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Vegetation succession and lichen diversity on dry coastal calcium-poor dunes and the impact of management experiments

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Abstract. The negative impact of grass and moss encroachment on the botanical diversity of West European coastal dunes attracted increasing attention in the 1990s. This paper focuses on moss encroachment during primary succession in the xeroseries. Until the mid-1970s, vegetation types rich in species of the lichen genera *Cladonia* and *Cladina* were found on the fixed, *Corynephorus canescens*-dominated, so-called grey dunes all over the island of Terschelling, The Netherlands. In addition, species of *Hypogymnia*, *Parmelia* and *Usnea*, which usually grow on trees, occurred here terrestrially on moss carpets or bare sand. These vegetation types are still present on the Noordsvaarder, a nature reserve in the western part of the island. They occur on parts of seven dune ridges parallel to the coast and form a chronosequence in which age increases with distance from the sea.

Our study found the highest lichen diversity on the second and third dune ridges in a stage of primary succession that can be assigned to the *Violo-Corynephoretum*. The changes from lichen-rich to moss-dominated stadia were significantly related to soil development and acidification in connection with the ageing of the dune soil.

The superficial cutting of sods in moss-encroached vegetation appeared to be unsuccessful as a management technique for restoring the biodiversity of cryptogams. Our findings suggest that the best option for maintaining lichen vegetation in the *Violo-Corynephoretum* is the blow-in of sand with a subneutral or neutral pH from reactivated and natural blowouts or from foredunes, with increasing lime content respectively.

Keywords: Acidification; Biodiversity; *Campylopus introflexus*; *Corynephorus canescens*; Chronosequence; Moss encroachment; Lime content; Sand drift; Sod cutting.

Nomenclature: Van der Meijden (1990) for higher plants; Touw & Rubers (1989) for mosses; Purvis et al. (1992) for lichens. A set of lichen specimens has been deposited at the herbarium of Dr. A. Aptroot (C.B.S. Baarn) – herbarium code ABL (Taxon 44: 258).

Introduction

In the last 30 years there has been a serious decline in the plant diversity in the dunes dominated by grey hairgrass *Corynephorus canescens*, the so-called grey dunes of the phytogeographic 'Waddendistrict' of The Netherlands (Ketner-Oostra 1992; Westhoff 1994; Ketner-Oostra & van der Loo 1998). To a large extent the species-rich, open dry dune grasslands along the Dutch coast have changed into a vegetation dominated by tall grass species or by mosses (Vertegaal et al. 1991). In particular the encroachment by the neophytic moss *Campylopus introflexus* (van der Meulen 1987) has drastically reduced species diversity (Kooijman & de Haan 1995; Kooijman & van der Meulen 1996).

Terschelling is one of the West Frisian islands (Fig. 1). Most of these islands are characterized by dune sand low in $CaCO_3$-content, usually below 0.5% (Eisma 1968). Terrestrial lichens, mainly from the genera *Cladonia* and *Cladina* but also several rare, usually epiphytic species used to grow all over the grey dune area of these islands, and were especially well developed on Terschelling (Brand & Ketner-Oostra 1983). However, by the 1990s, only a few areas with well-developed terrestrial lichen communities remained.

For the period between 1937 and 1946, Westhoff (1947) described a high cryptogamic biodiversity in the dry dune grasslands of the three westernmost islands in the Wadden Sea. From 1966 to 1972 all lichen-rich phases within this *Violo-Corynephoretum* Westhoff ex Boerboom 1960 were reviewed for Terschelling, from open pioneer, half-closed *Cladonia*-rich vegetation to closed reindeer lichen carpets (Ketner-Oostra 1989). Types transitional to dwarf shrub heath (composed of *Empetrum nigrum*, *Calluna vulgaris* and *Salix repens*) were also present, dominated by mosses, mainly *Dicranum scoparium*. Lichens, such as *Bryoria fuscescens*, *Evernia prunastri*, *Hypogymnia physodes*, *H. tubulosa*, *Parmelia sulcata*, *Pseudevernia furfuracea* and *Usnea subfloridana*, which are usually epiphytic, were growing on these moss carpets, but they also occurred in open sites

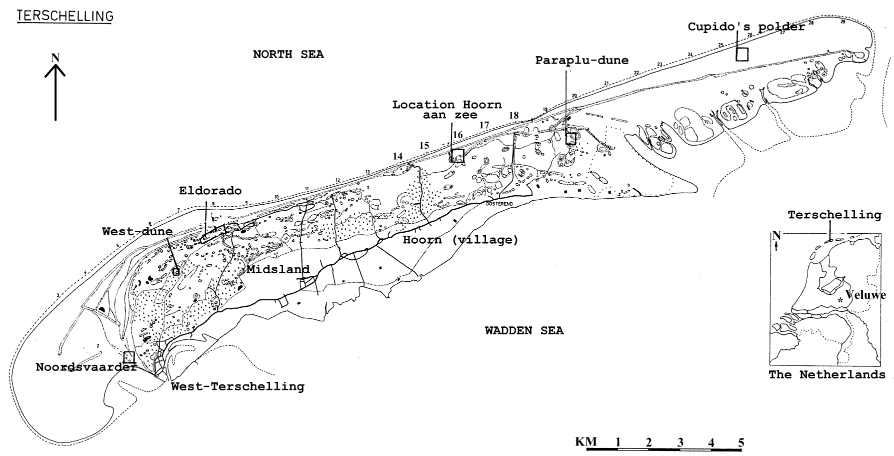


Fig. 1. Location of the study sites.

with only *Corynephorus canescens* (Ketner-Oostra 1972; Brand & Ketner-Oostra 1983). Both Westhoff (1947) and Barkman (1958) mentioned these special lichen-rich 'variants' within the *Violo-Corynephoretum* , which resemble the assemblage found elswhere on the NW side of the trunks of living trees. The epiphytic association *Parmelietum furfuraceae* includes the lichens mentioned here and is an aerohygrophytic and toxiphobic association, that is also strongly wind resistent. The habitat on moss-covered dune soil may be characterized by (1) a electrolyte concentration, (2) drought periods controlled by the frequency of precipitation and fog and (3) rate of evaporation, (4) water capacity whereas (5) illumination and (6) actual pH as direct factors are less important (Barkman 1958). Since 1975 this epiphytic association, occurring in The Netherlands in some refugia, has decreased considerably; the decline has been ascribed to the large emission of ammonia from the bioindustry (van Herk et al. 2000).

Between 1990 and 1995 the combination of these usually epiphytic species and several *Cladonia* species could only be found on Terschelling on relatively young dune ridges on the Noordsvaarder (Fig. 2), a sandbank grown together with the western side of the main island since 1900 (Fig. 3). This combination of lichens was also present on the slopes of the 'Paraplu-dune', where the vegetation is still influenced by moving sand (Ketner-Oostra 1997).

Terschelling dry dune vegetation has changed over large areas because of the encroachment of graminoids, mainly *Ammophila arenaria* and *Carex arenaria* (van der Meulen et al. 1996), while on secondary open sand the dominance of *Campylopus introflexus* is increasing (Ketner-Oostra & van der Loo 1998; Westhoff 1994). Biermann (1996, 1999) noted this trend in *Corynephorus* vegetation on the East Frisian islands (Germany).

In 1991 a nation-wide project (EGM, effect-oriented management against acidification and eutrophication of

Table 1. Frequency and characteristic cover of terrestrial lichens and mosses, as compared with those of graminoids, on the 2nd - 5th dune ridges on the Noordsvaarder. Frequency classes 1 = < 20%; 2 = 21 - 40 %; 3 = 41 - 60 %; 4 = 61 - 80 %; 5 > 80%. Cover estimates (%) from relevés of 2 m× 2 m (Ketner-Oostra 1997). The decreasing number of relevés points to increasing homogeneity.

Table 1.

