# Succession in lichen-rich vegetation in coastal dunes between 1995 and 2005.

Rita Ketner-Oostra, Bennekom (NL) & Karlè V. Sýkora, Wageningen (NL)

**Abstract.** Succession in lichen-rich stages of primary succession in calcium-poor coastal sand dunes was monitored from 1995 to 2005. The changes from lichen-rich to moss-dominated stages in *Corynephorus canescens* grassland were related to acidification in connection with ageing of calcium-poor dune soil. Lichen diversity decreased and the terrestrial growing usually epiphytic species disappeared. The final stage in succession in the *Violo-Corynephoretum* (V.-C.) with mats of *Cladina portentosa* changed very slowly and this stage needs protection, especially from grazing, as it is a very vulnerable, and, if fragmented, it will be replaced by the neophytic moss *Campylopus introflexus*.

Lichen diversity was neither restored by superficial cutting of sods in moss-encroached vegetation nor by fire in graminoid encroached *V.-C.* The best option in maintaining lichen vegetation in the *V.-C.* is to allow sand with a relatively high  $CaCO_3$  content to blow in. For sustainable conservation, formation of new dune ridges by natural processes is optimal or even necessary.

# 1 Introduction

In 1995 the State Forestry Service (province of Friesland) commissioned the first author to monitor actual lichen-rich *Corynephorus* grassland, threatened by moss and grass encroachment. The Monitoring project was initiated because of concern with the biodiversity decline in the 'grey dunes' on the West Frisian Islands. According to Natura 2000, within Europe, the Netherlands has a special responsibility for this habitat type. These lichen-rich 'grey dunes' were well developed in the dry coastal calcium-poor dunes in the Netherlands, and especially on the island of Terschelling (Fig. 1).

Until the mid-1970s these dunes were famous for their lichen-rich pioneer grasslands, developed in the course of primary succession in the xeroseries. The greater part of the older dune slopes was covered by short grassland, dominated by grey hairgrass (*Corynephorus canescens*) and sand sedge (*Carex arenaria*) and rich in the lichen genera *Cladonia* and *Cladina*. Lichens, such as *Bryoria fuscesens*, *Evernia prunastri*, *Hypogymnia physodes*, *H. tubulosa*, *Platismatia glauca* and *Pseudevernia furfuracea*, which are usually epiphytic, were growing terrestrially on dune sand or on moss carpets (WESTHOFF 1947; BRAND & KETNER-OOSTRA 1983).

Since the 1970s the vegetation changed over large areas due to encroachment of graminoids, mainly *Ammophila arenaria* and *Carex arenaria*, while on secondary open sand the dominance of *Campylopus introflexus* increased (BIERMANN & DANIËLS 1995; KETNER-OOSTRA & VAN DER LOO 1998). These changes in the flora, both of phanerogams and cryptogams, in dry oligotrophic habitats, have been attributed to increased dry and wet atmospheric deposition of nitrogen (NH<sub>4</sub>-N, NO<sub>3</sub>-N and organic compounds) throughout

the Netherlands as a result of intensified livestock farming, the so-called bio-industry, and industrial output. The results of this increase in nitrogen deposition have been monitored for Terschelling by comparing the cryptogam vegetation inside dry dune-grassland in the 1960s, a time with a relatively low deposition of atmospheric nitrogen, with the same vegetation in the 1990s, a time with strongly increased deposition (KETNER-OOSTRA & SÝKORA 2004).



Fig. 1: The island Terschelling, with some of the mentioned study sites.

Earlier investigations showed a high biodiversity in the *Violo-Corynephoretum* (V.-C.), mainly of lichens in recently formed dunes outside the main stabilized sand dune area of Terschelling (KETNER-OOSTRA & SÝKORA 2000). Such lichen-rich pioneer vegetations were found on slightly calcareous dune ridges on the Noordsvaarder, within groups of dunes in Cupido's polder and on the slope of a mobile dune, the Paraplu-dune. These locations as well as the final stages of succession in the *V.-C.* with carpets of reindeer lichens in the stabilized dunes north of Midsland were selected to be monitored.

Some sites were managed by the State Forestry Service, for instance by sod cutting. Moreover, the effect of blowing-in of sand, resulting from changes in coastal management by the National Institute of Coastal and Marine Management (Rijkswaterstaat), was included. Like the wildfire in 1993 and 2004, these are examples of 'unintended management' (WESTHOFF 1985). The aim was to ascertain the effect of such management and to give advice on future management.

We set out with the following research questions:

a. Will natural succession in lichen-rich vegetation lead to decrease in biodiversity?

- b. Are the effects of former management or of a wildfire and sand-suppletion temporary?
- c. What future management can be advised?

