Journal of Coastal Conservation 3: 179-190, 1997

Vegetation development in coastal foredunes in relation to methods of establishing marram grass (*Ammophila arenaria*)

van der Laan, D.[1], van Tongeren, O.F.R.[2], van der Putten, W.H.[1]* & Veenbaas, G.[3]

[1]Netherlands Institute of Ecology, P.O.Box 40, NL-6666 ZG, Heteren, The Netherlands;
[2]Data-analysis Ecology, Waemelslant 27, NL-6931 HS, Westervoort, The Netherlands;
[3]Hydraulic Engineering Division of the Ministry of Transport, Public Works and Water Management, P.O.Box 5044, NL- 2600 GA, Delft, The Netherlands;
[*]Corresponding author: Tel. +31 2647 91203; Fax +31 2647 23227; E-mail putten@cto.nioo.knaw.nl

Abstract. In coastal foredunes marram grass (*Ammophila arenaria*) is used to stabilize windblown sand. The development of traditionally planted *Ammophila* into a more natural foredune vegetation may take 5 - 10 yr. For economic reasons, traditional planting may be replaced by alternative techniques such as planting seeds or disk-harrowing rhizome fragments. In this paper, we compare the initial vegetation development of traditionally planted stands with stands established from seeds and from rhizomes.

The experiments were conducted on an artificial foredune originating from dredged sea sand. The total experimental area covered more than 100 ha and the vegetation development was studied for 6 yr. The data were analysed by *a priori* grouping of plant species according to their ecology, as well as by Principal Components Analysis (PCA) and Redundancy Analysis (RA) of the percentage ground cover per plant species.

Comparing ecological groups of plants showed that all planting methods delivered equal numbers of plant species that are indicative for coastal dunes. PCA and RA showed that methods based on the use of rhizome material resulted in a higher percentage cover of clonal perennials (*Calammophila baltica, Festuca rubra* ssp. *arenaria, Carex arenaria* and *Cirsium arvense*) than the traditionally planted stands and the stands obtained from seeds. The latter two were characterized by the dominance of annuals, bi-annuals and (mostly non-rhizomatous) perennials.

Initially, the rates of succession were highest in the stands obtained from rhizomes. However, after 3 - 6 yr there were no differences between the various stands. During the first four years, the percentage cover by rhizomatous foredune plants developed faster than that of annuals, bi-annuals and perennials. After 6 yr, the latter contributed almost as much to the percentage cover as the clonal species.

Keywords: Clonal plant; Dune management; Dune reinforcement; Sand dune; Sand stabilization; Succession.

Nomenclature: van der Meijden et al. (1990) for plant species. The plant species were classified into ecological groups according to van der Meijden et al. (1991) and Mennema et al. (1980).

Introduction

Coastal foredunes, when managed as a sea defence system, are usually ridges between the beach and the dune system planted with vegetation to stabilize the sand. The coastal foredunes in the Netherlands are among the most intensively managed in the world. Only 10 % of the Dutch foredunes are still natural (Arens & Wiersma 1994). The need for proper management of the Dutch foredunes is essential, because approximately one third of the country is below sea level and about 90 % of the 350 km long coastline is defended by dunes (van Bohemen & Meesters 1992; Hillen & Roelse 1995). The safety level of the foredunes is prescribed by law (Anon. 1989). For safety reasons, dune height should be at least 8 m above ‘Dutch Ordinance Level’ and dune width at the base should be at least 100 m.

Internationally, the dimensions of coastal foredunes may vary widely, but management practices are similar. In regions with a temperate climate *Ammophila arenaria* (marram grass) is mainly used for sand stabilization and planting techniques vary little (Brown & Hafenrichter 1948; Adriani & Terwindt 1974; Barr & McKenzie 1976). Bundles of culms are planted manually in grid patterns, which in the Netherlands is recorded as early as 1423 (Pilon 1988). Also, *Ammophila breviligulata* and *Uniola paniculata*, two sand stabilizing plant species used on the Atlantic coast of North America are planted in a similar way (Knutson 1978).

Field trials have shown that *Ammophila* may be sown, provided that the sand surface is temporarily stabilized until the germinated seedlings have become established (Adriani & Terwindt 1974; Mitchell 1974; Tsuriëll 1974; Barr & McKenzie 1976; van der Putten 1990; van der Putten & Kloosterman 1991). Some other methods are oblique planting of culms (Hobbs et al. 1983) and disk-harrowing rhizome fragments (van der Putten 1990).

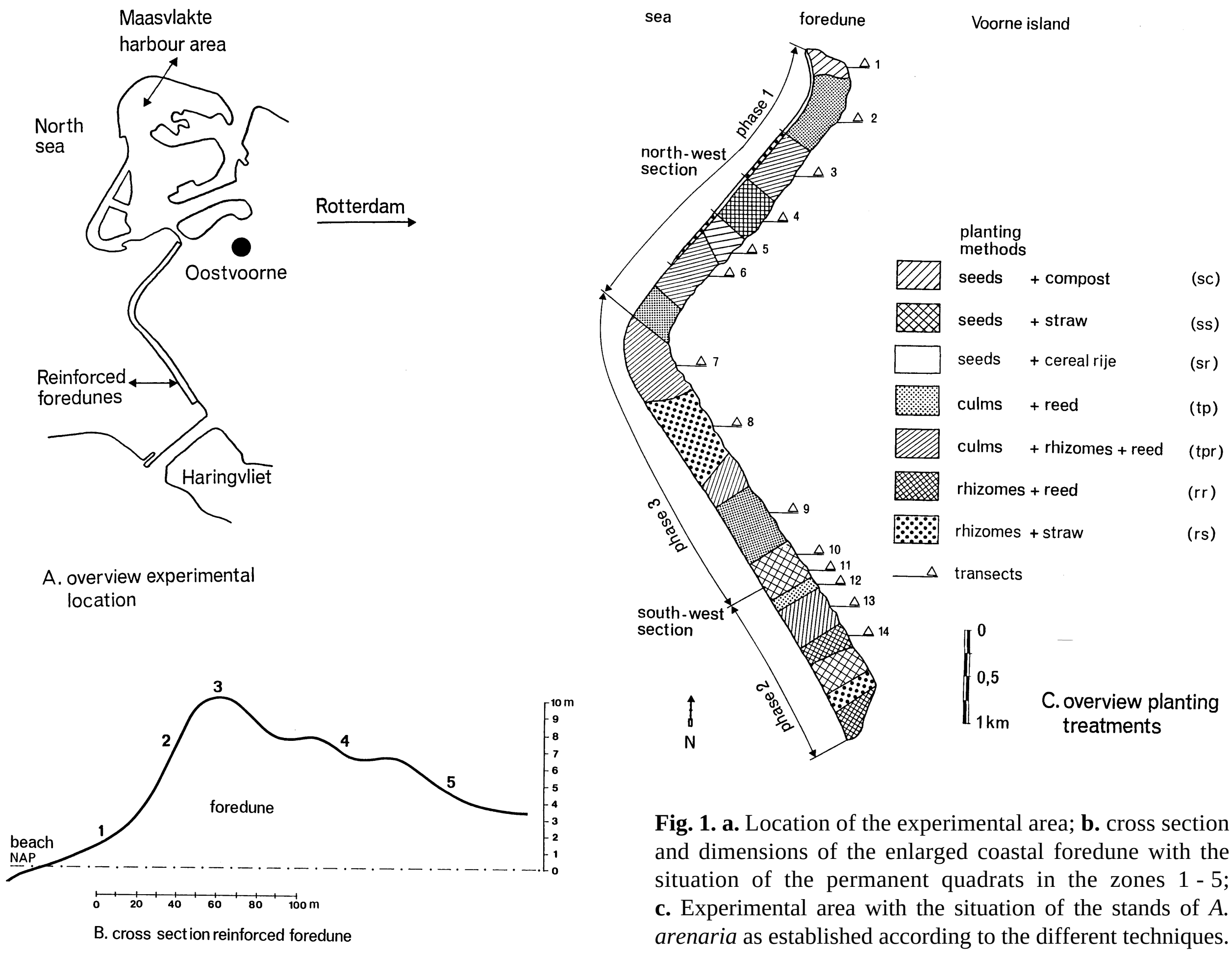

Fig. 1. a. Location of the experimental area; **b.** cross section and dimensions of the enlarged coastal foredune with the situation of the permanent quadrats in the zones 1 - 5; **c.** Experimental area with the situation of the stands of *A. arenaria* as established according to the different techniques.