Dune ridge	**2**	**3**	**4**	**5/6**
Number of relevés	14	7	6	4***
Graminoids				
Ammophila arenaria	3* (1)**	-	5 (7)	5 (2)
Corynephorus canescens	5 (8)	5 (18)	5 (8)	4 (5)
Festuca rubra	5 (2)	3 (<1)	4 (2)	2 (2)
Carex arenaria	2 (4)	5 (4)	5 (2)	4 (2)
Mosses				
Ceratodon purpureus	5 (17)	5 (5)	-	-
Brachythecium albicans	4 (20)	1 (<1)	-	-
Cephaloziella divaricata	4 (5)	3 (4)	-	2 (<1)
Hypnum cupressiforme	2 (5)	4 (9)	5 (27)	2 (<1)
Dicranum scoparium	2 (<1)	2 (5)	5 (40)	3 (50)
Campylopus introflexus	1 (7)	3 (10)	4 (10)	3 (95)
Polytrichum juniperinum	1 (<1)	2 (<1)	1 (2)	2 (2)
Hypnum jutlandicum	1 (<1)	1 (<1)	2 (2)	2 (30)
Tortula ruralis ssp. *ruraliformis*	1 (1)	-	-	-
Polytrichum piliferum	1 (<1)	-	-	-
Lichens				
Cladonia scabriuscula	4 (20)	5 (9)	5 (1)	-
Cladonia foliacea	3 (10)	5 (30)	2 (<1)	2 (8)
Cladonia pocillum	3 (8)	3 (1)	-	-
Cladonia furcata	1 (2)	4 (4)	1 (<1)	-
Cladonia chlorophaea s.l.	1 (7)	3 (1)	3 (<1)	-
Coelocaulon aculeatum	2 (2)	4 (6)	-	-
Cladonia ramulosa	3 (4)	3 (4)	-	2 (<1)
Cladonia subulata	3 (3)	3 (1)	-	-
Cladonia macilenta	1 (<1)	2 (<1)	-	2 (2)
Cladonia merochlorophaea	1 (3)	1 (<1)	-	-
Cladonia humilis	2 (7)	-	1 (<1)	-
Cladonia rangiformis	1 (<1)	-	-	-
Cladonia fimbriata	1 (<1)	-	-	-
Cladonia glauca	-	3 (3)	3 (1)	2 (<1)
Cladonia floerkeana	-	2 (<1)	-	-
Cladina portentosa	-	-	2 (<1)	-
Cladina coccifera	-	-	-	2 (2)
Micaria prasina	-	-	-	2 (<1)
Normally epiphytic lichens				
Hypogymnia physodes	3 (1)	1 (<1)	1 (<1)	-
Hypogymnia tubulosa	2 (<1)	-	-	-
Parmelia sulcata	2 (<1)	-	-	-
Evernia prunastri	1 (<1)	-	-	-

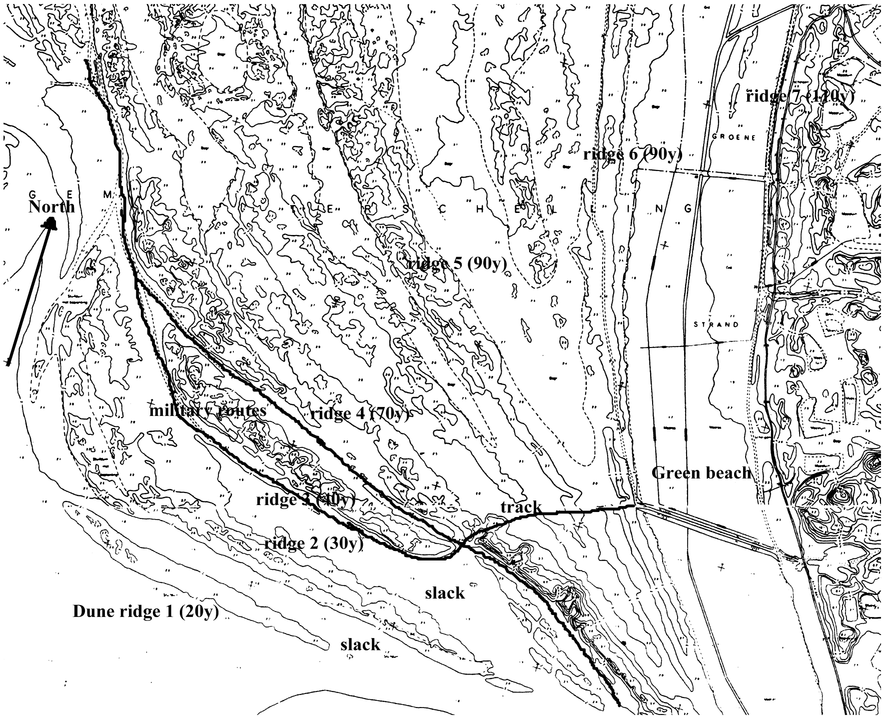


Fig. 2. Dune ridges on the Noordsvaarder, alternating with dune slacks, some of which are still connected with the sea.

dry dunes) was launched in The Netherlands. Measures to restore open dry dune grasslands were aimed at controlling grass encroachment and improving the competitive position of characteristic species, including cryptogams (Vertegaal et al. 1991). Two locations on Terschelling were included in this project (see Fig. 1) with large-scale vegetation removal from 11 dune slopes at Eldorado, a dune area NE of the village of West-Terschelling (van der Meulen et al. 1996). Small-scale mowing and sod cutting experiments were carried out on a former research dune (Ketner-Oostra 1992), north of Oosterend (van der Meulen et al. 1996; Veer & Kooijman 1997). In this project vegetation and soil research focused on the hypothesis that grass encroachment is related to aerial deposition of nitrogen. One of the conclusions was that atmospheric N-input is an important source of N, whereas in grass-dominated plots mineralization largely exceeds the input of N (Veer 1997).

The natural and man-induced soil acidification in the dry dunes was studied by de Vries et al. (1994). In calcium-poor dry dunes changes in the soil solution chemistry are the result of silicate weathering; they are dominated by the dissolution of aluminium hydroxides. In the almost pure quartz, sand grains, low in free minerals (Eisma 1968) silicates are expected to loose secondary metal ions under influence of plant growth. This process is important in the soil buffer system between pH 6.5 and 4.5 (the silicate buffer range). The dissolution of Al-hydroxides involves the loss of Al^{3+}-ions (de Vries et al. 1994). This aluminium buffer range becomes important below pH 4.5. The secondary metal ions mentioned should be studied to assess the state of soil acidification, as they are connected to the humic complex and form a natural buffering system against natural plant acids and 'acid rain'.

In 1995 the State Forestry Service, province of Fryslân (Friesland) commissioned the first author to start a programme to monitor actual lichen-rich *Corynephorus* vegetation threatened by moss and grass encroachment in the Terschelling dunes (Ketner-Oostra 1997). This project was initiated because of concern with the decline in biodiversity of the grey dunes in the Wadden district. The aim was to ascertain the effect of former management and to give advice on future management. It is questionable whether management will have any effect at all, as normally, in the grey dunes, cryptogam diversity is a temporary successional stage leading to successive stages with moss carpets, as forerunners of dune heath (Barendregt 1982; Ketner-Oostra 1989).

We based the following hypotheses on these considerations:

1. In the Wadden district, lichen communities are especially well developed in the earlier stages of the succession or when calcareous substrate is still being supplied by wind.
2. This lichen diversity is a time-limited phenomenon, related to soil development, i.e. a decrease in pH, leach-

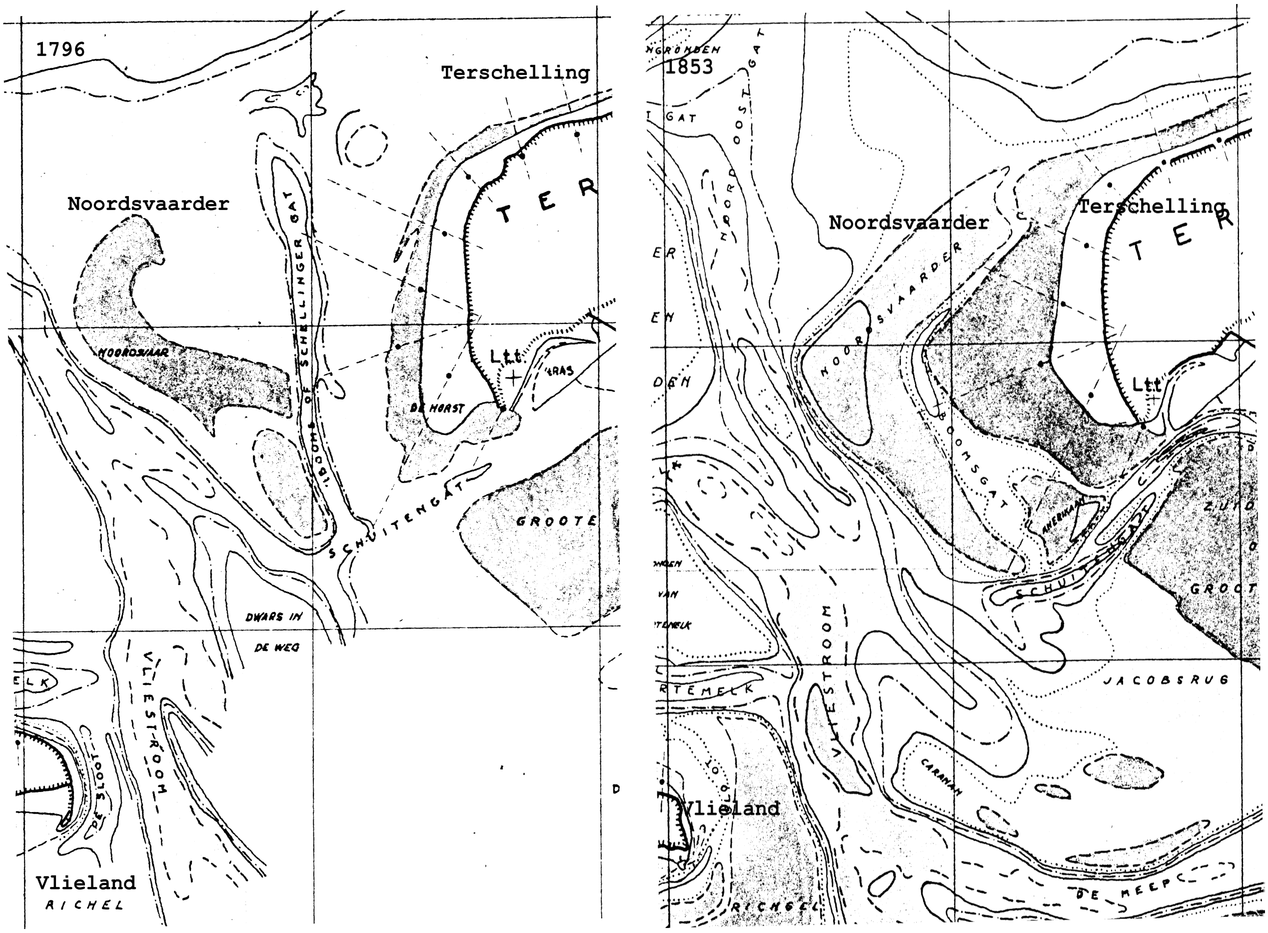


Fig. 3. The process of the joining of the Noordsvaarder sand bank to the main island of Terschelling from (**a**) 1796, via (**b**) 1853 to (**c**) 1898, as illustrated by old maps.

ing of calcium from the topsoil and an increase in organic matter.

