Lichen-rich coastal and inland sand dunes (Corynephorion) in the Netherlands: vegetation dynamics and nature management

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Lichen-rich coastal and inland sand dunes (Corynephorion) in the Netherlands: vegetation dynamics and nature management

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LICHEN-RICH COASTAL AND INLAND SAND DUNES (CORYNEPHORION) IN THE NETHERLANDS: VEGETATION DYNAMICS AND NATURE MANAGEMENT

General introduction

Rita Ketner-Oostra

Chapter 1. General introduction

1.1. Lichen-rich grasslands in nutrient-poor sand dunes in the Netherlands before the 1970s

Until the mid-1970s the dry coastal calcium-poor dunes in the phytogeographical Wadden district in the Netherlands (van der Meijden 1996) were famous for their lichen-rich pioneer grasslands, developed in the course of primary succession in the xeroseries (Westhoff 1947). The greater part of the older dune slopes was covered by a short grassland, the Violo-Corynephoretum Westhoff ex Boerboom 1960 (V.-C.), dominated by grey hairgrass (*Corynephorus canescens*) and sand sedge (*Carex arenaria*) and rich in the lichen genera *Cladonia* and *Cladina*, the latter called reindeer lichens. These lichen-rich 'grey dunes' were especially well developed on the island of Terschelling (Brand & Ketner-Oostra 1983). Lichens that are usually epiphytic, such as *Bryoria fuscensens*, *Evernia prunastri*, *Hypogymnia physodes*, *H. tubulosa*, *Pseudevernia furfuracea* and *Usnea* spp., grew on moss carpets, but also on open sites with only *Corynephorus canescens* (Barkman 1958; Ketner-Oostra 1972).

Apart from these calcium-poor coastal dunes, there are considerable areas of non-calcareous inland sand dunes in the Netherlands originating from Pleistocene deposits (Koster 2005). Many of these once large areas have been reduced in size since the late 19th and early 20th centuries as a result of afforestation. One of the largest remaining areas of these semi-natural inland sand-dune ecotopes is the Kootwijkerzand. Here, short pioneer grasslands with *C. canescens* assigned to the Spergulo-Corynephoretum Libbert 1932 (S.-C.) are part of the xeroseries. Until the 1970s the intermediate and terminal succession stages and the spatial gradients to heath were rich in the lichen genera *Cladonia* and *Cladina*. The relation between vegetation, soil and microclimate in these heathlands and inland dunes was studied by Stoutjesdijk (1959).

An integrated research and teaching training project of the University of Utrecht (Department of Vegetation Science of the Institute of Systematic Botany) on inland and coastal heathland was set up by de Smidt in the early 1960s (de Smidt 1966) and extended with study of the inland and coastal sand dunes in the mid-1960s. The cryptogam richness of these ecotopes was studied in detail by Oostra (1968) and Sipman (1969) for the coastal dunes, and by Daniëls (1983) and Pos (1968) for the inland dunes.

1.2. Changes in sand dune vegetation since the 1970s

Since the 1970s, nitrogen (NH_4-N, NO_3-N and organic compounds) has been an important acidifying and eutrophicating pollutant throughout the Netherlands as a result of the increased dry and wet atmospheric deposition. Nutrient enrichment increases the productivity in nutrient-poor ecosystems, enabling more competitive species to oust species that are characteristic of these ecosystems (Bobbink et al. 1998). In the calcium-poor coastal dunes this became apparent in the dominance of tall graminoids, especially *Ammophila arenaria*, which changed the aspect of the vegetation (Ketner-Oostra 1993), while other grasses dominated the vegetation of inland sand dunes (Masselink 1994) and heathlands (Diemont 1996). Changes in the flora, both of phanerophytes and cryptogams, in dry oligotrophic habitats, have been partly correlated with acidification caused by the high emission of SO_2 (Quené-Boterenbrood 1988). That emission declined considerably from the end of the 1970s onwards. However, since then, nitrogen (N) deposition has been the main polluting factor, partly as an effect of intensified livestock farming. In the central part of the country in 1990 the mean nitrogen deposition was 50 kg N ha^{-1} and for the West Frisian islands it was estimated to be 20 kg N ha^{-1} (Bleeker & Erisman 1996). From 1990 N deposition gradually decreased, to a mean value of 40 kg N ha^{-1} in 2001, but near areas with high livestock concentrations the N deposition is still high, with peak values exceeding 60 kg N ha^{-1} yr^{-1} (Buijsman 2004).

In the inland sand dunes the decrease in surface area of dry oligotrophic ecotopes was accompanied by an increase of the abundance and size of graminoids. Berendse et al. (1993) pointed to an accelerated vegetation succession on nutrient-poor sandy soils as one of the effects of N deposition. Another effect was that mosses became dominant (Daniëls et al. 1987). The neophytic moss *Campylopus introflexus*, a species adapted to acid open sand, invaded both coastal and inland dunes and reduced the area of open sand and the lichen richness in both ecotopes (van der Meulen et al. 1987; Biermann & Daniëls 1997). In the 1990s the State Forestry Service Region Veluwe-Achterhoek showed interest in the current lichen-diversity and the lichen communities on the Kootwijkerzand and I was assigned to their vegetation study combined with that of the soil. This resulted in setting out Permanent quadrats (PQs) in these lichen communities (Figure 6.1a) and in 1993 the monitoring of the vegetation development began (Ketner-Oostra 1994).

1.3. EGM (= Effect-oriented Management Measures) in coastal dunes

In the mid-1980s, an explicit objective of Dutch nature conservation policy was to halt the decline in biodiversity. However, attempts to reverse the influence of acidification and eutrophication in natural landscapes were rarely successful. In 1989 the Ministry of Agriculture, Nature and Fisheries began to fund restoration practices. A survival plan for forests and nature ('Overlevingsplan Bos en Natuur' (OBN) 1995-2010 was launched (LNV 1994) and an Expert Network for Coastal and Inland sand dunes was set up to advise on new restoration measures. Since then, 'Effect-oriented Management Measures' (EGM), i.e. additional restoration measures against acidification, eutrophication and desiccation in different nature target types, have been funded. Part of the available budget has been used for knowledge development.

Calcium-poor coastal dunes were included in a nation-wide EGM research project that aimed to restore former biodiversity in dry dunes (Vertegaal et al. 1991). In phase 1 (1991-1995) the University of Amsterdam (Department of Physical Geography and Soil Research) implemented large-scale management in 15 former blow-outs in the dune area of Eldorado on the island of Terschelling. In the final report on phase 1 van der Meulen et al. (1996) concluded that elongating the blow-outs in the direction of the prevailing westerly wind was particularly successful. The superficial layer of the accumulated sand proved to be neutral (pH-CaCl 7.1-7.8) and a pioneer vegetation established. However, the duration of the period in which sand was still blowing seemed restricted. Veer (1997) did small-scale experiments with mowing, sod-cutting and sand suppletion in open Violo-Corynephoretum and grass encroached V.-C. in plots of dune grassland on Terschelling. She found that atmospheric nitrogen input was an important source of N in open V.-C., but in grass-dominated V.-C. plots it was largely exceeded by mineralization. Kooijman et al. (1998) found that in the calcium-poor dune sands of the Wadden district, phosphorus was available, but N was limited; atmospheric N input had much more effect here than in the calcium-rich dunes of the Renodunale district, where phosphorus availability was limited.

1.4. Small-scale restoration measures in inland sand dunes before 1990

Since the 1960s, the sand dune management has been mainly small scale. Foresters have felled self-sown trees or a few ha of pinewood with chainsaws. One of the fieldwork areas for this thesis, the Kootwijkerzand, has been managed this way by the State Forestry (see Daniëls & Krüger 1996; Ketner-Oostra & Huijsman 1998). Small-scale management has also been practised in the Hulshorsterzand (owned by Natuurmonumenten), the Wekeromse Zand (Het Geldersch Landschap) and De Hoge Veluwe National Park (Daniëls & Krüger 1996). In the Harskamperzand, the army burn dry grassland and heath as a precaution against fires starting during their shooting exercises (Haveman et al. 1999).

In these early attempts to preserve the drift-sand ecotopes the main strategy was to maintain and restore wind erosion by keeping a stretch of sand open in the prevailing direction of the wind, which in the Netherlands is southwest to northeast. In the Kootwijkerzand a long stretchof blowing sands (supposed to be 300 ha) still exists, which is indeed oriented southwest to northeast. This is the result of small-scale management by the State Forestry Service since the 1960s: self-sown pine trees and *Prunus serotina* have been felled along the borders of the open sand dune and in the mosaics of grassland with heath, often combined with litter removal. Even a few ha of pinewood were cut: the stumps were dragged out and the branches burned (Daniëls & Krüger 1996, Ketner-Oostra & Huijsman 1998). More recently, the woody material has been chipped in situ and transported away from the site. In the past, litter was removed and sold to local azalea nurseries (Ketner-Oostra & Huijsman 1998). Other common small-scale measures were disk harrowing and sod removal.

1.5. Large-scale (EGM) management measures in inland sand dunes

In the large-scale management since the 1990s (EGM), the same practice of keeping one long stretch of blowing sand has been adopted. Two conditions have to be fulfilled to maintain or restore aeolian processes in sand dune landscape (Jungerius 2003). To move sand particles, wind force must exceed the critical velocity. The critical velocity for dry sands on the Veluwe with a mean diameter of 0.2 to 0.3 mm is about 6.5 m/sec (Bagnold 1954). To satisfy this condition, trees (like the planted pinewood on the southwestern border of the open sand) and other obstacles in the approach of the wind can be removed. The second precondition is a low resistance of the sand surface, which must be kept free of all vegetation (including algae) and organic soil material.

Large-scale management (in German 'Management durch Katastrophen', Riecken et al. 1998: 'catastrophic management') to restore the early stages of the drift-sand landscape was effectuated in both large and small inland sand dune areas. In 1992, the Hulshorsterzand, in the northern part of the Veluwe was one of the first nature reserves to be reactivated by large-scale cutting of pine trees and removal of topsoil (Frentz & van Griethuysen 1992). Similar measures were carried out in the much smaller Wekeromse Zand in 1992-1993 (Ketner-Oostra 1995) and in De Hoge Veluwe National Park in 2001 (Hasse et al. 2002). Inside the Wekeromse Zand the existing narrow stretch of bare sand was widened and a large area of trees (35 ha) was cut to reinforce the wind velocity (Ketner-Oostra 1995). It became common practice to remove also the upper (humus-rich) soil layer, to expose the mineral sand. In De Hoge Veluwe National Park, heavy machinery was used to do this and the topsoil removed was sold to road construction firms. Such projects are preceded by a preliminary research project that produces restoration proposals, as Hasse et al. (2002) did for De Hoge Veluwe, and have to be approved by the Expert Network for Coastal and Inland sand dunes. The restoration project in the former river dunes in North Limburg is the most recent example of this procedure (van den Ancker et al. 2002).

1.6. Monitoring and evaluating restoration measures

Regular monitoring of vegetation, fauna and soil is necessary in order to be able to evaluate interventions in the natural succession, and to help plan future management. Mosses and lichens have to be included in the monitoring, as these organisms provide the main part of plant diversity in coastal and inland sand dune vegetation, and relate to the fauna in general and to insect life in particular (Bakker et al. 2003). Part of this thesis is based on data from several such monitoring programmes.

1.6.1. Monitoring coastal dunes

As part of my own research project on vegetation succession and lichen diversity (Ketner-Oostra & Sýkora 2000) I followed the large-scale restoration measures in the coastal dunes of Eldorado (Terschelling), using relevés and including lichens and mosses.

In 1993 a wildfire abruptly terminated the small-scale EGM experiments of Maike Veer on a research dune north of Oosterend, Terschelling (Veer 1998). However, as fire could possibly be a useful restoration measure in dune grassland (V.-C.) dominated by long graminoids, for eight years I monitored the recovery of dune grassland after that fire (Ketner-Oostra et al. 2006).

In 1995, the State Forestry, province of Fryslân (Frisia), commissioned me to start a 10-year programme to monitor actual lichen-rich V.-C. threatened by moss and grass encroachment in the Terschelling dunes (Ketner-Oostra 1997). The project was initiated because of concern about the decline in biodiversity of the 'grey dunes' in the Wadden district. The aim was also to ascertain the effect of former management and to produce recommendations for future management.

1.6.2. Monitoring inland dunes

Daniëls & Krüger (1996) evaluated the small-scale management such as burning, soil damage by tractors removing cut Scots pines and litter dumping on the Kootwijkerzand and the Caitwickerzand. The impact of these restoration measures was still visible after ten years. However, in the same time period the undisturbed lichen-rich *C. canescens* vegetation appeared to have hardly changed.

In 1995 the former small-scale restoration projects implemented by the State Forestry Service in 13 locations on the Kootwijkerzand between 1960-1985 were evaluated by consulting the archives of the State Forestry. A comparison was made with the current vegetation in 1995 (Ketner-Oostra & Huijsman 1998). In certain locations the management was a failure because after 10-15 years there was too much encroachment of grasses or mosses. The pioneer vegetation of *C. canescens* with some mosses and lichens and the succession stages to heath were important for the preservation of biodiversity in the sand dune landscape and were very important for birds and for insects like butterflies, beetles and grasshoppers (Bink 1995). However, when Scots pines and/or self-sown trees had been removed from blown-out gravel-rich depressions, their place was taken by large carpets of the moss *Campylopus introflexus*. In 2005 these 13 locations were re-visited to record the longer-term effect of the management (Ketner-Oostra & Riksen 2005). In another project, the vegetation recovery after a wildfire in moss-encroached inland dunes north of Kootwijk was monitored for five years (Ketner-Oostra 2002).

1.7. Aim of the research

The aim of the research described in this thesis was to investigate long-term changes in the composition of the cryptogam-rich pioneer communities of the Corynephorion (Alliance of *Corynephorus canescens*), the coastal Violo-Corynephoretum and the inland Spergulo-Corynephoretum and their transformation into subsequent succession stages. The effect of grass and moss encroachment on lichens was studied. Small- and large-scale management measures aiming at restoring the former sand dune landscape with its high biodiversity as occurred before the 1970s, were evaluated for both coastal and inland nutrient-poor sand dunes. The prospects for lichen diversity in the coastal V.-C .and the inland S.-C. of the Netherlands, a country in which atmospheric pollution of N compounds is still high, were assessed.

1.8. Outline of the thesis

The changes that have taken place in the dry, lichen-rich pioneer grassland vegetation of the coastal calcium-poor dunes of Terschelling over a 30-year period are presented in **Chapter 2.** The influence of the invasion of the moss *Campylopus introflexus*, an alien moss species in this ecosystem, is discussed.

In **Chapter 3** a spatial sequence of differently aged coastal dune ridges is used to study temporal changes within sand dune vegetation. The development of vegetation and soil after sod cutting is described and the effect of blown in sand on the lichen diversity is presented and discussed.

The effect of fire on grass-dominated coastal dune vegetation (V.-C.) is analysed (**Chapter 4**), including the effect of fire on moss-rich grassland vegetation (S.-C.) in inland dunes near Kootwijk. The suitability of fire as a restoration practice is discussed.

The origin and development of inland drift-sand ecotopes in the Netherlands and their rapid decline after 1960 is presented in **Chapter 5.**

Chapter 6 describes the difference between former and actual successional pathways from open sand, through lichen-rich pioneer grassland to heath and forest. The changes in vegetation succession in general and in the diversity of cryptogams in particular of an inland sand dune area, the Kootwijkerzand, are presented for a period of nearly 40 years**.** These changes are related to acidification and eutrophication, the effects of the increased atmospheric N deposition since the 1970s, and to the invasion of *Campylopus introflexus*. The impact of natural and artificial disturbance, like a large archaeological excavation and of several restoration projects, is discussed.

Chapter 7 presents a synthesis of the botanical changes found in both coastal and inland calcium-poor sand dunes in the research period 1966-2006, and relates them to changes in environmental factors in that period. Differences between the developments in the coastal V.-C. and the inland S.-C. are discussed in relation to their specific environment, such as soil and climatic factors. The recommendations for future restoration management in coastal and inland dunes discussed in the previous chapters are re-examined.

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Chapter 2

DECLINE OF LICHEN DIVERSITY IN CALCIUM-POOR COASTAL DUNE VEGETATION SINCE THE 1970s, RELATED TO GRASS AND MOSS ENCROACHMENT

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Chapter 2. Decline of lichen diversity in calcium-poor coastal dune vegetation since the 1970s, related to grass and moss encroachment

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Abstract

Since the 1970s the encroachment by tall graminoids, especially of *Ammophila arenaria* and *Carex arenaria*, has changed the aspect of the calcium-poor 'grey dunes' of the Wadden Sea island Terschelling (the Netherlands) formerly dominated by *Corynephorus canescens*. In addition, the neophytic moss *Campylopus introflexus*, a species adapted to acid open sand, invaded these dunes. In this paper the cryptogam vegetation inside dry dune-grassland (the Corynephorion, the Tortulo- and Polygalo-Koelerion) and dune-heath (Empetrion) before (the 1960s) and after these changes (the 1990s) are compared. It was found that the lichen diversity in several plant communities was very high, amounting to a total of 45 species, among which 10 epigeic growing species that are usually epiphytes mainly occurring in the former period. In the latter period, *C. introflexus* not only outgrew the rare lichens from the pioneer stage of the Violo-Corynephoretum, but also the more common pioneer species of decalcified sand. However, when this moss has lower vitality through desiccation or being blown-over by sand, common humicolous lichens and some pioneer species may act as secondary pioneers on these withered moss carpets. In the 1990s some relatively open communities were still present in a transition stage of the Violo-Corynephoretum to the Phleo-Tortuletum and in the Phleo-Tortuletum itself, forming a suitable environment for some lichen pioneer species of subneutral sand, including some of the epigeic growing epiphytes.

Keywords: Acidification; *Ammophila arenaria*; *Campylopus introflexus*; *Carex arenaria*; *Empetrum nigrum*; Nitrogen deposition; Species diversity; Succession; Violo-Corynephoretum.

2.1. Introduction

During the previous decades grass and moss encroachment of coastal dune vegetation took place all over the Netherlands (van der Meulen et al. 1987, 1996, Vertegaal et al. 1991). This process affected biodiversity, as did encroachment with shrubs and competitive grasses in dune areas of the U.K. and N. Ireland after abandonment of grazing by cattle or dramatic crashes in the rabbit population following the outbreak of myxomatosis (Ranwell 1960, Binggeli et al. 1992, Packham & Willis 2001). In the Netherlands encroachment with graminoids is connected to increased acid rain and nitrogen deposition (Veer 1997, Kooijman et al. 1998). In the calcium-poor dunes of Terschelling it changed the microbial community in dune grasslands in favour of *Ammophila arenaria*-growth (de Boer et al. 1998). The decline in grazing pressure of rabbits, the resulting of the myxomatosis epidemic, must also be taken into account (Heil et al. 1990).

In the Violo-Corynephoretum Westhoff ex Boerboom 1960, as the characteristic plant community of dunes poor in calcium, pre-eminently lichens are the organisms that contribute greatly to the biodiversity (Erichsen 1957, Oostra 1968, Ketner-Oostra 1989).

Violo-Corynephoretum (V.-C.) on coastal sand dunes

In 1937, Westhoff (1947) started to study the xeroseries on the West Frisian islands, using the Braun-Blanquet-method. Then, in the so-called yellow dunes, the vegetation was still in a pioneer stage without lichens, while in the so-called grey dunes (James et al. 1977), *Corynephorus canescens* and lichens from the genera *Cladonia* and *Cladina* dominated in the V.-C. Westhoff (1947) thoroughly studied the *Cladina*-mats on western slopes and in shallow dry depressions, a vegetation similar to that described by Böcher (1941) of the lichen heaths on the island Læsø in the Kattegat (Denmark). Both Westhoff (1947) and Barkman (1958) mentioned lichen-rich 'variants' of the V.-C. characterized by *Evernia prunastri, Hypogymnia physodes, H. tubulosa, Pseudevernia furfuracea* and *Usnea subfloridana*. The epiphytic association Parmelietum furfuraceae Hil. sensu Ochsn. 1925 includes the above-mentioned lichens, generally found on the north-western side of the trunks of living trees. Barkman (1958) stated that these lichens benefit from the specific habitat conditions on moss-covered dune soil, a phenomenon comparable with epiphytes becoming terrestrial in other treeless regions, as has been observed at the alpine and the arctic timberline.

Effect of acid rain and nitrogen deposition

Since 1975 the above-mentioned toxiphobous epiphytic association has decreased considerably in their refugia in the Netherlands. This decline has been blamed partly on SO_2 emissions, partly on the high emissions of ammonia (van Dobben 1993). With SO2 influence maximized in the 1960s beard mosses disappeared from a wood refugium on the Veluwe (in the centre of the Netherlands; van Herk et al. 2000), but they were still present on Terschelling at that time. Since the 1970s the animal production, the so-called bio-industry effectuated an atmospheric dry and wet deposition of nitrogen (NH_4-N, NO_3-N and organic compounds) all over the

Netherlands, with an average of 50 kg N ha^{-1} yr^{-1} in the country's middle, and estimated for the West Frisian islands as 20 kg N ha^{-1} yr^{-1} (Bleeker & Erisman 1996). This corresponds with the estimated value of 10-20 kg N ha^{-1} yr^{-1} for the East Frisian island Spiekeroog (Gerlach 1993). Van Herk et al. (2000) found that in the last decennia many epiphytes in the mentioned wood refugium on the Veluwe received a final blow by this increased nitrogen deposition.

De Vries et al. (1994) predicted a disastrous effect of this high N deposition on dry dune vegetation in general. This atmospheric input on calcium-poor soils, was calculated through a model of natural and man-induced soil acidification, where almost no buffering system against acidification was present.

In the early 1990s large areas of dry dune vegetation along the Dutch coast appeared to have changed because of encroachment with tall graminoids. Terschelling was included in a nation-wide research project to restore former biodiversity in dry dunes (EGM, effect-oriented management against acidification and eutrophication of dry dunes, Vertegaal et al. 1991). As participants in this project Veer (1997) and Veer & Kooijman (1997) demonstrated that the atmospheric nitrogen-input was an important source of N in plots of open dune grassland, whereas in grass-dominated plots mineralization largely exceeded atmospheric nitrogen-input. Kooijman et al. (1998) found that the calcium-poor dune sands of the 'Wadden district' had a relatively high phosphorus availability, but were N-limited. This revealed the increased effect of the nitrogen-input.

In the late 1980s it was found that on more stabilized dunes behind the first foredunes marram grass (*Ammophila arenaria*) declined owing to fungal pathogens in their rhizosphere (van der Putten & Troelstra 1990). Afterwards, it was proved for Terschelling that in the rhizosphere of the acidic dune grasslands the microbial community 'in total' suppressed the activity of these fungal pathogens, resulting in a vigorous growth of *Ammophila arenaria* (de Boer et al. 1998).

Since the 1970s, the neophytic invader *Campylopus introflexus* both endangered the biodiversity of the calcium-rich dunes of the Netherlands (van der Meulen et al. 1987) and the calcium-poor dunes of the Dutch and German Wadden Sea islands (Biermann 1996, 1999). The local effect of this moss-encroachment was demonstrated in two previous studies on Terschelling, one north of Oosterend (Ketner-Oostra 1992) and one north of Midsland (Ketner-Oostra & van der Loo 1998; see also Figure 2.3).

Research objectives and related key questions

The aim of our study was to assess 25 years of vegetation change in the 'grey dunes' throughout Terschelling by comparing the species composition of lichen and moss vegetation from the 1966 - 1972 period (Oostra 1968, Ketner-Oostra 1989) with that of a revision study in the same area in the 1990 - 1996 period.
On the considerations given above we based the following hypotheses:

1. In the calcium-poor dunes of the 'Wadden district', lichen communities are especially well developed in the earlier succession stages of the 'grey dunes'.
2. This lichen diversity is a time-limited phenomenon, followed by moss encroachment.

3. This natural vegetation succession is probably influenced and accelerated by acid rain and nitrogen deposition.
4. The decline of epigeic growing epiphytes indicates changes in atmospheric deposition.

To verify these hypotheses we set out to answer the following questions:

1. How did vegetation composition change between the periods 1966-1972 and 1990-1996?
2. How did the vegetation of both periods differ in plant communities? Are vegetation types from the first period still present? Did they disappear? Did new or transitional types develop?
3. Can disappearance of certain vegetation types be used as an indication for changes in air quality?

2.2. Study area and environmental conditions

2.2.1. Soil origin and characteristics

Terschelling (Figure 2.1) is the third island from the west in the chain of West Frisian Islands in the Dutch part of the North European coastal dunes, the phytogeographic ‘Wadden district’. In many aspects different from the ‘Renodunaal district’ south of Bergen (North-Holland), it includes the dunes of the Wadden Sea islands and a small dune area north of Bergen (van der Meijden 1996). It is mainly characterized by Early and Middle Pleistocene sands, re-deposited in the Holocene (Saalien) west of Texel and Vlieland 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 a limited amount of weatherable minerals, notably iron and lime, are present (Eisma 1968, Klijn 1981). Most mineral ions are less bound than in the calcium-rich dunes. Natural acidification reinforced leaching, thereby leaving the older dunes almost completely decalcified. Phosphorus availability in the dune soils may be rather substantial, due to the comparatively loose nature of phosphorus sorption, resulting in nitrogen limitation (Kooijman et al. 1998).

2.2.2. Vegetation history

Two beach ridges (the longest 15 km), remnants of the Holocene sand bar with dune formation in the Atlanticum, developed into the West-Frisian island Terschelling. Northwest of the since the 9th century inhabited beach ridges extended a vast dune area of 9000 ha (85% of the total island), consisting of very calcium poor, movable sands (Westhoff 1947). Throughout the ages people used these dunes extensively for fuel gathering and rough grazing. When in the 13th century rabbits reached the West Frisian islands, not only their diet of grasses and dwarf shrubs but moreover their digging activity added to the destruction of dune vegetation (Wallage-Drees 1988). Periods of prosperity with importation of fuel from the mainland and recovery of the vegetation, alternated with poverty and sand drifts threatening villages and fields (Holkema 1870).

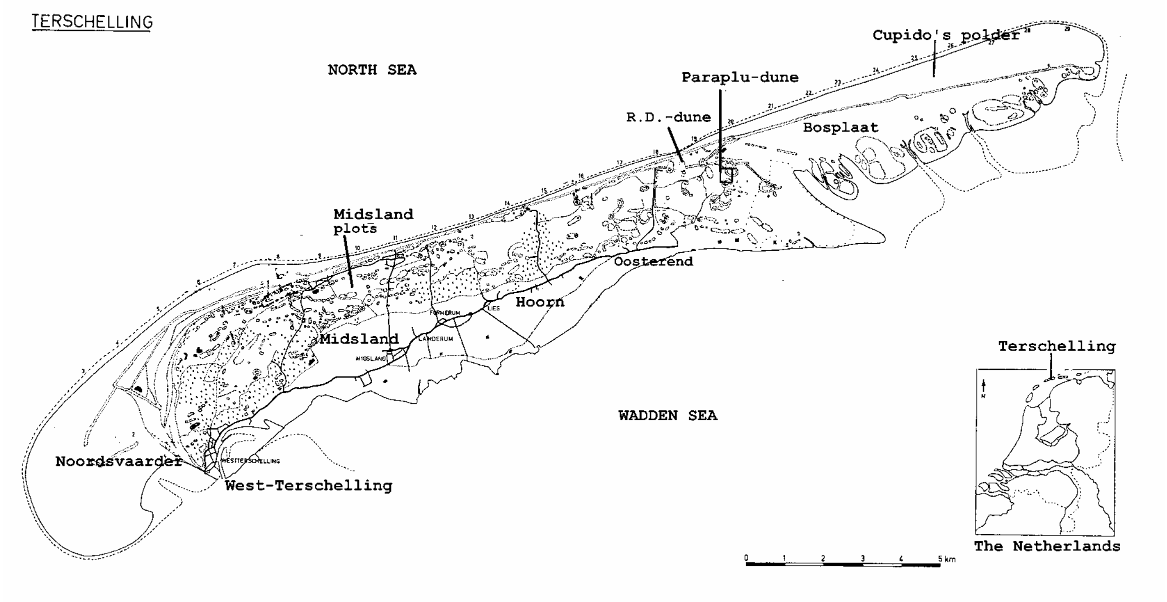

Figure 2.1. The island Terschelling, with some of the mentioned study sites

From 1846 onwards, as a reaction on the disastrous situation, the local and State government implemented an overall marram grass planting campaign, starting from West-Terschelling in an eastern direction (Figure 2.1). Around 1900 the east end of the island was reached as far as the salt marsh area of the Bosplaat and all kinds of dune formations were definitively fixed, effectuating in vegetation and soil development (van Dieren 1934, Klijn 1981). The newly formed dunes on the west- and east-end of the island, respectively on the Noordsvaarder and in Cupido's Polder, are an exception, as these dunes have not been fixed and are still mobile (Westhoff & van Oosten 1991). Moreover, in many parts of the dunes blowouts still provide aeolic rejuvenation with pioneer vegetation of *Festuca rubra, Carex arenaria* and *Corynephorus canescens*

2.2.3. Climate

Due to the surrounding sea, the climate on the West Frisian Islands can be described as almost extreme oceanic (Ellenberg et al. 1992). Compared with the inland area of the Netherlands, the mean summer temperature is lower and in winter there are fewer days with frost. In July the average daily maximum temperature is 20°C and in January 4°C. Both average daily temperature and the seasonal temperature variations are smaller than on the mainland. The total average rainfall of 720 mm y^{-1} is probably only slightly lower than that on the mainland, but less in spring and the growing season.

Winter and spring are more foggy than inland (Ketner 1972) with 29 days of fog at 14h. Moreover, the windy macroclimate resulting in a penetrating salt spray may favour terrestrial growth of epiphytic lichens on the sandy substrate of the dunes (Stoutjesdijk & Barkman 1992).

2.3. Methods

2.3.1. Vegetation research

Between 1966 and 1972 a total of 246 vegetation samples (relevés) was recorded in order to show the total variation of lichen-containing vegetation. These relevés were distributed proportionally over the dune area (Figure 2.2a). In the 1990-1996 period the vegetation of the same area was resampled with 238 relevés (Figure 2.2b). Again the survey focused on description of the total variation of lichen-containing vegetation. The newly formed dunes in Cupido's Polder (Figure 2.1) were not visited in the first period, because at that time they were in a very early stage of development (Westhoff & van Oosten 1991).

The size of the homogenous relevés (according to Braun-Blanquet 1928) varied between 0.25 m^2 and 4 m^2, but the smallest size was still in accordance with the minimum area size used for lichen communities (0.1 – 1 m^2 after Müller-Dombois & Ellenberg 1974 and 0.09 m^2 after Paus 1997). The Braun-Blanquet scale as modified by Barkman, Doing & Segal (Barkman et al. 1964, Westhoff & van der Maarel 1973) was used. The values were transformed into the ordinal 1-9 scale (van der Maarel 1979). All relevés were stored in the TURBOVEG database (Hennekens & Schaminée 2001).

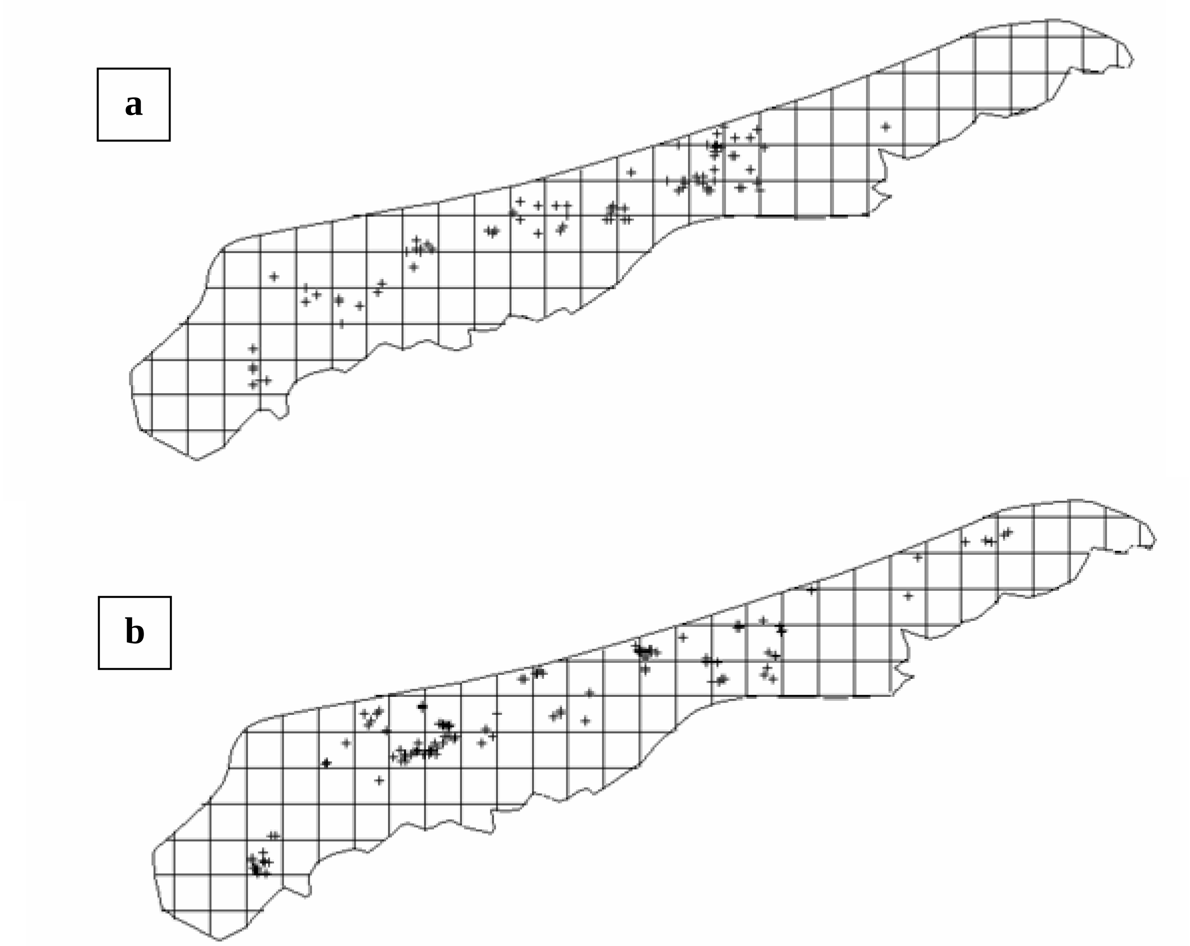

Figure 2.2. Location of the relevés on Terschelling (in km^2 squares) in the 1966-1972 period (a) and in the 1990-1996 period (b).

2.3.2. Data analysis

The total of 484 relevés was both ordinated and classified by means of multivariate analysis techniques. For classification we used TWINSPAN (Hill 1979). The final table has been summarized into a 'synoptic table', indicating presence class and characteristic cover. Species with comparable syntaxonomic status have been grouped into syntaxonomical species groups.

For each of the 23 clusters as derived from TWINSPAN a mean relevé was calculated (cluster centroid). The cluster centroids were subjected to Detrended Correspondence Analysis (DCA), resulting in an ordination of plant communities. In the resulting ordination diagram the clusters as derived from the TWINSPAN table are indicated.

2.3.3. Nomenclature

The nomenclature for the phytosociological identification and syntaxonomic assignment of the plant communities follows Weeda et al. (1996) and Stortelder et al. (1998). A number of so-called unsaturated plant communities have been distinguished. A plant community that is considered to be coenologically saturated is recognizable at the association level, because sufficient character species at this level are present. With increasing disturbance, and sometimes also due to natural dynamics, character species of lower levels of classification disappear. A plant communitiy can then only be assigned to the level of alliance, order or class and is referred to as a frame community (Kopecký & Hejný 1974).

The nomenclature for the phanerogams follows van der Meijden (1996), for the mosses Touw & Rubers (1989), and for the lichens Aptroot et al. (1999). A total of 45 lichen species is recorded. Some are a combination of two morphological identical species, as *Cladina arbuscula* s.l includes *C. mitis* and *Cladonia coccifera* includes *C. pleurota*. We use *Cladonia cervicornis* s.l. (van Herk & Aptroot 2003) and *Cladonia chlorophaea* s.l. (Ketner-Oostra & Sýkora 2000). When *Cladina ciliata* is mentioned, the var. *tenuis* is meant, for *Cladonia uncialis* it is ssp. *biuncialis* and for *Cladonia crispata* it is var. *cetrariiformis* (Purvis et al. 1992). *Peltigera rufescens* includes *P. canina*, while *P. neckeri* includes *P. polydactyla* (Aptroot et al. 1999). *Usnea subfloridana* is chemically identified by P.W. James (British Museum, London) and both *U. fulvoreagens* and *U. filipendula* were identified by M. Brand (Leiden).

Sets of lichen specimen have been deposited in U and ABL for the 1960 period and 1990 period respectively.

2.4. Results

2.4.1. Results of the TWINSPAN-clustering

We distinguished a total of 23 clusters and 15 plant communities (Table 2.1). Their syntaxonomic assignment and number of relevés in the1960 and the 1990 period is given in Table 2.2.

Table 2.1. Syntaxonomic table of cryptogam containing plant communities on Terschelling, based on relevés from the 1966-1972 and 1990-1996 period. In the first column of every cluster the presence class is given (r = present only in < 1% of the relevés, + = in < 5%, I = 6-20%, II = 21-40%, III = 41-60%, IV = 61-80% and V = 81-100%). In the second column the characteristic cover is given according to the ordinal scale. The characteristic cover is the mean cover of a species in one cluster, if present. Presence class and characteristic cover in **bold** means differentiating within the same community (syntaxonomic unit).

d* means differential species in a syntaxonomic sense; pref.ch*, preferential characteristic species; pr.opt.*, presence optimum; w.pref.*, weak preferential. For explanation of the plant communities, see the text.

Usnea spp.** includes *U. filipendula*, *U. fragilescens* and *U. subfloridana*.

Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**
Number of relevés	4	5	10	7	9	4	8	4	7	21	10	20	57	13	14	37	50	17	30	35	26	31	43
CALLUNO-ULICETEA																							
Calluna vulgaris	**V7**	IV5	III6	.	.	.	.	II2	.	III4	V5	II4	+4	+3	.	.	I4	I4	r4	r5	.	.	.
Hypnum jutlandicum	V3	IV5	V5	III3	III5	IV4	III5	III2	II3	.	+3	.	.	+2	.	+4	.	.	.	.	r2	.	r5
Pleurozium schreberi	II4	.	**IV5**	.	II8	.	II5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Genista anglica	.	I2	I4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Campylopus flexuosus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r2	.	.	.	.	.	.	.
Ptilidium ciliare	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r4	.	.	.	.	.	.
Campylopus pyriformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r4	.	.	.	.	.	.
EMPETRION																							
Empetrum nigrum	IV5	**V8**	**V8**	V7	V8	.	V6	V6	I2	II3	III3	IV4	r4	IV3	I3	II3	II4	II4	+4	.	.	.	+3
Carici arenariae-Empetretum																							
Cladina portentosa d	II6	**IV4**	**IV3**	V4	.	**III2**	**IV3**	IV2	II2	V7	V5	V6	IV5	IV5	III3	III3	IV4	II3	III4	III3	II3	r2	+5
Cladonia gracilis d	II2	I6	I3	.	.	.	.	.	.	II4	II4	II3	II3	II4	I2	.	II3	II3	II4	I4	I2	.	.
Cladonia chlorophaea s.l. d	.	**III2**	**V2**	V4	I2	.	**III2**	III2	IV2	IV3	III3	II2	I2	II2	II2	V3	IV3	V4	III3	II2	II3	II4	I2
Cladonia glauca d	.	**IV2**	**IV2**	IV3	.	.	I2	.	II2	+2	III4	III2	+2	II2	II2	IV3	V4	V5	V4	IV3	II3	+3	I2
Cetraria aculeata d	.	.	I2	II2	.	.	**II2**	.	I2	I3	III2	IV2	II3	II2	II2	IV3	V3	V3	V4	V4	V4	II3	I2
Cladonia subulata d	.	.	.	.	.	.	.	.	.	.	+2	+2	+2	I4	.	II2	II2	I3	II2	I2	+4	**II3**	.
Cladonia floerkeana d	.	I2	.	I2	.	.	.	.	I2	r2	II2	I2	I2	.	.	II2	III2	V2	IV2	III2	I3	r2	.
Cladina arbuscula d	.	.	.	.	.	.	.	.	.	+2	+2	+5	+2	I2	.	+5	II5	I4	+3	I5	r2	.	r2
Polypodio-Empetretum																							
Charisteristic combination:																							
Empetrum nigrum	IV5	**V8**	**V8**	V7	**V8**	.	V6	V6	I2	II3	III3	IV4	r4	IV3	I3	II3	II4	II4	+4	.	.	.	+3
Polypodium vulgare	.	**III2**	**II2**	III4	V5	IV6	IV6	V3	V5	+5	.	II3	+2	V3	**IV3**	II2	II4	+2	.	r2	.	I2	II3
Ammophila arenaria d	III4	III2	III2	V3	V5	V8	V4	III3	III2	V3	II3	V3	V5	V4	V5	III2	V2	III2	IV3	IV3	IV3	IV3	V3
Viola canina d	**II2**	.	+2	.	.	.	**II2**	IV2	II3	+2	.	+2	r2	III2	I2	II2	II2	I2	II2	IV2	II2	II3	II3
Hieracium umbellatum d	II2	III2	III2	II2	II2	V2	**V2**	V3	V2	I2	II2	V3	II2	V3	V3	V3	V2	V2	III3	II2	+3	V4	V4
Salici-Empetretum																							
Salix repens d	II2	III3	III5	.	**III6**	.	I5	**V8**	**V8**	+5	.	+4	r6	II6	.	I6	I4	.	r4	.	.	r2	.
Carex trinervis d	**III4**	**III3**	+3	.	.	.	.	.	.	r2	+2	.	r2	.	.	.	r5	.	.	r2	.	.	.
Erica tetralix d	**III4**	I6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Genista tinctoria	.	I2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Genista anglica d	.	I2	I4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pyrolo-Salicetum																							
Pyrola rotundifolia	.	.	.	.	.	.	.	**IV4**	.	.	.	.	.	.	.	.	r2	.	.	.	.	.	.
Rhinanthus minor d	.	.	.	.	.	.	.	**II2**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pyrola minor	.	.	.	.	.	.	.	.	**II3**	.	.	.	.	.	.	r5	.	.	.	.	.	.	.
Hippophae rhamnoides d	.	.	.	.	I7	.	I7	.	I7	.	.	.	.	+3	.	+6	.	.	.	.	.	+4	II4
Poa pratensis d	.	.	.	.	.	.	.	.	.	.	.	.	r2	.	+2	.	.	.	.	.	.	r3	II3
Linum catharticum d	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r2
Euphrasia stricta d	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r3
CALLUNO-ULICETEA + KOELERIO-CORYNEPHORETEA																							
Dicranum scoparium	V5	V5	V6	V7	II3	V5	**V6**	V5	III5	V6	V5	V7	IV6	V8	V6	IV4	V6	V4	III3	+2	III3	+2	II3
KOELERIO-CORYNEPHORETEA																							
Carex arenaria	IV4	V3	V2	V2	V3	V7	V4	IV2	V2	V4	IV4	V4	V5	V4	V5	V3	V3	V2	V3	V2	V4	II3	**V3**
Hypnum cupressiforme	III3	.	II3	III4	I4	.	**IV7**	III6	III6	I4	.	I3	+3	III3	**IV4**	V4	I3	III3	I3	.	+4	II4	**V7**
Corynephorus canescens	.	.	.	I2	.	III3	.	.	I2	III3	II3	IV3	V5	V5	V4	V5	V5	V4	V5	V5	V5	**V4**	III4
Galium verum	.	.	.	.	.	.	**II2**	.	I2	.	.	I2	.	I4	I3	I3	.	.	.	.	.	I4	II5
Aira praecox	.	.	.	.	.	.	.	.	.	+2	.	.	I2	II2	**IV2**	IV2	I3	I2	+3	.	II3	IV2	IV3
Ceratodon purpureus	.	.	.	.	.	.	.	.	.	r2	.	I2	+3	.	I5	III4	I2	I3	I3	+2	III5	**V5**	I3
Hieracium pilosella	.	.	.	.	.	.	.	.	.	r2	.	r3	.	+4	.	.	.	.	.	.	.	.	r4
Cerasti semidecandrum	.	.	.	.	.	.	.	.	.	.	.	.	.	+2	+2	I2	.	.	.	.	.	II2	III2
Leontodon saxatilis	.	.	.	.	.	.	.	.	.	.	.	.	r2	+2	II3	+2	.	+2	.	.	.	**V3**	**III3**
Peltigera rufescens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**r2**	**II4**
Sedum acre	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+2	.	.	.	.	.	**IV3**	II3
Erophila verna	.	.	.	.	.	.	.	.	.	.	.	r2	.	.	.	.	.	.	.	.	.	I2	+2
Arenaria serpyllifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r2	.	.	.	.	.	I2	**III2**
Anthyllis vulneraria	.	.	.	.	.	.	.	.	.	.	.	.	.	+2	.	r2	r2	.	.	.	.	I2	.
Racomitrium canescens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r3
Koeleria macrantha	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+2
CORYNEPHORETALIA + CLADONIO-KOELERIETALIA																							
Cladonia furcata	II2	II3	**V2**	V2	I2	II2	**IV2**	III3	IV2	I2	+2	IV2	II2	IV2	II2	V3	IV3	V3	V3	IV3	III3	II3	III3
Cladonia foliacea	.	.	I4	I2	.	II2	.	.	I2	II2	III2	II2	IV3	II3	III2	V4	IV3	V4	V5	III3	IV3	III3	II3
CORYNEPHORETALIA + TRIFOLIO-FESTUCETALIA																							
Jasione montana	.	.	.	.	.	III3	I2	.	II3	+2	.	IV2	I2	V2	**IV3**	V3	III2	III2	III2	III2	I2	IV2	III3
TRIFOLIO-FESTUCETALIA + CLADONIO-KOELERIETALIA																							
Brachythecium albicans	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I3	.	.	.	.	r2	**III5**	**II5**
Taraxacum laevigatum	.	.	.	.	.	.	.	II2	.	.	.	.	.	+2	.	.	.	.	.	.	.	+2	II2
Veronica arvensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I2
Vicia lathyroides	.	.	.	.	.	.	.	.	.	.	.	.	.	+2	.	.	.	.	.	.	.	+2	I2
Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**

Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**
Number of relevés	4	5	10	7	9	4	8	4	7	21	10	20	57	13	14	37	50	17	30	35	26	31	43
KOELERIO-CORYNEPHORETEA + FESTUCO-BROMETEA + MOLINIO-ARRHENATHERETEA + TRIFOLIO-GERANIETEA																							
Festuca rubra	.	.	+2	III2	.	V5	**II4**	V2	III3	.	+2	III3	I3	V4	**V3**	IV3	II3	IV2	II2	III2	I2	V4	V5
Lotus corniculatus s.l.	.	.	.	II2	.	.	**II2**	IV3	II5	.	.	+3	.	II3	**II4**	III3	+2	.	r2	+2	.	I3	**III3**
Senecio jacobaea ssp dunensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r2	.	+3	II3
Plantago lanceolata	.	.	.	.	.	.	.	II2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r6
Poa pratensis	.	.	.	.	.	.	.	.	.	.	.	.	r2	.	+2	.	.	.	.	.	.	r3	II3
FESTUCO-BROMETEA + NARDETEA																							
Rumex acetosella	**II3**	.	.	.	.	II2	**II4**	.	I2	II2	I2	III2	II3	IV3	**IV3**	**III2**	**II2**	**II2**	.	r2	I2	I2	**III2**
Luzula campestris	**III2**	.	+2	.	.	.	**II2**	II2	II3	I2	I2	III3	I3	IV4	II4	**IV3**	**II3**	**II3**	.	.	.	.	**IV3**
Festuca ovina	**III3**	I2	.	.	.	.	I4	.	.	**V5**	III4	II4	**II4**	I2	.	+3	I4	+5	+3	r5	I4	.	I3
CORYNEPHORION																							
Cetraria aculeata	.	.	I2	II2	.	.	**II2**	.	I2	I3	III2	IV2	II3	II2	II2	IV3	V3	V3	V4	V4	V4	II3	I2
Cladonia ramulosa	.	**II2**	+2	.	.	.	.	.	.	I2	II2	r2	**II2**	I3	.	III2	I2	IV2	I2	r2	II2	II3	+2
Polytrichum piliferum	.	.	.	.	.	.	.	.	.	I5	I3	II3	+4	.	.	I4	I3	II6	II6	r2	II4	+4	r3
Cladonia macilenta	.	I2	.	.	.	.	.	.	.	+2	I3	I2	+2	.	.	I2	+2	+2	+2	+3	I2	+2	r2
Cladonia cervicornis	.	.	+2	.	.	.	.	.	.	.	I3	r2	+3	+2	.	I3	I3	.	II4	+3	II5	+3	r2
Cladonia crispata	.	.	.	I5	.	.	.	.	.	r5	.	.	.	.	.	.	r6	.	.	.	.	.	.
Cladonia zopfii	.	.	.	.	.	.	.	.	.	.	.	.	+3	.	.	.	.	.	.	+7	+3	.	.
Cetraria muricata	.	.	.	.	.	.	.	.	.	.	.	.	r7	.	.	.	.	.	.	.	.	.	.
Differentiating CORYNEPHORION in relation the rest of the KOELERIO-CORYNEPHORETEA:																							
Cladina portentosa	II6	**IV4**	**IV3**	V4	.	III2	**IV3**	IV2	II2	V7	V5	V6	IV5	IV5	III3	III3	IV4	II3	III4	III3	II3	r2	+5
Cladonia gracilis	II2	I6	I3	.	.	.	.	.	.	II4	II4	II3	II3	II4	I2	.	**II3**	**II3**	**II4**	I4	I2	.	.
Cladonia glauca	.	**IV2**	**IV2**	IV3	.	.	I2	.	II2	+2	III4	III2	+2	II2	II2	IV3	V4	V5	V4	IV3	II3	+3	I2
Cladonia coccifera	.	I2	.	III3	.	.	.	.	I2	III3	V3	III3	III2	III2	II2	III2	V3	V4	IV4	IV2	IV3	r2	.
Cladonia floerkeana	.	I2	.	I2	.	.	.	.	I2	r2	II2	I2	I2	.	.	II2	III2	V2	IV2	III2	I3	r2	.
Violo-Corynephoretum																							
Hypogymnia physodes	II2	I4	**V5**	V4	I2	.	I2	II2	V4	r2	IV2	III3	r2	II4	.	III3	V3	V4	III2	I2	.	II2	r2
Cladina ciliata	**IV5**	.	+6	II5	.	.	I2	.	.	+5	+4	III4	.	+5	.	r2	II3	+2	+3	.	.	.	r2
Hypogymnia tubulosa	.	.	**II2**	II2	.	.	I2	.	II2	.	.	r2	.	+2	.	**II3**	**II2**	.	.	.	.	I2	r2
Platismatia glauca	.	.	.	I2	.	.	.	.	.	I2	I3	+3	.	.	.	+4	II3	III5	I3	.	.	.	.
Usnea spp.**	.	.	.	.	.	.	.	.	II3	.	.	.	.	.	.	r2	+2	.	.	r2	.	.	.
Pseudevernia furfuracea	.	.	.	.	.	.	.	.	.	.	.	+4	.	.	.	r2	+4	I3	I3	.	.	.	.
Dicranoweisia cirrata	.	.	.	.	.	.	.	.	.	.	.	r3	.	.	.	r2	+5	+2	+2	.	r3	.	.
Evernia prunastri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I2	I2	+5	r2	.	.	II2	.
Parmelia sulcata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I2	.	.	.	.	.	I2	.
Bryoria fuscescens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r3	.	.	II5	.	.	.

