

Chapter 4

Natural Plant Diversity Development on a Man-Made Dune System

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4.1 Introduction

Natural formation of coastal foredunes involves interaction among sand, sea, wind, and plant growth (Carter 1988; Klijn 1990; Nordstrom et al. 1990; Martinez and Psuty 2004). The subsequent development of the dunes implies a gradual increase in species richness as a result of the combined effect of biotic and abiotic conditions and processes, related to dune age and distance to the sea (Carter 1988; McLachlan 1991; Lichter 1998; Hesp 1999).

Natural dunes make up a valuable natural resource because of their relatively high biodiversity and the occurrence of many specialized species of plants and animals. Coastal dunes, however, may include areas that are not purely naturally formed. Thus, many dune systems play an important role in coastal protection or may serve as an important resource for recreation or the catchment of drinking water (van der Maarel 1979; van der Meulen and Jungerius 1989). Because of the erosion, restoration measures are often needed in such dune systems (van der Meulen and van der Maarel 1989; De Lillis et al. 2004; Kiehl and Isermann (2007).

In Denmark, large dune areas occur along the North Sea coast of Jutland (Doody 1991). However, dunes also occur along the coastlines of the Kattegat and as part of the barrier coasts along the Baltic. As they are important resources for recreation and coastal protection, many Danish dunes, however, are currently restored and maintained by the local mechanical leveling of sharp dune edges and the planting of *Ammophila* to prevent sand drift, or by replenishment by means of sand nourishment (Jensen 1994, 2008).

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The general pattern of dune succession from embryonic to fixed dunes is also documented by several studies in Danish dunes (e.g., Warming 1909; Heykena 1965; Vestergaard 1991; Frederiksen et al. 2006). However, succession studies in relation to restoration measures in dunes have not been carried out.

This chapter reports a 24-year study of the development of a beach–dune system in Denmark, which in the 1970s was designed and established to meet local recreational and coastal protection purposes (Nielsen 1990). Even if the establishment and development of this system is not an example of restoration according to the narrow definition of the term—to move a degraded system to a stable target state (Hobbs et al. 2007)—the results and observations gained from the study may be relevant in a restoration context, because they indicate how a human-modified dune might be restored by natural processes.

On a global scale, structural and adaptational characteristics of beach and dune vegetation are similar, even if the taxonomic spectrum differs (Doing 1985). Therefore, the use of plant functional types, i.e., sets of species sharing similar structural and functional attributes (Box 1996), may permit ecological comparisons among coastal dunes on a more general scale than would be possible by using a taxonomic approach (Shao et al. 1996; Garcia-Mora et al. 1999). A widely used functional type system is the life form classification of Raunkjær (1907, 1934), which has been applied in several studies on sand dune zonation and succession (e.g., Ranwell 1959; Hundt 1985; Olf et al. 1993). Other functional traits, important for understanding plant colonization and succession processes in coastal dunes, are mechanisms of the dispersal of diaspores (Andersen 1993; Davy and Figueroa 1993) and tolerance to burial by sand and salinity (Hesp 1991; Garcia-Mora et al. 1999; Gallego-Fernández and Martínez 2011).

The aim of the present study was to investigate the relationship between plant diversity and dune development processes in the human-initiated dune system, and to discuss whether those processes are similar to those known to be characteristic of natural dune succession.

4.2 Locality and Methods

4.2.1 Initial Morphology of the Man-Made Beach-Dune System

The study site is located in the Køge Bay Seaside Park at the Baltic coast of Zealand, Denmark, about 15 km southwest of Copenhagen (55°36'N, 12°22'E). The seaside park consists of an artificial barrier, 8 km long, about 300 m wide, established in 1977–1978, comprising a sandy beach, an artificial foredune and a grassland area landward of the dune (Fig. 4.1). The system was created from sediment, supplied to the beach by pumping calcareous marine sand upon previously existing, natural low sandy bars (Fig. 4.1; Thougard 1980; Nielsen 1990). During the planning of the barrier, the structure of a natural barrier island, the