3. The lichen-rich stages can be conserved or restored by management practices.

Based on these hypotheses we wished to answer the following questions:

1. What is the relation between the species composition of the vegetation, the occurrence of lichens and soil quality?

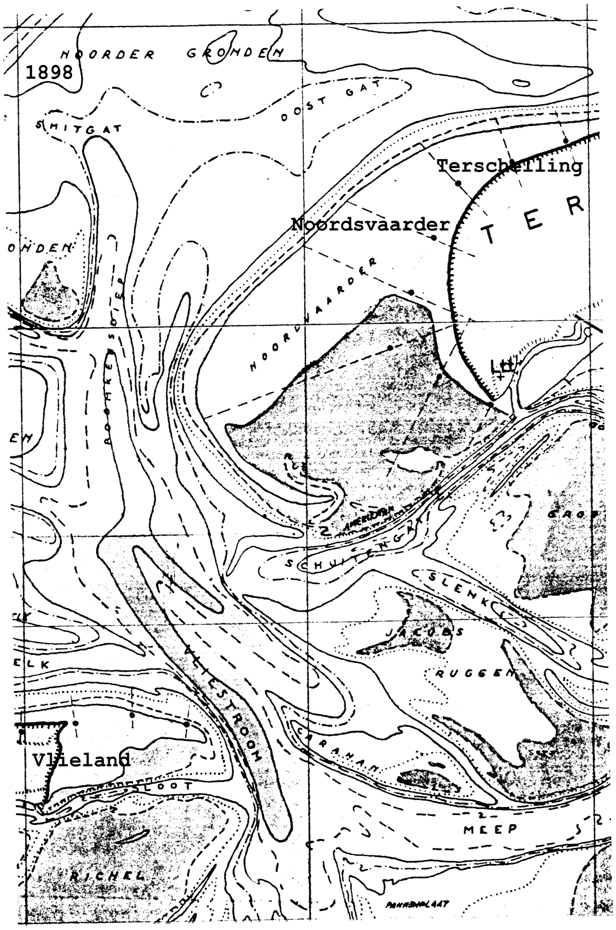
2. To what extent are changes from lichen-rich to moss-dominated *Violo-Corynephoretum* communities due to natural developments in vegetation composition and soil quality?

3. Is it possible to maintain or revitalize lichen-rich dune vegetation through special management?

Material and Methods

Soil origin and characteristics

Terschelling is the third island from the southwest in the chain of West Frisian islands phytogeographically forming the so-called Wadden district. This district is mainly characterized by Early and Middle Pleistocene sands redeposited in the Saalien by the rivers Meuse and Rhine (Eisma 1968). This parent material is poor in lime and iron, and in recent times no shell fragments have been deposited, partly because the coast is retreating. The result is that only limited amounts of weatherable minerals, notably iron and lime, are present (Eisma 1968). Furthermore the mineral ions are less bound than in the calcium-rich dunes. Through natural acidification leaching was reinforced and the older dunes almost completely decalcified. The dune soils may have a relative high phosphorus availability, due to the comparatively loose nature of phosphorus sorption. As a result the area is nitrogen-limitated (Kooijman et al. 1998).



Climate

Due to the surrounding sea the climate on the West Frisian islands is almost extreme oceanic (Ellenberg et al. 1992). Compared with the inland area of The Netherlands, summer temperatures are lower and in winter there are fewer days with frost. Both average daily temperature (in July > 14 °C) and the seasonal temperature variations are less than on the mainland. There are less than five summer days (temperature > 25°C) and the number of icy days (with a max. temperature < 0 °C), 10, is smaller than inland. Because there are more hours with sun in the growing season the evapotranspiration is high, especially in the dry dunes where the interstitial pores are small. This is an important factor for lichen and moss vegetation. Diurnal evapotranspiration is greater than inland, especially in autumn and winter when there are strong winds and much sun. The average wind velocity is 6 m/sec, which is almost twice as much as inland. Compared with the mainland, in spring rainfall is 15% less and in the growing season is 11% less, but the total mean of 720 mm/yr is probably only slightly lower. Winter and spring are foggier than inland, but there is generally less mist (Ketner 1972).

Sites at Terschelling (Fig. 1)

1. Dune ridges on the 'Noordsvaarder' (Fig. 2).

This nature reserve originates from a wide sandbank in the North Sea, west of the village of West-Terschelling and moving eastwards. The process of reaching and finally growing together with the main island started in 1850 and was completed by the end of the 19th century (Fig. 3). Since then a system of dune ridges has developed, separated by salt-water slacks. Untill 1995 this area was not much frequented by the public, as a large part was air-force training area, with no noise control.

Mr. C.A. Swart[1] estimated the age of these ridges based on the presence of military traffic routes running between the ridges that were used in the 1950s en 1960s (Fig. 2). The following dune systems, all with a height of 2 - 5 m above sea level, were studied:

- The youngest dune ridge closest to the sea is ca. 20 yr old, the second and the third ridge are 30 and 40 yr old, respectively. The ridges run parallel to each other, roughly from SSE to NNW. On the more inland dune ridges Marram grass (*Ammophila arenaria*) was planted.
- Ridges 4 to 6. Ridge 4 is estimated to be 70 yr old, while both ridges 5 and 6 are 90 yr old; all three are oriented SE-NW.
- Two NW-oriented dune slopes in the stabilized dunes on the main island were included in the research: the seventh ridge, a 10 m high dune ridge estimated to be 110 yr old, is nearest and runs parallel to ridge 6. It is separated from the Noordsvaarder by a low-lying dune slack, subjected to marine influence. This so-called Groene strand (green beach) is characterized by the presence of communities from the more sandy salt-marsh substrata.
- The 10 - 15 m high West dune is situated 2 km further north and is estimated to have stabilized ca. 130 yr ago (see Fig. 1).

2. Parallel dune ridges in Eldorado, a 80-ha dune area NE of West-Terschelling.

3. Parallel dune ridges along the North Sea coast in a former stabilized grey dune area NE of Hoorn, between beach marker posts 15 to 17. In this project it is referred to as 'Hoorn aan zee' (Fig. 1).

[1] Local Director of the National Coastal and Marine Management Institute (Rijkswaterstaat).

4. The Paraplu-dune, a mobile dune at the east side of the island in the Bosplaat nature reserve, is rarely frequented by the public. Shifting sand occurs on the outer, steep SW-facing slope of this 'ring dune' (Klein 1981).

5. Cupido's Polder, a very young dune area at the eastern end of the island. It has developed since 1940 on the wide beach flat north of an artificial sand embankment (Visser 1994).

Dune management

In 1990, an experiment was carried out for the State Forestry Service: 200 m^2 of dry dune grassland on the fourth dune ridge (Fig. 2) with a high moss cover (*Campylopus introflexus* and *Dicranum scoparium*) were cleaned from mosses by sod cutting. The sods were cut with a spade until the mineral sand was reached and all organic material was manually removed. In 1991 artificially stabilized blowouts at Eldorado were articially reactivated on a large scale as part of a large monitoring project on grass encroachment along the Dutch coast (EGM, see Introduction). The vegetation and uppermost soil layer of 11 dune slopes were removed down to the mineral sand. The effects of blowing sand on soil and vegetation were monitored until the end of 1994 (van der Meulen et al. 1996).

Stabilized dunes between Hoorn and Oosterend were exposed to reactivated sand from the first foredunes and the beach. At first this was the result of the change in the natural coastline (Klijn 1981). From 1990 onwards the National Institute for Coastal and Marine Management changed its management for coastal protection in this area and left the dunes unmanaged. To stop further retreat of the coastline a pilot project was implemented in 1993 (Spanhoff 1998). The artificial supply of sand on the seabed offshore from Hoorn and Oosterend between beach marker posts 14 and 18 intensified the inland transportation of sand.

Vegetation research

Between 1990 and 1995 phytosociological relevés (2 m × 2 m) were made according to the Braun-Blanquet method (Westhoff & van der Maarel 1973). A modified version of the Braun-Blanquet scale was used (Barkman et al. 1964). The values were transformed into the ordinal 1-9 scale (van der Maarel 1979).