# 2 Study Area

# 2.1 Soil origin and characteristics

Terschelling is one of the West Frisian Islands. It is part of the so-called Wadden district. This phytogeographic district is mainly characterized by Early and Middle Pleistocene sands re-deposited in the Saalien by the rivers Meuse and Rhine (EISMA 1968). The parent material is poor in lime and iron, and no shell fragments have been deposited in recent times, partly because the coast is retreating. The result is that only a limited amount of weatherable minerals, like 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. According to KOOIJMAN et al. (1998), phosphorus availability in these dune soils may be relatively high, due to the comparatively loose nature of phosphorus sorption, resulting in nitrogen-limitation

# 2.2 Climate

The climate of the Wadden sea area can almost be called 'eu-atlantic', especially as far as temperature, humidity and wind are concerned. The average rainfall is 720 mm yr<sup>-1</sup>. Winter and spring are foggier than inland. For more details, see KETNER (1972) and KETNER-OOSTRA & SÝKORA (2000).

Compared with the inland area of the Netherlands, in Terschelling the summer temperatures are lower and in winter there are fewer days of frost. Because there are more hours with sun in the growing season, the evapotranspiration is high, especially in the dry dune sands, where the interstitial pores are small. This is especially important for lichen and moss vegetation.

## 2.3 Sites at Terschelling (Fig. 1)

Five monitor areas are spread over Terschelling, each with several sites to study natural succession and to study intended and unintended dune management.

#### 2.3.1 Sites to study natural succession

#### 2.3.1.1 Noordsvaarder

Pioneer vegetation was studied by two PQs on a succession of young dune ridges on the Noordsvaarder at the west-end of the island (Fig. 1). The youngest dune ridge closest to the sea was about 20 yr old, and consisted of drifting sand with 0.3% CaCO<sub>3</sub> and a pH<sub>KCl</sub> of 6.9 The second and the third ridge, with each a PQ, are respectively 30 and 40 yr old with in the superficial soil layer (0-2 cm), respectively 0.3% and 0.0% CaCO<sub>3</sub>, and respectively a pH<sub>KCl</sub> of 5.6 and 4.5 in 1995 (KETNER-OOSTRA & SÝKORA 2000).

#### 2.3.1.2 Paraplu-dune

The Paraplu-dune, a mobile dune at the east side of the island in the Bosplaat nature reserve, has a pioneer vegetation on the outer, steep, SW-facing slope with shifting sand. Here one PQ was laid out in 1995. 0.1% CaCO<sub>3</sub> and pH<sub>KCl</sub> of 6.0 was measured in the 0-2 cm layer in 1995 (KETNER-OOSTRA & SÝKORA 2000).

#### 2.3.1.3 Cupido's polder

The Cupido's polder, a young dune area at the eastern end of the island developed since 1940 on the wide beach flat north of an artificial sand embankment. Here two PQs were laid out in 1995, both with an equal distance to the foredune. The shifting sand in this foredune had 1.2% CaCO<sub>3</sub> and a pH<sub>KCl</sub> of 8.1 in 1995. The superficial soil layer (0-2 cm) in the two PQs had respectively 0.2% and 0.1% CaCO<sub>3</sub> and respectively a pH<sub>KCl</sub> of 6.8 and 6.5 in 1995 (KETNER-OOSTRA & SÝKORA 2000).

## 2.3.1.4 Midsland

On the older stabilized dunes north of Midsland, the end of succession in the *V.-C* is characterized by a dune grassland with *Festuca ovina* s.l. and a high cover of *Cladina portentosa* and *Cladonia uncialis* (BÖCHER 1952; BIERMANN 1999; KETNER-OOSTRA & SÝKORA 2004). Here two PQs were laid out. 0.0% CaCO<sub>3</sub> was found and the pH<sub>KCl</sub> in the superficial layer was 3.5 and 3.7 respectively. We studied the re-establishment of the mentioned lichens with one PQ in a nearby, more open vegetation with some in-blowing slightly acid sand (0.0% CaCO<sub>3</sub> and pH<sub>KCl</sub> 4.3).

#### 2.3.2 Sites to study intended and unintended dune management

#### 2.3.2.1 Sod cutting

In order to restore biodiversity, the State Forestry Service cleaned 200 m<sup>2</sup> of dry dune grassland with a high moss cover (*Campylopus introflexus* and *Dicranum scoparium*) from mosses by sod cutting on dune ridge four on the Noordsvaarder (Fig. 1). The sods were superficially cut with a spade until the mineral sand was reached ( $pH_{KC1}$  4.3 and 0.0% CaCO<sub>3</sub> in 1995). All organic matter was manually removed and barrowed away (KETNER-OOSTRA & SÝKORA 2000). This site was studied since 1990 with one PQ.

#### 2.3.2.2 Wildfire

Vegetation recovery after a wildfire in 1993 in former grass-encroached dry dune vegetation, could be studied north of Oosterend. This so-called R.D.-dune or Rita's dune (Fig. 1) had a monitoring history going back to 1966. It was studied in 1990 to reveal the differences between the graminoid-encroached dune vegetation on acid dune soil ( $pH_{KCI}$  4.1

in the 0-10 cm layer) and the original lichen-rich vegetation of 1966. With one PQ the regenerating vegetation after fire was yearly followed (KETNER-OOSTRA et al. 2006).

On the Jan Thijssens-dune graminoid-encroached dune vegetation was studied with two adjoining PQs till 2004 when the vegetation burned down by a wildfire. In the two PQs the regenerating vegetation was recorded in 2004 and 2005, however, with a combined soil sample for the two PQs, taken at three depths according par. 3.2.

