5 Vegetation Dynamics and Succession on Sand Dunes of the Eastern Coasts of Africa

R.A. LUBKE

5.1 Introduction

Studies on dunes systems on the eastern coast of Africa (Fig. 5.1) have not been a priority but recent studies of the dynamics of dunes have been undertaken (Tinley 1985; Lubke et al. 1997), of particular interest being the large prograding dune systems on the KwaZulu Natal coast (Moll 1969; Pammenter 1983; Avis 1992) and the impressive transgressive dune fields of the Eastern Cape coast (Lubke 1983; Lubke and Avis 1988; Talbot and Bate 1991).

Some coastal systems have been disturbed by the invasion of alien species and their introduction (Shaughnessy 1980); their effects on the dune systems have been documented by Hertling (1997). The control of aliens (e.g. *Acacia cyclops* from Australia) is often essential as they disrupt ecosystems, but some species, (e.g.*Ammophila arenaria),* are potentially good stabilisers, not invasive and do not displace indigenous species (Hertling 1997; Lubke and Hertling 2001).

This chapter is a critical analysis of natural prograding and eroding dunes and mobile dune fields providing a baseline for successional change in dune systems, and the effects of aliens and predictions made regarding the changes on the dynamics of the dune systems are described. On the basis of this research suggestions are made regarding management of dune systems.

5.2 Successional Change Along the South-Eastern African Coast

Studies along this coastline (Fig. 5.1) have elucidated the successional changes and processes under different initial conditions and the effects of indigenous pioneer species as opposed to introduced alien plant invasion in the dune ecosystem.

> Ecological Studies, Vol. 171 M.L. Martínez, N.P. Psuty (Eds.) Coastal Dunes, Ecology and Conservation © Springer-Verlag Berlin Heidelberg 2004

Fig. 5.1. Map of the southeast African coastal regions

The coastal dune communities (Fig.5.2) are often quite distinct consisting of monospecific stands of pioneer plants. In other cases there may be a gradation from the pioneers into thickets so that the different communities are not that distinct. Piecing together the dynamics of successional change has taken place by analysis of the spatial relationships between the various communities and also through temporal studies of fixed plots over an extended time period.

5.2.1 Studies on Prograding Dune Fields

Along prograding coastlines there is a continuous supply of sand and new habitats are available for colonisation by pioneer species. The dunes at the Mlalazi Nature Reserve, at Mtunzini on the Kwa-Zulu/Natal coast (Fig. 5.1), provide an excellent example of succession on a prograding coastline (Fig. 5.2A). High summer rainfalls and supply of sand due to soil erosion from sugarcane fields into the Tugela River ensures a continuous deposition of

Fig. 5.2. Types of coastline and the coastal vegetation.**A** Thicket and/or forest are the climax vegetation on many prograding dune fields.**B** Community change on transgressive dune fields, which are often eroding, is not that obvious.**C** Coastal grasslands are climax vegetation types on rocky shores. **D** Coastal fynbos is climax vegetation on the south coast dunes, where alien species, e.g. *Acacia cyclops* and *Ammophila arenaria* are often present

sand and silt at the river mouth and by longshore drift northwards to the Mlalazi dunes. First well documented by Moll (1954), Weisser et al. (1982) related successional changes to the chronology of dune development using aerial photographs to date the parallel dune ridges of the region. They showed that dune advancement occurred in pulses with dune advancement from 1.2 m year⁻¹ (1937–1957) to 3.56 m year⁻¹ (1957–1965) to 5.67 m year⁻¹ (1965–1977) and in 1982/1983 a dune ridge would be formed about every five

Fig. 5.3. Profile diagrams of the three transects sampled across the Mtunzini dune field, showing position of sample sites in relation to topographical variation and community type recognised in the field, and the position of the eight dune ridges. The *x*-axis is both distance from the sea and age (inferred from Table 5.1). *P* Pioneer; *EP* enriched pioneer; *OS* open dune scrub; *CS* from Avis 1992)

years. The age of the dune ridges were estimated in this way for a study carried out in 1987 (Table 5.1). A quantitative study of this dune system was carried out by sampling 34 random relevés along three transects across the dune ridges (Fig. 5.3).