Soil research

Soil sampling

In 1991 soil samples were taken at three depths (0-2 cm, 2-7 cm and 7-17 cm (Table 2). In 1993 and 1995 the 0-10 cm mineral layer was examined – in the framework of the national EGM programme (Vertegaal et al. 1991). Because the surface layer is important for cryptogams, the topmost samples were subdivided into subsamples of 0-2 cm and 2-10 cm. Samples were a mixture of 8-10 subsamples, taken on a short distance (10-15 cm) from, and uniformly distributed around, the permanent plots or relevés.

Chemical analyses

The soil samples were chemically analysed at the Bedrijfslaboratorium voor Grond- & Gewasonderzoek, Oosterbeek, The Netherlands. Before analysis the samples were dried at 40 °C, ground and sieved, using a 2-mm sieve.
1. pH-H_2O was determined in a suspension of 1 volume-part soil and 5 volume-parts H_2O after standing for 16 hr. pH-KCl determination followed in the same manner, but using 5 volume-parts KCl 1 M instead of H_2O.
2. $CaCO_3$ determination followed the Scheibler method – shaking with 3.2% HCl for 1 hr. The CO_2 released was captured in a gas burette.
3. For C-elementary (or organic) determination a certain amount of soil was burned in an oxygen stream of 950 °C. The CO_2 released was purified and captured in a diluted alkaline solution. The change in conductivity of this solution was used as a measure for the CO_2 amount, with a correction for inorganic C.
4. N-total determination followed the destruction method of Jodlbauer (1961) by destroying with phenol H_2SO_4 and catalyst. NH_4 was spectrophotometrically analysed with 660 nm, after colouring with indophenol (van Schouwenburg & Walinga 1974).
5. P-total was determined after destruction with Fleischmann acid. After colouring with ammonium molybdate, antimony and ascorbic acid, P was spectrophotometrically analysed with 882 nm (Murphy & Riley 1962).
6. CEC (Cation Exchange Capacity) was calculated from the% Ca^{2+} exchangeable,% Mg^{+} exchangable,% K^{+} exchangeable,% Na^{+} exchangeable and H^{+} occupation values (de Vries et al. 1994). To determine the cation occupation, a subsample was percolated with NaCl 1 M, followed by determination of Ca^{2+} and Mg^{+} by AAS. Percolation with ammonium nitrate 1 M preceded determination of Na^{+} and K^{+} via VES; percolation with calcium acetate pH 8.2 preceded determination of H^{+} via titration with NaOH 0.1 M towards phenolphthaline.
7. For Al oxalate, Fe oxalate and P oxalate determination, 1 weight-part of soil was extracted with 100 volume-parts of a solution of oxalic acid / ammonium oxalate 0.01 M. P^{+} was spectrophotometrically determined with 882 nm after colouring with ammonium

molybdate, antimony and ascorbic acid (Murphy & Riley 1962). Al^{2+} and Fe^{2+} were determined via AAS.

Data analysis

The relevés were both ordinated and classified using multivariate analysis. The 141 relevés from all research locations studied were clustered using TWINSPAN (Hill 1979). The TWINSPAN table is not reproduced here; instead the TWINSPAN dendrogram is shown (Fig. 5).

The frequency of occurrence and the characteristic cover of grass species, mosses and lichens was calculated for the relevés of the second, third, fourth and fifth/sixth dune ridges. The fifth and sixth dune ridges were combined. With progressive homogeneity of the vegetation on the separate dune ridges a decreasing number of relevés was made. Characteristic cover was the sum of the cover of a species within a cluster, divided by the number of relevés within this cluster, in which the species actually occurred.

Ordination

The relation between vegetation and environment was studied using the following ordination diagrams:

1. The 35 relevés made on the dune ridges of the Noordsvaarder forming a chronosequence, were subjected to Detrended Correspondence Analysis (DCA). In this ordination diagram the clusters as derived from the TWINSPAN table are indicated. In addition, the successive years of the sod cutting experiment are marked as S1, S2, S3 and S4 (Fig. 6).

2. The significance of the relation between species composition and separate environmental parameters was tested by Monte-Carlo Permutation test using Canonical

Table 2. Results of the soil analysis in 1991 for six locations on the Noordsvaarder and three in the adjoining dune area; two of these on the West dune (from Ketner-Oostra 1997). Results of the $CaCO_3$ analysis for the 0 - 2, 2 - 7 and 7 - 17cm layers of the first foredune row are 0.3%, 0.2 % and 0.2 %, respectively; for the second row zero, < 0.1 % and < 0.1 %, respectively. All other locations had no demonstrable lime. Data on Al-oxalate, Fe-oxalate and P-oxalate are in mmol/kg.* = data set not used in the Monte-Carlo permutation test. The green beach is a dune slack separating the Noordsvaarder from the adjoining dune area. ** no data available.

Depth (cm)	pH_w 0 - 2	pH_w 2-7	pH_w 7-17	pH_{KCl} 0-2	pH_{KCl} 2-7	pH_{KCl} 7-17	% C 0-2	% C 2-7	% C 7-17	% N 0-2	% N 2-7	% N 7-17	C:N 0-2	C:N 2-7	C:N 7-17	% P 0-2	C:P 0-2	Al_{ox} 0-2	Fe_{ox} 0-2	P_{ox} 0-2
Ridge 1*	6.9	7.0	7.1	6.8	7.2	7.2	0.08	0.02	0.03	0.003	0.001	0.001	27	20	30	0.010	8	1.5	3.0	1.05
Ridge 2	6.3	6.2	6.2	5.1	5.9	6.1	0.4	0.08	0.07	0.035	0.007	0.007	11	11	10	0.015	27	1.7	2.7	1.40
Ridge 3	5.8	6.2	6.4	4.4	5.2	5.8	0.3	0.08	0.08	0.03	0.008	0.007	10	10	11	0.011	27	2.0	3.0	1.05
Ridge 4																				
Sods cut*	5.5	5.7	5.9	4.5	4.7	4.7	0.18	0.13	0.1	0.021	0.01	0.009	9	13	11	**	**	**	**	**
Not cut	5.3	5.5	5.8	3.9	4.2	4.6	0.92	0.3	0.07	0.061	0.03	0.01	15	10	7	0.013	71	2.0	3.0	1.10
Ridge 5/6	5.4	5.2	5.2	4.0	4.4	4.4	0.56	0.18	0.09	0.053	0.015	0.008	11	12	11	0.011	51	2.5	3.0	1.20
Green beach																				
Ridge 7	5.1	5.3	5.2	3.6	4.1	4.3	0.98	0.14	0.1	0.076	0.018	0.01	13	8	10	0.013	75	2.0	3.5	1.50
West dune																				
Open*	6.3	5.3	5.3	5.4	4.5	4.4	0.12	0.08	0.06	0.018	0.007	0.003	7	11	20	0.012	10	1.5	3.0	1.30
Moss	5.5	5.2	5.4	4.2	4.4	4.6	0.34	0.15	0.1	0.036	0.012	0.003	9	13	33	0.014	24	1.5	3.0	1.50

Table 3. Results of the soil analysis of the 0-10 cm layer for Eldorado in 1993 and for four other locations on Terschelling in 1995 (from Ketner-Oostra 1997). Values for pH, % carbon, Cation Exchange Capacity (CEC) and percentage basic ions are from eight permanent plots on the Noordsvaarder ridges 1, 2, 3; Hoorn aan zee 1, 2, 3; Paraplu-dune and Cupido's polder collected at the start of the monitoring programme. A second value for the 0-2 cm layer is added, if different from the 0-10 cm layer. * = with influence of blown-in sand.

Dune ridge		pH-H_2O	pH-KCl	% $CaCO_3$	% C	% N	% P	C:N	C:P	CEC	% ion
Eldorado	1	8.6/7.9	9.0/8.8	1.00	0.19	0.002	0.027	95	7		
	2	4.9/4.5	3.9/3.5	0.20	1.02	0.080	0.021	13	48		
	3*	6.2/6.3	5.4/5.5	0.05	0.29	0.019	0.016	15	18		
Noordsvaarder	1	6.9	6.9	0.30	0.14	0.001	0.008	140	18	6.9	75
	2	6.2/6.1*	5.7/5.6	0.22 / 0.3	0.30	0.011	0.009	27	33	10.2	70
	3	5.5/5.7	4.4/4.5	0.04 / 0.01	0.43	0.020	0.009	22	48	14.0	40
	4	5.5/5.4	4.3/4.1	0.03	0.79	0.051	0.011	15	72		
Hoorn aan zee	1	7.2	7.4	0.80	0.12	0.004	0.014	30	9	8.0	90
	2*	6.5	6.0/6.1	0.05 / 0.03	0.64	0.049	0.027	13	24	31.0	80
	3*	5.9/6.1	4.6/5.4	0.04 / 0.13	0.51	0.039	0.023	13	22	17.2	45
Paraplu-dune*		6.8/6.1	6.2/6.0	0.12 / 0.09	0.28	0.013	0.013	22	22	11.5	75
Cupido's polder	1	7.9	8.1	1.20	0.19	0.001	0.016	190	12	8.3	75

Correspondence Analysis (CCA) (ter Braak 1987). For this test seven relevés from the chronosequence on the Noordsvaarder and the corresponding environmental variables in three soil layers (0-2 cm, 2-7 cm, 7-17 cm) were used (Table 2).