V.-C. typicum																							
Ammophila arenaria d	III4	III2	III2	V3	V5	V8	V4	III3	III2	V3	II3	V3	V5	V4	V5	III2	V2	III2	IV3	IV3	IV3	IV3	V3
Hieracium umbellatum d	II2	III2	III2	II2	II2	V2	**V2**	V3	V2	I2	II2	V3	II2	V3	**V3**	**V3**	**V2**	**V2**	III3	II2	+3	V4	V4
Cladonia coccifera d	.	I2	.	III3	.	.	.	.	I2	III3	V3	III3	III2	III2	II2	III2	V3	V4	IV4	IV2	IV3	r2	.
Cladonia floerkeana d	.	I2	.	I2	.	.	.	.	I2	r2	II2	I2	I2	.	.	II2	III2	V2	IV2	III2	I3	r2	.
V.-C. typicum with *D. scoparium* dominance																							
Dicranum scoparium	V5	V5	V6	V7	II3	V5	**V6**	V5	III5	V6	V5	V7	IV6	V8	V6	IV4	V6	V4	III3	+2	III3	+2	II3
V.-C. koelerietosum																							
Cladina ciliata d	**IV5**	.	+6	II5	.	.	I2	.	.	+5	+4	III4	.	+5	.	r2	II3	+2	+3	.	.	.	r2
Galium verum d	.	.	.	.	.	.	**II2**	.	I2	.	.	I2	.	I4	I3	I3	.	.	.	.	.	I4	II5
Phleum arenarium d	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r2	.	.	.	.	.	I2	I2
Koeleria macrantha d	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+2
CLADONIO-KOELERIETALIA																							
Cerastium semidecandrum pr.opt.	.	.	.	.	.	.	.	.	.	.	.	.	.	+2	+2	I2	.	.	.	.	.	**II2**	**III2**
Viola curtisii	.	.	.	.	.	.	.	.	.	.	.	r2	.	I3	.	II2	r2	I2	.	+2	r2	I2	**III2**
Cladonia rangiformis	.	.	I4	.	.	.	.	.	I2	.	.	r2	.	I5	.	II5	r3	+3	.	.	.	II5	III5
Sedum acre pr.opt.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+2	.	.	.	.	.	**IV3**	**II3**
Myosotis ramosissima	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+2	I2
Koeleria macrantha	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+2
Ononis repens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r7
TORTULO-KOELERION																							
Tortula ruralis v. *ruraliformis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+3	.	.	.	.	.	**III4**	**II5**
Phleum arenarium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r2	.	.	.	.	.	I2	I2
Erodium cicutarium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r3
Phleo-Tortuletum																							
Ceratodon purpureus pr.opt.	.	.	.	.	.	.	.	.	.	r2	.	I2	+3	.	I5	III4	I2	I3	I3	+2	III5	**V5**	I3
Phleo-T. cladonietosum																							
Cladonia foliacea d	.	.	I4	I2	.	II2	.	.	I2	II2	III2	II2	IV3	II3	III2	V4	IV3	V4	V5	III3	IV3	III3	II3
Cladonia furcata d	II2	II3	**V2**	V2	I2	II2	**IV2**	III3	IV2	I2	+2	IV2	II2	IV2	II2	V3	IV3	V3	V3	IV3	III3	II3	III3
Cetraria aculeata d	.	.	I2	II2	.	.	**II2**	.	I2	I3	III2	IV2	II3	II2	II2	IV3	V3	V3	V4	V4	V4	II3	I2
Racomitrium canescens d	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r3
Phleo-T. brachythecietosum																							
Brachythecium albicans d	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I3	.	.	.	.	r2	**III5**	**II5**
Leontodon saxatilis d	.	.	.	.	.	.	.	.	.	.	.	.	r2	+2	II3	+2	.	+2	.	.	.	**V3**	III3
Hieracium umbellatum d	II2	III2	III2	II2	II2	V2	**V2**	V3	V2	I2	II2	V3	II2	V3	**V3**	**V3**	**V2**	**V2**	III3	II2	+3	V4	V4
Hypochaeris radicata d	II2	I2	III2	III2	.	IV4	**II2**	II2	V2	II2	+2	IV3	III2	V3	**V3**	**IV3**	**IV2**	**III2**	I2	I2	II2	III3	IV3
Jasione montana d	.	.	.	.	.	III3	I2	.	II3	+2	.	IV2	I2	V2	**IV3**	**V3**	III2	III2	III2	III2	I2	IV2	III3
Anthyllis vulneraria d	.	.	.	.	.	.	.	.	.	.	.	.	.	+2	.	r2	r2	.	.	.	.	I2	.
Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**

Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**
Number of relevés	4	5	10	7	9	4	8	4	7	21	10	20	57	13	14	37	50	17	30	35	26	31	43
Tortello-Bryoerythrophylletum																							
Cladonia pocillum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+6	.	.	r3	.	r2	II3	.
POLYGALO-KOELERION																							
Salix repens d	II2	III3	III5	.	**III6**	.	I5	**V8**	**V8**	+5	.	+4	r6	II6	.	I6	I4	.	r4	.	.	r2	.
Calamagrostis epigejos d	**II3**	.	.	.	II2	III8	III4	II4	I2	.	.	r4	r2	.	II3	.	r3	.	.	.	.	r2	II3
Polygala vulgaris d	.	.	.	.	.	.	.	II2	.	.	.	r2	.	.	+2	.	.	.	.	.	.	r2	I2
Hylocomium splendens	.	.	+7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Erigeron acris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r3
Differentiating species e.g.																							
TORTULO-KOELERION																							
Pseudoscleropodium purum d	.	I2	+2	.	**II4**	II2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula campestris d	**III2**	.	+2	.	.	.	**II2**	II2	II3	I2	I2	III3	I3	IV4	II4	**IV3**	II3	II3	.	.	.	.	**IV3**
Lotus corniculatus s.l. d	.	.	.	II2	.	.	**II2**	IV3	II5	.	.	+3	.	II3	**II4**	**III3**	+2	.	r2	+2	.	I3	**III3**
Linum catharticum d	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r2
Euphrasia stricta d	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r3
TRIFOLIO-FESTUCETALIA																							
Hypochaeris radicata	II2	I2	III2	III2	.	IV4	**II2**	II2	V2	II2	+2	IV3	III2	V3	**V3**	**IV3**	**IV2**	**III2**	I2	I2	II2	III3	IV3
Anthoxanthum odoratum d	.	.	.	.	.	.	.	.	II3	.	.	r2	.	II3	.	+4	.	.	.	.	.	.	.
Achillea millefolium d	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r2
Trifolium dubium d	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r3
PLANTAGINI-FESTUCION																							
Festuco-Galietum																							
Carex arenaria w.pref.*	IV4	V3	V2	V2	V3	V7	V4	IV2	V2	V4	IV4	V4	V5	V4	V5	V3	V3	V2	V3	V2	V4	II3	**V3**
Rumex acetosella pref.ch*	**II3**	.	.	.	.	II2	**II4**	.	I2	II2	I2	III2	II3	IV3	**IV3**	**III2**	**II2**	**II2**	.	r2	I2	I2	**III2**
Agrostis capillaris pref.ch	.	.	.	.	.	.	I6	II2	.	+2	.	+4	r2	I5	I3	r2	r2	+2	r2	.	.	.	+2
Koeleria macrantha d	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+2
Trifolium arvense d	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r2	.	.	.	.	.	.	r2
Ammophiletum																							
Ammophila arenaria d	III4	III2	III2	V3	V5	**V8**	V4	III3	III2	V3	II3	V3	V5	V4	V5	III2	V2	III2	IV3	IV3	IV3	IV3	V3
Sonchus arvensis v. maritimus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r2
Eryngium maritimum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r3	.
Calammophila baltica	.	.	.	.	I2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+3
Hippophaetum																							
Hippophae rhamnoides	.	.	.	.	I7	.	I7	.	I7	.	.	.	.	+3	.	+6	.	.	.	.	.	+4	II4
Asparagus officinalis ssp prostratus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r2
FRAME COMMUNITIES (Fc)																							
Fc *Campylopus*-[Koelerio-Corynephoretea]																							
Campylopus introflexus	.	.	.	.	.	II4	.	.	.	+2	I2	r2	**V6**	.	**V5**	+4	.	.	+5	.	**IV5**	I4	r2
Fc *Dicranum scoparium*-																							

[Koelerio-Corynephoretea]																							
Dicranum scoparium	V5	V5	V6	V7	II3	V5	**V6**	V5	III5	V6	V5	V7	IV6	V8	V6	IV4	V6	V4	III3	+2	III3	+2	II3
D. scoparium (dead)	.	.	.	.	.	.	.	.	.	+8	V6	II6	.	.	.	r5	+6	+3	.	.	.	.	.
Fc *Salix repens*-																							
[Polygalo- Koelerion]																							
Salix repens d	II2	III3	III5	.	**III6**	.	I5	V8	V8	+5	.	+4	r6	II6	.	I6	I4	.	r4	.	.	r2	.
Remaining species:																							
Rosa pimpinellifolia	**III6**	.	.	.	.	.	.	.	.	+4	.	r6	.	.	.	.	.	.	.	.	.	.	.
Viola canina	**II2**	.	+2	.	.	.	**II2**	IV2	II3	+2	.	+2	r2	III2	I2	II2	II2	I2	II2	IV2	II2	II3	II3
Taraxacum officinale s.s	.	I2	.	.	.	.	.	II2	I2	r2	.	.	.	.	+2	+2	r2	.	.	.	.	I2	II2
Holcus lanatus	.	.	.	.	.	II2	I2	IV3	I2	.	.	+2	.	I5	**II2**	**II3**	.	.	.	.	.	r2	I2
Cerastium fontanum s.l.	.	.	.	.	.	.	I2	.	.	.	.	.	.	.	+2	I2	.	.	.	.	.	r2	I2
Veronica officinalis	.	.	.	.	.	.	.	II2	I5	.	.	r2	.	I2	.	I3	r2	.	.	.	.	r2	II3
Leontodon autumnalis	.	.	.	.	.	.	.	II2	.	r2	.	+3	r2	+2	+3	I3	+2	I2	.	.	.	r3	r4
Hieracium peleterianum	.	.	.	.	.	.	.	II3	.	.	.	+5	.	.	.	.	.	.	.	.	.	.	I6
Cerastium diffusum	.	.	.	.	.	.	.	.	.	.	.	.	.	+4	.	r2	.	.	.	.	r2	II2	I2
Mosses and lichens:																							
Lophocolea bidentata	II2	.	I2	.	I2	.	I3	.	.	.	.	.	.	I2	.	.	.	.	.	.	.	.	.
Eurhynchium praelongum	.	.	+2	.	I2	.	.	II3	I2	.	.	.	.	.	.	.	.	.	.	.	.	.	+4
Polytrichum juniperinum	.	.	.	.	I2	.	I2	.	.	III4	IV5	II4	r3	II2	II3	I3	I4	.	.	.	+3	I2	+2
P. juniperinum (dead)	.	.	.	.	.	.	.	.	.	.	III6	r4	.	.	.	.	r8	.	.	.	.	.	.
Cephaloziella divaricata	.	.	.	.	.	.	.	.	.	.	+2	I2	r2	.	.	III4	II3	V6	V4	I3	II3	II4	I2
Cladonia uncialis	.	.	+3	.	.	.	.	.	.	II6	.	r4	r5	+6	.	.	.	.	+7	.	.	.	.
Cladonia squamosa	.	.	+2	I2	.	.	.	.	.	.	+2	II2	.	.	.	.	+2	.	r2	r2	.	.	.
Cladonia cornuta	.	.	.	II3	.	.	.	.	.	+2	+2	I2	.	.	.	.	I2	.	+2	+2	.	.	.
Cladina rangiferina	.	.	.	I2	.	.	.	.	.	.	.	.	.	.	.	.	r5	.	.	.	.	.	.
Cladonia scabriuscula	.	.	.	.	.	.	I2	.	.	.	.	.	r2	.	II2	I5	.	.	r6	.	r3	II4	I3
Cladonia fimbriata	.	.	.	.	.	.	.	.	.	r2	.	r2	.	+2	.	r2	.	.	.	.	.	r2	+2
Placynthiella icmalea	.	.	.	.	.	.	.	.	.	I2	.	.	r3	.	.	.	.	.	.	.	+3	.	.
Placynthiella uliginosa	.	.	.	.	.	.	.	.	.	.	I3	.	.	+2	.	r2	I3	I2	II3	III2	I4	+2	.
Trapeliopsis granulosa	.	.	.	.	.	.	.	.	.	.	+2	.	+3	.	.	+4	.	+2	II2	I2	II2	.	r2
Peltigera neckeri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+3	.	.	.	.	.	.	+3
Cladonia humilis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I4	r2
Algae:																							
Gloeocystis polydermatica	.	I5	.	.	.	.	.	.	.	II5	V6	III4	I4	.	+4	r3	+5	.	.	.	I4	I5	.
Green algae	.	I5	.	.	.	.	.	.	.	+2	I3	r2	+4	.	I4	I2	r3	+3	II4	I2	III5	+5	+3
Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**

Remaining higher plants: *Agrostis canina* cluster 10(r5); *Agrostis stolonifera* 23(r3); *Carex nigra* 8(II2); *Carex panicea* 2(I2); *Cytisus scoparius* 7(I4); *Geranium molle* 23(+2); *Galium saxatile* 14(+2); *Lonicera periclimenum* 5(II5); *Poa annua* 23(r2); *Populus tremula* 2(I5); *Rhinanthus angustifolius* 8(II4), 9(I2); *Rubus spec.* 9(I2); *Sagina nodosa* 23(r2); *Senecio vulgaris* 16(I3),23(+2); *Senecio sylvaticus* 23(r3); *Tanacetum vulgare* 14(+4); *Trifolium repens* 23(I2); *Veronica chamaedrys* 8(II2); *Vicia sativa* 16(r2).

Remaining mosses and lichens: *Brachythecium rutabulum* 23(r2); *Bryum amblydon* 23(r6); *Bryum argenteum* 16(r2); *Bryum capillare* 16(r7); *Dicranum polysetum* 3(+2); *Lophozia excisa* 23(r2); *Pohlia nutans* 18(r4), 19(+2); *Cladonia coniocraea* 20(+2); *Micarea prasina* 13(r2); *Placynthiella oligotropha* 21(I2).

Table 2.2. Syntaxonomic allocation of the clusters from the synoptic table. The total number of relevés is listed. The total number of lichens, including the terrestrial growing epiphytes is listed. Separately, only the number of terrestrial growing epiphytes is listed.
* Fc means frame community, ** V.-C. means Violo-Corynephoretum, **bold**: community predominantly present in one period.

Cluster	Alliance	Plant community	Total number relevés	Number relevés Period 1966-72	Number relevés Period 1990-96	Total number lichens	Terrestrial growing epiphytes
1	Empetrion	Carici-Empetretum	4	2	2	5	1
2		Carici-Empetretum	5	2	3	10	1
3		Carici-Empetretum	10	**10**	0	15	2
4		Transition C.-E. to Polypodio-Empetretum	7	7	0	16	3
5		Polypodio-Empetretum	10	5	5	3	1
6		Fc* with *Ammophila / Carex arenaria*	4	0	4	3	0
7		Polypodio-Empetretum	7	5	2	9	2
8		Pyrolo-Salicetum	4	2	2	4	1
9	Polygalo-Koelerion	Fc with *Salix repens*	7	7	0	12	3
10	Corynephorion	Fc with *Festuca ovina* and reindeer lichens	21	3	**18**	20	2
11		Fc with *Calluna vulgaris*, dead mosses covered by algae	10	3	7	21	2
12		V.-C.** typicum with *Dicranum scoparium* dominance	20	14	6	24	4
13		Fc with *Campylopus introflexus*	57	0	**57**	22	1
14		Fc with *Dicranum scoparium*	13	7	6	19	2
15		Fc with *Campylopus introflexus*	14	0	**14**	9	0
16		V.-C. typicum	37	**27**	10	28	9
17		V.-C. typicum	50	**49**	1	25	9
18		V.-C. typicum	17	**17**	0	21	4
19		V.-C. typicum	30	**28**	2	26	4
20		Initial stage V.-C.	35	**35**	0	23	3
21		Fragmentary V.-C.	26	1	**25**	21	0
22	Tortulo-Koelerion	Phleo-Tortuletum ruraliformis subass. brachythecietosum with *Ceratodon purpureus*	31	6	**25**	23	4
23		Phleo-Tortuletum ruraliformis subass. brachythecietosum with *Hypnum cupressiforme*	43	9	**34**	19	2

The following plant communities have been distinguished:

Dry dune heath: Empetrion. The dry dune heath is represented by:

* The Carici arenariae-Empetretum (clusters 1-3). In cluster (cl.) 1 the Red list species *Cladina ciliata* (Aptroot et al. 1998) occurs in the moss layer, which mainly consists of *Dicranum scoparium* and *Hypnum jutlandicum*. The moss

layer of cl. 2 is comparable to that of cl. 1 and contains ten lichen species in a low frequency. Both clusters are present in both research periods. The species rich moss layer of cl. 3 contains eight moss and one liverwort species. Among the lichens (15 species) especially *Hypogymnia physodes* has a high frequency and cover. Cluster 3 is only present in the1960s.

* Transitional community between Carici arenariae-Empetretum and the Polypodio-Empetretum (cluster 4). In this *Calluna vulgaris* and *Salix repens* are absent and Empetrum *nigrum* is dominant, while the cover of *Polypodium vulgare* is higher. The moss layer seems to be dryer than in cl. 3 and is dominated by *Dicranum scoparium*. Reindeer lichens like *Cladina portentosa* occur in a high frequency together with the Red list species *Cladina ciliata and C. rangiferina.* The Red list species *Cladonia cornuta* and *C. crispata* grow on the moss cover between the *Empetrum*-shrubs together with the terrestrial epiphytes *Hypogymnia physodes, H. tubulosa* and *Platismatia glauca.* Cluster 4 is only present in the sixties.

* The Polypodio-Empetretum (clusters 5 and 7). In cl. 5 the number of moss and lichen species is low. In cl. 7 nine lichen species occur with low cover on the moss layer, which is dominated by *D. scoparium* and *Hypum cupressiform*. The Polypodio-Empetretum is equally present in both the old and the new relevés.

* The Pyrolo-Salicetum (cluster 8). Here the moss layer mainly consists of *D. scoparium* and *Hypnum cupressiforme.* Besides *Eurynchium praelongum* occurs. The number of lichen species is small. Cluster 8 is found in both research periods.

Transition between vegetation of young to fixed dunes and dry grasslands on sandy soil:

* Cluster 6 is considered to be a fragmentary or coenologically unsaturated, so-called frame community (Kopecký & Hejný 1974). As it is clearly transitional between two different classes it is assigned to the frame community *Ammophila arenaria – Carex arenaria* [Ammophiletea/Koelerio-Corynephoretea]. Although some V.-C. species are still present, it is substantially grass-encroached by *Ammophila arenaria, Carex arenaria* and *Festuca rubra*. In the moss layer *Dicranum scoparium* and *Hypnum jutlandicum* and only a few lichens are present. This cluster is only present in the 1990s.

Dry grasslands and pioneer communities on sandy soil
Frame communities of the Koelerio-Corynephoretea (Fc. Corynephorion):

* The frame community of *Festuca ovina* (cluster 10) has only small patches of *Calluna vulgaris* and *Empetrum nigrum* (both in low frequency) and an exceptionally high cover of *Cladina portentosa* and *Cladonia uncialis*. Most relevés originate from the 1990 period.

* The frame community with *Calluna vulgaris* (cluster 11) is characterized by a moss carpet of largely dead *Dicranum scoparium* and *Polytrichum juniperinum,* covered by *Gloeocystis polydermatica* (Kützing) Hindák. Besides 23 lichen species are present. Two-thirds of the ten relevés originate from the nineties.

* The frame community of *Campylopus introflexus* (clusters 13 and 15), following Weeda et al. (1996). It consists of a short Koelerio-Corynephoretea

vegetation with small dwarf shrub patches. *Campylopus introflexus* with *Dicranum scoparium* form a closed carpet, with *Hypnum cupressiforme* in a lower but still substantially high presence. In cl. 13 many lichen species (22) are present, growing on and between the mosses, in cl. 15 only nine, but in both hardly any terrestrial growing epiphytes. In cl. 13 all 57 relevés are from the 1990 period, as are all14 relevés of cl. 15.

* The frame community of *Dicranum scoparium*- [Koelerio-Corynephoretea] (cluster 14, Weeda et al. (1996). Because characteristic species of the association are very scarce we do not assign it to the V.-C. typicum with *Dicranum scoparium* dominance (Biermann 1999). Several herbs occur and subneutral lichens like *Cladonia furcata* and *C. rangiformis* (Ellenberg 1992). This community is very poor in terrestrial growing epiphytes, only both *Hypogymnia* spp. are present. An equal number of relevés is made in both periods.

Frame community of the Polygalo-Koelerion:

* The frame community of Salix repens- [Polygalo-Koelerion] (cluster 9, Weeda et al. 1996) is dominated by *Salix repens*. Terrestrial growing epiphytes are frequent on the moderate moss cover of *Dicranum scoparium* and *Hypnum cupressiforme*. Of these species *Hypogymnia physodes*, a character species of the V.-C. is most frequent, besides in two relevés *H. tubulosa* and *Usnea* spp. are found. All seven relevés are from the 1960s.

Violo-Corynephoretum:

* Violo-Corynephoretum typicum with *Dicranum scoparium* dominance (after Biermann 1999, cluster 12). The *D. scoparium* cover (with an average of 40%) goes together with 24 lichen species, among which reindeer lichens, including *Cladina ciliata*, and *Cladonia gracilis* in a high cover. Terrestrial growing epiphytes like *Pseudevernia furfuracea* and *Dicranoweisia cirrata* are present. Two-third of the relevés are from the 1960s.

* Violo-Corynephoretum typicum (conform Weeda et al. 1996 and Biermann 1999, clusters 16, 17, 18 and 19). The species composition in cl. 16 indicates a transition to the Cladonio-Koelerietalia, i.c. the Phleo-Tortuletum. In the moderate moss cover *Hypnum cupressiforme* has the highest presence, but it is mixed with some *Dicranum scoparium*, next are *Ceratodon purpureus* and *Cephaloziella divaricata*, with occasionally *Tortula* or *Brachythecium*. Of the 28 lichen species *Cladonia foliacea* is most frequent and covers most, followed by *C. furcata* and *C. chlorophaea* s.l. Several terrestrial epiphytes are present in a low presence and cover, with *Hypogymnia physodes* most frequent, followed by *H. tubulosa, Evernia prunastri, Parmelia sulcata*, *Platismatia glauca*, *Pseudevernia furfuracea* and the rare *Usnea* spp. Two-thirds of the 37 relevés of this cluster is from the former period. The relevés from the recent period are made on slightly calcareous locations (0.1-0.3% $CaCO_3$): on young dune ridges at the Noordsvaarder, West-Terschelling, in dynamic dunes near the first dune ridge north of Hoorn, and on the Paraplu dune in the Bosplaat nature reserve (Ketner-Oostra & Sýkora 2000).

This plant community presents itself in cl. 17 with *Dicranum scoparium* in the highest mean characteristic cover and with the terrestrial growing epiphytes the most abundant. The epiphytic moss *Dicranoweisia cirrata* and the same lichens as in cl. 16 are found, including *Bryoria fuscescens* but except *Parmelia sulcata*. These lichens are attached on or between the moss carpet and only very small patches of dwarf shrubs are present (Ketner-Oostra 1972, 1989). From the 50 relevés 49 originate from the sixties.

In cl. 18 *Dicranum scoparium, Hypnum cupressiforme* and *Cephaloziella divaricata* have a high frequency but a relatively low cover. Like in the former two cls. and in cl. 19 *Dicranoweisia cirrata* is sparsely found. The lichen cover is almost complete due to many *Cladonia*-species with high frequency and cover, like *Cladonia coccifera, C. foliacea, C. furcata* and *C. glauca.* Only four terrestrial epiphytes are present.

Cluster 19 shows a low frequency and cover of *Dicranum scoparium*, whereas the liverwort *Cephaloziella divaricata* occurs with a high frequency. Many lichen species (26) are present, with the subneutral species *Cetraria aculeata*, *Cladonia foliacea* and *C. furcata* with high frequency and cover. The pioneer species *Cladonia cervicornis* s.l. is present here and in cl. 21. Four terrestrial growing epiphytic lichens occur, but all with a lower frequency and cover as in cluster 18. In this cl. 28 from 30 relevés are from period one.

* Initial stage of the Violo-Corynephoretum canescentis (cluster 20, Biermann 1999). It contains almost no mosses but many lichen species, mainly pioneers. In the 1960s this is the special habitat for *Bryoria fuscescens* on bare sand (Ketner-Oostra 1972). The Red list species *Cladonia coniocraea, C. cornuta* and *C. zopfii* and are also recorded. All 35 relevés are from the 1960 period.

* Association fragment of the V.-C. typicum (cluster 21). This is characterized by the presence of many moss species, including *Campylopus introflexus, Ceratodon purpureus, Dicranum scoparium* and *Polytrichum piliferum*. From the lichens especially the pioneer species, like *Cetraria aculeata, Cladonia foliacea, C. furcata, C. pocillum* and *C. zopfii* occur. In this cluster terrestrial epiphytes do not appear, only *Dicranoweisia cirrata* once. For both periods we find here the highest presence and cover of green algae, colonizers of movable sand. Almost all of the 26 relevés are from period 2.

Phleo-Tortuletum ruraliformis:

* Phleo-Tortuletum ruraliformis brachythecietosum. In clusters 22 and 23 the Corynephorion and V.-C. element is still present. However, as the presence of most species of this species group is low and as the Cladonio-Koelerietalia element prevails, these communities are assigned to the Phleo-Tortuletum ruraliformis brachythecietosum.

In the moss layer of cl. 22 *Ceratodon purpureus* shows a high frequency and a relatively high cover. From the 23 lichen species present, *Cladonia foliacea* is most frequent, followed by *C. rangiformis, C. scabriuscula, C. furcata, C. pocillum* and *C. humilis*. All these species indicate a subneutral habitat and the last two species are indicators for calcium in the substratum. Terrestrial growing epiphytes present

Figure 2.3. Two pictures of lichen-rich dune grassland (*Violo-Corynephoretum*) north of Midsland: before (1970) and after (1993) grass and moss encroachment.

are *Hypogymnia physodes,* followed by *H. tubulosa, Evernia prunastri* and *Parmelia sulcata*. Four-fifth of the relevés is from the 1990 period.

From all 23 clusters cl. 23 contains the highest number of herb species (44). Of the 19 lichen species *Cladonia rangiformis* and *C. furcata* are most frequent, followed by *C. foliacea* and *Peltigera rufescens*. *Cladonia humilis* and *Peltigera neckeri* are almost restricted to this vegetation type. The two mentioned *Peltigera*–species are exclusively epigeic growing lichens (Purvis et al. 1992) and not part of the terrestrially growing epiphytes. Their occurrence is in accordance with the habitat preference of the Phleo-Tortuletum ruraliformis. In this cluster the relevés are mainly from the 1990s.

2.4.2. Results of the ordination

For the ordination of the 23 cluster centroids as derived from the TWINSPAN-table we refer to Figure 2.4. The first axis with Eigenvalue .35 corresponds to a gradient in acidity from very acid on the left to (sub-) neutral and basiphilous on the right side of the diagram. The second axis with Eigenvalue .24 represents a transition from closed vegetation at the base, to open vegetation at the top.

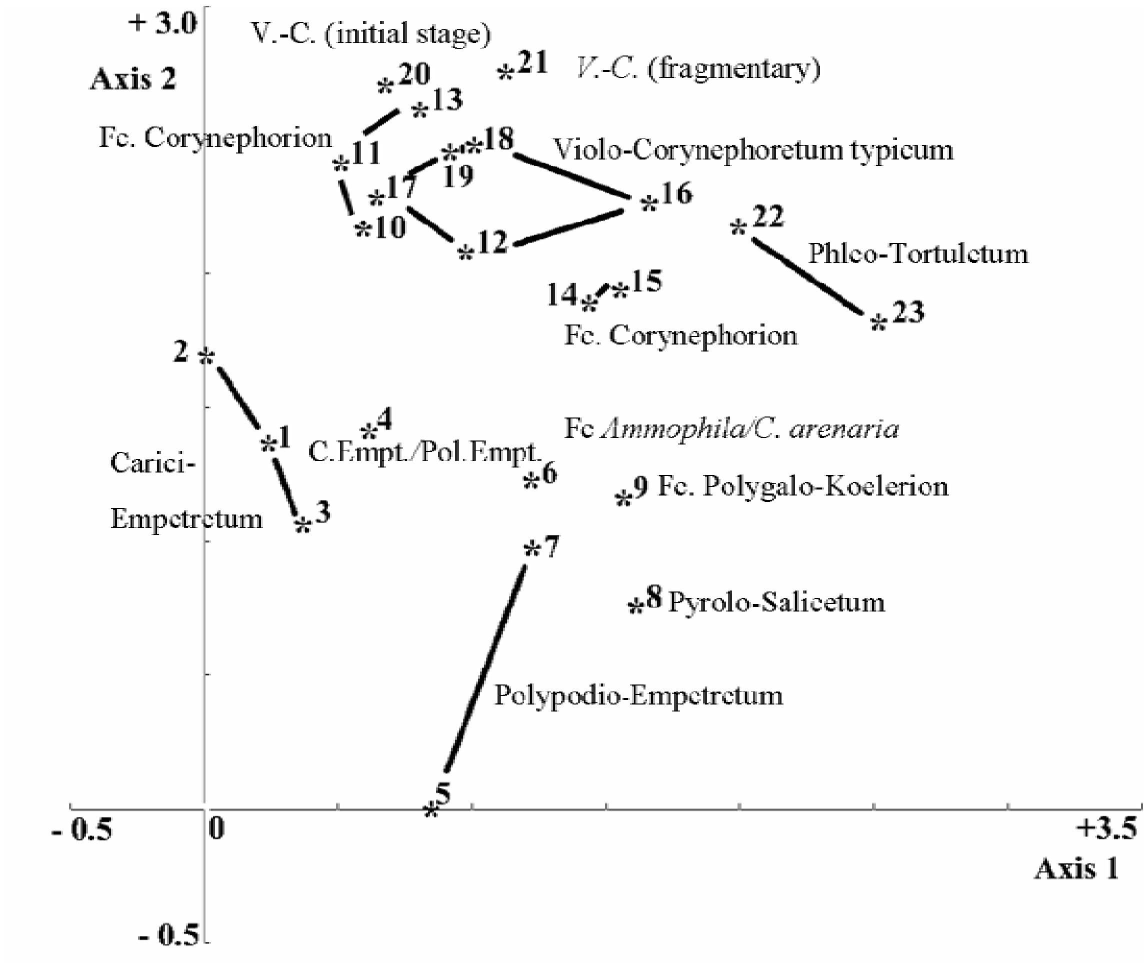

Figure 2.4. Ordination diagram representing a DCA of the 23 cluster centroids derived from the TWINSPAN table

In the ordination diagram, a clear gap is visible, partitioning the ordination space into two groups of clusters: (a) the dune heath communities forming later stages in the succession in the Ca-poor so-called ‘black dunes’ and (b) initial vegetation and open grasslands on Ca-poor dune sands, the ‘grey dunes’. Group (b) is plotted in the upper half of the ordination diagram and consisted of different stages of the V.-C., frame communities of the Corynephorion and of the Phleo-Tortuletum ruraliformis.

The cls. 1-5 and 7 represent two different dune heath communities characteristic of Ca-poor dunes, the Carici-Empetretum (1-4) on more level sites and the Polypodio-Empetretum (5 and 7) more or less restricted to northern and eastern slopes (Stortelder et al. 1996). Also belonging to the Empetrion is cl. 6, the *Fc. Ammophila/Carex arenaria*, dominated by tall graminoids like *Ammophila arenaria* (frequency V and mean cover 65%). It is close to cl. 9, Fc with *Salix repens* dominance, assigned to the Polygalo-Koelerion, which indicates a less acid soil. In both frame communities *Polypodium vulgare* occurs with high presence and 20% cover. The Pyrolo-Salicetum, cl. 8, can be found on mainly decalcified dune sites covered by acid litter (Stortelder et al. 1996).

The V.-C. typicum (cls. 12, 16-18 and 19), consists mainly of relevés from the former period. The frame communities of the Corynephorion are divided into two groups, one on the utmost left side of the diagram (cls. 10, 11 and 13) and one occurring in the middle, near the Empetrion communities (cls. 14 and 15). Cluster 10 is dominated by *Festuca ovina* and is rich in reindeer lichens, cl. 11 is characterized by *Calluna vulgaris* and a dead moss layer, covered by algae. Cluster 13 is from recent origin. It consists of a moss carpet of both *Campylopus introflexus* and *Dicranum scoparium*, in combination with several V.-C.-species, especially lichens, and also with patches of dwarf shrubs. It is close to the cls. 18 and 17, the most lichen-rich V.-C. typicum of the former period, but both with a low mean percentage of mosses (respectively < 1% and 20%). However, cl. 12, present in both periods, is very moss-rich with *D. scoparium*, and is considered V.-C. typicum with *D. scoparium* dominance. Both frame communities (cls. 14 and 15) are also moss-rich with dominance of *D. scoparium* and *Campylopus introflexus,* respectively, and have very small patches of dwarf shrubs. These types are only found in the 1990s and are strewn with tall graminoids (*Ammophila arenaria* and *Carex arenaria*). The connection between cl. 14 and cl. 6 (the FC *Ammophila/Carex* arenaria belonging to the *Empetrion*, and also dominated by tall graminoids) is clear.

The initial stage of the V.-C. (cl. 20), is plotted at the top of the diagram. It originates from the 1960 period and consists of pioneer species, both of mosses and lichens, including *Bryoria fuscescens*. Cluster 21 represents a recent pioneer community with *Campylopus introflexus*, green algae and several pioneer lichen species.

Cluster 16, a V.-C. typicum, found in both periods, contains species from the Phleo-Tortuletum and can be considered to be transitional to the Phleo-Tortuletum ruraliformis brachythecietosum (cls. 22 and 23). The latter two clusters have many differential species of this sub-association (Table 2.1) and are very lichen-rich (Table 2.2).

2.5. Discussion

The dune vegetation on Terschelling has undergone many changes since the end of the 19th century when intensive exploitation ceased and an overall *Ammophila*-planting fixed the dunes. For the first half of the 20th century van Dieren (1934) and Westhoff (1947) described many early succession stages in the dry dune vegetation, several rich in lichens.

By comparing our vegetation relevés from the 1960 period with those of the 1990s, lichen diversity in the former period was especially in the initial stage of the V.-C. and within the V.-C. typicum (the quadrangular in Figure 2.4).

The initial stage of the V.-C. with mainly pioneer lichen species on slightly decalcified sand, was only present in the former period. In the 1990s the early succession stages of the V.-C. with *Cladonia*-species could still be found, but these were accompanied by *Campylopus introflexus* (V.-C. fragmentary in Figure 2.4). Due to the expansion of this neophytic moss characteristic of calcium-poor acid sand (Biermann 1996, 1999), lichen-diversity is no longer guaranteed. The pioneer lichen species like *Cetraria aculeata, Cladonia foliacea, C. furcata* and *C. zopfii* disappeared from open, now more acid sand (de Boer et al. 1998) due to competition with this moss (Ketner-Oostra & van der Loo 1998). Hypothesis 1 stating that in the calcium-poor dunes of the phytogeographic 'Wadden district', lichen communities are especially well developed in the earlier succession stages of the 'grey dunes' applies mainly for the past but not for the present.

In the ordination diagram (Figure 2.4) the V.-C. typicum with *Dicanum scoparium* dominance (cl. 12) is close to Fc Corynephorion with *D. scoparium* dominance (cl. 14), representing a mosaic vegetation of the V.-C. with small dwarf shrubs, and related to the Empetrion-clusters. This supports our second hypothesis that lichen diversity is a time-limited phenomenon, followed by moss encroachment or dominance of competitive lichens, mainly reindeer lichens (Bültmann & Daniëls 2001). Also in the former period this succession from the V.-C. to the dune heaths went through such stages (Ketner-Oostra 1989). This is demonstrated by cl. 4, mainly with relevés from the former period, uniting *Dicanum scoparium*, *Cladina portentosa*, *C. ciliate* and *C. rangiferina* (a for the Netherlands very rare reindeer lichen and declared 'absent' by Aptroot et al. 1998), with several epigeic growing epiphytes like *Pseudevernia furfuracea* and the moss *Dicranoweisia cirrata*.

Recent relevés in moss-rich succession stages, characterized by the dominating *Campylopus introflexus* (cls. 13 and 15), are enclosed in the Fc Corynephorion, following Weeda et al. (1996) and not Biermann (1999), who distinguished a new subassociation V.-C. rumicetosum acetosellae, characterized by *C. introflexus*, and a subtype with *Dicranum scoparium* dominance. According to our view the high frequency and cover of *C. introflexus* and *D. scoparium* are insufficient to distinguish a new subassociation and subtype as differentiating species against the V.-C. typicum are lacking.

The expansion of *C. introflexus* in the present time compared with that of *D. scoparium* in the past might be an indication for an accelerated vegetation succession, as in our third hypothesis is postulated. That this neophyte can interfere with the normal succession in calcium-poor dune grassland is one of the effects of acid rain (Biermann 1996, 1999). However, that this moss profits from the nitrogen deposition is not yet proved.

Weeda et al. (1996) stated that the V.-C.-typicum is (or rather was) the typical subassociation for terrestrial growing epiphytic lichens. This is in accordance with our data as the cls. 17-19 contain mostly relevés from the 1960 period. In this period *Hypogymnia physodes* was the most frequent of the ten terrestrial growing epiphytic lichens, followed in frequency by *H. tubulosa, Platismatia glauca, Evernia prunastri, Pseudevernia furfuracea, Parmelia sulcata*, and the Red list species *Bryoria fuscescens, Usnea subfloridana, U. filipendula* and *U. fulvoreagens*. In the latter period these last four lichens were not found again. In 1970 *Bryoria fuscescens* was discovered on Terschelling abundantly growing on bare sand (Figure 2.5, Ketner-Oostra 1972) and in the former period was also found on the West Frisian islands Vlieland and Ameland, but occurred in the dunes of the East Frisian islands only on Langeoog (Brand & Ketner-Oostra 1983). The usually epiphytic moss *Dicranoweisia cirrata* occurs in all clusters of the V.-C. typicum

Figure 2.5. *Bryoria fuscescens* on dune sand in 1970

quadrangular (Figure 2.4) and was refound terrestrially on Terschelling only once in the 1990s.

The disappearance of the four most rare beard-like lichen species from the V.-C. typicum and the severe decline in presence and cover of the *Hypogymnia* spp. (fourth hypothesis) might be linked to the acidification of the soil surface, but probably mainly as a consequence of their intolerance to NH_3, as is proved by their decline in epiphytic habitats in the Netherlands (van Herk et al. 2000).

In the 1960 period the V.-C. typicum contained 28 lichen species (Table 2.1). Nevertheless, in the 1990s the frame community with *C. introflexus* (cl. 13) exhibited many common *Cladonia* species on top and between the mosses, according to what was noticed by van der Meulen et al. (1987) in the dunes along the Dutch coast. We found that when *C. introflexus* is failing in vitality through desiccation or is covered by algae (mainly by *Gloeocystis polydermatica*), it may act as a substrate for common humicolous lichen species (i.e. growing on humus-rich substrata) like *Cladonia coccifera, C. floerkeana, C. macilenta, C. ramulosa, Micarea prasina, Placynthiella* spp. and for *Cladina portentosa*. In the 1990s *Hypogymnia physodes* was the only epiphytic lichen growing very sparcely epigeic on these moss-carpets. Especially when the influence of in-blowing sand is observed, which harms the *Campylopus*-carpet even more and provides mineral ions for the lichens (Ketner-Oostra & Sýkora 2000), also some pioneer species like *Cetraria aculeata*, *Cladonia foliacea* and *C. furcata* were present. All mentioned

Figure 2.6. *Usnea* and *Hypogymnia* spp., growing terrestrially on a moss carpet in 1970

lichen species seemed to establish themselves as 'secondary pioneers' on these withering moss carpets.

The frame community Corynephorion, characterized by *Festuca ovina* and dominated by reindeer lichens (cl. 10), mainly consists of recent relevés. In the ordination diagram a relation to the Empetrion is made clear. Westhoff (1947) described *Cladina*-mats in the V.-C., like Böcher (1941) did in the lichen heath on the Danish island Læsø, while Böcher (1952) stressed the permanent state of these reindeer mats as a lasting climax vegetation. Both authors did not mention grass encroachment with *F. ovina* as we found. Paus (1997) mentions *F. ovina* s.l. and the occurrence of *Ammophila arenaria* in the Cladonietum mitis of coastal dunes in Northwest Germany. On Terschelling former grazing by goats and the presence of rabbits might cause *F. ovina* encroachment.

The real Polypodio-Empetretum, present in both periods, is found to be rather lichen-poor. The frame community with *Salix repens* (Fc. Polygalo-Koelerion) present in the 1960s, is related to the Pyrolo-Salicetum, with a moss layer on which epiphytic lichens like *Hypogymnia* spp. and *Usnea* spp. were growing terrestrially at that time (Figure 2.6).

Effect of encroachment with tall graminoids

The frame community *Ammophila arenaria/Carex arenaria* with several species of the V.-C. and substantially grass-encroached by *Ammophila arenaria, Carex arenaria* and *Festuca rubra* contains also *Polypodium vulgare* with a high presence

Figure 2.7. *Parmelia sulcata* growing epigeic in a *Corynephorus canescens* vegetation on the Noordsvaarder in 1991

and cover (average 20%). This frame community of tall graminoids is a key to the present state of the formerly lichen-rich dune grassland of Terschelling (Figure 2.3).

The transition of a short-grassland vegetation with a high biodiversity into a long grassoid vegetation with a reduced biodiversity is also related to the fluctuating grazing pressure of rabbits (Heil et al. 1990, Packham & Willis 2001), as their population on Terschelling is frequently decimated by outbreaks of virus-diseases.

By our phytosociological research the quantity of grass-encroached vegetation cannot be deduced, as describing lichen-rich vegetation was for both periods our basic assumption and main attention. However, in the Terschelling 1998-1999 vegetation mapping project of Buro Bakker (2000), their GIS total-up of the Fc. *Ammophila* got to 518 ha, the Fc *Carex arenaria* 76 ha and the Fc *Polypodium* 46 ha. This is in marked contrast with the area of 5 ha of their V.-C.rich in *Cladonia's* (undisturbed) and 57 ha slightly disturbed. Moreover their V.-C. rich in reindeer lichens (undisturbed) covered 7 ha and slightly disturbed 170 ha. This disturbance meant in both cases that species of other vegetation types penetrated, like *Ammophila arenaria*, *Carex arenaria, Calamagrostis epigeios*, and/or *Salix repens*. This mapping project has revealed the dramatic decline of the undisturbed lichen-rich V.-C. on Terschelling.

In the 1990s lichens can still thrive in the more open dune grassland with a low cover of tall graminoids (< 5%, Table 2.1), i.e. the transitional stage from V.-C. typicum to the Phleo-Tortuletum ruraliformis and the subassociation brachythecietosum of that Phleo-Tortuletum ruraliformis. According to our data many *Cladonia*-species and in addition several terrestrial growing epiphytes like *Hypogymnia physodes, H. tubulosa, Evernia prunastri* and *Parmelia sulcata* (Figure 2.7) can still be found, but only in young, recently formed dune ridges on the Noordsvaarder and in Cupido's Polder, in subneutral habitats with slightly calcareous sand blown-in (Ketner-Oostra & Sýkora 2000).

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Chapter 3

VEGETATION SUCCESSION AND LICHEN DIVERSITY ON DRY COASTAL CALCIUM-POOR DUNES AND THE IMPACT OF MANAGEMENT EXPERIMENTS

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Chapter 3. 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 *Cladonia* and *Cladina* species were found on the fixed, grey hairgrass (*Corynephorus canescens*) dominated, so-called grey dunes all over the island of Terschelling (the Netherlands). In addition, species like *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 west part of the island. They occur on parts of seven dune ridges parallel to the coast and forming 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 ageing of 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 sub-neutral or neutral pH from reactivated and natural blowouts or from foredunes, with increasing lime content respectively.

Key words: Acidification; Biodiversity, *Campylopus introflexus*; *Corynephorus canescens*; Chronosequence; Moss encroachment; Lime; Sand-drift; Sod cutting.

Nomenclature: Higher plant taxonomy follows van der Meijden (1990), the nomenclature of the mosses is according to Touw & Rubers (1989) and that of the lichens to Purvis et al. (1992). A set of lichen specimen has been deposited at the herbarium of Dr. A. Aptroot (C.B.S. Baarn) herbarium code ABL (Taxon 44: 258)

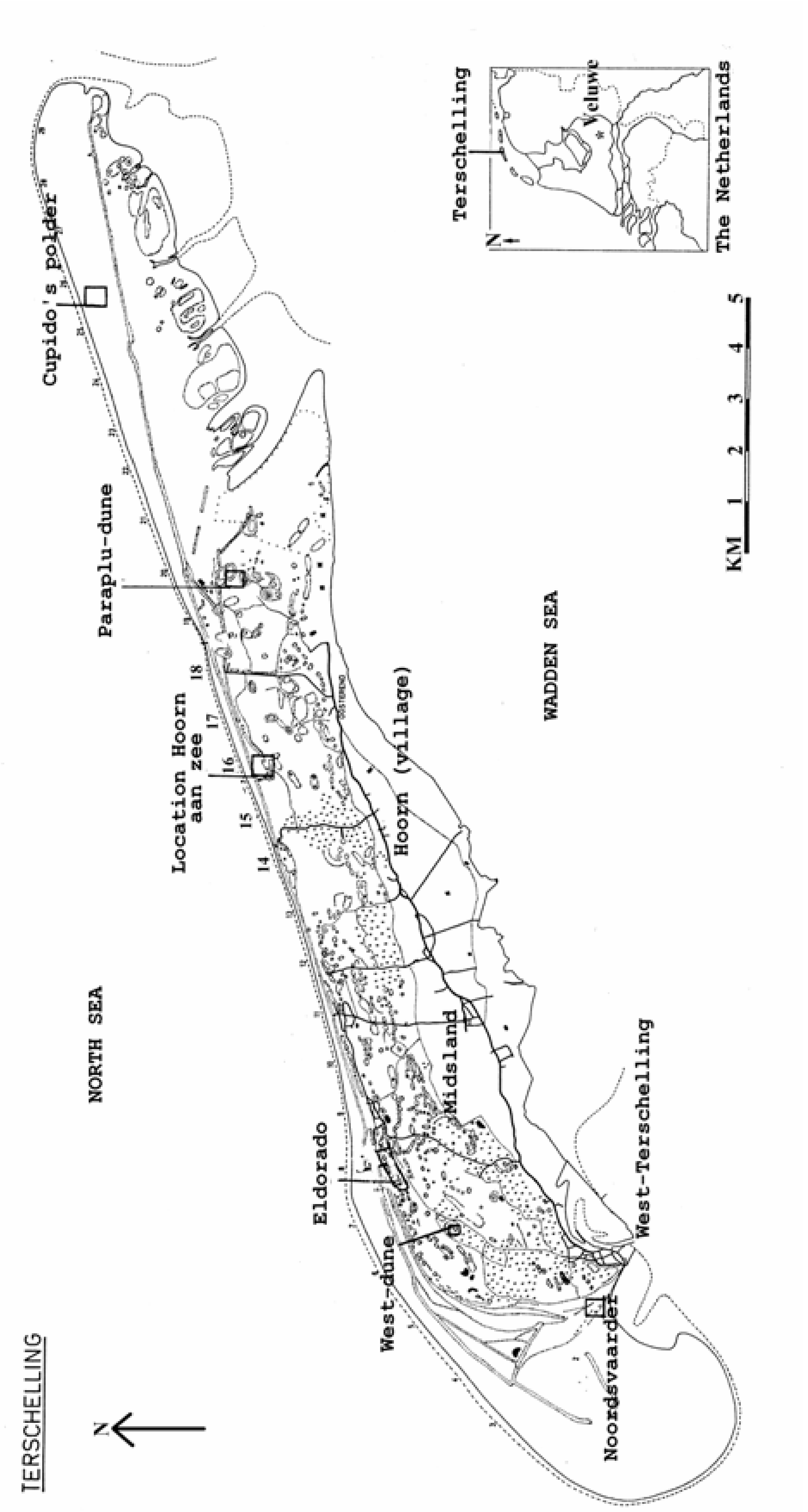


Figure 3.1. Location of the study sites

3.1 Introduction

In the last 30 years there has been a serious decline in the plant diversity in the grey hairgrass (*Corynephorus canescens*) dominated, 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 vegetation dominated by tall grass species or by mosses (Vertegaal et al. 1991). The encroachment by the neophyte *Campylopus introflexus* (van der Meulen 1987) in particular has drastically reduced species diversity (Kooijman & van der Meulen 1996).

Terschelling is one of the West Frisian Islands (Figure 3.1). Most of these islands are characterized by dune sand low in $CaCO_3$, 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 on open 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 elsewhere on the NW side of the trunks of living trees. The epiphytic association Parmelietum furfuraceae Hil. sensu Ochsn. includes the lichens mentioned here and is an aero-hygrophytic and toxiphobic association, that is also strongly wind resistent. The habitat on moss-covered dune soil may be characterized by (1) electrolyte concentration, (2) drought periods controlled by the frequency of precipitation and fog, (3) rate of evaporation, (4) water capacity, whereas (5) illumination and (6) actual pH as direct factors are second in importance (Barkman 1958). Since 1975 this epiphytic association, occurring in the Netherlands in some in refugia, has decreased considerably; the decline has been ascribed to the emissions of ammonia from the bio-industry (van Herk et al. 2000).

Between 1990-1995 these usually epiphytic species, in combination with a rich *Cladonia* assortment, could only be found on Terschelling on relatively young dune ridges on the Noordsvaarder (Figure 3.2), a sandbank joined to the

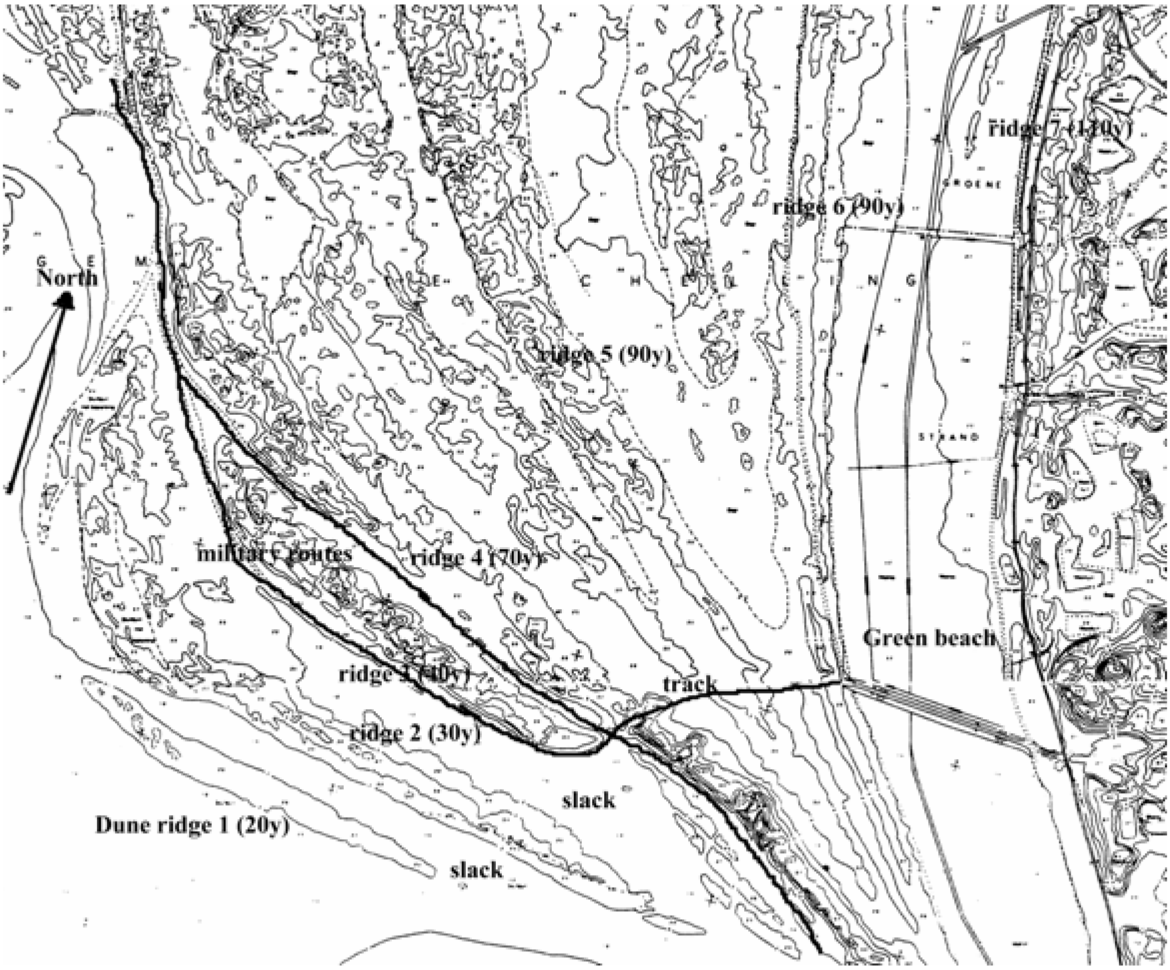


Figure 3.2. Dune ridges on the Noordsvaarder, alternating with dune slacks, some of which are still connected with the sea

western side of the main island since 1900 (Figure 3.3). 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).

On Terschelling the 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 in Germany.

In 1991 a nation-wide project (EGM, effect-oriented management against acidification and eutrophication of dry dunes) was launched in the Netherlands. Measures to restore open dry dune grasslands were aimed at controlling the grass-encroachment and improving the competitive position of characteristic species, including cryptogams (Vertegaal et al. 1991). Two locations on Terschelling were

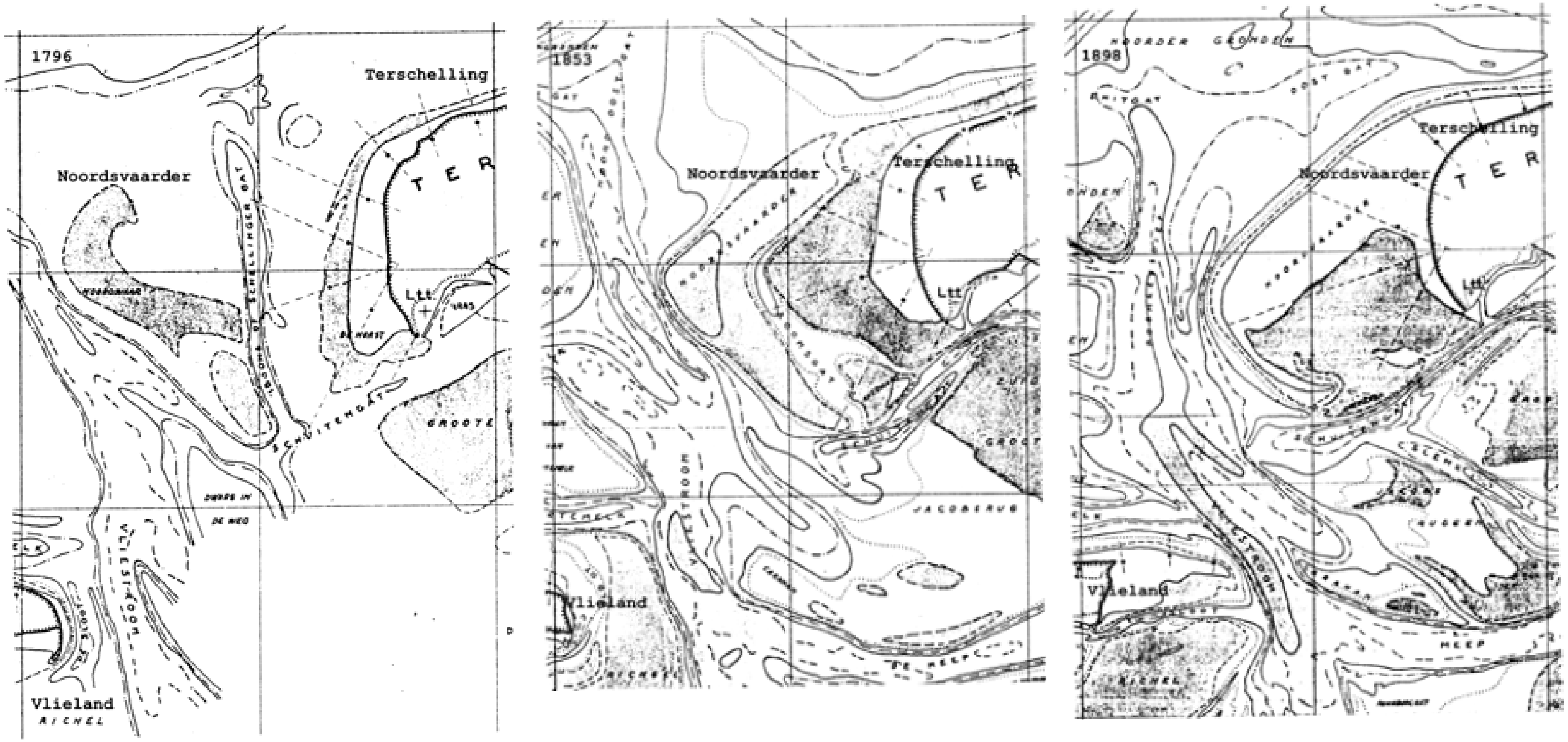
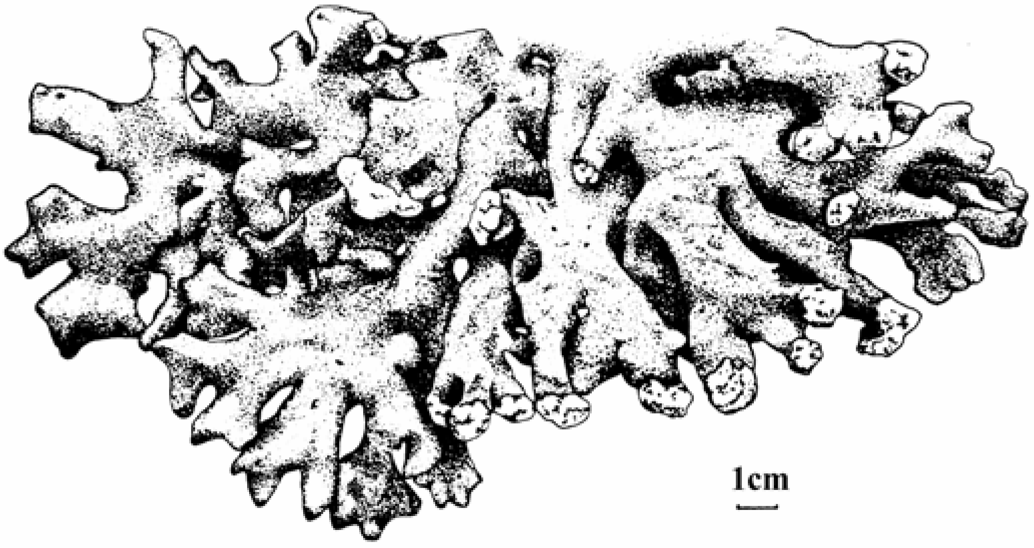


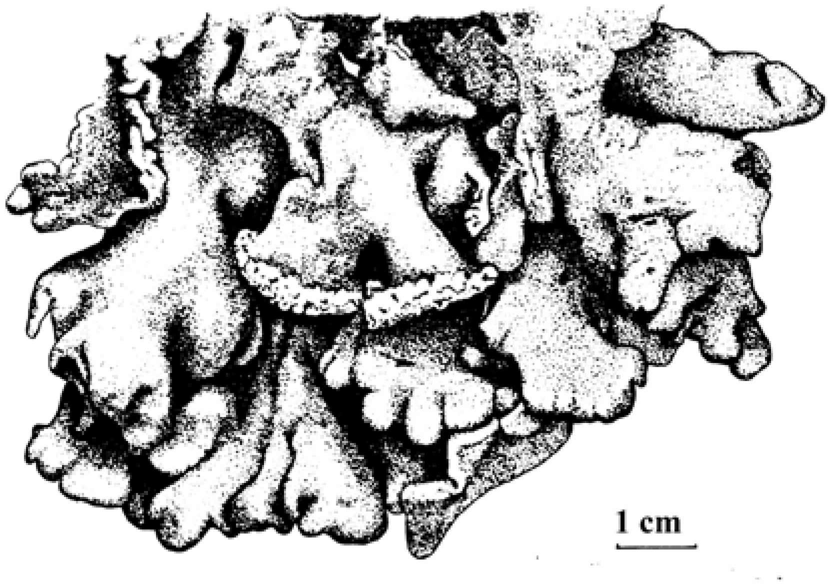
Figure 3.3. The process of the joining of the Noordsvaarder sand bank to the main island of Terschelling from (a) 1796, via (b) 1853 to (c) 1898, as illustrated by old maps

Table 3.1. Frequency and characteristic cover of terrestrial lichens and mosses, as compared with those of graminoids, on the 2d - 5th dune ridges on the Noordvaarder. Frequency classes 1 = < 20%; 2 = 21 - 40%; 3 = 41-60%; 4 = 61-80%; 5 = > 80%. Cover estimates (%) from relevés of 2 m x 2 m (Ketner-Oostra 1997). 3* living; (1)** standing dead; *** the decreasing number of relevés points to increasing homogeneity.