Seedlings of S*caevola plumieri* have been observed to establish on the drift line as a result of seeds rolling down from the first foredune covered with mature *Scaevola plumieri* plants. Knevel (2001) monitored seed production and establishment of *S. plumieri* over a 3-year period on different sites on similar dunes at Kleinemonde). Under high rainfall conditions seedlings rapidly establish and form hummock dunes, which coalesce to form parallel linear dune ridges. Other pioneers, such as *Ipomoea pes-caprae,* also occur but the continuous stem elongation and root production of *S. plumieri* are the important factors in sand stabilisation and foredune development. On the second dune ridge, there is an abundance of other herbaceous species, where grasses, herbs and some shrubs become established. *S. plumieri* is an accomplished pioneer when subjected to sand deposition and salt spray, but does not thrive on the second dune ridges (Pammenter 1983).

Eight communities were identified along a gradient of increasing distance from the sea and increasing age of the dunes: pioneer, enriched pioneer, open dune scrub, closed dune scrub, bush clumps, bush clump/forest margin transition, forest margin and forest (Fig. 5.4). Communities showed an increase in species richness, cover, stature and biomass.

Table 5.1. Rate of sand movement (from Weisser and Backer 1983), mean distance between dune ridges and approximate dune ages, when the study was carried out in 1987 on the Mtunzini dune field. (Avis 1992)

Dune ridge	Mean rate of sand Movement $(m \text{ year}^{-1})$	Mean distance from previous ridge(m)	Age (years) from previous ridge	Approximate accumulative age (years)
1	5.67	5	5	5
$\overline{2}$	5.67	39.3 ± 5.6	$39.5/5.67 = 6.9$	12
3	5.67	25.3 ± 5.5	$25.3/5.67=4.5$	17
$\overline{4}$	4.5	41.3 ± 5.8	$41.3/4.5=9.2$	26
5	2.4	30.7 ± 3.7	$30.7/2.4 = 12.8$	39
6	1.25	27.3 ± 1.76	$27.3/1.25 = 27.8$	61
7	1.25	$34.7 + 4.4$	$34.7/1.25 = 27.8$	89
8	1.25	39.3 ± 1.8	$39.3/1.25 = 31.4$	120

Fig. 5.4. Ordination of relevés of the Mtunzini dune field, showing the distribution of plant communities identified by TWINSPAN age of the communities estimated from aerial photographs. (Avis 1992)

As succession progresses, species diversity increases, but sometimes reaches a maximum value prior to the climax community, whereupon it decreases (Margalef 1968). Simpson Diversity Index (from density data) shows a sharp increase from pioneer to enriched pioneer communities, and remains fairly constant except for decreases in closed dune scrub and forest margin communities. This variability in the alpha diversity along the chronosequence supports Drury and Nisbet's (1973) statement that diversity is a result of microtopographic and other influences, and that it is not uniformly expressed in all parts of the community.

One would expect beta diversity to be highest and the coefficient of community (CC) lowest, for communities furthest apart, since they do not have many shared species (Table 5.2). The CC value decreases steadily as communities become more disjunct. The pioneer community has no similarity with forest margin and forest communities, with no shared species. Likewise, open dune scrub has a lower CC value with forest margins and forest than closed dune scrub, and values for the latter are lower than for bush clumps. The number of shared species decreases steadily from pioneer to forest communities suggesting that species turnover is very rapid along this 300-m successional gradient.

The edaphic factors also showed changes along the chronosequence, which are usually associated with successional changes in vegetation. Total organic

Community	Pioneer	Enriched pioneer	Open dune scrub	Closed dune scrub	Bush clump	Bush clump forest margin	Forest Forest margin	
Pioneer	8	0.695	0.516	0.139	0.093	0.045	Ω	$\mathbf{0}$
Enriched pioneer	8	15	0.666	0.526	0.320	0.235	0.122	0.076
Open dune scrub	7	13	24	0.765	0.508	0.333	0.103	0.065
Closed dune scrub	3	10	18	23	0.620	0.406	0.175	0.100
Bush clump	$\overline{2}$	8	15	18	35	0.732	0.579	0.500
B/Forest margin	\mathbf{I}	6	10	12	26	36	0.685	0.547
Forest margin	0	3	3	5	20	24	34	0.845
Forest	0	2	\overline{c}	$\overline{3}$	18	21	30	37