3. From the locations Noordsvaarder, Hoorn aan zee, Eldorado and Paraplu-dune, 12 relevés including many soil data from the 0-10 cm (Table 3) depths were available. Again the significance of the relation between species composition and separate environmental parameters was tested with a Monte-Carlo Permutation test in CCA.

4. A third set of eight relevés from four different dune locations with soil data from 0-10 cm depth, including values of CEC (Table 3), was subjected to a Monte-Carlo Permutation test.

Results

Vegetation

1. The Noordsvaarder chronosequence

In Table 1 the relevés from the separate dune ridges forming a chronosequence, are clustered and the frequency and characteristic cover have been calculated. This table clearly shows the high abundance of lichens on the dune ridges 2 and 3 (30 and 40 yr, respectively). These ridges differ from ridges 4 and 5/6 (Fig. 2) by having the calciphilous mosses *Ceratodon purpureus* and *Brachythecium albicans* and the lichens *Cladonia pocillum*, *C. ramulosa*, *C. subulata*, *C. macilenta* and *C. merochlorophaea*.

The second dune ridge is characterized by the presence of usually epiphytic growing lichens *Hypogymnia physodes*, *H. tubulosa* (Fig. 4), *Parmelia sulcata* and *Evernia prunastri*. Species differentiating the third dune ridge are *Cladonia furcata*, *Coelocaulon aculeatum* and *Cladonia floerkeana*. This ridge is also characterized by the relatively large cover of *Cladonia foliacea*. The older ridges are characterized by the relatively high cover of mosses, *Hypnum cupressiforme* and *Dicranum scoparium* on ridge 4 and *D. scoparium* and the neophyte *Campylopus introflexus* on ridges 5 and 6. In the latter the cover of *D. scoparium* is almost complete (95%).The reindeer lichen *Cladina portentosa* was only found on ridge 4. The lichens *Cladonia coccifera* and *Micaria prasina*, growing on humus, occurred only on ridges 5 and 6.

Fig. 6 shows the DCA ordination diagram of all Noordsvaarder relevés except those from the embryonic *Elymus farctus* dunes which are outliers.

Although reléves from dune ridges with different ages overlap, the first axis is clearly related to age. The second and the third dune ridges on the left of the diagram are

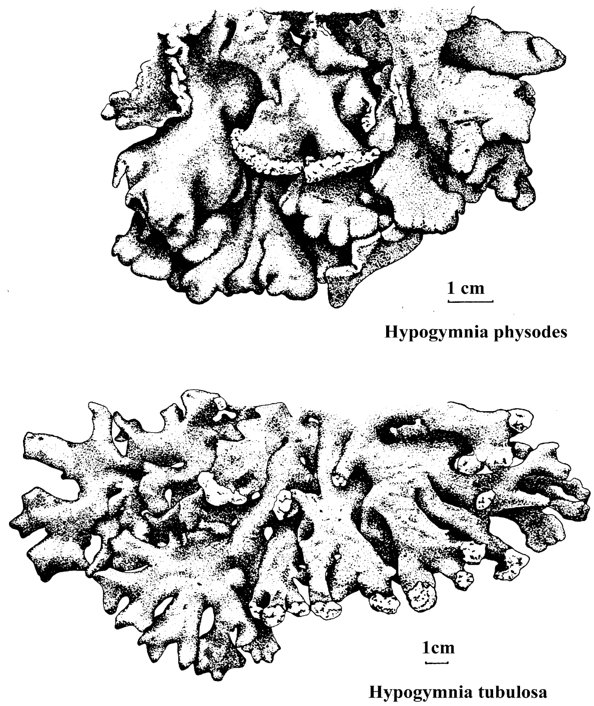


Fig. 4. *Hypogymnia physodes* and *H. tubulosa*, usually epiphytic lichens can still be found as epiphytes (e.g. on *Salix* shrubs) but also occur terrestrial. Their frequency has declined considerably since the 1970s. Drawing by R. Koeman. From van Dobben (1978).

characterized by the presence of many lichens. The combined fourth and fifth/sixth dune ridges occurring in the middle of the diagram are moss-dominated. These moss- dominated relevés are separated along the second axis. The relevés in the lower part of the diagram are dominated by *Dicranum scoparium*, with the exception of one relevé which is dominated by *Hypnum cupressiforme*. The relevés in the upper part of axis two are dominated by *Campylopus introflexus*. The relevés from the sod cutting experiment (S1 - S4) appeared in the area dominated by *C. introflexus*.

Sod cutting experiment. The vegetation development in four years time after sod cutting in 1990, is shown in Table 4. The area of bare sand decreased by 60%. In the second year 20% of the soil was covered by green algae. In the third year the vegetation was dominated by *Corynephorus canescens* and *Campylopus introflexus*. In year 5 *Corynephorus* declined while *Campylopus* remained dominant and was joined by five other mosses. Full moss cover increased up to 25% cover. However, *Campylopus introflexus* in particular appeared to be almost dead in 1994, due to sand blown in as an effect of the dry summer. Lichens were still very sparse, only two species were present, with a cover of < 1%.

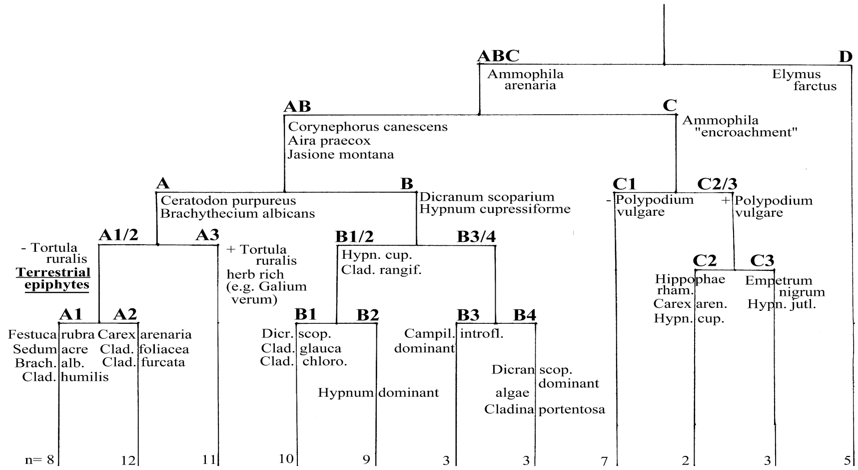


Fig. 5. TWINSPAN dendrogram of the total data set of Terschelling relevés from the period 1990 - 1995. Cluster groups A, B, C and D (see Text) are indicated. The number of relevés in each cluster is indicated by *n*. At each dichotomous division the main differential species are indicated.

2. All sites studied

Fig. 5 consists of a TWINSPAN dendrogram based on the total data set of 85 relevés from the period 1990-1995. The 11 clusters distinguished were grouped into four groups: A, B, C and D. The embryonic dunes dominated by *Elymus farctus* (group D) were separated from the other groups at the first division (Fig. 5).

The vegetation of group C is assigned to the *Elymo-Ammophiletum* (C1), a *Hippophae rhamnoides* scrub (C2) and the *Polypodio-Empetretum* (C3).

Groups A and B are characterized by species characteristic of the *Violo-Corynephoretum*. Further differentiation is based on the absence or presence of different moss and lichen species, on differences in moss- and lichen-cover, on the presence and cover of *Ammophila arenaria*, *Carex arenaria* and other higher plant species. It appears that the four, usually epiphytic, lichen species are almost exclusively present in cluster A1/A2 (see Fig. 5). Cluster A3 can be assigned to the *Phleo-Tortuletum ruraliformis*, a community of sunny, dry sites on calcium containing dune sand poor in humus.

Group B differs from group A in the cover and species composition of the moss layer. Whereas group A is characterized by the calciphilous mosses *Ceratodon purpureus* and *Brachythecium albicans*, group B is characterized by *Hypnum cupressiforme*, *Dicranum scoparium* and *Campylopus introflexus*. In B1 *D. scoparium* is constant and dominant. B2 is dominated by *H. cupressiforme* and B3 by the neofyte *C. introflexus*. B4 forms a transition to dwarf shrub heath (*Empetrion nigri*) and consequently to group C3.