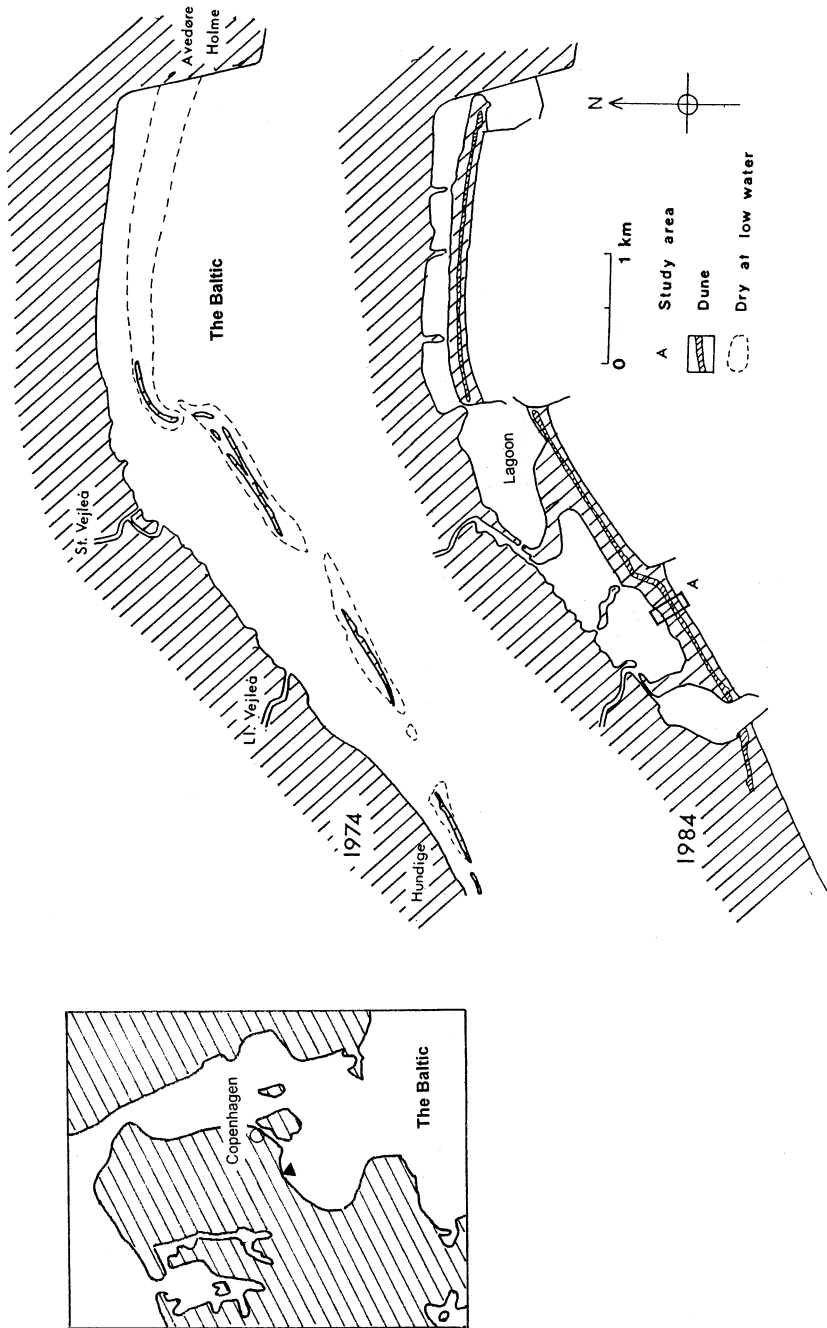


Fig. 4.1 Sketch maps based on aerial photographs from 1974 and 1984, showing the natural sandy bars existing before the construction of the Køge Bay Seaside Park, and the situation after the establishment of the artificial barrier. The arrow on the inset map indicates the position of the seaside park

Ølseagle Revle, further south in the bay of Køge Bugt, which was studied by Gravesen and Vestergaard (1969), served as a model (Nielsen 1990).

The total size of the seaside park is about 500 ha. The park is managed by the I/S Køge Bugt Strandpark. The total price for the establishment of the seaside park amounted to approximately 91 million Danish krone (about 13 million US dollars). The annual management amounts to around 5 million crowns (about 0.7 million US dollars) (Valgren et al. 1986).