Table 5.2. Matrix showing the number of species shared by the eight communities (*italic*), the species richness in each community (*bold*) and the Sorenson's co-efficient of community (CC), in a study of succession on the Mtunizini dune field

matter increased (0.5–6.1 %) with community complexity and pH decreased (8.5–7.3). An increase in the exchangeable bases was also noted, and the substratum became more stable with increasing distance from the sea. Changes in the soil properties can be related to changes (increases) in community complexity and also represent an increase in total biomass of the more complex communities. Salisbury (1925) first showed that organic content of dune soils increased along progressive dune ridges, and that soil changes could be correlated with changes in the vegetation. He also noted a leaching of carbonates with increasing age, and a change in pH from alkaline to acid. Lubke (1983) and Lubke and Avis (1982) noted similar edaphic changes with dune community succession at Kleinemonde in the Eastern Cape.

The Mtunzini area was most suitable for a comparative study on plant succession, since the age of the dunes was determined and the communities related to a chronosequence. Similar results were found by Olson (1958) and Morrison and Yarranton (1973), but in both cases dunes were much older (thousands of years). The rate of succession at Mtunzini is rapid due to the high rainfall and rapid accretion of sand along this coastline (Table 5.1). The succession is probably along a single pathway, at least in the early stages when pioneer communities are very similar, as indicated by their relative distribution along the median of axis 2 of Fig. 5.4. The position of relevés from forest margin and forest groups on the outer edges of axis 2 suggests that multiple pathways may occur at this stage. A multiple pathway succession, with three trajectories from pioneer to woodland vegetation was described by van Dorp et al. (1985) in the Netherlands over a 10–15-year period. DCA of the vegetation data supported the hypothesis that this increase in community complexity is related to an increase in the age of dunes, and species with similar environmental requirements appeared to be grouped together along the chronosequence gradient (Fig. 5.4) rather than evenly distributed along a continuum.

5.2.2 Studies on Transgressive Dune Fields and Partially Eroding Coastlines

In other regions of the coast there is no distinct chronological sequence, since the coastline is not prograding uniformly and is often eroding (Fig. 5.2B).Avis and Lubke (1996) sampled relevés ranging from pioneer communities to closed dune thicket in a number of localities at Kleinemonde, east of Port Alfred. Results were similar to those obtained at Mtunzini, except that pioneer foredune communities are dominated by a number of pioneer species (see Fig. 5.6), whereas the dune thicket was dominated by a single tree, the coastal white milkwood, *Sideroxylon inerme.* Although not linearly positioned along a transect across the dune field, the various communities sampled were located along a gradient of increasing community complexity (Avis and

Fig. 5.5. The percentage cover of the major plant species groups over 20 years in a dune slack at Kleinemonde, Eastern Cape. (Lubke and Avis 2001)

Lubke 1996). At Kleinemonde the foredunes provide indirect facilitation by protecting the more mesic dune slacks from factors such as salt spray and sand movement, whereas this facilitation is more direct on prograding systems such as Mtunzini.

Studies on the dune slacks, which act as centres of diversity within the mobile dune field, were carried out by establishing fixed plots, which were monitored over 5, 17 (Lubke and Avis 1988, 2000) and 20 years (Fig. 5.5). The dynamic changes in the dune slack community result from the movement of sands parallel to the coastline, from the west to the east, due to predominantly southeasterly or westerly winds in the region (Fig. 5.6).As transgressive dunes advance they bury the western side of the slack, while other pioneer species are colonising the eastern margins. Vegetation can establish in these slacks due to the high water table and the protection afforded by the foredunes. Our site was covered with numerous *Scirpus nodosus* seedlings in 1978: and other herbaceous species, such as *Vellereophyton vellereum* and *Chironia decumbens*, became abundant in the early stages (Lubke and Avis 1982, 1988), but were replaced by woody species after about four years (Fig. 5.5). This study is continuing and as yet larger trees, i.e. *Brachylaena discolor, Sideroxylon inerme,* etc. have not yet been recorded. It supports concepts presented in an

Fig. 5.6. Hypothetical model of dune succession at Kleinemonde. (Lubke and Avis 1988)

earlier model of succession for this region (Lubke and Avis 1988; Fig. 5.6). We have postulated that dune thicket communities (Fig. 5.2B) will not progress because rainfall in the eastern Cape is erratic with long drought periods. Sufficient rainfall for an extended period is crucial in the successional development of patches of thicket vegetation from dune slack vegetation into the transgressive and migratory dune field.