The vegetational development of traditionally established stands (i.e. planted as bundles of culms) takes at least 5 to 10 years (Hewett 1970; Hansen & Vestergaard 1986), so that periodic disturbances (e.g. caused by replanting) may prevent the development of natural vegetation. It is not known whether, and if so how differently, the alternative methods of establishing *Ammophila* from seeds and rhizomes affect the re-establishment of natural vegetation. This question became the subject of a study when the dunes of Voorne, The Netherlands, were raised and widened on a large scale. From 1985 to 1988, 9 km of coastal foredunes were raised with dredged sea sand (van der Putten & Kloosterman 1991). Stands of *Ammophila* were established from bundles of culms (the traditional method), from seeds and from rhizomes. As *Ammophila* had not previously been established from seeds or rhizomes on such a large scale, a cost-benefit evaluation was made to compare the sowing and rhizome methods with the traditional one. After both one and two growing seasons, quantitative assessment by remote sensing showed that the methods, when applied optimally, were equally productive. The stands from seeds were the most heterogeneous, whereas those planted traditionally were the most homogeneous (van der Putten & Kloosterman 1991). Sowing was the cheapest and the traditional planting of bundles of culms the most expensive method.

As the sand used originated from the sea floor, the newly created dunes will not have contained a seed bank. The entire new foredune adjoined the old one, so that dispersal distances were generally the same. Therefore, the large-scale experiment at Voorne enabled us to study the re-establishment of natural vegetation in relation to the method of planting of *Ammophila*. In this paper we present the results of the first six years of vegetation development. The results are discussed in relation to colonization strategies of plant species in coastal foredunes and the management of coastal foredune vegetation.

Material and Methods

Description of the experimental site

The large-scale experiment was carried out at Voorne, the Netherlands (51 ° 5' N; 4 ° 05' E). The foredune faces Northwest in the northern area and Southwest in the southern part. In the northern part the influence of the sea is reduced, due to sheltering by the offshore harbour area ‘Maasvlakte’ (Fig. 1a). As a result, environmental factors such as sand deposition and salt spray do not have such a dynamic influence in the northern dunes as compared to the southern (van der Laan 1985). Between 1985 and 1988, the 9.4-km long foredune ridge was raised and widened and, subsequently, planted with *Ammophila* (Fig. 1b). The work was carried out in three phases (Fig. 1c). Each phase was started in winter with the offshore dredging of Pleistocene sand and storage at a depot on the beach. Between March and September, the sand surface was temporary stabilized with 5000 kg/ha of disk-harrowed straw, which prevented erosion by wind. Due to natural rainfall the salt content of the sand was reduced from 2000 mg Cl/kg sand to 100 mg/kg (Voogt 1988). In the subsequent winter, the sand depots were reshaped into a foredune landscape by bulldozers, cranes and scrapers, and *Ammophila* was established from seeds, culms and rhizomes (Voogt 1988).

The Northwest area was raised in the winter of 1984-1985 and planted in the subsequent winter. The southwest area was raised in the winter of 1985-1986 and planted in the subsequent winter, and the central area was raised in winter 1986-87 and planted in the winter of 1987-1988 (Fig. 1c).

Planting methods for the establishment of Ammophila arenaria

Seven different treatments were used for establishing *Ammophila*. The treatments were based on three types of plant material: culms (traditional), seeds (sowing), and underground stems to be compared with rhizomes. By combining culms and rhizomes (mixed planting), as well as by combining types of plant materials with types of temporary sand stabilization (compost, straw, cereal rye as cover crop, or reed) seven treatments were obtained: (1) seeds with compost, (2) seeds with straw, (3) seeds with cereal rye, (4) culms with reed, (5) culms and rhizomes with reed, (6) rhizomes with reed and (7) rhizomes with straw (Fig. 1c).

All plant material had been collected from the local foredune area: the bundles were collected from optimal stands by cutting using a hand shovel at 10 cm depth. The seeds were manually harvested in July of the preceding year and originated from vigorous stands where inflorescences were abundant. Mechanical threshing was applied to collect the caryopses. The rhizomes were mechanically collected from the upper 2 - 4 m of the soil profile of vigorous stands by a modified tulip bulb harvesting machine.

After planting the culms, sowing the seeds or disk-harrowing the rhizomes, the sand was temporarily stabilized until the vegetation had developed well enough to take over. The traditional, as well as the mixed planting, was applied in combination with bundles of dry reed (*Phragmites australis*). The sown stands were stabilized by disc-harrowed wheat straw (*Triticum aestivum*) or by broadcasted liquid compost. In one case cereal rye (*Secale cereale*) was sown as a cover crop. The rhizomes were protected by planted reed or disk-harrowed wheat straw. Thus seven treatments (i.e. combinations of planting techniques and temporary sand stabilization) were used. Fences were constructed around the new plantings to prevent rabbit browsing. Further details are given by van der Putten & Kloosterman (1991).

Permanent quadrats (PQs) and recording of vegetation development

14 transects of ca. 150 m each were established across the reinforced foredune ridge: six transects in 1986 in the Northwest area (planted winter 1985/1986) and eight in 1988: four in the Southwest foredunes (planted winter 1986-1987) and four in the central area (planted winter 1987-1988) (Fig. 1c). In the northern and central transects vegetation development was mapped from the first growing season, whereas the survey in southwestern transects started in the second growing season.

The transects were established perpendicular to the coast line. Most transects contained five permanent quadrats (PQs) of 10 m $\times$ 10 m which were stratified into five zones: (1) lower seaward slope, (2) upper seaward slope, (3) top, (4) landward slope and (5) depression down the landward slope (Fig. 1b). From 1986 to 1992 the vegetation in the PQs was recorded each year at the end of the growing season using Braun-Blanquets’ scale (Westhoff & van der Maarel 1973) as transformed according to van der Maarel (1979).

