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Vegetation succession and habitat restoration in Dutch lichen-rich inland drift sands

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Abstract

Between 1996 and 2006 the vegetation succession in drift sands and in blown-out gravel-rich depressions, located in the nature reserve Hulshorsterzand in the central Netherlands, was studied. Within this Natura 2000 habitat (type 2330: inland dunes with open *Corynephorus* and *Agrostis* grasslands) so-called lichen steppes are included, famous for their biodiversity, both in flora (cryptogams), and in fauna. With multivariate analysis, the relation between the primary succession, the species composition of the vegetation and the soil quality was studied in three different biotopes i.e. 1. drift sand, 2. blown-out gravel-rich depressions and 3. drift sand after management. With a total of up to 34 species, lichen diversity in the study area appeared to be high. Biotope 1, i.e. the pioneer vegetation with *Corynephorus canescens* on blowing sand, is rather scarce in lichens. Between 1996 and 2006 green algae, *C. canescens* and *Polytrichum piliferum* appeared, with the result that much of the former open drift sand area was covered by pioneer stages of the *Spergulo-Corynephoretum.* If sand stopped blowing in, a combination of *P. piliferum* with the neophyte C*ampylopus introflexus* occurred. The terminal stages of lichen succession on drift sand, a vegetation with mainly *Festuca ovina* s.l., *Deschampsia flexuosa* and reindeer lichens (*Cladonia* subgen. *Cladina*), proved to be rather stable. Since 1996 the lichen steppes occurring in biotope 2 were increasingly grass-encroached. Where some sand was still blowing in, lichen diversity did not change much, but gradually *C. introflexus* increased. However, without sand blowing-in, a decreasing lichen cover and loss of some Red List lichens occurred. In general, in this grass-rich vegetation *Calluna vulgaris* will germinate and gradually a dry heath might develop. However, where dynamics had stopped and *Pinus sylvestris* seedlings established, succession to a young forest started. Vegetation change from open sand to lichen-rich vegetation is clearly related to a decrease in pH, an increase in organic matter, in % total N and in % total P. The lichen composition is clearly related to this gradient. The applied restoration measures on steep sand dunes in the eastern area, both of cutting pine trees and removing topsoil down to the mineral soil layer, proved to be successful. The sand kept drifting and the pioneer community thriving, including the lichen *Stereocaulon condensatum* characteristic of pioneer conditions, while the neophytic moss hardly increased between 1996 and 2006.

Zusammenfassung: Sukzession und Lebensraumrenaturierung in flechtenreichen Binnendünen der Niederlande

Wir untersuchten in den Jahren 1996–2006 die Sukzession der Vegetation mobiler Binnendünen und ausgeblasener, kiesreicher Senken im Naturschutzgebiet Hulshorsterzand im Zentrum der Niederlande. Zu diesem Natura-2000-Habitat (Typ 2330: Offene Grasflächen mit *Corynephorus* und *Agrostis* auf Binnendünen) gehören auch sogenannte „Flechten-Steppen“, die für ihre Biodiversität sowohl an Pflanzen (Kryptogamen) als auch an Tieren bekannt sind. Wir analysierten mittels multivariater Methoden die Zusammenhänge zwischen Primärsukzession, Artenzusammensetzung der Vegetation und Bodeneigenschaften für drei verschiedene Biotoptypen: 1. Binnendünen; 2. ausgeblasene, kiesreiche Senken; 3. Binnendünen nach erfolgtem Management. Mit insgesamt 34 Arten war die Flechtenartenvielfalt im Gebiet insgesamt hoch. Biotoptyp 1, d. h. Pioniervegetation mit *Corynephorus canescens* auf mobilen Sanddünen, war dagegen eher flechtenarm. Zwischen 1996 und 2006 traten Grünalgen, *C. canescens* und *Polytrichum piliferum* neu auf, wodurch erhebliche Teile der ehemals weitgehend vegetationsfreien Dünenbereiche jetzt mit Pionierstadien des *Spergulo-Corynephoretum* bestanden sind. In Bereichen, wo die Sandbewegung aufhörte, trat die Kombination von *P. piliferum* mit dem neophytischen Moos *Campylopus introflexus* auf. Das Endglied der Flechtensukzession auf Binnendünen, welches durch *Festuca ovina* s.l., *Deschampsia flexuosa* und Rentierflechten (*Cladonia* subgen. *Cladina*) gekennzeichnet ist, erwies sich als recht stabil. Seit 1996 haben sich in den Flechten-Steppen des Biotoptyps 2 mehr und mehr Gräser ausgebreitet. In Bereichen, in denen eine gewisse Sandbewegung fortbestand, hat sich die Flechtendiversität kaum verändert, doch nahm allmählich die Deckung von *C. introflexus* zu. In Bereichen ohne Sandbewegung konnten sich dagegen *Pinus sylvestris*-Keimlinge

etablieren, und die Entwicklung zu einem Vorwald begann. Die Sukzession von offenen Sandflächen hin zu flechtenreicher Vegetation war verknüpft mit einer Versauerung der Böden sowie einer Zunahme an Humus, Gesamt-N- und Gesamt-P-Gehalten. Die Flechtenartenzusammensetzung änderte sich entlang dieses Gradienten. Die im östlichen Teil des Gebietes im Bereich steiler Sanddünen angewandten Managementmaßnahmen, (a) Fällen von Kiefern und (b) Entfernung des humusreichen Oberbodens, erwiesen sich als erfolgreich. Hier setzte die Sandbewegung wieder ein und damit entwickelten sich die Pioniergesellschaften einschließlich der Flechtenart *Stereocaulon condensatum* vital, welche für solche Standortbedingungen bezeichnend ist. Dagegen hat sich die Deckung des neophytischen Mooses in den Managementbereichen von 1996 bis 2006 kaum verändert.