5.2.3 Studies on Rocky Shores and Eroding Coastlines

Along some of the southeast coast and Transkei coast (Fig. 5.1), there are rocky shores with wave-cut platforms and eroding cliffs (Fig. 5.2C). Above the rocky shores and cliffs coastal grassland is the climax vegetation. Detailed studies on these grasslands (Judd 2000) have revealed much information about the types of communities, but little about the origin of the grasslands. In some areas along these eroding shores bays and stretches of sandy dunes occur with prograding shorelines.Here,successional changes to forest or thicket are similar to that of the southeast coast. KwaZulu-Natal coastal grasslands are secondary in origin developing where thicket or forest was cleared for grazing or cultivation of crops (Weisser 1978; Lubke et al. 1991). Thus, these grasslands may also be secondary in these regions but this warrants further study.

5.3 Changes in Dune Succession Due to Invasive Aliens

Alien plant invasion has a large influence on the indigenous flora and plant communities of southern Africa (Shaughnessy 1980; Richardson et al. 1997).

5.3.1 The Effect of *Ammophila arenaria* **as a Dune Pioneer on the Southern Cape Coast**

Hertling and Lubke (1999a, 2000) and Lubke and Hertling (2001) studied the distribution of *Ammophila arenaria* (marram grass) communities and the dynamics of the system in various coastal dune systems, especially on the south coast (Fig. 5.1) where coastal fynbos is dominant (Fig. 5.2D). Marram grass becomes well established as a pioneer on foredunes in regions where the rainfall is high enough and consistent without lengthy drought periods. However, unlike other invader plants (see Sects. 5.3.2 and 5.3.3) it does not show traits of an outwardly aggressive behaviour in ecosystems. It forms dense stands and is able to tolerate burial like *Scaevola plumieri* as has been recorded by Maun and Lapierre(1984) in *A. breviligulata*, a similar species on the Lake Michigan dune shores. Although apparently excluding indigenous species, a quantitative assessment showed that the *A. arenaria* communities appear similar to those of indigenous dune plant communities with respect to species richness. Simpson's species diversity indices were, however, considerably lower (1.55±0.08 and 2.39±0.14 respectively), indicating a higher abundance of *A. arenaria* relative to other species in the marram stands. Although having a slight negative impact, *A. arenaria* does not show extreme dominance to the exclusion of other species, as it does on the North American Pacific coast (Weidemann and Pickart 1996).

Studies were carried out in a stabilisation area in the vicinity of the mouth of the Heuningnes River, at De Mond Nature Reserve, (Fig. 5.1) in the Southern Cape by Lubke and Hertling, (2001) in order to determine the succession from monospecific *Ammophila arenaria* stands. Stabilisation started in the late 1930s as the mouth was repeatedly blocked by drift sands in the winter, causing flooding of the Augulhas Plain. Between 1942 and 1958, 283 ha were stabilised and in 1996, when our study was undertaken, the stabilised area extended over 90 ha. Aerial photographs and a map showing dates of stabilisation were used to document the ages of the dune stabilisation and sampling was carried out in 20x1 m^2 quadrats in 42 stands which could be dated. Evidence for succession was detailed by Detrended Correspondence Analysis (DCA) of the stands, which were split into communities identified by TWINSPAN (Fig. 5.7). We found that stands stabilised in the 1980s now have a rich and dense dune scrub vegetation. This could be due to favourable

Dune fynbos / enriched dune scrub				
dune fynbos 22 - 60 years	D. enriched scrub 35 - 60 years	C. dune scrub $13 - 35$ years	в. stabilised dunes $6 - 20$ years	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 zevheri	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 Trachvandra divaricata Sutherlandia frutescens	Ammophila arenaria Elymus distichus Arctotheca populifolia Didelta carnosa Senecio elegans

Fig. 5.7. Detrended correspondence analysis of De Mond stands results in the 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 by canonical correspondence analysis. The four stages relate well to the stabilisation times of respective stands determined from a map of the stabilisation of the area. (Lubke and Hertling 2001)

habitat features such as a sheltered dune slack site with high organic matter and 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 characterised by greater sand movement, where *A. arenaria* profits from its superior sand burial tolerance. In sheltered dune slack locations, *A.arenaria* does not have this niche advantage and is replaced by other species, such as *Myrica cordifolia*, which was prevalent in these stands (e.g. community C, Fig. 5.7).