### 2.3.2.3 In-blowing sand

The effect of in-blowing sand over acid dune grassland was studied along the coastline between Hoorn-aan-zee and Oosterend with six PQs, three installed in 1995 and three in 2000. From 1990 onwards the National Institute for Coastal and Marine Management changed its management for coastal protection in this area and left these dunes unmanaged. The artificial sea bed replenishing just offshore between Hoorn and Oosterend in 1993 (SPANHOFF 1998) intensified the inland transportation of sand. Stabilized dunes between Hoorn and Oosterend were exposed to reactivated sand from the first foredunes and the beach with 0.8% CaCO<sub>3</sub> and pH<sub>KCl</sub> 7.4 in 1995.

# 3 Vegetation and soil analysis

# 3.1 Vegetation sampling

Fourteen permanent quadrates (PQs), with a plot size of 4 to 16  $m^2$ , were laid out in 1995 to study changes in vegetation in detail in 1998, 2000, 2002 and 2005. In 2000 three more PQs were added and followed in 2002 and 2005 to follow the effects of inblowing sand over existing vegetation. In the sod cutting experiment on the Noordsvaarder the original PQ relevé of 1990 was added, as was the PQ relevé on the R.D.-dune from before the wildfire (1990) and the one on the Jan Thijssens-dune after the wildfire in 2004.

A total of 40 relevés resulted from the PQs at the sites with natural vegetation development and 46 relevés from the PQs at the sites with vegetation development after management, including the repetitive studies.

The PQs were monitored according to the Braun-Blanquet method (WESTHOFF & VAN DER MAAREL 1973) with a modified version of the Braun Blanquet scale (BARKMAN et al. 1964). The values were transformed into the 1-9 scale (VAN DER MAAREL 1979).

# 3.2 Soil sampling

In 1995 (results used in KETNER-OOSTRA & SÝKORA 2000) and 2005, soil samples were taken at a distance of 10-15 cm from all PQs. Besides, in the same years, from the first dune ridge (foredune) with drifting sand, on the Noordsvaarder, near Hoorn-aan-zee and

in Cupido's polder, respectively, one soil sample was taken for reference. Bulked samples consisting of 8-10 subsamples per plot were used in all cases.

The soil samples were taken and analysed stratified from 0-2 cm, 2-10 cm and 10-30 cm depth. As the reference samples from the foredunes were taken from 0-10 cm depth, the values of 0-2 cm and the 2-10 cm layer from the PQs were recalculated into one value for the 0-10 cm layer. Besides differences between the 0-2 cm upper layer (important for cryptogams) and the total 0-10 cm layer were made visible.

The soil samples were chemically analysed for  $pH_{KCl}$  and % CaCO<sub>3</sub>. For methods of analysis, see KETNER-OOSTRA & SÝKORA (2000).

## 3.4 Data analysis

#### 3.4.1 Vegetation classification and ordination

The total of 86 relevés originating from the PQs in all research locations, see above, were both ordinated and classified using multivariate analysis (TWINSPAN, HILL 1979). The TWINSPAN table (not reproduced here) was used to construct a TWINSPAN dendrogram, based on presence and characteristic cover. Characteristic cover is 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.

#### 3.4.2 Vegetation change

The coverage of the phanerogams, bryophytes, lichens, bare sand and litter in the relevés of some PQs, and as such reported in KETNER-OOSTRA (2006), are used in diagrams to depict the vegetation change in the period 1995-2005. Selected were four PQs in the pioneer stage, three on slightly calcareous sand dunes (one on the third dune ridge at the Noordsvaarder, one on the slope of the Paraplu-dune, one in Cupido's polder) and one in the stabilized acid dunes north of Midsland. These PQs were the most explicit in their vegetation change seen from the perspective of lichen-development during the 10-year period.

#### 3.5 Nomenclature

The nomenclature of the plant communities follows WEEDA et al. (1996) and STORTEL-DER et al. (1996). The nomenclature for the phanerogams follows VAN DER MEIJDEN (1996), with the exception of *Festuca ovina* which has always been treated as sensu lato. For the mosses we follow DIRKSE et al. (1999), and for the lichens APTROOT et al. (2004).

# 4 Results

# 4.1 Vegetation of all study sites

Table 1 consists of a TWINSPAN dendrogram based on the total data set of 86 relevés. The 15 clusters distinguished were grouped into three groups: A, B and C (see Table 1). The three groups are characterized by the presence of species characteristic of the *Koelerio-Corynephoretea*. Group AB contains the pioneer and subsequent succession stages and group C covers the graminoid-encroached situation.

Within group AB, group B differs from group A in the cover and species composition especially of the moss layer. Whereas group A is characterized by the calciphilous mosses *Ceratodon purpureus* and *Brachythecium albicans* and lichens *Cladonia humilis* and *C. pocillum*, group B is characterized by a higher proportion of phanerogams.