Dune ridge **Number of relevés**	**2** **14**	**3** **7**	**4** **6**	**5/6** **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)	-
Cladonia 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)	-	-	-



Hypogymnia tubulosa



Hypogymnia physodes

Figure 3.4. *Hypogymnia physodes* and *Hypogymnia 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)

included in this project (see Figure 3.1) with large scale vegetation removal from eleven 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 N. One of the conclusions was that atmospheric N-input is an important source of N, whereas in grass-dominated plots mineralization largely exceeds N-input (Veer 1997).

The natural and man-induced soil acidification in the dry dunes has been studied by de Vries et al. (1994). In calcium-poor dry dunes changes in the soil solution chemistry are the result of silicate weathering, but 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 lose 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 aluminium 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 in the Fryslân Region (the province 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).

On these considerations we based the following hypotheses:

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, leaching 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 set out 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?

3.2. Material and Methods

3.2.1. Soil origin and characteristics

Terschelling is the third island from the south west in the chain of West Frisian islands in the Dutch part of the North European coastal dunes, 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). 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 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. The dune soils may have relative high phosphorus availability, due to the comparatively loose nature of phosphorus sorption, resulting in the area being nitrogen-limitated (Kooijman et al. 1998).

3.2.2. 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, the summer temperatures are lower and in winter there are fewer days with frost. Both average daily temperature (in July > 14^o C) and the seasonal temperature variations are less than on the mainland. There are less than five summer days (temperature $>25^o$) and the number of 10 icy days (max. temperature $<0^o$ C) 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 s^{-1}, 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 average of 720 mm y^{-1} is probably only slightly lower. Winter and spring are foggier than inland, but in annual average there is less fog (Ketner 1972).

3.2.3. Sites at Terschelling (Figure 3.1)

1. Dune ridges on the ‘Noordsvaarder’ (Figure 3.2). This nature reserve originates from a wide sandbank situated in the North Sea, west of the village West-Terschelling and moving eastwards. The process of reaching and finally joining the island started in 1850 and was completed at the end of the 19th century (Figure 3.3). Since then a system of dune ridges has developed, separated by brackish slacks. Until 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, who was born and bred on Terschelling and is now the local director of the National Coastal and Marine Management Institute, estimated the age of these ridges. His observations were mainly based on the presence of military traffic routes running between the ridges that were used in the 1950s en 1960s (Figure 3.2).

The following dune systems were studied:

- The youngest dune ridge closest to the sea is ca. about 20 yr old, the second and the third ridge are 30 and 40 yr old, respectively. All ridges are more or less oriented from SSE to NNW and run parallel to each other. On the more inland dune ridges Marram grass has been planted.
- Ridges 4 to 6. Ridge 4 is estimated to be 70 yr old, while both ridges 5 and 6 are 90 years old; all three are oriented SE-NW. In all cases mentioned above the height varies between 2-5 m above sea-level.
- Two NW-oriented dune slopes in the stabilized dunes on the main island were included in the research: the seventh, a 10 m high dune ridge estimated to be 110 yr old, is nearest and parallel to the sixth dune ridge. 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 two km further north and is estimated to have stabilized about 130 years ago (see Figure 3.1).

2. Parallel dune ridges in what is called Eldorado, a 80-ha dune area NE of the village of West-Terschelling.

3. Parallel dune ridges along the North Sea coast in a former stabilized grey dune area NE of Hoorn, situated between beach marker posts 15 to 17. In this project it is referred to as Hoorn aan zee (Figure 3.1).

4. The Paraplu dune, a mobile dune at the east side of the island in the Bosplaat nature reserve, 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).

3.2.4. Dune management

In 1990, an experiment was carried out by the State Forestry Service: 200 m^2 of dry dune grassland on the fourth dune ridge (Figure 3.2) 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 and barrowed away. In 1991 artificially stabilized blowouts at Eldorado were reactivated on a large scale with an excavator, as a part of a large research project on grass encroachment along the Dutch coast (EGM, see Introduction). The vegetation and uppermost soil layer of eleven dune slopes were removed until clean mineral sand daylighted. 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 Rijkswaterstaat (the National Institute for Coastal and Marine Management) changed its management for coastal protection in this area and left these dunes unmanaged. To stop further retreat of the coastline a pilot project was implemented in 1993 (Biegel & Spanhoff 1996; Spanhoff 1998). The artificial supply of sand on the sea bed offshore from Hoorn and Oosterend between beach marker posts 14 and 18 intensified the inland transportation of sand.

3.2.5. Vegetation research

Between 1990 and 1995 vegetation relevés (size 2 x 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).

3.2.6. Soil research

Soil sampling: In 1991 soil samples were taken at three depths (0-2 cm, 2-7 cm and 7-17 cm (Table 3.2). In 1993 and 1995 the stipulations of the national EGM programme were followed (Vertegaal et al. 1991) and the 0-10 cm mineral layer was examined. 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 plot, or relevés.

Chemical analysis: The soil samples were chemically analysed at the Bedrijfslaboratorium voor Grond- & Gewasonderzoek, Oosterbeek, the Netherlands. The samples were dried at 40^0 C, ground and sieved, using a 2-mm sieve. The following analyses were performed:

1. pH-H_2O was determined in a suspension of 1 volume-part soil and 5 volume-parts H_2O after standing for 16 hours. pH-KCl determination followed the same line, but using 5 volume-parts KCl 1 M instead of 5 volume-parts H_2O.
2. $CaCO_3$ determination followed the Scheibler method of shaking with 3.2% HCl for one hour. 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 950^0 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, the P was spectrophotometrically analysed with 882 nm (Murphy & Riley 1962).

6. CEC (Cation Exchange Capacity) was calculated from the % Ca^{2+} exchangeable, % Mg^+ exchangeable, % K^+ exchangeable, % Na^+ exchangeable and H^+ occupation values (de Vries et al. 1994). To determine the cation occupation, a sub sample 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.

3.2.7. Data analysis

The relevés were both ordinated and classified using multivariate analysis. The 141 relevés originating from all research locations studied were clustered using TWINSPAN (Hill 1979). The TWINSPAN table (not reproduced here) was used to construct a TWINSPAN dendrogram. 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.

3.2.8. 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 ordered using 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.
2. The significance of the relation between species composition and separate environmental parameters was tested by Monte-Carlo Permutation test using Canonical Correspondence Analysis (CCA) (ter Braak 1987). For this test 7 relevés from the chronosequence on the Noordsvaarder and the corresponding environmental variables in three soil layers (0-2cm, 2-7cm 7-17 cm) were used.
3. From the locations Noordsvaarder, Hoorn aan zee, Eldorado and Paraplu dune, 12 relevés including many soil data from the 0-2cm and 2-10 cm depths, were available. Again the significance of the relation between species composition and separate environmental parameters was tested by Monte-Carlo Permutation test using CCA.
4. A third set of 8 relevés from four different dune locations with soil data from 0-10 cm depth, including values of CEC, was subjected to a Monte-Carlo Permutation test using CCA.

Table 3.2. 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 amd 7 - 17 cm 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^{-1}. * data set not used in the Monte-Carlo permutation test. ** no data available. The Green beach is a dune slack separating the Noordsvaarder from the adjoining dune area.

Analysis	**pH_w**	**pH_w**	**pH_w**	**pH_{KCl}**	**pH_{KCl}**	**pH_{KCl}**	**% C**	**% C**	**% C**	**% N**	**% N**	**% N**	**C:N**	**C:N**	**C:N**	**% P**	**C:P**	**Al_{ox}**	**Fe_{ox}**	**P_{ox}**
Depth (cm)	**0-2**	**2-7**	**7-17**	**0-2**	**2-7**	**7-17**	**0-2**	**2-7**	**7-17**	**0-2**	**2-7**	**7-17**	**0-2**	**2-7**	**7-17**	**0-2**	**0-2**	**0-2**	**0-2**	**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	0.40	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	0.30	0.08	0.08	0.030	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	0.10	0.021	0.010	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	0.030	0.010	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	0.10	0.076	0.018	0.010	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	0.10	0.036	0.012	0.003	9	13	33	0.014	24	1.5	3.0	1.50

Tabel 3.3. Results of the soil-analysis of the 0-10 cm layer for Eldorado and four other locations on Terschelling in 1995 (from Ketner-Oostra 1997).Values for pH, % carbon, Cation Exchange Capacity (CEC, in mequiv.kg^{-1}) and percentage basic ions are from eight permanent plots on the Noordvaarder 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	SW-facing slope*	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

3.3. Results

3.3.1. Vegetation

1. The Noordsvaarder chronosequence. In Table 3.1 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 great abundance of lichens on the second and third dune ridges that are 30 and 40 yr old, respectively. These dune ridges differ from ridges four and five/six (Figure 3.2) 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* (Figure 3.4), *Parmelia sulcata* and *Evernia prunastri*. Species differentiating the third dune ridge are *Cladonia furcata*, *Cetraria aculeata* and *Cladonia floerkeana*. It is also characterized by the relatively high cover of *Cladonia foliacea*. The older ridges are characterized by the relatively high cover of mosses, respectively *Hypnum cupressiforme* and *Dicranum scoparium* on the fourth ridge and *Dicranum scoparium* and the neophyte *Campylopus introflexus* on the fifth/sixth ridges. In the latter the cover of *Dicranum*

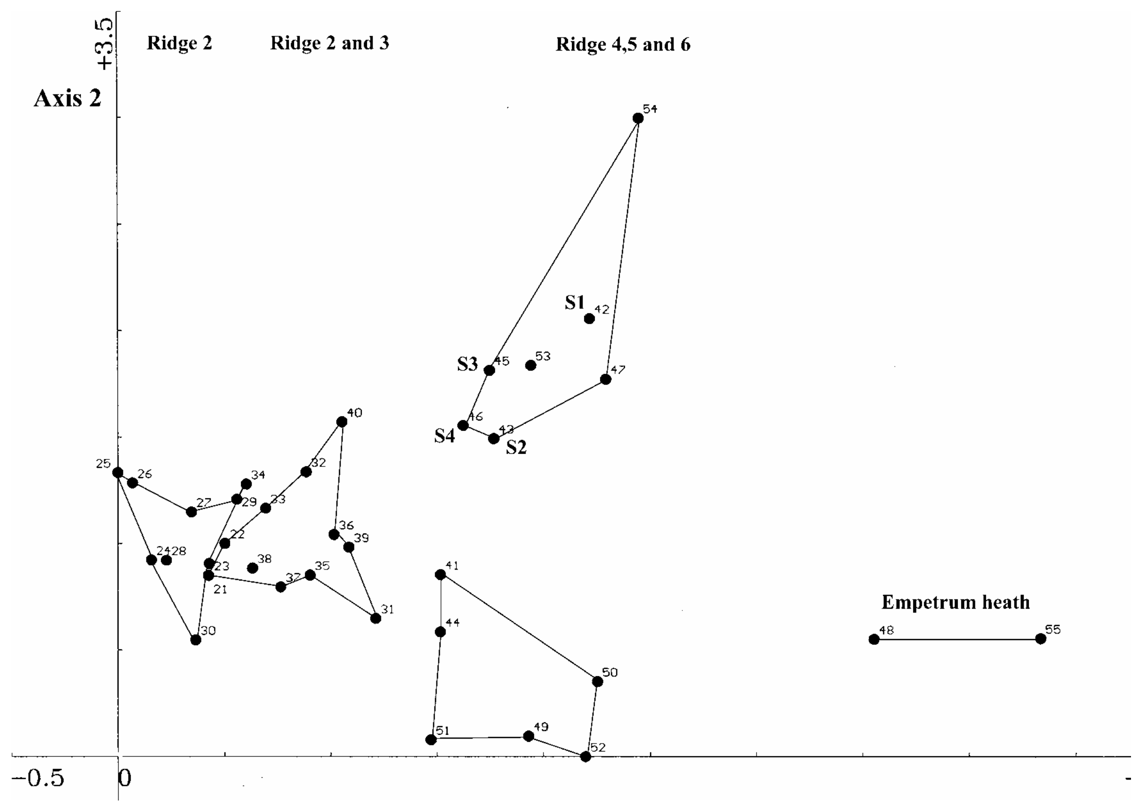


Figure 3.5. Ordination diagram representing a DCA of all Noordsvaarder relevés except those from the first foredune. TWINSPAN clusters are outlined. The four relevés (S1-S4) were made in four consecutive years after sod cutting

scoparium is almost complete (95%).The reindeer lichen *Cladina portentosa* was only found on the fourth ridge and the on humus growing lichens *Cladonia coccifera* and *Micaria prasina* occured only on the fifth/sixth ridges.

Figure 3.5 shows an ordination diagram representing a DCA of all Noordsvaarder relevés except those from the embryonic *Elymus farctus* dunes, which are outliers. Apart from the ordination the data have been subjected to TWINSPAN clustering (table not presented in this paper). The relevés belonging to one TWINSPAN cluster have been outlined.

Although relèves 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 characterized by the presence of many lichens. The combined fourth and fifth/sixth dune ridges ocurring 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*.

Table 3.4. 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 the 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

Sod cutting experiment. The vegetation development in four years time after sod cutting in 1990, is shown in Table 3.4. In four years the area of bare sand declined 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 *C. introflexus*. In the fifth year *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 coverage of < 1%.

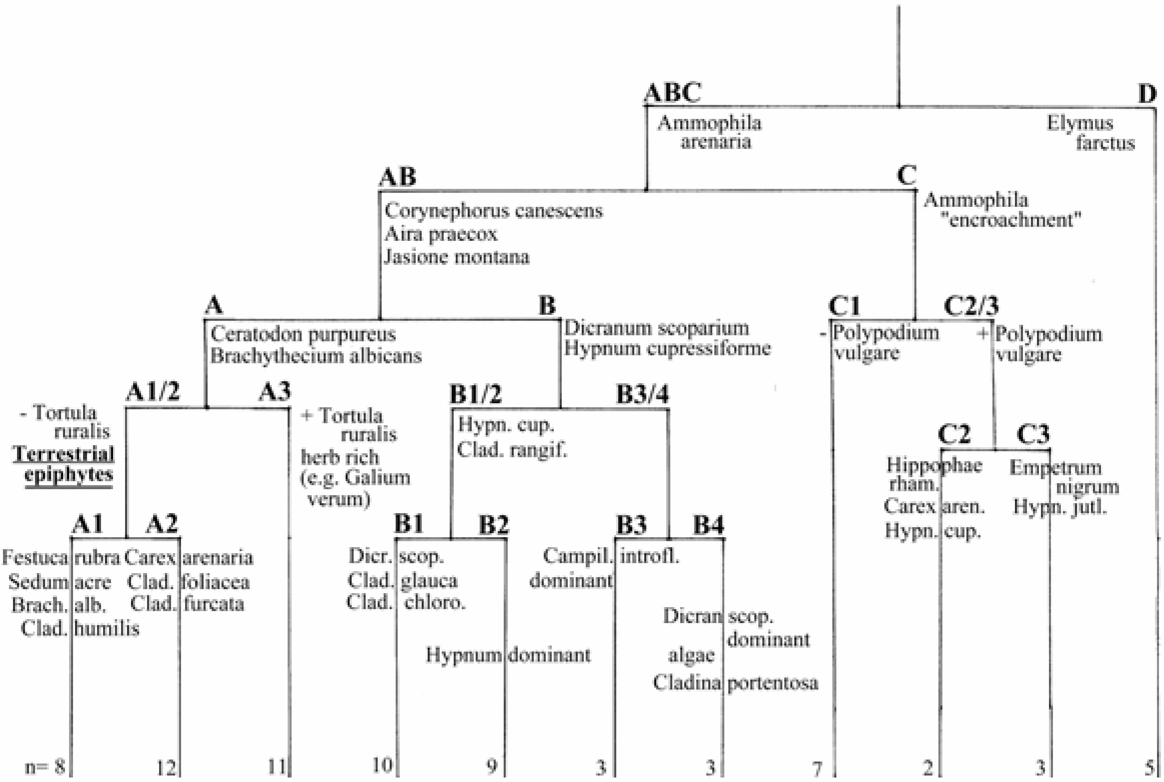


Figure 3.6. TWINSPAN-dendrogram of the total data set of Terschelling relevés in the period 1990-1995. Cluster groups A, B, C and D (see Text) are indicated. The number of relevés in each cluster is indicated by *n*. At each dichotomous division the main differential species are indicated

<u>2. All sites studied.</u> Figure 3.6 consists of a TWINSPAN dendrogram based on the total data set of 85 relevés from the period 1990-1995. The eleven 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 (Figure 3.6).

The vegetation of group C assigned to the Elymo-Ammophiletum (C1), a *Hippophae rhamnoides* scrub (C2) and a 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 Figure 3.6). 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

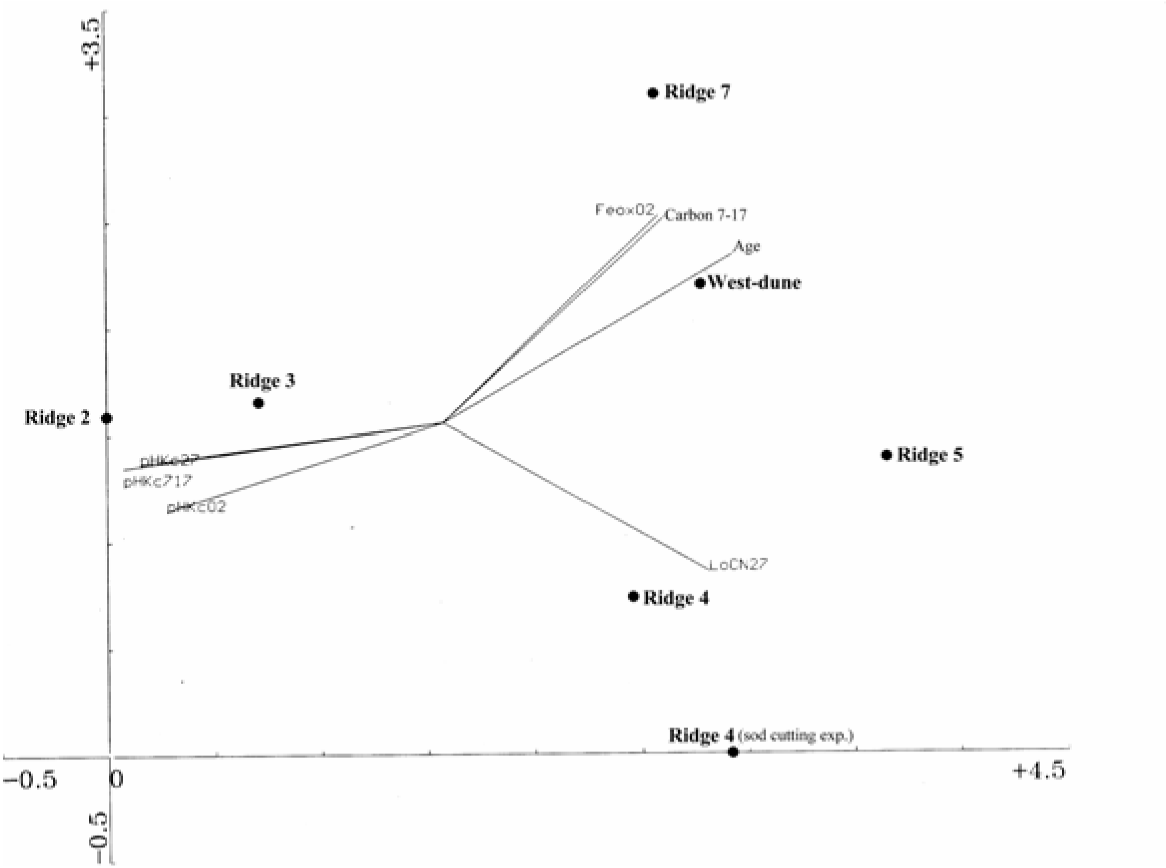


Figure 3.7. Relation between seven parameters and the first two axes of a DCA, based on the relevés from the chronosequence at the Noordsvaarder (Ridge 2 - Ridge 5/6). Ridge 7 and the West-dune are from the adjoining dunes. Carbon7-17 signifies % C at the soil depth 7-17 cm; Feox02 signifies % Fe-oxalaat at the soil depth of 2-7 cm; pH-Kc02 = pH-KCl in the surface layer of 0-2 cm; pH-Kc27 = pH-KCl at 2-7 cm; pH-Kc717 = pH-KCl at 7-17 cm.

Dicranum scoparium is constant and dominant. B2 is dominated by *Hypnum cupressiforme* and B3 by the neofyte *Campylopus introflexus*. B4 forms a transition to dwarf shrub heath (Empetrion nigri) and consequently to group C3.

3.3.2. 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 respectively 12 and eight relevés.

Set 1. Noordsvaarder chronosequence. Figure 3.7 shows the relation between seven parameters and the first two axes of a DCA based on the relevés from the chronosequence on the Noordsvaarder and matching soil data (Table 3.2). Only parameters that appeared to be significant or almost significant 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 can be expected, these data were strongly correlated with the pH-KCl values.

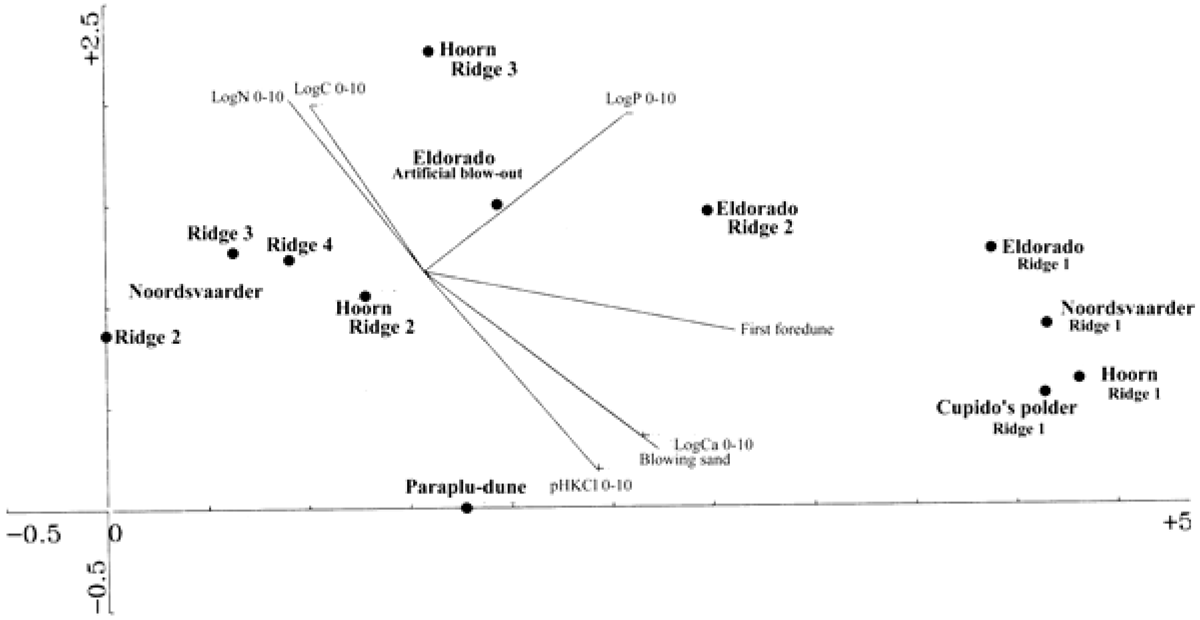


Figure 3.8. Relation between seven parameters (in the 0-10 cm soil layer) and the first two axes of a DCA, based on a selection of 12 relevés from four locations along the dune coast, the artificial blowout in Eldorado and the natural blowing sands on the Paraplu dune.

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 increases 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 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 connected to the vegetation.

Set 2. All dune sites studied. The second DCA (Figure 3.8) 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 3.3. Again, only factors appearing to be significantly or almost significantly (see Table 3.5) related to the variation in the species composition of the vegetation using a Monte-Carlo Permutation test are displayed in Figure 3.8. The location of relevés on the first foredunes (forming a closed coastal ridge along the beach, the so-called 'zeereep') appears to be a highly significant factor, as is the presence of blowing sand (see Table 3.5). Some factors (such as % calcium) were also highly significantly correlated to 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.

Table 3.5. Rate of significance of parameters connected to the vegetation of 12 releves along the Terschelling dune coast, tested with Monte-Carlo permutation test. $p = 0.05$ is the chosen significance margin.

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

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

The relevés in Figure 3.8 can be ranked according to decreasing nitrogen and organic carbon and with increasing pH, calcium and in-blowing 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 in-blowing sand after artificial erosion;
- Eldorado second dune ridge and Paraplu dune; and
- All relevés from the first foredunes.

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

Set 3. Several dune sites studied, parameters including CEC. In the third set eight relevés are available, with values of CEC (in meq/kg) and % basic ion content, measured at four different dune locations (Table 3.3). The first dune ridge of the Hoorn aan zee location with 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. Also the value for the blowing sand on the slope of the Paraplu dune is in the same order of 75%.

3.4. Discussion

3.4.1. Vegetation

Our research shows that the second and third dune ridges on the Noordsvaarder appear to be 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 to Violo-Corynephoretum, but in which *Sedum acre* and *Festuca rubra* are abundant (clusters A1 and A2 in the TWINSPAN table, here represented in Figure 3.6 as a dendrogram). The lime content of 0.3% to a depth of 10 cm in the first foredune had fallen to < 0.1% for the 0-2 cm layer of the second and third ridges (Table 3.2). In Table 3.3 this seems to be only true for the third ridge. Perhaps in this set of results the second ridge received some fresh accretion in the superficial layer. The epiphytic lichen *Evernia prunastri* was also growing terrestrially in the Paraplu dune relevés that were classified in cluster A2, having a similar vegetation, also growing on decalcified sand of 0,09% Ca CO_3 in the surface layer (Table 3.3).

Biermann (1999) studied the syntaxonomy and ecology of these succession stages from foredunes (so-called white dunes) to grey dunes on several Dutch and German Wadden Islands, including dune areas in the north of Denmark. He 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 (Biermann 1999). On Terschelling we also found the highest richness in *Cladonia* species in this succession stage: clusters A1 and A2 contained 14 *Cladonia* species, with *Cladonia foliacea* and *C. scabriuscula* reaching 70% cover in some of the 2 x 2 m relevés and *Cladonia rangiformis* and *C. pocillum* reaching 40%. In this stage of primary succession on dune ridges in the xeroseries 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 *Cladonia furcata* and *C. rangiformis* occurred as co-dominants. *Tortula 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 respectively 1.0%, 0.8% and 1.2%, respectively, which is substantially higher than that on the Noordsvaarder, which is 0.3% (Table 3.3). Biermann (1999) 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.

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 *Hypnum cupresiforme* and *Dicranum scoparium* in combination with reindeer lichens. Here, *Campylopus introflexus appears* as a co-dominant (cluster B3).

3.4.2. 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 (Figure 3.7) 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 Figure 3.8 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 in-blowing 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 in-blowing 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 (Figure 3.7) it can be seen that with ageing, the carbon content and acidity increase and 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 3.3).

Of the ridges 2 till 7 on the Noordsvaarder the C:N ratio was about 10 to 11 (Table 3.2), the same as Olff (1992) found in the dune succession range at 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 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 3.3).

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 however 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 compostion 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 3.2).

In the data set containing all Terschelling locations with available soil data (Tabel 3.3), 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 in the 2nd and 3rd plots 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 Figure 3.8 (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 with the management in Eldorado.

The oxalate determinations in the 1990-1995 period (Table 3.2) 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 aluminium oxalates convincingly present an increased buffer capacity with soil ageing. This becomes clear when we compare the coastal dunes with the inland dunes of the Veluwe consisting of much older Pleistocene deposits (see Figure 3.1). For all Terschelling plots the mean value is 2 (+1/-1) mmol kg^{-1} compared with 18 (+7/-5) mmol kg^{-1} 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 Figure 3.7) 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^{-1}. 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^{-1} (Ketner-Oostra 1995). For P oxalate the mean of all Terschelling plots was 1 mmol kg^{-1}, the same as for the 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 3.3). Barkman (1958) has suggested that this terrestrial occurrence of epiphytes was linked to specific ecological factors, with in the first place electrolyte concentration.

3.4.3. Management

3.4.3.1. 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 (Figure 3.5) shows that the relevés of the sod cutting experiment on the Noordsvaarder remained in the area dominated by *Campylopus introflexus*. Also in Figure 3.7 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 3.4).

3.4.3.2. 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 Figure 3.8).

Kooijman et al. (1998) state that though the Wadden district in general might be nitrogen-limited, it has a relatively high available phosphorus, 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 four yr after re-activating 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 re-activated 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 3.3). Hardly any sand accretion was visible, but it sustained the lichen richness, as our observations over several years showed.

3.4.3.3. 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 re-vitalised by neutral sand of pH-KCl 7.4 and 0.8 % $CaCO_3$ blowing in from the first foredune. The in-blowing 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 3.3). On these dune ridges *Cladonia rangiformis* and *C. foliacea*, characteristic of neutral or basic grassland (Purvis et al.1992) are growing together with sub-neutral species such as *Cladonia scabriuscula*, *C. furcata* and *Cetraria aculeata* 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 *Cla. arbuscula* s.l. These last two reindeer lichens are not mentioned by Ellenberg and can be considered to be acidophilic species as well.

The in-blowing 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 in-blowing sand (70-80% basic ion-content; see Table 3.3). 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.

3.5. 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 years for the succession from first foredune vegetation to a lichen-rich dune vegetation and another 30-40 years 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 sub-neutral sand with some lime content and a relatively high base content from natural and re-activated 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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Chapter 4

RESTORATION OF LICHEN DIVERSITY IN GRASS-DOMINATED VEGETATION OF COASTAL DUNES AFTER WILDFIRE

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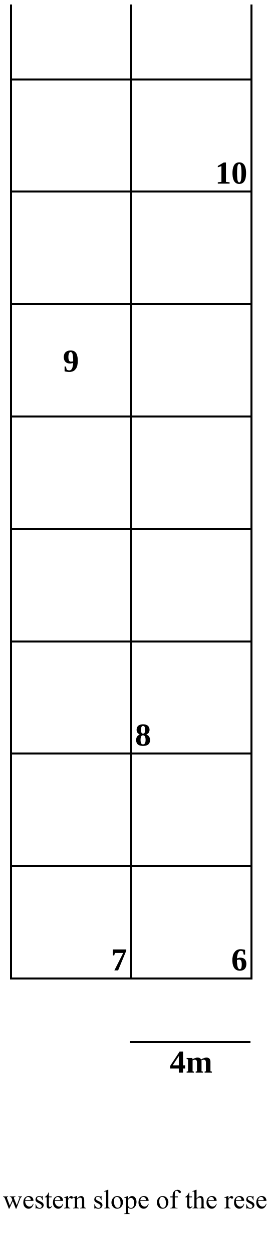

Part of the transect on the western slope of the research dune (RD), compiled of 4 m x 4 m blocks with PQs (6 – 10) included.

Photo page 73 (top): Research dune, five days after the wildfire in March 1993 (photo: Maaike Veer); (bottom): Research dune in June 1993.

Chapter 4. Restoration of lichen diversity in grass-dominated vegetation of coastal dunes after wildfire

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Abstract

Question: Can lichen diversity of an earlier succession stage be restored in dune grassland after fire in a region with high nitrogen deposition?
Location: Calcium-poor coastal dunes in the Wadden district, the Netherlands.
Methods: We sampled dune grassland by using a large continuous transect of 4 m x 4 m blocks on both a south slope and a west slope. The sampling was conducted in the lichen-rich Violo-Corynephoretum in 1966, in the vegetation dominated by tall graminoids in 1990 and in the recovering vegetation for eight years after a wildfire in 1993. Vegetation succession in the blocks is visualised in stacked bar graphs and ordination diagrams (DCA). In 1966 relevés were made within the blocks, and from 1990 until 2001 permanent quadrats were studied.
Results: Between 1966 and 1990 the lichen-rich open grassland became dominated by tall graminoids and developed partly into a dwarf-shrub heath, resulting in a severe loss of lichen diversity. After the fire a lush vegetation of tall graminoids with an abundant moss cover developed. In 2001 the vegetation was still very different from the lichen-rich vegetation in 1966.
Conclusions: Fire alone will not change dunes dominated by tall graminoids into open lichen-rich grasslands in an area with high aerial nitrogen deposition. After fire, additional intervention is recommended, such as large-scale clearing of the burned vegetation and actively promoting deposition of sand, either blown in from foredunes, from re-activated blow-outs or artificially brought to the site.

Keywords: Ammophila arenaria; *Campylopus introflexus*; *Carex arenaria*; *Cladonia*; Colonization; Invasive species; Management; Moss dominance; Nitrogen deposition; Terricolous lichen; Violo-Corynephoretum.

Abbreviations: L = Light; N = Nitrogen; NMDS = Non-metric multidimensional scaling; PQ = Permanent quadrat; R = Acidity reaction; RD = Rijks-Driehoeksmeting; VC = Violo-Corynephoretum.

Nomenclature: Phanerogams: van der Meijden (1996); Mosses: Dirkse et al. (1999); Lichens: Aptroot et al. (2004).

4.1 Introduction

4.1.1. Plant diversity threatened in northwest European dunes

The cover of mosses and tall graminoids has, since the 1970s, increased considerably on coastal and inland sand dune grasslands throughout the Netherlands (Veer & Kooijman 1997) and NW Germany (Biermann 1996, 1999). Terrestrial lichen diversity has previously been very high in these dunes, especially in those with calcium-poor sand of Pleistocene origin. In the past, grazing by cattle and rabbits kept the coastal dune grasslands in a condition of short grasses with patches of bare sand, where succession was frequently restarted (van Dieren 1934). In these 'grey dunes' the *Corynephorus canescens* vegetation on decalcified sand was rich in lichens (Westhoff 1947; Erichsen 1957; Oostra 1968). Since the 1970s the lichen-rich plant community Violo-Corynephoretum (VC) occurring on coastal dunes (Weeda et al. 1996; Biermann 1999) was affected by a lush growth of tall graminoids such as *Ammophila arenaria*, *Calamagrostis epigejos* and *Carex arenaria.* Other grasses began to dominate the lichen-rich Spergulo-Corynephoretum on calcium poor inland dunes, and both communities were invaded by the exotic moss species *Campylopus introflexus* (van der Meulen et al. 1987).

Increased grass dominance has been connected to increased deposition of atmospheric nitrogen (N), which, in the 1990s, amounted to 20 kg $N.ha^{-1}.y^{-1}$ on the West Frisian islands, the Netherlands (Bleeker & Erisman 1996). Ammonia initially acts as a nutrient enrichment, but in the soil it also turns into nitric acid, which causes the acidification of the dune soils. The calcium poor dunes had a relatively high P availability but were N-limited, resulting in a large effect of this increased N-input (Kooijman et al. 1998) and accelerated succession (Veer & Kooijman 1997). The vigorous growth of *Ammophila arenaria* was also due to acidification, which altered the plant-parasitic microbial community in the dune grasslands on Terschelling (de Boer et al. 1998). The decrease in rabbit population due to viral diseases accelerated the dominance of these graminoids (ten Harkel & van der Meulen 1996).

4.1.2. Fire as a management tool to regain lichen diversity

Fire has been frequently used to manage heathland (Gimingham 1994), and nowadays fire is considered as a management tool in grass-dominated dune grasslands. Knowledge of the effect of fire on soil lichens and their re-establishment could provide basic information for future management measures to regain former biodiversity in coastal and inland dune grasslands.

Vestergaard & Alstrup (2001) studied the effect of a wildfire on the biodiversity in coastal dune heath in NW Jutland (Denmark). Müller et al. (1997) studied controlled burning to conserve and revitalize large areas of heathland on Pleistocene nutrient-poor sands in the Lüneburger Heide (NW Germany). The establishment of terricolous lichens, mainly *Cladonia* species and the pioneer species *Placynthiella uliginosa* showed a good post-fire regeneration in open sites as early as one year after burning (Müller et al. 1997). A wildfire in moss-dominated inland sand dunes (*Spergulo-Corynephoretum*) at the Veluwe (the

Netherlands) was monitored for possible lichen recolonization with permanent plots from 1995-2000 (Ketner-Oostra 2002). *Campylopus introflexus* reappeared in flat and undulating dunes. Only on the steep south and east exposed slopes did the desired pioneer vegetation in with *Polytrichum piliferum* blowing sand arise and promoted the re-establishment of lichen diversity.

4.1.3. The wildfire on the Terschelling research dune

An opportunity for research presented itself after a wildfire in 1993, which removed most of the vegetation on a dune body in the coastal dunes of Terschelling. This dune had a monitoring history going back to the lichen-rich vegetation in 1966, when the vegetation on this large dune was described, both quantitatively with large blocks in transects and qualitatively with relevés (Oostra 1968). In 1990 this dune was studied again to document the decline in species richness as result of increased dominance of *Ammophila arenaria*, *Calamagrostis epigejos* and *Carex arenaria*. After a very dry period in early spring 1993 this lichen-poor dune, dominated by tall graminoids and with much standing dead plant material and litter, was intensively burned by a wildfire. The field layer turned into ash, and the dwarf-shrubs (*Empetrum nigrum*) on the upper part of the western slope burned deeply into their root system. The bottom layer turned partly into ash and the high temperatures killed all cryptogams. Only a few blocks with patches of reindeer lichens at the bottom of the western slope were not burned. However, the root system of many *Ammophila arenaria* plants survived, and some shoots appeared as soon as the first monitoring took place in June 1993, as did some rosette plants.

The aim of this study was to assess the regeneration of burned dune grassland vegetation with possible restoration of the former open dry dune grassland rich in lichens (Oostra 1968). We tested the hypothesis that burning can be used to restore terricolous lichen diversity in former ‘grey dunes’ (VC), dominated by tall graminoids.

4.1.4. Site description

The study site is located on the dune with the wildfire history. It is known as the RD dune – it is marked by a sign Rijks-Driehoeksmeting; State Triangular Mapping Survey – in the eastern part of the coastal dunes of the Frisian island of Terschelling, the Netherlands (53°25' N, 5°25' E). It has a size of ca. 4 ha, and results from large sand movements in the 19th century and subsequent consolidation by *Ammophila* planting around 1920 (van Dieren 1934). The RD dune has a steep southern slope and a long, more heterogeneous gently sloping western slope.

4.2. Methods

4.2.1. Vegetation sampling

We studied a total of 24 blocks (4 m x 4 m) in a transect (three blocks wide by eight blocks long) on the southern slope of the RD dune and 52 blocks in another transect (two blocks wide by 26 long) on the western slope. Cover of five major moss species, dwarf-shrubs (*Empetrum nigrum*) and total cover of living and dead vascular plants (graminoids and herbs), litter, mosses, lichens, bare sand and ash were estimated in 1966, 1990 and, after the fire in 1993, annually until 2001, except in 2000. In 1966, the following blocks were not recorded: three at the top of the southern slope, 12 at the top and four at the foot of the western slope. One third of the transect on the southern slope (eight blocks) with intensely burned vegetation was not recorded in 1993.

Percent cover was estimated for each 4 m x 4 m block in 1990-2001. In 1966 a count scale, I - IV, was used for vascular plants, mosses and lichens: I = 1-10% cover; II = 11-25%; III = 26-50%; IV = 51-75%, with no higher values present. We used the midpoint of each of these cover classes in the data analysis. Standing dead material was assumed to be 10% of living graminoids and herbs, conforming to their cover in the VC community of today.

In addition, in 1966 relevés of variable size (with a mean size of 0.4 m x 0.4 m), were subjectively located within the blocks, 20 on each slope (Oostra 1968). These were used for species diversity and estimation of cover-abundance, according to the Braun-Blanquet method, as modified by Barkman et al. (1964). In 1990, permanent quadrats (PQs), 2 m x 2 m, were subjectively located within the block transects, six PQs on the southern slope and nine PQs on the western slope. They were sampled before the fire (1990) and annually after the fire, from 1993 until 2001, except for 2000. Presence and quantity of all plant species was recorded as in 1966.

4.2.2. Data analysis

We created stacked bar graphs for each slope, based on the data from the blocks, to describe the pattern of vegetation change. The data from the individual blocks were analysed with Detrended Correspondence Analysis (DCA, Hill 1979) separately for the southern slope and the western slope. The objective of the multivariate analysis was to address the spatial and temporal variation in the vegetation. The response variables, i.e. percentage cover of living *Empetrum nigrum* (only for the western slope), living graminoids and herbs and standing dead, bare sand (including the percentage surface covered by ash), total lichen cover and the cover of five moss species, were log transformed before analysis.

The DCA was based on a total of 227 and 504 blocks for the southern slope and western slope, respectively. To express the heterogeneity of the long western slope, after copying the ordination diagram, year groups of different clusters of relevés were outlined to emphasize major differences in the vegetation of 1990 and 1993. The four clusters consist of a burned major part of the western slope (a total of 272 blocks), the burned upper part, rich in dwarf-shrubs in 1990 (160 blocks), a burned part at the foot of the slope, lichen-rich in 1990 (45 blocks), and an unburned part at the same foot, also lichen-rich in 1990 (27 blocks). To check the reliability of the DCA we also applied Non-metric Multidimensional Scaling (NMDS) as recommended by Økland (1996). The results were very similar for the western slope and similar for the southern slope, although in the case of the southern slope the DCA patterns were clearer than the NMDS patterns. The lichen diversity on the southern slope and on the western slope was analysed from 20 relevés (0.4 m x 0.4 m) on each slope, established in 1966 (Oostra 1968), and from the six PQs of 2 m x 2 m on the southern slope and nine on the western slope from 1990-2001. Mean lichen cover was calculated for each year. The lichens were categorized according to ecology and with Ellenberg indicator figures indicating preference for light (L) and acidity (R); see Wirth (1992).

For Ellenberg indicator figures, light (L) gives a scale of relative light intensity: 5 = semi-shade, rarely in full light; 6 = between 5 and 7; 7 = in a well lit place, but also in partial shade; 8 = mostly in light; 9 = in full sunlight; Indiff. = indifferent. Reaction (R) gives a gradient of soil acidity and lime content where 1 = extremely acid (pH < 3.4); 2 = very acid (pH 3.4-4.0); 3 = quite acid (pH 4.1-4.8); 4 = between 3 and 5; 5 = moderately acid (pH 4.9-5.6); 6, between 5 and 7; 7 = subneutral (pH 5.7-6.5); 8 = neutral (pH 6.6-7.5).

4.3. Results

4.3.1. Vegetation composition on the southern slope

In 1966 the vegetation composition on the southern slope was characterized by a combination of much bare sand (60%), vascular plants (28%), mosses (5%) and lichens (8%; Figure 4.1a).

Lichens from the pioneer stage of the VC, such as *Cladonia foliacea*, *C. furcata* and *Cetraria aculeata,* with high Ellenberg L-values, had moderate cover (Table 4.1a). Their Ellenberg R-values resemble the pH-values found in 1966, with a pH-H_2O of 5.5 (soil layer 0-5 cm deep; Oostra 1968). The humicole species of the later succession stages such as *Cladonia glauca* and *C. chlorophaea* were not as well developed on the southern slope as they were on the western slope (Table 4.1a, b).

In 1990 the southern slope was dominated by tall graminoids with hardly any bare sand left (Figure 4.1a). The cover of graminoids and herbs (living plus dead) was more than 85% and much litter had accumulated. The abundance of graminoids in relation to herbs varied considerably over the slope: from 100% graminoids at the top to 15% at the foot; with 2% herbs at the top and 5% at the foot (data from PQs); very few lichens remained (Table 4.1a).

Directly after the spring fire in 1993, both graminoids and rosette plants re-occurred. The cover of ash and bare sand was high (Figure 4.1a). After two years the cover of ash had decreased rapidly, after only two to four years the cover of herbs, graminoids and litter had increased, and after three to eight years the plant cover (including standing dead material) remained at a constant high level with much litter. The abundance of graminoids in relation to herbs still varied considerably over the slope during those years, especially the four years (1993-1997) following the fire. This situation stabilized in the period 1998-2001: from 85% graminoids at the top to 20% at the foot; with 20% herbs both at the top and at the foot (data from the PQs). The total moss cover increased from zero in the first year after the fire, to 40% in the second year and reached 65% after six years (Figure 4.1a; Figure 4.2).

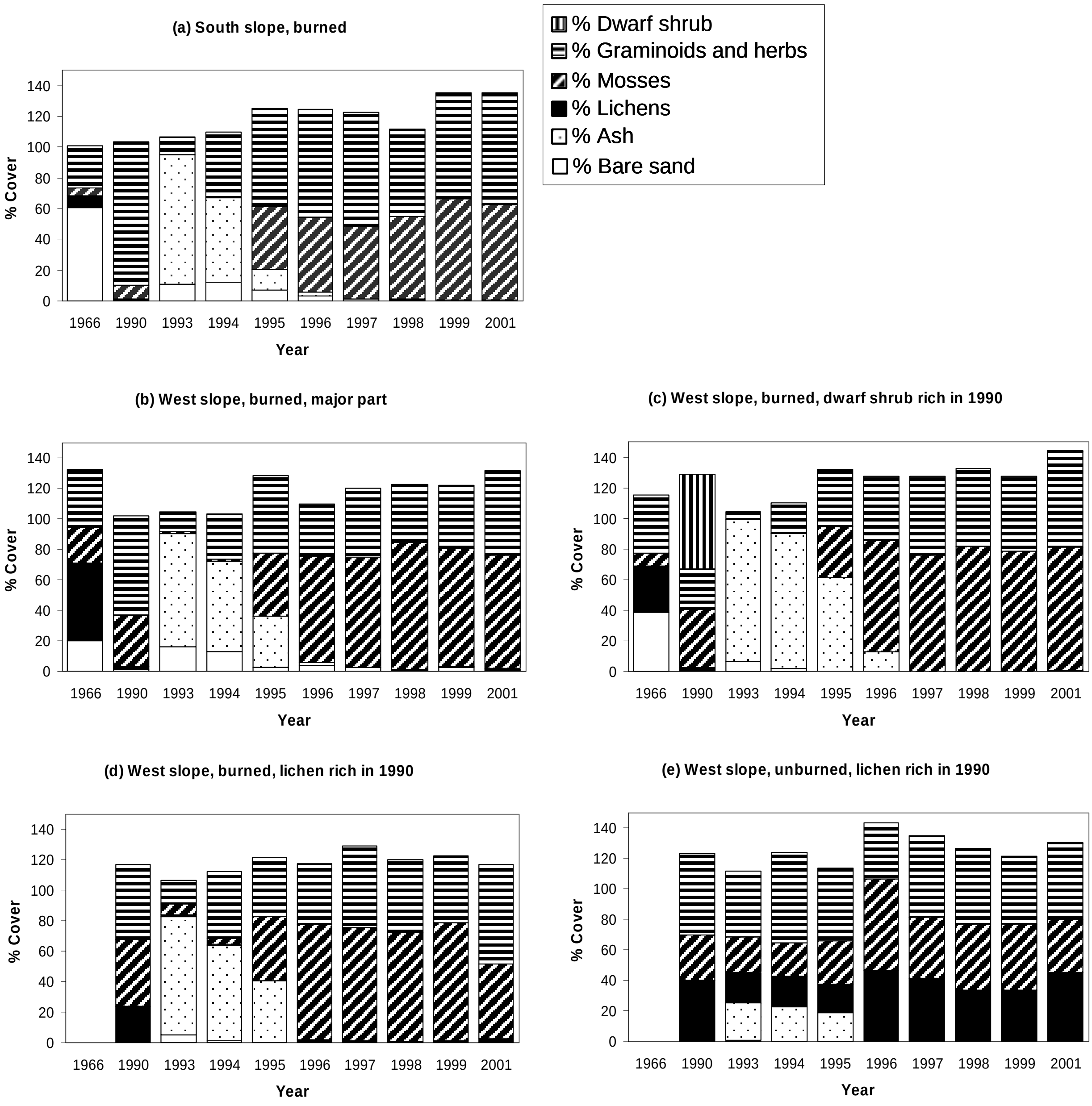

Figure 4.1. Changes over time in the cover of vegetation elements, bare sand and ash. a. Southern slope; b. Western slope, burned, major part; c. Western slope, burned, rich in dwarf-shrubs in 1990; d. Western slope, burned, lichen-rich in 1990; e. Western slope, unburned, lichen-rich in 1990.

Two lichen species were present three years after the fire (1996) and six species after five years. Only a minor increase in number of lichen species and cover was found during the following years (Table 4.1a).

4.3.2. Vegetation composition on the western slope

In 1966 the western slope was covered by a well developed VC, very rich in lichens with high cover and much bare sand (Figure 4.1b, c). Lichen species from the pioneer stage of the VC, such as *Cladonia foliacea*, *C. furcata* and *Cetraria aculeata*, had high cover. They were growing in locations exposed to full sunlight

(Table 4.1b). The humicole species of the later successional stages such as *C. glauca* and *C. chlorophaea* were growing abundantly on and between mosses (*Hypnum cupressiforme* and *Dicranum scoparium*), a substrate with a pH-H_2O of 4.8 (Oostra 1968). They were growing in well lit places, but also in partial shade. At that time only a few aero-hygrophytic species, such as the reindeer lichen *Cladina portentosa,* were present. The generally epiphytic lichens *Hypogymnia physodes*, *Platismatia glauca* and *Pseudevernia furfuracea*, were growing on sand and moss covered dune soil (Ketner-Oostra & Sˇkora 2004), a substrate with a pH-H_2O of 5.0 (Oostra 1968).

In 1990 the major part of this slope was dominated by tall graminoids with some herbs and mosses. The cover of lichens and bare sand was very small (Fig 1b). On the upper part of the slope (inclination 10°), an *Empetrum nigrum* heath developed, with much *D. scoparium* and few lichens (Figure 4.1c). At the foot of the slope the lichen cover was relatively high (Figure 4.1d, e).

Directly after the fire a high proportion of the studied blocks were covered by ash with some bare sand (Figure 4.1b-d). *Empetrum nigrum* on the upper part of the

Table 4.1. Change in lichen cover % 1966-2001. In 1966, means of 20 relevés (0.4 m x 0.4 m). **a**. On the southern slope, 1990-2001: means of six PQs (2 m x 2 m); **b.** On the western slope, 1990-2001: means of nine PQs.

	Light*	**R****	**Species**	**1966**	**1990**	**1993** (Fire)	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2001**
a. Southern slope													
P	9	4-8	*Cladonia foliacea*	6.4	0.1	-	-	-	-	-	-	0.1	0.1
	8	2-7	*Cetraria aculeata*	3.7	0.1	-	-	-	-	-	-	-	-
	6-8	3-5	*Cladonia furcata*	1.9	0.2	-	-	0.1	0.2	0.4	0.6	0.6	0.6
	Indiff.	1-3	*Trapeliopsis granulosa*	0.1	-	-	-	-	-	-	-	-	-
	6-8	5-7	*Cladonia scabriuscula*	-	-	-	-	-	-	-	0.1	0.1	0.5
	8	7	*Cladonia rangiformis*	-	-	-	-	-	-	-	-	+	+
H	7	2	*Cladonia glauca*	2.5	-	-	-	-	-	-	-	-	-
	7	2-3	*Cladonia chlorophaea*	1.7	-	-	-	-	-	0.1	0.1	0.1	0.3
	7	2	*Cladonia floerkeana*	1.6	-	-	-	-	-	-	-	-	-
	7	3-5	*Cladonia coccifera*	0.3	0.1	-	-	-	-	-	-	-	-
	Indiff.	2-3	*Cladonia ramulosa*	0.2	-	-	-	-	-	-	-	0.1	0.1
	8-9	2	*Placynthiella uliginosa*	-	-	-	-	-	-	+	+	-	-
	8	3	*Cladonia subulata*	-	-	-	-	-	-	-	+	+	+
A	7	1-5	*Cladina portentosa*	0.1	0.4	-	-	-	+	+	0.1	0.1	0.3
	8	1-5	*Cladina arbuscula*	0.3	-	-	-	-	-	-	-	-	-
E	7	3	*Hypogymnia physodes*	0.3	-	-	-	-	-	-		-	-
b. Western slope													
P	9	4-8	*Cladonia foliacea*	10.3	0.3	0.1	0.1	0.2	0.2	0.3	0.3	0.7	0.8
	6-8	3-5	*Cladonia furcata*	2.0	0.4	0.1	+	0.1	0.2	0.2	0.7	0.7	1.6
	8	2-7	*Cetraria aculeata*	2.7	-	+	-	+	-	+	-	+	-
	6-8	5-7	*Cladonia scabriuscula*	-	-	-	-	-	+	0.1	0.2	0.3	0.7
	9	5-7	*Cladonia humilis*	-	-	-	-	-	-	-	-	+	0.2
	8	7	*Cladonia rangiformis*	-	-	-	-	-	-	-	-	-	0.1
H	7	2	*Cladonia glauca*	16.2	-	-	-	-	-	-	-	-	-
	7	2-3	*Cladonia chlorophaea*	7.7	-	+	0.1	0.1	0.1	0.2	0.3	0.3	0.3
	7	3-5	*Cladonia coccifera*	3.3	0.3	-	-	-	-	+	+	0.1	0.1
	7	3	*Cladonia gracilis*	0.6	-	-	-	-	-	-	-	0.1	0.1
	8	3	*Cladonia subulata*	-	-	-	-	-	-	+	+	+	0.2
	7	2	*Cladonia floerkeana*	0.9	-	-	-	-	-	-	-	-	-
	Indif	2-3	*Cladonia ramulosa*	0.4	-	-	-	-	-	-	-	0.1	0.1
	8-9	2	*Placynthiella uliginosa*	0.1	-	-	-	-	-	-	-	-	-
A	7	1-5	*Cladina portentosa*	0.5	2.9	0.1	0.1	0.1	0.1	0.1	0.6	0.6	0.8
E	7	2-5	*Platismatia glauca*	6.1	-	-	-	-	-	-	-	-	-
	7	3	*Hypogymnia physodes*	2.1	-	-	-	-	-	-	+	-	-
	8	2	*Pseudevernia furfuracea*	0.2	-	-	-	-	-	-	-	-	-

P = Pioneer spp.; H = humicole spp.; A = Aero-hygrophytes; E = Epigeic epiphytes. *For Light and **Reaction (acidity) figures, see Methods.