This study shows a significant example of succession involving *A. arenaria*, where the grass provides temporary stability of dune sands until indigenous dune plants take over. On a smaller scale, the succession from *A.arenaria* to indigenous plant species has been observed at other sites along the coast (Hertling 1997; Hertling and Lubke 1999b).

5.3.2 The Effect of Invasive Communities of *Acacia cyclops* **in the Southern and Eastern Cape**

Acacia cyclops and *A. saligna* from Australia, introduced to stabilise the sandy Cape Flats (Fig. 5.1), have invaded mobile dune fields along the southeastern coast (Richardson et al. 1997). These species have a high invasive potential (Hertling and Lubke 1999b) and in some cases, e.g. headland bypass systems, have resulted in stabilised mobile dune fields causing the lack of supply of sand to beaches in the bays upwind from the dune systems (Lubke 1985). Although not foredune pioneers, these woody species, being nodule-forming legumes, are extremely successful in low-nutrient sands and may fill a niche that is vacant on open dunes. The bird-dispersed seeds of *A. cyclops* have been carried inland into some grassland and thicket communities as well as northwards into the dunes along the Cape coast.

In South Africa, a Working for Water Programme (DWAF 2002) was introduced with the objective to remove alien invader species, thus increasing biodiversity of indigenous species, to supply more water to streams and reservoirs as the water-thirsty aliens are removed and to provide work and job security for the local people. Consequently, along some of the Eastern Cape Coast and at dune fields at Kleinemonde (Fig. 5.1) *Acacia cyclops* has been removed. Five 100-m2 permanent plots have been established and 20 random 1-m2 quadrats are sampled periodically to record the changes in plant diversity as indigenous species return following alien removal. These data have yet to be analysed but on open foredunes and on dune ridges the pioneers (e.g. *Scaevola plumieri* and *Ipomoea pes-caprae*) are rapidly returning, while in dune slacks some of the shrubs (e.g. *Passerina rigida)* have become established as seedlings and others (e.g. *Myrica cordifolia)* are expanding vegetatively into *A. cyclops* cleared areas. Seeds of *A. cyclops* were still found to occur in 63 % of the sample sites in a seed bank study of the dunes by Knevel (2001) so that a maintenance programme will be necessary to remove returning invading plants as they germinate.

5.3.3 The Introduction of *Casuarina equisetifolia* **as a Dune Stabiliser**

Along KwaZulu Natal, Mozambique and East African coasts, a commonly introduced tree is *Casuarina equisetifolia*, the Australian beefwood. These trees have been planted for shade on the hot tropical coasts and are able to grow in the pioneer and dune grassland zone very successfully (Lubke et al. 1991). However, in KwaZulu Natal, concern has been expressed as to their invasive potential, as they have spread in some areas where natural blowouts occur.

Avis (1992, 1995) made a study of the Department of Forestry records and sampled 17 sites where dune stabilisation had been carried out along the Eastern Cape coastline from 1965 to 1982.At this time, Forestry no longer uses the invasive woody species for dune stabilisation (Cobby 1988) but many invasive species persist.

At the Gulu River Mouth site, 20 km southwest of East London (Fig. 5.1), mobile sand from the dunes was thought to be responsible for silting up the river mouth, and to prevent further siltation it was decided to stabilise the dunes (Fig. 5.8). In 1975, over 6000 *Casuarina equisetifolia* trees were planted, due to its non-invasive and rapid growth rate. Indigenous shrubs such as *Rhus crenata* and *Passerina rigida,* together with pioneer species were either planted or seeded, and usually formed a number of distinct plant communities.