Keywords: *Campylopus introflexus*, chronosequence, *Cladonia*, dry grasslands, management, nitrogen deposition.

Abbreviations: CCA = canonical correspondence analysis; CEC = cation exchange capacity; DCA = detrended correspondence analysis; EIV = Ellenberg indicator value; PQ = permanent quadrat.

1. Introduction

In large areas of the central part of the Netherlands (the Veluwe, Fig. 1) an inland dune landscape has developed on sandy aeolian sediments of Pleistocene origin, deposited in the Late Glacial, 13,000–10,000 years ago (KOSTER 2005). These sands are acidic and nutrient-poor. 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, extreme storm events in the Middle Ages and vegetation degradation by anthropogenic over-exploitation in more recent centuries. At the end of the 19th century and at the beginning of the 20th century, the greater part of these dunes was afforested with Scots pine trees (*Pinus sylvestris*: see RIKSEN et al. 2006). After the afforestation some drift sand areas remained as nature reserves or military exercise grounds (Fig. 2).

Inside the nature reserve Hulshorsterzand the drift sands and the gravel-rich depressions are famous for their biodiversity, both in flora (cryptogams) and in fauna (insects and birds). According to Natura 2000, the Netherlands have a special responsibility for these so-called lichen steppes (habitat type 2330: open grasslands with *Corynephorus* and *Agrostis* species on inland dunes). Criteria for an advisable conservation status for this habitat type are a substantial proportion of lichen species and the presence of characteristic fauna elements (mainly insects) related to the extreme conditions, with several Red List species (BAL et al. 2001, NIJSSEN & SIEPEL 2010).

Fig. 1: Map of the Netherlands with the location of the Veluwe.
Abb. 1: Karte der Niederlande mit der Lage der Landschaft „Veluwe“.

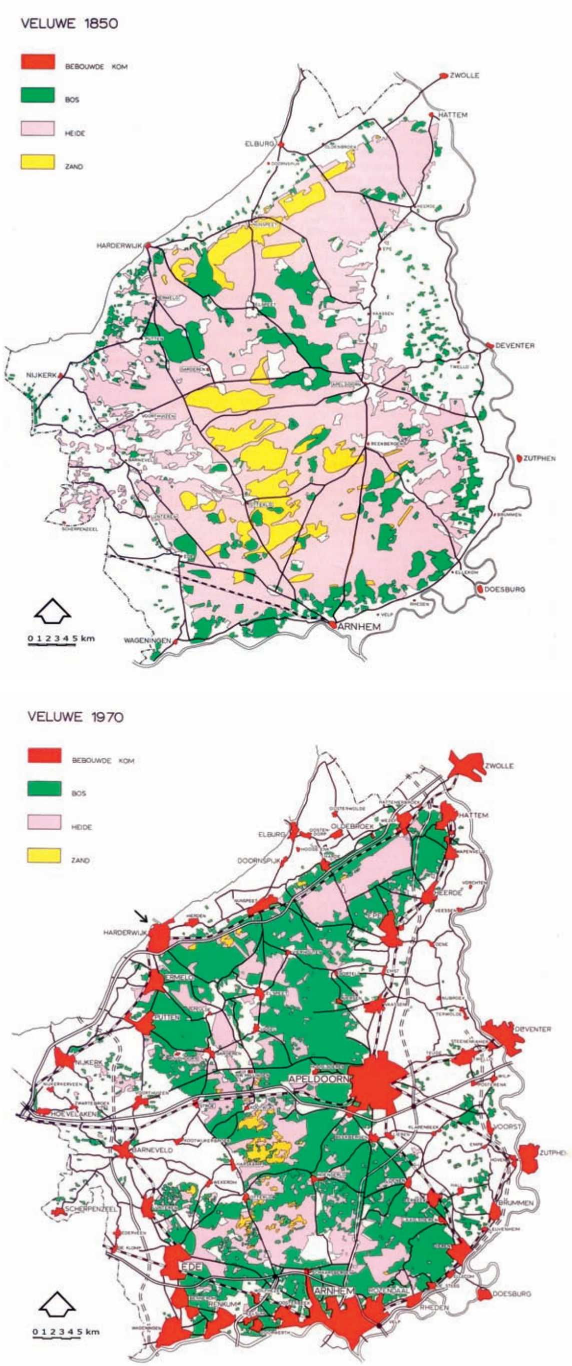


Fig. 2: Land use and landscape structure in the Veluwe 1850 (top) and 1970 (bottom) (both from SCHIMMEL 1975). Legend: →: town of Harderwijk with the Hulshorsterzand 7 km eastward; red: built-up area; green: woodland, pink: heath and yellow: sand.