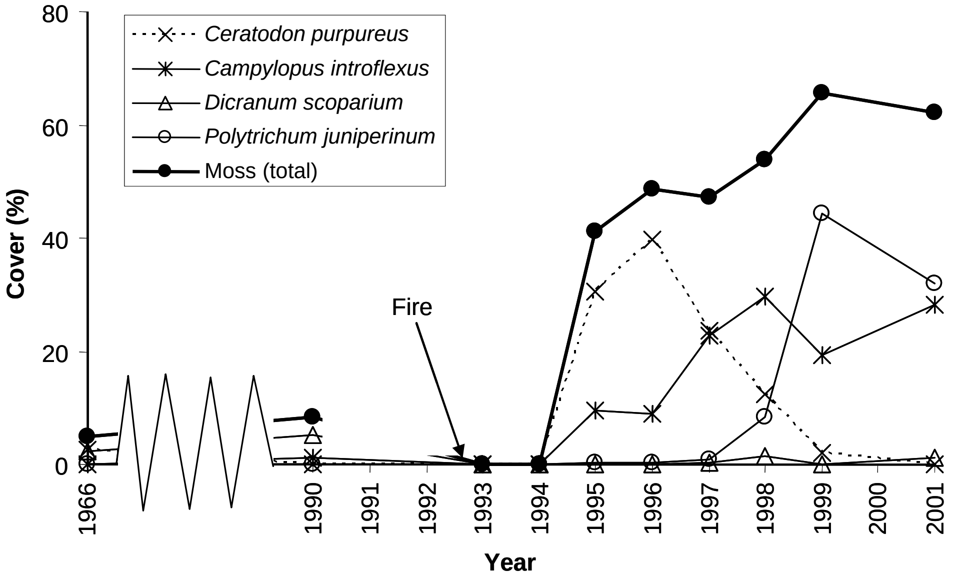

Figure 4.2. Changes in the cover of four moss species and total moss cover on the southern slope between 1966-2001. Mean cover of 24 blocks.

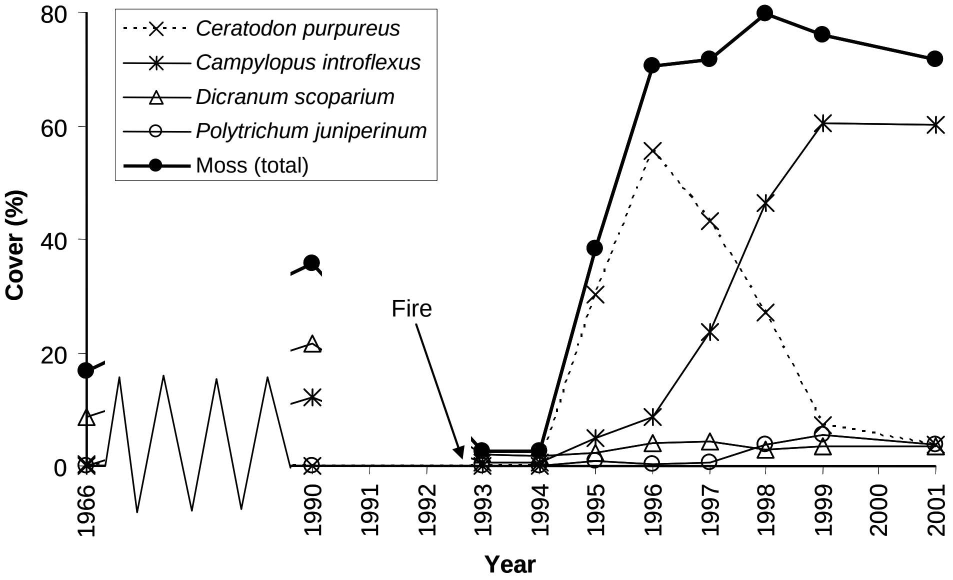

Figure 4.3. Changes in the cover of four moss species and total moss cover on the western slope between 1966-2001. Mean cover of 52 blocks.

slope did not reappear after the fire. In all burned blocks, the cover of higher plants (including standing dead material) and mosses quickly increased immediately after the fire, resulting in dominance in 2001, a build up of litter and very low abundance of lichens (Figure 4.1b-d). Only on the unburned lower slope (lichen-rich in 1990), mosses and higher plants remained at about the same level, while lichen cover remained high (Figure 4.1e). The moss increase (Figure 4.3) was partly different compared to the south slope (Figure 4.2).

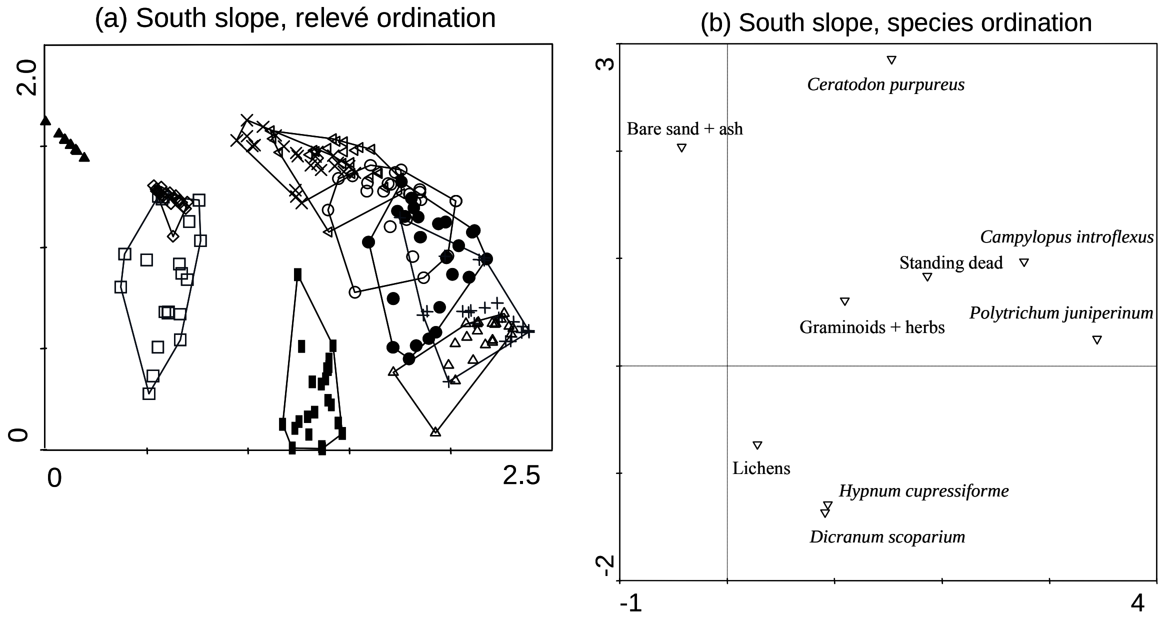

Figure 4.4. Axis 1 and 2 of a DCA ordinations of the blocks on the southern slope. Relevés from different years are enveloped separately. **a.** Relevés, burned; **b.** Species. The length of each axis was extended to allow all species to be displayed. For explanation of symbols, see Figure 5.

The lichens were slow to colonize after the fire. Five species occurred after three years, with *Cladonia foliacea* and *C. furcata* as the main pioneers, while eight species occurred after five years. The humicole species *C. chlorophaea* was found on burned stumps of *Ammophila arenaria*. Colonization by some species typical of subneutral sand such as *C. rangiformis* and *C. humilis* led to 11 species in 1999, probably the result of sand blowing in, while some increase in cover was apparent in 2001 (Table 4.1b). However, the total lichen cover of the studied blocks was still low in 2001.

4.3.3. Main direction of vegetation change

The main direction of vegetation change is visualized in the DCA ordination diagrams (Figures 4.4 and 4.5). The eigenvalues for the first two axes of the ordination for the southern slope are 0.28 and 0.18; the first species axis explains 37% and the cumulative variance of axes 1 and 2 is 60%. For the western slope the eigenvalues are 0.37 and 0.28 and the cumulative variance amounts to 29% (axis 1) and 51% (axes 1 and 2).

On the southern slope (Figure 4.4a) the vegetation changes from very open in the upper left part of the diagram (after the fire in 1993), to increasingly closed, dominated by mosses and higher plants, in the right lower part. The grass and moss increase from 1966 to 1990 is clearly indicated by the shift in the relevés in the lower right direction, followed by a strong shift to the utmost left upper part after the fire. Subsequently, the direction of change, leading again to increased cover of mosses, herbs and graminoids, can clearly be followed as the relevés gradually shift downward and in a right direction. The main difference compared to 1990 is a

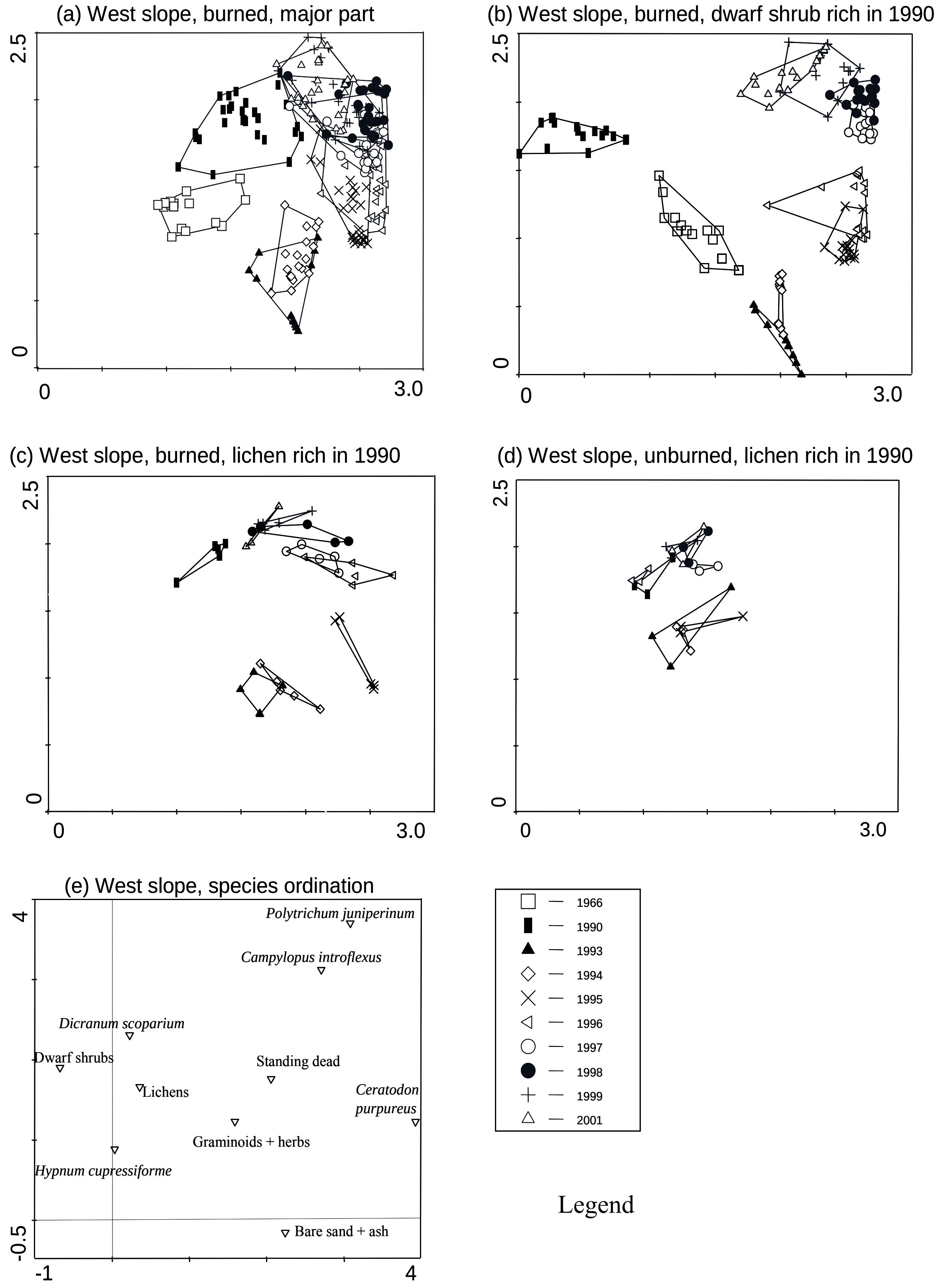

Figure 4.5. Axis 1 and 2 of DCA ordinations of the blocks on the western slope. The same ordination of relevés is copied four times to show successional pathways in different parts of the slope. Relevés from different years are outlined separately.

much higher moss cover in 2001 (Figure 4.1a). The successive dominance of the three moss species *C. purpureus*, *C. introflexus* and *P. juniperinum* (see Figure 4.2) can also be deduced from Figure 4.4b.

The vegetation change in the more heterogeneous western slope is shown in four DCA ordination diagrams in which the different initial stages are presented (Figure 4.5a-d). The gradient from open (after the fire in 1993) to closed vegetation is now from lower right to top right. On the burned, major part of the slope (Figure 4.5a) the vegetation shift was very similar to that on the southern slope. The same applies for the burned lichen-rich vegetation at the foot of the western slope. The relevés follow the same successional pathway as on the southern slope but are more compressed. This is because of the presence of dwarf-shrubs while the southern slope lacked a dwarf-shrub stage. The dwarf-shrub vegetation present in 1990 also developed from the lichen-rich open vegetation in 1966. After burning, however, the succession followed the same path as on the burned, major part of the slope and dwarf-shrubs (*Empetrum*) did not reappear (Figure 4.5b). In the burned part at the foot of the slope, lichen-rich in 1990 (Figure 4.5c), the vegetation composition followed the same route as that of the burned, major part of the slope (Figure 4.5a), not returning to the composition of 1990. The unburned blocks at the foot of the slope that were lichen-rich in 1990 (Figure 4.5d) remained little changed, in the upper part of the diagram. Due to ash blown in, a slight downward shift can be seen for 1993, 1994 and 1995. The sequential dominance of *C. purpureus* and *C. introflexus*, and the relatively late increase of *P. juniperinum* (Figure 4.3), are indicated by their positions in the species ordination (Figure 4.5e).

4.4. Discussion

Between 1966 and 1990, both slopes of RD developed from a lichen-rich Violo-Corynephoretum into grassland dominated by tall graminoids. The upper part of the western slope changed into a dwarf-shrub heath with *Empetrum nigrum* (Ketner-Oostra & Sýkora 2000). In the bottom zone of that slope, the aero-hygrophytic *Cladina portentosa* remained partly unburned between the tall graminoids, probably due to higher availability of capillary water (Westhoff 1947).

4.4.1. Vegetation recovery after fire

During the first years after the fire, some of the mineral ions originating from the burned plant material-were obviously used for the regrowth of both vascular plants and mosses. However, part of the ash might have been blown off and the free minerals lost through leaching. A similar vegetation as before the fire became established, partly from surviving perennial plant remains, partly from nearby areas of unburned vegetation, in accordance with the findings of Vestergaard & Alstrup (2001) in calcium-poor Jutland dunes. However, the development of vegetation during later years was most probably a result of the same environmental factors that promoted dominance of graminoids before the fire, 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 *Ammophila arenaria* (de Boer et al. 1998) and (3) litter decomposition and soil formation during succession (Veer & Kooijman 1997; Kooijman & Besse 2002).

4.4.2. Moss increase after fire

The total quantity of mosses in 1966 and 1990 was low compared with the rapid increase in moss cover after the fire (Figure 4.1a, b). The moss *Ceratodon purpureus*, a species strongly favoured by fire, reached a peak three years after the fire (southern slope 40%; western slope 55%). This moss is among the early colonizers in post-fire succession in heathland in Brittany (Gloaguen 1990) due to its wide diaspore dispersion (Clément & Touffet 1990). In contrast, mosses had a subordinate role in the recovery after fire in Jutland dunes (Vestergaard & Alstrup 2001). *Campylopus introflexus* gradually took over as succession proceeded. Later in the succession the habitat on the southern slope appeared to be particularly suitable for the xerophytic moss *P. juniperinum*. It increased from < 1% in 1995 to 45% in 1999, with a simultaneous decrease in cover of *C. introflexus* to 20%. *C. introflexus* is an alien moss species in this ecosystem (van der Meulen et al. 1987), characteristic of acid calcium-poor sand. The interference of this moss with the normal succession in acid dune grassland has been shown to be the result of the high asexual reproductive effort at an early succession stage, which leads to dominance of this invasive species and impedes lichen establishment (Biermann 1996). Likewise, on flat and undulating inland dunes, *C. introflexus* had the same cover before, and five years after, a wildfire (in 1995) and only a few lichens colonized (Ketner-Oostra 2002). This was due to the much higher N deposition at the Veluwe (Bleeker & Erisman 1996). However, *C. introflexus* has been shown to be at a disadvantage in the more extreme microclimate on southern slopes. In these inland dunes the xerophytic moss *Polytrichum piliferum* increased, while *P. juniperinum* increased in the studied coastal dunes, especially on the southern slope (Figure 4.2).

4.4.3. Limited lichen recolonization

We found a slow and very limited re-establishment by lichens after the wildfire, especially on the southern slope. We found no living fragments indicating that our wildfire must have been very intense. Some lichen species had established on the western slope (11 species in total), but their total cover was very low (< 2 % after eight years, 2001). This can be compared with a mean cover of 42% in the original ‘grey dunes’ of 1966. Lichens here are dependent on open vegetation with much bare sand. In our research area lichen colonization was probably limited by the fast colonizer *C. purpureus*, soon followed by *C. introflexus*. An important factor was the quick regrowth of vascular plants (graminoids and rosette plants), which has previously been shown to be caused by high N deposition in calcium poor dune ecosystems (Kooijman et al. 1998).

Lichens require sufficient light for photosynthesis and growth. This was seen in 1966 with the presence of lichens with high Ellenberg L-values for plants in full sunlight (Table 4.1). The decrease of lichen richness in the Terschelling dunes since the 1970s has been connected to the high biomass of graminoids and herbs in the former lichen-rich VC (van der Meulen et al. 1996; Ketner-Oostra & Sýkora 2004). Light reaching the soil was shown to be substantially limited. In 1992, in grass-dominated VC only 25% of the light was found to reach the soil compared with 77% in reference vegetation having lower abundance of grasses; in a VC in 1966 light passage must have been much higher (van der Meulen et al. 1996). The more constant humid microclimate in tall grasslands might also reduce lichen growth. The poikilohydric uptake and loss of water in lichens are connected with the passive accumulation of macronutrients through alternating periods of drying out and remoistening (Nash 1996). The open dry dune grasslands of 1966 with short grasses such as *C. canescens* and lichens, may have been warm and moist after rain, but were usually dry again after one day of sunny weather. The main difference with the tall dense graminoid dune vegetation of the 1990s is that this recent grassland maintains a moist microclimate over a much longer period of time (Stoutjesdijk & Barkman 1992).

4.5. Conclusion

Our results show clearly that fire alone is not sufficient for management aimed at restoration of lichen-rich dune grasslands in calcium-poor coastal dunes, influenced by a relatively high N deposition. At the end of the study period (2001), the vegetation composition in the burned blocks was still quite different from the original composition in 1966. Even the *Cladina* mats, present at the foot of the western slope in 1990, did not recover after the fire. Additional measures are recommended, such as large-scale clearing of the burned vegetation to the mineral soil layer and promoting sand to be blown in. The sand will physically harm and dry out the remaining mosses and *C. introflexus* especially has been shown to be sensitive to such treatment (Ketner-Oostra & Sýkora 2000; Ketner-Oostra 2002). Neutral or sub-neutral sand might be blown in from foredunes, from reactivated blowouts, or artificially brought to the site. We conclude that this is especially important for the colonization and maintenance of lichen vegetation in the first stages of the VC in these calcium-poor Terschelling dunes, based on earlier research (Ketner-Oostra & Sýkora 2000; Ketner-Oostra 2001).

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Chapter 5

WILL WE LOSE THE LAST ACTIVE INLAND DRIFT SANDS OF WESTERN EUROPE? THE ORIGIN AND DEVELOPMENT OF THE INLAND DRIFT-SAND ECOTYPE IN THE NETHERLANDS

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Photo page 91: Southern part of the drift-sand area Kootwijkerzand (Aerial photo © ESW group Wageningen University, 2005).

Chapter 5. Will we lose the last active inland drift sands of Western Europe? The origin and development of the inland drift-sand ecotype in the Netherlands

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Abstract

In the Netherlands the total active drift-sand area has been declining rapidly during the last 50 years. To preserve the inland drift sands, it is necessary to understand its origin and development and the role of human activity in this semi-natural ecotype. The objective of this literature review is to describe the development of the drift-sand ecotopes, to explain the rapid decline of the active drift sands, and to develop a management strategy for the remaining active drift sands.

Inland drift-sand landscapes are relatively young landscapes of Holocene age. They often occur as oval-shaped cells with a length of 1.5 to over 6 km in the direction of the prevailing wind. These cells presumably represent reactivated deposits of Younger Cover Sands. Large-scale erosion events in combination with human activity suppressed the development of vegetation. After the change in land use in the first half of the 20th century in which most of the drift sands were re-afforested, the vegetation succession started to show a progressive development. In this stage inland drift-sand ecotopes developed in most of the remaining drift sands with all forms of the typical succession stages from bare sand to forest. The rate at which this development took place mainly depended on the geomorphological development stage of the area, the area size and human activity.

Since the 1960s the increased nitrogen deposition has accelerated the vegetation succession, not only resulting in a further decline of the drift sands, but also in a loss of the fragile balance between the different ecotopes and loss of its typical habitants like the Tawny Pipit (Aves) and the Tree Grayling (Lepidoptera).

Most drift-sand vegetation and fauna need the presence of bare sand nearby and a certain level of erosion activity to survive. To preserve the drift-sand ecotype, it is therefore recommended to keep the area affected by erosion sufficiently large (process management). In the meantime one should also ‘maintain’ or increase the wind force in the drift-sand area by suppressing the growth of high vegetation and removing trees, which form a wind barrier. In areas which are less suitable for reactivation, one could restore the mosaic vegetation by removing the vegetation on a limited scale (pattern management). More research is needed to develop a more balanced management strategy and to develop a management tool for the managers of inland drift sands. Also the role of the increased nitrogen deposition in the regeneration process needs further investigation in order to find an effective way to suppress its effect. The development of management strategies for the Dutch inland drift sands might be of great value to drift-sand areas in Western Europe where nature conservationists start to show more interest in the restoration of former drift-sand areas.

Key words: Drift-sand ecotype, Nature conservation, the Netherlands, Wind erosion.

5.1. Introduction

In today's Europe, the interest in the inland drift-sand landscape is on the rise. The inland drift sands are appreciated for their unique landscape, their cultural/historical value and their unique flora and fauna. They are also appreciated for recreational purposes.

Inland drift sands, also known as drift sands, form a separate group within aeolian forms and deposits and can be defined as (Koster 2005): aeolian deposits, irrespective of their form as sheets or dunes, resulting from reactivation of sandy deposits by human impact during the late Holocene. In this they differ from other aeolian forms such as coastal dunes or coastal drift sands, river dunes or cover sands.

The extent of inland drift sands in northwest Europe alone has been estimated at 3000-4000 km^2 (Castel et al. 1989), but outside the Netherlands, active drift-sand landscapes have almost completely disappeared. With this landscape, several Red-list species such as the Tawny Pipit (Aves: *Anthus campestris*) become extinct, along with various lichens (Bal et al. 2001). In the Netherlands several active drift-sand areas have been saved from the large re-forestation projects and officially turned into nature reserves. However without a certain level of erosion activity, these 'active' drift sands evolve in a forest.

To preserve these drift sands simply by buying them and turning them into a protected area is therefore not enough. All kinds of negative external influences may influence their existence. For the preservation of the present biodiversity or the re-entry of lost species, the natural differentiating processes should first be restored. This new nature approach is focused on management of systems (processes). The question is whether the inland drifts-sand ecotype can be preserved in a sustainable way by this approach. In some cases large-scale reactivation of drift-sand areas by removing all the vegetation including the topsoil has led to a loss of the for drift sands characteristic dunes. To be able to manage these drift sands in a more sustainable way it is necessary to know how they have been developed. What are the stages in the development of the present drift-sand ecotype, and what are today's main bottlenecks? For a better management of the remaining active drift-sand areas and reactivation strategies, a more multi-disciplinary process-oriented approach is needed.

This paper presents an overview of the development of the inland drift sands in the Netherlands. First a description is given of the origin and development of inland drift sands in the Netherlands before 1960 (Section 5.2). Section 5.3 describes the rapid decline of the remaining active drift sands in the Netherlands after 1960 and the role of the increased atmospheric nitrogen deposition and the introduction of invasive species in the drift-sand ecotopes in this.

Section 'Discussion and conclusions' (Section 5.4) discusses the consequences of these developments for the management of the drift sands and proposes a few topics for further research.

5.2. Origin and development of inland drift-sand ecotopes in the Netherlands

5.2.1. Late glacial dune fields and cover sands

Drift sands are mainly derived from late-Pleistocene sands. In Europe during parts of the Last Glacial, cold desert-like conditions prevailed. Extensive aeolian deposits were formed in the 'European Sand Belt' (Koster 1978; Castel et al. 1989) which extends from the north-western and central European lowlands, to the Polish-Russian border and beyond. Small areas with similar deposits are found in England most of them in East Anglia (Castel et al. 1989; Riksen & de Graaff 2001). Koster (2005) recognizes various types of aeolian forms and deposits, based on a combination of geomorphology, sediment and depositional environment. Most important are the *cover sands* and *dune fields* (mainly river dunes).

From west to east across the European lowlands the proportion of cover sands to dune fields changes; cover sands are found mainly in the western part whereas dune fields predominate in the east (Koster 2005). Within the cover sand region, a distinction is made between the almost level 'Older Cover Sand', which occasionally contains loamy laminae, and the undulating to rolling 'Younger Cover Sand' in which loam is absent (Pannekoek 1956). The more pronounced relief of the younger sands is attributed to the trapping of sand in the vegetation, which followed the warming-up of the climate at the transition from the Pleistocene to the Holocene. Cover sands are commonly fine-grained with a modal grain size between 105 and 210 µm (Koster 2005).

During the Holocene, the aeolian sands were gradually covered with forests. A brown forest soil developed in the upper part of the sands. Starting with the settlement of farmers in the Neolithic Age, about 5000 years ago, the forests were destroyed and replaced by heath land. The soil profile changed to a heath podzol.

5.2.2. Inland drift sands

Drift-sand landscapes are relative young landscapes of Holocene age. Several theories on the initiation of the sand drifts have been proposed. The most popular theories attribute drift sands to agricultural practices, roads and cattle/sheep drifts or in some cases to the falling water table (Slicher van Bath 1977). Heidinga (1984) found indications that the formation of the first drift sands coincides with periods of extreme droughts and heavy winds during the 10th century AD, and that the drift sands developed on bare arable fields. Their main expansion however, took place after 1150 AD (Koster 2005) after large-scale deforestation by men changing the landscape from a nearly closed to an open landscape with mainly heath land.

The communal heath lands were used for heath cutting to manure the arable fields. Heather sods together with sheep dung was used to manure the arable fields. For 1 ha of arable land a sod digging area of about 3 to 7 ha was needed. The great need for heather sods sometimes created large bare sandy surfaces, vulnerable to wind erosion.

Apart from sod digging, this agricultural practice needed a large area of heath land for grazing. Grazing and burning the heath lands also contributed significantly to the development of drift sands by keeping the landscape open and making the topsoil vulnerable to wind erosion.

Another theory links the drift sands with roads and cattle/sheep drifts, which in the loose sands were always unstable and often had to be shifted as Tesch et al. (1926) described for the Veluwe. This theory is more popular in Germany, because heath cutting for agricultural purposes was not practiced east of Schleswig Holstein (Pape 1970). One of the few examples in the Netherlands is the recently discovered road of Late Bronze Age/Early Iron Age across the heath in SE North Brabant near the Belgian border (van den Ancker & Jungerius 2003).

Although deforestation, agricultural practices, roads and cattle/sheep drifts may have triggered their formation and maintained their activity, recent research by Koomen et al. (2004) points to a geomorphological control of the drift sands. They often occur as oval-shaped cells with a length of 1.5 to over 6 km in the direction of the prevailing south-westerly wind. These cells presumably represent reactivated deposits of the Younger Cover Sands, which are more sensitive to wind erosion than the Older Cover Sands due to their stronger relief and low loam content (Koomen et al. 2004). The structure within the cells shows a fairly regular pattern. At the south-west end the original cover sand morphology is replaced by a deflation plain in the cover sand, dotted with isolated nabkhas (dunes of drift sand formed around plants). Towards the north-east the deflation plain expands due to the gradual erosion of the nabkhas and the formation of vegetated parabolic dunes. This part is still active in the large sand drift areas of the Netherlands. Scattered remnant knobs, so-called 'forts', testify to the former pattern of these nabkhas. The wind accumulates the drift sand in a wide zone around the deflation plain. Here parabolic dunes can develop due to erosion at the windward side of the deposits in combination with deposition at the lee side of the erosion dune. The lithology and morphogenesis of the inland drift sands is well described by Castel et al. (1989).

Koomen et al. (2004) found that all these occurrences have in common that they hardly show any change in outline in the 200 years that reliable topographic maps are available. The main period of aeolian activity as the dominant landscape differentiating process apparently took place earlier.

However, once the wind got a grip on the bare sand these spots easily expanded during extreme erosion events, causing the deposition of large quantities of poor cover sand in the surrounding vegetation. Locations where the vegetation died or was completely covered by the sand also became vulnerable to wind erosion. Hereafter the interaction between large scale wind erosion activity, vegetation development and human activity played a more dominant role in their further development. The number of documents between 1532 and 1855 in which the government speaks about the problems caused by wind erosion or measures to control the drift sands as listed by Tesch et al. (1926), indicate periods of relative low erosion activity followed by periods with increased wind erosion damage. It seems that only severe storms of high intensity and duration can generate sufficient sediment transport into the vegetated zones adjacent to the bare sand. Under the given land use in combination the openness of the landscape, the large area bare sand and an extreme micro-climate, the erosion risk remained high. In this situation the first vegetation development was easily suppressed during the periods with high erosion activity as schematically presented by Figure 5.1.

This development changed with the major land use changes, which started in the second half of the 19th century. With the introduction of fertilizers, the collapse of the wool industry and the increased demand for wood for the mine industry it became interesting for the Dutch government to invest in the afforestation of the drift sands. Additionally this would reduce the off-site damage on community properties, e.g. farm land, settlements and roads, caused during the extreme wind erosion events. Earlier attempts to control the drift sands had no or little effect due to a lack of neither economical benefit by the government nor financial benefits for the local farmers. In the Netherlands, about 60 km^2 of the original drift-sand area still existed in the mid-1960s (Bakker et al. 2003). These 60 km^2 have been saved for their unique landscape value, or for recreation or military use, like Aekingerzand in Drenthe, Kootwijkerzand and Harskamperzand at the Veluwe, and the Loonse en Drunense Duinen in North Brabant. Figure 5.2 shows the largest remaining active drift-sand areas in the Netherlands.

5.2.3. Effects of the land use changes on the further development of the drift sands

The land use change, which took place in the period between 1850 and 1960, had a major effect on the development of the remaining active drift sands. These effects were a direct corollary of:

1. The afforestation; and
2. The change in human activity in the remaining drift-sand areas: activities that disturbed the vegetation growth and/or the soil surface.

The effects of re-forestation

Since the late 19th century most drift-sand areas in the Netherlands were reforested successfully mainly with an exotic pine species Scottish pine (*Pinus sylvestris*), as

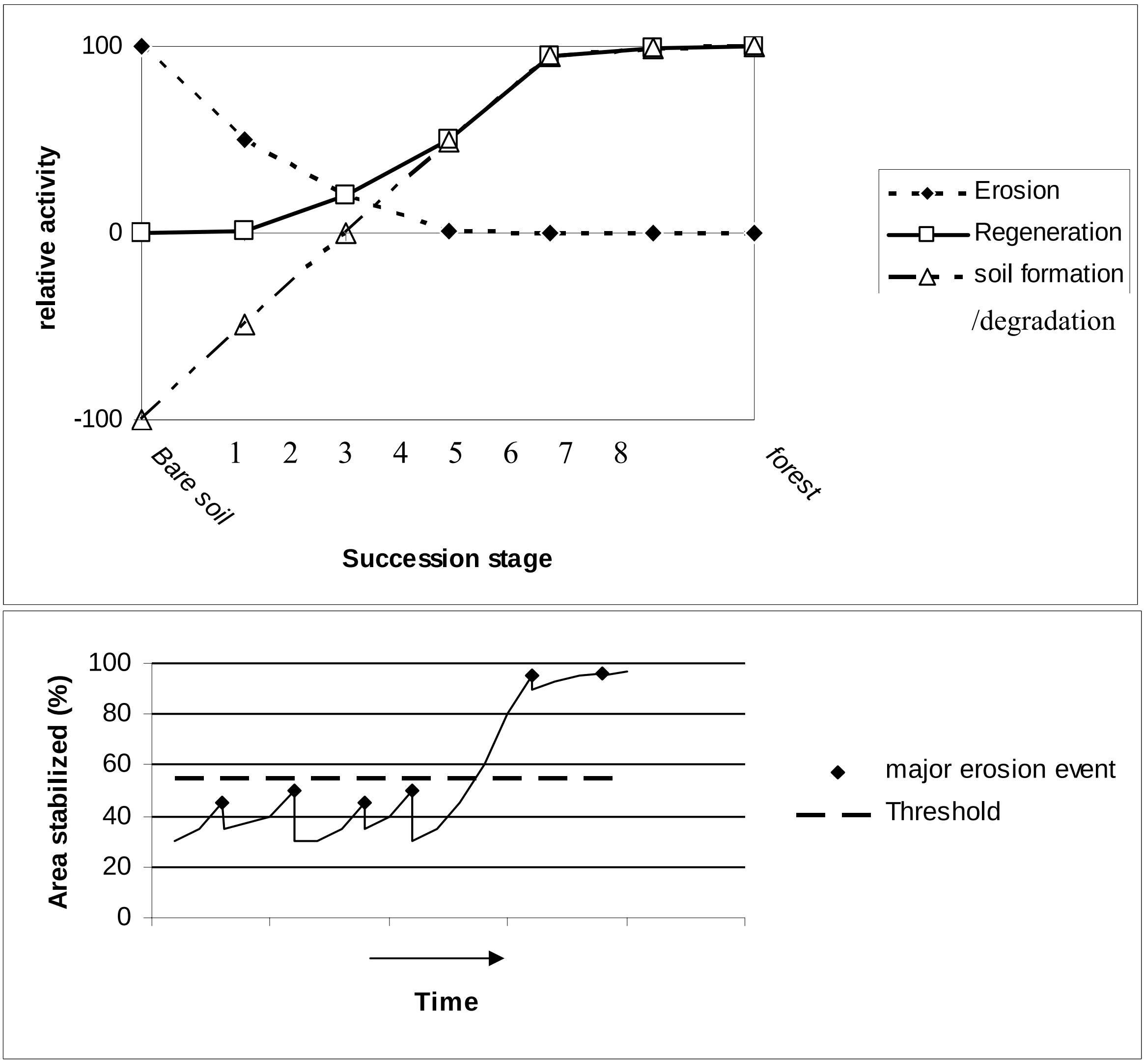


Figure 5.1. Schematically representation of the interaction between soil degradation caused by wind erosion and regeneration by vegetation development on drift sands. Top: Relation succession stage and relative activity of the different processes. Bottom: Role of wind erosion at landscape level: When the area covered with vegetation exceeds the threshold the effect of the extreme wind erosion events will become too small to have a significant influence on the landscape development.

in the Veluwe, Brabant and Drenthe (Tesch et al. 1926; Schimmel 1975; Castel al. 1989). As a result the remaining drift-sand areas are small compared to the size they had before re-forestation as illustrated by Figure 5.3. for Kootwijkerzand. The re-forestation has changed the landscape from open into closed or half-open. This reduced the average wind velocities in these landscapes, thereby diminishing the wind's erosive force. As a consequence wind activity in the zones close to the forest is low, and regeneration is not seriously hampered. In these zones vegetation and algae develop rapidly and inhibit wind erosion. The seed of *P. sylvestris* (Scottish pine) will easily geminate and survive. These seedlings grow fast and can form a closed forest within a few decades. Schimmel (1975) found for the drift-sand area

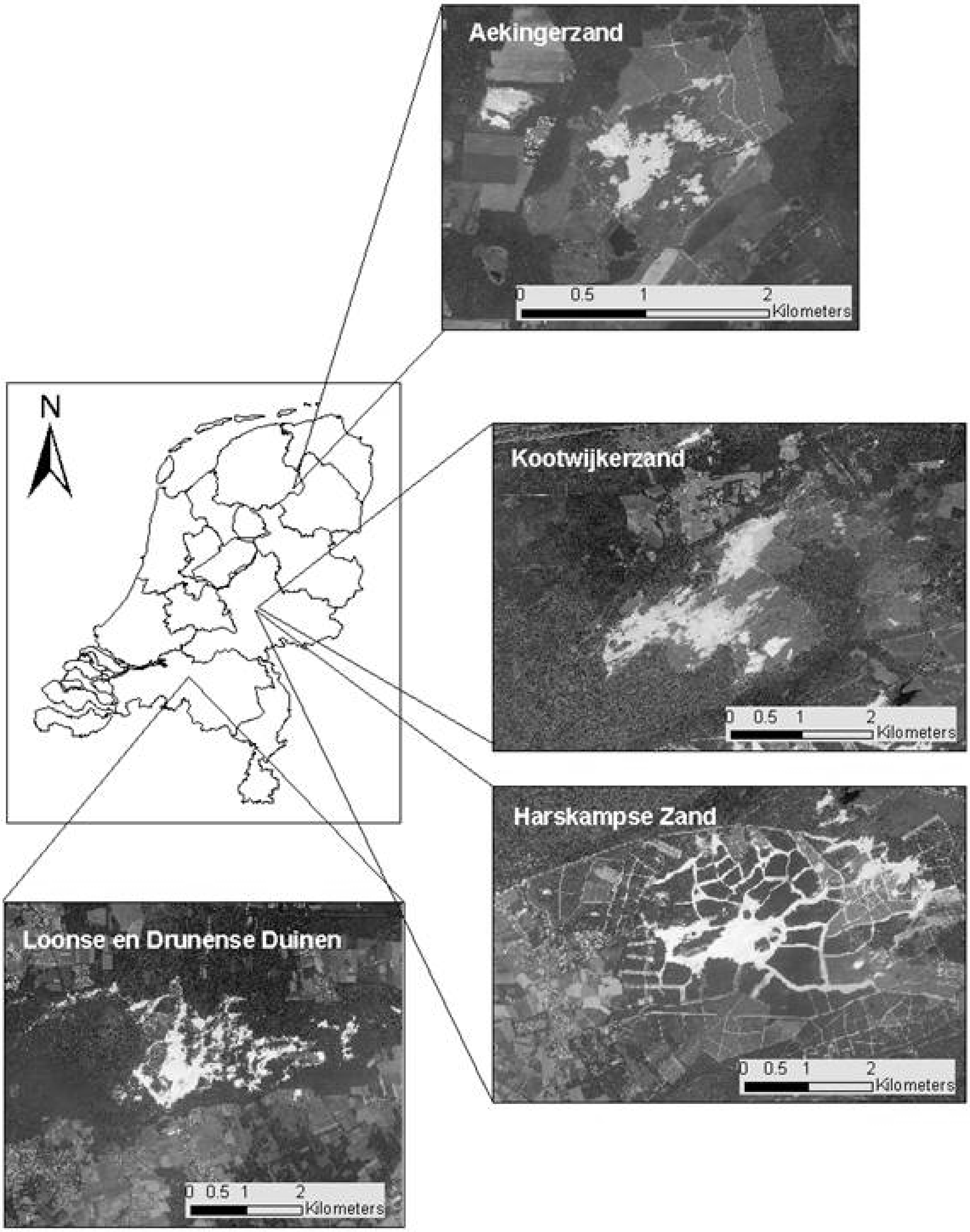


Figure 5.2. Major active drift-sand areas in the Netherlands (aerial photograph: © Eurosense, 2003).

Harskamperzand (the Veluwe, the Netherlands) that between 1950 and 1973 the area under vegetation had increased by 70%, with mainly *P. sylvestris*.

With the forestation of large parts of the drift-sand areas and their surrounding regions, the remaining active areas became spatially fixed and could no longer in line with with the drift-sand structure as described in Section 5.2.2.

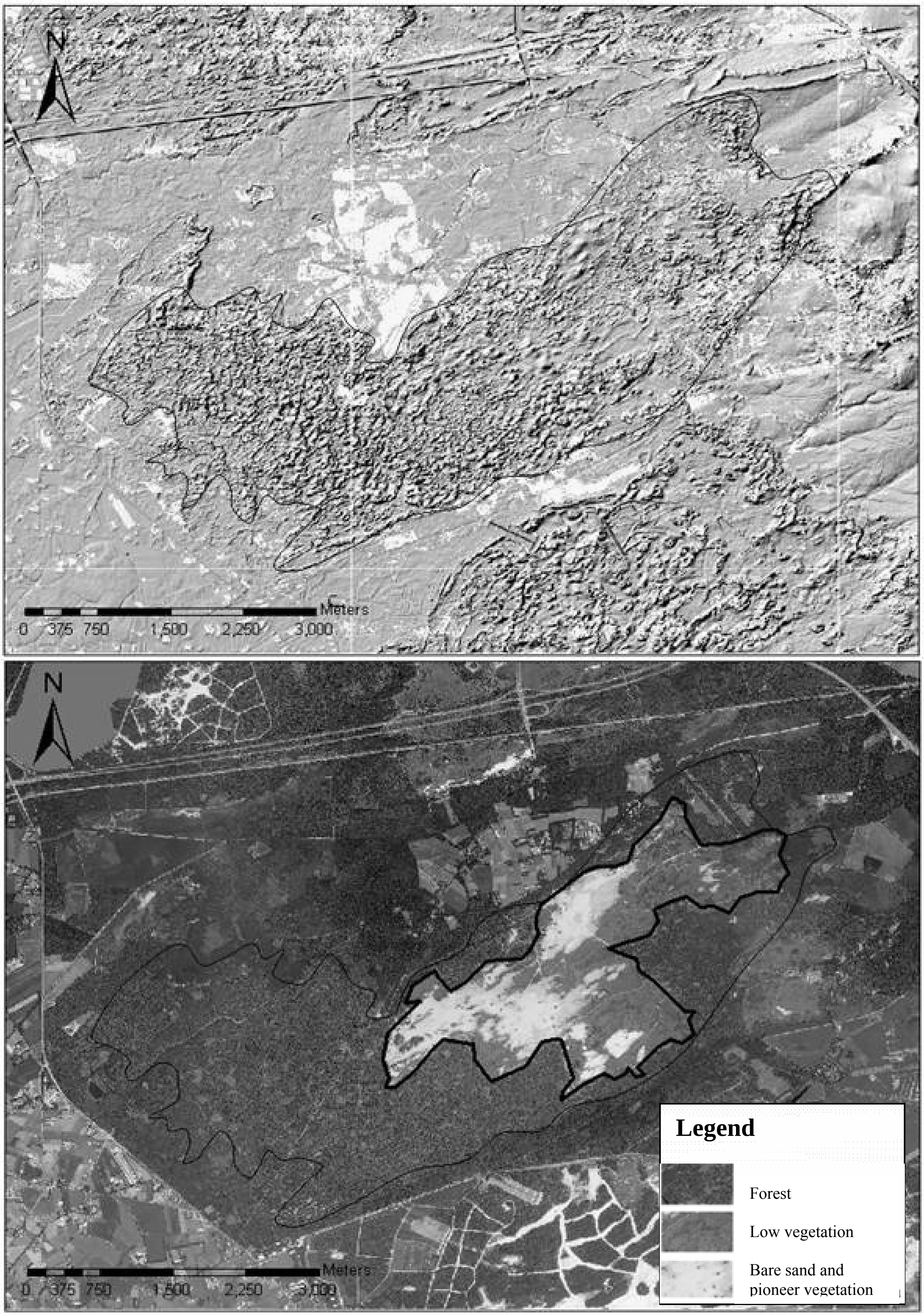


Figure 5.3 Top: Original size drift-sand area Kootwijkerzand based on relief shaded model (Source: AGI-ITC Rijkswaterstaat 2004). Bottom: Remaining active drift-sand area Kootwijkerzand in 2003 (aerial photograph: © Eurosense, 2003).

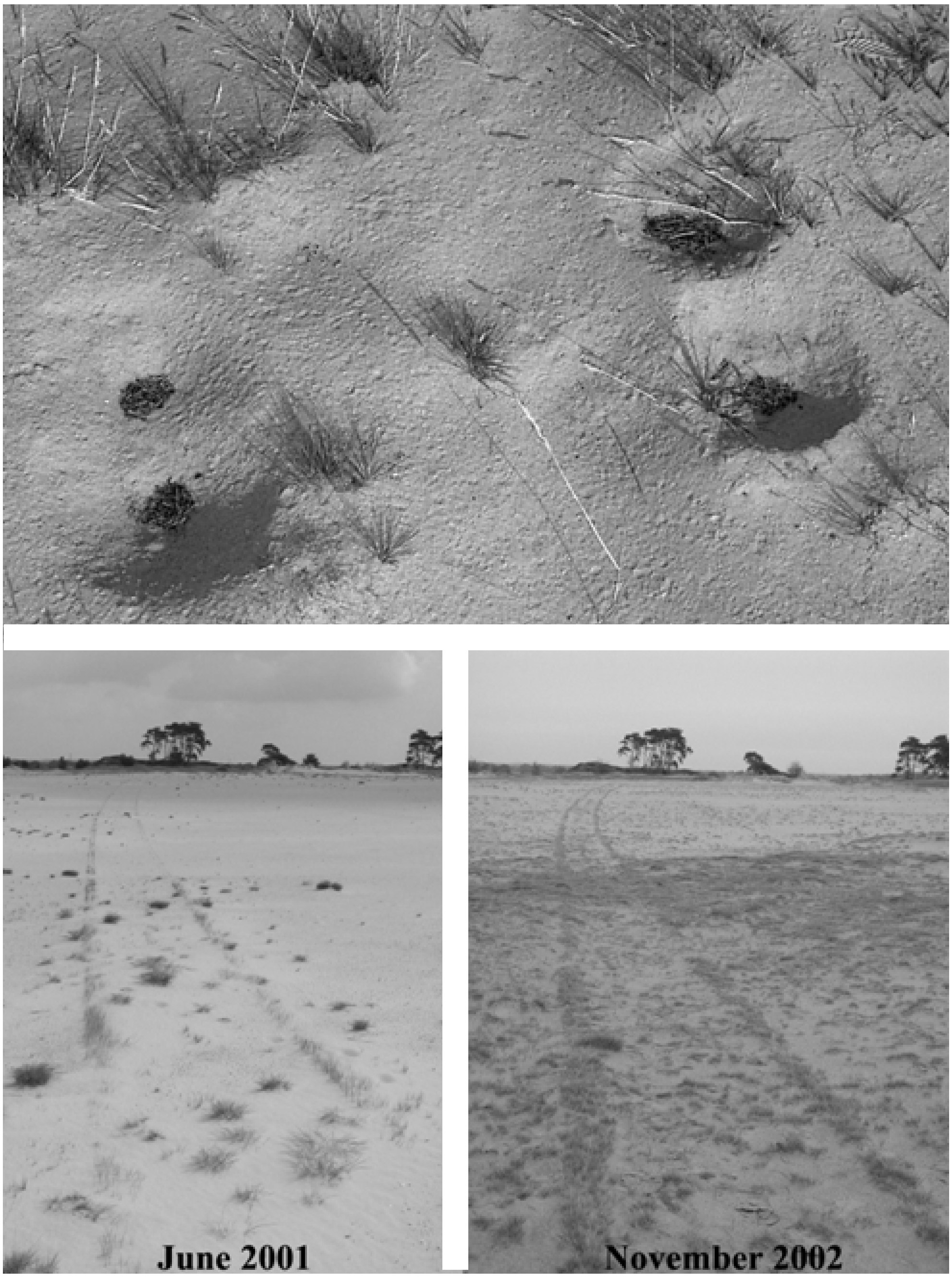


Figure 5.4. Effect of footprints and tracks on vegetation development. Top: Organic material trapped in footprints. Bottom left: Vegetation developed in car tracks have formed vegetated ridges. Bottom right: 17 months later: rapid vegetation development due to lack of erosion activity.

Wind erosion was thus reduced to a local process, and the fine sand could no longer be transported over long distances. Drift sand that is trapped in the forest's borders is usually no longer available for subsequent wind erosion because of the sheltering effect caused by the forest. In the deflation zone, on the other hand, the increase in coarse material at the surface can form a non-erodible desert pavement, or due to the lowering of the surface the ground water table (or another non-erodible geological layer) may be reached so that wind erosion no longer occurs.

Furthermore, the forest at the border of the drift-sand areas inhibits the formation of new sources for deflation. Under these conditions wind erosion activity is low, and the natural regeneration of these soils can take place in more or less undisturbed conditions. Sandblasting, burying and blowing out of vegetation no longer take place at a sufficiently large scale and a sufficiently short time interval. No new dunes are formed in the zones of deposition due to the lack of a sufficient amount of sand transport.

Change in land-use

The abolition of communal land use in the 19th century (van den Bergh 2004) was an important intervention in the drift-sand areas of the Veluwe (central Netherlands). The large-scale communal landscape was reclaimed and transformed into many small 'private' plots, each bordered by hedges to delimit property and to control cattle (Staring 1862). Together with the introduction of fertilizers and the collapse of the wool industry at the end of the 19th century agricultural practices like intensive grazing, burning heath lands and collecting heather sods to manure the arable fields, slowly disappeared. As a consequence no new highly erodible hotspots could develop from where new deflation plains could grow into larger drift-sand areas, and sheep and cattle flocks no longer crossed the drift-sand areas.

Table 5.1. Number of higher plants, mosses and lichens in eight succession phases (vegetation type 1-8) of drift-sand vegetation at the Kootwijkerzand in 1993 (after: Masselink 1994; Ketner-Oostra 1994a, b; Ketner-Oostra & Huijsman 1998).

Vegetation type	**Description**	**Number of**			**Vegetation cover (%)***
		Higher plants	**Mosses**	**Lichens**	
0	No vegetation	0	0	0	0
1	Patches of pioneer grasses	5	0	0	< 5
2	Fixation of bare sand by *Corynephorus. canescens* and green algae	2	1	0	50 – 80
3	Fixation as in type 2, and also by mosses	5	1	0	40 – 75
4	Moss carpets, partly covered by algae (*Gloeocystis polydermatica*)	5	2	0	70 - 100
5	Dying moss carpets through ageing and effects of covering by algae	7	5	11	70 - 100
6	Lichen growth on partly dead moss carpets	7	2	20	90 - 100
7	Species-rich lichen vegetation, including reindeer lichens	9	7	18	90 - 100
8	Mosaic vegetation of drift-sand vegetation with heath (*Calluna vulgaris*) including *Juniperus communis*	11	5	21	90 - 100

* The actual vegetation cover varies between the different seasons.

New types of land use, particularly recreation and military use came instead. Land-use types as recreation and military use may positively or negatively affect the development of drift sands, depending on their frequency and intensity. Only intensive tread will keep the vegetation away. Extensive use will result in footmarks or tracks which trap organic matter and seeds. On these spots new vegetation develops and reduces the erosion activity (see Figure 5.4). A disadvantage of intensive tread by recreation or military activity is the disturbance it will cause for the fauna, especially during the breeding season.

5.2.4 The development of the drift-sand ecotopes

Due to these changes in land use, which led in most cases to a reduction of soil degradation caused by the disturbance by wind erosion and /or human activity, natural regeneration process became the more dominant process in the remaining open drift sands. As result a clear distinction can be made in the present Dutch drift-sand areas between zones of a different vegetation composition. In general eight types (Table 6.1), which represent the succession stages from bare sand to the development of heath, can be distinguished. The presence of all these stages seems to be of importance for the typical drift-sand fauna.

5.2.4.1. Natural succession

The bare (moving) sand is generally very poor in organic matter and nutrients. If the parent material at the soil surface consists of cover sand the organic matter content is negligibly small. The organic matter content for Dutch drift sand is approximately 0.3 % (Table 5.2).

Table 5.2. Description of the soil for the different drift-sand succession stages (Source: Ketner-Oostra & Riksen 2005).

Succession stage	**Description**	**Soil profile**	**OM* 0 – 5 cm (%)**	**pH-KCl 0 – 2 cm**
0	No vegetation	C	0.30	4.7
1	Patches of pioneer grasses	C	0.30	4.7
2	Fixation of bare sand by *Corynephorus. canescens* and green algae	C	0.34	4.6
3	Fixation as in type 2, and also by mosses	C	0.58	4.5
4	Moss carpets, partly covered by algae (*Gloeocystis polydermatica*)	AC	0.79	4.0
5	Dying moss carpets through ageing and effects of covering by algae	AC	0.88	3.5
6	Lichen growth on partly dead moss carpets	AC	1.37	3.5
7	Species-rich lichen vegetation, including reindeer lichens	AC	1.64	3.5
8	Mosaic vegetation of drift-sand vegetation with heath (*Calluna vulgaris*) including *Juniperus communis*	A(B)C	5.25	3.2

* OM= organic matter

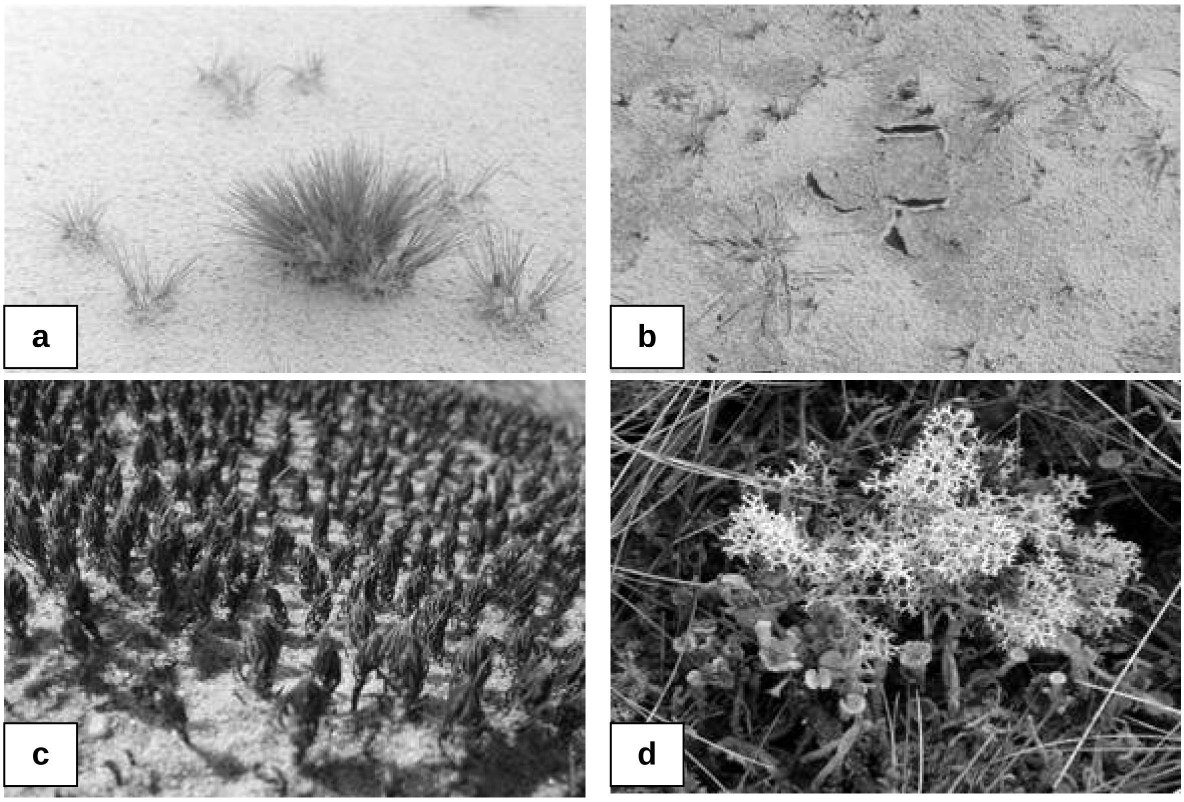


Figure 5.5. Drift-sand vegetation: (a) Gray hairgrass (*Corynephorus canescens*) (Photo: M. Riksen); (b) Algae crust (Photo: M. Riksen); (c) The pioneer moss *Polytrichum piliferum* (Photo: M. Riksen); (d) the lichens *Cladonia coccifera* and *Cladina portentosa* (Photo: A. Aptroot)

The early pioneer species are adjusted to growing in moving sand, like *Ammophila arenaria* and *Festuca rubra* ssp. *commuta*, both extending with an underground rhizome system. The maritime species *A. arenaria* has been introduced in inland sand dunes for retaining blowing sands in the past (Tesch et al. 1926; van Embden & Verwey 1968). A species as *Carex arenaria* is adapted to extend with creeping underground rhizomes producing shoots at intermediate distances over an open sand surface.