Data analysis

First, data were analysed by classifying the species into nine ecological groups according to van der Meijden et al. (1991) and Mennema et al. (1980). Species not belonging to any of these groups were combined into a separate group, number 0. A complete species list, including their classification into ecological groups, is presented in App. 1. For each ecological group the contribution to the average number of species per PQ and to

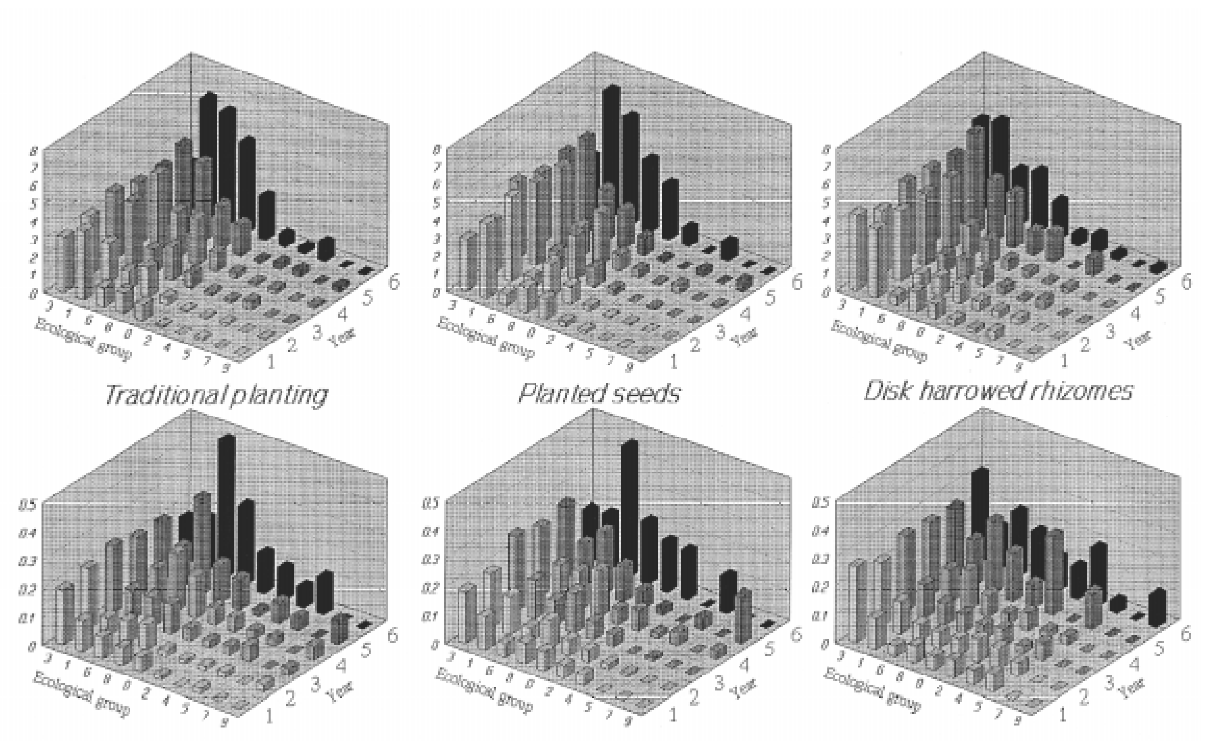

Fig. 2. Contribution of the ecological species groups (for explanation of groups see App. 1) during six successive years to the developing vegetation after establishing *Ammophila arenaria* by traditional planting, seeds in combination with straw and disk-harrowed rhizomes in combination with straw. Upper row: average number of plant species per ecological group. Lowest row: average fraction, expressed as the average number of species from each ecological group, divided by the total number of species in that ecological group present in the total data set.

the total cover (transformed) per PQ was calculated using combinations of plot age, transect and treatment (i.e. planting technique in combination with sand stabilization) as independent factors. For the calculations, the 1987 data of phase 1, the 1988 data of phase 2 and the 1989 data of phase 3 were all considered as records of two-year-old vegetation. In order to make the ecological groups suitable for comparison of treatments, mean fractions of species were computed by relating the number of species per ecological group of each record to the total number of species in that ecological group found in all PQs together. Treatments were compared by plotting the number of species per group, the mean fractions per group and the ground cover per group of six subsequent years of development after establishing *Ammophila*. As the large-scale experiment was not set up as a balanced design, treatments were not randomized for their position along the coast line. Therefore no statistical (e.g. χ^2) tests of independence were applied.

Ordination techniques were applied in order to evaluate the effects of the different planting methods on individual plant species. Because most of the plant species show monotonous relationships in space and time, principal component analysis (PCA) was applied. Redundancy analysis (RA) was performed with age, transect number and treatment as independent factors to optimally display the development with time, at different exposures (zones 1 - 5 as passive variables) along the coastline and the effects of the treatments (Rao 1973; ter Braak 1988). The seven treatments were digitally coded as dummy variables (0/1). Age was defined as time after planting (in years).

In order to correct for the unbalanced design and high correlations between the sets of independent variables, i.e. because not every treatment was repeated, or even used, during each phase of dune reinforcement, weighing and covariables were applied. The records were divided into 14 classes: seven treatments each applied at two coastal sections, i.e. the relatively unexposed northern stretch (phase 1) and the exposed south-western and central stretches (phases 2 and 3, respectively). From each class the number of records was counted. To each record a weight was assigned equal to

1/(max. no. of records from the class the record belongs to). (1)

As the maximum number of records per class was 30, the lowest weight assigned to a record was 1/30 = 0.03.

If a treatment was unique for one of the sections, all records of that treatment received an arbitrary weight of 0.02, as its weight then became somewhat lower than that of records from the most abundant, and therefore the most heterogeneous, class. As the plots with an age of 6 years were present in only one section (i.e. in the Northwest foredune area), they also received the arbitrary weight of 0.02. Covariables were used to remove the effect of position within the transect (distance from the shoreline) and for the effect of the position along the coast (phase 1 versus phases 2 and 3).

Results

Development of Ammophila

The development of biomass and soil cover of the establishing *Ammophila* stands were measured by remote sensing. The stands established by culms produced less biomass and soil cover than the other stands in the first year, but the reverse appeared in the second year (van der Putten & Kloosterman 1991). Culms gave the most homogeneous soil cover and seeds the least. During subsequent years, the stands subject to sand burial (usually PQs 1 and 2) developed into tussocks of vigorous *Ammophila*, whereas at PQs 3 - 5 the vigour of *Ammophila* gradually diminished and successive plant species established.

Plant species in ecological groups

The comparison of species classified into groups according to their ecology did not reveal many differences between planting methods. Therefore, only the results of traditional planting, as well as those of sowing and rhizomes in combination with disk-harrowed straw, are shown (Fig. 2). In all differently established stands, three to four plant species on average belonged to ecological group 3: ‘plants of sea dunes, salt water and salt marshes’ (Fig. 2a). The number of these species represented 18 - 25 % of the total number of species of this ecological group occurring in all permanent quadrats together (Fig. 2b). The species of ecological group 3 contributed, especially until 5 yr after planting, more to the percentage cover (12 - 16 %; cover data not shown) than any other ecological group of species. The second dominant group of plant species belonged to ecological group 1: ‘Plants of cultivated and dry waste places’. This also concerned a mean of three to four plant species (Fig. 2a). However, as the total number of species in this group was higher than in group 3, these plant species represented a lower proportion than those of the group 3 species (Fig. 2b). The species of ‘cultivated lands’ contributed less to the percentage cover than the ‘sea dunes’ (data not shown). Generally, the planting methods were rather similar when comparing them for the absolute and proportional number of species from the ecological group numbers 3 and 1 (Fig. 2a, b).

Most of the remaining plant species belonged to ecological group 6 (‘Plants of dry grasslands and walls’), group 8 (‘Plants of fell-fields, woodland margins and shrubs’) and group 0 (‘other plants’). The latter were introduced as cover crops or by the wheat straw. Virtually no plant species from the remaining ecological groups were recorded in the PQs.