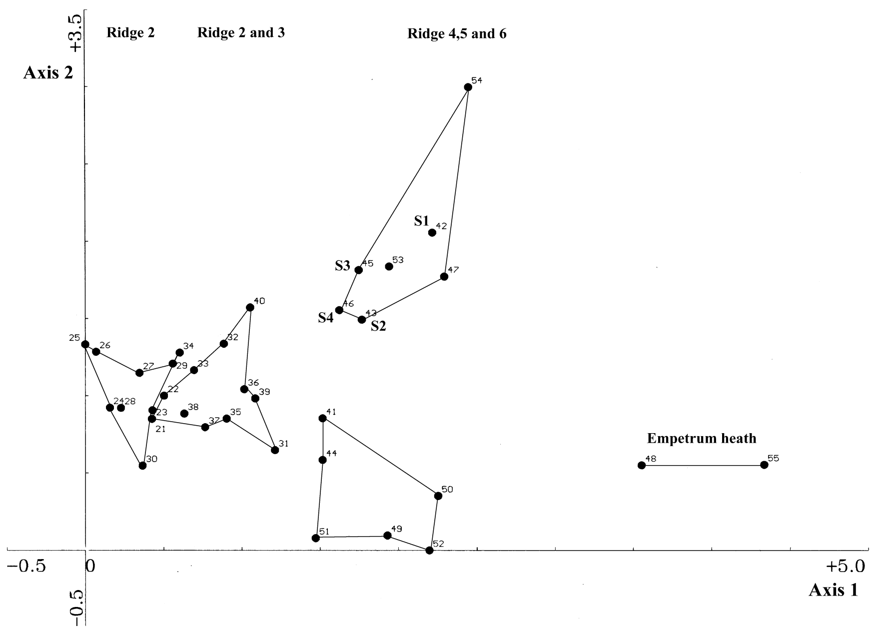


Fig. 6. Ordination diagram representing a DCA of all Noordsvaarder relevés except those from the first foredune. TWINSPAN clusters are outlined. The four relevés (S1-S4) were made in four consecutive years after sod cutting.

Table 4. Four years of succession in a permanent plot on the 4th dune ridge on the Noordsvaarder, after sod cutting in 1990. Values in 0 - 9 scale according to van der Maarel (1979). * In 1990 M.P. van Zuijen made a reference relevé in the moss-encroached area before sod cutting. ** Algae not recorded.

Year in 199.	0	1	2	3	4
Number of relevé (TURBO-veg)	*42	43	45	46	
Total number of species	15	6	15	17	20
Cover of bare sand (in %)	10	90	80	60	40
Cover of higher plants	15	2	5	16	20
Cover of mosses	80	0	1	12	25
Cover of lichens	1	0	0	<1	<1
Cover of algae	**	5	20	10	<1
Graminoids					
Ammophila arenaria	2	2	2	2	1
Carex arenaria	4	2	1	2	3
Corynephorus canescens	5	-	2	8	3
Aira praecox	1	-2	2	1	
Luzula campestris	1	-	-	-	-
Calamogrostis epigeios	-	-1	2	1	
Holcus lanatus	-	-	1	-	1
Festuca rubra	-	-	-	2	1
Herbs					
Hypochaeris radicata	1	1	1	1	1
Jasione montana	3	-	1	1	2
Rumex acetosella	1	-	1	1	3
Leontodon saxatilis	2	-	1	-	-
Taraxacum spec.	1	-	-	-	-
Hieracium umbellatum	-	1	2	1	1
Lotus corniculatus	-	-	1	1	1
Cerastium semidecandrum	-	-	1	-	-
Mosses					
Campylopus introflexus	8	1	-	5	6
Polytrichum juniperinum	5	-	1	2	2
Hypnum cupressiforme	-	-	-	1	2
Ceratodon purpureus	-	-	-	-	3
Dicranum scoparium	-	-	-	-	2
Lichens					
Cladonia foliacea	3	-	-	1	1
Coelocaulon aculeatum	2	-	-	1	1
Cf. *Cladonia subulata*	1	-	-	-	-
Green algae	**	3	6	5	1

Relation between vegetation and soil

The relation between the vegetation and environmental parameters was studied using three different sets: a set with seven relevés from the chronosequence on the Noordsvaarder, and two sets from several locations on the island with 12 and 8 relevés, respectively.

Set 1. Noordsvaarder chronosequence

Fig. 7 shows the relation between seven parameters and the first two axes of a DCA based on the relevés from the chronosequence on the Noordsvaarder. Only parameters that appeared to be significant or almost so after a Monte-Carlo permutation test are displayed in the diagram. Significant parameters that were not displayed are pH-H_2O values for several depths. As expected, these values were strongly correlated with the pH-KCl. The species composition of the vegetation appears to be related to age,% C-organic at 7-17 cm, Fe-oxalate, acidity (pH) and C:N ratio. With age, carbon and Fe-oxalate content increase and the soil acidifies.

Using forward selection both pH-H_2O and pH-KCl values proved to be highly significant; pH.KCl was chosen because it was most informative (p = 0.027; 0.005 and 0.001 for pH.KCl at the depths 0-2, 2-7 cm and 7-17 cm respectively). The C:N ratio in the 2-7 cm layer was significant (p = 0.023) and% C in the 7-17 cm layer almost significant (p = 0.091). With the Monte-Carlo permutation test only Fe-oxalate was almost significantly correlated to the variation in vegetation.

Table 5. Rate of significance of parameters connected to the vegetation of 12 relevés along the Terschelling dune coast, tested with a Monte-Carlo permutation test. p = 0.05 is the chosen significance margin.

Parameter	Soil depth	p
First dune ridge	-	0.001
pH_{KCl}	0-2 cm	0.173
	2-10 cm	0.059
	0-10 cm	0.061
Log $CaCO_3$	0-2 cm	0.047
	2-10 cm	0.003
	0-10 cm	0.002
Log C-organic	0-2 cm	0.055
	2-10 cm	0.057
	0-10 cm	0.052
Log N-total	0-2 cm	0.015
	2-10 cm	0.024
	0-10 cm	0.013
Log P-total	0-2 cm	0.052
	2-10 cm	0.073
	0-10 cm	0.054
Blowing sand present	-	0.013

Set 2. All dune sites studied

The second DCA (Fig. 8) is based on a selection of 12 relevés from four locations along the dune coast, and from the slope of the Paraplu-dune. For the matching soil data (pH,% C-organic,% N-total,% P-total and% $CaCO_3$) see Table 3. Again, only factors appearing to be significantly or almost significantly (Table 5) related to the variation in the species composition of the vegetation using a Monte-Carlo permutation test are displayed in Fig. 8. The location of relevés on the first foredunes (forming a closed coastal ridge along the beach) appears to be a highly significant factor, as is the presence of blowing sand (see Table 5). Some factors (such as% calcium) were also highly significantly correlated with the vegetation when data from the 0-2 cm and 2-10 cm soil layers were used. However, for all factors only the data from the undivided 0-10 cm layer are displayed in the diagram.

As expected, the arrows representing first foredune, calcium content, and pH point in the direction of all first foredune relevés and of the Paraplu-dune, a dune system which has been blown out secondarily.

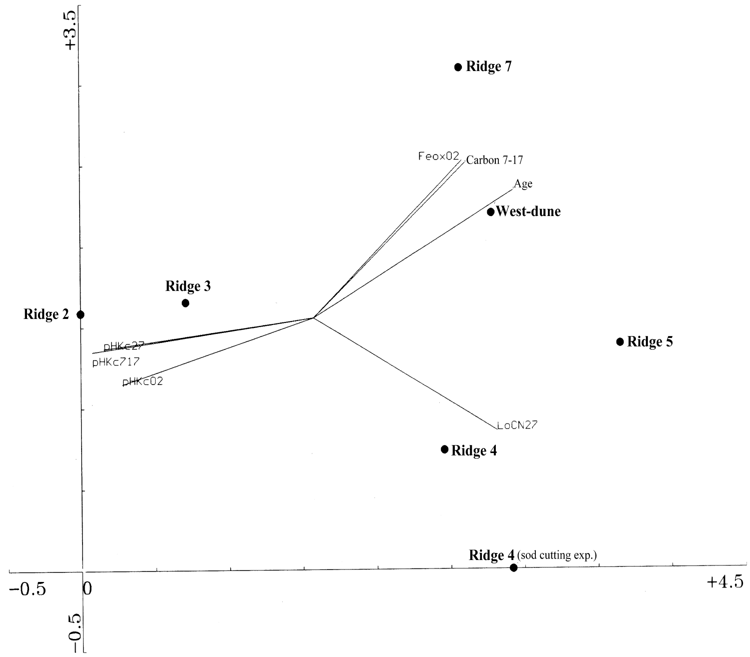


Fig. 7. Relation between seven parameters and the first two axes of a DCA, based on the relevés from the chronosequence on the Noordsvaarder (Ridge 2 - Ridge 5/6). Ridge 7 and the West dune are from the adjoining dunes. Carbon7-17 signifies % C at the soil depth 7-17 cm; Feox02 signifies % Fe oxalate at the soil depth of 2-7 cm; pH-Kc02 = pH-KCl in the surface layer of 0-2cm; pHKc27 = pH-KCl at 2-7cm; pHKc717 = pH-KCl at 7-17cm.

The relevés in Fig. 8 can be ranked according to decreasing nitrogen and organic carbon and with increasing pH, calcium and inblowing sand as follows:
- stabilized dunes of Hoorn aan zee;
- dune ridges 2, 3 and 4 of the Noordsvaarder;
- Hoorn aan zee with blowing sand;
- Eldorado with inblowing sand after artificial erosion;
- Eldorado second dune ridge and Paraplu-dune;
- First foredunes.

The arrow for% P indicates an increase in the P-content in the direction of the stabilised dunes at location Hoorn aan zee, the second dune ridge of Eldorado and the first foredunes.