The establishment of the pioneer grass *Corynephorus canescens* (Figure 5.5a) depends on its spread by wind. Seed and organic material is often found in higher concentrations behind small obstacles, in foot prints or in tracks. Most seeds therefore geminate in the deposition zone behind or between the existing vegetation. Successfulness of the germination of these grass seeds probably mainly depends on the weather conditions. In a period with dry and windy conditions it only geminates very locally whereas in periods with rainy conditions it geminates in a more widespread, uniform pattern. Under the latter conditions the algae present in the top soil show an increased growth and may develop a crust (Figure 5.5b). It is believed that the formation of such biotic crusts enables the successful germination of pioneer vegetation like *C. canescens* and the winter annuel *Spergula morisonii*. Weeda (1985) claims that humus should be present in the latter case. *Pinus* seeds might germinate in bare or nearly bare sand, but generally do not survive a dry season. In Table 5.1 these first pioneering plants are summarized under Vegetation type 1.

Soil formation in the first succession stage is limited. The acidity of the parent soil material (e.g. drift sand or cover sand) in the un-vegetated zone and in the top soil of this first vegetation type remains at pH-KCl 4.6 and remained largely unchanged over the last 10 years (Ketner-Oostra 1994ab; 2003; Ketner-Oostra & Riksen 2005). With an increasing soil cover the vegetation reduces the sand transport and thus the regular deposition of nutrient-poor sand as shown in Figure 5.6. The organic matter content in the topsoil will slowly increase, which creates favourable conditions for species that cannot bear the poor conditions and/or the high sediment deposition rates found near an active deflation/transport zone.

As more sand is stabilized plaques of green algae might develop between the tussocks of *C. canescens*, followed by protonemata of mosses. In this early stage with still significant sediment transport (Figure 5.6) the pioneer moss *Polytrichum piliferum* (Figure 5.5c) is found. This species expands through perennial underground rhizomes. Individual shoots may live for several years continuing forming annual segments. A mat of *P. piliferum* may consist of circular colonies up to 1 m in diameter, being clones (Hobbs & Pritchard 1987; During 1990). In the top two centimetres of sand inside this *C. canescens* vegetation dominated by *P. piliferum* (Vegetation type 3 in Table 5.1) some humus has formed resulting in a small decrease of the pH-KCl (see Table 5.2).

After 1-3 years spore capsules might be formed as part of the life cycle of the dioecous *P. piliferum*. This mostly occurs in a fine maze over the moss carpet, in which not all plants sporulate (Hobbs & Pritchard 1987). After sporulating these moss plants might die. The mucous containing algae *Gloeocystis polydermatica* intensifies this process by the covering of the moss layers. During rain the algae absorb nearly all the water until they have formed a more or less impermeable layer over which the surplus of rain is discharged that might otherwise be available for development of the new shoots from the rhizomes (Vegetation type 4 in Table 5.1).

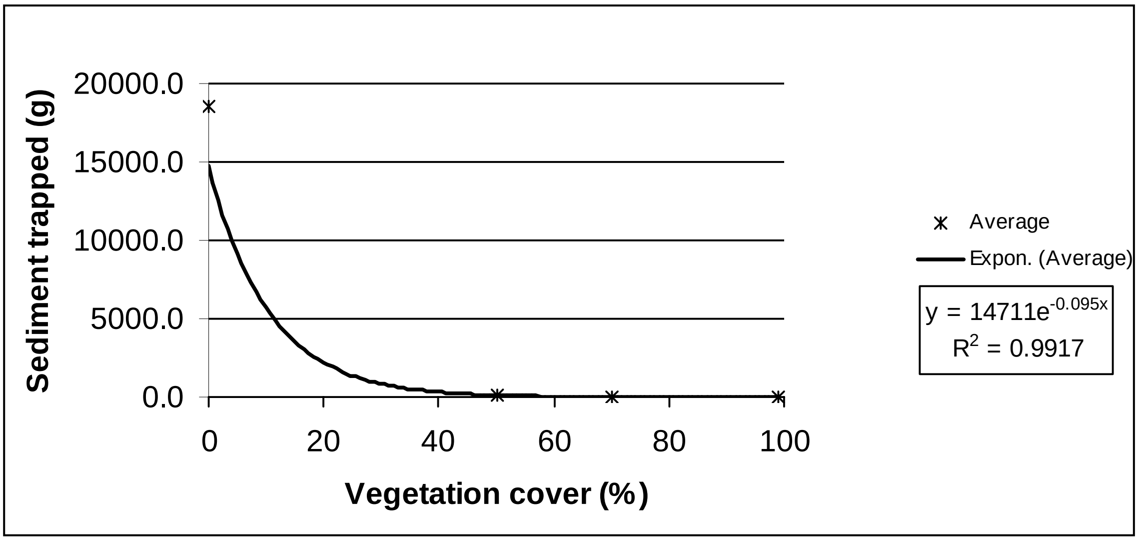


Figure 5.6. Relation vertical accumulation flux and vegetation cover (after: Ketner-Oostra & Riksen 2005).

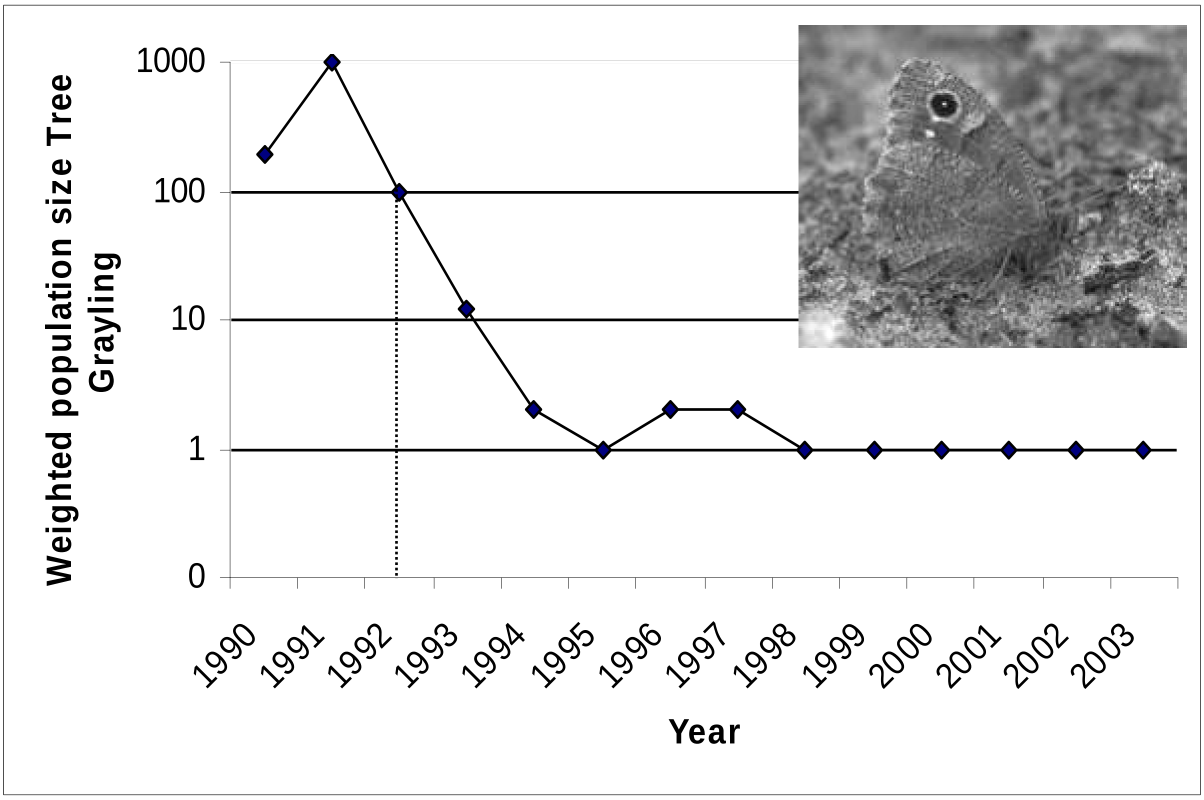
On the carpet of partly dead mosses lichens will start to colonize (Table 5.1, Vegetation type 5). These are mostly common humicolous species such as *Cladonia coccifera* (Figure 5.5d), *C. macilenta, C. glauca* and *C. floerkeana*. But also more rare species might develop such as the Red List species (Aptroot et al. 1998) *C. zopfii, C. crispata* and *C. monomorpha*. In Vegetation type 6 this has added up to 22 species (Ketner-Oostra 1994ab). Real pioneer species like *Cetraria aculeata*, *Cladonia foliacea* and *C. cervicornis* can also be found, species mentioned so far behaving as secondary pioneers on dead moss (van der Meulen et al. 1987; Biermann & Daniëls 1997). In Vegetation type 5-6, clear acidification has taken place as shown in Table 5.2. With the lowering of the pH the efficiency of the N-mineralization will probably increase resulting in a higher biomass production (Bakker et al. 2003).

At the drift-sand area Kootwijkerzand near Kootwijk, the Netherlands, the climax in lichen-richness is reached when aero-hygrophylous reindeer lichens (Figure 5.5d) have settled in, like *Cladina portentosa* (Figure 5.5d) and *C. arbuscula* s.l. (Vegetation type 7). This type consists of more grasses, like *Festuca ovina* s.l. and *Agrostis vinealis*, the latter when there is clearly more soil moisture available in flat gravel-rich locations where cover sand is surfacing (Ketner-Oostra 2003). The acidity is as low as in the former Vegetation type (see Table 5.2) but even detectable in the 10-30 cm layer. In this grass and herb-rich vegetation *Calluna vulgaris* might germinate and form a mosaic with the moss and lichen-rich grass vegetation (Vegetation type 8 in Table 5.1). Gradually a dry heath will develop, mainly with *Calluna vulgaris*. This succession from initial species-poor grey hairgrass vegetation (Vegetation type 1) into lichen-rich final phases (Vegetation type 8) might take 10-12 years, while they might stay for years more or less without succession until the age of 20 years (Daniëls & Krüger 1996). However, little is known about the influence on the succession of the location in the drift-sand landscape. On a former deflation plain the succession will probably take longer than on stabilized drift-sand deposits or in the zone close to the forest due to the lower nutrient content.

5.2.4.2 Drift-sand fauna

With the development of the typical drift-sand vegetation as described above, a selective number of fauna species has settled down. The composition and distribution of the characteristic fauna communities of the Dutch inland drift sands is closely related to the extreme conditions in this landscape. Relatively few fauna species can cope with these extreme conditions. Therefore inland drift sands accommodate a species poor, but very characteristic fauna community. This community is however under severe ecological pressure, though only little is known about the exact mechanisms underlying the decline of characteristic species.

Most characteristic fauna species belong to the insects (*Insecta*), especially wasps and ants (*Aculeata*; *Hymenoptera*) and beetles (*Coleoptera*) (Mörzer Bruijns & Westhoff 1951). Only three species are known to be restricted to inland drift sands in the Netherlands: Tawny Pipit (Aves: *Anthus campestris*), Tree Grayling (Lepidoptera: *Hipparchia statilinus*) and Giant Earwig (Dermaptera: *Labidura riparia*). The Red-Listed Tawny Pipit has recently reached the point of extinction.



The year 1992 is 100

Figure 5.7. Relative abundance of Tree Grayling in the Netherlands since 1990 (data Dutch Butterfly Foundation; photo by Kars Veling, 1992, Dutch Butterfly Foundation).

From the 250-350 breeding pairs present in the period 1940-1960, only 21-23 were left in 2000, in 2003 only one territory was occupied and in 2004 no territories were present (van Turnhout 2005). Populations of the Red-Listed Tree Grayling have also declined rapidly in the last three decades (Figure 5.7). This butterfly species now only occurs in three areas in the central part of the Netherlands. The Tawny Earwig (*Labidura riparia*) is probably found on many, but not all, inland drift sands and on these places it seems not to be threatened yet.

Many other fauna species of inland drift sands are also found in coastal dunes, dry heath lands or dry calcareous grasslands. Species which are found mainly, but not solely, in drift sands are the Grey Spider Wasp (*Pompilus cinereus*) and its parasite *Ceropales maculata*. Many other species of digging wasps (Specidae), wasps (Apidae) and spider wasps (Pompilidae) find their optimum habitat in inland drift sands. Other interesting insect species are the ant species *Myrmica specioides*, *Lasius psammophyllus* and *Formica lusatica*, Snow Scorpion Fly *(Boreus hymealis*), Spotted Ant-lion (*Euroleon nostras*), the Red-Listed Blue-winged Grasshopper (*Oedipoda caerulescens*), the ground beetles *Amara infima*, *Cymindis macularis* and *Harpalus neglectus*, the tiger beetle *Cycindela maritima* and the Red-Listed butterflies Silver-spotted Skipper (*Hesperia comma)* and Grayling (*Hipparchia semele*) (Bakker et al. 2003). Furthermore inland drift sands and the surrounding dry heaths and forests accommodate significant parts of the Dutch populations of some Red-Listed breeding birds: European Nightjar (*Caprimulgus europeus*), Northern Wheatear (*Oenanthe oenanthe*), Wryneck (*Jynx torquilla*) and Great Grey Shrike (*Lanius excubitor*), which has almost disappeared from the Netherlands. European Thicknee (*Burhinus oedicnemus*) probably used to breed in small numbers on inland drift sands until a few decades ago, but reliable records of confirmed breeding are lacking (SOVON 2002).

Due to physiological adaptations or life cycle adjustments, most characteristic fauna species are resistant against or dependent on extreme climatic conditions, mainly high or fluctuating temperatures and drought, and low nutrient availability. Examples of physiological adaptations are metallic colours and long hair as a response to heat (Almquist 1971) and slow growth and a long larval period as a response to the use of low nutritious food such as Tree Grayling and its host plant *Corynephorus canescens*. Furthermore several behavioural adaptations occur, such as burrowing in bare sand by different *Harpalus* species and Tawny Earwig, and hiding under fallen branches or trees during daytime (probably many species). Because of low nutrient availability there is a high specialisation rate of feeding guilds. Most species are parasites or carnivorous. However in carabid beetles some very characteristic species have developed the faculty to feed (partly) on plants, especially seeds of grasses and the herb *Spergula morisonii*. Many aculeate species feeding on nectar or pollen are small and find enough food on *Spergula morisonii* and shrubs of *Rhamnus-species* in adjacent woodlands. Species that occur on the most dynamic places of drift sands are characterized by high mobility, a short life cycle and one or several generations per year. Species of fixed dunes generally have a low dispersal power and a life cycle of more than 1 year. Many fauna species depend on two or more ecotope types within the inland dune landscape to fulfil their needs and complete their life cycle. Tree Grayling for instance needs stands of *Calluna vulgaris* to facilitate its nectar demand during its mature stage and vital stands of the pioneer grass *Corynephorus canescens* during its larva stage.

Because of the dependence on extreme conditions many characteristic species have a southern and/or eastern distribution in Europe and occur on the north-western border of their range in the Netherlands such as Tawny Pipit, Tree Grayling and Blue-winged Grasshopper. Their reproduction surplus in general is probably low and strongly depends on weather conditions. Local extinction of populations may be significant in years with low temperatures and/or high precipitation, especially in small and isolated areas.

5.3. The rapid decline of the active drift sands after 1960: causes and consequences

Since the 1960s the remaining inland drift-sand areas have shown a rapid decline in size. From the 60 km^2 that remained in the Netherlands after the major period of reforestation, only 40 km^2 were left around 1980 (Bakker et al. 2003). Bakker et al. (2003, pp. 103-105) estimated the total area of *active* drift sand less then 1.5 km^2.

Figure 5.8 shows the rapid extension of the vegetation at the drift-sand area Kootwijkerzand between 1964 and 2004.

Besides the ongoing decline due to natural regeneration on the one hand and a lack of erosion activity and human activity on the other, the regeneration seems to have changed in speed as well as in pattern after 1960 due to external factors:

- eutrophication by relatively high atmospheric nitrogen deposition; and
- invasive (exotic) species.

5.3.1. Atmospheric nitrogen deposition

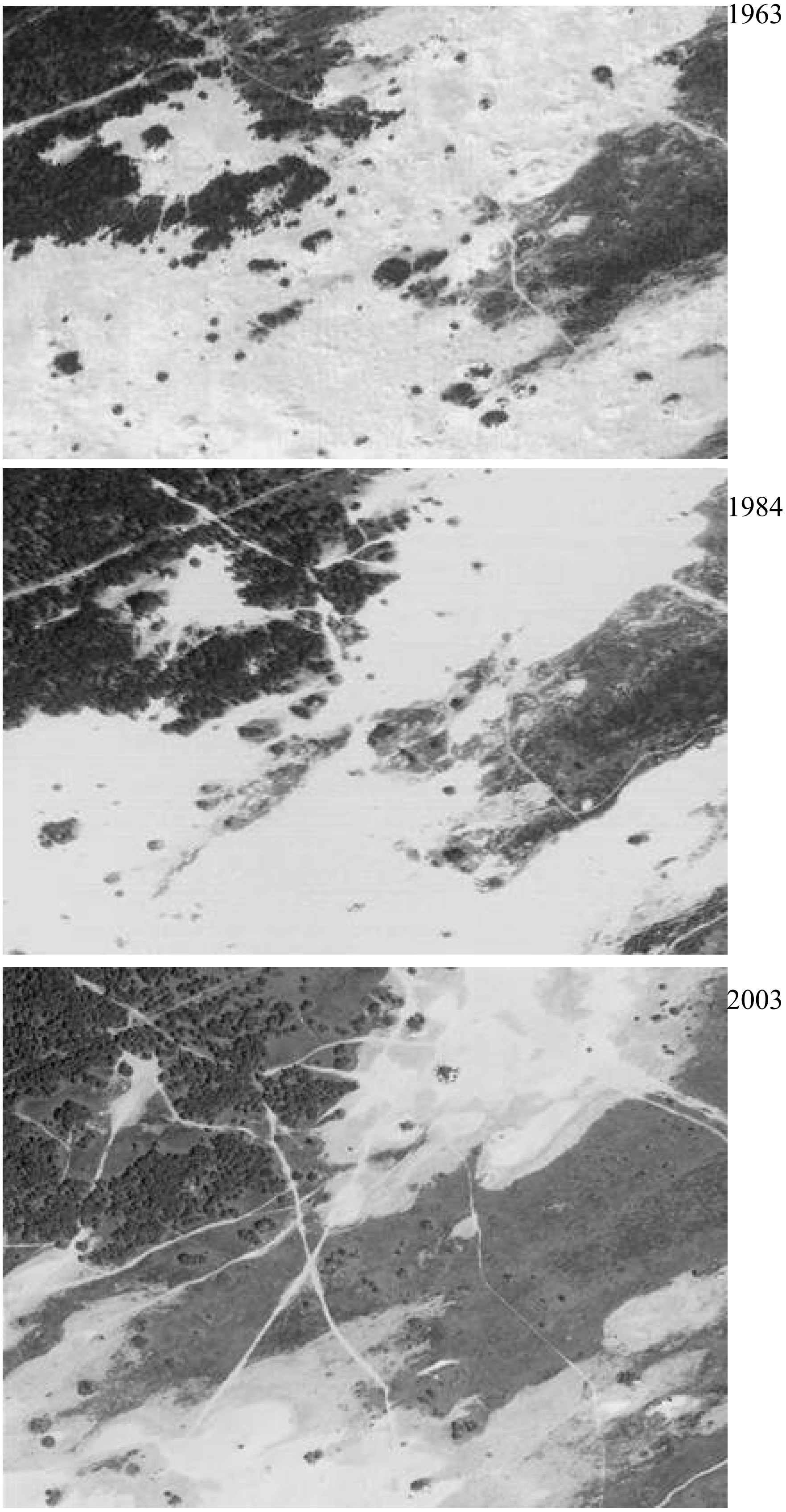
In the Netherlands, the increase in atmospheric N deposition led to an increase in biomass production and, consequently, a more rapid succession. The nitrogen mainly originates from animal husbandry and the bio-industry. Although the N deposition reduced from 3000 mol ha^{-1} y^{-1} in 1990 to 2350 mol ha^{-1} y^{-1} in 2001 (Buijsman 2004), in and near areas with high livestock concentrations the N deposition is still high with values above 3500 mol ha^{-1} y^{-1} (Buijsman 2004). In combination with sufficient available moisture nitrogen can stimulate the growth of algae. On locations with moderate or little wind erosion activity the algae can form a few millimetre thick crust, which effectively stops erosion (Pluis 1994). For this reason this problem is often observed in the smaller drift-sand areas and in zones in the wind shadow of obstacles, but also in zones covered by more then 30% grey hairgrass, where the wind erosion activity is relatively low. The atmospheric N deposition also accelerated the succession in the drift-sand vegetation. The algae not only form a non-erodible crust but also fixate the nitrogen that normally would have been leached out. Another algae that has accelerated the succession since the 1980s is the mucous containing algae *Gloeocystis polydermatica*, the development of which boomed due to the increase in aerial N deposition. This has intensified the covering of the moss layers by these algae.

Eutrophication also enhances the invasion of *P. sylvestris,* especially in the zone along the forests.

5.3.2 Invasive (exotic) species

Another external factor is the introduction of invasive species by human (activities). These species can overtake the place of local species in the succession. The most important exotic species that influences the succession of inland drift sands in the Netherlands is the moss *Campylopus introflexus*, which originates from South America. Since the 1980s this neophytic moss has invaded the inland sand dunes (van der Meulen et al. 1987; Masselink 1994). It disperses very actively by stem tops or leaflets. This life strategy (During 1979) made it suitable to invade large areas of partly degenerating *P. piliferum*, but also humus containing sandy areas that have low dynamics. But *C. introflexus* is not adapted to blown-in sand like *P. piliferum* and will wither or die when it is covered by sand.

On oligotrophic sites inside the Dutch Veluwe district *C. introflexus* probably takes advantage from the high aerial nitrogen deposition (Londo 2002). Apart from the aggressive growth of *C. introflexus*, grass encroachment by *F. ovina* s.l. and/or *A. vinealis* is also observed.



1963

1984

2003

Figure 5.8. Development of vegetation at Kootwijkerzand, the Netherlands in the period 1963 – 2003. (Source aerial photographs: Topografische Dienst Emmen; © Eurosense, 2003)

This does not lead to an increase of the mosaic drift-sand vegetation with heather (which is so important for several fauna elements), however. It was also found that the germination of *Calluna vulgaris* seeds is strongly inhibited by thick moss carpets of *C. introflexus* (Equihua & Usher 1993).

5.3.3. Effects of the decline of active drift sands on fauna

Many characteristic fauna species of inland drift sands have shown a long-term decrease in both numbers and distribution (Bakker et al. 2003). Initially, it was assumed that this was caused by the decline in the total area of active drift sands in the Netherlands due to the re-forestation and because the remaining drift sands had become too small and fragmented. Typical species such as Tawny Pipit and Tree Grayling require a relatively large habitat within a site to sustain viable populations, and it is clear that only few such sites are left.

Since the sixties, as a result of atmospheric deposition, nitrophilic grasses such as *Festuca ovina*, *Deschampsia flexuosa* and *Agrostis vinealis* and the moss *Campylopus introflexus* have become dominant. Low, open vegetations with a dry microclimate, and large temperature fluctuations between day and night, have been replaced by tall, closed vegetations with a constant cool and relatively moist microclimate (Biermann & Daniëls 1997). These changes in the vegetation of drift sands are enhanced by the decrease of Rabbit (*Oryctolagus cuniculus*) populations due to viral diseases, as a result of which grazing pressure on grasses is low (Bakker et al. 2003). The above described developments will have contributed to the decline of characteristic fauna species, but the exact mechanisms remain largely unknown.

Here we present some hypotheses for the causes of the decline of Blue-winged Grasshopper, Tree Grayling and Tawny Pipit.

For the Blue-winged Grasshopper the decrease in the amount of bare sand may have reduced the possibilities for display and oviposition. Furthermore, a taller vegetation enhances the extinction of sun light near the soil surface, resulting in lower temperatures in the top layer of the soil. As a result of this, the time needed for the development of grasshopper eggs increases, leaving not enough time to complete the year cycle before winter arrives (Kleukers et al. 1997). For some grasshopper species a cooler microclimate also increases the development time of juveniles (Schaedler & Witsack 1999).

Adults of Tree Grayling will be adversely affected by a decrease of both bare sand and lichen abundance, because they use these ecotopes for warming up. For the related species Grayling (*Hipparchia semele*), it was demonstrated that egg-laying females use dark grey lichen species (*Cladonia spp.*) not only for warming up in early morning, but also during the rest of the day for resting, because the butterflies are best camouflaged here (Shreeve 1990). At some sites the disappearance of *Calluna vulgaris* through grass encroachment will have resulted in food shortage for Tree Graylings. However, caterpillars are believed to be more sensitive to habitat changes than adults. First of all, the infection rate of caterpillars by pathogens may increase when microclimate levels out, resulting in a decrease of winter survival. This was demonstrated once again by the Grayling (Bink 1992).

Furthermore, eutrophication reduces the nutritional value of the food plant *Corynephorus canescens*. Finally, the caterpillars pupate in bare sand, a process which takes 21-46 days (Bink 1992). Grass and moss encroachment reduce the amount of bare sand, which causes a third possible bottle-neck for Tree Grayling caterpillars.

Many other characteristic invertebrate species of inland drift sands face comparable problems as described for Blue-winged Grasshopper and Tree Grayling (Bakker et al. 2003). Indeed in *Campylopus*-dominated vegetations, grasshoppers and probably many other invertebrate species, appear to be rare (Nijssen et al. 2001) and a shift occurs from day-active to night-active carabid and spider species (Vogels 2004). This will have seriously affected the food supply for the insectivorous Tawny Pipit, which is the most probable cause for the observed decrease in breeding success of this species (Bijlsma et al. 2001; van Turnhout 2005). Furthermore, disturbance by recreation will have been another important cause for the decline of the Tawny Pipit in the Netherlands. Bijlsma (1978) showed a correlation between the local extinction of the Tawny Pipit and the accessibility of the site to the public. As many other ground breeders, Tawny Pipits are very shy when they have young in the nest. Young may starve or nests abandoned when people are constantly around, as is the case in many of the Dutch drift sands nowadays. Besides, Tawny Pipits have only one clutch a year and breed relatively late in the season, when recreation pressure is high. This makes them very susceptible to disturbance (Bijlsma 1990).

5.4. Discussion and conclusions

The decline of active inland drift sand in northern Europe is explained by various factors. The landscape differentiating processes are not longer functioning according to the geomorphological structure of the original drift-sand area. The major change in land use that took place at the begin of the 20th century can be seen as its main cause. Wind erosion activity in the remaining drift-sand areas is tempered by the reduced size of the potential erodible area on the one hand, and the reduced wind force on the other. In most cases the lack of erosion activity is not compensated for by human activity, e.g. recreation, military use. Only in areas with regular intensive human activity the pioneer vegetation and algae crust is suppressed effectively.

Other factors, such as increased N deposition, accelerate the regeneration process. Also, in many drift-sand areas the establishment of exotic plant species has significantly disturbed the balance between degradation and regeneration. Invasive species like Scots pine and the neophytic moss *Campylopus introflexus* spread more rapidly, causing a higher biomass production and a more rapid soil formation, resulting in a more rapid evolution of the succession towards a closed forest. This development causes increasing landscape roughness and therefore a further reduction of the area with maximum wind erosion activity. Only severe storms of high intensity and duration can generate sufficient sediment transport into the vegetated zones to set succession back. If the area of bare sand becomes too small, sand transport during these severe storms also becomes too small and the influence on the regeneration process will be minimal. Most pioneer vegetation needs to be regularly covered with a small amount of blown-in sand to remain vital. For the typical drift-sand fauna the combination of bare sand with a vital transition zone and other ecotopes seems to be crucial to survive. In the present drift sands the distance between the bare sand including the transition zone with other drift-sand ecotopes has become too large so that for fauna necessary connection between the different ecotopes seem to be lost. However at this stage too little is known about the role of the different drift-sand ecotopes and their connections for the different fauna species. There is also a lack of knowledge about the effect of algae on the regeneration process, and about the direct effect of these algae on the fauna.

In general one can conclude that, under present condition, wind erosion no longer acts as a large-scale landscape differentiation process as was the case during the development stage of the drift-sand areas, but has become a local process. Without proper management the erosion activity will further decline and will no longer influence the regeneration as schematically represented in Figure 5.1.

The best way to reactivate inland drift sands is to restore the natural processes by removing the forests and the A-horizont at the upwind side of the active areas. The main problems faced here are the high costs of such measures, legislation, the presence of infrastructural works or private property in the area, and the risk the measures would bring to community interests.

In most situations the stakeholders prefer to preserve the drift sand in the present setting. In this setting it is recommendable to keep the area with erosion activity sufficiently large by taking management measures in the first succession stages. A good balance between the area with bare sand and the area covered with pioneer vegetation can be achieved by relatively simple and cheap tilling measures. These measures should be taken on a regular base to destroy the algae crust and the other vegetation, and keep the active areas connected to guarantee a sufficiently large potential sediment transport. To support the characteristic fauna it is important that the area with the first succession stages is not treated at once but phased, and/or to leave small areas untreated.

In the meantime the wind force in the drift-sand area should be ‘maintained’ or improved by suppressing the growth of tall standing vegetation and removing trees that shelter the sands from the wind.

In the remaining area the effect of the high nitrogen deposition on vegetation development and soil formation should be counteracted by pattern-based management, by small scale removing of the unwanted vegetation including the top soil.

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Chapter 6

LONG-TERM VEGETATION SUCCESSION IN LICHEN-RICH DRIFT SAND IN THE CENTRAL NETHERLANDS AS INFLUENCED BY HABITAT RESTORATION

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Chapter 6. Long-term vegetation succession in lichen-rich drift sand in the central Netherlands as influenced by habitat restoration

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Abstract

In this paper we compare the cryptogam vegetation in the Spergulo-Corynephoretum and Genisto-Callunetum at the inland drift-sand area Kootwijkerzand in 1968, 1993 and 2004. In the early period the lichen diversity in these plant communities appeared to be very high. The aspect was formed by *Corynephorus canescens* and *Polytrichum piliferum*. Since the 1970s the neophytic moss *Campylopus introflexus*, a species adapted to acid open sand, has invaded these dunes. These changes have been attributed to the high aerial deposition of N in this central part of the Netherlands. In the more recent periods the actual lichen diversity did not really diminish, but the cover was clearly reduced when encroaching mosses outgrew the lichens in all succession stages. However, when *C. introflexus* is less vital because of ageing, desiccation or burial under wind-blown sand, common humicole, aero-hygrophytic and even pioneer lichen species may locally establish on or between the moss cushions. The former succession series starting with *P. piliferum* and ending with lichen-rich *Calluna* heath (1968) has been partly replaced by one including *C. introflexus* (1993 and 2004).

Process management is nessesary to keep the sand blowing and hereby reduce the colonization by *C. introflexus*. Habitat restoration by small-scale management consisting of cutting down self-sown trees and removing the canopy has positively influenced lichen diversity and needs to be continued.

Keywords: Acidification; Biodiversity; *Campylopus introflexus*; *Cladonia*; Colonization; Genisto-Callunetum; Invasive species; Management; Moss dominance; Nitrogen deposition; Spergulo-Corynephoretum; Terricolous lichen.

6.1. Introduction

In the central part of the Netherlands, the Veluwe, Pleistocene sands have been deposited and blown into inland sand dunes. Here large areas of non-calcareous and nutrient-poor drift sand existed until the end of the 19th century when they were afforested with Scots pine trees (*Pinus sylvestris*). For the purpose of nature conservation, certain areas were deliberately not planted with trees. One of these open areas was preserved east of the village of Kootwijk on the Veluwe (province of Gelderland), probably for aesthetic reasons (Tesch et al. 1926). This Kootwijkerzand was designated a State Nature Reserve in 1928.

Without management, through succession, the pioneer communities on the drift sand change into grassland, followed by heath and finally by woods consisting of self- sown Scots pine or deciduous trees. If left unchecked, ultimately only a small area of the open drift-sand ecotope will survive. This process has been taking place on drift-sand areas all over the Netherlands since the 1970s, and biodiversity has declined alarmingly as result of high aerial deposition (Quené-Boterenbrood 1988; de Smidt 1995).

After being designated a nature reserve, the Kootwijkerzand was not managed for 30 years, resulting in an increase of several ha of self-sown trees. In the 1960s the State Forestry implemented management measures, with the intention of maintaining 700 ha of open area, 300 ha of which was to be more or less open sand (Ketner-Oostra & Huijsman 1998).

In 1959 the first vegetation survey on inland sand dunes and heath of the Veluwe was published (Stoutjesdijk 1959). It paid much attention to the relation between landscape structure, vegetation, soil and microclimate. Until well into the 1970s mats of reindeer lichens locally covered the transition belt between the sand dune ecotope and heath, especially in blown-out depressions near the edges of the planted pine wood. Inside the planted pine wood around the Kootwijkerzand the Cladonio-Pinetum sylvestris Juraszek 1927 was present on the most nutrient-poor sands (Leijs 1964; Bannink et al. 1973).

Since the 1960s, interest in the botany of the inland and coastal heath and sand dunes has grown; there have been vegetation surveys by de Smidt (1966; 1977) and detailed descriptions of the cryptogam richness of these ecotopes by Pos (1968) and Daniëls (1983) and Daniëls et al. (1987). The Kootwijkerzand was recognized as an important relict of the West European sand dune landscape from former centuries (de Smidt 1969; Schimmel 1975). Two MSc students, van Embden and Verwey, who did their dissertations on the Kootwijkerzand, investigated the cryptogam vegetation. They found that lichens determined the high biodiversity in the succession series from open sand with *Corynephorus canescens* and the moss *Polytrichum piliferum* to the establishment of *Calluna vulgaris* heath. In the terminal stages many moss and liverwort species were also present (van Embden & Verwey 1968).

6.1.1. Effect of atmospheric SO_2 and nitrogen deposition

After the surveys of Stoutjesdijk (1959) and van Embden and Verwey (1968) emission of sulphur dioxide (SO_2) peaked in 1979 and then declined sharply

Table 6.1. Critical deposition values for nitrogen in different vegetation types (after Klein et al. 1996)

Vegetation type	Critical deposition value (mean) in kg.ha.yr^{-1}
Deciduous wood and coniferous wood	18
Heathland (Calluno-Ulicetea)	13
Heathy grasslands (Nardetalia)	15
Pioneer community of dry acid sand (Corynephorion canescentis)	21

(RIVM 1976-1986). However, dry and wet nitrogen (N) deposition (NH_4-N, NO_3-N and organic compounds), especially of ammonia, has greatly increased since the 1970s, as a direct result of intensive animal farming (bio-industry) with the top values occurring in the 1980s.

Before the 1970s N deposition was not measured, but from the explosive increase of livestock since the 1970s one may conclude that until the 1960s N deposition influenced vegetation change little, if at all. Ammonia in particular can adversely influence many vegetation types, as not only does it act as a nutrient enrichment, but in the soil it also turns into nitric acid, thereby acidifying the sandy soils (Erisman 2000). Deposition data are available from the 1980s and 1990s (Bleeker & Erisman 1996); they show that the critical load (the amount of deposition an ecosystem may tolerate without loss of biodiversity: de Vries 1994) was exceeded. The more sensitive the vegetation is for ammonia, the lower the critical value (Table 6.1 from Klein et al.1996).

The critical deposition value for open sand is probably higher than that for pioneer communities with *Corynephorus canescens* (Table 6.1), as N leaches out relatively fast in sand without humus. In 1982 the deposition of ammonia in the Kootwijkerzand was 68 kg N ha^{-1} yr^{-1}, 90% of which originated from the Geldersche Vallei, an area with intensive pig and chicken farms, located 10 km to the west (Buijsman et al. 1984). The deposition declined sharply from 51 kg N ha^{-1} yr^{-1} in 1990 to 40 kg N ha^{-1} yr^{-1} in 2001 (Buijsman 2004), in response to changes in manure spreading made mandatory by legislation passed in 1990. Since then, the RIVM has reported the deposition in km grid squares. With the ammonia deposition in this part of the Veluwe somewhat reduced, it has been suggested (van Herk 2004) that some peaks in the deposition during the year might do much harm. Van Herk investigated epiphytic lichens on trees and found their decrease or increase on the Veluwe to be related to the ammonia values as measured by the TNO ammonia monitoring network (Bleeker et al. 2003).

The increased nitrogen deposition has enhanced plant growth in most (natural) ecosytems (Fangmeier et al. 1994). The overall changes imposed on the nutrient-poor terrestrial ecosystems rich in lichens, were most desastrous (Daniëls et al. 1987; de Smidt 1995). Grass dominance in heath vegetation has been proved to be related to increased N deposition since the 1970s (de Smidt 1979; Diemont & Heil 1984; Diemont 1996). The increasing quantities of mosses in several grassland communities may also be attributable to nutrients supplied by aerial deposition (Londo 2002). Quené-Boterenbrood (1988) included the Kootwijkerzand in a survey of the effects of ammonia deposition on all vascular plants. However, she blamed the decrease in *Selago* species on SO_2 emission in the national peak year of 1979. In their comparative research of epiphytic lichens on the Veluwe, van Herk et al. (2000) reported that the high SO_2 emission in that year had killed certain lichen species.

In the Spergulo-Corynephoretum the decrease of species from dry oligotrophic biotopes was accompanied by an increase in the size and abundance of graminoids. Moss encroachment, with the alien moss species *Campylopus introflexus* forming a large biomass, had a direct impact on succession. Since the 1970s, this alien moss species, which originates from the southern hemisphere, has been gradually increasing in coastal and inland sand dunes of Western Europe (van der Meulen et al. 1987). Older cushions of *C. introflexus* are two-layered: a fresh green layer occurs on top of a semi-humified layer that contributes greatly to the humus content of the sand. The moss's rapid dispersal and its high humus production are the main threats to the inland sand dune ecosystem.

6.1.2. Research objectives and related key questions

In 1992 the available information on the lichen species and the lichen communities of the Kootwijkerzand was updated. Permanent quadrats (PQs) were set out in the lichen communities (Figure 6.1a) and in 1993 the monitoring of the vegetation development began (Ketner-Oostra 1994a).

In 1996 the effects of former small-scale management by the State Forestry and large archaeological excavations on the current lichen vegetation were studied (see Figure 6.1b and Table 6.2 from Ketner-Oostra 1996; Ketner-Oostra & Huijsman 1998). In 2004, the development in the PQs over 11 years was evaluated. The extended effects of former management and recent management experiments by Riksen were studied (Ketner-Oostra & Riksen 2005).

The aim of study described here was to assess 36 years of vegetation change (1968-2004) on the Kootwijkerzand.

We set out with the following hypotheses:

1. Before the 1970s the cryptogam vegetation in the earlier succession stages was especially well developed.
2. At that time, natural, intermediate and terminal succession stages were still rich in cryptogams.
3. Since the 1970s acidification and eutrophication have affected the cryptogam composition.
4. Since the 1970s the expansion of *Campylopus introflexus* has changed, accelerating the succession in the inland sand dunes, thereby negatively influencing lichen diversity.
5. Habitat restoration by small-scale management has a positive effect on the development and maintenance of lichen-rich vegetation.

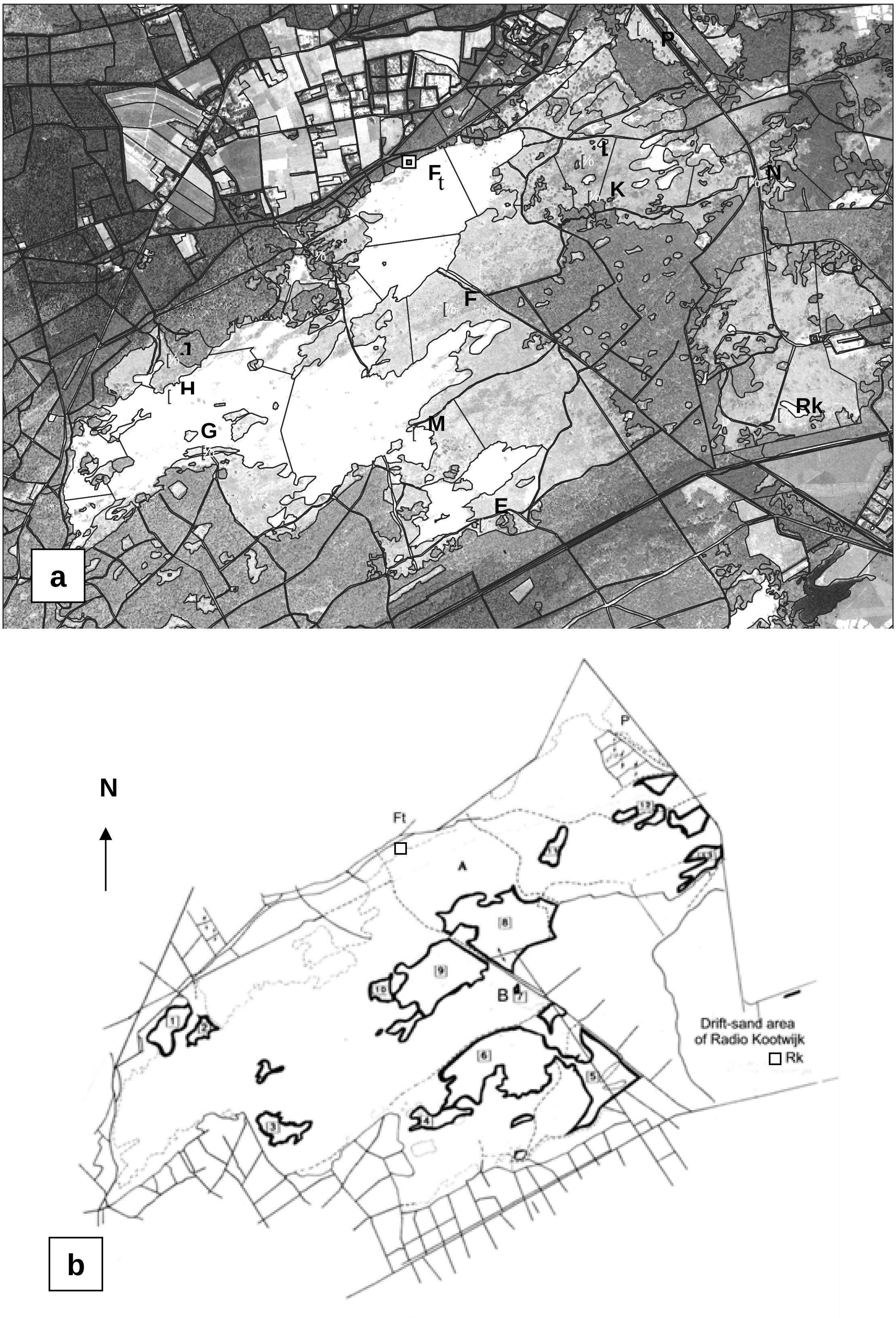


Figure 6.1. **a)** Overview of the Kootwijkerzand with the Reference plot H, the PQs E - P and two additional lichen-rich relevés in 2004 (Ft and Rk);
b) Locations 1 - 13 with management measures
A = area of 'De Dikke Bart', B = area of detailed mapping in 1968 and 1995. For the explanation of the different management measures (see Table 6.2).

Table 6.2. Study sites (locations 1-13 from Figure 6.1b) for vegetation evaluation of small-scale nature management in the Kootwijkerzand, aimed at restoring the drift-sand area after invasion by self-sown trees in 1960-1985 (from Ketner-Oostra & Huijsman 1998)

Location	1.	2.	3.	4.	5.	6.	8.	9.	11.	12.	13.
Year 19..	80	60	80	80	78	80	78	62	80	80	80
Area[1]	6ha	sP	10ha	sP	sP	sP	sP	15ha	3ha	4ha/sD	13ha
Management:											
trunks dragged out	+	+	+	+	chip[2]	+	chip	+	+	+	+
branches burned	+	+	+	+	+/chip	+	+	+	+	+	+
litter[3] removed	+	+	+/-	-	+/-	?	+/-	-	+	+	+
effects on[4]:											
a) local area	-	+/-	+/-	-	+/-	+	+	+	+	+/-	+
b) surrounding area	-	-	+	+	-	+/-	+	+	+	-	-

[1] rather closed area with *Pinus sylvestris*; sP, scattered self-sown *Pinus*; sD, self-sown Deciduous trees

[2] locally chipped and transported

[3] + removed or – not removed; +/- partly removed; ?, unknown

[4] + positive or - no effect; +/- partly positive effect

6.2. Methods

6.2.1. Site description and soil origin

The Kootwijkerzand is located in the Veluwe District (province of Gelderland, the Netherlands). The inland dune landscape has developed on sandy sediments of Pleistocene origin deposited in the Late Glacial, 13 000-10 000 years ago (Koster 2005). These Pleistocene sediments belong to the Wierden Member of the Formation of Boxtel (de Mulder et al. 2003). Koster (pers. comm.) gave the following (updated) definition of drift sands and cover sands: '(a) Drift sands are aeolian sand deposits, originating by local redeposition of terrestrial (mainly aeolian) Pleistocene deposits. These sands are of Holocene age and usually display a dune-relief. The sands are well-sorted, with loose grain-packing, usually with a low organic matter content and yellow-grayish in colour. (b) Cover sands are the Late Pleistocene aeolian sand deposits of primarily cold-climate or periglacial origin. These sands are also indicated as sand sheets because of their typical low undulating relief. Both sand types are nutrient-poor and very calcium-poor to non-calcareous '.

During the Holocene, the aeolian sands were gradually covered with forests. In the Neolithic Age, about 5000 years ago, human activity (farming) exposed the sand and it became windblown again. The sand drift continued in periods of extreme drought in the Middle Ages (Heidinga 1984) and of over-exploitation of heath in more recent centuries (Koster 1978); for a historical review, see Chapter 5.

Figure 6.2. Area of 'De Dikke Bart' showing the site of archaeological excavations in the mid 1970s (from Heidinga 1987)

6.2.2. Management and archaeological excavations between 1960-2004

The total area of drift-sand ecotope of the Kootwijkerzand has been maintained at about 700 ha, 300 ha of which is kept active by small-scale management (Ketner-Oostra & Huijsman 1998). Self-sown trees, mainly *Pinus sylvestris*, but also the invasive species *Prunus serotina* and other deciduous trees from the surrounding wood, constantly threaten to reduce the area of open sand. From the 1960s onward, self-sown trees and a few ha of pine wood were cut by the State Forestry with chainsaws (Daniëls 1990; Daniëls & Krüger 1996; Ketner-Oostra & Huijsman 1998). Figure 6.1b shows the main locations where small-scale management was effectuated between 1960 and 2004. In the main relatively open sand area called 'De Dikke Bart' an extensive archaeological excavation of mediaeval villages took place between 1973-1975 (Figure 6.2). Afterwards the entire site was levelled by heavy machinery, leaving an area of bare sand (Heidinga 1987). Moreover, east of that central location, near the eastern border of the planted pine wood, 15 ha of self-sown pine trees had already been felled and removed in 1962 (location 9) and many large pine trees were removed at the end of the 1970s (location 8 in Figure 6.1b). The main purpose of removing pines in the southwest of the Kootwijkerzand (locations 1 - 3) was to strengthen the impact of wind on the sand dunes. This met with varying success, however, especially near the western edge of the surrounding wood. However, the cutting of 3 ha of trees in location 13 in the northeast has had the long-term effect of increasing the wind speed across the area to the northeast (Ketner-Oostra & Huijsman 1998).

6.2.3. Vegetation research

In 1968 (period 1) a total of 78 vegetation samples (relevés) were recorded in the drift-sand area of the Kootwijkerzand by van Embden & Verwey in order to show the total variation of vegetation containing lichens (van Embden & Verwey 1968). The vegetation of the same area was re-sampled in 1993, with 83 relevés (Ketner-Oostra 1994a), and in 2004, with 78 relevés (Ketner-Oostra & Riksen 2005). Just as in 1968, these surveys (henceforth referred to as periods 2 and 3, respectively) focused on describing the total variation of lichen-containing vegetation.

The relevés (according to Braun-Blanquet 1964) varied between 1 m^2 and 6 m^2 in period 1, and were 4 m^2 in periods 2 and 3, so were larger than the minimum area used for lichen communities (0.1 – 1 m^2 after Müller-Dombois & Ellenberg 1974). The scales used were the Braun-Blanquet scale (Braun-Blanquet 1964) in period 1 and the Braun-Blanquet scale as modified by Barkman, Doing & Segal (Barkman et al. 1964; Westhoff & van der Maarel 1973) in periods 2 and 3. All values were transformed into the ordinal 1-9 scale (van der Maarel 1979). All relevés were input into the TURBOVEG database (Hennekens & Schaminée 2001).

6.2.4. Soil research

Soil sampling. In 1993 and 2004, soil samples were taken according to the EGM protocol (Effect-oriented measures against acidification: de Vries 1990). Because the surface layer is important for cryptogams, the samples were subdivided into sub-samples of 0-2 cm, 2-10 cm and 10-30 cm Soil samples for determination of oxalate and cation ion content (CEC) were taken only from a depth of 0-10 cm. At a distance of 10-15 cm from the PQs or relevés, 8-10 sub-samples were taken at regular intervals and pooled.

Chemical analysis. The soil samples were chemically analysed for pH-H_2O, pH-KCl, % C (C-elementary), % N (N-total), % P (P-total), exchangeable ions (for CEC), % Al oxalate, Fe oxalate and P oxalate. For methods of analysis, see Chapter 3 (Ketner-Oostra & Sýkora 2000).

6.2.5. Data analysis

Multivariate analysis was used to study the spatial and temporal variation in the vegetation. All 239 relevés were ordinated and classified.

Classification. For classification we used TWINSPAN (Hill 1979). The final table has been summarized into a synoptic table, indicating presence class and characteristic cover. Species with comparable syntaxonomic status have been grouped into syntaxonomic species groups.

Ordination of cluster centroids. For each of the 16 clusters as derived from TWINSPAN a mean relevé was calculated (cluster centroid). The cluster centroids were subjected to Detrended Correspondence Analysis (DCA), resulting in an ordination of plant communities. The clusters are indicated in the resulting ordination diagram, which visualizes the main direction of change.

Relevés and soil parameters. A total of 18 relevés was analysed with DCA and CCA: seven PQs from 1993 (period 2), the same seven PQs in 2004 (period 3), two relevés with a monitoring history from 1994 onwards, and two relevés from very lichen-rich vegetation in 2004. The main direction of change is visualized in the DCA ordination diagram.

Species composition was related to the following environmental variables: pH-KCl in three soil layers (0-2 cm, 2-10 cm and 10-30 cm); % C-total in two soil layers (0-2 cm and 2-10 cm); % N-total in two soil layers (0-2 cm and 2-10 cm); % P-total in three soil layers (0-2 cm, 2-10 cm and 10-30 cm). As the % C-total and % N-total values in the 10-30 cm soil layer were below the limit of detection they were excluded from further analysis.

Response variables were transformed as follows: pH of the 0-2 cm and 2-10 cm soil layers, log (pH-KCl); the 10-30 cm soil layer was divided into three classes: class 1, pH-KCl < 4.4; class 2, pH-KCl 4.5 - 4.7; class 3, pH-KCl 4.8 - 4.9; percentage C-total, log (% C + 0.5); percentage N-total 0-2 cm soil layer log(% N + 0.02) and 2-10 cm log (% N + 0.01); % P-total 0-2 cm and 2-10 cm soil layers log (% P).

The significance of the relation between species composition and environmental variables was tested by Monte Carlo permutation test within Canonical Correspondence Analysis (CCA; ter Braak & Looman 1995). Both relevé and species ordination diagrams are presented.

6.2.6. Ellenberg indicator figures

The lichens were assigned to categories according to their ecology and with Ellenberg indicator figures indicating preference for light (L) and acidity (R); see Wirth (1992; 1995). For Ellenberg indicator figures, light (L) gives a scale of relative light intensity: 5 signifies semi-shade, rarely in full light; 6, between 5 and 7; 7 in a well-lit place, but also in partial shade; 8, mostly in light; 9, in full sunlight; Indiff. means indifferent. Reaction (R) gives a gradient of soil acidity and lime content where 1 signifies extremely acid (pH < 3.4); 2, very acid (pH 3.4-4.0); 3, rather acid (pH 4.1-4.8); 4, between 3 and 5; 5, moderately acid (pH 4.9-5.6); 6, between 5 and 7; 7, subneutral (pH 5.7-6.5); and 8, neutral (pH 6.6-7.5).

6.2.7. Nomenclature

The nomenclature for the phytosociological identification and syntaxonomic assignment of the plant communities follows Weeda et al. (1996) and Stortelder et al. (1996). The nomenclature for the phanerogams follows van der Meijden (1996), with the exception of *Festuca ovina* s.l. For the mosses we follow Dirkse et al. (1999), and for the lichens Aptroot et al. (2004).

In our vegetation table some species are a combination of two morphologically identical species, as *Cladina arbuscula* s.l includes *C. mitis*. We use *Cladonia cervicornis* s.l. for the former three subspecies of *C. cervicornis*, namely ssp. *cervicornis*, ssp. *verticillata* and ssp. *pulvinata* (van Herk & Aptroot 2003). When *Cladina ciliata* is mentioned, it is the var. *tenuis*. *Cladonia coccifera* includes *C. pleurota* and *C. borealis*. *C. crispata* is var. *cetrariiformis* and *C. uncialis* is ssp. *biuncialis* (Purvis et al. 1992).

Both Stoutjesdijk (1959) and van Embden & Verwey (1968) may have overlooked *C. ramulosa*, but perhaps this species was scarce at that time. The latter two authors do not mention *C. glauca* and probably recorded it as *C. cornutoradiata* (= *C. subulata*) instead. From former field observation we decided that *C. glauca* was most probable, so in the tables *C. glauca* includes *C. subulata*.

In earlier publications *Cladonia chlorophaea* and *C. merochlorophaea* were distinguished with their paraphenylene positive and negative varieties (Ketner-Oostra 1994a and b; Paus 1997). These species and their varieties could have been present in the PQs of 2 m x 2 m between 1993 and 2004, but in order to avoid damage were not tested. We decided to use *C. chlorophaea* s.l., by keeping to morphological distinctions, as had been done earlier (Biermann 1999; Ketner-Oostra & Sýkora 2004). *Cladonia chlorophaea* s.l. also seems appropriate for the data from 1968, where van Embden and Verwey used *C. pyxidata*, which at that time included *C. pyxidata* var. *chlorophaea* and var. *grayi* (van Embden & Verwey 1968). The real *C. pyxidata* has recently been renamed *C. monomorpha* (Aptroot et al. 2001).

6.3. Results

6.3.1. Lichen flora

Forty lichen species were found in the sand dune ecotope of the Kootwijkerzand in the three fieldwork periods (Table 6.3). However, since 1968 five lichen species have disappeared: three of them (*Cetraria nivalis*, *Cladina rangiferina* and *Cladonia deformis*) have disappeared from the Netherlands, one (*C. cornuta*) has disappeared from the inland dunes, and one (*Hypogymnia physodes*) is no longer growing epigeically on the inland dunes; see Table 6.3.