Abb. 2: Landnutzung und Landschaftsstruktur in der Veluwe 1850 (oben) und 1970 (unten; beide Abbildungen aus SCHIMMEL 1975). Legende: →: Stadt Harderwijk., 7 km östlich von welcher der Hulshorsterzand liegt; rot: Siedlungsfläche; grün: Wald; violett: Heide; gelb: offene Sandflächen.

Fig. 3: a. Early succession stage in drift sand with *Corynephorus canescens*. b. High moss cover with *Polytrichum piliferum* and the neophyte *Campylopus introflexus* in PQ.B in 2001. c. *Stereocaulon condensatum* in *P. piliferum* vegetation. d and e. *Corynephorus* grassland rich in *Cladonia* species.

Abb. 3: a. Frühes Sukzessionsstadium auf Binnendünen mit *Corynephorus canescens*. b. Hohe Moosdeckung mit *Polytrichum piliferum* und dem Neophyten *Campylopus introflexus* in PQ.B im Jahr 2001. c. *Stereocaulon condensatum* in einer *P. piliferum*-dominierten Vegetation. d and e. *Cladonia*-reicher Silbergrasrasen.

Between 1996 and 2006, vegetation and soil were studied in permanent quadrates (PQs). These included the early succession stage with only *Corynephorus canescens* (Fig. 3a), the moss-rich pioneer communities (Fig. 3b), their transformation into lichen-rich succession stages (*Spergulo-Corynephoretum*; WEEDA et al. 1996) (Fig. 3c–d) and dry heath vegetation (*Genisto anglicae-Callunetum*; STORTELDER et al. 1996).

Increased grass and moss encroachment facilitates self-sowing of trees, mainly *Pinus sylvestris*, but also the invasive species *Prunus serotina* and other deciduous trees. These tree species constantly threaten to reduce the area of open sand with their seed easily dispersing from the surrounding wood. In cool and humid spring and autumn, seeds may germinate, but in hot summers young plants may soon die.

Since the 1960s, sand-dune management was mainly carried out on a small scale by the non-governmental organization (NGO) 'Natuurmonumenten', which owns this sand dune area. Cutting of self-sown trees or a few hectare of pine wood was effectuated by foresters or labourers with small machinery.

The growing influence of atmospheric nitrogen (N)-deposition on nutrient-poor sandy soils made management on a larger scale necessary. Dry deposition in particular, but also wet N-deposition in the form of NH_4^+, NO_3^-, and gaseous ammonia (NH_3) has greatly increased since the 1970s, as a direct result of intensive animal farming (bio-industry) with the top values occurring in the 1980s. Nutrient enrichment increases the productivity in nutrient-poor ecosystems (BOBBINK et al. 1998), and an accelerated vegetation succession is one of the effects of N-deposition on nutrient-poor sandy soils (BERENDSE et al. 1993). This manifested itself in grass and moss encroachment, a danger for the survival of the lichen-diversity, like was recorded in similar sand dune reserves on the Veluwe (BIERMANN & DANIËLS 1997; KETNER-OOSTRA & SÝKORA 2008). As the critical N-deposition value for the habitat type of drifting sands is 10.4 kg ha^{-1} yr^{-1} and for the end stage of dry heath it is 15 kg ha^{-1} yr^{-1} (VAN DOBBEN & VAN HINSBERG 2008), also the Hulshorsterzand was in danger, as the mean N-deposition on the Veluwe was 50 kg ha^{-1} in 1990. However, since then a decrease gradually set in with values between 30–50 kg ha^{-1} in 2003 (RIVM 2003).

Part of our study is related to large-scale management of cutting planted pine wood at the Hulshorsterzand in 1991 with as main purpose to strengthen the impact of wind on the sand dunes and keep the area of drifting sand at a constant size (FRENTZ & VAN GRIETHUYSEN 1992).