C. equisetifolia plantations are distinct from communities planted with indigenous vegetation, and have a species diversity of less than half that of the latter areas. Competitive exclusion results from their rapid growth rate, ability to rapidly utilise available nutrients, production of dense, fibrous roots covering several square metres of soil around each tree and copious leaf litter with an allelopathic effect on most other species. The only species able to survive was the herbaceous composite *Senecio litorosus*. Thus, despite being non-

Fig. 5.8. Map showing the vegetation of the Gulu West stabilisation sites. Note the patches of *Casuarina equisetifolia* with very low species diversity, compared with other indigenous communities. (Avis 1992, 1995)

invasive this alien species is not suitable for dune stabilisation as, unlike *Ammophila arenaria,* it persists and will need to be physically removed to enable indigenous species to become established (Avis 1995).

5.4 Discussion

5.4.1 Distinguishing the Mechanism of Succession with Indigenous Pioneers

The only sequential assessment of dune communities and dune vegetation dynamics along the southern African coastline is that of Tinley (1985). Later studies have looked at areas along the east coast of Africa more exactly (e.g. Frazier 1993). Studies of the communities along gradients of increasing age as in our studies at Mtunzini and over a temporal sequence at Kleinemonde are unique on the south-east African coastline. In studies on sand dune systems at Malindi (Fig. 5.1) in Kenya, Musila et al. (2001) record similar results to Mtunzini with different plant species but without age determination of the dune system. The change in species richness which they recorded across the dune field was from 2–5 species on young dunes to 40–60 species in mature communities, and thus compares to our Mtunzini results (Table 5.2 and Avis 1992).

The distinct separation of relevés into communities (Table 5.1) along a gradient of increasing age (Figs. 5.2, 5.3 and 5.4) suggests that these communities do not integrade continuously along the environmental gradients (Whittaker 1975). They appear to form distinct, clearly separated zones more in line with the "community concept" (Clements 1916). However, this does not prove that this concept applies to the vegetation sequence at Mtunzini, since one cannot prove the one hypothesis by rejecting the other (Shipley and Keddy 1987). The situation is even more confusing when one considers that at the scale of individual species turnover (Table 5.2), there is overlap with no sharp boundaries between species, suggesting that species turnover follows the individualistic hypothesis of Gleason (1926). However, Shipley and Keddy (1987) have shown that the individualistic concept is unfalsifiable at the level of pattern analysis, allowing one to favour the "community-unit concept". The ordination diagram (Fig. 5.4) suggests an organisational structure of the communities (*vide* Clements 1916), but changes at the species level (Avis 1992) suggest that the communities integrate continuously along this gradient (Whittaker 1975) in an individualistic manner (Gleason 1926). However, ordination methods cannot provide unequivocal evidence for the continuum concept (Austin 1985), but the low level of similarity between communities less than 100 m apart (Table 5.2) suggests that species only intergrade over short distances. Possibly,

as stated by Shipley and Keddy (1987), one needs to deny this dichotomy and to consider multiple working hypotheses of community structure.

Problems and shortfalls in successional theory led to the Connell & Slatyer (1977) models, and these support our Facilitation Model. There are also a number of other studies which support these models. Olson(1958) presented evidence for an autogenic succession on the Lake Michigan sand dunes, and he showed that two Connell and Slatyer models (mechanisms *vide* Picket et al. 1987) play a role in this succession.

5.4.2 Effects of Aliens and the Need for Dune Stabilisation

Many of the large-scale dune stabilisation programmes on this coastline have the primary objective of preventing sand movement which threatens human well-being. Often, therefore, the use of alien vegetation has been promoted both here and overseas (Weidemann and Pickart 1996) but potentially invasive species should not be used due to the threats they pose to adjoining ecosystems. Once the need for a stabilisation programme has been determined, the creation of functional, aesthetic ecosystems should be the primary objective of such programmes. Our studies show that indigenous species can be used successfully on our coastline (Lubke 1983) but the process is costly, time consuming and slow, often necessitating detailed studies to be undertaken prior to the initiation of a stabilisation programme and ongoing monitoring. If stabilisation is necessary under harsh, adverse conditions, *Ammophila arenaria* has been shown to be most suitable (Lubke and Hertling 2001).

5.4.3 Conservation of Biodiversity and Dune Ecosystems and Future Studies

Introduction or programmes such as the "Working for Water" clearance of aliens (DWAF 2002) have long-term goals of restoration of biodiversity and reestablishment of ecosystems. The effect of alien species on diversity in dune systems has been shown (Avis 1996) and removal of aliens at Kleinemonde has shown how diversity can increase. Our unique coastal systems (Fig. 5.2) need to be protected and fortunately many reserves are sited along coastal areas for recreational proposes. Studies on the use of indigenous species for dune stabilisation (Knevel 2001) have shown that these pioneers have the potential for dune stabilisation, but more studies on their application in the field is required for dune management.