In the 5-yr-old stands, the relative contribution of the unexposed northern part of the foredune area to the averages increased, as no 5-yr-old stands from the westward exposed central foredune area were available. The 6-yr-old stands were only those of the relatively unexposed northern part of the foredune, so that the apparent increase of species from groups 1, 6, 8 and 0 is an artefact caused by the absence of data from the central amd southern foredune, rather than by a successional development in the vegetation.

Cover per species analyzed by PCA and RA

The results of principal component analysis (PCA) and redundancy analysis (RA) solutions resembled each other closely. PCA solution is presented, as it optimally displays variation in plant species composition. The first four axes calculated by PCA explain 43.1 % of the species data and 74.4 % of the relation between species and ‘independent’ environmental variables, i.e. age and treatment (Table 1). Redundancy analysis revealed two main trends in abundance of plant species: one trend related to the number of years after planting (indicated by the arrow ‘Age’) and the other related to the transect number (indicated by the arrow ‘Transect’) (Fig. 3a). For clarity, the species vectors were omitted from Fig. 3a. The species from the centre are plotted separately in Fig. 3b.

The development with age clearly demonstrates a

Table 1. Summary of ordination results from principal component analysis of plant species composition in stands of *Ammophila arenaria* that were established by (seven) different planting techniques.

Axes	1	2	3	4	Total variance
Eigenvalues	0.187	0.114	0.070	0.061	1.000
Species-environment correlations	0.842	0.790	0.705	0.567	
Cumulative percentage variance of:					
Species data	18.7	30.1	37.0	43.1	
Species- environment relations	38.1	58.6	68.6	74.4	
Sum of all unconstrained eigenvalues					1.000
Sum of all canonical eigenvalues					0.347

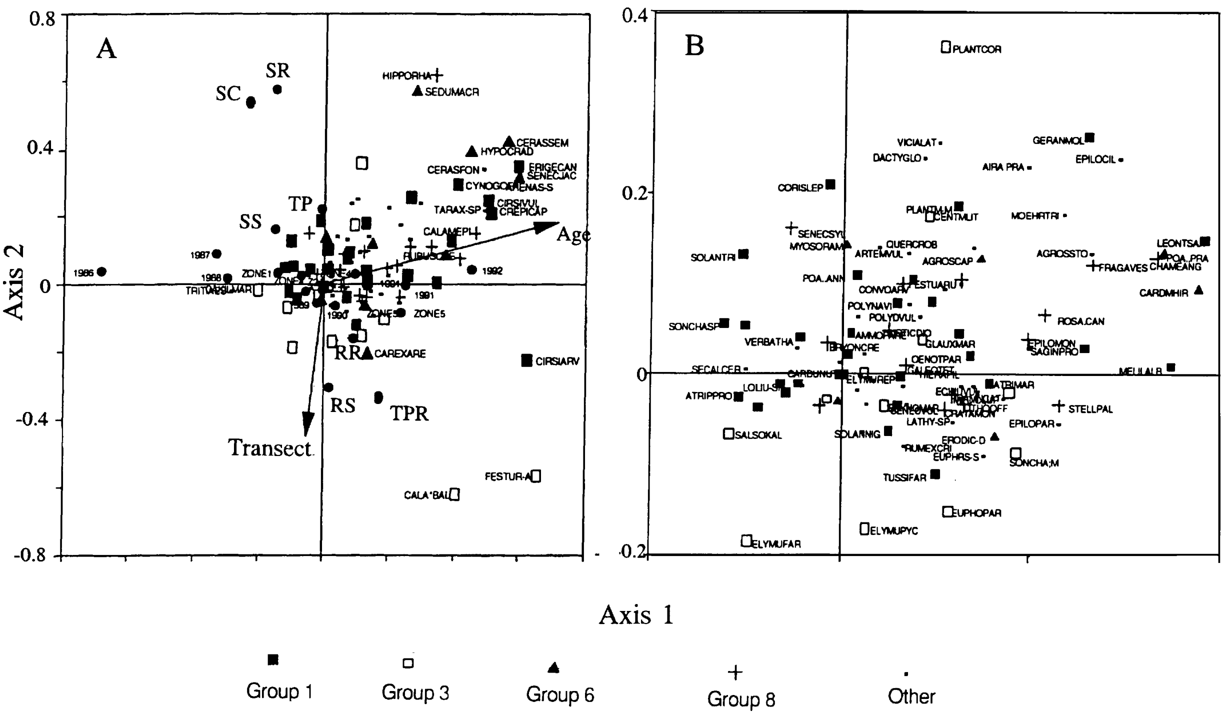

Fig. 3. Ordination diagram with axes 1 and 2: Correlation biplot of species (species names abbreviated with first letters of genus and species names; see App. 1 for complete list of species names (species vectors not drawn) and environmental variables (age and transect number). The mean data of the treatments are plotted as centroids, scaled down by a factor 2. Codes for treatments as used in Figs. 1 and 5. Note that distances in the direction of axis 2 are exaggerated. The four most important species groups (1, 3, 6 and 8) are indicated by symbols. **a.** Overview; **b.** Detail of the centre of the plot.

successional process even within this relatively short period of time. The centroids (i.e. means) of the different years of vegetation surveying (1986-1992) show the youngest stands to be on the left and the oldest on the right in the diagram (Fig. 3a). When interpreting these centroids it should be realized that, except in 1986-1987 in the centroids, permanent plots of three different ages have been combined. The temporal development shows that in the early years of development of pioneer species such as *Cakile maritima* and *Corispermum leptopterum* were at their maximum and that dune grassland and shrub species became more abundant with time (Fig. 3a, b).

The transect arrow is related to the gradual north-south changes along the coast line that remain after correction for the two coastal sections (Fig. 1c). Fig. 3a also shows the centroids of the plots for the different planting treatments. Differences in abundance of species among treatments may be derived from the correlations of the species with the axes 1 and 2 and the treatment centroids in the diagram. The abundance of each species increases in the direction of the vector (the arrow) connecting the origin with the species position. The main contrast between the different planting methods is due to a more pronounced development of rhizome-forming plant species (*Calammophila baltica*, *Festuca rubra* ssp. *arenaria*, *Carex arenaria* and *Cirsium arvense*) in the stands established by methods based on the use of *Ammophila* rhizomes than in other stands. These species were all at the lower side of the diagram. On the other hand, in stands established from seeds in combination with spraying compost or in combination with cereal rye and, to a lesser extent, seeds in combination with disk-harrowed straw, as well as traditionally planted culms (without disk-harrowed rhizomes) annuals, bi-annuals and (mostly non-rhizomatous) perennials, such as *Sedum acre*, *Cerastium fontanum*, *Hypochaeris radicata*, *C. semidecandrum*, and *Hippophaë rhamnoides* were relatively dominant. These species are all at the upper side of the diagram. From the positions of the centroids, sowing in combination with compost or cereal rye and methods based on the use of rhizomes differed the most. The differences between rhizome methods and sowing with straw or the traditional planting method were less, but still apparent (Fig. 3a).