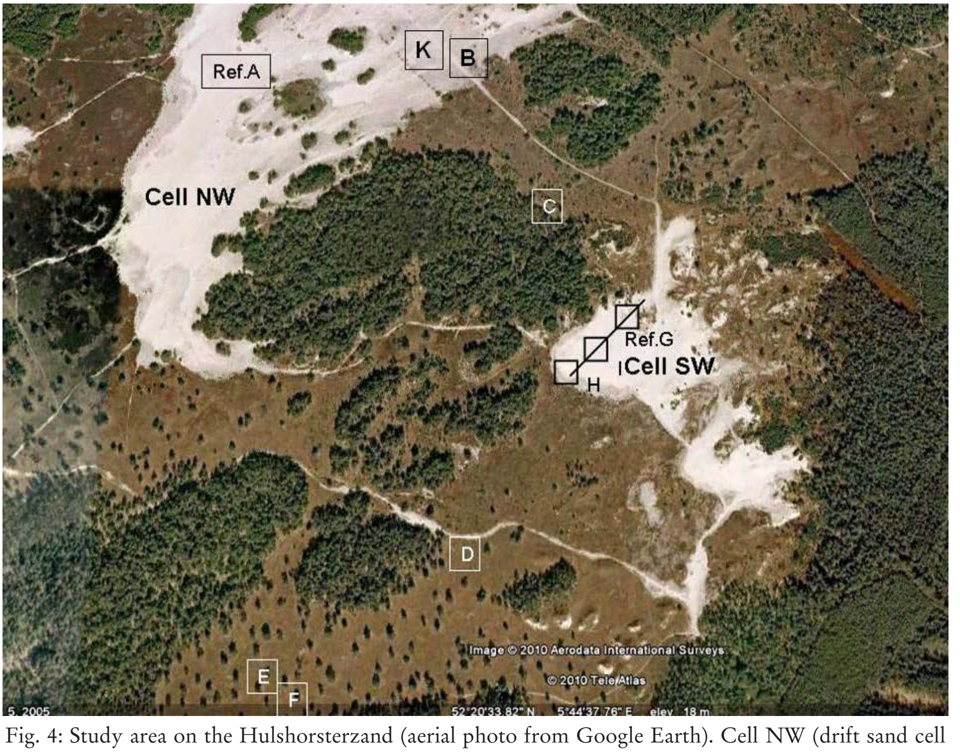


Fig. 4: Study area on the Hulshorsterzand (aerial photo from Google Earth). Cell NW (drift sand cell northwest, with Ref.A (Reference plot A), PQ.K, PQ.B and PQ.C; cell SW (drift sand cell southwest) with PQ.D, PQ.E, PQ.F, Ref.G (Reference plot G), PQ.H and PQ.I.

Abb. 4: Untersuchungsgebiet im Hulshorsterzand (Luftfoto aus Google Earth). Die Flächenbezeichnung kann der englischen Legende entnommen werden.

Considering both spontaneous development (not managed for a long period) and the effect of management, we set out to answer the following questions:
a. What is the relation between the species composition of the vegetation, the occurrence of lichens and soil quality?
b. Will spontaneous succession, due to natural changes in vegetation composition and soil quality, lead to decrease in biodiversity?
c. Is it possible to maintain or revitalize lichen-rich dune vegetation by management? Or are the effects of former management measures temporary?

2. Study area and former management

The study area, the Hulshorsterzand, is located in the northwestern peripheral of the Veluwe District (province of Gelderland, the Netherlands, 52° 22' N, 5° 44' E), 7 km east of the town of Harderwijk (Fig. 2). After the afforestation of this area around the turn of the 19th to 20th century, four drift sand cells (after JUNGERIUS & RIKSEN 2010) with comb dunes in their leeward side were left as nature reserve. Our research took place in cell NW and cell SW (Fig. 4), consistent with the naming of the cells in JUNGERIUS & KETNER-OOSTRA (2006).

During the period 1991–1992 trees were cut in order to strengthen the force of the mainly southwestern wind on the open sand of cell NW. However, no topsoil was removed after the cutting of the pine trees. Our study site was around 2 km northeast from this intervention and subject to a constant influx of sand. On the dune slopes in cell SW *Pinus sylvestris* trees were cut and here the topsoil was removed down to the mineral soil layer in 1991 (FRENTZ & VAN GRIETHUYSEN 1992).

3. Methods

3.1. Vegetation sampling and analysis

Both spontaneous vegetation and soil development, and that after management, were studied with vegetation relevés and permanent quadrates (PQs). Extra relevés to show the variation in sand dune vegetation were made in 1996, moreover 24 relevés to describe the transitional phase to dry heath vegetation in 2006. During the research period in total 90 relevés were made, partly as the result of monitoring of the PQs in 1998, 2001, 2003 and 2005.

In all PQs, cover and abundance were estimated using the extended Braun-Blanquet scale (WESTHOFF & VAN DER MAAREL 1973). The PQ size varied between 1 m^2 and 16 m^2, with some of 25 m^2 in drifting sand. All cover-abundance values were transformed into the 9-point ordinal scale (VAN DER MAAREL 1979).

For the distribution of the PQs in the three biotopes, see Table 1.

3.1.1 PQs chosen to study spontaneous succession on drifting sand (biotope 1)

These sites were located in the drift sand cell NW (Fig. 4) and were influenced by a strong mainly southwestern wind, causing here active drifting sands. In the open sand the Reference point A (Ref. A) was chosen and two research plots for vegetation development, one with only *Corynephorus canescens* (PQ.K) and one with *C. canescens* and *Polytrichum piliferum* (PQ.B). The third plot was chosen in the final succession stage of lichen development with reindeer lichens in a sheltered location near the base of a sand dune (PQ.C).

3.1.2 PQs in blown-out depressions (biotope 2)

The research plots with high lichen diversity were chosen on sites with gravel-rich perifluvioglacial sand in the lichen desert of the southwestern cell (SW in Fig. 4), one plot more central in this area (PQ.D) and two plots in the southern part (PQ.E and PQ.F). PQ.D was located in the open, while PQ.E and PQ.F were located in the semi-sheltered park-landscape with scattered *Pinus sylvestris* trees. In the soil of PQ.F ashes, the remnants of a former fire were present. The soil profile of the first plot showed 25 cm of blown-in sand on top of gravel-rich perifluvioglacial sand. In the other two plots 10 cm of the upper layer of this perifluvioglacial sand was mixed with some blown-in sand.