Group A1-3 can be assigned to the *Phleo-Tortuletum ruraliformis* (*Ph.-T.*), a community of sunny, dry sites on calcium containing dune sand, poor in humus with in Group A1+2 an open *Hippophae rhamnoides* shrub, with the sub-neutral *Cladonia foliacea* in cluster A1 and *Eryngium maritium* and the calciphilous moss *Tortula ruralis* ssp. *ruraliformis* in cluster A2. Cluster A3 consits of a transition between the *Ph.-T.* and the *V.-C.* with calciphilous herbs, like *Galium verum*, and the lime-indicating lichens *Peltigera rufescens* and *Cladonia rangiformis*.

Cluster A4 is characterized by the almost exclusive presence of the usually epiphytic lichen species *Hypogymnia physodes*, *H. tubulosa* and *Parmelia sulcata*.

Group B1-6 contains, apart from eutrophic grasses, sub-neutral lichens, while group B7+8 consists of pioneer vegetation on artificially or naturally bare soil characterized by Green algae and mosses.

Group B1-4 is characterized by *Holcus lanatus* and *Campylopus introflexus*, while group B5+6 has more herbaceous species, among which *Hieracium peleterianum*. The latter species combined with *Empetrum nigrum* is also differentiating group B1+2 against group B3+4. Due to overblowing with sand, species of the foredune are present in cluster B1, while cluster B2 represents a typical *Pyrolo-Salicetum*, a *Salix repens* scrub with *Empetrum nigrum* and *Pyrola rotundifolia*.

In group B3+4 species of the V.-C. are combined with *Campylopus introflexus*. Cluster B3 represents the final stage after sod cutting, which forms a transition to dwarf shrub heath and is as such a connection to cluster B2 and B5 with a high cover of herbaceous plants and a moss cover of 80% (not to see in Tab.1). Cluster B4 consists of a V.-C. with pioneer lichens, like *Cladonia foliacea*, *C. scabriuscula* and *C. furcata*, but with an increase of mosses during succession, like *Campylopus introflexus* and *Dicranum scoparium* (*D. scoparium* not differential on this level, but frequent according to the TWINSPAN table).

Group B5+6 are richer in herbaceous species, typical of rabbits grazing and with influence of airborne sand. Here *Hieracium peleterianum*, *Veronica officinalis* and *Cladonia rangiformis* have their optimum. While in cluster B5 succession into the

*Polypodio-Empetretum* can be seen, cluster B6 represents an earlier succession stage without dwarf shrubs.

Within the pioneer vegetation of group B7+8, cluster B7 contains vegetation that developed after sod cutting or after a wildfire, and cluster B8 represents the succession on naturally open acidic sand with intrusion of the neophyte *Campylopus introflexus*.

Group C with the graminoid-encroached situation contains group C1+2 with cluster C1 representing the pre-fire situation and cluster C2 the recovering vegetation after wildfire in a time sequence (both from the R.D.-dune and the Jan Thijssens-dune). Cluster C3 finally covers the end of succession in the *V.-C.* with *Festuca ovina* and mats of *Cladina portentosa* and *Cladonia uncialis*.

# 4.2 Sites to study natural succession

## 4.2.1 Noordsvaarder

In the research period 1990-1995 the second and the third dune ridge on the Noordsvaarder were characterized by a *V.-C.* very rich in *Cladonia*-species, with some species characteristic for lime-rich dune sand, like *Cladonia pocillum* and usually epiphytic lichens growing terrestrially (KETNER-OOSTRA & SÝKORA 2004).

Between 1995 and 2005 on the second dune ridge still several of such epiphytes like *Hypogymnia physodes*, *H. tubulosa, Evernia prunastri* and *Parmelia sulcata* were present (Tab.1, cluster A4). In the relatively high moss cover the species composition changed from 1995 to 2005, with *Ceratodon purpureus* almost disappearing and *Dicranum scoparium* and *Hypnum cupressiforme* increasing, the latter species from 5% till 60% between 1995 and 2005. These changes are clearly related to the decrease of CaCO<sub>3</sub>. In 1995 the top soil layer of the second dune ridge contained 0.3% CaCO<sub>3</sub>, decreasing till < 0.1% in 2005, which was also measured in the 0-10 cm layer; however for both soil layers the pH<sub>KCl</sub> indicated a sub-neutral habitat (Tab. 2).

In 2005 the vegetation of dune ridge 2 on the Noordsvaarder very much resembled that of dune ridge 3 in 1995. Both *Hypogymnia*-species disappeared from the second dune ridge since 2003 and sub-neutral *Cladonia*-species like *Cladonia foliacea*, *C. scabriuscula* and *C. humilis* remained (TWINSPAN table; not shown here).

On dune ridge 3 (Tab.1, cluster B4) the lichen cover diminished from 75% to 7% while the moss layer increased from 8% to 85% between 1995 and 2005, with *Dicranum scoparium* as dominant species (Fig. 2). Locally, an *Empetrum nigrum* heath developed, covering 50% of the PQ in 2005, while its  $pH_{KCl}$  in both the 0-2 cm and the 0-10 cm soil layer stabilised around 4.5 (Tab. 2).



Fig. 2: Change in cover % of different vegetation elements between 1995 and 2005 in the PQ on the third dune ridge of the Noordsvaarder. After: KETNER-OOSTRA (2006).