Aspects in the dune successional process still need to be answered such as the role of the various species in facilitating the process, if in fact they do have a role. Ecophysical studies and the application of functional ecology principles need to be considered, requiring more studies on the life histories and the behaviour of the species. Finally, the explanation of the successional process of coastal grasslands along our rocky shores still needs to be studied in detail to show their relationship to the more widespread thicket climax communities on sandy shores.

Acknowledgements. I would like to thank my postgraduate students for the contribution they have made to our understanding of the dune systems through long hours in the field, laboratory and discussions on dune processes. The undergraduate students and others who also contributed in gathering data are also thanked. Finally, the Rhodes University is acknowledged for funding this research.

References

- Austin MP (1985) Continuum concept, ordination methods and niche theory. Aust Rev Ecol Syst 16: 39–61
- Avis AM (1992) Coastal dune ecology and management in the eastern Cape. Unpubl PhD Thesis, Rhodes Univ, Grahamstown
- Avis AM (1995) An evaluation of the vegetation developed after artificially stabilizing South African coastal dunes with indigenous species. J Coastal Conserv 1:41–50
- Avis AM, Lubke RA (1996) Dynamics and succession of coastal dune vegetation in the Eastern Cape, South Africa. Landscape Urban Plann 34:347–254
- Cobby JE (1988) The management of diverse ecological types of the Directorate of Forestry. In: Bruton MN, Gess FW (eds). Towards an environment plan for the Eastern Cape. Rhodes Univ, Grahamstown. pp 126–163
- Clements FE (1916) Plant succession. Carnegie Institute, Washington, DC, Publ 242
- Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. Am Nat 111:1119–1144
- Drury WH, Nisbet ICT (1973) Succession. J Arnold Arboretum 54:331–368
- DWAF Department of Water Affairs and Forestry (2002) http://www.dwaf.pwv.gov.za/ Projects/wfw/
- Frazier JG (1993) Dry coastal ecosystems of Kenya and Tanzania. In: van der Maarel E (ed) Dry coastal ecosystems – African, America, Asia and Oceania. Ecosystems of the world 2B. Elsevier Amsterdam, pp 129–150
- Gleason HA (1926) The individualistic concept of plant association. Ibid 53:7–26
- Hertling UM (1997) *Ammophila arenaria* (L.) Link. (marram grass) in South Africa and its potential invasiveness. PhD Thesis, Rhodes Univ, Grahamstown, South Africa, 279 pp
- Hertling UM, Lubke RA (1999a) Indigenous and *Ammophila arenaria*-dominated dune vegetation on the South African Cape coast. J Appl Veg Sci 2:157–168
- Hertling UM, Lubke RA (1999b) Use of *Ammophila arenaria* for dune stabilization in South Africa and its current distribution – perceptions and problems. Environ Manage 24:467–482
- Hertling UM, Lubke RA (2000) Assessing the potential for biological invasion the case of *Ammophila arenaria* in South Africa. S Afr J Sci 96:520–527
- Judd R (2000) The Coastal Grasslands of the Eastern Cape, West of the Kei River. PhD Thesis. Rhodes Univ, Grahamstown, South Africa
- Knevel IC (2001) The life history of selected coastal fore dune species of Eastern Cape, South Africa. PhD Thesis, Rhodes Univ, Grahamstown, South Africa, 291 pp
- Lubke RA (1983) A survey of the coastal vegetation near Port Alfred, Eastern Cape. Bothalia 14:725–738
- Lubke RA (1985) Erosion of the beach at St. Francis Bay, eastern Cape. Biol Conserv 32:99–127
- Lubke RA, Avis AM (1982) Factors affecting the distribution of *Scirpus nodosus* plants in a dune slack community. S Afr J Bot 1(4):97–103
- Lubke RA, Avis AM (1988) Succession on the coastal dunes and dune slacks at Kleinemonde, Eastern Cape, South Africa. Monogr Syst Bot Missouri Bot Gard 25:599–622