In the centre of Fig. 3a, many species from ecological group 3 ('plants of sea dunes, salt waters and salt

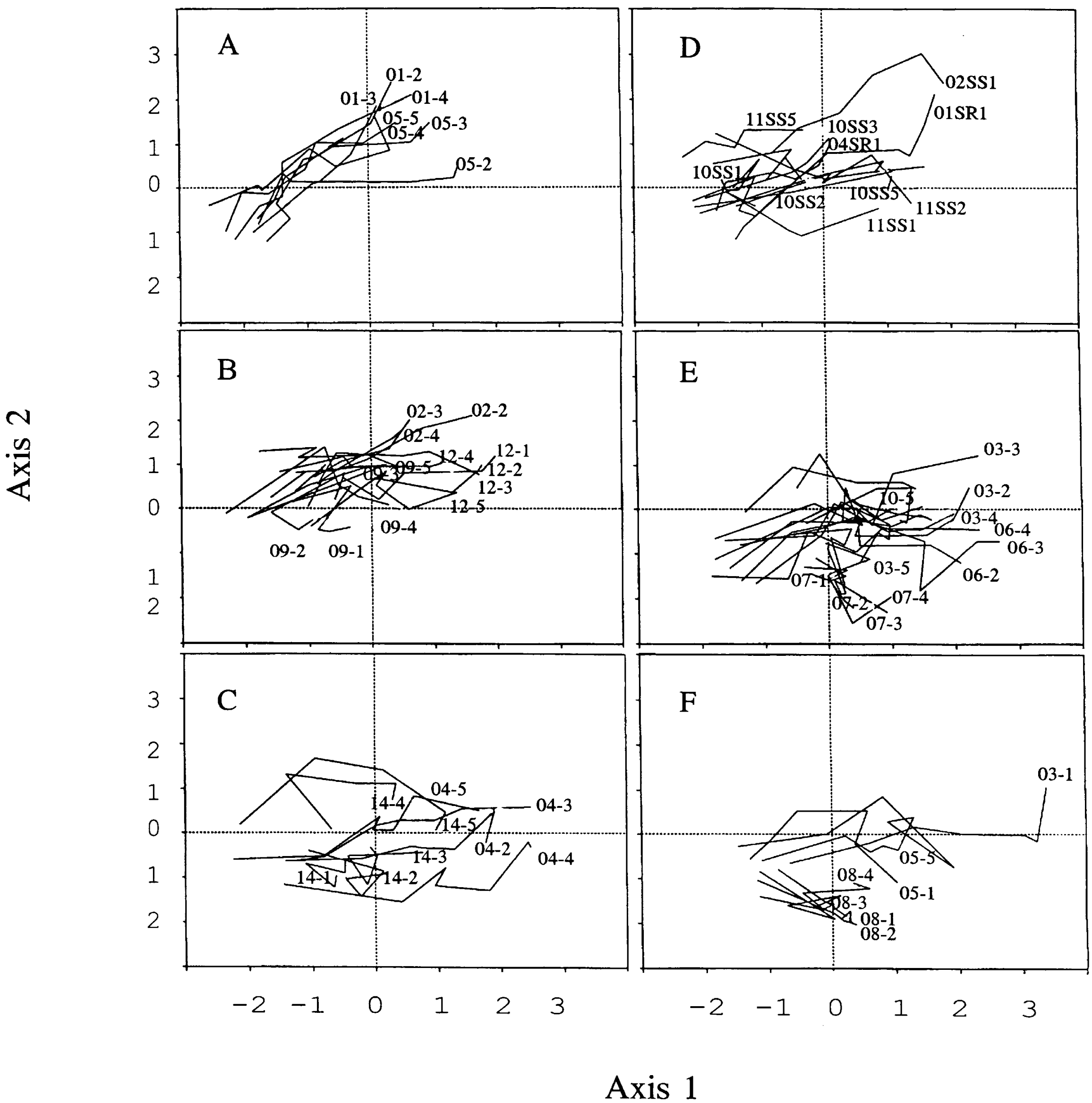

Fig. 4. Pathways of the succession, plotted in the ordination diagram of axes 1 and 2. Note that the distances in the direction of axis 2 are exaggerated. **a.** Seeds with compost; **b.** Traditional planting; **c.** Rhizomes with reed bundles; **d.** Seeds with straw (SS) or cereal rye (SR); **e.** Traditional planting in combination with rhizomes; **f.** Rhizomes with straw. Each line represents one permanent quadrat and is coded, e.g. 01-2; The first symbols indicate the transect number (as explained in Fig. 1c) and the two final symbols identify the situation of the PQ (Fig. 1b).

marshes') and 1 ('plants of cultivated and dry waste places') were present. Among them was *Ammophila*, the only one to be targeted in the vegetation establishing programme (Fig. 3b). All other plants may have been co-dispersed with the planting material, or reached the new foredune by natural dispersal.

The highest rate of development occurred in zones 4 and 5, as the centroids of these zones were shifted, from left of the centre to the right, in correspondence with the direction of the 'Age' arrow (Fig. 3a, b). Zone 1 remained in a rather early stage of succession, which was to be expected considering its exposed position (Fig. 1b). Rates of development did not vary much between treatments. All differences in the locations of the centroids may be explained by time of development or by the position within the transect, for which the treatment centroids have not been corrected.

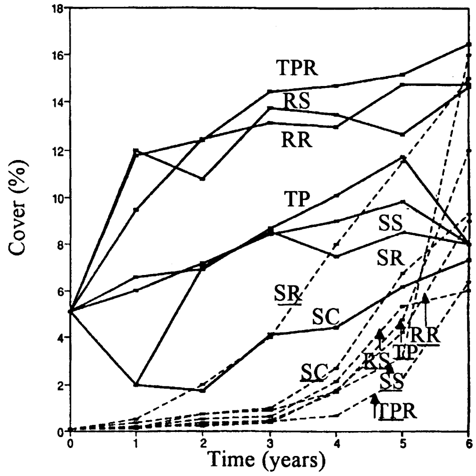

Fig. 5. Sum of percentage ground cover (van der Maarels' transformation of Braun Blanquets' scale) meaned for treatments, of two species groups, derived from the ordination diagram (Fig. 3a) during the first six years of vegetation development. Solid lines represent clonal plant species of the lower right part of the ordination diagram and dashed lines the non-rhizome-forming species from the upper left part. SC = seeds with compost, SS = seeds with straw, SR = seeds with cereal rye, TP = traditional planting, TPR = traditional planting in combination with rhizomes, RR = rhizomes with reed bundles, and RS = rhizomes with straw.

Rates of succession

In order to be able to analyse the rates of succession in more detail, the successional pathways of the individual PQs were plotted in the ordination diagrams (Fig. 4). As 6-yr-old records were only available for stands of the northern foredune area, not much weight should be given to the rightmost part of the lines. From these plots and a plot of sample scores on axes 3 and 4 (not shown) it appears that stands established from rhizomes with bundles of dry reed showed the largest vegetation development progress in the first year (Fig. 4e, f). However, after the first year the rate of succession slowed down and as a result there were no longer any among-treatment differences after 2 years of development (Figs. 4e, f vs 4a - d). Transects 7, 8, 9 and 10 (Figs. 4b, c, d, f) showed poor development, which could be due to their relatively young age. These transects were situated in the stands that became established during the third phase, so that there were only data from four years of development instead of five (phase 2) and six years (phase 1) (Fig. 1c).

Based on the results of the ordination, two groups of plant species may be distinguished that are expected to best express the differences between treatments. The first group consists of *Hippophaë rhamnoides*, *Sedum acre*, *Cerastium fontanum*, *Hypochaerus radicata* and *Cerastium semidecandrum* (Fig. 3a). The second group consists of *Calammophila baltica*, *Festuca rubra* ssp. *arenaria*, *Carex arenaria*, *Elymus farctus*, *Elymus athericus*, *Euphorbia paralias* and *Sonchus arvensis* ssp. *maritima* (Fig. 3a, b). All species from the second group are rhizomatous and able to establish vegetatively. The plot of total cover of these two groups of plant species against time clearly demonstrates that it is mainly the group of rhizome-forming perennials that differs between the treatments (Fig. 5). The treatments based on applying rhizomes of *Ammophila* show a comparable, relatively high, development of the percentage cover in relation to time, due to the rhizomatous perennials. Traditional planting, sowing in combination with straw and, somewhat distinct, sowing in combination with cereal rye showed a different development, as rhizomatous perennials contributed less to the percentage cover (Fig. 5). The development of the percentage ground cover of the perennials in the treatment 'sowing in combination with spraying compost' was lowest of all methods.