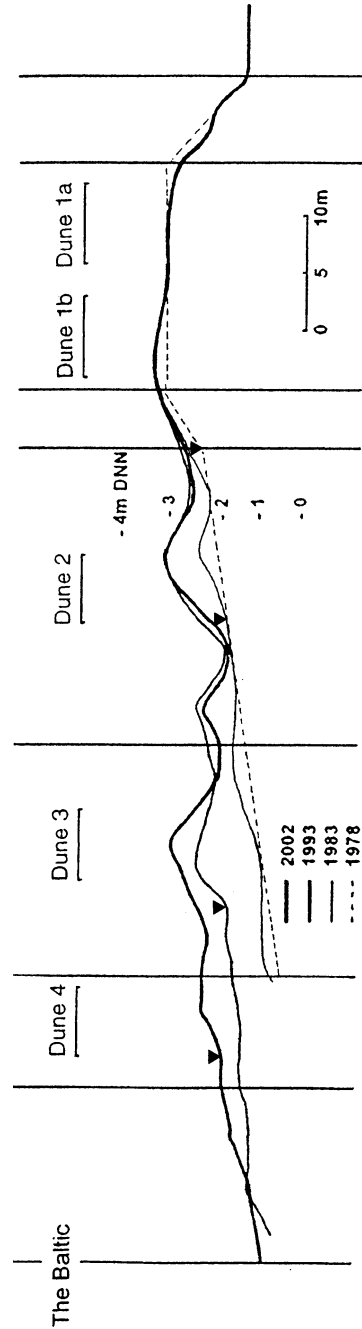
The initial relief of the artificial beach and dune is shown in Fig. 4.2. The beach, about 45 m wide, was built up to +2.3 m DNN (Danish Mean Sea Level). The initial dune consisted of a horizontal plateau at +3 m DNN, approximately 20 m wide, delimited by a seaward and a landward slope. The dune plateau and the seaward slope were planted with *Ammophila arenaria*. The planting was carried out according to the traditional Danish method (Jensen 2008). At about ten regularly distributed points per square meter, 2–4 *Ammophila* shoots, cut at a depth of 10–20 cm below the sand surface in established *Ammophila* dune elsewhere, were planted. After the planting, the area was fertilized with NPK fertilizer. The area landward of the dune was sown with a mixture of perennial grasses, mostly *Festuca rubra*, and locally planted with low shrubs: the native *Hippophaë rhamnoides*, which is rather widely distributed along Danish coasts, and the non-native *Rosa rugosa*. Even if *Rosa rugosa* is non-native and now known to be invasive, it was earlier commonly planted along Danish coasts for its ornamental value and its sand-binding ability (Weidema et al. 2007).

4.2.2 Data Collection

In 1979, a study area across the barrier, 100 m wide, was selected (“A” in Fig. 4.1). Along a line transect, perpendicular to the shore, six permanent plots were established. This chapter is based on four of these plots, each 5×10 m²: two plots from the inner and outer part of the dune plateau (“dune 1a” and “dune 1b”) and two from the inner and outer parts of the beach (“dune 2” and “dune 3”; Fig. 4.2). Because of later gradual seaward widening of the beach, an additional plot was established in 1993 (“dune 4”).

The species composition and species diversity of the permanent plots were recorded in July or August on 11 occasions between 1979 and 2002. The distance to the sea of the plots was recorded, and from 1980 the plots were leveled in relation to DNN. A quantitative estimate of the species composition was attempted using a fixed system of 20 sampling circles of 0.1 m². In the circles rooted species of vascular plants were recorded, and the cover of each species was estimated using the Hult–Sernander 1–5 cover scale (1: cover <6 %, 2: cover 6–12.5 %, 3: cover 12.5–25 %, 4: cover 25–50 %, 5: cover > 50 %) (Malmer 1974; Hansen 1981, nomenclature). From these data, frequency (%) and mean cover of the species in each plot were calculated. In total 43 relevées (plot-years) were analyzed.

Fig. 4.2 Structure and change of the profile of the dune system between 1978 and 2002, with localization of the permanent plots. The year 1978 represents the initial profile. The *arrows* indicate the limit between the beach (backshore) and the dune



4.2.3 Plant Data Analysis

The species diversity in the permanent plots was expressed by the number of species as well as by the Shannon–Wiener diversity index. These measures were found to be highly significantly positively correlated (Fig. 4.3). Therefore, the discussion of the trends in plant diversity development presented here will be based on the number of species per plot.

For each of the dunes, the correlation between the number of species per plot and the following dune attributes was investigated: number of years since establishment, dune height, distance to the sea, and total plant cover. The plant species were classified according to their life forms (Raunkiær 1907, 1934), and diaspore dispersal strategy, following Andersen (1993).

The frequency and Hult–Sernander cover data were combined into a 1–9 cover–abundance scale (Vestergaard 2006). Based on this scale, the species composition of the relevés was subjected to TWINSpan classification analysis, cut levels 0–2–4–6–8, using the program PC-ORD (McCune and Mefford 1999).

4.3 Results

4.3.1 Change in Dune Morphology 1978–2002

The morphology of the landward part of the initial man-made dune remained fairly unchanged during the study period, while in other parts, the morphology changed substantially (Fig. 4.2).

In the seaward part of the initial dune, a net accumulation of up to approximately 0.4–0.5 m of windblown sand was recorded. On the beach, new foredune ridges, parallel to the initial dune, gradually developed, supported by *A. arenaria*, which spread from the planting in the initial dune, as well as by other dune-forming grasses. Thus, in the inner part of the beach, the dune, represented by “dune 2,” accreted rapidly (0.15 m year^{-1}) to about the same height as the top of the initial dune, +3 m DNN (Figs. 4.4, and 4.5). After 1990, this dune stabilized, and the height did not change significantly. On the outer part of the beach, another new dune, represented by “dune 3,” developed, albeit a little more slowly (0.1 m year^{-1}). In 2002 this dune was about 0.5 m lower than “dune 2.”