Fig. 3: Change in cover % of different vegetation elements and bare sand between 1995 and 2005 in the PQ on the Paraplu-dune. After: KETNER-OOSTRA (2006).

## 4.2.2 Paraplu-dune

In 1995 the Paraplu-dune was covered with a transition between an open *Ph.-T.* and a *V.-C.* rich in lichens, including some terrestrial growing epiphytes (Tab.1, cluster A3) and with 0.1% CaCO<sub>3</sub> in the 0-2 cm soil layer of in-blowing sand. Since 1995 the amount of bare sand clearly decreased and much litter was produced (Fig. 3). In 2005 no (0.0%) calcium was found and the pH<sub>KCl</sub> dropped from 6.0 to 5.3 (Tab.2) in the 0-2 cm soil layer. Mosses were the winners (Fig. 3). Among the mosses, *Hypnum cupressiforme* increased from 2% to 45% and replaced the calciphilous *Tortula ruralis* ssp. *ruraliformis* (TWINSPAN table, not shown here). The original seven lichen species remained with an equal cover of 8%, from which *Cladonia foliacea* and *C. rangiformis* indicated the sub-neutral habitat. However, the terrestrial growing epiphyte *Evernia prunastri* disappeared since 1998, while the calciphilous *Peltigera rufescens* increased in cover in the research period.

## 4.2.3 Cupido's polder

The young dunes in Cupido's polder were not very lichen-rich in 1995, but with much limerich in-blowing sand from the foredune (1.2% CaCO<sub>3</sub> in 1995) more lichens were expected in the following years (two PQs, one as cluster A1 and one in cluster A2 in Tab. 1). Indeed, total lichen cover increased from 20% to 80% in the research period, while the moss layer with the calciphilous *Tortula ruralis* ssp. *ruraliformis* and *Brachythecium albicans* (TWINSPAN table; not shown here) decreased from 50% to 5% (Fig. 4). Species like *Cladonia pocillum, C. humilis* and *C. fimbriata* had a temporary optimum, while the rare *C. cariosa* was found only in 2002 (KETNER-OOSTRA 2006). The soil is gradually reaching the sub-neutral phase with not much lime in the 0-2 cm and 0-10 cm layer. However, the samples of the 10-30 cm layer (not shown here) contained 0.4 % CaCO<sub>3</sub> in 2005, which explained the lasting presence of the deeper rooting *Hippophae rhamnoides* and *Eryngium maritimum*.



Fig. 4: Change in cover % of different vegetation elements between 1996 and 2005 in a PQ in Cupido's polder. After: KETNER-OOSTRA (2006).

Tab. 1: TWINSPAN dendrogram of the total data set of Terschelling relevés in the period 1995-2005, including one pre-fire relevé and some relevés after sod cutting in 1990. Cluster groups A, B, C and D (see Text) are indicated. At each dichotomous division the main differential species are indicated.

Division 1	2	3	4	5	6
AB	Α	A1-3	A1-2	A1	
Corynephorus canescens	Sedum acre	Fetuca rubra dead	Hippophae rhamnoides	Hippophae rhamnoides	
Festuca rubra	Phleum arenarium	Ammophila arenaria	Festuca rubra	Festuca rubra	
Hypnum cupressiforme	Cerastium diffusum	Leontodon saxatilis	Cladonia foliacea	Cladonia foliacea	
Cladonia foliacea	Ceratodon purpureus	Arenaria serpyllifolia	Cladonia pocillum	A2	
Cladonia furcata	Brachythecium albicans Cladonia humilis	Hypochaeris radicata Tortula ruralis	Cladonia scabriuscula	Eryngium maritimum Polypodium vulgare	
	Cladonia pocillum	Tortula furails		Phleum arenarium	
	r			Jasione montanum	
				Tortula ruralis	
			A3		_
			Corynephorus canescens		
			Galium verum		
			Viola canina Eryngium maritimum		
			Cladonia rangiformis		
			Peltigera rufescens		
			Coelocaulon aculeatum		
		A4			
		Dicranum scoparium			
		Campylopus introflexus			
		Cephalozielle divaricata Cladonia scabriuscula			
		Hypogymnia physodes			
		Hypogymnia tubulosa			
		Parmelia sulcata			
	В	B1-6	B1-4	B1+2	B1
	Lotus corniculatus	Agrostis capillaris	Holcus lanatus	Hieracium peleterianum	Ammophila arenaria
	Luzula campestris	Holcus lanatus	Campylopus introflexus	Empetrum nigrum	Sonchus arvensis
	Calamagrostis canescens	Cladonia foliacea			Salsola kali
	Cerastium fontanum Cladina portentosa	Cladonia scabriuscula			Lonicera peryclimenum B2
	Ciadina portentosa				Salix repens
					Pyrola rotundifolia
					Polypodium vulgare
					Dicranum scoparium
					Cladina portentosa
				B3+4	B3
				Corynephorus canescens	Leontodon saxatilis
				Aira praecox	Agrostis capillaris
				Holcus lanatus Hieracium umbellatum	Festuca rubra dead Ammophila arenaria dead
				Rumex acetosella	B4
				Campylopus introflexus	Cladonia foliacea
					Cladonia furcata
					Cladonia scabriuscula
					Campylopus introflexus
			B5+6	B5	
			Hieracium peleterianum Veronica officinalis	Empetrum nigrum Polypodium vulgare	
			Viola curtisii	Festuca ovina	
			Arenaria serpyllifolia	Ammophila dead	
			Cladonia rangiformis	Dicranum scoparium	
			-	Cladina portentosa	
				B6	
				Negatively differentiated	
		B7+8	B7	by absence of species B5	
		B/+8 Green algae	B7 Festuca rubra		
		Polytrichum juniperinum	Aira praecox		
		Ceratodon purpureus	Jasione montana		
		Campylopus introflexus	Hieracium umbellatum		
			Hypochaeris radicata		
			Polytrichum juniperinum		
			B8		
			Cladonia zopfii Cladonia cervicornis		
			Placynthiella icmalea		
С	C1-2	C1		1	
Ammophila arenaria alive					
Carex arenaria alive	Carex arenaria alive	Ammophila arenaria dead			
	Hieracium umbellatum	Dicranum scoparium			
		Campylopus introflexus			
		Cladina portentosa			
		C2			
		Negatively differentiated by absence of species C1			
	C3	e, absence of species CI			
	Festuca ovina	1			
	Corynephorus canescens				
	Jasione montana				
1	Dicranum scoparium				
	Cladina portentosa				
	Cladonia uncialis				