With respect to the plant species occurring in the upper part of Fig. 3a (annuals, bi-annuals and, mainly, non-rhizomatous perennials), all planting methods except sowing in combination with cereal rye showed a more or less comparable development. The contribution of these plant species to the percentage ground cover was initially low, but increased from the fourth year onwards (Fig. 5).

Discussion

The large scale experimental establishment of *Ammophila arenaria* on the raised and strengthened coastal foredunes of Voorne offered a unique opportunity to compare the effects of different planting methods on the subsequent vegetation development. Initially, the bare sand-body did not contain a seed bank, so that all plants recorded were either dispersed with the planting material, by the straw used for short-term sand stabilization or by natural (anemochorous or zoochorous) modes of transport. Most planted fields (except some of the smaller fields in transects 1-6) were at an equal distance from the old foredune, so that dispersal distances could not have affected the resulting vegetation development. Within each phase of foredune reinforcement, there was virtually no replication of planting treatments, since these were usually applied once in each phase. However, most treatments were carried out in all three phases, so that they were repeated in subsequent years. Occasional variability in the sources of natural seed dispersal will, therefore, not have caused the observed differences between planting methods.

Two principally different methods of data analysis have been applied. The first method was based on an *a priori* lumping of plant species into ecological groups. According to this comparison there were no substantial differences between the various planting methods. As all differently established stands possessed both a similar number and a similar percentage cover of plant species characteristic of coastal foredunes, no differences in degrees of naturalness among planting methods could be observed.

The *a priori* mode of comparison, however, turned out to be too coarse for examining the actual effects of planting methods on vegetation development. The main distinction between vegetation development in relation to planting methods was due to the relative abundance of clonal perennials in all variations after applying the rhizome method. Stands established from seeds or bundles of culms were relatively sparsely covered by clonal perennials; they were characterized rather by species with a non-clonal life history (Figs. 3, 5). These results are partly in line with earlier reports on poor seedling establishment of foredune plants, especially clonal perennials (e.g. Hewett 1970; Huiskes 1977; Maun 1994; van der Putten & Peters 1995). However, as Hewett (1970) observed colonization of *Festuca rubra* and *Agrostis stolonifera* by outgrowth from traditionally planted stands using bundles of culms, we had expected that the traditionally planted stands would be more comparable to the stands from rhizomes than to those from seeds. There may be three possible explanations: (1) the sites of origin of bundles of culms contained less accompanying plant species than the sites from where rhizomes originated; (2) the collection of plant material for the traditional method may have been more selective than for rhizomes; or (3) the stand architecture may have affected the establishment of the various plant species differently.

Under natural conditions, seedling establishment of *Ammophila* is mostly restricted to moist sites, such as dune slacks (Huiskes 1977). Factors that may have contributed to the large-scale establishment of *Ammophila* could be the artificial surface stabilization between sowing and establishment, fertilizer application (van der Putten 1990) or the relatively moist conditions due to a better water-holding capacity of the dredged sand than of windblown dune sand. The straw may also have enhanced the water-holding capacity of the soil.

Seedling establishment of *H. rhamnoides* was recorded from the first growing season. Unless the seeds have been exposed to acid, they need a stratification period of more than one year. As the new plantings were surrounded by fences it is most likely that birds dispersed the seeds. The seed coat may have been weakened while passing through the bird's gut thus facilitating germination. Van Dieren (1934) mentioned dispersal of *H. rhamnoides* by birds from the inner to the outer dunes.

We expected no *Calammophila baltica*, the sterile hybrid of *Ammophila arenaria* and *Calamagrostis epigejos* (Westergaard 1943; Rihan & Gray 1985) to appear in the sown stands. However, a few specimens were found. Apparently, in this case *A. arenaria* acted as the mother plant receiving pollen of *C. epigejos*.

The development rates of the different stands have also been compared. One of the rhizome methods seemed to have a relatively high rate of development during the first year, but after 3 - 5 yr, this apparent difference disappeared (Fig. 4). The main difference in stand development occurred along the transects. The most seaward zones stayed in an early stage of development, dominated by *Ammophila*, whereas the most landward zones showed the highest rate of development (data not shown). Although the most landward PQs were at the shortest dispersal distance from the original foredune, the gradient in abiotic changes (mainly salt spray and sand deposition) will have had the largest impact on the differences in the development rate in the different zones. Comparison between the northern (relatively unexposed) and southern (exposed) parts of the foredune confirm the dominant effect of the gradient in abiotic factors on the rates of development in the PQs. These will be mainly sand burial (Sykes & Wilson 1990) and salt spray (Sykes & Wilson 1988). Sand burial was only observed in PQs 1 and 2. Salt spray has not been actually measured and older data could not be used because of the heavy geomorphological changes during the past decade.

Conclusions

Vegetation development was affected by the method of establishing *Ammophila*. Methods based on the application of rhizomes favoured the development of clonal perennial plants, whereas the traditional planting and sowing methods resulted in a vegetation dominated by (mostly) non-clonal dicots. At exposed sites along the beach, the vegetation did not develop further than an *Ammophila*-dominated vegetation type, which was in accordance with expectations. Landward, the development of vegetation proceeded, as expected, with the highest rate in the most inner zone. The different developments in the various zones is most likely due to the gradient in abiotic factors, such as salt spray and sand deposition. It is very difficult to draw conclusions on the degree of 'naturalness' of the developing vegetation, as this may be defined in many ways. If the degree of naturalness of vegetation is expressed as the contribution of plants from the foredune environment to both the number of species and the percentage cover, no differences could be distinguished between methods of establishing *Ammophila*.

Implications for management

The differences in development of vegetation as affected by the planting technique could be especially useful at foredune sites where sand deposition is insufficient to guarantee ample vigour of *Ammophila* for erosion control. At such sites, artificial replacement of degenerated *Ammophila* by establishing successional plant species appeared to be constrained by water repellency of the soil and rabbit browsing (van der Putten & Peters 1995). When, at such sites, methods based on the use of rhizomes are applied, all elements for development of a sand-stabilizing vegetation will be introduced at once, which will be in favour of the replacement of degenerating *Ammophila*. At other sites more exposed to sand deposition, the vegetation development will be affected by environmental factors more than by the method of planting. At such exposed sites, therefore, the vegetation development does not have to be a major consideration when choosing between the various methods of establishing *Ammophila* for erosion control. A cost-benefit evaluation of the different planting methods has been made by van der Putten & Kloosterman (1991).

Acknowledgements. Thanks are due to Hans Koelewijn for supporting data management. This study was financially supported by the Hydraulic Engineering Division of the Ministry of Transport, Public Works and Water Management.

References

Anon., 1989. *Guide to the assessment of the safety of dunes as a sea defence*. Report Technical Advisory Committee on Water Defence, Delft.

Adriani, M.J. & Terwindt, J.H.J. 1974. *Sand stabilization and dune building*. Rijkswaterstaat Communications no. 19.