The total width of the beach–dune system increased from approximately 75 m in 1978 to 100 m in 2002, owing to the accretion of additional beach formed by less calcareous marine sand (Vestergaard 2006). On this beach, a low dune, represented by “dune 4,” had developed in 2002 (Figs. 4.2, and 4.4). This propagation and development of new foredunes is similar to those examined by for example Hesp (1989) and McLean and Shen (2006).

Fig. 4.3 Correlation between number of species and the Shannon–Wiener diversity index in the permanent plots (r -value for the linear trend line: $r = 0.948$, $p < 0.001$, $n = 43$)

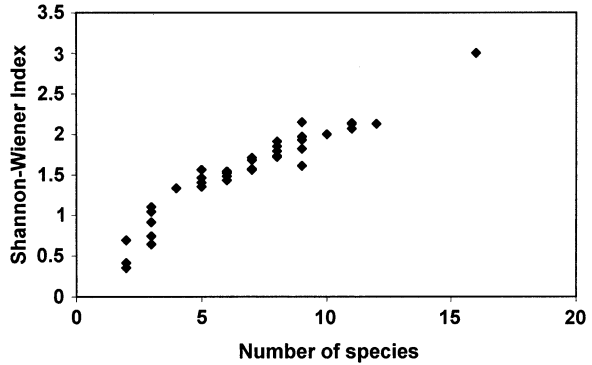
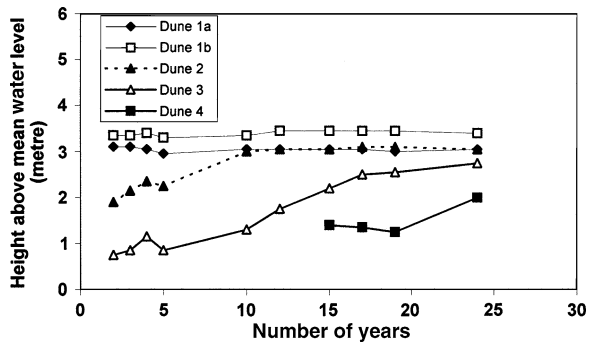


Fig. 4.4 Growth of the dunes from 1980 to 2002, expressed by the increasing height of the permanent plots above the Danish Mean Sea Level



4.3.2 Development in Species Diversity

The planted *A. arenaria* was the only species present in the beach–dune system from the very beginning. In 1979, seven species were recorded in the permanent plots, and from 1979 to 2002, the total number of species in the permanent plots gradually increased to 26 after some fluctuations, especially during the first years (Fig. 4.6a). The proportion of coast species, i.e., species exclusively or predominantly growing in coastal habitats, also changed, from 71 % in 1979 to 38 % in 2002.

The species richness in the plots changed over time, with changes in relief and distance to the sea and with total plant cover, but the changes differed among the dunes (Fig. 4.6, Table 4.1). In the relatively stable landward part of the man-made dune, “dune 1a,” the number of species varied significantly only with total plant cover. In the less stable part of the man-made dune, “dune 1b,” the number of species also increased significantly over time and over distance to the sea. In “dune 2” and “dune 3,” which developed from beach to foredunes during the study period, compare Figs. 4.2 and 4.5: the number of species increased significantly with all the factors involved in the dune development, recorded in the present study: dune age, distance to the sea, dune height, as well

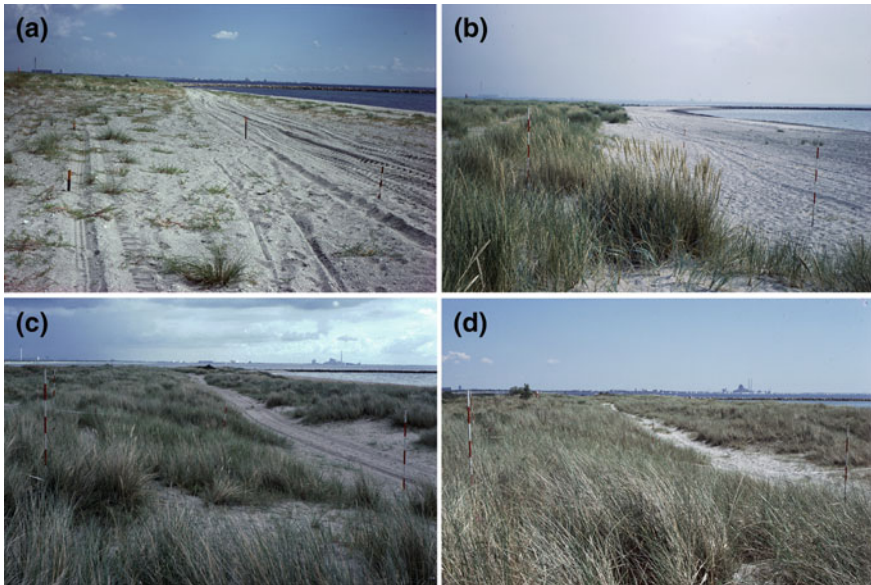


Fig. 4.5 a–d Development of the permanent plot, representing “dune 2” from 1979 to 2002, seen in a northeasterly direction. Compare with Fig. 4.2. On the right of the photos the development of “dune 3” can also be followed. *Photos* P. Vestergaard. **a** 1979, **b** 1983 **c** 1993, **d** 2002

as total plant cover. In the plot of the youngest dune, “dune 4,” the number of species also increased, albeit not significantly, owing to the low number of observations.