The pioneer species have high Light figures (Wirth 1992; 1995), mostly 8, meaning that they are light-loving. Only *C. foliacea* is indicated as a lichen from full light (Light figure 9). No pioneer species have disappeared from the Kootwijkerzand, but many are on the Red List for the Netherlands (Aptroot et al. 1998). *Stereocaulon condensatum* is a species from that Red List, but is doing rather well in areas where sand has blown out from between *P. piliferum* plants on the Kootwijkerzand. However, the very rare *S. saxatile* was last found here by Westhoff in 1948 (Brand & Sipman 1978). Since 1968 some humicole and aero-hygrophytic species have disappeared from the Kootwijk sand dune area, such as *Cladonia squamosa*, *C. phyllophora* and the terrestrial *Hypogymnia physodes*. Most humicole species are doing well in the research area and aero-hygrophytic species have increased in vitality since 1993 (Ketner-Oostra & Riksen 2005). Their Light figures are around 7, which means growing in well-lit places but also occurring in partial shade.

The pioneer species have Reaction figures (Wirth 1992; 1995), which indicate a wide amplitude: from 2-7 (*Cetraria aculeata*) or 4-8 (*Cladonia foliacea*). This indicates their adaptation to acid and also to more (sub-) neutral habitats. Most humicole and aero-hygrophytic species have a Reaction figure between 1 and 3, which indicates extreme to rather acid biotopes.

Table 6.3. List of lichen species in period 1 (1968), 2 (1993) and 3 (2004) with their Red List status after Aptroot et al. (1998). *For Light and ** Reaction (acidity) figures, see Methods. In the Red List status CR means critical, EN endangered, VU vulnerable, DIS disappeared.

Ecology	**Species**	**Research period**	**Red list status**	**L***	**R****
Pioneer spp.	*Cetraria aculeata*	1, 2 ,3		8	2-7
	Cetraria muricata	2, 3			
	Cladonia cervicornis s.l.	1, 2, 3			
	= *C. cervicornis* s.s.	3			
	= *C. verticillata*	3			
	= *C. pulvinata*	3	VU		
	Cladonia foliacea	1, 2, 3		9	4-8
	Cladonia furcata [1]	3		6-8	3-5
	Cladonia strepsilis	1, 2, 3	EN		
	Cladonia zopfii	1, 2, 3	VU		
	Diploschistes muscorum [1]	3	VU		
	Placynthiella icmalea	2, 3			
	Stereocaulon condensatum	1, 2, 3	VU		
	Trapeliopsis granulosa	1, 2, 3		Indiff.	1-3
Humicole spp.	*Cladonia borealis* [1]	3			
	Cladonia chlorophea s.l.	1, 2, 3		7	2-3
	Cladonia coccifera	1, 2, 3		7	3-5
	Cladonia callosa	2, 3			
	Cladonia cornuta [2]	1	EN		
	Cladonia deformis [3]	1	DIS		
	Cladonia digitata	1	VU		
	Cladonia fimbriata [1]	3			
	Cladonia floerkeana	1, 2, 3		7	2
	Cladonia glauca [4]	1, 2, 3		7	2
	Cladonia macilenta	1, 2, 3			
	Cladonia monomorpha [5]	1, 2, 3			
	Cladonia ramulosa	2, 3		Indiff.	2-3
	Cladonia phyllophora [3]	1	DIS		
	Cladonia polydactyla [6]	2, 3	EN		
	Cladonia squamosa	1, 2	CR		
	Cladonia subulata	1, 2, 3			
	Micarea leprosula	3			
	M. viridileprosula	3			
Humicole/Aero-h.	*Cladonia crispata*	1, 2, 3	VU		
	Cladonia gracilis	1, 2, 3			
	Cladonia uncialis	1, 2, 3			
Aero-hygrophytes	*Cetraria nivalis* [3, 7]	1	DIS		
	Cladina arbuscula s.l.	1, 2, 3	VU	8	1-5
	Cladina ciliata	2	EN		
	Cladina portentosa	1, 2, 3		7	1-5
	Cladina rangiferina [3, 8]	1	DIS		
Epigeic epiphytes	*Hypogymnia physodes* [9]	1	DIS	7	3

---

[1] From Radio Kootwijk inventorization (Klinge et al. 2004)
[2] In: Schimmel (1975)
[3] DIS, disappeared from the Netherlands
[4] includes *Cladonia subulata* in 1968
[5] in period 1 marked as *Cladonia pyxidata*
[6] = *Cladonia degenerans* in de Smidt (1969)
[7] in: Pos (1968)
[8] in: Leys (1964)
[9] DIS means here: almost disappeared growing epigeic

6.3.2. Vegetation

6.3.2.1 Classification

We distinguished a total of 16 clusters and 14 plant communities (Table 6.4). The syntaxonomic assignment of the clusters, the number of relevés in 1968, 1993 and 2004, and corresponding number of plants (higher plants, mosses, liverwort and lichens), is given in Table 6.5. The following plant communities were distinguished:

I Dry grasslands and pioneer communities on sandy soil

Grey hairgrass vegetation = Spergulo-Corynephoretum, Corynephorion canescentis

I.1 Spergulo-Corynephoretum subassociation inops (clusters 1-4)
The data set for 1968 contains only a few relevés of this subassociation. Van Embden & Verweij (1968) focussed on grassland and heath vegetation with lichens, but did not study the ecotope of blowing bare sand in detail.

I.1.a) variant with *Ammophila arenaria* (cluster 1)
In this very species-poor community *Ammophila arenaria* is abundant but dead in parts. This variant is further characterized by a low presence of green algae and *Corynephorus canescens*; it occurs on the crests of small dunes that are being buried by sand blowing over them (Weeda et al. 1996). It was probably present in all three periods, but was only recorded in 1993.

I.1.b) variant on bare sand without *Polytrichum piliferum* (cluster 2)
This variant has almost no green algae. *Corynephorus canescens* has a high presence but a low cover, and is dead in parts. The presence of *Festuca rubra* might indicate much fresh sand is being blown in. Mainly recorded in periods 2 and 3, but present in one relevé in 1968.

I.1.c) variant on bare sand with *Polytrichum piliferum* (clusters 3 and 4)
This variety has the highest presence and cover of green algae, colonizers of shifting sand. Lichens are sparse, only some *Cetraria aculeata* is found. Cluster 3 is mainly present in 1993 and 2004.

Cluster 4 includes *Festuca ovina* s.l. (Weeda et al. 1996) and has less green algae than cl. 3. The lichen *Stereocaulon condensatum* is present in cluster 4 (see Weeda et al. 1996), and in cl. 5, 6 and 7 (Spergulo-Corynephoretum cladonietosum). This species thrives in areas of eroding sand, where the thallus is left atop small pillars of sand in blown-out *Corynephorus* vegetation. Two thirds of the relevés are from 1968, one third from 2004. Only one relevé is from 1993: PQ.M, situated on a dynamic dune crest, with both *Ammophila arenaria* and *F. rubra*.

I.2 Spergulo-Corynephoretum subassociation cladonietosum (clusters 5-11)
This lichen-rich subassociation was the main object of study in all three research periods.

I.2.a) variant with *Polytrichum piliferum*, *Cetraria aculeata* and *Cladonia zopfii* (cluster 5).

This cluster was only recorded in 1968. The variant has been described by Masselink (1994), but we follow the syntaxomic classification according to Weeda et al. (1996). The high presence and relatively high cover of *C. aculeata* is typical of 1968; all 37 relevés are from that year. Moreover, 17 lichen species and three liverwort species are present.

I.2.b) variant with *Polytrichum piliferum* living but with some dead patches, overgrown by the green algae *Gloeocystis polydermatica* Künzing (Hindák) (clusters 6 and 7).

Note that cluster 6 was recorded in 1993 (19 relevés) and 2004 (11 relevés). The unicellular green algae mentioned produce a mucous film which hardens upon drying (Barkman 1958; Ettl & Gärtner 1995). When wet, the moss carpets are covered with a slimy layer, and when dried out, a crust is formed, which keeps water off the mosses or grasses below. Moss carpets that are dead in parts may form a substrate for lichen species. In cl. 6 half of the *P. piliferum* mats are alive and half are dead and covered with *G. polydermatica*. In this cluster, live *Campylopus introflexus* has established in the *P. piliferum* mats with minor presence and cover. *Cladonia coccifera* is the first lichen to establish on and between the mosses, followed by other *Cladonia* species and *Stereocaulon condensatum*, but all with very low presence and cover.

PQ.L was set out in 1993 in a relatively open situation with a pioneer stage without lichens, situated on a dynamic sand ridge with influence of nearby management (cutting of trees), which accelerated the force of the wind. PQ.G was also situated in a dynamic situation with sand blowing in, but with much dead *P. piliferum* and a few lichens.

Cluster 7 has much living and dead *P. piliferum*, covered by *G. polydermatica*, but has been separated from cl. 6 because of the many lichen species with a high presence and cover. Moreover, in this cluster live *Campylopus introflexus* has established in the *P. piliferum* mats with moderate presence and minor cover. This cluster is restricted to 1993 and 2004.

In 1993 PQ.E (which contained many lichen species) was marked off near the eastern edge of the *Pinus* wood bordering the Kootwijkerzand, as was PQ.K on the northeastern border, where cover sand is being exposed. In 2004 these two PQs are still in this cluster. In 2004 the cluster includes PQ.M (in cl. 4 in 1993) and the two PQs L and G (in cluster 5 in 1993). The very lichen-rich relevé Pk with cover sand near the surface, which was recorded in the Radio Kootwijk research in 2004 (Klinge et al. 2004), is part of this cluster.

I.2.c) variant with *Campylopus introflexus* (cluster 8)

This variant is characterized by a high presence of *C. introflexus*, half of which are dead and partly covered by *G. polydermatica*. Although *P. piliferum* is still rather abundant, in this variant its cover is very low. This cluster is only present in the more recent years 1993 and 2004. This community has been described by Weeda et al. (1996) as 'derivative community of Campylopus introflexus-[Koelerio-Corynephoretea]'.

Table 6.4. Syntaxonomic table of plant communities on the Kootwijkerzand containing cryptograms, based on relevés from 1968, 1993 and 2004. For every cluster the presence class is given (r = present in only < 1% of the relevés, + = in < 5%, I = 6-20%, II = 21-40%, III = 41-60%, IV = 61-80% and V = 81-100%). The characteristic cover is given in superscript in each column according to the ordinal scale 1 - 9. The characteristic cover is the mean cover of a species in one cluster, if present.

Ch* = characteristic species, d** = differential species. For explanation of the plant communities, see the text. For each cluster the presence of a permanent quadrat (PQ) is indicated; no asterisk indicates PQ in 1993, * indicates PQ in 2004.

Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Permanent quadrat				**M**		**G L**	**G* K** **L* E** **Rk E***	**K*** **J***	**P*** **Ft**		**N**		**F** **F*** **N***			
Number of relevés	2	12	12	14	37	22	30	27	7	6	18	16	15	8	3	0
Mean number of species	3	2	3	4	10	9	15	13	17	19	13	18	16	17	7	11
Community with *Ammophila*																
Ammophila arenaria	V ^{4}	I ^{3}	-	II ^{3}	I ^{1}	-	+ ^{5}	-	-	-	-	I ^{2}	-	-	-	-
*Ammophila arenaria (*dead)	V ^{5}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
KOELERIO-CORYNEPHORETEA																
Corynephorus canescens	III ^{5}	V ^{3}	V ^{4}	V ^{5}	V ^{5}	V ^{3}	V ^{3}	V ^{3}	V ^{3}	V ^{5}	IV ^{3}	IV ^{3}	II ^{1}	III ^{3}	II ^{3}	-
*Corynephorus canescens (*dead)	-	II ^{2}	I ^{2}	I ^{3}	-	II ^{2}	III ^{3}	II ^{3}	-	I ^{3}	I ^{1}	-	-	-	-	-
Carex arenaria ch*	-	-	-	-	I ^{2}	-	-	-	-	II ^{2}	I ^{2}	I ^{2}	II ^{2}	-	-	I ^{5}
Hypnum cupressiforme	-	-	-	-	-	-	-	-	-	-	-	I ^{3}	I ^{2}	II ^{5}	II ^{2}	IV ^{6}
Hypochaeris radicata ch	-	-	-	-	I ^{3}	-	-	-	-	-	-	-	-	I ^{1}	-	-
Festuca rubra d**	-	II ^{2}	-	II ^{3}	-	I ^{2}	-	-	-	-	-	-	-	-	-	-
Ceratodon purpureus ch	-	-	-	-	-	+ ^{1}	-	-	-	I ^{5}	-	-	-	-	-	-
Diploschistes muscorum	-	-	-	-	-	-	+ ^{1}	-	-	-	-	-	-	-	-	-
CORYNEPHORETALIA CANESCENTIS CORYNEPHORION																
Polytrichum piliferum	-	I ^{4}	IV ^{4}	III ^{6}	V ^{7}	V ^{7}	V ^{6}	IV ^{2}	III ^{4}	III ^{3}	III ^{3}	IV ^{4}	I ^{2}	II ^{3}	II ^{2}	I ^{5}
Cetraria aculeata	-	-	I ^{2}	-	V ^{3}	-	III ^{2}	I ^{1}	III ^{2}	V ^{2}	II ^{2}	IV ^{2}	-	-	-	-
Cladonia macilenta	-	-	-	-	II ^{2}	+ ^{1}	IV ^{2}	IV ^{1}	V ^{2}	IV ^{2}	II ^{1}	II ^{2}	IV ^{1}	-	-	I ^{2}
Cladonia cervicornis s.l.	-	-	-	-	I ^{3}	+ ^{1}	II ^{2}	II ^{2}	II ^{1}	IV ^{2}	I ^{3}	III ^{2}	I ^{1}	-	-	-

Cladonia crispata	-	-	-	-	+^{1}	I^{2}	II^{2}	II^{2}	III^{2}	V^{3}	II^{2}	I^{2}	II^{1}	-	-	-
Cladonia zopfii	-	-	-	-	II^{3}	+^{2}	II^{1}	I^{1}	III^{1}	II^{2}	II^{3}	III^{3}	I^{1}	-	-	-
Cladonia ramulosa	-	-	-	-	-	+^{1}	III^{4}	II^{2}	IV^{4}	V^{5}	II^{1}	-	III^{2}	-	-	I^{1}
Differentiating CORYNEPHORION																
Cladina portentosa	-	-	-	-	I^{4}	-	I^{2}	II^{2}	V^{4}	V^{5}	V^{5}	V^{3}	IV^{3}	I^{2}	-	II^{2}
Cladonia gracilis	-	-	-	-	II^{2}	-	II^{2}	II^{1}	V^{4}	V^{5}	V^{4}	IV^{3}	II^{2}	-	-	-
Cladonia glauca	-	-	-	-	III^{3}	II^{1}	V^{3}	III^{2}	V^{2}	V^{2}	II^{2}	V^{3}	III^{2}	I^{2}	-	II^{1}
Cladonia coccifera	-	-	-	-	IV^{3}	IV^{2}	V^{4}	V^{2}	V^{4}	V^{3}	IV^{2}	V^{3}	V^{2}	I^{2}	II^{2}	II^{2}
Cladonia floerkeana	-	-	-	-	I^{2}	I^{1}	V^{2}	III^{2}	IV^{3}	V^{2}	I^{1}	I^{2}	III^{2}	-	-	I^{1}
Spergulo-Corynephoretum																
Polytrichum piliferum ch	-	I^{4}	IV^{4}	III^{6}	V^{7}	V^{7}	V^{6}	IV^{2}	III^{4}	III^{3}	III^{3}	IV^{4}	I^{2}	II^{3}	II^{2}	I^{5}
Spergula morisonii ch	-	-	II^{1}	I^{1}	IV^{3}	IV^{2}	IV^{1}	IV^{1}	III^{1}	V^{1}	I^{1}	III^{2}	II^{1}	-	-	I^{1}
Agrosits vinealis	-	-	-	III^{4}	V^{4}	+^{1}	II^{2}	III^{3}	III^{3}	III^{3}	V^{2}	V^{4}	III^{2}	V^{4}	V^{4}	I^{2}
Cladonia zopfii ch	-	-	-	-	II^{3}	+^{2}	II^{1}	I^{1}	III^{1}	II^{2}	II^{3}	III^{3}	I^{1}	-	-	-
Cladonia cervicornis s.l. ch	-	-	-	-	I^{3}	+^{1}	II^{2}	II^{2}	II^{1}	IV^{2}	I^{3}	III^{2}	I^{1}	-	-	-
Cladonia strepsilis ch	-	-	-	-	II^{2}	I^{1}	I^{3}	I^{3}	I^{1}	IV^{2}	II^{3}	I^{2}	-	I^{2}	-	-
Cladonia crispata d	-	-	-	-	+^{1}	I^{2}	II^{2}	II^{2}	III^{2}	V^{3}	II^{2}	I^{2}	II^{1}	-	-	-
Stereocaulon condensatum ch	-	-	-	I^{5}	II^{2}	I^{1}	II^{2}	-	-	-	-	II^{2}	-	-	-	-
Cladina ciliata ch	-	-	-	-	-	-	-	-	-	-	I^{1}	-	-	-	-	-
Cladonia foliacea d	-	-	-	-	+^{1}	-	+^{1}	-	-	II^{1}	-	-	I^{1}	-	-	-
Jasione montana d	-	-	-	-	-	-	-	-	-	-	-	I^{2}	-	II^{4}	-	-
Spergulo-Corynephoretum inops variant with *Polytrichum piliferum*																
Polytrichum piliferum	-	I^{4}	IV^{4}	III^{6}	V^{7}	V^{7}	V^{6}	IV^{2}	III^{4}	III^{3}	III^{3}	IV^{4}	I^{2}	II^{3}	II^{2}	I^{5}
with *Ammophila*																
Ammophila arenaria	V^{4}	I^{3}	-	II^{3}	I^{1}	-	+^{5}	-	-	-	-	I^{2}	-	-	-	-
with *Festuca ovina*																
Festuca ovina s.l.	-	-	I^{2}	IV^{2}	V^{4}	IV^{3}	III^{2}	V^{3}	II^{4}	III^{2}	IV^{5}	V^{5}	V^{4}	V^{6}	IV^{7}	-
Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**

Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Permanent quadrat				**M**		**G L**	**G* K** **L* E** **Rk E***	**K*** **J***	**P*** **Ft**		**N**		**F** **F*** **N***			
Festuca ovina (dead)	-	-	-	-	-	+ ^{3}	I ^{3}	II ^{3}	-	-	-	-	II ^{5}	-	-	-
with Green algae																
Green algae	III ^{5}	I ^{2}	V ^{6}	I ^{3}	+ ^{7}	III ^{3}	II ^{2}	I ^{2}	II ^{3}	II ^{2}	-	-	I ^{2}	-	-	-
Stereocaulon condensatum	-	-	-	I ^{5}	II ^{2}	I ^{1}	II ^{2}	-	-	-	-	II ^{2}	-	-	-	-
S.-Corynephoretum cladonietosum																
Cladina portentosa d	-	-	-	-	I ^{4}	-	I ^{2}	II ^{2}	V ^{4}	V ^{5}	V ^{5}	V ^{3}	IV ^{3}	I ^{2}	-	II ^{2}
Cladonia gracilis d	-	-	-	-	II ^{2}	-	II ^{2}	II ^{1}	V ^{4}	V ^{5}	V ^{4}	IV ^{3}	II ^{2}	-	-	-
Cladonia floerkeana d	-	-	-	-	I ^{2}	I ^{1}	V ^{2}	III ^{2}	IV ^{3}	V ^{2}	I ^{1}	I ^{2}	III ^{2}	-	-	I ^{1}
Cladonia glauca d	-	-	-	-	III ^{3}	II ^{1}	V ^{3}	III ^{2}	V ^{2}	V ^{2}	II ^{2}	V ^{3}	III ^{2}	I ^{2}	-	II ^{1}
Cladonia uncialis d	-	-	-	-	I ^{2}	-	-	-	I ^{1}	III ^{1}	IV ^{3}	I ^{2}	I ^{1}	-	-	-
Cladonia cervicornis s.l.	-	-	-	-	I ^{3}	+ ^{1}	II ^{2}	II ^{2}	II ^{1}	IV ^{2}	I ^{3}	III ^{2}	I ^{1}	-	-	-
Variant with *Cladonia zopfii* and *Cetraria aculeata*																
Cladonia zopfii	-	-	-	-	II ^{3}	+ ^{2}	II ^{1}	I ^{1}	III ^{1}	II ^{2}	II ^{3}	III ^{3}	I ^{1}	-	-	-
Cetraria aculeata	-	-	I ^{2}	-	V ^{3}	-	III ^{2}	I ^{1}	III ^{2}	V ^{2}	II ^{2}	IV ^{2}	-	-	-	-
Cetraria muricata	-	-	-	-	-	-	I ^{1}	-	-	II ^{1}	-	-	-	-	-	-
Variant with *Cladonia strepsilis*																
Cladonia strepsilis	-	-	-	-	II ^{2}	I ^{1}	I ^{3}	I ^{3}	I ^{1}	IV ^{2}	II ^{3}	I ^{2}	-	I ^{2}	-	-
Variant with *Polytrichum piliferum* dead																
Polytrichum piliferum	-	I ^{4}	IV ^{4}	III ^{6}	V ^{7}	V ^{7}	V ^{6}	IV ^{2}	III ^{4}	III ^{3}	III ^{3}	IV ^{4}	I ^{2}	II ^{3}	II ^{2}	I ^{5}
Polytrichum piliferum (dead)	-	-	-	II ^{6}	-	V ^{7}	V ^{8}	II ^{5}	-	II ^{4}	I ^{3}	-	I ^{5}	-	-	-
Gloeocystis polydermatica	-	-	-	-	+ ^{7}	V ^{7}	V ^{7}	III ^{6}	V ^{6}	III ^{6}	I ^{6}	-	V ^{6}	-	-	III ^{6}
Variant with *Campylopus introflexus*																
Campylopus introflexus	-	-	I ^{2}	-	-	III ^{3}	IV ^{4}	V ^{8}	V ^{5}	II ^{2}	II ^{4}	-	IV ^{5}	-	-	III ^{3}
Campylopus introflexus (dead)	-	-	-	-	-	+ ^{6}	-	IV ^{7}	V ^{6}	-	I ^{2}	-	II ^{5}	-	-	-

***Cladina* variant**																
Cladina portentosa	-	-	-	-	I^{4}	-	I^{2}	II^{2}	V^{4}	V^{5}	V^{5}	V^{3}	IV^{3}	I^{2}	-	II^{2}
Cladina arbuscula s.l.	-	-	-	-	+^{2}	-	+^{1}	-	I^{1}	III^{2}	IV^{2}	II^{2}	II^{1}	-	-	-
Cladonia uncialis	-	-	-	-	I^{2}	-	-	-	I^{1}	III^{1}	IV^{3}	I^{2}	I^{1}	-	-	-
COELERIO-CORYNEPHORETEA and CALLUNO-ULICETEA																
Dicranum scoparium	-	-	-	-	-	+^{3}	-	-	I^{2}	-	III^{4}	I^{3}	III^{4}	-	II^{3}	V^{3}
*Dicranum scoparium (*dead)	-	-	-	-	-	+^{3}	-	-	-	-	-	-	I^{6}	-	-	-
CALLUNO-ULICETEA																
Calluna vulgaris	-	-	-	-	I^{2}	-	+^{1}	I^{2}	-	I^{5}	II^{3}	V^{6}	V^{5}	IV^{6}	V^{5}	V^{8}
Hypnum jutlandicum	-	-	-	-	-	-	-	-	-	-	I^{2}	-	-	-	-	II^{3}
Pleurozium schreberi	-	-	-	-	-	-	-	-	-	-	-	-	I^{1}	-	-	I^{6}
Campylopus flexuosus	-	-	-	-	-	+^{2}	-	-	-	-	I^{3}	III^{4}	-	-	-	III^{1}
Ptilidum ciliare	-	-	-	-	-	-	-	-	-	-	-	I^{2}	I^{1}	-	-	-
Campylopus pyriformis	-	-	-	-	I^{5}	-	-	-	-	-	I^{2}	II^{3}	II^{1}	-	-	II^{2}
Juniperus communis	-	-	-	-	-	-	-	-	-	-	-	-	I^{3}	I^{6}	-	-
Dicranum spurium	-	-	-	-	-	-	-	-	-	-	-	I^{2}	-	-	-	-
Calluno-Ulicetalia and Calluno-Genistion pilosae																
Pohlia nutans d	-	-	-	-	I^{5}	+^{1}	-	-	-	-	I^{2}	V^{4}	I^{1}	IV^{7}	IV^{7}	I^{2}
Campylopus flexuosus d	-	-	-	-	-	+^{2}	-	-	-	-	I^{3}	III^{4}	-	-	-	III^{1}
Campylopus pyriformis d	-	-	-	-	I^{5}	-	-	-	-	-	I^{2}	II^{3}	II^{1}	-	-	II^{2}
Deschampsia flexuosa d	-	-	-	-	-	I^{2}	-	I^{2}	II^{2}	I^{1}	III^{2}	I^{2}	V^{3}	-	-	IV^{2}
Polytrichum commune	-	-	-	-	-	-	-	+^{5}	-	-	-	-	I^{2}	-	-	I^{3}
Genisto anglicae-Callunetum																
Polytrichum piliferum	-	I^{4}	IV^{4}	III^{6}	V^{7}	V^{7}	V^{6}	IV^{2}	III^{4}	III^{3}	III^{3}	IV^{4}	I^{2}	II^{3}	II^{2}	I^{5}
Festuca ovina s.l.	-	-	I^{2}	IV^{2}	V^{4}	IV^{3}	III^{2}	V^{3}	II^{4}	III^{2}	IV^{5}	V^{5}	V^{4}	V^{6}	IV^{7}	-
Calluna vulgaris	-	-	-	-	I^{2}	-	+^{1}	I^{2}	-	I^{5}	II^{3}	V^{6}	V^{5}	IV^{6}	V^{5}	V^{8}
Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**

Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Permanent quadrat				**M**		**G L**	**G* K** **L* E** **Rk E***	**K*** **J***	**P*** **Ft**		**N**		**F** **F*** **N***			
G.-C cladonietosum																
Cladonia macilenta	-	-	-	-	II^{2}	+^{1}	IV^{2}	IV^{1}	V^{2}	IV^{2}	II^{1}	II^{2}	IV^{1}	-	-	I^{2}
Cladonia chlorophaea s.l.	-	-	-	-	I^{2}	+	III^{2}	III^{1}	IV^{2}	III^{3}	III^{1}	IV^{2}	IV^{3}	-	-	III^{2}
Cladonia crispata	-	-	-	-	+^{1}	I^{2}	II^{2}	II^{2}	III^{2}	V^{3}	II^{2}	I^{2}	II^{1}	-	-	-
Pohlia nutans	-	-	-	-	I^{5}	+^{1}	-	-	-	-	I^{2}	V^{4}	I^{1}	IV^{7}	IV^{7}	I^{2}
Campylopus pyriformis	-	-	-	-	I^{5}	-	-	-	-	-	I^{2}	II^{3}	II^{1}	-	-	II^{2}
Campylopus flexuosus	-	-	-	-	-	+^{2}	-	-	-	-	I^{3}	III^{4}	-	-	-	III^{1}
Cladonia squamosa d	-	-	-	-	-	-	-	-	-	-	I^{1}	IV^{2}	-	-	-	-
G.-C. lophozietosum ventricosae																
Lophozia ventricosa d	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	I^{3}
Cladonia glauca d	-	-	-	-	III^{3}	II^{1}	V^{3}	III^{2}	V^{2}	V^{2}	II^{2}	V^{3}	III^{2}	I^{2}	-	II^{1}
Empetrum nigrum ch	-	-	-	-	-	-	-	-	-	-	-	-	-	-	V^{8}	-
Pleurozium schreberi	-	-	-	-	-	-	-	-	-	-	-	-	I^{1}	-	-	I^{6}
Ptilidum ciliare	-	-	-	-	-	-	-	-	-	-	-	I^{2}	I^{1}	-	-	-
Hypnum jutlandicum	-	-	-	-	-	-	-	-	-	-	I^{2}	-	-	-	-	II^{3}
Barbilophozia barbata d	-	-	-	-	-	-	-	-	-	-	-	I^{2}	-	-	-	-
Scapanea nemorea d	-	-	-	-	-	-	-	-	-	-	-	I^{3}	-	-	-	-
FRAME COMMUNITIES (Fc)																
Fc Campylopus -																
[Koelerio-Corynephoretea]																
Campylopus introflexus	-	-	I^{2}	-	-	III^{3}	IV^{4}	V^{8}	V^{5}	II^{2}	II^{4}	-	IV^{5}	-	-	III^{3}
Campylopus introflexus (dead)	-	-	-	-	-	+^{6}	-	IV^{7}	V^{6}	-	I^{2}	-	II^{5}	-	-	-
Rumex acetosella	-	-	-	-	I^{3}	-	+^{3}	+^{1}	II^{1}	II^{2}	IV^{3}	II^{3}	I^{2}	-	-	-
Wood encroachment																
Pinus sylvestris	-	I^{1}	-	I^{2}	I^{1}	I^{1}	I^{1}	II^{1}	III^{3}	III^{1}	II^{1}	II^{2}	I^{2}	II^{2}	-	-

Cluster	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Quercus robur	-	-	-	-	-	-	-	I^{1}	-	-	II^{1}	III^{2}	I^{1}	II^{2}	II^{1}	-
Prunus serotina	-	-	-	II^{1}	-	-	-	-	-	-	-	II^{2}	-	II^{1}	II^{2}	-
Sorbus aucuparia	-	-	-	-	-	-	-	-	-	-	-	-	-	I^{1}	-	-
Rhamnus frangula	-	-	-	-	-	-	-	-	-	-	-	I^{2}	-	-	-	-
Remaining species Querco-fagetea + Querceto r-p																
Quercetea robori-petraeae																
Dicranella heteromalla ch	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	I^{2}
Querco-fagetea																
Eurhynchium striatum ch	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	I^{1}
Remaining species																
Cephaloziella divaricata	-	-	-	-	+^{2}	-	-	-	-	-	-	I^{2}	-	-	II^{2}	IV^{1}
Trapeliopsis granulosa	-	-	-	-	+^{1}	-	I^{1}	-	I^{1}	-	-	-	-	-	-	-
Lophozia excisa	-	-	-	-	+^{2}	-	-	-	-	-	-	-	-	-	-	-
Lophozia incisa	-	-	-	-	+^{2}	-	-	-	-	-	-	I^{3}	-	-	-	-
Placynthiella icmalea	-	-	-	-	-	-	I^{2}	-	-	-	-	-	II^{2}	-	-	-
Micarea leprosula	-	-	-	-	-	-	I^{1}	-	-	-	-	-	I^{1}	-	-	I^{1}
Cladonia callosa	-	-	-	-	-	-	I^{1}	+^{1}	I^{1}	-	-	-	-	-	-	-
Agrostis capillaris	-	-	-	-	-	-	-	+^{1}	-	I^{1}	-	-	I^{1}	-	-	-
Cladonia polydactyla	-	-	-	-	-	-	-	+^{2}	-	-	I^{1}	-	-	-	-	-
Hypogymnia physodes	-	-	-	-	-	-	-	-	-	-	-	$\boxed{\text{III}^{2}}$	-	I^{1}	-	-
Lophocolea bidentata	-	-	-	-	-	-	-	-	-	-	-	I^{2}	-	-	II^{2}	-
Gymnocolea inflata	-	-	-	-	-	-	-	-	-	-	-	I^{2}	-	-	-	I^{1}
Polytrichum formosum	-	-	-	-	-	-	-	-	-	-	-	-	I^{6}	-	-	I^{1}

Remaining phanerophytes: *Arnica montana* cluster 12 (I^{2}); *Danthonia decumbens* cluster 12 (I^{5}); *Dryopteris carthusianum* cluster 16 (I^{1})*; Erica tetralix* cluster 13 (I^{1})*; Holcus lanatus* cluster 13 (I^{1})*; Poa pratensis* cluster 11 (I^{1})*; Potentilla erecta* cluster 12 (I^{2})*; Rubus* sp. cluster 12 (I^{2}). **Remaining cryptogams:** *Aulacomnium palustre* cluster 12 (I^{2}); *Brachythecium rutabulum* cluster 16 (I^{2}); *Cephalozia* sp. cluster 12 (I^{2}); *Micarea viridileprosula* cluster 16 (I^{1}); *Nardia geoscyphus* cluster 14 (I^{6}); *Cladonia deformis* cluster 12 (I^{2}); *Cladonia digitata* cluster 16 (I^{1}).

Table 6.5. Syntaxonomic allocation of the clusters from the synoptic table. The total number of relevés is listed. The total number of phanerophytes, mosses, liverworts and lichens is listed. * self-sown, **bold** = community present predominantly in one period.

Cluster	**Alliance**	**Community**	**Number of releves**				**Number of plants**			
			Total	in 68	in 93	in 04	phanerophytes	mosses	liverworts	lichens
1		Community with *Ammophila arenaria*	2	0	2	0	2	0	0	0
2	Corynephorion	Spergulo-Corynephoretum inops,variety without *Polytrichum piliferum*	12	1	6	5	3 + 1 tree*	1	0	0
3		S.-C. inops, variety with *P. piliferum* and Green algae	12	0	**9**	**3**	3	2	0	1
4		S.-C. inops, variety with *P. piliferum* and *Festuca ovina*	14	8	1	5	6 + 2 trees	1	0	1
5		S.-C. cladonietosum, variety with *P. piliferum* and *Cetraria aculeata*	36	**36**	0	0	9 + 1 tree	3	3	17
6		S.-C. cladonietosum, variety with *P. piliferum* living, partly dead and covered with algae (*Gloeocystis polydermatica*)	23	0	**19**	**4**	5 + 1 tree	6	0	11
7		S.-C. cladonietosum, variety with *P. piliferum* living, partly dead and covered with algae (*G. polydermatica*)	30	0	**19**	**11**	7 + 1 tree	2	0	23
8		S.-C. cladonietosum, variety with *Campylopus introflexus*	27	0	**6**	**21**	8 + 2 trees	3	0	15
9		S.-C. cladonietosum, *Cladina* variety with *C. introflexus* living and partly dead and covered with algae (*G. polydermatica*)	7	0	**1**	**6**	6 + 1 tree	2	0	17
10		S.-C. cladonietosum, *Cladina* variety with *Cladonia strepsilis*	6	0	**3**	**3**	9 + 1 tree	3	0	16
11		S.-C. cladonietosum, *Cladina* variety with *F. ovina* and *Rumex acetosella*	18	5	10	3	9 + 2 trees	6	0	18
12	transitional	S.-C. cladonietosum, *Cladina* variety with *F. ovina* and *Calluna vulgaris* / G.a.-C. cladonietosum with *C. aculeata* and *Hypogymnia physodes*	16	**16**	0	0	14 + 4 trees	7	9	18
13	transitional	S.-C. cladonietosum, *Cladina* variety with *F. ovina* and *Calluna vulgaris* / G.a.-C. cladonietosum with *C. introflexus* and algae (*G. polydermatica*)	15	0	**6**	**9**	12 + 2 trees	8	1	16
14	Calluno-Genistion	Genisto anglicae-Callunetum cladonietosum with *Pohlia nutans*	8	**8**	0	0	8 + 4 trees	3	1	5
15		G.a.-C. cladonietosum / lophozietosum ventricosae with *P. nutans* and *Empetrum nigrum*	3	**3**	0	0	5 + 2 trees	3	2	1
16		G.a.-C. cladonietosum / lophozietosum ventricosae with *Dicranum scoparium* and *Deschampsia flexuosa*	10	1	1	8	6			
		Total number of releves	239	78	83	78				

On and between the mosses 15 lichen species have been counted. Here PQ.J was laid out in 1993 when the moss layer had been almost totally turned upside down by birds searching for insects; until 2004 it was monitored for the re-occurrence of the lichens.

I.2.d) variant with *Cladina* spp. and *Campylopus introflexus* (cluster 9)
This variant is characterized by the combination of both living and dead *Campylopus introflexus,* partly covered by *G. polydermatica,* and a high number and presence of lichen species.

There are 17 lichen species, among which *Cladina portentosa* and *Cladonia gracilis* with a high presence and a moderate cover. Also present are *C. zopfii*, *C. uncialis* and *Cladina arbuscula* s.l. Two relevés were classified in this cluster. The first is PQ.P, which was marked out in a very lichen-rich *Corynephorus* vegetation in 1995, probably in a formerly levelled area of blowing sand between a road and a *Pinus* forest. In 2004 relevé Ft was placed in a lichen-rich area that probably developed inside the *Pinus* forest after removal of self-sown trees and litter. The variant with *Cladina* spp. and *Campylopus introflexus* is only present in the recent years 1993 and 2004.

I.2.e) variant with *Cladina* spp. and *Cladonia strepsilis* (cluster 10)
A *Cladonia strepsilis* variant of the Spergulo-Corynephoretum cladonietosum has been described by Weeda et al. (1996) for blown-out planes and depressions with loamy sand. Cluster 10 is characterized by the combination and high presence of *C. strepsilis* and *Cetraria aculeata*. In this community *P. piliferum,* dead in parts and covered by *G. polydermatica,* both with presence class III, occurs, as well as *C. introflexus* with presence class II. Because the relevés were large (2 x 2 m) 16 lichen species are found in combination. They include the pioneer species *Cetraria aculeata*, *Cladonia strepsilis, C. cervicornis* s.l. and *C. foliacea* and also many humicolous species, as well as *Cladina portentosa*, *Cla. arbuscula* s.l., *Cladonia gracilis* and *C. uncialis.* As lichen synusia (Barkman 1968) are small, micro-communities are often distinguished (Paus 1997). The variant with *Cladina* spp. and *Cladonia strepsilis* therefore consists of a mosaic of different micro-communities. This cluster is composed of relevés from 1993 and 2004.

I.2.f) variant with *Cladina* spp., *Festuca ovina* s.l., *Rumex acetosella* (cluster 11)
This variant is characterized by the relatively high cover and presence of *Festuca ovina* s.l., *Cladina portentosa*, *Cla. arbuscula* s.l., *Cladonia gracilis* and *C. uncialis*. The total lichen cover in the 2 m x 2 m plots was 50%. This cluster is present in all three years and is found at the edges of the pine forest along the border of the Kootwijkerzand. PQ.N represented in this cluster, was marked out in 1993 between a large self-sown Scots pine and deciduous roadside trees.

II Transitional community between Spergulo-Corynephoretum subassociation cladonietosum / Genisto anglicae-Callunetum subassociation cladonietosum

The vegetation in clusters 12 and 13 is transitional between the Spergulo-Corynephoretum cladonietosum and the Genisto-Callunetum cladonietosum.

II.1.a) variant with *Cetraria aculeata* and *Hypogymnia physodes* (cluster 12)
This variant has many (18) lichen species and also six moss species and nine liverwort species. It occurred on north-facing slopes and on gently sloping sand dunes near the edge of surrounding *Pinus* wood and represents intermediate successional stages colonized by *Calluna vulgaris. Hypogymnia physodes* is growing epiphytically on dead *Calluna* twigs, and also terrestrially on open sites. This species is very sensitive to air pollution, as is *Cladonia squamosa* occurring in this variant with presence class IV. The relevés from this community were all from 1968.

II.1.b) variant with *Campylopus introflexus* and algae (*G. polydermatica*) (cl. 13).
This variant is characterized by *Calluna* in combination with *Campylopus introflexus* and algae like *G. polydermatica.* It mainly occurred along the eastern edges of the Kootwijkerzand, where the State Forestry has removed self-sown Scots pine. This cluster has many lichen species but only one liverwort. It is only represented by relevés from 1993 and 2004. PQ.N started in cl. 11 in 1993 and ended in cl. 13 in 2004. PQ.F was classified in this cluster both in 1993 and in 2004. In the area where PQ.F was laid out in 1993, 15 ha of self-sown pine was cut down in 1962. Moreover, the branches were burned, but the litter not removed (Table 6.2). In this part of the Kootwijkerzand a mosaic vegetation has developed of different varieties of Spergulo-Corynephoretum with *Calluna* heath and *Juniperus communis* bushes.

III Dry heath vegetation: Calluno-Genistion
The dry inland heath belongs to the Genisto anglicae-Callunetum (Stortelder et al. 1996) and is represented in our table by the subassociation *cladonietosum* (cluster 14) and a transition between the *cladonietosum* and the *lophozietosum ventricosae* (cl. 15 -16).

III.1 Genisto anglicae-Callunetum cladonietosum
III.1.a) variant with *Pohlia nutans* (cluster 14)
In this variant *Pohlia nutans* has a high presence and cover. Both *Festuca ovina* s.l. and *Agrostis vinealis* have a high presence, while *F. ovina* has the same moderate cover as *Calluna vulgaris* (6). *Juniperus communis* is present, as in cl. 12. This variant is poor in lichens and only one liverwort (*Nardia geoscyphus*) has been found. The high presence and cover of *Pohlia nutans* and the presence of *Hypogymnia physodes* point to a succession stage exclusive to 1968. The many seedlings from deciduous trees indicate the start of the last succession stage into wood as it occurred near the edge of the wood. All relevés in this cluster are from 1968.

III.2 Genisto anglicae-Callunetum cladonietosum / lophozietosum ventricosae
III.2.a) variant with *Pohlia nutans* and *Empetrum nigrum* (cluster 15)
This variant is characterized by the dominance of *Empetrum nigrum.* Furthermore it is comparable to cluster 14 with *Calluna vulgaris, Festuca ovina* s.l. and *Agrostis vinealis* having a high frequency and a moderate cover and *Pohlia nutans* being the dominant moss. Likewise there are very few lichen and liverwort species: only two

liverwort species (*Lophocolea bidentata* and *Cephaloziella divaricata*) occur and both communities have *C. coccifera* in common. This variant was only found in 1968.

III.2.b) variant with *Dicranum scoparium* and *Deschampsia flexuosa* (cluster 16)
In this variant *Calluna vulgaris* and *Deschampsia flexuosa* co-occur with 13 moss species, the maximum present in one cluster, among which much *Dicranum scoparium*, *Hypnum cupressiforme*, *Campylopus flexuosus* and *C. introflexus*. In 2004 three liverwort species were found (*Lophozia ventricosa, Cephaloziella divariata* and *Gymnocolea inflata*) and ten lichen species. The variant was mainly described from north slopes of young dunes in the eastern part of the Kootwijkerzand in 2004, but in 1968 and in 1993 it was also represented by one relevé.

6.3.2.2. Ordination of TWINSPAN clusters (Figure 6.3)

The first axis corresponds to a gradient from open, pioneer vegetation on the left-hand side to a late successional stage consisting of a closed heath vegetation on the right-hand side. This successional gradient starts with almost open sand with *Ammophila*, followed by the following sequence of successional stages: Spegulo-Corynephoretum (S.-C.) inops, S.-C. cladonietosum, transition between S.-C. and Genisto anglicae-Callunetum (G.a.-C.), G.a.-C., and finally G.a.-C. with dominance of *Empetrum nigrum*. In the clusters plotted in the upper part, *Campylopus introfexus* has a high presence and/or cover, whereas in the clusters in the lower part of the diagram *Campylopus* is absent or present with low frequency and cover. The clusters that are exclusively from 1968 are restricted to the lower part of the diagram.

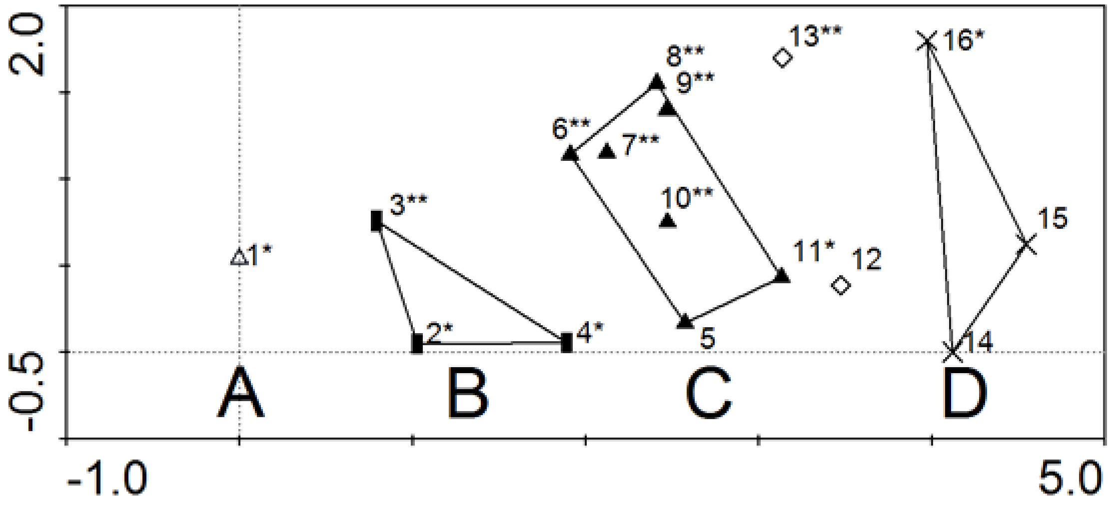


Figure 6.3. Ordination diagram representing a DCA of all relevés on the Kootwijkerzand in the three research periods. (a) TWINSPAN clusters; (b) species. A = community with *Ammophila*; B = Spergulo-Corynephoretum inops; C = Spergulo-Corynephoretum cladonietosum; D = Genisto-Callunetum cladonietosum. Unasterisked clusters = only present in 1968, clusters with * = present in all three periods, and with ** = only present in the recent periods (1993 and 2004).

In 1968 the succession from open sand went through a stage with *P. piliferum* and a considerable presence and cover of *Cetraria aculeata*, followed by *Cladonia* and *Cladina* species and forming a lichen-rich transition to *Calluna* heath, with some mosses included (Table 6.4). The recent periods 1993 and 2004 show a succession from the stage with *P. piliferum*, where many patches of this species are dying, covered by a slimy (or crusty) layer of green algae and often invaded by the alien *C. introflexus*. *Cladonia* species appear in this stage, followed by the transition to *Calluna* heath, which is rather rich in grasses, mosses and *Cladina* spp.

All syntaxa occur in all years, but not all variants do. In all years the S.-C. inops variant with *Ammophila arenaria* was recorded and so were the variant on bare sand without *Polytrichum piliferum* and the variant on bare sand with *Polytrichum piliferum,* the lichen *Stereocaulon condensatum* and limited green algae (cluster 4). The variant on bare sand with *P. piliferum* and much green algae (cluster 3) was only present in later years.

The S.-C. cladonietosum variant with *P. piliferum*, *Cetraria aculeata* and *Cladonia zopfii* (cluster 5) was only found in 1968. The variant with *Cladina* spp., *Festuca ovina* s.l. and *Rumex acetosella* (cluster 11) was found in all years. The variants with *P. piliferum* that is dead in parts and overgrown by the green algae *Gloeocystis polydermatica* (cl. 6-9), with *Campylopus introflexus* (cluster 8), with *Cladina* spp. and *C. introflexus* (cluster 9) and with *Cladina* spp. and *Cladonia strepsilis* (cluster 10) were only recorded in the more recent periods 1993 and 2004. From the transition between S.-C. and G.a.-C., the variant with *Cetraria aculeata* and *Hypogymnia physodes* (cluster 12) was only found in 1968, whereas the variant with *C. introflexus* and algae (*G. polydermatica*) (cluster 13) was only found in the two more recent years.

The G.a.-C. cladonietosum variants with *Pohlia nutans* (cluster 14) and with *P. nutans* and *Empetrum nigrum* (cluster 15) were restricted to 1968; the variant with *Dicranum scoparium* and *Deschampsia flexuosa* (cluster 16) was found in all years.

The number of lichen species is lowest in the initial (S.-C. inops) and late (G.a.-C.) stages of succession. The highest numbers of lichen species are found in the S.-C. cladonietosum, irrespective of the period. In all years, variants of this subassociation are found, with many lichen species.

Successional stages and soil properties in 1993

Reference values were measured in open sand without vegetation. In 1993 the pH-H_2O and pH-KCl in the 0-2 cm layer were respectively 5.6 and 4.7. The pH hardly changed in 2004 (pH-H_2O 5.5 and pH-KCl 4.9); see Table 6.6. In 1993 the pH-KCl in the separate soil layers was hardly different. In 2004 all layers were only slightly less acid than in 1993. This means that the topsoil consisted of more or less sub-neutral sand.

Acidification appears to be related to succession stage. The pH values are gradually decreasing, especially in the 0-2 cm layer, from moss-rich S.-C. inops (PQ.G), to lichen-rich S.-C. cladonietosum variant with *Polytrichum piliferum*, overgrown by the green algae *Gloeocystis polydermatica* (PQ.K and PQ.E), followed by the lichen-rich S.-C. cladonietosum variant with *Cladina* spp., *Festuca*

Table 6.6 Results of the soil analysis in three layers (0-2 cm, 2-10 cm and 10-30 cm) in a Reference plot H, seven PQs in 1993 and 2004, and in four additional lichen-rich relevés in 2004.

	$\mathrm{pH_{w}}$	**$\mathrm{pH_{KCl}}$**	**$\mathrm{pH_{KCl}}$**	**$\mathrm{pH_{KCl}}$**	**% C**	**% C**	**% C**	**% N**	**% N**	**% N**	**% P**	**% P**	**% P**
Depth (cm)	0-2	0-2	2-10	10-30	0-2	2-10	10-30	0-2	2-10	10-30	0-2	2-10	10-30
Reference H 1993*	5,6	4,7	4,6	4,6	0,33	0,27	0,28	0,003	0,003	0,003	0,008	0,008	0,008
PQ.M Ammophila '93*	5,6	4,5	4,4	4,4	0,43	0,36	0,32	0,021	0,013	0,008	0,011	0,010	0,009
PQ.L Corynephorus '93*	5,2	4,5	4,5	4,4	0,42	0,42	0,42	0,005	0,005	0,016	0,010	0,010	0,010
PQ.G Polytrichum '93*	5,1	4,0	4,2	4,6	0,71	0,55	0,29	0,036	0,015	0,005	0,010	0,008	0,009
PQ.E Lichen-rich '93*	4,4	3,6	4,0	4,4	1,03	0,57	0,44	0,089	0,03	0,008	0,014	0,009	0,009
PQ.K Lichen-rich '93**	4,8	3,8	4,1	4,5	0,74	0,46	0,28	0,057	0,024	0,007	0,013	0,011	0,012
PQ.N reindeer lichens '93*	4,4	3,5	4,0	4,2	1,04	0,46	0,32	0,084	0,021	0,009	0,017	0,008	0,008
PQ.F Calluna mosaic '93**	4,4	3,8	3,5	4,3	0,83	1,73	0,74	0,045	0,162	0,011	0,017	0,023	0,014
Reference H 2004*	5,5	4,9	4,9	4,8	*0,25*	*0,25*	*0,25*	*0,01*	0,039	*0,02*	0,009	0,009	0,008
PQ.M Ammophila '04*	5,1	4,0	4,5	4,8	1,13	*0,25*	*0,25*	0,065	0,149	*0,02*	0,013	0,009	0,009
PQ.L Corynephorus '04*	4,9	3,9	4,5	4,6	0,77	*0,25*	*0,25*	0,049	0,076	*0,02*	0,013	0,011	0,009
PQ.G Polytrichum '04*	5,0	3,9	4,5	4,9	1,37	*0,25*	*0,25*	0,067	0,102	*0,02*	0,015	0,010	0,010
PQ.E Lichen-rich '04*	5,2	3,6	4,3	4,8	1,17	0,32	*0,25*	0,061	*0,02*	*0,02*	0,014	0,010	0,009
PQ.K Lichen-rich '04**	4,9	3,8	4,4	4,7	1,02	*0,25*	*0,25*	0,069	*0,02*	*0,02*	0,014	0,011	0,011
PQ.N reindeer lichens '04*	4,7	3,5	4,2	4,8	1,64	0,34	*0,25*	0,077	*0,02*	0,02	0,017	0,009	0,010
PQ.F Calluna mosaic '04**	4,6	3,1	3,9	4,5	5,25	0,69	*0,25*	0,279	0,069	0,067	0,035	0,017	0,014
J04 with disturbed moss*	4,9	3,6	4,4	4,7	1,16	0,34	*0,25*	0,105	0,065	0,031	0,015	0,012	0,013
P04 lichen-rich S.-C.*	4,7	3,5	4,1	4,7	1,93	0,26	*0,25*	0,117	0,083	*0,02*	0,022	0,013	0,015
Rk4 lichen-rich RadioKootwijk**	5,1	3,6	4,2	4,9	1,42	0,38	*0,25*	0,120	0,078	0,010	0,023	0,013	0,013
Ft4, lichen-rich in forest*	4,5	3,4	3,9	4,7	5,54	0,67	*0,25*	0,487	*0,02*	*0,02*	0,041	0,014	0,013

*******	$\mathrm{Al_{ox}}$	$\mathrm{Fe_{ox}}$	$\mathrm{P_{ox}}$	CEC	$\%_{\mathrm{basic}}$
Depth (cm)	0-10	0-10	0-10	0-10	0-10
Reference H 1993*	21	5	1	11	0,5
PQ.G Polytrichum '93*	14	5	1	23	19
PQ.E Lichen-rich '93*	10	6	1	22	10
PQ.K Lichen-rich '93**	10	7	1	23	5
PQ.N reindeer lichens '93*	9	6	1	30	39
PQ.F Calluna mosaic '93**	12	12	1	45	6

* on blowing sand, ** on cover sand. *** Al, Fe and P oxalate in mmol.kg^{-1} and CEC in mequiv.kg^{-1}. Italicised *0.25*, *0.01* and *0.02* signify that analysis results were < 0.25, < 0.01 and < 0.02.

ovina s.l. and *Rumex acetosella* (PQ.N) and finally by the transitional community between S.-C. subassociation cladonietosum / G.a.-C. subassociation cladonietosum (PQ.F). The acidification is paralleled by humus production (% C and % N).

In 1993 the % basic ions (Table 6.6) was lowest in the Reference plot (0.5%) followed by the lichen-rich S.-C. cladonietosum (PQ.K) and the transition to *Calluna* heath on former forest soil (PQ.F). The highest value was found in the quadrat rich in reindeer lichen (PQ.N) with cover sand at a depth of 70 cm.

The calculated CEC (Table 6.6) was the lowest in the Reference plot on blowing sand (11 meq.kg^{-1}), gradually increasing during succession to 23 meq.kg^{-1} in moss-rich PQ.G, lichen-rich PQ.E, PQ.K and the reindeer-lichen-rich (PQ.N). The highest CEC was found in PQ.F the transition to *Calluna* heath (45 meq.kg^{-1}). PQ.K and PQ.F have cover sand at the surface and PQ.N has cover sand at a depth of 70 cm (see soil profiles in Ketner-Oostra & Riksen 2005). These cover sands are near the surface in the eastern part of the Kootwijkerzand and with their relatively high content of cations form a suitable substrate for lichens, as is also seen in the sand dune vegetation of 'Radio Kootwijk' (Klinge et al. 2004).

The oxalate determinations in 1993 (Table 6.6) were intended to provide information on the buffer capacity of the sand, as the amounts of Al, Fe and P ions are dissociated under influence of plant growth (de Vries et al. 1994). The Al oxalate values of 18 (+7/-5) mmol kg^{-1} are an indication of the age of these Pleistocene sands; the much younger calcium-poor coastal dunes have 2 (±1) mmol kg^{-1} (Ketner-Oostra & Sýkora 2000). The increase in Fe oxalate from open sand to *Calluna* heath (from 5 to 12 mmol kg^{-1}) shows the dissociation of Fe ions from the parent material with vegetation development. By comparison, the mean value in the calcium-poor coastal dunes was 3.2 mmol kg^{-1} (+0.8/-02). The mean value of P oxalate for the Kootwijk plots was the same as for the calcium-poor dunes (1 mmol kg^{-1}), both dune areas being rather poor in phosphorus ions.

Relation between vegetation and soil

The relation between vegetation and environmental parameters was studied using a set of 18 relevés (seven PQs from 1993, the same PQs in 2004 and four lichen-rich relevés from 2004) and 10 external variables. The DCA ordination is shown in Figure 6.4. The first axis, corresponding to a vegetation change from the open sand to heath, is clearly related to a decreasing pH and an increase in organic matter, % total N and % total P.