Set 3. Several dune sites, parameters including CEC

In the third set eight relevés are available, with values for CEC (in meq/kg) and% basic ion content, measured at four different dune locations (Table 3). The first dune ridge of the Hoorn aan zee location with

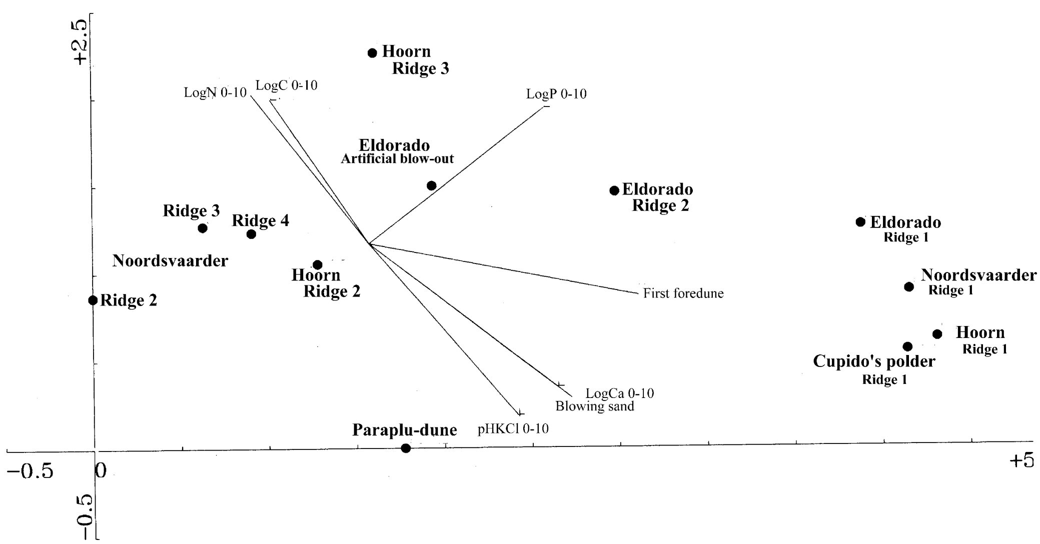


Fig. 8. Relation between seven parameters (in the 0-10 cm soil layer) and the first two axes of a DCA, based on a selection of 12 relevés from four locations along the dune coast, the artificial blowout in Eldorado and the natural blowing sands on the Paraplu-dune.

incoming sand from the beach had the highest% basic ions (90%). The third dune ridge on the Noordsvaarder and that of Hoorn aan zee had the lowest% basic ions: 40%. The first foredunes on the Noordsvaarder and in Cupido's Polder, with 75%, were still rather rich in base content. The value for the blowing sand on the slope of the Paraplu-dune is also similar with 75%.

Discussion

Vegetation

According to our results, the second and third dune ridges on the Noordsvaarder are refugia for lichens, especially for lichens such as *Hypogymnia physodes*, *H. tubulosa*, *Evernia prunastri* and *Parmelia sulcata* that normally occur as epiphytes elsewhere, but are terrestrial on the Wadden Islands. These species were found in combination with a moss layer of the calciphilous mosses *Ceratodon purpureus* and *Brachythecium albicans*, in a plant community that can be assigned marginally to the *Violo-Corynephoretum*, but in which *Sedum acre* and *Festuca rubra* are abundant (clusters A1 and A2 in the TWINSPAN table; Fig. 5). The lime content of 0.3% to a depth of 10 cm in the first foredune had decreased to < 0.1% for the 0 - 2 cm layer of the second and third ridges (Table 2). In the 1995 data this seems true for the third ridge only (Table 3). Perhaps in this set of results the second ridge received some fresh accretion in the superficial layer. The epiphytic lichen *Evernia prunastri* also grew terrestrially in the Paraplu-dune relevés that were classified in cluster A2, having a similar vegetation, also growing on decalcified sand of 0.09% $CaCO_3$ in the surface layer (Table 3).

Biermann (1999), studying succession stages from foredunes to grey dunes on Dutch and German Wadden Islands and in North Denmark, described a transitional stage between the *Festuco-Galietum veri* and the *Violo-Corynephoretum*, which is characterized by *Brachythecium albicans*, *Polytrichum juniperinum* and *Rumex acetosella* and by many lichens. On Terschelling we also found the highest richness in *Cladonia* species in this succession stage: clusters A1 and A2 contained 14 *Cladonia* species, with *C. foliacea* and *C. scabriuscula* reaching 70% cover in some of the 2 m × 2 m relevés and *C. rangiformis* and *C. pocillum* 40%. In this stage of primary succession on dune ridges in the xerosere the normally epiphytic macrolichens still grew terrestrially.

In cluster A3 the normally epiphytic lichens were few because of the abundance of *Tortula ruralis* var. *ruraliformis* and of other mosses and higher plants. In this *Phleo-Tortuletum ruraliformis*, including later succession stages with *Hypnum cupressiforme*, a few lichens such as *C. furcata* and *C. rangiformis* occurred as co-dominants. *T. ruralis* var. *ruraliformis* is indicative of a fairly calcareous soil (ca. 1% Ca) and an annual accretion of about 3 mm of incoming sand (van Boxel 1997). The calcium contents of the top 10 cm of the first foredunes in Eldorado, at the beach NE of Hoorn, and in Cupido's Polder are 1.0%, 0.8% and 1.2%, respectively, which is substantially higher than that on the Noordsvaarder, which is 0.3% (Table 3). Biermann described the *Tortulo-Phleetum arenariae* (synonymous with *Phleo-Tortuletum ruraliformis*) as a transitional stage between the *Ammophilion arenariae* and the *Koelerion arenariae* and, indeed, as being less lichen-rich than the transitions within the *Corynephorion* (Biermann 1999).

As demonstrated in the Results, the next succession stage of the xeroseries on the Terschelling dunes occurs on the older ridges, the fourth to seventh dune ridges on the Noordsvaarder (> 70 yr old), as well as on all other older locations we investigated (clusters B1 and B2). It contains the mosses *H. cupressiforme* and *D. scoparium* in combination with reindeer lichens. Here, *Campylopus introflexus* appears as a co-dominant (cluster B3).

Relation between vegetation and soil

In the chronosequence on the Noordsvaarder we found the changes in the composition of the vegetation to be significantly related to the age of the ridges, to an increase in soil acidity at all three depths (0-2 cm, 2-7 cm and 7-17 cm) from neutral to moderately acid (Ellenberg et al. 1992) and to an increasing carbon content at the 7-17 cm depth. This change in soil quality is a significant feature, accompanying the changes from lichen-rich to moss-dominated stages during succession.

In the ordination diagram (Fig. 7) the relevés of the lichen-rich second and third dune ridges appeared at the far left side of axis one and opposite all the moss-rich ridges, including the sod cutting experiment on the fourth ridge.

In Fig. 8 the second, third and fourth dune ridges and the stabilized dune ridge of Hoorn aan zee (Hoorn ridge 3) are all plotted by DCA in the direction of the arrow indicating an increase in% nitrogen and% carbon. This is in contrast to the relevés from the foredunes and from dunes with inblowing sand. In these younger or rejuvenated dunes the calcium content and consequently the pH is higher. Given that the second and third dune ridges are an important biotope for the epiphytes growing terrestrially it can be inferred that the decrease of inblowing sand and a certain increase of nitrogen and carbon, accompanied by a certain acidification, are important for their decline. In the biplot of relevés from the chronosequence of the Noordsvaarder (Fig. 7) it can be seen that with ageing, the carbon content and acidity increase while the vegetation changes into lichen-poor and moss-rich communities. Our research shows that lichen-rich communities are clearly restricted to subneutral soils (Ellenberg et al. 1992) with a pH-H_2O between 5.7 and 6.3 in the superficial layer (Table 3).

Of the ridges 2 till 7 on the Noordsvaarder the C:N ratio was ca. 10 to 11 (Table 2), the same value as Olff (1992) found in the dune succession range at the Wadden Island of Schiermonnikoog. From his finding and the results of other studies on nutrient limitation in sand dunes, Olff concluded that nitrogen was an important limiting nutrient and that it was strongly correlated with the organic matter content of the soil. The very high C:N ratio of the first dune ridges with *Ammophila* and/or *Elymus farctus* on the Noordsvaarder, in Eldorado and Cupido's polder is, however, not informative and is due to almost not measurable C and N concentrations (Table 3).

In forward selection the relation between vegetation (including the sod-cutting experiment) and log C:N in the 2 - 7 cm layer appeared to be significant ($p = 0.023$). However, the differences in C:N values are very low. Although the C:N ratio in the 7 - 17 cm layer doubled to 20 and reached 30 in the moss-covered West dune, its relation with vegetation composition was found to be not significant.

The C:N ratio in the topmost 2 cm of the plot at the fourth dune ridge where sods were cut, fell from 15 to 9, probably indicating a high nitrification rate. After sod-cutting the pH-KCl in deeper layers remained low (4.7) and approximately at the same level as before sod cutting (4.5). This pH value is similar to the pattern shown in the moss-rich relevés where the moss cover had not been removed (Table 2).