4.3.3 *Species Composition Dynamics and Functional Traits*

Based on the TWINSPAN analysis, six groups of plot-year relevées (“plant communities”) could be defined (Tables 4.2, and 4.3). The distribution pattern of the groups in the dune system could be related to a combination of the factors time and distance to the sea (Table 4.4).

Group A (8 relevées) represents the species composition of “dune 1a” and “dune 1b” during the first years, as well as the first year of the plot of the most landward of the new foredunes, “dune 2.” The cover of the planted *A. arenaria* was mostly high, but there were also many beach and inland annuals (62 %). Most species were dispersed by wind (54 %).

Group B1 (14 relevées) represents the first years of development of “dune 3” and “dune 4” and also some years of “dune 1b.” The relevées are characterized by strong sand movement and sand accretion and by dune-building rhizome

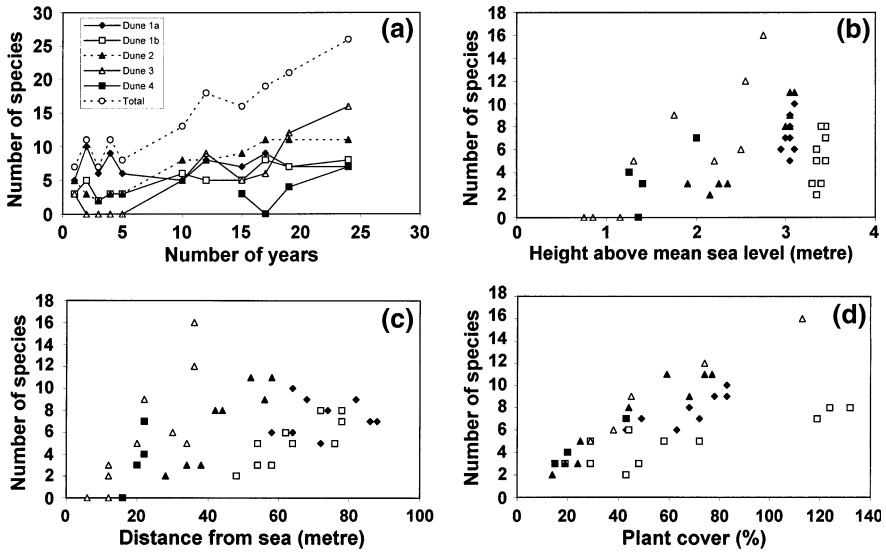


Fig. 4.6 **a** Development in the number of species in the permanent plots over time (1979–2002), with **b** dune height above the mean sea level, and **c** the distance to the sea and **d** total plant cover. For the correlation, see Table 4.1

Table 4.1 Correlation (*r*-values for linear trend lines) between the number of plant species in the permanent plots, and age, height above mean sea level, distance to the sea, and total plant cover of the plots

	Time	Height	Distance	Plant cover
Dune 1a	$r = 0.074$ ns	$r = 0.354$ ns	$r = 0.138$ ns	$r = 0.808^{**}$
Dune 1b	$r = 0.867^{**}$	$r = 0.539$ ns	$r = 0.838^{**}$	$r = 0.845^{**}$
Dune 2	$r = 0.928^{**}$	$r = 0.937^{**}$	$r = 0.935^{**}$	$r = 0.958^{**}$
Dune 3	$r = 0.902^{**}$	$r = 0.871^{**}$	$r = 0.833^{**}$	$r = 0.986^{**}$
Dune 4	$r = 0.792$ ns	$r = 0.749$ ns	$r = 0.898$ ns	$r = 0.997^*$

Number of observations: dune 1a–3: $n = 7–11$; dune 4: $n = 3–4$. Levels of significance: ns $p > 0.05$; * $p < 0.05$; ** $p < 0.01$)

geophytes, *A. arenaria*, *Leymus arenarius*, and *Elytrigia junceiforme*. The proportion of annuals was still high (46 %). Because of the relatively low elevation above sea level of most relevées, about 1 m DNN (Fig. 4.4), water was the most important agent of diaspore dispersal (46 %), and most species are salt tolerant.

