temporary stability of dune sands until indigenous dune plants take over. On a smaller scale, the succession of *A. arenaria* by indigenous plant species has been observed at several other sites along the coast (Hertling 1997; Hertling & Lubke 1999b), such as Kleinkrantz near Wilderness (southern Cape) or in the Alexandria dune field near Port Elizabeth (eastern Cape).

By maintaining a continuous management programme using mainly *A. arenaria* the littoral foredune has kept the mouth of the Heunings River open throughout the year. This has resulted in a dynamic estuarine system with no further flooding to the interior Agulhas Plain since the 1940s. In contrast the Salt River now remains closed and forms the De Hoopvlei and Papiesfontein Marsh within the De Hoop Nature Reserve (Fig. 2), which is also an important Ramsar site.

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