Table 1: Outline of the 90 relevés made in the period 1996–2006 and used in this study. Biotope 1 is in naturally drifting sand, biotope 2 is in a blown-out gravel-rich depression and biotope 3 is in drifting sand after management. The relevés of the PQ recordings during the monitoring years 1998, 2001, 2003 and 2005 are underlined.

Tabelle 1: Übersicht der 90 Vegetationsaufnahmen aus dem Zeitraum 1996–2006, die in dieser Arbeit Verwendung fanden. Biotoptyp 1 sind mobile Binnendünen, Biotoptyp 2 ausgeblasene, kiesreiche Senken und Biotoptyp 3 Binnendünen nach erfolgtem Management. Die Wiederholungsaufnahmen von Dauerquadraten (PQ) sind unterstrichen.

	1996	1998	2001	2003	2005	2006	Sum
Biotope 1	Ref A						
id.	PQ.K	PQ.K	PQ.K	PQ.K	PQ.K		5
id.	PQ.B	PQ.B	PQ.B	PQ.B	PQ.B		5
id	PQ.C	PQ.C	PQ.C	PQ.C	PQ.C		5
Biotope 2	PQ.D	PQ.D	PQ.D	PQ.D	PQ.D		5
id.	PQ.E	PQ.E	PQ.E	PQ.E	PQ.E		5
id	PQ.F	PQ.F	PQ.F	PQ.F	PQ.F		5
Biotope 3	PQ.G (=Ref.G)	PQ.G	PQ.G	PQ.G	PQ.G		5
id.	PQ.H	PQ.H	PQ.H	PQ.H	PQ.H		5
id	PQ.I	PQ.I	PQ.I	PQ.I	PQ.I		5
id.				3a, 3b, 3c	3a, 3b, 3c		6
Extra relevés	15					24	39
Total							90

3.1.3 PQs to study the effect of management (biotope 3)

After the planted pine forest was cleared off in 1991, several transects and a fixed measuring point, still present in 1996, were laid out on a large dune slope in the drift sand cell SW (FRENTZ & VAN GRIETHUYSEN 1992). Three research plots (Fig. 4), were located in the first transect near the fixed measuring point, PQ.G, also used as a Reference point (Ref.G) as the sand kept here blowing during the research period, PQ.I with only some individuals of *Corynephorus canescens* and PQ.H with *C. canescens*, *Polytrichum piliferum* and the lichen *Stereocaulon condensatum*. Close to PQ.H, three plots (relevés 3a–c) were laid out in 2003 to study the effect of inblowing sand on litter left after the removal of a pine tree.

3.2. Soil sampling and analysis

In 1996 and 2005 soil samples were taken at a distance of 10–15 cm from all PQs (see KETNER-OOSTRA 2006). Besides, in the same years, a soil sample was taken for reference in the open drifting sand of the NW area (Ref.A) and one from the eastern area, were the management had occurred in 1991 (Ref.G = PQ.G). In 2005 the sampling of PQ.I was left out, as it seemed to have the same amount of moving sand as Ref.G; instead the sampling of PQ.K (pioneer stage with *C. canescens* only) was added. Bulked samples consisting of 8–10 subsamples per plot were used in all cases.

The soil samples were taken at 0–2 cm and 2–10 cm depth. As the reference samples from the areas with drifting sand were taken from 0-10 cm depth, the values of 0–2 cm and 2–10 cm depth were recalculated into one value for the 0–10-cm layer. The differences between the 0–2 cm upper layer, important for cryptogams, and the total 0–10-cm layer are made visible in Table 4. Soil samples for oxalate and cation content were partly taken from a depth of 0–10 cm and partly from the 0–2-cm layer (see Table 4). The soil samples were chemically analysed for pH-H_2O (not in 2005), pH-KCl, % C (C-elementary), % N (N-total) and % P (P-total). % Al oxalate, Fe oxalate and P oxalate. Cation exchange capacity (CEC) was calculated from the % Ca^{2+} exchangeable, % Mg^{+} exchangeable, % K^{+} exchangeable, % Na^{+} exchangeable and H^{+} occupation values. For methods of analysis, see KETNER-OOSTRA & SÝKORA (2000).

3.3. Vegetation classification and ordination

All 90 relevés were ordinated and classified using DCA, CCA (TER BRAAK & SMILAUER 2002) and TWINSPAN (HILL 1979).

DCA was used to show the main variation in species composition independent of the external variables (indirect ordination analysis). The relation between the main variation in species composition and the external variables is shown after constructing the ordination diagram and represented by arrows. In order to relate the change in species composition in time with the main explaining factors a CCA was run, using forward selection. Significance was tested using Monte Carlo Permutation test (reduced model, number of permutations 499) .