Arens, S.M. & Wiersma, J. 1994. The Dutch foredunes; inventory and classification. *J. Coast. Res.* 10: 189-202.

Barr, D.A. & McKenzie, J.B. 1976. Dune stabilization in Queensland, Australia, using vegetation and mulches. *Int. J. Biometeorol.* 20: 1-8.

Brown, R.L. & Hafenrichter, A.L. 1948. Factors influencing the production and use of beachgrass and dunegrass clones for erosion control. II. Influence of density of planting. *J. Am. Soc. Agron.* 40: 603-609.

Hansen, K. & Vestergaard, P. 1986. Initial establishment of vegetation in a man-made coastal area in Denmark. *Nord. J. Bot.* 6: 479-495.

Hewett, D.G. 1970. The colonization of sand dunes after stabilization with marram grass (*Ammophila arenaria*). *J. Ecol.* 58: 653-668.

Hillen, R. & Roelse, P. 1995. Dynamic preservation of the coastline in the Netherlands. *J. Coastal Conserv.* 1: 17-28.

Hobbs, R.J., Gimingham, C.H. & Band, W.T. 1983. The effects of planting technique on the growth of *Ammophila arenaria* (L.) Link and *Leymus arenarius* (L.) Hochst. *J. Appl. Ecol.* 20: 659-672.

Huiskes, A.H.L. 1977. The natural establishment of *Ammophila arenaria* from seed. *Oikos* 29: 133-136.

Knutson, P.L. 1978. Planting guidelines for dune creation and stabilization. In: *Coastal Zone. Proceedings of the Symposium on Technical, Environmental, Socioeconomic and Regulatory Aspects of Coastal Zone Management 1978*. pp. 762-779. ASCE, San Francisco, CA.

Maun, M.A. 1994. Adaptations enhancing survival and establishment of seedlings on coastal dune systems. *Vegetatio* 111: 59-70.

Mennema, J., Quené-Boterenbrood, A.J. & Plate, C.L. 1980. *Atlas of the Netherlands Flora. 1 Extinct and very rare species.* Dr. W. Junk, The Hague.

Mitchell, A. 1974. Plants and techniques used for sand dune reclamation in Australia. *Int. J. Biometeorology* 18: 168-173.

Pilon, J.J. 1988. Kustafslag op Voorne in het verleden. *Waterschapsbelangen* 73: 255-259.

Rao, C.R. 1973. *Linear statistical interference and its applications.* 2nd. ed.. Wiley, New York, NY.

Rihan, J.R. & Gray, A.J. 1985. Ecology of the hybrid marram grass × *Calammophila baltica* in Britain. *Vegetatio* 61: 203-208.

Sykes, M.T. & Wilson, J.B. 1988. An experimental investigation into the response of some New Zealand sand dune species to salt spray. *Ann. Bot.* 62: 159-166.

Sykes, M.T. & Wilson, J.B. 1990. An experimental investigation into the response of New Zealand sand dune species to different depths of burial by sand. *Acta Bot. Neerl.* 39: 171-181.

ter Braak, C.J.F. 1988. *CANOCO - a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1).* Groep Landbouwwiskunde, Wageningen.

Tsuriëll, D.E. 1974. Sand dune stabilization in Israel. *Int. J. Biometeorology* 18: 89-93.

van Bohemen, H.D. & Meesters, H.J.N. 1992. Ecological engineering and coastal defence. In: Carter, R.W.G., Curtis, T.G. & Sheehy-Skeffington, M.J. (eds.) *Coastal dunes. geomorphology, ecology and management.* Proceedings of the Third European Dune Congress, Galway/Ireland, pp. 369-378. A.A. Balkema, Rotterdam, Brookfield.

van der Laan, D. 1985. Changes in the flora and vegetation of the coastal dunes of Voorne (The Netherlands) in relation to environmental changes. *Vegetatio* 61: 87-95.

van der Maarel, E. 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 39: 97-114.

van der Meijden, R., Weeda, E.J., Holverda, W.J. &

Hovenkamp, P.H. 1990. *Heukels' Flora van Nederland.* Wolters-Noordhoff, Groningen.
van der Meijden, R., van Duuren, L., Weeda, E.J. & Plate, C.L. 1991. Standaardlijst van de Nederlandse Flora 1990. *Gorteria* 17: 75-127.
van der Putten, W.H. 1990. Establishment and management of *Ammophila arenaria* (marram grass) on artificial coastal foredunes in The Netherlands. In: Davidson-Arnott, R. (ed.) *Proceedings Canadian symposium on coastal sand dunes*, pp. 367-387. Associate Committee on Shorelines, National Research Council and Guelph University, Guelph.
van der Putten, W.H. & Kloosterman, E.H. 1991. Large-scale establishment of *Ammophila arenaria* and quantitative assessment by remote sensing. *J. Coastal Res.* 7: 1181-1194.
van der Putten, W.H. & Peters, B.A.M. 1995. Possibilities for the management of coastal foredunes with deteriorated stands of *Ammophila arenaria* (marram grass). *J. Coast. Conserv.* 1: 29-39.
van Dieren, J.W. 1934. *Organogene Dünenbildung: eine geomorphologische Analyse der Dünenlandschaft der West-Friesischen Insel Terschelling mit pflanzensoziologischen Methoden.* Martinus Nijhoff, Den Haag.
Voogt, H. 1988. Verzwaring van de zeereep en problemen met helmbeplanting. *Waterschapsbelangen* 73: 208-213.
Westergaard, M. 1943. Cyto-taxonomical studies on *Calamagrostis epigejos* (L.) Roth, *Ammophila arenaria (*L.) Link, and their hybrids *(Ammophila baltica* (Fluegge) Link)*. Biol. Skr.* 2: 1-68.
Westhoff, V. & van der Maarel, E. 1973. The Braun-Blanquet approach. In: Whittaker, R.H. (ed.) *Ordination and classification of communities.* Handbook of Vegetation Science. Part I. pp. 617-726. Junk, The Hague.

Received 25 June 1996;
Revision received 25 June 1997;
Accepted 2 July 1997.

App. 1 on page 190

App. 1. Survey of ecological groups (E.G.) with species name abbreviation as used in ordination plots is according to the first letters of both the genus and species names), and presence. Figures are numbers of plots per year of survey. Finally, total numbers of species and numbers of recorded permanent quadrats are given for each year.