The parameters that appeared to be significant after the Monte-Carlo permutation test and forward selection are displayed in the CCA (Figure 6.5a, b). The first axis appears to be significantly related to a decreasing pH-KCl in the 0-2 cm layer and an increase in % C and % N in this layer. From the % P values only the 2-10 cm layer appeared to be significant.

From 1993 to 2004 all permanent quadrats shift from the left-hand side of the diagram to the right-hand side, indicating changes to more organic and acid conditions with more nitrogen. The strongest shift was in the S.-C. inops with much bare sand and *Ammophila* (M93), the S.-C. cladonietosum with *Polytrichum*

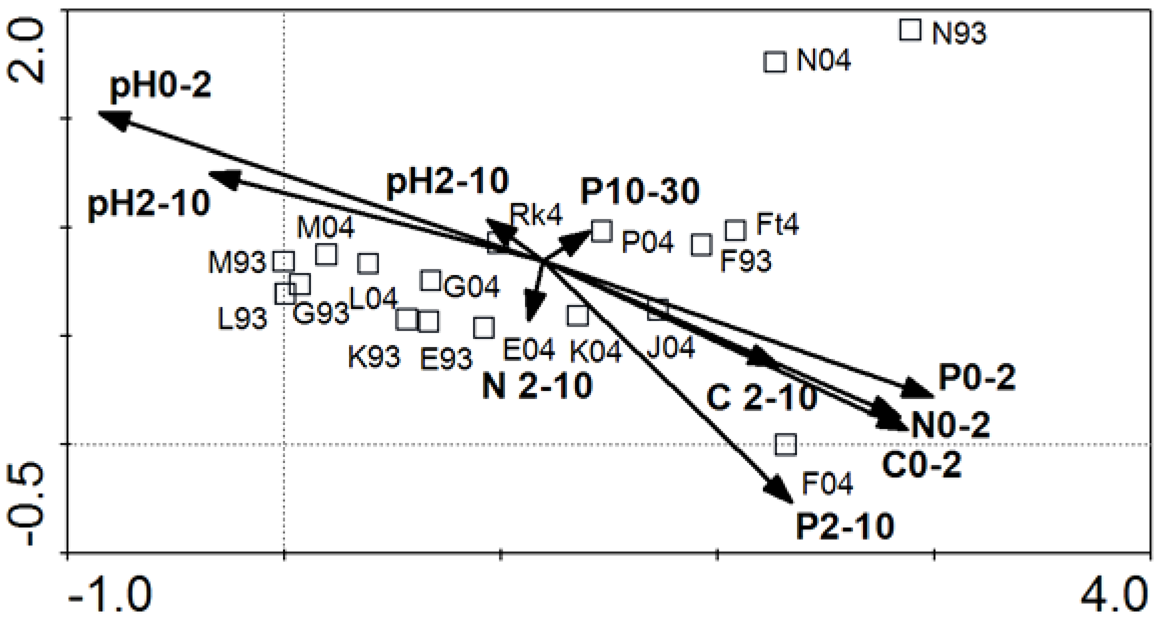
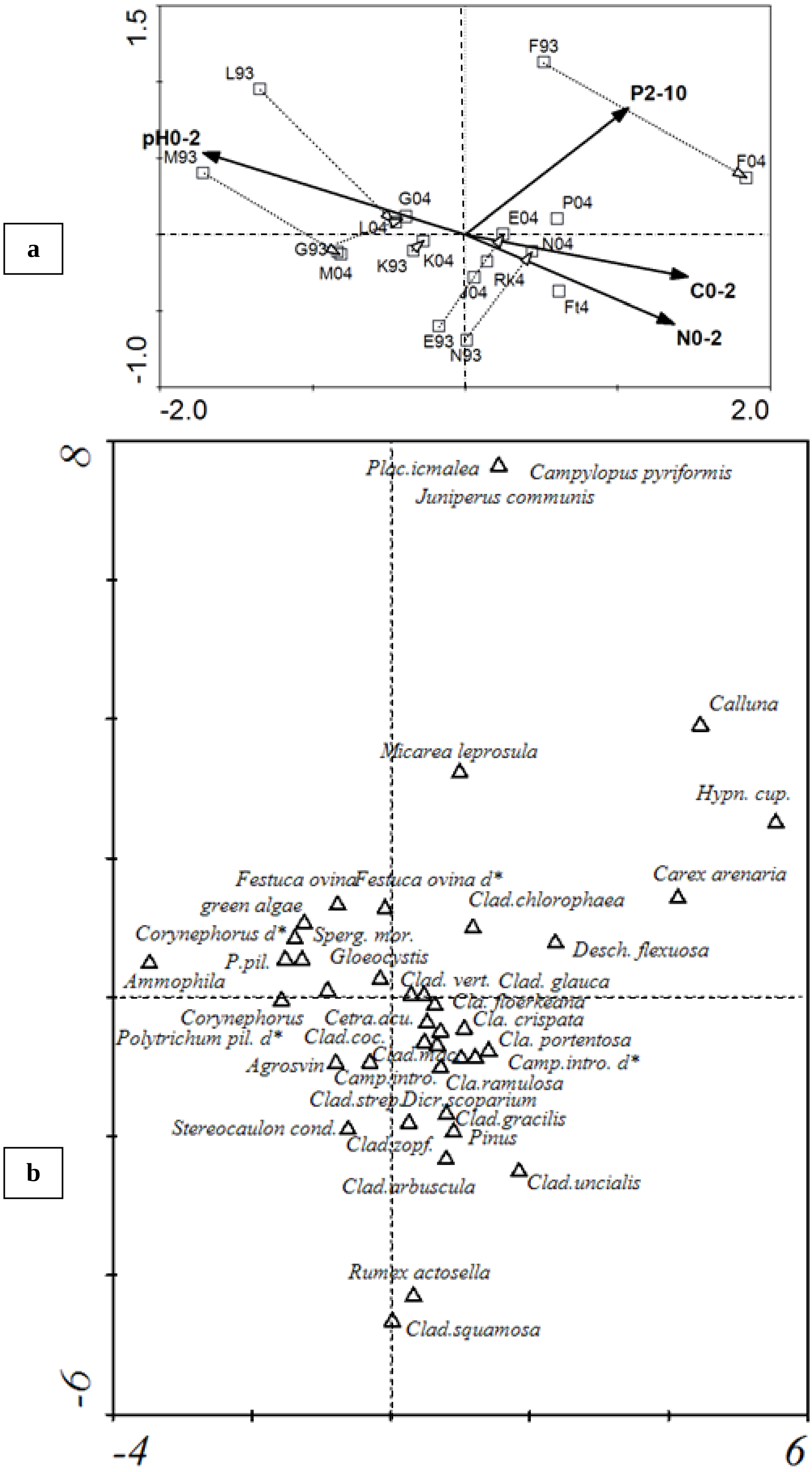


Figure 6.4. Relation between 10 parameters (in the 0-2 cm, 2-10 cm and 10-30 cm soil layers) and the first two axes of a DCA, based on a selection of 18 relevés including seven PQs (E - N) from 1993, and the same seven PQs in 2004, and four additional lichen-rich relevés in 2004 (J, P, Rk and Ft, see Table 6).

overgrown with green algae (L93) and F93 with a vegetation of the G.a.-C. cladonietosum situated on cover sand where the forest was cleared in the 1960s.

S.-C. cladonietosum variant with *Polytrichum piliferum* overgrown by the green algae *Gloeocystis polydermatica* (E93, K93, both near the eastern edge of a pine wood) and the variant with *Cladina* spp., *Festuca ovina* s.l. and *Rumex acetosella* (N93, between a large self-sown Scots pine and deciduous roadside trees) shifted in the direction of increasing % P, where F93 (the permanent quadrat on cover sand where forest had been cleared) is plotted. The lichen-rich moss layer of K93 was inverted by wild boar in 2000, but in 1994 the species richness seemed to have recovered. In 1993 and 2004, *Calluna vulgaris* and *Juniperus communis* were both growing in F93 and F04, situated on cover sand. In the species diagram (Figure 6.5b) the connection between the relatively high % P in the 2-10 cm layer and *Calluna vulgaris*, *Juniperus communis* and *Deschampsia flexuosa* is visible. *Cladonia chlorophaea* s.l is characteristic of litter from *Calluna* and grasses.

The lichen-rich reference relevés Rk4 (Radio Kootwijk), Ft4 (after forest management), J04 (originating from inverted *C. introflexus* vegetation) and the lichen-rich S.-C. cladonietosum variant with *Cladina* spp. and *Campylopus introflexus* (P04, uprooted by wild boar) are all plotted on the lower right-hand side of the diagram. The presence of many lichen species in this part of the diagram is clearly visible in the species ordination (Figure 6.5b).


a
1.5
-1.0
-2.0
2.0
L93
F93
P2-10
pH0-2
M93
F04
G04
P04
E04
L04
N04
G93
K04
M04
K93
C0-2
Rk4
J04
Ft4
E93
N0-2
N93
b
8
-6
-4
6
Plac.icmalea
Campylopus pyriformis
Juniperus communis
Calluna
Micarea leprosula
Hypn. cup.
Carex arenaria
Festuca ovina
Festuca ovina d*
green algae
Clad.chlorophaea
Corynephorus d*
Sperg. mor.
Desch. flexuosa
P.pil.
Gloeocystis
Ammophila
Clad. vert.
Clad. glauca
Cla. floerkeana
Corynephorus
Cetra.acu.
Cla. crispata
Polytrichum pil. d*
Clad.coc.
Cla. portentosa
Clad.mac
Camp.intro. d*
Agrosvin
Camp.intro.
Cla.ramulosa
Clad.strep
Dicr.scoparium
Clad.gracilis
Stereocaulon cond.
Pinus
Clad.zopf.
Clad.uncialis
Clad.arbuscula
Rumex actosella
Clad.squamosa

Previous page Figure 6.5. Relation between 10 parameters (in the 0-2 cm and 2-10 cm soil layers) and the first two axes of a CCA, based on a selection of 18 relevés (PQs) from 1993 and 2004, and four additional lichen-rich relevés in 2004 (J, P, Rk and Ft) after the Permutation test. (**a**) relevés (PQs); (**b**) species. d* signifies dead.

6.4. Discussion

The lichen diversity did not change much between 1968 and 2004, with up to 34 species in the more recent periods (Table 6.3). The decrease of *Hypogymnia physodes* in epiphytic and terrestrial habitats has been signalled by Aptroot et al. (1998) and is probably mainly because of the SO_2 pollution before the1970s or the NH_3 pollution since then, as van Herk et al. (2000) demonstrated for the epiphitic form in a wood on the Veluwe. *Cladonia cornuta*, *C. deformis, C. phyllophora* and *C. squamosa* were probably already scarce in 1968 and their almost total disappearance since then might have another cause. *Cladonia digitata* and *C. squamosa* still occur inside woods on rotting wood (Aptroot & van Herk 2005) and *C. cornuta* is still present in the V.-C. in the Wadden district (Ketner-Oostra & Sýkora 2004). *Cetraria nivalis* and *Cladina rangiferina* have vanished from the Netherlands. As the Netherlands is at the southern border of these species' mainly boreo-alpine distribution, their extinction has been linked to climatic change (van Herk et al. 2002). However, detailed inventories revealed that many lichens still were present in 1993 and 2004, and in addition, certain terrestrial growing crustose species were found.

Contrary to our **Hypothesis 1**, stating that cryptogam vegetation was especially well developed in the early succession stages of the sand dune ecotope in 1968, we did not find much difference between the lichen vegetation of the pioneer stage (S.-C. inops) in the three research periods. The group of clusters of the S.-C. inops (a) is plotted on the left-hand side of the ordination diagram (B in Figure 6.3). It consists mainly of relevés from all three periods (cl. 1, 2 and 4). Cluster 3 has a high presence and cover of green algae, and is only present in periods 2 and 3. Cluster 4 with *P. piliferum* has less green algae and is mainly from period 1 and 3. We conclude that there were probably fewer green algae present on the bare sand in 1968, perhaps because aerial deposition of N was minor at that time.

However, the next stages of natural succession in *Corynephorus* grassland (S.-C. cladonietosum), the cryptogam-rich intermediate and terminal stages, and gradient stages to heathland, are quite different in the three periods. In agreement with **Hypothesis 2**, they are very well developed in period 1. In the ordination diagram, the clusters from the early periods and the later period are separated: the early period is in the lower part whereas the later periods are mainly in the upper part. The development in 1968 is shown from left to right: from the S.-C. inops to the S.-C. cladonietosum (cl. 5 and 11), followed by the transition between S.-C. and G.a.-C. cladonietosum (cl. 12), and finally the G.a.-C. with *Pohlia nutans* (cl. 14 and 15). All these clusters occur mainly in period 1. At that time the successional stages were rich in lichens, but also displayed a moderate cover of mosses (*Pohlia nutans*, *Campylopus flexuosus*, *Polytrichum piliferum* and *Dicranum scoparium*), with liverwort species being particularly numerous in cl. 12 (nine species).

However, in 1993 and 2004 a high presence and cover of *Festuca ovina* s.l., *Deschampsia flexuosa* and *Rumex acetosella* (cl. 11) is seen in the succession stages from *Corynephorus*-grassland to heath, including mosses and lichens, but impoverished by the apparent decrease of liverwort species (cl. 13). This indicates that eutrophication by deposition of N has been influential in the succession to heath – which corroborates the repeat study of the 1960/1970 survey of de Smidt in heath vegetation of the Veluwe by van Ree & Meertens (1989). The disappearance of *Arnica montana*, *Jasione montana*, *Hypochaeris radicata*, *Potentilla erecta* and *Danthonia decumbens* (only present in cl. 12 in 1968) points to acidification, which is documented for the Kootwijkerzand as the effect of 'acid rain' by Quené-Boterenbrood (1988). Our results agree with the publications mentioned above and support **Hypothesis 3** that stated 'Since the 1970s acidification and eutrophication have affected the cryptogam composition'.

For 1993 and 2004, the clusters in the upper part of the diagram show the same order of plant communities: again the S.-C. inops is followed by the cladonietosum(cl. 6-10), the transition to heath (cl. 13) and finally the G.a.-C. cladonietosum (cl. 16). However, in all these clusters now *Campylopus introflexus* is present, living and some of it dead, together with the algae *G. polydermatica*.

Hypothesis 4 was that 'since the 1970s the expansion of *Campylopus introflexus* has changed and accelerated the succession in the inland sand dunes, thereby negatively influencing lichen diversity'. In accordance with this hypothesis *C. introflexus* did indeed influence species composition, but the sequence of plant communities remained the same and lichen diversity remained high. The communities of reindeer lichens (*Cladina portentosa*, *Cla. arbuscula* s.l.) and other fruticose species (*Cladonia gracilis*, *C. crispata* and *C. uncialis*) are well developed in clusters 9 and 10 (both in 1993 and 2004) and cl. 11 (all three periods). Stoutjesdijk (1959) described such communities for the 1950s and their occurrence in open pine plantations into the early 1970s is confirmed by Leijs (1964) and Bannink et al. (1973). Their presence in 1993 and 2004 might be the effect of the small-scale management in the preceding period (locations 5-8 in the east and 10-13 in the northeast of the Kootwijkerzand: Figure 6.1b). It is quite likely that these communities were scarcer in 1993 and 2004 than in 1968, as in more recent times the relevés with fruticose lichens were singled out for study.

However, this large number of lichen species refutes the second part of **Hypothesis 4**, which states that the expansion of *Campylopus introflexus* after 1970 reduced lichen diversity. It does seem true that lichen abundance was reduced, though.

6.4.1. How Campylopus introflexus interferes with the life strategy of Polytrichum piliferum

In 1968 *Polytrichum piliferum* appeared to be the only pioneer moss species on bare sand. In its life cycle some of the shoots from the rhizomes may form male and female reproduction organs, the latter becoming sporophytes. This sporulation follows a fine-meshed net which does not include all plants at the same time (Hobbs & Pritchard 1987). After the sporulation some of these moss plants die, but some grow into a new plant on top of the old one, especially if sand is still blowing in. In wet and probably eutrophic circumstances (N deposition) algae like *Gloeocystis polydermatica* may cover the carpet, and more plants will die. This slimy layer of algae probably keeps water away from the rejuvenating shoots of *P. piliferum*. The neophyte *C. introflexus* has a life strategy with mainly vegetative establishment from leaves or stem tops (During 1979) but also a generative life strategy, with spores. It intrudes into the *P. piliferum* carpets when they are less vital. *C. introflexus* also establishes on sand with a certain humus content, often after disturbance by management measures, such as removal of felled pine trees (Daniëls & Krüger 1996).

6.4.2. Lichens as secondary pioneers on and between moss carpets

There is little difference in the number and presence of lichen species in the intermediate stages of lichen succession, between periods 1968, 1993 and 2004. Cluster 6 represents an early succession stage, comprising PQs L and G in 1993. Due to a change in the vegetation composition, after 11 years these PQs shifted to cluster 7 (Table 6.4). The high number of lichens (23 species) in this cl. 7 indicates that the intrusion of *C. introflexus* into the moss carpet of *P. piliferum* had no influence on lichen establishment. Pioneer species like *Cetraria aculeata*, *Cladonia cervicornis* s.l., C. *strepsilis* and *C. zopfii* are present, as are humicole species and aero-hygrophytic species – the latter with low presence and cover. Cluster 8 has a higher cover of *C. introflexus* and less lichen species (15 species), with greater numbers of humicole species, but also including the abovementioned pioneer species in low frequency and cover. Cluster 9, with dominance of the aero-hygrophytes, like *Cladina portentosa* and *Cladonia gracilis*, also has many humicole lichen species, but some pioneer species too. In cl. 13, the next stage in the transition from S.-C. to the G.a.-C. cladonietosum, with much *F. ovina* s.l. and *C. introflexus*, 16 lichen species are present, both humicole and aero-hygrophytic species, but the pioneer species have the lowest presence and cover. Cluster 16, a *Calluna* heath representing the latest succession stage in our research, has less lichen species (10) and only humicole species, all in a very low presence and cover. However, many moss species (13) and three liverwort species were found here, including the Red List species *Gymnocolea inflata* and *Lophozia ventricosa* in 2004.

We conclude that species of all the lichen groups mentioned (pioneer, humicole and aero-hygrophytes) can establish themselves on and between the mosses (live, or dead in parts, or humified) in a mixed carpet of *P. piliferum* and *C. introflexus* (cl. 6-11) and also when *C. introflexus* is the dominant species in the transition between S.-C. and G.a.-C. (cl. 13). This feature has also been described for inland dunes by Biermann & Daniëls (1997; 2001) and Hasse (2005), for calcium-rich coastal dunes by van der Meulen et al. (1987) and for calcium-poor dunes on Terschelling by Ketner-Oostra & Sýkora (2004); see Chapter 2.

6.4.3. Changes in the soil between 1993-2004 (see DCA and CCA)

The pioneer stage with almost no lichens had a pH-KCl value of 4.5. Succession coincides with humus production inside the vegetation (% C and % N). From 1993 to 2004 all permanent quadrats shift from the left-hand side of the CCA diagram (Figure 6.5a) to the right-hand side, indicating a change to more organic and acid conditions with more nitrogen. In plots that already had lichens, the acidity remained constant between 1993 and 2004 at a pH-KCl of 3.6 (+0.2/-0.1). Only in the transition between S.-C. and heath did the pH-KCl drop from 3.8 in 1993 to 3.1 in 2004, in response to the unusually high litter and humus production. Here the % P (2-10 cm layer) is the highest (Table 6.6).

On the left-hand side of the species diagram (Figure 6.5b), with the least acid sand, the lichen pioneers like *Stereocaulon condensatum*, *Cladonia strepsilis* and *C. callosa* are seen. In the centre, most humicole species are present (*C. coccifera*, *C. macilenta* and *C. glauca*), with the aero-hygrophytes (*Cladina portentosa*, *Cladonia gracilis* and *C. uncialis*) immediately to the right. Here the % C and % N is the highest and the pH-KCl is low. The humicole *Cladonia chlorophaea* s.l. and *Placynthiela icmalea* (particularly the latter) are near *Juniperus communis*, which relates them to a high % P (2-10 cm layer) and to *Calluna*, together with a high % C and % N. These values seem to have been high in cover sand where pine trees had been removed some time ago (Figure 6.1b, location 9). Permanent quadrat N93 characterized by *Festuca ovina* s.l. and *Rumex acetosella* and situated between a large self-sown Scots pine and deciduous roadside trees, shifted in the direction of increasing P, where PQ.F occurs in the ordination diagram (Figure 6.5a).

6.4.4. Seasonal effect on moss encroachment

In extremely hot summers the topsoil dries out. This will promote sand ablation and the death of mats of *C. introflexus*. However, the xerophyte *P. piliferum* is more adapted to such circumstances. Lichens will also survive such periods as poikilohydrics that can use dew and mist in the early morning (Nash III 1996). However, increasing rainfall and more moisture in springtime and autumn, both brought about by climatic change, may allow the rapid grower *C. introflexus* to recover after summer drought. A study done after a wildfire in the same ecotope two kilometres away found that between 1997 and 2000 *C. introflexus* had overgrown a lichen-rich control plot and reduced the lichen cover from 35% to 8%, with a species reduction from 12 to 10 (Ketner-Oostra 2002). Biermann & Daniëls (2001) reported the same decline in the lichen richness of an S.-C. vegetation after the extremely cold and dry winters of 1985 and 1986, and noted the high reproductive and dispersal ability of *C. introflexus* thereafter.

However, in spring the high moss production of the preceding seasons is often visible. Such increased moss production may be linked to the still high N deposition, as Londo (2002) showed for *Rhytidiadelphus squarrosus* in various grassland communities. Climatic change with a slight rise in temperature and more rainfall in winter and spring might also be an issue. In their UB-V experiments Lud et al. (2001) found that a rise of 2-4 °C led to an increase in the biomass of grasses and mosses, but not of lichens.

The high grass and moss abundance is clearly shown in the recent vegetation map of the Kootwijkerzand from 2002 (Groeneweg 2004) in which the *Corynephorus* type (Z1) in its typical form (Z1a) covers 26 ha, in a form with *P. piliferum* (Z1b) covers 69 ha, and a grass-dominated form (Z1c) covers 107 ha. The subdivision including *C. introflexus* shows a total of 40 ha (Z1a*, Z1b* and Z1c*). The total area of 298 ha of the *Corynephorus* type, including intermediate complexes, indicates a sand dune landscape dominated by grasses and mosses. Only 92 ha of bare sand was found in 2002; a further 69 ha was in a complex of 70% bare sand and 30% of the different *Corynephorus* forms. A map like this gives a snapshot of the different types of vegetation. If a severe storm were to occur, the picture might change. However, such wind erosion events are rare (Riksen & Goossens 2006).

6.4.5. Effects of disturbance from management and archaeological excavations

Almost all the vegetation types studied, especially those from periods 2 and 3, were influenced by disturbances (Figure 6.1a/b). In 1993 the effect of management measures to strengthen the wind velocity was visible in PQ.M, G and L. However, after 11 years of succession, more stabilized vegetation developed.

At the location of the archaeological excavations in 1973-1975 (Figure 6.2) a large area of bare sand existed in 1993, with some establishment of *Corynephorus* vegetation, sometimes with *P. piliferum*. This area subsequently shrank in 2004: see vegetation mapping project in 2002 (Groeneweg 2004) and Ketner-Oostra & Riksen (2004).

In 1993 the vegetation in location B (Figure 6.1b) was remapped and compared with that in 1968 to visualize this process (van Embden & Verwey 1968) in 1993 (see Ketner-Oostra 1996). Within 25 years, the border of open sand without vegetation retreated 120 m in a southwesterly direction. The *Cladonia*-rich *P. piliferum* 'steppe' changed into a *C. introflexus* field, probably because of the nearby management and also the sheltered location with restricted dynamics. Daniëls (1990) has evaluated such side-effects of management with machinery in sites with few dynamics on the Kootwijkerzand and the nearby Caitwickerzand.

Hypothesis 5 'Habitat restoration by small scale management has a positive effect on development and maintenance of lichen-rich vegetation' appears to apply to the southwestern area that has been opened up to restore the action of wind force and to the central eastern border of the Kootwijkerzand, where many self-sown trees were cut in the past. Here, small- scale management, so-called pattern management (Borkent et al. 2005), proved to have a positive effect, resulting in the present lichen-rich vegetation. A mosaic vegetation has developed, consisting of different varieties of S.-C. with *Calluna* heath and *Juniperus communis* bushes.

6.4.6. Effects of uprooting by animals

When densities of wild boar were high, large areas of moss-dominated grassland were uprooted by boar searching for insect larvae in the humus layer. In 2000 some lichen-rich PQs were damaged in this way. However, *P. piliferum* and lichens immediately regrew on the partly (20% in PQ.P) exposed underlying mineral sand. The monitoring of 2004 revealed that the lichen richness in PQ.P had recovered to

11 *Cladonia* species, with a total cover of 50%. In PQ.K the uprooting resulted in a carpet of *Campylopus* with 12 *Cladonia* species with a total cover of 5%. The very restricted change in species composition in PQ.K is demonstrated in the CCA, where both 1993 and 2004 were plotted close together.

Inverted moss carpets, especially of *C. introflexus*, are partly the effect of mechanical tension inside the cushions, due to alternate wetting and drying of the cracks (van der Meulen et al. 1987), but partly also due to birds, pecking for insect larvae in the underlying humus layer. In PQ.J the establishment of lichens on clumps of moss inverted and partly covered by the algae *G. polydermatica*, was monitored from 1993 onwards. In an early stage *Cladonia coccifera* was recorded, but it was soon followed by the pioneer species *C. cervicornis* s.l., the Red List species *C. zopfii* and later *C. crispata*, ending with a lichen richness of 12 species in a total cover of 2% in PQ.J4 in 2004. Sand blowing in from adjacent open sand was probably an important factor influencing lichen establishment.

6.5. Conclusions and recommendations

1. Vegetation development on the drift-sand ecotope is related to dynamics, mainly those caused by the strength of the wind. Large-scale disturbances like the archaeological excavations in the 1970s have had a long-term effect on the presence of open blowing sand, but in 30 years, part of that area has been recolonized by *Corynephorus* and *Polytrichum piliferum*. Dynamics introduced by fauna, such as the uprooting of vegetation in intermediate or terminal stages of succession, showed a positive effect, especially on the re-establishment of lichens.

2. The establishment of *Campylopus introflexus*, partly in less vital *P. piliferum* carpets covered with algae, and partly on sand with a certain humus content, resulted in a different and accelerated succession, followed by a high production of humus.

3. At present, much of the former open area of blowing sand is covered by pioneer succession stages of the S.-C. with green algae and/or with *P. piliferum* or a combination of this moss species with *C. introflexus*. However, *C. introflexus* can be damaged and killed by sand blowing in. The best way to keep the sand blowing and to reduce colonization by *C. introflexus* seems to be large-scale management in the central open area and the surrounding belt with *Corynephorus* and *P. piliferum*.

4. With up to 34 species, lichen diversity is still high in the beginning of the 21st century. Most humicole species are doing well in the research area and aero-hygrophytic species have increased in vitality since 1993. However, a much smaller area is covered by the lichen vegetation now than at the end of the 1960s. At that time, the transition zone between the sand dune ecotope and heath near the edges of the pine forest was locally covered by mats of reindeer lichens. This former succession series in the Spergulo-Corynephoretum starting with *P. piliferum* and ending with lichen-rich *Calluna* heath (1968) has been partly replaced by one

including *C. introflexus* in the intermediate and late successional stages (1993 and 2004). Common pioneer lichens, humicole and aero-hygrophytic species have locally established on top or between withering moss cushions of both *P. piliferum* and *C. introflexus*, which are often covered by the mucous layers of the green algae *Gloeocystis polydermatica*.

5. The S.-C. cladonietosum in its rich species composition is still found where cover sand is at or near the surface, like in more remote areas on the eastern side of the Kootwijkerzand and in the area around 'Radio Kootwijk' that has no influence from recreation. The lichen diversity was found to be related to sand containing more phosphate and a relatively high content of assimilable cations.

6. Small-scale management in this eastern part of the Kootwijkerzand has positively influenced the area's biodiversity. Where trees were cut in the past (mainly the 1975-1985 period) *Calluna* heath with *Juniperus communis* is now present. Here the lichen-rich intermediate and late successional stages of succession in S.-C. cladonietosum and from S.-C. cladonietosum to heath vegetation are still found, such as those with reindeer lichens and other fruticose lichens, albeit in low abundance. In the future, cutting trees, pulling out tree seedlings, removing litter, or removing the upper layer of vegetation on a small scale, will also be necessary from time to time.

7. The N emission from livestock farming should be further reduced in the future, so that the remaining lichen diversity can be used as a source for more lichen dispersion in order to increase lichen cover in the inland heath and sand dune ecotope.

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Chapter 7

SYNTHESIS

Rita Ketner-Oostra

Chapter 7. Synthesis

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Introduction: Lichens as biological indicators of environmental quality

Lichens (*Flechten* in German, *korstmossen* in Dutch) are prominent examples of symbiotic organisms, in which fungi and algae and/or cyanobacteria form an intimate biological union (Nash III 1996). They are pre-eminently suited for indicating changes in the environment, such as air pollution, as was already recognized in the 19th century (Grindon 1859). However, not all lichens are equally sensitive, and several species of epiphytic lichens, i.e. lichens growing on trees and shrubs, have a differential sensitivity to specific air pollutants and are used to monitor the effects of dry deposition. 'Lichen deserts' have developed around cities and in areas with much industry (Sernander 1926). Barkman (1958) found the same features in some areas with high pollution in the Netherlands and related them to SO_2 emission.

In the UK, a mapping system to monitor environmental quality was developed using lichens as biological indicators (Hawksworth & Rose 1970). In the Netherlands, the *Werkgroup Herkartering Epiphyten Nederland* (Dutch working group for remapping epiphytes) started a survey of epiphytic lichens, departing from the results of Barkman (1958). Lichen frequency was presented in the Netherlands per 5 km^2 grid cell. It was proved that the more sensitive species had disappeared from large areas (de Wit 1976). Since 1984 the air quality in the Netherlands has been monitored in a provincial network of epiphytic lichens on oak trees (van Herk et al. 2002). The effect of a decrease in SO_2 emission and a recovery of the epiphytic flora became gradually visible during the 1980s; van Dobben & de Bakker (1996) reported the increasing influence of the pollutant ammonia on epiphytes.

Repetitive inventories like those mentioned above are lacking for terrestrial (growing on soil) lichens. The influence of atmospheric deposition on these lichens, both of SO_2 before the 1980s and of nitrogen (N) thereafter, might have been less disastrous than on epiphytes, but effects on vitality and size – even injuries – have been found at species level (Søchting 1995; Aptroot & van Herk 2001, see Figure 7.1). However, since the 1970s the increased N deposition, caused by the animal production, the so-called bio-industry, has enhanced plant growth in most (natural) ecosytems (Fangmeier et al. 1994). N deposition has accelerated vegetation succession on nutrient-poor sandy soils (Berendse et al. 1993), the core area of terrestrial lichens. The overall changes in the nutrient-poor terrestrial ecosystems rich in lichens, have been disastrous (Daniëls et al. 1987; de Smidt 1995; Ketner-Oostra 1992).

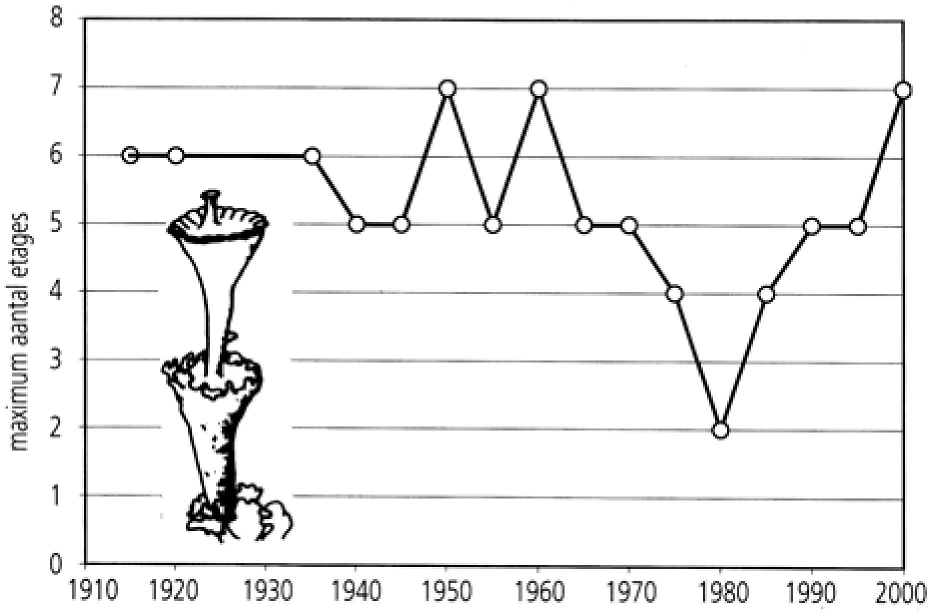

Figure 7.1. The maximum number of 'storeys' (proliferations in the centre) of *Cladonia cervicornis* in 5-year periods, as an example of the change in vitality of terrestrial lichens between 1915 and 2000. Based on measurements of specimen in the herbaria of Leiden, Utrecht and Soest by A. Aptroot en L. Spier. From: Aptroot & van Herk 2001.

7.1. Changes in lichen diversity in calcium-poor coastal dunes since the 1970s

The initial diversity and abundance of lichens in terrestrial ecosystems of sand dunes has been well documented, especially in the calcium-poor coastal dune vegetation of the phytogeographic Wadden district (Westhoff 1947). Apart from many *Cladonia* and *Cladina* species, Westhoff (1947) and Barkman (1958) mentioned that lichens that usually grow as epiphytes were also growing terrestrially in the Violo-Corynephoretum (V.-C.).

My vegetation survey of 1966 (Oostra 1968) and that of the 1966-1972 period (Ketner-Oostra 1989) in a time with a relatively low deposition of atmospheric N serve as a base for comparison with a more recent survey in the 1990-1996 period, a time in which the increased deposition had clearly left its mark (Ketner-Oostra 1997a).

7.1.1. Changes in the stabilized dry dunes of Terschelling

In **Chapter 2** a detailed description is given of the changes in lichen diversity in the formerly 'grey dunes' on this Wadden sea island between the1966-1972 period and the 1990-1996 period. The frame community of tall graminoids *Ammophila arenaria – Carex arenaria* with several species of the V.-C. exemplifies the present state of the formerly lichen-rich dune V.-C. (Veer 1997; Kooijman et al. 1998).

The initial stage of the V.-C. with mainly pioneer lichen species on slightly decalcified sand, was only present in the 1960s (Table 2.2). In the 1990s the early succession stages of the V.-C. with *Cladonia* species could still be found, but these were accompanied by *Campylopus introflexus*. The expansion of this neophytic moss characteristic of nutrient-poor acid sand (Biermann 1999), is threatening lichen diversity. Competition with this rapidly growing moss is probably the reason for the disappearance of the pioneer lichen species like *Cetraria aculeata, Cladonia foliacea, C. furcata* and *C. zopfii* from open, now rather acid sand (Ketner-Oostra & van der Loo 1998; Ketner-Oostra 2005).

The next successional stage, the V.-C.-typicum, is (or rather was) the typical subassociation for terrestrial growing epiphytic lichens (Weeda et al. 1996). In the 1960s, *Hypogymnia physodes* was the most frequent of the ten terrestrial growing normally epiphytic lichens, followed in frequency by *H. tubulosa, Platismatia glauca*, *Evernia prunastri, Pseudevernia furfuracea, Parmelia sulcata*, *Bryoria fuscescens* and three *Usnea* spp.

In the 1960s, the succession from the V.-C. to the dune heaths went through a moss-rich stage with *Dicranum scoparium*, which was also very lichen-rich. Apart from many *Cladonia* and *Cladina* species, the reindeer lichen *Cladina rangiferina* and the epiphytic lichens and the normally epiphytic moss *Dicranoweisia cirrata* were found epigeic.

Recent vegetation relevés in moss-rich succession stages characterized by the dominating *Campylopus introflexus* have been assigned to the Corynephorion as Fc (frame community) with *Campylopus introflexus* (Weeda et al. 1996). The current expansion of *C. introflexus* compared with the expansion of *D. scoparium* in the past might be one of the aspects of an accelerated vegetation succession. This neophyte's interference with the normal succession in calcium-poor dune grassland is an effect of acid rain (Biermann 1999). However, it has not yet been proved that this moss profits from the increased N deposition.

In the 1990s, the disappearance of the *Bryoria* and *Usnea* spp. from the V.-C. typicum and the severe decline in presence and cover of the *Hypogymnia* spp. were probably mainly a consequence of their intolerance to NH_3, as evidenced by their decline in epiphytic habitats in the Netherlands (van Herk et al. 2000). In the 1960s lichen diversity in the studied plant communities as a whole was very high: 45 lichen species (Table 2.1). Nevertheless, in the 1990s we found that when *C. introflexus* was losing vitality through desiccation and/or being covered by algae (mainly by *Gloeocystis polydermatica*), it could act as a substrate for many common humicolous and aero-hygrophytic lichen species such as *Cladonia coccifera, C. floerkeana, C. macilenta, C. ramulosa, Micarea prasina, Placynthiella* spp. and for *Cladina portentosa*, as reported in other Dutch coastal dunes (van der Meulen et al. 1987). Some pioneer species like *Cetraria aculeata*, *Cladonia foliacea, C. furcata* and *C. scabriuscula,* were also present. All the lichen species mentioned seemed to establish as 'secondary pioneers' on these withering moss carpets and followed in permanent plots (Ketner-Oostra 2005).

7.1.2. Succession in young coastal dunes on Terschelling

On the Noordsvaarder, a nature reserve in the western part of Terschelling, a system of young, recently formed dune ridges has developed, separated by brackish slacks. This spatial sequence of differently aged coastal dune ridges was part of our study of temporal changes within sand dune vegetation (**Chapter 3).** In the 1990s, lichens still thrived in the more open dune grassland on the second and third dune ridges in a stage of primary succession with a low cover of tall graminoids, i.e. the transitional stage from V.-C. typicum to the Phleo-Tortuletum ruraliformis (Figure 3.5). Many *Cladonia*-species and several terrestrial occurring epiphytes like *Hypogymnia physodes, H. tubulosa, Evernia prunastri* and *Parmelia sulcata* were still present, but only on the Noordsvaarder in subneutral habitats with slightly calcareous blown-in sand.

At the eastern end of the island, north of the embankment built on the Bosplaat in the period 1931–1937, there are very young dunes with a calcium carbonate content of about 1%. In this so-called Cupido's Polder, several groups of young dunes have developed on the wide beach flat since 1950. Here, the dry open grasslands have proved to be an ideal biotope for many lichen species, such as the calciphilous *Cladonia cariosa*, *C. rangiformis* and *C. symphycarpa* (Masselink & Sipman 1985); in 2000, *Bacidea bagliettoana*, *B. saxenii* and *Diploschistes muscorum* were also recorded (Aptroot et al. 2000). In the phase with decalcification in the top 0–2 cm of soil, *Cladonia* species such as *C. foliacea*, *C. humilis* and *C. pocillum* occur, some of which are increasing in abundance, as revealed by 10 years of monitoring permanent quadrats (Ketner-Oostra 2005). Moreover, Aptroot et al. (2000) recorded epiphytes like *Evernia prunastri*, *Hypogymnia physodes*, *H. tubulosa*, *Parmelia sulcata*, *Pseudevernia furfuracea* and *Ramalina farinacea* growing terrestrially here.

7.2. The origin and development of the inland drift sands in the Netherlands

Early accounts on lichen-rich terrestrial ecosystems of the inland non-calcareous sand dunes in the phytogeographic Pleistocene district can be found in Stoutjesdijk (1959) and Leijs (1964). However, the total active drift-sand area has been declining rapidly during the last 50 years. To preserve the inland drift sands and their biodiversity, it is necessary to understand their origin and development and the role of human activity in this semi-natural ecotype.

The development of the drift sands from late Pleistocene deposits is described in **Chapter 5**. In Europe during part of the last Glacial, cold desert-like conditions prevailed. Extensive aeolian deposits were formed in the 'European Sand Belt' that extended from Northwest and central European lowlands, to the Polish–Russian border and beyond (Koster 2005). Based on geomorphology, sediment and depositional environment, cover sands and dune fields (mainly river dunes) are distinguished. Within the cover sand region 'Older Cover Sands' and 'Younger Cover Sands' are distinguished, the latter having a more pronounced relief and almost no loamy laminae.

During the Holocene, the aeolian sands were gradually covered with forests and a brown forest soil developed on the sands. Starting with the settlement of farmers in the Neolithic Age, about 5000 years ago, the forests were gradually destroyed and superseded by heath land with heath podzol development.

Drift-sand landscapes are relatively young landscapes of Holocene age. Several theories on the initiation of the sand drifts have been proposed. Heidinga (1984) points to periods of extreme droughts during the 10th century. The falling water table in their wells forced farmers near Kootwijk to leave their homesteads. Sand then drifted over their bare arable fields (Heidinga 1987); see Figure 6.2. Most attribute drift sands to farming practices, such as managing the heath lands to promote sheep grazing. Another theory links the drift sands with routes well trodden by livestock or people, which in the loose sands were always unstable and often had to be shifted.

Although the interventions mentioned above may have triggered the formation of the drift sands, recent research (Koomen et al. 2004) points to a geomorphological control of the drift sands. They often occur in oval cells 1.5 to over 6 km long aligned in the direction of the prevailing southwesterly wind. These cells represent reactivated deposits of Younger Cover Sands, as these are more sensitive to wind erosion than Older Cover Sands.

In the first half of the twentieth century most of the drift sands were afforested with Scots pine (*Pinus sylvestris*); as explained in Chapter 5, this accounts for the rapid decline of active drift sands. The remaining active areas became stabilized, with wind erosion reduced to a local process. The forest bordering the drift-sand area inhibits the formation of new sources of deflation. Under these conditions there is very little wind erosion, so in the remaining drift sands and blow-outs, natural regeneration with all forms of the typical stages of succession from bare sand to forest with their gradual soil formation has developed (Tables 5.1 and 5.2). The pace of progress in this development is set by the geomorphological stage of the area, the area's size and human activity. The succession is lagging behind at the Harskamperzand, bordering the Kootwijkerzand at the east side, which is a military training ground with many open tracks. Intensive recreation also hampers regeneration and keep the sands in a pioneer stage. Under these conditions, there are few opportunities for lichen establishment, the number of species is low and those present are easily disturbed by trampling (Bayfield et al. 1981). If the aim is to increase biodiversity by encouraging lichens, recreation can be influenced by zoning, as has been done by the State Forestry Service on the Kootwijkerzand. Here, access to the sand dune area has been encouraged on the western side, by laying out several parking lots there. The eastern and northern sides are not accessible to cars, with the result that here there has been almost no influence of recreation on the development of lichen-rich vegetation.

Since the 1960s, the increased atmospheric N deposition has accelerated the vegetation succession and has had a particularly marked effect on sandy soils poor in nutrients (Berendse et al. 1993); the terrestrial ecosystems rich in lichens have been most affected (Daniëls et al. 1987; de Smidt 1995). Not only has the area of bare drift sand shrunk still more (Figure 7.2), the fragile balance between the different ecotopes has been disrupted and many of its typical habitants like the Tawny pipit (Aves: *Anthus campestris*) and the Tree Grayling (Lepidoptera: *Hipparchia statilinus*; Figure 5.7) have been lost.

Riksen & Goossens (2005) developed management techniques to reactivate aeolian erosion on the inland drift sand of the Kootwijkerzand in order to keep its central open area blowing and of a certain size. In their experiments they used a 'beach sand cleaner', a rotary cultivator, a disk harrow and an excavator. The tilling with the first two machines produces a loosely packed topsoil while the other two

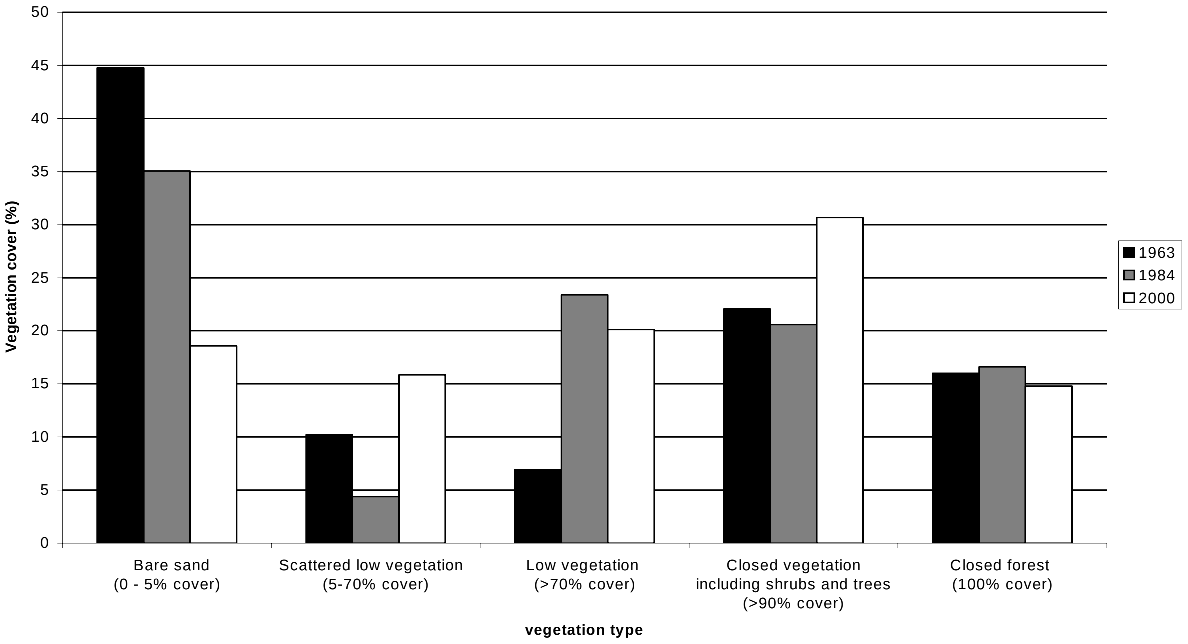

Figure 7.2. Change in vegetation between 1963, 1984 and 2000 at the Kootwijkerzand. Based on aerial photographs. After: Ketner-Oostra and Riksen (2005).

compact the topsoil. Compaction of the topsoil enhances the water-holding capacity and makes the surface fit for recolonization by algae. This type of management is attractive not only because of the physical results, but also because of its low cost. These findings might be of great value for the restoration of former drift-sand areas with their interesting biodiversity all over Western Europe (Riksen 2006).

7.3. Changes in lichen diversity in non-calcareous inland dunes since the 1970s

In the 1960s the inventories of inland sand dunes were mostly done as part of a heath and sand dune survey by MSc students of Utrecht University (Institute of Systmatic Botany, Department of Vegetation Science). For instance, for the Kootwijkerzand the successional stages from open sand, through lichen-rich pioneer grassland to heath were well documented (van Embden & Verwey 1968).

In **Chapter 6** the vegetation relevés of van Embden & Verwey were used as a base for comparison with my recent surveys (Ketner-Oostra 1996; Ketner-Oostra & Riksen 2005). With up to 34 species, lichen diversity at the Kootwijkerzand was still high in the beginning of the 21st century (Table 6.3) and identical to the present lichen diversity of the Deelense Zand in De Hoge Veluwe National Park, a stabilized drift-sand area in the centre of the Veluwe (Hasse 2005). Since the 1960s, only a few species have disappeared, probably as a result of high SO_2 deposition in the past, or climatic change (Aptroot & van Herk 2001). Several others are endangered and as such are on the Red List (Aptroot et al. 1998). However, the surface area covered by the lichen vegetation is probably much smaller than it was at the end of the 1960s. At that time the transition zone between the sand dune ecotope and heath was locally covered by the final stage of succession in the S.-C., rich in *Cladonia* species and with mats of reindeer lichens (van Embden & Snuif-Verwey, pers. comm.). Such lichen-rich mats also occurred locally in the open pine forest on nutrient-poor sand (Leijs 1964), the Cladonio-Pinetum sylvestris and has since disappeared inland (van der Werf 1991).

The former succession series in the Spergulo-Corynephoretum (S.-C.), starting with *Polytrichum piliferum* and ending with lichen-rich *Calluna* heath (Genisto anglicae-Callunetum, G.a.-C.), has been partly replaced by one including the neophytic moss *Campylopus introflexus* in the intermediate and late successional stages, present in 1993 and 2004 (Tables 6.4 and 6.5). Establishment of *C. introflexus*, partly in less vital *P. piliferum* carpets covered by algae, and partly on sand with a certain humus content, resulted in a different and accelerated succession (Figure 6.3), followed by a high production of humus (Table 6.6; Figure 6.5). However, this does not lead to an increase of the mosaic drift-sand vegetation with heather, which is so important for several fauna elements. It was found that the germination of *Calluna vulgaris* seeds is strongly inhibited by thick moss carpets of *C. introflexus* (Equihua & Usher 1993).

At present, the former open area of blowing sand is reduced in size and mainly covered by pioneer succession stages of the S.-C. with green algae and/or with *P. piliferum*, or with a combination of this moss species with *C. introflexus*. However, *C. introflexus* was found to be damaged and killed by inblowing sand.

In the area, lichens have established on ageing, less vital moss carpets of *P. piliferum*, but also on carpets including *C. introflexus*, which are often covered by a slimy layer of the green algae *Gloeocystis polydermatica* and have partly died as a result of desiccation or burial under windblown sand. These lichens are common lichens, such as humicole and aero-hygrophytic species, but pioneer lichens such as *Cetraria aculeata*, *Cladonia foliacea* and *C. zopfii* also occur (Table 6.4).

Cover sands are near or at the surface in more remote locations on the eastern side of the Kootwijkerzand and around 'Radio Kootwijk' where the public was denied access for a long time. The S.-C. cladonietosum in its rich species composition with several Red List species is still found here, on sand with a relatively high content of phosphate and exchangeable cations (Table 6.6).

7.4. Similarities and differences between the vegetation changes in the coastal sand dunes (V.-C.) and inland sand dunes (S.-C.) in the research period 1966-2006

The differences in botanical composition between the coastal and the inland sand dunes are mainly due to differences in climate and geology (Londo 1997). Apart from a much higher wind force and lower mean temperatures during the year, at the coast the salty sea spray supplies a considerable amount of exchangeable cations, within a gradient from the beach to the stabilized dunes on Terschelling (Kooistra 1971); coastal fog early in the afternoon is also more common. The total average annual rainfall (long-range) near the coast and inland is about the same with 792 mm yr^{-1} (KNMI klimatologie 2006), but its distribution over the year is different.

In the 1990s the effect of increased deposition of atmospheric N on the younger, Pleistocene sands redeposited along the Dutch coast in the Holocene by the rivers Meuse and Rhine (Eisma & Fey 1982) and on the older Pleistocene inland dune sands (Koster 2005) was found to be quite different.

7.4.1. Effect of increased N deposition on the soil of calcium-poor coastal dunes

Veer (1997) demonstrated that even though the atmospheric N deposition in open dune grasslands on Terschelling was only half as much as the deposition inland, it was an important source of N, as these soils had a relatively high phosphorus availability but were N-limited (Kooijman et al. 1998). Ammonia, the main pollutant, initially acts as a nutrient enrichment, but in the soil it also turns into nitric acid, causing the dune soil to acidify. The acidification has a direct effect on the microbial community of the dune soil, which is the indirect cause of the vigorous growth of *Ammophila* (de Boer et al. 1998).

In 1994, de Vries et al. (1994) predicted a disastrous effect of the heavy N deposition on dry dune vegetation in general by using a model of natural and anthropogenic soil acidification, where almost no buffering system against acidification was present (**Chapters 2 and 3**). We did indeed find a very low buffering capacity for the Terschelling plots through our oxalate tests, with a mean value for all Terschelling plots of 2 (+1/-1) mmol kg^{-1} aluminium oxalate (Chapter 3). We found an increased buffer capacity of 18 (+7/-5) mmol kg^{-1} Al oxalate for inland dunes as result of a longer history of vegetation development (Chapter 6).

The recently formed dunes outside the main stabilized sand dune area of Terschelling are slightly calcareous, such as dune ridges on the Noordsvaarder and within groups of dunes in Cupido's Polder (Figure 2.1). Here, soil acidification is still in progress and lichens thrive in the more open dune grasslands with a low cover of tall graminoids.

7.4.2. Effect of increased N deposition on the soil of non-calcareous inland dunes

The effect of ammonia acting as nutrient and causing soil acidification is also found in the inland dunes with nutrient-poor sand without calcium (**Chapter 6**). The open, still blowing sand in the centre of the Kootwijkerzand was found to be very acid (reference value of pH-KCl 4.7) with a very low percentage of basic ions (Table 6.6). Here, the pollutant ammonia has twice the concentration as in the Wadden district and acts as a nutrient enrichment and makes the soil more acid. However, in the inland sand dunes, no dominance of long grasses is found, as *Ammophila arenaria*, which is indigenous to the coastal dunes, has been planted only locally in inland dunes. In the S.-C. on the Veluwe, an increase in vitality and cover of the short grasses *C. canescens* and *F. ovina* s.l. was recorded, while in certain vegetation types, *Agrostis vinealis* and *Deschampsia flexuosa* were dominant. This is probably the result of the N deposition, as has been shown for grass encroachment in *Calluna* heath (Diemont 1996). Ammonia as a source of N is probably also used by algae and mosses in their expansion. In the soil, ammonia turns into nitric acid, making the soil more acid. The lowest pH-KCl of 3.1 was found in a mosaic vegetation of *F. ovina* s.l. with *Calluna vulgaris*, including *Juniperus communis* (Table 6.6).

Table 7.1. Incoming and reflected radiation (albedo %) in: (a) open V.-C. with 12% total plant cover with 7% *Corynephorus canescens* and 3% *Cladonia* spp. and (b) V.-C. with a closed carpet of reindeer mosses = *Cladina* spp. with some *Dicranum scoparium*. The radiation was measured with a solarimeter for outdoor installation (Kipp & sons, Delft). * slightly cloudy conditions.

Date in 1971	**29.03**	**22.04**	**22.04**	**19.05**	**19.05***
Time	13 h.	10 h.	13 h.	7 h.	13 h.
Incoming radiation in $W.m^{-2}$	159.5	139.6	167.8	176.2	157.9
(a) open V.-C.with 3% lichens					
Albedo in %	17.7	16.7	15.8	12.7	14.2
(b) closed V.-C. with *Cladina*					
Albedo in %	14.6	14.9	16.8	13.2	14.7

7.4.3. Changes in the microclimate since the end of the 1960s

The climate in Terschelling is almost extreme oceanic (see **Chapter 2**) and the weather pattern seems not to have changed much in the research period. The many hours of sunshine in the growing season cause high evapotranspiration, but in the inland dunes too, there is high evapotranspiration in pioneer vegetation after extremely high temperatures (Stoutjesdijk 1959). Large fluctuations in temperature between day and night favour lichens over phanerogams in the pioneer phase. Lichens require sufficient light for photosynthesis and growth. This can be seen both in the coastal dunes (in 1966) and inland dunes (in 1968), from the presence of lichens with high Ellenberg Light figures (Wirth 1992) for plants in full sunlight: see Tables 4.1 and 6.3. The decrease of lichen richness in the Terschelling dunes since the 1970s has been attributed to the high biomass of graminoids and herbs, which intercepts light (van der Meulen et al. 1996; Veer & Kooijman 1997) so that much less light reaches the soil. In grass-dominated V.-C. in 1994, only a few percent of the light was found to reach the soil compared with 70% in open dune grassland, a reference vegetation with lower abundance of grasses (Veer & Kooijman 1997). Much more light was probably received at the soil in the V.-C. of the late 1960s. This is shown in my albedo measurements of the V.-C. in 1971 (Table 7.1).