Group B2 (6 relevées) represents the next seral stage of “dune 2” and “dune 3” after these dunes had built up to about the same height as that of the initial dune (Fig. 4.4). The rhizome geophytes, which dominated group B1, were still dominating, but they were accompanied by *Ammophila x baltica*. The number of species increased, and the hemicryptophytes, e.g., *F. rubra*, became the most important life form, even if their cover was still low. In this group, as well as in the following groups, wind was the dominating agent for diaspore dispersal.

Table 4.2 Important vascular plant species of the TWINSPAN groups

TWINSPAN group	A	B1	B2	C1	C2	C3
Total number of species	13	13	21	21	12	12
<i>Cakile maritima</i>	X	o	o			
<i>Senecio vulgaris</i>	X			o		
<i>Chenopodium album</i>	X					
<i>Festuca rubra</i>	X	o	X	X	X	X
<i>Ammophila arenaria</i>	X	X	X	X	X	X
<i>Leymus arenarius</i>		X	X	o		
<i>Elytrigia junceiforme</i>		X	X	o	o	
<i>Salsola kali</i>	o	X				
<i>Ammophila x baltica</i>			X	o		
<i>Taraxacum</i> sp.			X	X	X	X
<i>Erigeron acre</i>			X	o		o
<i>Cirsium arvense</i>			X	o		
<i>Conyza canadensis</i>	o		X	o		
<i>Senecio vernalis</i>	o	o	X	X	o	X
<i>Epilobium montanum</i>			o	X		
<i>Lathyrus japonicus</i>		o		X	X	o
<i>Cirsium vulgare</i>	o		o	X		o
<i>Anthyllis vulneraria</i>						X
<i>Trifolium arvense</i>				o		X
<i>Cerastium semidecandrum</i>			o		X	X
<i>Rosa rugosa</i>				o	X	
<i>Chamaenerion angustifolium</i>			o	o	X	o

X species present in >40 % of the relevées; o important species also present in the group in question, but in <40 % of the relevées

Group C1 (7 relevées) represents the seral situation of “dune 1a” and “dune 1b” between years 5 and 12. It also represents the situation of “dune 2” between years 19 and 24, starting about 10 years after the stabilization of the dune. The vegetation is characterized by a high number of species and increasing *F. rubra*. In “dune 1a” and “dune 1b,” *A. arenaria* declined, while *A. arenaria* and *A. x baltica* have kept their position in “dune 2” so far.

Group C2 (4 relevées) represents the seral situation of “dune 1b” between years 12 and 24. Hemicryptophytes were the dominating life form. *F. rubra* dominated, but *A. arenaria* and *Lathyrus japonicus* were also important, indicating that some sand movement still occurred. The invasive phanerophyte *Rosa rugosa* became established in year 17 and increased further to year 24.

Group C3 (4 relevées) represents the seral situation of “dune 1a” between years 12 and 24. The surface was stable, and the vegetation had become similar to northwest European and Baltic grassland-like fixed dune with a high percentage of hemicryptophytes, dominated by *F. rubra*, and with, for example, *Trifolium arvense* and *Anthyllis vulneraria*, but still with *A. arenaria* present (e.g., Böcher 1954; Pålsson 1995; Thorell et al. 2001).

Table 4.3 Life form and diaspore dispersal strategy spectra of the TWINSPAN groups

TWINSPAN group	A	B1	B2	C1	C2	C3
Life form, % of species						
Rhizome geophytes	8	31	24	19	17	8
Root geophytes	0	0	10	14	8	8
Hemicryptophytes	31	23	43	33	42	50
Annuals	62	46	24	29	25	33
Phanerophytes	0	0	0	5	8	0
Dispersal strategy, % of species						
By wind	54	23	57	67	42	67
By seawater	8	46	10	10	8	8
By wind shaking	8	8	5	0	8	0
Epizoic	0	0	5	0	0	0
Endozoic	0	0	0	5	8	0
No special strategy	31	23	24	19	33	25

Table 4.4 The distribution of the TWINSPAN groups in the permanent plots from 1979 to 2002

	Dune 1a	Dune 1b	Dune 2	Dune 3	Dune 4
1979	A	A	A	B1	
1980	A	A	B1		
1981	A	A	B1		
1982	A	B1	B1		
1983	C1	B1	B1		
1988	C1	C1	B2	B1	
1990	C1	C1	B2	B1	
1993	C3	C2	B2	B1	B1
1995	C3	C2	B2	B1	
1997	C3	C2	C1	B2	B1
2002	C3	C2	C1	B2	B1

4.4 Discussion

4.4.1 Beach and Dune Dynamics

The initial relief of the beach–dune system in the seaside park differed from the relief of the natural barrier island, Ølsemagle Revle, further south in the bay of Køge Bugt, especially with regard to the amount of beach sand (Gravesen and Vestergaard 1969).