	Year of survey						
	1986	1987	1988	1989	1990	1991	1992
E.G. 1. Plants of cultivated and dry places							
Cirsium arvense	6	20	40	47	50	54	58
Convolvulus arvensis	0	0	0	0	0	1	2
Epilobium ciliatum	0	5	11	19	15	17	18
Artemisia vulgaris	0	0	0	1	1	1	1
Erigeron canadensis	0	23	44	57	51	52	54
Solanum triflorum	0	8	7	7	6	2	0
Lolium perenne	8	6	15	13	8	9	3
Sonchus asper	0	0	2	0	0	0	0
Sonchus oleraceus	8	7	27	30	21	17	5
Capsella bursa-pastoris	0	0	4	2	0	0	0
Plantago major ssp. *major*	0	0	2	2	1	2	2
Lolium multiflorum	0	0	1	0	0	0	0
Tussilago farfara	0	3	9	7	7	6	7
Senecio vulgaris	0	0	0	0	2	0	0
Crepis capillaris	0	0	0	2	12	25	30
Senecio viscosus	0	0	6	4	4	5	2
Carduus nutans	1	0	0	0	0	0	0
Lactuca serriola	0	2	3	1	0	0	0
Verbascum thapsus	0	0	1	0	0	0	0
Chenopodium polyspermum	5	2	0	0	0	0	2
Elymus repens	0	0	2	6	3	1	2
Sagina procumbens	0	0	0	1	1	1	3
Chenopodium album	0	0	0	4	12	3	0
Polygonum persicaria	0	0	3	2	0	0	0
Matricaria maritima	6	9	10	10	8	10	9
Echium vulgare	0	0	1	3	2	3	5
Corispermum leptopterum	9	3	6	10	11	10	5
Cirsium vulgare	1	2	5	19	24	33	35
Atriplex prostrata	3	0	1	0	0	0	0
Lepidium ruderale	0	1	0	0	0	0	0
Poa annua	11	12	16	10	13	11	13
Polygonum aviculare	3	1	5	3	5	3	2
Cynoglossum officinale	2	6	18	24	19	31	31
Melilotus alba	2	3	4	5	7	12	9
Geranium molle	0	0	1	1	3	6	10
Solanum nigrum	1	0	1	0	2	0	0
Verbascum nigrum	0	0	0	0	0	1	0
E.G. 2. Plants of disturbed or open, damp to wet soils, poor in humus							
Agrostis stolonifera	1	0	6	9	7	12	10
Pulicaria dysenterica	0	0	0	0	0	0	1
Rumex crispus	0	0	0	4	2	5	3
Festuca arundinacea	0	0	1	4	4	4	4
Sagina nodosa	0	0	0	0	0	0	2
Centaurium littorale	0	0	0	1	2	3	0
Leontodon autumnalis	0	0	0	1	1	0	0
Trifolium repens	2	1	2	1	3	3	0
Potentilla anserina	0	1	1	1	1	1	0
E.G. 3. Plants of sea dunes, salt water and salt marshes							
Elymus farctus	0	0	0	0	3	4	4
Eryngium maritimum	0	0	0	2	0	0	0
Festuca rubra ssp. *arenaria*	5	12	29	46	49	52	54
Ammophila arenaria	22	28	67	68	68	68	68
Plantago coronopus	0	0	0	1	2	3	2
Oenothera parviflora	0	0	0	0	1	1	1
Salsola kali	2	0	1	1	6	0	1
Glaux maritima	0	1	2	3	2	4	3
Calammophila baltica	14	12	44	45	47	48	51
Beta vulgaris ssp. *maritima*	0	0	0	0	1	0	0
Elymus athericus	0	0	0	2	1	1	1
Sonchus arvensis var. *maritimus*	9	22	59	68	62	65	60
Cakile maritima	4	2	0	0	12	9	5
Plantago maritima	0	0	0	0	0	0	1
Euphorbia paralias	0	0	3	4	3	3	3
Spergularia salina	0	1	0	0	0	0	0
E.G. 4. Plants of fresh water and neighbouring shores							
Salix purpurea	1	1	2	2	0	0	0
Solanum dulcamara	0	2	9	6	7	4	7
Epilobium hirsutum	0	0	0	0	0	1	1
Eupatorium cannabinum	0	0	7	6	5	7	7
Phragmites australis	0	0	1	1	1	0	1
Epilobium parviflorum	0	0	0	0	14	5	5
Lycopus europaeus	0	0	0	0	0	0	1

	Year of survey						
	1986	1987	1988	1989	1990	1991	1992
E.G. 5. Plants of fertilized grasslands on moderately rich to rich, moist to wet soils							
Holcus lanatus	0	0	2	1	0	2	1
Medicago lupulina	1	1	2	4	2	4	2
Dactylis glomerata	1	0	0	0	1	1	1
Daucus carota	1	0	1	1	1	0	0
Trifolium pratense	3	2	2	2	0	1	0
Plantago lanceolata	1	1	1	1	1	1	0
Poa pratensis	4	7	21	21	18	22	29
Rumex acetosa	0	0	4	0	0	0	0
E.G. 6. Plants of dry grasslands and walls							
Cerastium arvense	0	0	0	0	0	0	1
Carlina vulgaris	0	0	0	0	1	0	0
Erodium cicutarium ssp *dunense*	3	3	4	7	9	9	8
Viola curtisii	0	0	0	0	0	1	1
Eryngium campestre	0	0	0	1	1	1	1
Arenaria serpyllifolia ssp. *serpyl.*	0	0	0	1	7	25	36
Hypochaeris radicata	0	0	1	0	14	21	27
Agrostis capillaris	0	0	0	0	0	3	2
Senecio jacobaea	11	24	46	52	48	55	58
Leontodon saxatilis	0	0	0	1	6	2	12
Cardamine hirsuta	0	0	1	0	7	12	24
Vicia lathyroides	0	0	0	0	0	0	2
Hieracium pilosella	0	0	0	0	0	1	3
Sedum acre	0	1	4	2	8	11	13
Myosotis ramosissima	0	0	0	0	0	1	0
Erigeron acris	0	0	0	0	0	3	0
Veronica arvensis	0	0	0	0	0	0	2
Aira praecox	0	0	0	0	0	0	3
Cerastium semidecandrum	0	0	0	1	13	25	30
Carex arenaria	0	0	0	2	3	3	2
E.G. 7. Plants of moors, peat bogs, unfertilized grasslands and calcareous marshes							
Salix repens	0	0	0	0	0	0	1
Euphrasia stricta	0	0	0	0	1	0	2
E.G. 8. Plants of fell-fields, woodland margins and shrubs							
Epilobium montanum	0	0	0	0	0	4	5
Fragaria vesca	0	0	0	1	2	6	9
Senecio sylvaticus	22	25	53	51	52	38	51
Rubus caesius	0	0	7	12	22	29	29
Inula conyzae	0	0	0	1	1	4	6
Hippophaë rhamnoides	1	6	15	14	20	27	29
Calamagrostis epigejos	0	2	4	7	14	15	24
Stellaria pallida	0	1	4	3	6	8	9
Crataegus monogyna	0	0	0	0	0	2	1
Galeopsis tetrahit	0	1	2	1	1	2	0
Sambucus nigra	1	1	3	3	4	3	2
Lithospermum officinale	0	0	0	1	1	1	1
Urtica dioica	1	1	3	3	3	1	1
Bryonia cretica ssp. *dioica*	0	0	2	1	1	0	0
Rosa canina	0	0	1	1	2	3	5
Galium aparine	0	0	1	0	0	0	0
Rhamnus catharticus	0	0	1	0	2	4	3
Euonymus europaeus	0	0	0	1	1	1	0
Chamerion angustifolium	0	0	0	0	1	10	16
E.G. 9. Plants of woods							
Epipactis helleborine	0	0	0	0	0	0	1
Moehringia trinervia	0	0	0	0	1	2	8
Polypodium vulgare	0	0	0	0	0	0	2
Hieracium umbellatum	0	0	0	0	0	1	0
Quercus robur	0	0	0	0	1	1	0
E.G. 0. Other plant species							
Epilobium spec.	0	0	0	0	0	3	0
Trifolium spec.	0	0	0	0	0	2	0
Lathyrus spec.	0	0	0	0	1	0	1
Taraxacum spec.	1	9	33	39	39	44	43
Secale cereale	3	2	0	0	0	0	0
Triticum aestivum	8	6	16	5	0	1	0
Vicia spec.	0	0	0	1	1	1	1
Number of species	38	46	69	79	88	93	92
Number of permanent quadrats	24	26	68	68	68	68	68