The values of these albedo measurements (between 14.2 and 17.7%) demonstrate that in (a) the open V.-C with 3% lichens (*Cladonia* spp.) and (b) the closed V.-C. with reindeer mosses (*Cladina* sp.) the albedo values were close to the albedo for dry grasslands (albedo 20.4-21.0%) and distant from that for tall (production) grassland (albedo 21.3-26.0%; see Stoutjesdijk & Barkman 1992).

Diurnal curves, I made in 1971 in lichen-rich V.-C., showed that during a day with a clear sky, lichens gradually lost the moisture content that had been built up the previous night (Ketner-Oostra 2006). Such alternating periods of drying out and remoistening result in macronutrients accumulating passively in lichens, and are a prerequisite for lichen growth (Nash III 1996).

The open dry dune grasslands in the 1960s, with short grasses like *C. canescens* and lichens (Chapter 2), may have been warm and moist after rain, but were usually dry again after one day of sunny weather.

The main difference between an open pioneer V.-C. of the past and the tall dense graminoid dune vegetation of the present is that this recent grassland maintains a moist and cooler microclimate during a much longer period of time (Stoutjesdijk & Barkman 1992). The same is probably true when an open pioneer S.-C. with some lichens is compared with a S.-C. with a dense vegetation of very vital grasses and mosses. It is these changes in the microhabitat of the terrestrial lichens in the Corynephorion that might have been decisive in their low abundance nowadays. That these changes have impact on the insect fauna, is clear (see Chapter 5, p. 111).

7.4.4. Interaction of N deposition with climatic change

If climatic change were to result in more rain in spring and autumn and a higher mean annual temperature, our monitoring results of 1998 will give an impression of the effect this could have on inland sand dune vegetation. In my yearly monitoring of the Nieuw Milligerzand in 1998 (Ketner-Oostra 1999) a relation between an extreme high total cover of grasses and excessive rainfall during the growing season (March, April and June) was very clear, with an annual value of 1055 mm in 1998 compared with the mean long-term annual value of 792 mm yr^{-1} (KNMI klimatologie 2006). Another rapid vegetation development by green algae and *C. canescens* between June 2001 and November 2002 is visualized in Figure 5.4. This might be the effect of the high rainfall in September 2001 and the relatively high temperatures in October 2001, as autumn is the season for *C. canescens* to germinate and establish on the sand (Marshall 1967).

Increasing rainfall and more moisture in springtime and autumn, both brought about by climatic change, may also allow the rapidly growing moss C*ampylopus introflexus* to recover after summer drought. However, such increased moss production might also be linked to the still high N deposition, as Londo (2002) showed for *Rhytidiadelphus squarrosus* in various grassland communities.

During the year, especially in summer, the microclimate in the sand dune vegetation might still have such maximum and minimum extremes as were measured in the past (Stoutjesdijk 1959), and determine vegetation development in the long term. The restricted lichen establishment in the pioneer phase of the inland sand dune ecotope compared with that of the 1960s, needs more research.

7.5. Evaluation of former restoration management in the calcium-poor coastal dunes

7.5.1. Effect-oriented measures (EGM) against acidification and eutrophication

To halt the grass encroachment and stop the decline in biodiversity, large-scale management was implemented in Eldorado (Terschelling) in a University of Amsterdam project in the period 1991-1995. Independently of this work I did my vegetation survey in Eldorado: the relevés and soil sampling were (1) on the SW slope of the first foredune, (2) ditto on the second dune ridge and (3) further inland around the reactivated blow-outs, with influence of blowing sand on the lichen-rich vegetation (**Chapter 3**).

The management measures within the nationwide EGM project did not succeed fully, because *Ammophila arenaria* regenerated from root fragments and continued to dominate. 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, more lime and high dynamics (see Eldorado Ridge 2 in Fig. 3.8). One positive finding, four years after reactivating the blow-outs, was the establishment of the pioneer species of the Phleo-Tortuletum ruralifomis in the fresh sand accumulations around the blow-outs (van der Meulen et al. 1996). A prolonged positive effect on plant diversity was found by Zumkehr (1999), who mentioned the positive influence of rabbits.

My own lichen-rich plots in Eldorado, some of which had a 90% cover of lichens, were about 60 m SE of the high dune with the reactivated blow-out no. 11 (van der Meulen et al. 1996) and the soil to a depth of 10 cm showed a pH-KCl of 5.4 and 0.05% lime (see Eldorado Ridge 3 in Table 3.4). Hardly any sand accretion was visible, but it sustained the lichen diversity and frequency for many years (see Chapter 3).

7.5.2. Sod-cutting experiment at the fourth dune ridge on the Noordsvaarder

In 1990, as an experiment for the State Forestry Service, 200 m^2 of moss (*Campylopus introflexus* and *Dicranum scoparium*) were removed from dry dune grassland on the fourth dune ridge by volunteers (**Chapter 3**). Using spades, sods were cut until the mineral sand was reached and then all organic material was removed manually.

The ordination of the vegetation of the Noordsvaarder (Figure 3.6) shows that the relevés of the sod-cutting experiment remained in the area dominated by *C. introflexus*. Five years after the sod cutting, mosses started to dominate again on a soil characterized by a reduced lime content through soil acidification. From this it appeared that the removal of the moss-encroached vegetation did not result in lichen-rich pioneer vegetation comparable to that on the second and third dune ridges of the Noordsvaarder.

In 2005, 15 years after the experiment, a dwarf shrub heath with *Empetrum nigrum* and *Polypodium vulgare* covered 75% of the permanent plot with mainly *Hypnum cupressiforme* in the moss layer (Ketner-Oostra 2005). The conclusion is that after cutting sods in dune grassland (V.-C.) dominated by *Campylopus*, lichens do not return as succession proceeds into dune heath.

7.5.3. Effect of changes in coastal protection and offshore sand suppletion

Stabilized dunes between Hoorn and Oosterend (Terschelling) were exposed to reactivated sand from the first foredunes and the beach. From 1990 onwards Rijkswaterstaat (the National Institute for Coastal and Marine Management) ceased their management for coastal protection in this area and left these dunes unmanaged. To stop further retreat of the coastline, sand was dumped on the seabed offshore from Hoorn and Oosterend in 1993 (Spanhoff 1998). Here, inblowing sand with a pH-KCl 7.4 and 0.8 % $CaCO_3$ from these unmanaged foredunes revitalized the lichen diversity in my research plots with more acid soils on the second and third dune ridges (Ketner-Oostra 2001). In a total lichen cover of 90%, *Cladonia rangiformis* and *C. foliacea*, which are characteristic of neutral or basic grassland, are growing together with subneutral species such as *Cladonia scabriuscula*, *C. furcata* and *Coelocaulon aculeatum*, as well as with rather acidophilic species such as *Cladonia gracilis*, *Cladina portentosa* and *Cla. ciliata*. The inblowing sand mainly influenced the 0-2 cm layer of the plots, where the effect was clearly measurable (pH-KCl 6.1; see **Chapter 3**). Ten years later the lichen diversity was still high, but the moss *H. cupressiforme* had increased its cover considerably (Ketner-Oostra 2005).

I recorded the same increase of this moss on the Paraplu dune between 1995 and 2005. This mobile dune at the west side of the Bosplaat nature reserve (Figure 3.1) has shifting sand on the rather steep outer southwest slope. In 1995 the influence of active sand movement was visible (40% open sand) and among the lichens the epiphyte *Evernia prunastri* was found, here growing terrestrially on slightly calcareous sand (Table 3.3). Ten years later, open sand covered 6% and an increase of *H. cupressiforme* was found, but still seven subneutral lichen species were present with the same total cover of 8% (Ketner-Oostra 2005). Such an increase of mosses is partly due to natural succession, but it could be promoted by the atmospheric supply of N (see 7.5.4).

7.5.4. Fire as a management tool for restoring former lichen diversity in dry dunes

The possibility of restoring the lichen diversity of an earlier succession stage (Oostra 1968) was studied by investigating the long-term effect of wildfire on grass-dominated V.-C. (**Chapter 4**). Vegetation development after fire was followed in two transects for eight years (1993-2001). After the fire, the lichen-rich earlier succession stage did not redevelop; instead, the succession resulted in a graminoid-dominated vegetation similar to the one existing before the fire (1990).

The huge increase in mosses was not expected. Though *Ceratodon purpureus* was the first colonizer after the fire, *Campylopus introflexus* gradually took over as the succession proceeded; eight years after the fire there was a total moss cover of 63% on the southern slope and of 70% on the western slope (Figures 4.1 and 4.3). During the succession the habitat on the southern slope appeared to be particularly suitable for the xerophytic moss *Polytrichum juniperinum*.

After the wildfire, lichens were slow to re-establish and remained very limited compared with 1966. After eight years, eight species were recorded on the southern slope, compared with 12 species in 1966; on the western slope, 11 species were found, compared with 14 species in 1966: see Table 4.1. On the original 'grey dunes' of 1966 the mean lichen cover on the south and the west slopes was respectively 15% and 42%, while in 2001, eight years after the fire, it was only very low, with a total cover of < 2% for both slopes (Fig 4.1).

Lichens in calcium-poor coastal dunes are dependent on open vegetation with much bare sand. Lichen colonization after the wildfire 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. For some time the minerals from the ashes might work as fertilizer. But the development in later years, after the ash had been leached out or blown away, was most probably a result of the same environmental factors that promoted the dominance of graminoids before the fire (see Chapter 4).

A comparable development occurred after a wildfire that burned down grass- and moss-dominated inland sand dune vegetation on the Nieuw Milligerzand near Kootwijk, north of the A.1 motorway (Amersfoort–Apeldoorn), in 1995. After five years of monitoring, it became clear that the encroachment with the moss *C. introflexus* was at the same extent as before the wildfire. However, on south and east exposed slopes, the moss *Polytrichum piliferum* re-occurred and where sand was blowing over this vegetation, a gradual establishment of lichen species was recorded (eight species with a total cover of 3% in five years; Ketner-Oostra 2002). Our results clearly show that fire alone is not sufficient for management aimed at restoration of lichen-rich dune grasslands in nutrient-poor coastal and inland dunes, influenced by a relatively high N deposition. Additional measures are recommended, such as large-scale clearing of the burned vegetation down to the mineral soil layer and encouraging sand to blow in. The sand will physically harm and dry out the remaining mosses; *C. introflexus* in particular has been shown to be sensitive to such treatment. Neutral or subneutral sand might be blown in from foredunes, from reactivated blow-outs or imported to the site, and moreover, promote lichens to establish (Chapter 3). In inland dunes, even the slightly acid sand being blown in from the crest of a nearby bare dune helped the lichen diversity on withering *C. introflexus* to re-establish (Ketner-Oostra 2002).

7.6. Evaluation of former restoration management in non-calcareous inland sand dunes on the Veluwe

7.6.1. Management to increase wind velocity

In the Kootwijk research it was found that succession always overtakes implemented management to keep or restore certain vegetation types (Ketner-Oostra & Riksen 2005). Furthermore, large disturbances have a limited lifespan (**Chapter 6).** The large area of bare sand in the centre of the Kootwijkerzand ('De Dikke Bart'; Figure 6.1b) existed in 1993 at the site of the archaeological excavations in 1973-1975 (Figure 6.2), but by 2002 was much smaller (Groeneweg 2004). The remapping in 1993 of a vegetation map of 1968 (van Embden & Verwey 1968) made this reduction apparent in detail (Ketner-Oostra 1996).

In general, the management measures to enforce the wind velocity should be implemented in the southwestern part of the sand dune area, to open up a stretch of bare sand in the prevailing southwest to northeast direction of the wind.
This is illustrated by the following examples.

(a) Hulshorsterzand (the Netherlands: 52°22' N, 5°44' E).
In 1991, there was large-scale cutting down of forest in the southwest of this nature reserve, with the aim of intensifying the wind force on an area of open blowing sand to the northeast. After the trees had been felled, no vegetation and topsoil was removed. Another intervention occurred in the northeastern part of the reserve; here, pine trees were cleared from steep sand dunes and the vegetation plus topsoil

down to the mineral soil layer were removed (Frenz & Griethuysen 1992). In both areas, the vegetation development has been monitored since 1996 (Ketner-Oostra 1997b) and the management was evaluated in 2005 (Jungerius & Ketner-Oostra 2006). The management in the southwestern area kept the long stretch of open sand to the northeast very active, though some primary succession began along the edges. After the intervention in the northeast, the long slopes were influenced by the prevailing southwesterly wind, and there was still much active sand in 2005. The low cover of the pioneer moss *P. piliferum* combined with that of *Stereocaulon condensatum*, the lichen from deflation locations. Other lichens, such as *Cladonia spp*., only established on litter near the former stands of pine trees. (Jungerius & Ketner-Oostra 2006).

(b) Wekeromse Zand (the Netherlands: 52°06' N, 5°41' E).
EGM restoration management in the Wekeromse Zand in 1992-1993 was successful in widening a stretch of open sand in the prevailing southwesterly wind (Ketner-Oostra 2003). Lichen diversity is still present, but the abundance is very much reduced. Only on the eastern edge of tree plantation near the western borders of this sand dune reserve are terrestrial lichens still to be found, probably protected by the edge of the planted pine forest from the high ammonia emission originating from the surrounding farmland. The reduction of lichen abundance was studied between 1984 and 1994 (Ketner-Oostra & Masselink 1999); a further decrease in cover was found between 1994 and 2004 (Ketner-Oostra 2004). Although the management of 1993 seemed effective in enlarging the area of open sand, it mainly stimulated the increase of *Polytrichum piliferum* and not the establishment of more lichen species (Ketner-Oostra 2003; 2004).

(c) Kootwijkerzand (the Netherlands: 52°11' N, 5°47' E).
The small-scale management by Kootwijk/Loobos Forestry Service staff along the western border of the Kootwijkerzand (Figure 6.1b, locations 1 and 2) was not very successful, and a grass-dominated sand dune landscape (mainly with *Deschampsia flexuosa*) developed, with much of the invasive moss *Campylopus introflexus* (Ketner-Oostra & Riksen 2005). The reactivation techniques were evaluated by Riksen & Goossens (2005) and the newly developed management is now ongoing (2005-2006). It entails removing part of the forest in the southwestern corner of the sand dune area, including the vegetation plus topsoil, and clearing the pioneer vegetation on a regular basis (Riksen 2006).

Conclusion: in general, this management to enhance wind scour is useful in keeping the drift sands open, but scheduled maintenance is needed afterwards.

7.6.2. Small-scale management by cutting self-sown trees in the transitional zone between the sand dunes and the surrounding planted wood

In the eastern part of the Kootwijkerzand where cover sand is at or near the surface, the management of the 1975-1985 period did improve biodiversity. Here, the lichen-rich intermediate and late stages of succession in the sand dune ecotope to the heath ecotope are still found: the different varieties of S.-C. with *Calluna* heath and *Juniperus communis* bushes (the transitional community between S.-C. subassociation cladonietosum / Genisto anglicae-Callunetum subassociation cladonietosum; see **Chapter 6**). Although in low abundance, reindeer and other fruticose lichens were found in this mosaic vegetation.

For a limited period, the removal of large self-sown pine trees from gravelly flat deflation plains in the southeastern part of the Hulshorsterzand was sufficient to maintain the lichen diversity. In these restored 'lichen steppes' 21 lichen species were found, including the Red List species *Cladonia strepsilis*, *C. zopfii*, *C. crispata* and *Cladina arbuscula* s.l. (Jungerius & Ketner-Oostra 2006). The presence of the open water surface of the 'Veluwemeer' northwest of the area may positively influence the mesoclimate; additionally, the high biodiversity might also benefit from the farming around this large nature reserve being more restricted compared with that in the 'Veluwse Vallei', west of the Kootwijkerzand, central at the Veluwe. The Wekeromse Zand, located 20 km south of the Kootwijkerzand, is even more influenced by the high emissions of ammonia from the factory farms in the surrounding area; in 2003, lichens were still less abundant than they had been before 1984 (Ketner-Oostra 2004).

On the Kootwijkerzand (Ketner-Oostra & Riksen 2005) and on the Hulshorsterzand (Jungerius & Ketner-Oostra 2006) a gradual succession is observed from the S.-C. cladonietosum (the variant with *Festuca ovina* s.l. and *Rumex acetosella* with a high cover and presence of *Cladina portentosa*, *Cla. arbuscula* s.l., *Cladonia gracilis* and *C. uncialis*; see Chapter 6) into a community dominated by *Festuca ovina* s.l. Much litter production by the grasses and many self-sown pine trees endangered the abundance of the lichens after approximately 15-20 years.

Conclusion: cutting of self sown trees and removing the canopy of grass-encroached vegetation down to the mineral soil layer seems necessary (in strips: see 7.7.2) on a regular basis in order to preserve these 'lichen steppes'.

7.7. Recommendations for future restoration management in coastal and inland dunes

7.7.1. Calcium-poor coastal dunes in the Wadden district

The restoration practice in acid dunes with intermediate and terminal stages of succession seems rather arbitrary. When large carpets of reindeer lichens are present, management in general and by cattle grazing in particular, should be abandoned, as such vegetation is very vulnerable and is becoming rare in the coastal dunes (Ketner-Oostra 2005).

The removal of the vegetation plus topsoil in grass- and moss-encroached dune grassland is sensible only if carried out to a deeper, slightly subneutral mineral soil layer with a low humus content. Also, the area should be large enough for effective wind scouring.

Fire as a management tool is only useful if followed by large-scale clearing of the burned vegetation to the mineral soil layer and if sand deposition is actively promoted: sand blowing in from dunes with a relatively higher calcium content (from foredunes), sand from re-activated blow-outs or even sand imported to the site (**Chapter 4**).

The future for lichen diversity on Terschelling lies in the younger dune areas of the Noordsvaarder and in the coastal area north of Hoorn (**Chapter 3**). On the Noordsvaarder, new natural dune ridges are formed of sand with a pH-KCl 6.9 and 0.3% $CaCO_3$ (Table 3.3). In the coastal area north of Hoorn, sand blowing in from the foredunes with a pH-KCl 7.4 and 0.8 % $CaCO_3$ has consolidated lichen diversity in older dune vegetation. In the groups of young dunes in Cupido's Polder there is already a high lichen diversity in the calcium-rich biotope with a pH-KCl of 8.1 and 1% $CaCO_3$ (Aptroot et al. 2000), and where there is superficial acidification to pH-KCl 6.0 and 0.2% $CaCO_3$ (Ketner-Oostra 2005).

7.7.2. Inland non-calcareous sand dunes in the Pleistocene district

To reactivate inland drift sands we need more scouring by wind in the still open area of the drift-sand ecotope. Several hectares of the forest in the southwestern corner of the drift-sand area of the Kootwijkerzand are now in the process of being removed. The balance between the area with bare sand and the area covered with pioneer vegetation can be achieved by relatively simple and cheap tilling measures (Riksen & Goossens 2005). The characteristic fauna depending on vital *Corynphorus* plants makes it necessary to have a phased treatment.

Such 'process management' was also advised by van den Acker et al. (2002) and is now being practised in the Maasduinen National Park, a river dune landscape of Pleistocene origin in the north of Limburg (NL) in 2004. Here, the vegetation of former lichen-rich sand dunes (Cleef & Kers 1968) was replaced by grassland dominated by *Campylopus introflexus*, resulting from the very high nitrogen deposition in this part of the country in the past.

However, the lichen diversity in sheltered locations on the eastern edge of the tree plantation near the western borders of the Bergerheide was still high, with lichens growing on degrading moss carpets (Sparrius et al. 2000; Ketner-Oostra et al. 2005). To preserve such lichen-rich intermediate and late stages of succession in the border between the drift-sand landscape and the surrounding forest, it is necessary to provide special 'pattern' treatment on a regular basis (Borkent et al. 2005; Riksen 2006). This includes cutting self-sown trees and removing the vegetation plus topsoil down to the mineral soil layer. This should be practised in strips in order to maintain the biodiversity of such vegetation stages and guarantee the dispersion of flora (lichens) and fauna elements.

7.7.3. Monitoring as an essential condition after restoration management

The principles of OBN (*Overlevingsplan Bos en Natuur*, survival plan forest and nature; see Chapter 1) have been successfully implemented with the EGM restoration management in the coastal and inland dunes in the past decades. This could only be demonstrated by monitoring vegetation and soil for at least 10 years. In the future, fauna should be incorporated into such plans, in accordance with the current restoration advice (van de Ancker et al. 2005; Jungerius & Ketner-Oostra 2006).

As current high N emission still exceeds the critical deposition values for the coastal V.-C. and the inland S.-C., after such large-scale EGM restoration, additional measures in a scheduled maintenance trajectory are still necessary (Chapter 5).

A further reduction of N emission from livestock farming, industry and traffic should be pursued, so that the remaining biodiversity in the coastal and inland sand dune ecotope could be a source for more dispersion. This is not only essential for the lichen-diversity but for all still existing flora and fauna elements.

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Summary

The objective of this thesis was to describe long-term changes in the lichen-rich dry grassland communities of the Corynephorion in calcium-poor dunes of the Netherlands. Some of the changes that have occurred since 1966, the starting year of the research, are due to natural succession. Others are caused by human-induced eutrophication and acidification through increased aerial inputs of nitrogen (mainly ammonia) as a consequence of increased livestock farming since the 1970s. In the calcium-poor coastal dunes of the Wadden district, new succession stages have occurred in the Violo-Corynephoretum (V.-C.) where the short grass *Corynephorus canescens* has been replaced by tall graminoids like *Ammophila arenara* and *Carex arenaria*. In the Spergulo-Corynephoretum (S.-C.) of the non-calcareous inland dunes of Pleistocene origin, it was found that *Corynephorus canescens* was more vital, while *Festuca ovina* s.l. and *Agrostis vinealis* had increased. In both ecosystems, the invasion of the moss *Campylopus introflexus*, an alien species from the southern hemisphere, had major consequences for the lichen diversity and abundance. These effects of grass and moss encroachment on lichen-rich vegetation were studied by comparing relevés from before the 1970s with relevés from the 1990s and beginning of the 21st century.

Another topic covered in this thesis is evaluation of small- and large-scale management measures aiming at restoring the former sand dune landscape with its high biodiversity. The prospects for lichen diversity in the coastal and inland nutrient-poor sand dunes of the Netherlands, a country in which atmospheric pollution of nitrogen (N) compounds is still high, were assessed.

The changes that have taken place in the vegetation of dry, lichen-rich pioneer grasslands of the coastal calcium-poor dunes of the Wadden Sea island of Terschelling (the Netherlands) since the 1970s are presented in **Chapter 2.** The cryptogam vegetation inside dry dune-grassland (the Corynephorion, the Tortulo- and Polygalo-Koelerion) and dune heath (Empetrion) before (the end 1960s) and after these changes (the 1990s) are compared. It was found that in the former period the lichen diversity in several plant communities was very high: 45 species. Until the beginning of the 1970s, vegetation types rich in *Cladonia* and *Cladina* species were found all over the island of Terschelling, on the fixed ‘grey’ dunes dominated by grey hairgrass (*Corynephorus canescens*). In addition, species like *Bryoria fuscenscens*, *Evernia prunastri*, *Hypogymnia physodes*, *H. tubulosa*, *Platismatia glauca*, *Pseudevernia furfuracea* and *Usnea* spp., which usually grow on trees, occurred here terrestrially on bare sand or on moss carpets.

Since the 1970s the encroachment by tall graminoids, especially of *Ammophila arenaria* and *Carex arenaria*, has changed the aspect of these dune grasslands. In addition, *Campylopus introflexus*, a species adapted to acid open sand, invaded these dunes, outgrowing not only the rare lichens from the pioneer stage of the V.-C., but also the more common pioneer species of decalcified sand. However, where this moss is less vital as a result of desiccation or being blown over by sand, common humicolous lichens and some pioneer species may act as secondary pioneers on these withered moss carpets. In the 1990s, some relatively open communities were still present in a transition stage of the V.-C. to the Phleo-Tortuletum and in the Phleo-Tortuletum itself, forming a suitable environment for some lichen pioneer species of slightly calcareous or subneutral sand, including some of the epigeic epiphytes. Such biotopes can still be found in young recently formed dune ridges on the Noordsvaarder and on young dunes in Cupido's Polder.

In **Chapter 3** a spatial sequence of seven differently aged coastal dune ridges parallel to the coast is used to study temporal changes within sand dune vegetation on the Noordsvaarder. In this nature reserve in the west of the island Terschelling, lichen-rich vegetation types of the pioneer stage of the V.-C. are still present. In addition, species of *Hypogymnia*, *Parmelia* and *Evernia*, which are usually epiphytic, occurred here terrestrially on bare sand or on moss carpets. The vegetation types of the dune ridges formed a chronosequence in which age increases with distance from the sea. The greatest lichen diversity was found on the second and third dune ridges, in a stage of primary succession that can be assigned to the V.-C. The changes from lichen-rich to moss-dominated stages were significantly related to soil development and acidification associated with the ageing of dune soil. Inblowing sand with a $CaCO_3$ content of 1.2 - 0.1% corresponded with lichen-rich vegetation on the second ridge of the Noordsvaarder, as well as with such vegetation in the young dune area in the east part of the island (Cupido's Polder), in the lichen-rich 'grey dunes' with inblowing sand from the foredunes north of Hoorn, in reactivated blow-outs in Eldorado and on the Paraplu dune. Less inblowing sand and increasing soil development influence lichen biodiversity

The skimming off the sods in moss-encroached vegetation on the fourth dune ridge on the Noordsvaarder appeared to be unsuccessful as a management technique for restoring the biodiversity of cryptogams as was found on the second and third dune ridges. Our findings suggest that the best option for maintaining lichen vegetation in the V.-C. is to allow sand to blow in: sand with a subneutral, neutral or basic pH from reactivated and natural blowouts, or sand from foredunes (the latter with a relatively high $CaCO_3$ content).

In **Chapter 4**, the effect of a wildfire in 1993 on a V.-C. with dominance of tall graminoids in the calcium-poor coastal dunes of Terschelling is monitored for eight years, using large continuous transects of blocks of 4 x 4 m on two dune slopes. These results are compared with those of the same transects in the lichen-rich vegetation in l966 and the vegetation of 1990. Between 1966 and 1990 the lichen-rich open grassland became dominated by tall graminoids (*Ammophila arenaria* and *Carex arenaria*) and developed partly into a dwarf shrub heath, resulting in a severe loss of lichen diversity. After the fire, a lush vegetation of long graminoids with an abundant moss cover developed. In 2001 the vegetation was still very dissimilar from the lichen-rich vegetation in l966. It is concluded that fire alone will not change dunes dominated by tall graminoids into open lichen-rich grasslands in an area with heavy aerial nitrogen deposition.

A comparison is made with the effect of fire in 1995 on moss-rich grassland vegetation (S.-C.) in inland dunes near Kootwijk. The suitability of fire for restoring lichen diversity of an earlier succession stage in dune grassland in a region with heavy nitrogen deposition is discussed. After fire, additional intervention is recommended, both for coastal and inland dunes. Suitable interventions are the large-scale clearing of the burned vegetation and the active promotion of deposition of sand, either blown in from foredunes (on the coast), from reactivated blowouts, or imported to the site.

In **Chapter 5**, the origin and development of the inland drift-sand ecotype in the Netherlands and the rapid decline of the total active drift-sand area after 1960 is discussed. To preserve the inland drift sands, it is necessary to understand the origin, development and the role of human activity in this semi-natural ecotype. A management strategy is needed to halt the rapid decline of the remaining active drift sands.

Drift-sand landscapes are relatively young landscapes of Holocene age. They often occur as oval cells, 1.5 to over 6 km long in the direction of the prevailing wind. These cells presumably represent reactivated deposits of Younger Cover Sands. Large-scale erosion events in combination with human activity have suppressed the development of vegetation. After the change in land use in the first half of the twentieth century, in which most of the drift sands were re-afforested, the vegetation succession began a progressive development. The rate of this development mainly depended on the geomorphological stage of the area, the size of the area and human activity. Since the end 1960s the increased nitrogen deposition caused by the expanded animal production, has accelerated the vegetation succession, resulting not only in a further decline of the drift sands, but also in a loss of the fragile balance between the different ecotopes and loss of some of its typical birds like *Anthus campestris* and butterflies like *Hipparchia statilinus*.

Most drift-sand vegetation and fauna need the presence of bare sand nearby and a certain level of erosion activity to survive. To preserve the drift-sand ecotopes, it is therefore recommended to keep the area affected by erosion sufficiently large (process management). In the meantime one should also ‘maintain’ or increase the wind force in the drift-sand area by suppressing the growth of tall vegetation and removing trees, which form a wind barrier. In areas which are less suitable for reactivation, one could restore the mosaic vegetation by removing the grass-encroached vegetation including the topsoil on a limited scale (pattern management). More research is needed to develop a more balanced management strategy as a management tool for the managers of inland drift sands. The role of the increased nitrogen deposition in the regeneration process also needs further investigation, in order to find an effective way to suppress its effect. The development of management strategies for the Dutch inland drift sands might be of great value to drift-sand areas in Western Europe where nature conservationists are becoming more interested in the restoration of former drift-sand areas.

Chapter 6 describes the difference between former and actual successional pathways from open sand, through lichen-rich pioneer grassland to heath and forest. The changes in vegetation succession in general and in the diversity of cryptogams in particular of an inland non-calcareous and nutrient-poor sand dune area, the Kootwijkerzand (central Netherlands), are presented for a period of nearly 40 years**.** We compared the cryptogam vegetation in the Spergulo-Corynephoretum and Genisto anglicae-Callunetum in 1968, 1993 and 2004. In the early period, the lichen diversity in these plant communities appeared to be very high. The aspect was formed by *Corynephorus canescens* and *Polytrichum piliferum.*

Since the 1970s grass-encroachment and the invasion by the neophytic moss *Campylopus introflexus* altered these dunes. These changes have been attributed to the heavy aerial deposition of N in this part of the Netherlands, which caused eutrophication and acidification of the nutrient-poor soil.

In the more recent periods, the actual lichen diversity did not really diminish, with 34 different terrestrial lichen species still present; the cover was clearly reduced, however, when encroaching mosses outgrew the lichens in all succession stages. The former succession series starting with *Corynephorus canescens*, *Polytrichum piliferum* and ending with lichen-rich *Calluna* heath (in 1968) has been partly replaced by one including C*ampylopus introflexus* (in 1993 and 2004). When this neophytic moss becomes less vital because of ageing, desiccation or burial under wind-blown sand, common humicole, aero-hygrophytic and even some pioneer lichens may locally establish on or between the moss cushions. The S.-C. cladonietosum in its rich species composition is still found on since long established blowing sand and on cover sand, occurring in more remote areas on the eastern side of the Kootwijkerzand and in the former closed area around 'Radio Kootwijk'.

The changes from pioneer vegetation with open sand to moss-dominated stages were significantly related to soil development and acidification. The lichen diversity was found to be connected to sand containing more phosphate and assimilable cations.

The impact of natural (by the fauna) and artificial disturbance such as a large archaeological excavation and several restoration projects is discussed. Small-scale management by cutting down self-sown trees and removing the canopy has positively influenced lichen diversity and needs to be continued. Large-scale management is essential, to create a large open space in the central area in order to stimulate the blowing of sand.

Chapter 7 presents a synthesis of the vegetation changes found in coastal and inland sand dunes in the research period 1966-2006, and relates them to changes in environmental factors in that period. Differences between the developments in the coastal V.-C. and the inland S.-C. are discussed in relation to their specific environment, such as soil history and climatic factors. In the V.-C of calcium-poor coastal dunes, encroachment with tall graminoids has altered the specific microclimate which is essential for lichens.

EGM restoration management (Effect-oriented measures against acidification and eutrophication) in both the nutrient-poor coastal and inland dunes is evaluated using the data presented in this thesis and the recent end-evaluation of several long-term monitoring programmes. Recommendations for future restoration management to maintain or regain biodiversity in nutrient-poor coastal and inland dunes are given:

(a) The pioneer vegetation in young dune areas in the west and east of the island Terschelling (Noordsvaarder and Cupido's Polder respectively) is very promising for lichen diversity in the different dune ecotopes. Sand blowing in from foredunes north of Hoorn is maintaining the lichen-rich V.-C. in the older dunes. For the grass-encroached stabilized dunes, reactivation of former blow-outs is still an option for the future. Terminal lichen-rich stages with reindeer lichens need protection and should not be grazed.

(b) For inland non-calcareous dunes, large-scale management is essential in the early succession stage with pioneer vegetation, in order to create a large open space in the central area and to stimulate the sand blowing. Small-scale management in grass-encroached succession stages by cutting down self-sown trees and removing the canopy has positively influenced lichen diversity and needs to be continued. This should be practised in zones, in order to maintain the biodiversity of such vegetation stages and guarantee the dispersion of flora (lichens) and fauna elements.

Additional measures in a scheduled maintenance traject are recommended when large scale EGM restoration is applied. This seems necessary given that the current high N emission still exceeds the critical deposition values for the coastal and inland communities of the Corynephorion. A further reduction of N emission from livestock farming should be pursued, so that the remaining biodiversity in the coastal and inland sand dune ecotope could be a source for more dispersion. This is essential not only for the lichen diversity, but also for all existing flora and fauna elements.

Samenvatting

De korstmosrijke duinen langs de Nederlandse kust en in het binnenland: vegetatieontwikkeling en beheer in het Buntgras-verbond (Corynephorion)

In dit proefschrift worden de langetermijnveranderingen in de korstmosrijke plantengemeenschappen van het Buntgras-verbond (Corynephorion) voor de Nederlandse droge kalkarme duinen beschreven. Sinds het onderzoek in 1966 begon, is door natuurlijke successie de vegetatie veranderd, maar is er ook invloed van vermesting en verzuring zichtbaar als gevolg van de verhoogde atmosferische depositie van stikstof (vooral ammoniak) door de sinds de jaren zeventig (van de vorige eeuw) toegenomen veehouderij (bio-industie). In de de Duin-Buntgras-gemeenschap (Violo-Corynephoretum = V.-C.) van de kalkarme kustduinen in het Waddendistrict komen sindsdien nieuwe successiestadia voor. Het korte Buntgras (*Corynephorus canescens*) is vervangen door lange grasachtigen zoals Helm (*Ammophila arenaria*) en Zandzegge (*Carex arenaria*). In de Heidespurrie-Buntgras-gemeenschap (Spergulo-Corynephoretum = S.-C.) van de binnenlandse, van oorsprong Pleistocene kalkloze stuifzanden, is Buntgras vitaler geworden terwijl de hoeveelheid Schapengras (*Festuca ovina* s.l.) en Zandstruisgras (*Agrostis vinealis*) is toegenomen. Ook de invasie van de neofyt Grijs kronkelsteeltje (ook wel Tankmos genoemd = *Campylopus introflexus*), een uitheemse soort afkomstig van het zuidelijk halfrond, heeft grote gevolgen gehad voor de diversiteit en rijkdom aan korstmossen (lichenen) in beide ecosytemen. De effecten van vergrassing en vermossing op de korstmosvegetatie zijn onderzocht door vegetatieopnamen van voor 1970 te vergelijken met die uit de jaren negentig en begin 21e eeuw.

Een ander onderwerp in dit proefschrift is de evaluatie van kleinschalige en grootschalige beheersmaatregelen die tot doel hadden het vroegere duinlandschap met de bijbehorende hoge biodiversiteit te herstellen. Het toekomstperspectief voor de diversiteit aan korstmossen in de kust- en binnenlandse duinen wordt uiteengezet, waarbij de relatief hoge atmosferische stikstof (N)-depositie een negatieve factor van betekenis blijft vormen.

In **Hoofdstuk 2** worden de veranderingen beschreven die de pioniervegetatie van de droge korstmosrijke graslanden in de kalkarme duinen van het Waddeneiland Terschelling sinds 1970 ondergingen. De mos- en korstmosvegetatie in die duingraslanden, het kalkarme Buntgras-verbond, het verbond van de kalkrijke droge duingraslanden (Polygalo-Koelerion), het Duinsterretjes- (Tortulo-Koelerion) en het duinheide-verbond (Empetrion) van vóór 1970 en van na deze veranderingen (de jaren negentig), zijn vergeleken. In de eerstgenoemde periode was de diversiteit aan korstmossen in de verschillende plantengemeenschappen erg hoog en telde 45 soorten. Tot in het begin van de jaren zeventig waren over het hele eiland de door Buntgras gedomineerde zgn. grijze duinen te vinden, waarin de vegetatietypen voorkwamen die rijk waren aan korstmossoorten van het genus *Cladonia* en *Cladina* (de rendiermossen).

Bovendien groeiden soorten als *Bryoria fuscenscens, Evernia prunastri, Hypogymnia physodes, H. tubulosa, Platismatia glauca, Pseudevernia furfuracea* and *Usnea* spp., die meestal op bomen groeien, hier terrestrisch op het kale zand of op mostapijten.

Sinds de zeventiger jaren heeft de vergrassing met Helm en Zandzegge het aspect van de duingraslanden sterk veranderd. Bovendien zijn de duinen overgroeid met Grijs kronkelsteeltje, een soort die aangepast is aan verzuurd open zand, waarbij niet alleen de zeldzame korstmossen van het pionierstadium van het V.-C. zijn verdreven, maar ook de algemenere soorten van het ontkalkte duinzand. Waar dit mos echter minder vitaal is als gevolg van uitdroging of door overstuiving, kunnen algemene op humus groeiende korstmossen, evenals enkele pioniersoorten, als secundaire pioniers op de kwijnende mostapijten gaan groeien. In de 1990er jaren bestonden er nog relatief open vegetatietypen in de overgangsfase van het V.-C. naar het Phleo-Tortuletum (de Duinsterretjes-gemeenschap) en het echte Phleo-Tortuletum, die een passende ecotoop vormden voor pionierkorstmossoorten van subneutraal en zwak kalkhoudend zand, inclusief enkele normaliter epifytische soorten. Dergelijke biotopen komen nog steeds voor op recent ontstane duinrijen op de Noordsvaarder en op jonge duinen in Cupido's Polder.

In **Hoofdstuk 3** is de ruimtelijke opeenvolging van zeven duinrijen van verschillende leeftijd, die op de Noordsvaarder evenwijdig aan de kust liggen, gebruikt om de veranderingen te bestuderen die deze duinvegetatie in de loop van de tijd heeft ondergaan. In dit op westelijk Terschelling gelegen natuurreservaat zijn korstmosrijke vegetatietypen van het V.-C. nog steeds aanwezig. Bovendien groeien de normaliter epifytische korstmossen *Hypogymnia, Parmelia* en *Evernia* hier op kaal duinzand of op mostapijten. De vegetatietypen van deze duinrijen vormen een chronologische reeks waarbij de leeftijd toeneemt met de afstand tot de zee. De hoogste diversiteit aan korstmossen is aangetroffen op de tweede en derde duinrij, in een stadium van primaire successie binnen het V.-C. De veranderingen van korstmosrijke stadia naar door mossen gedomineerde stadia vertonen een significante relatie met bodemontwikkeling en verzuring die samenhangt met het ouder worden van de duinbodem. Er bleek een samenhang tussen het inwaaien van zand met een CaCO3 -gehalte van 1,2 - 0,1% en de rijkdom aan korstmossen van (1) de tweede duinenrij op de Noordsvaarder, (2) met die van het jonge duingebied oostelijk op het eiland (Cupido's Polder), (3) met die in het overstuivingsgebied op de tweede en derde duinrij ten noorden van Hoorn, (4) met die in de omgeving van gereactiveerde stuifkuilen in Eldorado en (5) met die van de vegetatie op het Paraplu-duin. Minder inwaaiend zand en verdere bodemvorming doen de rijkdom afnemen.

Het plaggen van vermoste duinvegetatie op de vierde duinrij van de Noordsvaarder om de biodiversiteit aan (korst)mossen zoals die op de tweede en derde duinrij aanwezig was, te herstellen, bleek als beheersmaatregel geen succes. Uit voornoemde resultaten blijkt dat de beste manier om een korstmosrijke Buntgras-vegetatie te handhaven of the bevorderen is het bevorderen van de verstuiving, te weten van duinzand met een subneutrale, neutrale of basische pH van gereactiveerde en natuurlijke stuifkuilen, of van zand afkomstig uit de zeereep met een relatief hoog CaCO3 -gehalte.

Hoofdstuk 4 beschrijft het vervolgonderzoek na een natuurlijke duinbrand in 1993 waardoor een vergrast V.-C. op een onderzoeksduin op Terschelling in de as werd gelegd. Acht jaar lang is op twee hellingen het herstel van de vegetatie gevolgd in een aaneengesloten transect bestaande uit blokken van 4 m x 4 m. De resultaten daarvan zijn vergeleken met die van dezelfde transecten met korstmosrijke vegetatie in 1966 en de vergraste vegetatie in 1990. Tussen 1966 en 1990 gingen Helm en Zandzegge het open korstmosrijke duingrasland domineren en ontwikkelde zich plaatselijk een dwergstruikheide van Kraaihei (*Empetrum nigrum*). Het resultaat was een sterke achteruitgang in de korstmossendiversiteit. Na de brand ontwikkelde zich een weelderige grasachtige vegetatie met een ondergroei van mossen. In 2001 verschilde de vegetatie sterk van de korstmosrijke vegetatie uit 1966 en leek op die uit 1990 maar met meer Grijs kronkelsteeltje. De conclusie was dat in een gebied met een relatief hoge N-depositie een brand de vergraste duinvegetatie niet zal veranderen in een open korstmosrijk duingrasland.

Dit resultaat is vergeleken met het effect van een brand (1995) op mosrijke Buntgras-vegetatie (S.-C.) in voedselarme duinen langs de snelweg ten noorden van Kootwijk. Daar is na vijf jaar ook een vergraste en vermoste vegetatie teruggekeerd, vergelijkbaar met die van voor de brand. Het blijft een punt van discussie of brand geschikt is als beheersmaatregel om een eerder successiestadium van het duingrasland terug te krijgen in gebieden met een hoge N-depositie. Na een brand in de kustduinen of in binnenlandse duinen worden extra beheersingrepen aanbevolen, zoals het op grote schaal verwijderen van de verbrande vegetatie en het actief bevorderen van zandtoevoer. Aan de kust kan dat door verstuiving vanuit de zeereep te stimuleren, of door het weer openmaken van stuifkuilen, wat ook opgaat in het binnenland, of zelfs door de aanvoer van zand om dat uit te strooien over het verbrande terrein.

In **Hoofdstuk 5** worden de oorprong en de ontwikkeling van het stuifzandecotype in Nederland beschreven waarbij de snelle afname van het totale stuifzandareaal na 1960 wordt besproken. Om de binnenlandse stuifzanden te behouden is het noodzakelijk de oorsprong van dit half-natuurlijke ecotype, de ontwikkeling ervan en de rol van de mens daarbij te leren kennen. Om het proces van de snelle achteruitgang van het nog bestaande actieve stuifzand tot staan te brengen, is een beheersstrategie noodzakelijk.

Stuifzanden zijn relatief jonge landschappen uit het Holoceen. Ze komen voor als ovale cellen van anderhalf tot meer dan 6 km lengte in de belangrijkste windrichting. Dergelijke cellen zijn waarschijnlijk gereactiveerde afzettingen van Jonger Dekzand. De combinatie van grootschalige erosie, zoals zandstormen als gevolg van droogteperioden en menselijke activiteiten, hebben de vegetatieontwikkeling afgeremd. Na de verandering in landgebruik in de eerste helft van de 20e eeuw werden de meeste stuifzandgebieden herbebost. Daarna kon zich in de meeste overgebleven stuifzanden een vegetatiedek ontwikkelen met alle karakteristieke successiestadia van open zand naar bos. De mate van die ontwikkeling hing grotendeels samen met de geomorfologie van het gebied, de omvang van het terrein en de menselijke activiteit die er plaatsvond. Sinds eind zestiger jaren heeft de toegenomen N-depositie als gevolg van de uitbreiding van de bio-industrie de vegetatiesuccessie versneld. Dit resulteerde in een verdere afname van het stuifzandareaal alsmede de teloorgang van de fragiele balans tussen de verschillende stuifzandecotopen en het verdwijnen van sommige specifieke vogels en vlinders, zoals de Duinpieper (*Anthus campestris*) en de Kleine heidevlinder (*Hipparchia statilinus*).

De stuifzandvegetatie en de bijbehorende fauna hebben kaal zand en een zekere mate van dynamiek nodig om te overleven. Om de stuifzandecotopen te behouden wordt daarom aanbevolen het areaal waar erosie-activiteit optreedt voldoende groot te houden (procesbeheer). Tegelijkertijd moet in het stuifzandgebied de windkracht gehandhaafd of zelfs vergroot worden door hoge vegetatie (opslag) te verwijderen en in sommige delen van het terrein bos te kappen dat een barrière voor de wind vormt. In terreindelen die minder geschikt zijn om te reactiveren kan de mozaïekvegetatie hersteld worden door de vergraste vegetatie op beperkte schaal te verwijderen (patroonbeheer). Er is meer onderzoek nodig om een uitgebalanceerde beheersstrategie te ontwikkelen die als handleiding voor beheerders van stuifzanden kan dienen. De rol van de toegenomen N-depositie in het regeneratieproces moet ook verder onderzocht worden om de effecten ervan op een doeltreffende manier tegen te kunnen gaan. De ontwikkeling van een beheersstrategie voor de Nederlandse stuifzanden kan voor heel West-Europa van grote waarde zijn. Europese natuurbeschermers tonen in toenemende mate belangstelling voor het herstel van vroegere stuifzandterreinen.

In **Hoofdstuk 6** wordt het verschil tussen de voormalige en huidige successiereeksen van open zand, via korstmosrijk pionierduingrasland naar heide en bos beschreven. Deze verandering in de vegetatieontwikkeling in het algemeen en van de biodiversiteit aan (korst)mossen in het bijzonder, is over een tijdsbestek van 40 jaar onderzocht voor het Kootwijkerzand, een binnenlands kalkloos en voedselarm stuifzandgebied. Daartoe is de vegetatie behorend tot de Heidespurrie-Buntgras-gemeenschap en de Stekelbrem-Struikhei-gemeenschap (Genisto-anglicae-Callunetum) van 1968, 1993 en 2004 vergeleken. In de oudste periode bleek de rijkdom aan korstmossoorten in genoemde plantengemeenschappen zeer hoog te zijn waarbij het aspect bepaald werd door Buntgras en Ruig haarmos (*Polytrichum piliferum*).

Sinds de jaren zeventig van de vorige eeuw is de neofyt Grijs kronkelsteeltje, een soort aangepast aan zuur open zand, het stuifzandterrein binnengedrongen, terwijl bovendien vergrassing toesloeg zoals ook elders in de binnenlandse duinen. Deze veranderingen worden toegeschreven aan de hoge stukstofdepositie in het centrale deel van Nederland, die vermesting en verzuring van de voedselarme bodem tot gevolg heeft.

In de twee recentere onderzoeksperioden bleek de diversiteit aan korstmossen niet echt achteruit te zijn gegaan, met 34 verschillende op de grond groeiende soorten, maar de mate van bedekking (abundantie) was dat echter wel, doordat vermossing met Grijs kronkelsteeltje de korstmossen in alle successiestadia bleek te verdringen. De vroegere successiereeks (in 1968) die begon met Buntgras en Ruig haarmos, eindigde met korstmosrijke Struikhei (*Calluna vulgaris*)-vegetatie. Deze is vervangen door een reeks waarin Grijskronkelsteeltje een plaats heeft gevonden (in 1993 en 2004) Als dit mos echter minder vitaal wordt door veroudering, uitdroging of door overstuiving, dan kunnen zich op of in spleten tussen de moskussens korstmossen vestigen - en wel de op humusgroeiende en luchtvochtigheid-minnende soorten, evenals sommige pioniersoorten. Het S.-C. cladonietosum kan in een rijke soortensamenstelling nog steeds gevonden worden op reeds lang geleden vastgelegd stuifzand of dekzand. Dit is aangetroffen in de meer afgelegen delen in het oostelijk deel van het Kootwijkerzand en in het terrein om 'Radio Kootwijk' dat voor lange tijd niet voor het publiek toegankelijk was.

Er bleek een significante relatie tussen de verandering van pioniervegetatie met veel open zand naar door mossen gedomineerde stadia enerzijds, en de bodemontwikkeling in combinatie met verzuring anderzijds. De diversiteit aan korstmossen bleek samen te hangen met een wat hoger gehalte aan fosfaat en opneembare kathionen in het onderzochte zand.

De effecten van natuurlijke (door fauna) en kunstmatige verstoringen zoals grote archeologische opgravingen en beheersingrepen, zijn geëvalueerd. Kleinschalig beheer als het kappen van opslag en plaggen heeft de diversiteit aan korstmossen positief beïnvloed en moet zeker voortgezet worden. Grootschalig beheer blijft in het centrale terrein noodzakelijk om daar een open vlakte te houden en verstuiving te bevorderen.

Hoofdstuk 7 geeft de synthese van de vegetatieontwikkeling zoals die in de onderzoeksperiode 1966-2006 is aangetroffen in de kalkarme duinen aan de kust en in de kalkloze stuifzanden in het binnenland. Deze vegetatieontwikkeling wordt in verband gebracht met de veranderingen in omgevingsfactoren in die periode. Verschillen tussen de ontwikkelingen in het V.-C. aan de kust en het S.-C. in het binnenland worden besproken in relatie tot hun specifieke omgeving, zoals bodem en klimaat. In het V.-C. van de kalkarme duinen heeft de vergrassing met hoge grasachtigen het specifieke microklimaat dat essentieel is voor korstmossen sterk veranderd.

EGM herstelbeheer (Effectgerichte Maatregelen tegen verzuring en vermesting) is zowel voor de voedselarme kustduinen als voor de binnenlandse duinen geëvalueerd. Daarbij zijn onderzoeksresulaten uit dit proefschrift gebruikt en die uit recente evaluatierapporten van langetermijn monitoringprogramma's. Aanbevelingen voor toekomstig herstelbeheer worden gedaan om de de biodiversiteit in dergelijke duingebieden te behouden of terug te krijgen:

(a) De pioniervegetatie in jonge duinen op westelijk en oostelijk Terschelling hebben een veelbelovende diversiteit aan korstmossen van uiteenlopende ecotopen. Inwaaiend zand vanuit de 'losgelaten' zeereep ten noorden van Hoorn bevordert de rijkdom aan korstmossen in gevestigd duingrasland (V.-C.). Voor de vergraste middenduinen van het eiland is het reactiveren van oude stuifkuilen nog steeds aan te bevelen.

(b) Voor de voedselarme stuifzanden in het binnenland zijn grootschalige beheersingrepen in de eerste successiestadia met pioniervegetatie van groot belang. Deze dienen om centraal in de zandverstuiving een voldoende grote open ruimte te maken en daar de verstuiving te bevorderen. Kleinschalig procesbeheer als het kappen van opslag en plaggen in vergraste successiestadia heeft in het verleden de diversiteit aan korstmossoorten bevorderd en moet daarom worden voortgezet. Dit moet echter strooksgewijs uitgevoerd worden om de biodiversiteit van die successiestadia te handhaven en de verspreiding van flora (korstmossen) en fauna-elementen te garanderen.

Na grootschalige EGM herstelmaatregelen wordt aanvullend beheer volgens een onderhoudsplan sterk aanbevolen. Dit lijkt nodig zolang de huidige hoge N-emissie de kritische depositiewaarde voor het V.-C. in de kustduinen en het S.-C. in de stuifzanden nog steeds overschrijdt. Naar een verdere afname van de hoofdzakelijk van de bio-industrie afkomsige N-uitstoot moet gestreefd worden. In de toekomst kan de nog aanwezige biodiversiteit in de ecotopen van kustduinen en stuifzanden dienen als verspreidingsbron. Dit is niet alleen van essentieel belang voor de diversiteit aan korstmossen maar voor alle nog aanwezige flora- en fauna-elementen.

Curriculum vitae

Op 13 november 1940 werd Rita Oostra in Eindhoven als derde van vier Oostra-kinderen geboren en voorzien van de 'voormoederlijke' namen Henderika Gepke Maria. Begin van de 1930-er jaren waren haar ouders vanuit Groningen naar de Brabantse lichtstad geëmigreerd, waar vader Oostra alle kansen kreeg zich bij Philips tot assistent onderzoeker te ontplooien.

Eindhoven was na de 2e wereldoorlog een bruisende stad met moderne scholen, jeugdwerk en bibliotheken. Daar werd door het gezin volop gebruik van gemaakt. In 1953 ging Rita naar het Gemeentelijk Lyceum waar zij in 1959 het diploma gymnasium β behaalde. Met de vakken biologie en scheikunde als favorieten koos zij voor de studie biologie aan de Rijksuniversiteit te Utrecht. Haar hoofdvak voor het doctoraal examen was Chemische dierfysiologie, waarvan een deel bestond uit onderzoek over insectenhormonen bij de vakgroep Entomologie aan de Landbouw Hogeschool te Wageningen. Haar bijvakken waren Fytopathologie en Vegetatiekunde, dat toen nog bij Systematische Plantkunde was ondergebracht. In het kader van dit laatste vak onderzocht zij de korstmosrijke duinvegetatie op Terschelling.

Na het doctoraalexamen in 1967, inclusief de eerste graad onderwijsbevoegdheid, gaf zij twee jaar biologieles aan het Corderius Lyceum in Amersfoort. Daarnaast werkte zij in deeltijd als wetenschappelijk medewerker bij prof. J. Lanjouw aan de voornoemde afdeling Vegetatiekunde van het Instituut voor Systematische Plantkunde aan de Utrechtse Universiteit. Haar doctoraal onderzoek op Terschelling werd uitgebreid en zij begeleidde studenten bij hun afstudeerprojecten op de Waddeneilanden. Na haar huwelijk met Pieter Ketner in 1969 verhuisde zij naar Terschelling, waar haar man al enige jaren als vegetatie-ecoloog werkte in het kader van het Internationaal Biologisch Programma (IBP). Zij bleef part-time aan de universiteit in Utrecht verbonden om haar onderzoek voort te zetten. Na de promotie van Pieter bij prof. V. Westhoff in Nijmegen vertrokken zij samen naar Kenia, waar hij een baan bij UNESCO kreeg.

Na terugkeer in 1975 vestigde het gezin zich in Wageningen waar haar man medewerker werd bij de vakgroep Vegetatiekunde en Plantenoecologie van de Landbouw Hogeschool. Naast de opvoeding van hun twee dochters werkte zij regelmatig als invalskracht voor Elsevier’s Attenderingsdienst afd. Milieuverontreiniging. Daarna werkte zij drie jaar als assistent van de redactie van 'Antonie van Leeuwenhoek', het tijdschrift van de Nederlandse Vereniging voor Microbiologie. Toen de kinderen naar school gingen verwerkte zij het vegetatieonderzoek uit de periode 1966-1972 op Terschelling. In 1983 werd het floristische deel samen met Maarten Brand gepubliceerd als het onderdeel over korstmossen in het Witboek Waddengebied. De vegetatiekundige resultaten kwamen in 1989 uit als rapport van het toenmalige Rijksinstituut voor Natuurbeheer (RIN).

Gestimuleerd door deze publicaties en gesteund door Ger Londo van het RIN, hervatte zij in 1990 haar onderzoek op Terschelling, waar de korstmosrijke duingraslanden inmiddels sterk vergrast waren. Kort daarna kwam er een opdracht van Staatsbosbeheer Regio Veluwe voor een inventarisatie van de korstmossen van het Kootwijkerzand, gevolgd door een van Het Gelders Landschap over effecten van herstelbeheer op het Wekeromse zand. Vanaf die tijd werkt zij als freelance vegetatiekundige in projecten van droge duinen en stuifzanden. In 1998 werd zij gevraagd lid te worden van het Deskundigenteam Droge duinen en Stuifzanden van het Expertise Centrum (EC) van het Ministerie LNV. De resultaten van haar eigen lange-termijn onderzoek naar de veranderingen in de korstmosrijke duingraslanden aan de kust en in het binnenland - met de effecten van maatregelen tot herstel van de oorspronkelijke biodiversiteit - zijn voor een deel gebundeld in dit proefschrift.

Naast haar wetenschappelijke contacten in de universitaire wereld bleef zij ook betrokken bij het studentenleven, namelijk door zich in te zetten voor de commissie van het Engelstalige studentenpastoraat 'Student Chaplaincy' in Wageningen.

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