The natural beach was 10–20 m wide and had a height of up to about 1.5 m above DNN. The man-made beach was much wider and higher (Fig. 4.2). The large amount of sand contained in the man-made beach had important implications for the later development of the whole system. Several foredunes were formed by natural processes—sand movement and plant growth—on the man-made beach within 24 years. These dunes were formed by two components of sand: the initial

nourishment sand and the sand subsequently deposited by the sea by natural coastal processes (Nielsen 1990). This gradually increased the width of the beach by 25 m in 24 years. The sand deposited by the sea was quite similar to the beach sand of the natural barrier in its pH and exchangeable calcium, but differed from the nourishment sand (Gravesen and Vestergaard 1969; Vestergaard 2006).

The system studied here seems to have behaved like the “high sediment supply system” described by Carter (1990), which is characterized by progressive seaward formation of several foredunes, each of which develops until the sand supply from the beach is cut off by the formation of a new foredune ridge. Thus, an important consequence of the successive seaward formation of the natural dunes on the beach in the seaside park has been a strongly reduced dynamic of the landward dunes, which instantly or within a few years stabilized at a dune height of 3 m DNN. This is typical of the prograding foredune systems such as those described by among others Carter (Carter 1990; Hesp 1999, 2002).

4.4.2 *Immigration of Plant Species*

The increase in species richness and development of vegetation in the dunes studied here includes the sequence of processes characteristic of primary succession in a new area (Bradshaw 1993). Among these processes, dispersal of diaspores and distance to species sources are essential for the rate and course of the succession (van der Maarel 1997; del Moral 1998; Walker and del Moral 2003).

In the nourishment sand, no seed bank was present (Hansen and Vestergaard 1986). Thus, apart from the initial planting of *A. arenaria*, the subsequent development of the vegetation in the permanent plots was due to natural influx of diaspores.

The minimum number of species dispersed into the beach and dune system can be estimated from the number of species that have been recorded in the permanent plots during the years, i.e., 38 species. Nothing indicates, however, that the influx of species to the plots has stopped. Thus, the number of species established in the beach and dune within the total study area (Fig. 4.1) was 55 (Vestergaard 2006), and in the natural Ølsemagle Revle barrier, 85 species were recorded within similar beach and dune habitats after about 37 years of development (Gravesen and Vestergaard 1969), and 102 species after a further 40 years (2008). Based on the above, it is thus expected that the species number will continue increasing, if the same trends are maintained during the coming years.

During the study period, the natural habitat of an increasing proportion of the species recorded is relatively dry, nutrient-poor inland grasslands and other open inland habitats (Hansen 1981). The source of these species is rather diffuse, but the species in question are all common and more or less widely distributed in Denmark (Vestergaard and Hansen 1989). The remaining species are found in coastal habitats. The source of these species was probably the nearby coasts along the bay of Køge Bugt and the island of Amager (Fig. 4.1). The relative increase in inland

species is supposed to be due to the reduced influence of the sea upon an increasing proportion of the dune area, caused by the seaward development of new foredunes.

A large proportion (54 %) of the species recorded in 2002 specializes in seed dispersal by wind. This indicates that the dune system after 24 years was still at an early stage of succession (Fenner 1985; Prach and Pysek 1999). However, for many species it is not possible to demonstrate evident morphological specialization for long-distance dispersal. Andersen (1993) points to humans as important dispersal agents for such species. This could well be the case in the seaside park, considering the strong recreational pressure in the area (Nielsen 1990; Andersen 1995). Many species with no special spreading device can, however, be dispersed by wind because of the small diaspore size (<2 mm; Andersen 1993). Thus, *F. rubra*, which dominated the later stages of succession in the dune, has small and light diaspores (Grime et al. 1988), which could easily have been blown into the dunes from the sown grassland just landward to the initial, man-made dune by the frequent westerly winds.

4.4.3 Species and Life Form Dynamics

The increase in species richness of the dune system from 1979 to 2002 implied a change in the proportion of the plant life forms in a spatial–temporal pattern also observed during primary succession in other beach and dune systems, e.g., Hundt (1985).

In the original, man-made dune, the *A. arenaria* that had been planted declined because of a decreasing supply of fresh, wind-borne sand (van der Putten 1989; van der Putten and Peters 1995; De Rooij-van der Goes 1995; van der Stoel et al. 2002), while *F. rubra* as well as inland annuals increased. *A. arenaria* expanded seaward, however, into the area of mobile sand and was the primary colonizer initiating and forming new foredunes on the beach.