The divisions of the TWINSPAN table (not reproduced here) were used to construct a TWINSPAN classification (Table 3), indicating the differential species representative of the different divisions. Differential species were distinguished based on their difference in presence and characteristic cover. Characteristic cover is the sum of the cover of a species within a cluster, divided by the number of relevés within this cluster, in which the species actually occurs.

3.4. Vegetation change in diagrams

The cover of the vascular plants, bryophytes, lichens, bare sand and litter in the relevés of some PQs, and as such reported in KETNER-OOSTRA (2006), are used in diagrams to depict the vegetation change between 1996 and 2006 (Figs. 5–7). Selected were three PQs, one in the pioneer stage, and two in the lichen-rich blown-out gravel-rich depressions. These PQs were the most explicit in their vegetation change seen from the perspective of lichen development during the research period.

3.5. Indicator values of terricolous lichens

In Table 2, the lichens were assigned to four categories according to their ecology (pioneer, humicole, aero-hygrophytes, epigeic epiphytes), for which we follow DURING (1992) and BÜLTMANN (2005). Species and their Red List status were added (from APTROOT et al. 2012). Table 2 is extended with Ellenberg indicator values (EIVs) for light and acidity for further ecological characterization for those species for which they are available; see WIRTH (1995, 2001) and BÜLTMANN (2006). EIV for light (L) is used because even in open habitats, without trees or shrubs, due to differences in vegetation structure, light availability still varies and influences the colonization by pioneer lichens, mosses or phanerogames. EIV for light 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. EIV for reaction (R) gives a scale of soil acidity and lime content: 1 is defined as 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).

3.6. Nomenclature

The nomenclature of the plant communities follows WEEDA et al. (1996) and STORTELDER et al. (1996). The nomenclature for the vascular plants follows VAN DER MEIJDEN (2005), with the exception of *Festuca ovina*, which has always been treated as sensu lato (s.l.). For the mosses, we follow SIEBEL & DURING (2006), and for the lichens APTROOT et al. (2012), with the exception of *Cetraria muricata* (BÜLTMANN 2006). We decided to use *Cladonia chlorophaea* s.l. (including *C. grayi*) and *Cladonia arbuscula* s.l. (including *C. mitis*) and thus not to recognize chemical microspecies (see also BIERMANN & DANIËLS 1997, KETNER-OOSTRA & SÝKORA 2008).

4. Results

4.1. Lichen flora

In the 20th century, a total of 41 terrestrial growing lichen species were recorded in the sand dune ecotope of the Hulshorsterzand, some of which are collective data, including three that are restricted to dead wood. During the 1996–2006 research period, 34 species were still present, eight with a Red List status (see Table 2).

The pioneer species have high EIVs for light (WIRTH 2001), mostly 8, meaning that they are photophilous. *Stereocaulon condensatum* is indicated as a lichen from full light (EIV L 9), as is *Cladonia foliacea* (BÜLTMANN 2006). With the pioneers *Cetraria aculeata*, *C. murica-*

Table 2: List of terrestrial growing lichen species of the Hulshorsterzand with their Red List status after APTROOT et al. (2012) and their Ellenberg indicator values (EIVs) for light and soil reaction, ordered by ecological group.

[1] In Project Hulshorst: A means, in herbarium A. Aptroot (Soest), herbarium code ABL (*Taxon* 44: 258); A: only w means, only growing on wood; L, in herbarium Leyden University, herbarium code L (*Taxon* 44: 258) and only collected in the mentioned period; v.H '97, collected by C.M. van Herk in 1997; KO, collected for and documentated in KETNER-OOSTRA (2006).

[2] Classification according ecology follows DURING (1992) and BÜLTMANN (2005).

[3] In the Red List status CR means critical, EN endangered, VU vulnerable, EXN extinct in the Netherlands, EXN[3x] means here: almost disappeared growing epigeic.

[4] EIVs for light (L) and [5] soil reaction (R), see Methods. Values from WIRTH (2001) are given regularly, those from WIRTH (1995) between brackets and those from BÜLTMANN (2006) are underlined.

Tabelle 2: Verzeichnis der epigäischen Flechtenarten im Gebiet Hulshorsterzand mit ihrem Rote-Liste-Status nach APTROOT et al. (2012) und ihren Ellenberg-Zeigerwerten für Licht und Bodenreaktion. Für die verwendeten Abkürzungen siehe die englische Legende.