- Lubke RA, Avis AM (2000) 17 years of change in a dune slack community in the Eastern Cape. Proc IAVS Symp 2000 IAVS, Opulus Press, Uppsala, pp 35–38
- Lubke RA, Hertling UM (2001) The role of European marram grass in dune stabilization and succession near Cape Agulhas, South Africa. J Coastal Conserv 7:171–182
- Lubke RA,Avis AM, Phillipson PB (1991) Vegetation and floristics. Reprinted from: Environmental impact assessment, eastern shores of Lake St Lucia (Kingsa/Tojan Lease Area) Specialist Reports. Coastal and Environmental Services, Grahamstown, 741 pp
- Lubke RA, Avis AM, Steinke TD, Boucher CB (1997) Coastal vegetation: In: Cowling RM, Richardson D (eds) Vegetation of South Africa. Cambridge University Press, Cape Town
- Margalef R (1968) Perspectives in ecological theory. University of Chicago Press, Chicago
- Maun MA, Lapierre J (1984) The effects of burial by sand on *Ammophila breviligulata*. J Ecol 72:827–839
- Moll EJ (1969) A preliminary account of the dune communities at Pennington Park, Mtunzini, Natal. Bothalia 10:615–626
- Morrison RG, Yarranton GA (1973) Diversity, richness and evenness during a primary sand dune succession at Grand Bend, Ontario. Can J Bot 51:2401–2411
- Musila WM, Kinyamario JI, Jungerius PD (2001) Vegetation dynamics of coastal sand dunes near Malindi, Kenya. Afr J Ecol 39:170–177
- Olson JS (1958) Rates of succession and soil changes on south Lake Michigan sand dunes. Bot Gaz 119:125–170
- Pammenter NW (1983) Some aspects of the ecophysiology of *Scaevola thunbergii*, a subtropical coastal dune pioneer. In: McLachlan A, Erasmus T (eds) Sandy beaches as ecosystems. Developments in hydrobiology, vol 19. W Junk, The Hague, pp 675–685
- Picket STA, Collins SL, Armesto JJ (1987) Models, mechanisms and pathways of succession. Bot Rev 53:335–371
- Richardson DM, Macdonald IAW, Hoffmann JH, Henderson L (1997) Alien plant invasions. In: Cowling RM, Richardson DM, Pierce SM (eds) Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp 535–570
- Salisbury EJ (1925) Note on the edaphic succession in some dune soils with special reference to the time factor. J Ecol 13:322–328
- Shaughnessy GL (1980) Historical ecology of alien woody plants in the vicinity of Cape Town, South Africa. PhD Thesis, University of Cape Town
- Shipley B, Keddy PA (1987) The individualistic and community-unity-concepts as falsifiable hypotheses.Vegetatio 69:47–55
- Talbot MMB, Bate GC (1991) The structure of vegetation in bush pockets of trangressive coastal dune fields. S Afr J Bot 57:156–160
- Tinley KL (1985) Coastal dunes of South Africa. South African National Scientific Programmes Report, No 109. CSIR, Pretoria.
- Van Dorp D, Boot R, Van der Maarel E (1985) Vegetation succession on the dunes near Oostvoorne, The Netherlands, since 1934, interpreted from air photographs and vegetation maps.Vegetatio 56:123–126
- Weidemann AM, A Pickart (1996) The *Ammophila* problem on the northwest coast of North America. Landscape Urban Plann 34:287–299
- Weisser PJ (1978) Changes in the area of grasslands on the dunes between Richards Bay and the Mfolozi River 1937–1974. Proc Grassland Soc S Afr 13:95–97
- Weisser PJ, Backer AP (1983) Monitoring beach and dune advancement and vegetation changes 1937–1977 at the farm Twinstreams, Mtunzini, Natal, South Africa. In: Mc Lachlan A, Erasmus T (eds): Sandy beaches as ecosystems. Developments in Hydrobiology, vol 19. Junk, The Hague, pp 727–740
- Weisser PJ, Garland LF, Drews BK (1982) Dune advancement 1937–1977 at the Mlalazi Nature Reserve, Natal, South Africa, and preliminary vegetation-succession chronology. Bothalia 4:127–130

Whittaker RH (1975) Communities and ecosystems, 2nd edn. MacMillan, London