## 4.2.4 Dunes north of Midsland

All relevés of the plant community of *Festuca ovina* s.l. with a high cover of *Cladina portentosa* and *Cladonia uncialis* in the dunes north of Midsland, occur together in one cluster (Tab.1, cluster C3). Gradually the cover of *Festuca ovina* increased, while *Corynephorus canescens* disappeared from the PQs in 2000. *Empetrum nigrum* and *Calluna vulgaris* seedlings established in the PQs and cover of *Dicranum scoparium* increased, but the reindeer lichens still had a high cover. A gradual succession into a heath might be possible in the future, however, an extreme hot summer might give a throw-back on the dwarf shrub seedlings.

In the PQ on a north-facing slope (Fig. 5) with 90% bare, acid sand (pH<sub>KCl</sub> 4.3) in 1995 and with several pioneer lichens like *Cladonia zopfii*, *C. cervicornis*, *C. foliacea* and *Cetraria aculeata* and covered by Green algae in the early monitoring years (Tab.1, cluster B8), moss encroachment with *Campylopus introflexus* followed, ending with 80% in 2005 (Fig. 5). However, the mentioned pioneer lichens survived.



Fig. 5: Moss-encroachment with *Campylopus introflexus* in a PQ with pioneer lichens (*Cladonia foliacea, C. zopfii, C. cervicornis* and *Cetraria aculeata*) in stabilized older dunes with acid sand north of Midsland between 1995 and 2005 (data in %%). After: KETNER-OOSTRA (2006).

## 4.3 Sites to study the effects of intended and unintended dune management

#### 4.3.1 Noordsvaarder

On the site at the Noordsvaarder with the sod cutting experiment in 1990 phanerogams and mosses were gradually increasing till 1995 (Tab.1, cluster B7; see also Table 4 in KETNER-OOSTRA & SÝKORA 2000). *Campylopus introflexus* died in the very dry summer of 1994

and was replaced by *Dicranum scoparium* and *Hypnum cupressiforme*. The latter species dominated in 2005 with 70% of the moss cover of 80%. In cluster B3 a high cover of herbaceous plants and a moss cover of 80% represents the final stage after sod cutting. This forms a transition to dwarf shrub heath. Between 2002 and 2005 the herb-rich vegetation was replaced by a *Polypodio-Empetretum*, with a 75% covering.

## 4.3.2 R.D.-dune

The results after the wildfire at the R.D.-dune in 1993 were published in KETNER-OOSTRA et al. (2006). These results, summarized in Fig. 6, were calculated from many subplots, yearly monitored between 1993 and 2001 (except 2000). They include the PQ of the monitoring project, which was also visited in 2003 and 2005. This graminoidencroached PQ (pre-fire in 1990) and the two graminoid-encroached PQs on the Jan Thijssens-dune (pre-fire in 1995, 1998, 2000 and 2003) are included in Tab.1, cluster C1, and after fire in cluster C2.

In 2005 it became apparent that the PQ on the R.D.-dune was additionally influenced by inblowing sand from the nearby foredune. This is clearly visible in the soil data, especially from the 0-2 cm soil layer (Tab. 2), where in 2005 the pH<sub>KCl</sub> was with 6.7 very clearly much higher than with 4.5 in 1995. Such a remarkable difference could not be found on the Jan Thijssens-dune, where one year after the wildfire (2005) almost no difference in the soil pH<sub>KCl</sub> is seen compared with the graminoid-encroached situation in 1995 (2005: 4.0, 1995: 3.9, both in the 0-10 cm soil layer). Here even the ashes seemed to make no difference.