In the new dunes, beach annuals, e.g., *Cakile maritima* and *Salsola kali*, which are typically limited to open, salty and unstable beach sand (Davy and Figueroa 1993; Packham and Willis 1997), were present during the first years of dune development, when the plant cover was sparse and the substrate was fresh marine sand. During the following years the beach annuals were replaced in the sequence “dune 2” → “dune 3” → “dune 4” by the dune-forming rhizome geophytes *A. arenaria*, *A. x baltica*, *L. arenarius*, *Elytrigia junceiforme*, which are tolerant to or even favored by deposition of fresh sand (Ranwell 1972; Packham and Willis 1997). During the last years of the study period hemicryptophytes, especially *F. rubra*, began to play a role in the sequence “dune 2” → “dune 3.”

Besides the plant groups mentioned, some additional plant groups colonized the dunes during the latter part of the study period: root geophytes, e.g., *Chamaenerion angustifolium*; hemicryptophytic dicots, e.g., *Erigeron acre*, Fabaceae, e.g., *L. japonicus*, *Anthyllis vulneraria*, *Trifolium arvense*; shrubs, e.g., *Rosa rugosa*, *Hippophaë rhamnoides*.

4.4.4 Species Composition Dynamics

The groups of relevées that resulted from the TWINSPAN analysis appear to be meaningful in several ways.

The gradual increase in species richness of the dune system from year 1 to year 24 was reflected in the number of TWINSPAN groups represented, which increased from two to five, indicating an increasing habitat variation within the dune system.

Second, the grouping clarifies, together with the changes in morphology, the developmental trends in the dune system in the seaside park up to 2002. The spatial position of the active dune formation, as indicated by the relatively high speed of dune growth, gradually moved seaward from 1979 to 2002, leaving behind an increasing area of stabilized dunes. This dynamic was reflected in the distribution of the TWINSPAN groups (Table 4.4). The initial, man-made dune during the first years was covered by group A vegetation, which was mostly based on the *Ammophila* that had been planted. After a few years this vegetation changed into group B1 or C1 vegetation, which after 14 years stabilized into C2 vegetation or dune grassland (C3). In the oldest of the new, naturally formed foredunes seaward to the man-made dune, the successional development followed the sequence (A →) B1 → B2 → C1, which reflects the increasing stability and species richness. The younger, more seaward dune in 2002 had only reached group B2 in this sequence, while the development of the youngest dune by 2002 had occurred within the variation of group B1.

Third, the sequence of the TWINSPAN groups largely matches the succession/zonations previously described from the younger parts of coastal dunes elsewhere at the Baltic and in northwest Europe (e.g., Warming 1909; Ranwell 1972; Olsson 1974; Hundt 1985; Vestergaard 1991; Packham and Willis 1997; Frederiksen et al. 2006). This indicates that the dune vegetation in the seaside park developed according to the same successional and ecological processes as in natural coastal dunes. This result agrees with the experience of De Lillis et al. (2004) with man-made dunes on the Mediterranean coast.

4.5 Conclusions

For 24 years, the initially man-made dune in the Køge Bay Seaside Park stabilized quite quickly, while the beach expanded seaward because of the natural accretion of marine sand. On the beach, three rows of coast-parallel foredunes developed successively. The gradual change in plant diversity of the dune system, expressed by a net increase in the species richness of the permanent plots from only one planted species in 1978 to 26 species in 2002, could be related to the combined effect of the following dune succession processes:

1. Increasing the number and height of the new foredunes, seaward of the man-made dune, based on the initial nourishment, calcareous marine sand, as well as subsequent accumulation of less calcareous marine sand.
2. Increasing the distance of the man-made dune, as well as that of the new dunes, from the sea, causing a decline in the relative influence of the sea and increasing stabilization.
3. Successive immigration of species from local and regional species pools.
4. Change in the dominating dispersal agent—the seawater—during the first years of dune building and the wind during the later stages.
5. Change from a high proportion of coastal plant species to a high proportion of inland plant species.
6. Replacement of beach annuals and dune-building rhizome geophytes by hemicryptophytes and inland annuals.
7. Increasing habitat differentiation in time and space.

The increasing habitat differentiation of the initially man-made dune system was indicated by the increasing number of TWINSPAN groups with increasing dune age and distance from the coastline. This differentiation matches well with dune succession found elsewhere in younger parts of natural dune systems. After 24 years of development there is no indication so far—neither from soil processes like leaching and acidification (Vestergaard 2006) nor from the presence of species typical of stabilized, acid dunes such as *Corynephorus canescens*—of continued succession toward plant communities found in the inner, older parts of natural Baltic and NW European dune systems (e.g., Olsson 1974; Hundt 1985). It can be expected, however, that the landward-most part of the dune system will in due course be invaded by *Rosa rugosa* scrub, as observed in other parts of the seaside park. Such a development will probably reduce the species richness of the dunes (Isermann 2008).

Acknowledgments Most of the field work was carried out in cooperation with the late Professor Kjeld Hansen. I wish to thank Hans Henrik Bruun, Marisa Martinez, Patrick Hesp, and Juan B. Gallego-Fernandez for constructive comments on the manuscript.

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