Project Hulshorst [1]	Ecology [2]	Species	Red list status [3]	L [4]	R [5]
A	Pioneer	*Baeomyces rufus*		5 6	3 3
KO	Pioneer	*Cetraria aculeata*		8 8	(2-7)
KO	Pioneer	*Cetraria muricata*		8 8	
KO	Pioneer	*Cladonia cervicornis*		8	3
KO	Pioneer	*Cladonia verticillata*		8 8	3 3
KO	Pioneer	*Cladonia pulvinata*		8	3
A	Pioneer	*Cladonia foliacea*		9 8	(4-8)
KO	Pioneer	*Cladonia furcata*		6-8	4
KO	Pioneer	*Cladonia strepsilis*	VU	8	3
KO	Pioneer	*Cladonia zopfii*		8	3
KO	Pioneer	*Stereocaulon condensatum*	VU	9	3
KO	Pioneer	*Trapeliopsis granulosa*		8	1 2
A	Humicolous	*Cladonia borealis*		8	3
KO	Humicolous	*Cladonia chlorophaea* s.l.		7 7	3
KO	Humicolous	*Cladonia coccifera*		7 8	3-5 3
L '59	Humicolous	*Cladonia cornuta*	CR	8	3
A: only w	Humicolous	*Cladonia digitata*		5 5	2 2
A: only w	Humicolous	*Cladonia fimbriata*		7 7	4
KO	Humicolous	*Cladonia floerkeana*		8	3
KO	Humicolous	*Cladonia glauca*		7	2 2
KO	Humicolous	*Cladonia macilenta*		7 7	2 2
KO	Humicolous	*Cladonia monomorpha*		7 8	4
KO	Humicolous	*Cladonia ramulosa*		8	(2-3)
A	Humicolous	*Cladonia scabriuscula*		7	-
L '59-'63	Humicolous	*Cladonia phyllophora*	VU	8	3
A: only w	Humicolous	*Cladonia polydactyla*		5 5	2 2
L '57-'68	Humicolous	*Cladonia squamosa*	CR	6 6	2 3
KO	Humicolous	*Cladonia subulata*		8 8	3
v.H '97	Humicolous	*Cladonia sulphurina*	EXN	7 7	1 2
KO	Humicolous	*Micarea leprosula*		8	3
A	Humicolous	*Micarea viridileprosa*		-	-
KO	Humicolous	*Placynthiella icmalea*		7	2 2
KO	Humicolous	*Placynthiella oligotropha*		7 8	2 3
KO	Humicolous	*Placynthiella uliginosa*		8	3
KO	Humicolous/Aero-h.	*Cladonia crispata*		8	3
KO	Humicolous/Aero-h.	*Cladonia gracilis*		7	3 3
KO	Humicolous/Aero-h.	*Cladonia uncialis*	VU	8 8	3
KO	Aero-hygrophyte	*Cladina arbuscula* s.l.	VU	8 8	(1-5)
KO	Aero-hygrophyte	*Cladonia portentosa*		7 7	(1-5)
L '47-'59	Aero-hygrophyte	*Cladonia ciliata*	EN	7 7	- -
L '47-'59	Aero-hygrophyte	*Cladonia rangiferina*	EXN	6 7	- -
A	Epigeic epiphyte	*Hypogymnia tubulosa*	EXN [3x]	7	3

ta, *Cladonia zopfii* and *C. strepsilis* they were still present in 2006. Humicolous and aero-hygrophytic species have EIV values for light around 7, which means growing in well-lit places but also occurring in partial shade.

The pioneer species *Cetraria aculeata* and *Cladonia foliacea* have EIVs for soil reaction (WIRTH 1995, 2001) with wide amplitude. This indicates their adaptation to acid and also to more (sub-) neutral habitats. EIV for reaction of 3 for *Stereocaulon condensatum* means rather acid (pH 4.1–4.8) and explains their constancy in the rather acid succession stage B2 (Table 3). Most humicolous and aero-hygrophytic species have an EIV for reaction between 1 and 3, which indicates extreme acid to rather acid biotopes.

4.2. Vegetation of all study sites

Table 3 is based on a TWINSPAN classification of the total data set of 90 relevés. The 10 clusters distinguished were grouped into three groups: A, B and C (see Table 3).

The three groups are characterized by the presence of species characteristic of the *Koelerio-Corynephoretea*. Group A represents the open drift sand, while group BC includes pioneer and subsequent succession stages with *Corynephorus canescens* and *Polytrichum piliferum* as main characteristic species. Within BC, group B differs from group C with a dominant cover of the moss *P. piliferum* and one lichen that can stand the critical environmental stress of drifting sand, *Stereocaulon condensatum*. Group C represents the stage where several grasses, many lichen species and *Calluna vulgaris* follow in the succession.

Within group BC, group C differs from group B in the cover and species composition especially of the moss layer. Whereas group B is characterized by a high cover of the pioneer moss *P. piliferum*, group C is characterized by a high number of lichen species.

Group B1–2 can still be assigned to the *Spergulo-Corynephoretum inops* (WEEDA et al. 1996), a community of sunny, dry sites on acidic and nutrient-poor dune sand. Herein B1 represents the rather bare early succession stage with *P. piliferum* and B2 with *Festuca ovina* s.l., a following succession stage with partly dying *P. piliferum* covered with the slimy green alga *Gloecystis polydermatica*, and where the neophyte *Campylopus introflexus* is settling in the open spots.

Group C1–4 is still characterized by *Corynephorus canescens*, but *Campylopus introflexus* has a high cover, accompanied by several humicolous lichen species. Group C5+6 is characterised by tall grasses and some aero-hygrophytic mosses and lichens. However, both groups are part of the *Spergulo-Corynephoretum cladonietosum* (WEEDA et al. 1996).