Fig. 6: Changes in cover % of different vegetation elements, bare sand and ash on the R.D.dune, Oosterend, between 1966 and 2001. From: KETNER-OOSTRA et al. (2006).

Tab. 2: Results of the soil analysis of the 0 - 10 cm layer for five locations on Terschelling in 1995 and 2005. All plots on Dune ridge 1 are Reference plots, all other plots are Permanent quadrats (PQs). A second value for the 0 - 2 cm layer is added, if different from the 0 - 10 cm layer. Bold: clearly lime containing.

\* second dune with the same distance to Dune ridge 1; \*\* in 2000; \*\*\* after a wildfire in 2004; \*\*\*\* after a wildfire in 1993; \*\*\*\*\* with influence of inblowing sand.

	Dune ridge	pH <sub>KCl</sub> (1995)	pH <sub>KC1</sub> (2005)	% CaCO <sub>3</sub> (1995)	% CaCO <sub>3</sub> (2005)
Noordsvaarder	1	6.9	7.4	0.3	0.3
	2	5.7 (5.6)	6.2 (6.6)	0.2 (0.3)	<0.1
	3	4.4 (4.5)	4.6 (4.3)	< 0.1	<0.1
	4	4.3 (4.1)	4.3 (4.2)	<0.1	<0.1
Hoorn-aan-zee	1	7.4	8.1	0.8	1.0
	2	6.0 (6.1)	6.2 (6.4)	<0.1	< 0.1
	3	4.6 (5.4)	4.7 (5.2)	<0.1	<0.1
	4	-	5.0 (5.9)	-	<0.1
Paraplu-dune		6.2 (6.0)	5.7 (5.3)	0.1	<0.1
Cupido's polder	1	8.1	8.1	1.2	1.0
	2	7.0 (6.8)**	7.0 (6.4)	0.2**	<b>0.1</b> (<0.1)
	2*	7.0 (6.5)**	6.1 (5.8)	0.1**	< 0.1
Dunes north of	north slope	3.9 (3.7)	4.0 (3.8)	< 0.1	< 0.1
Midsland	+/- flat	3.7 (3.5)	4.1 (3.9)	<0.1	<0.1
	pioneer	4.3	4.5	<0.1	<0.1
Jan Thijssens-dune	south slope	3.9 (3.7)	4.0***	< 0.1	< 0.1
R.D dune (Rita's dune)	west slope	4.3 (4.5) ****	5.6 (6.7) ****	<0.1	<0.1 ( <b>0.1</b> )

#### 4.3.3 Dunes near Hoorn-aan-zee

In the dunes near Hoorn-aan-zee in-blowing sand is often signaled, however, it is not visible in the CaCO<sub>3</sub> content of the plots (Tab. 2). In the period 1995-2005 the soil in the 0-2 and in the 0-10 cm layer of dune ridge 2 continued to be sub-neutral. In the PQ on the second dune ridge *Hieracium peleterianum* increased from a 20% cover till 70%, with *Cladonia rangiformis* as the surviving sub-neutral species, but in this period decreasing from 20% in 1995 to 4% in 2005 (Tab.1, cluster B6, period 1995-2005).

In 1995, in the PQ on dune ridge 3 near Hoorn-aan-zee with acid soil of  $pH_{KCl}$  4.6 (Tab. 2), the lichen vegetation covered 90% and consisted of a mosaic of calciphilous, neutral and acidophilous lichen species (Tab.1, cluster B5). In 2005 the herb-layer and the moss layer had increased considerably with the composite *Hieracium peleterianum* settled in 2000 and *Hypnum cupressiforme* becoming the dominant moss with an increase from 4% to 60% between 1995 and 2005. The lichen cover decreased from 90% to 20% with *Cladonia rangiformis* diminishing from 40% to < 1% and the acidophilous *Cladina portentosa* remained at 20%. Some other acidophilous species like *Cladina ciliata*, *Cladonia ranulosa* and *Cetraria aculeata* were new arrivals.

On ridge 4 near Hoorn-aan-zee grows an interesting Pyrolo-Salicetum with Empetrum nigrum on a sub-neutral dune soil with probably some influence of in-blowing sand,

which seems to stabilize the *Pyrola rotundifolia* population already for decades (Tab.1, cluster B2).

Between Hoorn-aan-zee and Oosterend in-blowing sand gradually covered the original vegetation with *Empetrum nigrum*. *Ammophila arenaria* and species of the foredune established themselves on the sand, like *Salsola kali* and *Sonchus arvensis* var. *maritimus* (see in Tab.1, cluster B1), while some of the PQ relevés before 2002 are present in Tab.1, cluster B5.

# 5 Discussion

Concerning our first research question: natural succession in lichen-rich vegetation leads to a decrease in biodiversity. In 1995, relatively open dune grassland communities were still present in young recently formed young dunes, dune ridges and on the slopes of a mobile dune (KETNER-OOSTRA & SÝKORA 2000). At that time PQs were laid out in such transition stages of the *V.-C*. to the *Ph.-T*. and in the *Ph.-T*. itself, that formed a suitable environment for some lichen pioneer species of slightly calcareous or sub-neutral sand, including some of the epigeic growing epiphytes. In this ten-years study on these PQs changes from lichen-rich to moss-dominated stages were observed, together with a corresponding soil development and acidification associated with the ageing of dune soil.