In the data set including all Terschelling locations with available soil data (Table 3) , the relation between the C:P ratio in the 0 - 10 cm layer and the vegetation proved to be significant ($p = 0.033$). In all transects from the beach to the 4th dune ridge there was a clear increase from low to high values: on the Noordsvaarder from C:P 18, via 33 and 48 to 72. In Eldorado the sand accretion in the 3rd ridge lowered the C:P to 18, as it did for the 2nd and 3rd ridge in Hoorn aan zee which also received sand. Here the value of 22 was the same as in the Paraplu-dune plot with moving sand. In Fig. 8 (DCA for all locations) we decided to indicate log P ($p = 0.054$; almost significant) instead of log C:P, in order to have log P in the same diagram as log C and log N. The variation in% P will be discussed below in relation to the management in Eldorado.

The oxalate determinations in the 1990-1995 period (Table 2) were intended to provide information on the increasing buffer capacity of young dune soils, as the amount of Al-, Fe- and P-ions are dissociated under influence of plant growth (de Vries et al. 1994). The Al-oxalates convincingly suggest an increased buffer capacity with soil ageing. This becomes clear when we compare the coastal dunes with the inland dunes of the Veluwe which consist of much older Pleistocene deposits (see Fig. 1). For all Terschelling plots the mean value is 2 (+1/–1) mmol/kg compared with 18 (+7/–5) mmol/kg for the inland plots (Ketner-Oostra 1995). But for the Noordsvaarder this Al-oxalate did not increase significantly, only the Fe-oxalate did. Fe oxalate 0 - 2 cm arrow (in Fig. 7) points in the same direction as% C, which means that as the soil ages its buffer capacity increases. The mean value of Fe-oxalate for the Noordsvaarder is 3.0 (+0.5/–0.3) mmol/kg. The mean value for Fe oxalate for all 16 plots in the monitoring programme on Terschelling (Ketner-Oostra 1997) was 3.2 (+0.8/–0.2), with two plots of 0 - 10 cm depths inside this range of values. The concentrations in blowing sand in the older Pleistocene deposits on the Veluwe were not much higher: in six plots of 0 - 10 cm depth the mean value was 4.0 (+1.1/–0.9) mmol/kg (Ketner-Oostra 1995). For P-oxalate the mean of all Terschelling plots was 1 mmol/kg (+/–), the same as for the above-mentioned six plots in the inland dunes.

Basic ion-content (%) is remarkably high in the vegetation with the terrestrial growing epiphytic lichens on the second dune ridge of the Noordsvaarder and on the Paraplu-dune (Table 3). Barkman (1958) has suggested that this terrestrial occurrence of epiphytes was linked to specific ecological factors, with in the first place electrolyte concentration.

Management

The experimental sod cutting

This experiment on the fourth dune ridge on the Noordsvaarder is an example of internal management (Westhoff 1985) attempting to restore cryptogam diversity in moss-encroached dry dunes. The ordination of the vegetation of the Noordsvaarder (Fig. 6) shows that the relevés of the sod cutting experiment on the Noordsvaarder remained in the area dominated by *Campylopus introflexus*. Also in Fig. 7 the sod-cutting relevé was plotted near the moss-rich ridge 4. Here the soil is characterized by a reduced lime content because of leaching, the increase of carbon and soil acidification with depth. From this it appears that the cutting of sods in moss-encroached vegetation did not result in a restoration of lichen-rich vegetation comparable to that growing on the second and third dune ridges. Mosses started to dominate again with some increase in the number of higher plants compared with the starting point (Table 4).

The large-scale clearing of dune vegetation at Eldorado

This (internal) management project within the nationwide EGM project did not succeed fully, because *Ammophila arenaria* regenerated from root fragments and continued to encroach (van der Meulen et al. 1996). The abundance of *Hippophae rhamnoides* on the second dune ridge in Eldorado, greater than elsewhere on Terschelling, is probably connected with the relatively high% P in this area, more lime and rather high dynamics (see Eldorado Ridge 2 in Fig. 8).

Kooijman et al. (1998) stated that though the Wadden district in general might be nitrogen-limited, it has a relatively high available phosphorus amount, which, given current levels of atmospheric nitrogen deposition, favours grass encroachment. This relative abundance of phosphorus in the dunes in Eldorado probably makes them more susceptible to grass encroachment than certain other dune areas on Terschelling.

One positive finding 4 yr after re-establishing the blowouts, reported by van der Meulen et al. (1996), was the establishment of the pioneer species of the *Phleo-Tortuletum ruralifomis* in the fresh sand accumulations around the artificial blowouts. A prolonged positive effect on plant diversity was recently published by Zumkehr (1999), who mentioned rabbits for taking an active part in this success.

Van der Meulen et al. (1996) found that their research plots in the *Violo-Corynephoretum* did not change much, being outside the influence of incoming sand. The uninfluenced soil had a pH-$CaCl_2$ of 4.0 (+/– 0.7), while in the soil with 5 cm sand accretion the pH.$CaCl_2$ was between 7 and 8. Our lichen-rich plots in Eldorado, some of which were 90% covered with lichens, were ca. 60 m SE of the high dune with artificial blowout no. 11 (van der Meulen et al. 1996) and the soil showed a pH-KCl of 5.4 and 0.05% lime to a depth of 10 cm (see Eldorado Ridge 3 in Table 3). Hardly any sand accretion was visible, but it sustained the lichen richness, as our observations over several years showed.

The influence of sand blown in from the first foredunes

Continued lichen richness was also found in the plots on the second and third dune ridges along the Hoorn aan zee coast. Here artificial sand supply offshore was intended for coastal protection, and is an example of 'unintended' external management (Westhoff 1985). The sand used was obtained locally from a winning area in the sea and had roughly the same grain size and lime content as the beach sand (Biegel & Spanhoff 1996; Spanhoff 1998). In our research plots the lichen cover of 90% was still being revitalised by neutral sand of pH-KCl 7.4 and 0.8% $CaCO_3$ blowing in from the first foredune. The inblowing sand had its main influence on the 0 - 2 cm layer, where the effect was clearly measurable (pH-KCl 6.1 on the second dune ridge and 5.4 on the third;% $CaCO_3$ 0.03 and 0.13 respectively; see Table 3). On these dune ridges *Cladonia rangiformis* and *C. foliacea*, characteristic of neutral or basic grassland (Purvis et al. 1992) are growing together with subneutral species such as *Cladonia scabriuscula*, *C. furcata* and *Coelocaulon aculeatum* as well as with rather acidophilic species (pH-H_2O-range 4.1 - 4.8; Ellenberg et al. 1992) such as *Cladonia gracilis*, *Cladina portentosa* and *C. arbuscula*. These last two species are not mentioned by Ellenberg and can be considered to be acidophilic species as well.

The inblowing sand at Hoorn aan zee has a base content that was comparable with that of the lichen-rich second dune ridges of the Noordsvaarder and the lichen-rich plots in Cupido's Polder and on the Paraplu-dune, both influenced by inblowing sand (70 - 80% basic ion-content; see Table 3). From the foregoing it is apparent that the blowing in of sand with a neutral to subneutral pH, some lime and a relative high base content benefits lichen richness.

Conclusions

Species composition of the vegetation on dune ridges and the presence of lichen species appear to be clearly related to age. The greatest lichen richness, both in *Cladonia* species and in epiphytic lichens growing terrestrially, is still found on the second and third dune ridges on the Noordsvaarder. It took ca. 30 yr for the succession from first foredune vegetation to a lichen-rich dune vegetation and another 30 - 40 yr until gradually the moss-dominated stage took over.

Soil development during ageing of dune soil with increasing C and N percentages and acidification from pH-KCl from 7.0 till 3.6 are significant features, accompanying the changes from lichen-rich to moss-dominated stages during vegetation succession within the *Violo-Corynephoretum*. During the succession the C:N ratio still remained around 10 down to a depth of 17 cm, indicating a high nitrification rate. Higher C:N ratios developed only in deeper and older soil layers outside the Noordsvaarder. C:P ratios clearly increased during succession, but were only measured in the superficial soil layer.

The buffer capacity of the young dune soils at Terschelling proved to be very low compared with inland Pleistocene deposits and only Fe-ions were significantly released during soil ageing.

It is clear that the superficial sod cutting in moss-encroached vegetation has not been a successful management tool for restoring the former lichen-rich succession stages. The main reason for this failure was the former leaching of lime, the consequent soil acidification and the increased carbon content with depth. The blowing-in of neutral or subneutral sand with some lime content and a relatively high base content from natural and artificial blowouts or from foredunes proved to be important for maintenance of lichen vegetation in the first stages of the *Violo-Corynephoretum*. According to our observation lichen richness can be sustained with very little sand accretion.

The occurrence of the terrestrial growing epiphytic lichens in some of our plots is probably linked to a high percentage of basic ions.

Moss encroachment is also a problem in other dune ridge systems in calcium-poor Western European dunes. Our experiments made clear that only deep sod-cutting down to soil layers containing some calcium will be effective. Reactivation of former blowouts in grey dunes or keeping foredunes dynamic is a better option in order to generate a subtle sand flow over *Corynephorus canescens* vegetation that is endangered by moss-encroachment.

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