In several PQs the lichen-rich vegetation gradually changed in a moss-dominated vegetation with the increase of *Hypnum cupressiforme*, being the dominant moss in 2005. This resulted in the decrease in the lichen cover and mainly acidophilous *Cladonia* species remained, but still some sub-neutral lichen species were present in 2005.

In the main area of stabilized acid dunes, encroachment with long graminoids changed the dunes in the last decades (KETNER-OOSTRA & SÝKORA 2004). However, carpets of the reindeer lichen *Cladina portentosa* still occur, and are especially well developed north of Midsland. This final stage in succession in the *V.-C.* changed very slowly and the same applies to its biodiversity. This almost permanent condition was studied in the dunes on the island of Læsø (BÖCHER 1952, CHRISTENSEN 1989). On Terschelling this final stage needs protection from mechanical disturbance by the public or by new management measures like grazing. Grazing will very much harm the structure of these carpets, as was seen in autumn 2005, when the introduced goats totally disturbed some of the reindeer lichen PQs (KETNER-OOSTRA 2006). It will take decades to reach such a final stage and probably *Campylopus introflexus* encroachment will occur in open spaces (most moss cover in PQ shown in Fig. 5).

Most terrestrially growing epiphytes disappeared during the dune succession. At a first glance, a relation between the decrease of epiphytic lichens on soil and the decrease of % CaCO<sub>3</sub> seems the most obvious conclusion; however, it seems more plausible that the epiphytes established in rather open dry grassland with short grasses with much bare sand without much humus. The microclimate in such vegetation promotes the poikilohydric uptake and loss of water in lichens, which are connected with the passive accumulation of macronutrients through alternating periods of drying out and

remoistening (NASH III 1996; KETNER-OOSTRA 2007). Encroachment by mosses and graminoids maintains a moist microclimate over a much longer period of time, which is harmfull for lichens.

Besides the loss of epiphytes, natural succession in lichen-rich vegetation indeed leads to a decrease in lichen diversity, but this does not always apply for the diversity of phanerogams. However, when soil acidification succeeds, encroachment with graminoids and consequent species loss might occur (KETNER-OOSTRA & SÝKORA 2000).

Management by skimming off the sods in moss-encroached vegetation appeared to be an unsuccessful technique for restoring the biodiversity of cryptogams. Lichens did not return because succession proceeded into a graminoid-rich vegetation, which later turned into dune heath (KETNER-OOSTRA 2006). No positive effect was found, neither temporarily nor on the long-term. Only deep sod-cutting down to not leached sand will possibly be effective.

Also after the wildfire, lichen colonization was probably partly limited by the rapid moss colonization and partly by the quick regrowth of vascular plants (graminoids and rosette plants) from their unburned roots. Ashes as fertilizers also did not favour the little competitive lichens when the rapid moss encroachment occurred. After the ash had been leached out or blown away, vegetation turned to the graminoid dominant stage before the fire, most probably a result of the same environmental factors that promoted the dominance of graminoids before, namely (1) nitrogen deposition in combination with the available phosphates in the soil (KOOIJMAN et al. 1998); (2) the impact of acidification on the soil micro-organisms which has been shown to influence the regrowth of *Anmophila arenaria* (DE BOER et al. 1998) and (3) litter decomposition and soil formation during succession (KOOIJMAN & BESSE 2002).

As on present young dunes, lichen diversity is still high, and several rare lichen species, like the Red List species *Cladonia cariosa* and the epiphytes like *Evernia prunastri*, *Hypogymnia physodes*, *H. tubulosa*, *Pseudevernia furfuracea* and *Ramalina farinacea* can still be found (noted by APTROOT et al. 2000), blowing-in of fresh sand appears to be most effective in restoring lichen diversity. In the foredunes also the phanerogams seemed to profit from the supply of fresh sand, especially on the second and third dunes ridges. Here the composite *Hieracium peleterianum* is found and expanded into exuberance, which is spectacular for a species that established on Terschelling rather recently (WEEDA et al. 1991). If too much sand is blowing in older dune stages, the original vegetation is covered and replaced by *Ammophila arenaria* and species of the foredune can settle again.

Our findings suggest that the best option for future management in maintaining lichen vegetation in the *V.-C.* is to allow sand with a sub-neutral, neutral or basic pH from foredunes and from natural or reactivated blowouts to blow in (KETNER-OOSTRA & SÝKORA 2000). For the distant future it is necessary that new dune ridges will be stimulated to develop in order to guarantee the continued lichen richness in the 'grey dunes' for the future.

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Addresses of the authors:

Dr. Rita Ketner-Oostra, freelance ecologist Algemeer 42 6721 GD Bennekom The Netherlands E-mail: rita.ketner.oostra@gmail.com (corresponding author)

Prof. Dr. Karlè V. Sýkora Wageningen University Department of Environmental Sciences Nature Conservation and Plant Ecology Group Droevendaalsesteeg 3a 6708 PB Wageningen The Netherlands

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