Group C1–4 is divided in C1–2 and C3–4, with the first group negatively differentiated from the second, which has more aero-hygrophytic lichen species that prefer a higher air humidity, facilitated by the thicker soil and denser grass cover. The climax in lichen-richness is reached when such aero-hygrophylous reindeer lichens have settled in, like *Cladonia portentosa*, *C. arbuscula* and the podetia of *C. uncialis*. In this habitat type (group C1–4) several relatively tall grasses occur, like *Agrostis vinealis* and *Deschampsia flexuosa*, both when there is clearly more soil moisture available, especially in flat gravel-rich locations. Here *Calluna vulgaris* will germinate and form a mosaic with the moss and lichen-rich grass vegetation (C1).

Group C5–6 is characterised by *Deschampsia flexuosa*, *Dicranum scoparium* and *Cladonia portentosa. C. portentosa* increased in cover as it profits from a relatively high air moisture. Within group C5–6 *C. portentosa* has the highest cover in C5, but is accompanied by the slimy green alga *Gloeocystis polydermatica*, both on the grasses and on the cryptogams. C6 is characterised by *Molinia caerulea* and some more aero-hygrophytic species like *Polytrichum juniperinum*, *P. piliferum* and *Cladonia uncialis*.

4.3. Succession study on drift sand habitats

4.3.1 On drifting sand

In the NW area with active drifting sand, over the years PQ.K, characterised by only *Corynephorus canescens* and a low presence of *Polytrichum piliferum,* did hardly change

Table 3. TWINSPAN classification of the total data set of Hulshorst relevés in the period 1996–2006. Cluster groups A, B and C (see text) are indicated. At each dichotomous division, the main differential species are indicated. For each cluster, the number of fitting relevés is added between brackets.

Tabelle 3: TWINSPAN-Klassifikation des Gesamtdatensatzes aller Vegetationsaufnahmen von Hulshorst aus den Jahren 1996–2006. Für jedes Cluster ist die Anzahl der zugehörigen Aufnahmen in Klammern genannt; die Hauptcluster A, B und C sind im Text vorgestellt. Für jeden dichotomen Teilungsschritt sind die hauptsächlichen Differenzialarten angegeben.

<table>
<tr><td>Division 1</td><td colspan="2">A (9)</td><td colspan="8">BC: Spergulo-Corynephoretum (81)</td></tr>
<tr><td></td><td colspan="2">Open drift sand</td><td colspan="8">Corynephorus canescens, Polytrichum piliferum</td></tr>
<tr><td>Division 2</td><td>A1 (7)</td><td>A2 (2)</td><td colspan="2">B: Spergulo-Corynephoretum inops (27)</td><td colspan="6">C: Spergulo-Corynephoretum cladonietosum (54)</td></tr>
<tr><td></td><td>Bare sand with green algae</td><td>Ammophila arenaria, Festuca rubra s.l.</td><td colspan="2">Polytrichum piliferum (cover), Polytrichum piliferum †, Stereocaulon condensatum, Cladonia coccifera (low cover)</td><td colspan="6">Agrostis vinealis, Cladonia coccifera (cover), Cetraria aculeata s.l., Cladonia chlorophaea s.l., Cladonia crispata, Cladonia floerkeana, Cladonia glauca, Cladonia gracilis, Cladonia macilenta, Cladonia portentosa, Cladonia ramulosa, Cladonia uncialis, Cladonia zopfii</td></tr>
<tr><td>Division 3</td><td colspan="2"></td><td>B1 (8)</td><td>B2 (19)</td><td colspan="4">C1-4 (35)</td><td colspan="2">C5-6 (19)</td></tr>
<tr><td></td><td colspan="2"></td><td>Negatively differentiated by absence of species B2</td><td>Festuca ovina s.l., Polytrichum piliferum †, Gloeocystis polydermatica (alga), Campylopus introflexus, Stereocaulon condensatum</td><td colspan="4">Corynephorus canescens, Campylopus introflexus (cover), Cetraria aculeata s.l., Cladonia glauca, Cladonia zopfii</td><td colspan="2">Deschampsia flexuosa, Dicranum scoparium, Cladonia portentosa (cover)</td></tr>
<tr><td>Division 4</td><td colspan="8"></td><td>C5 (13)</td><td>C6 (6)</td></tr>
<tr><td></td><td colspan="8"></td><td>Cladonia portentosa (cover), Cladonia chlorophaea s.l., Gloeocystis polydermatica (alga)</td><td>Molinia caerulea, Polytrichum juniperinum, Polytrichum piliferum, Cladonia uncialis</td></tr>
<tr><td>Division 5</td><td colspan="4"></td><td colspan="2">C1-2 (17)</td><td colspan="2">C3-4 (18)</td><td colspan="2"></td></tr>
<tr><td></td><td colspan="4"></td><td colspan="2">Negatively differentiated by absence of species C3-4</td><td colspan="2">Cladonia chlorophaea s.l., Cladonia gracilis, Cladonia uncialis, Cladonia portentosa</td><td colspan="2"></td></tr>
<tr><td>Division 6</td><td colspan="4"></td><td>C1 (8)</td><td>C2 (9)</td><td>C3 (10)</td><td>C4 (8)</td><td colspan="2"></td></tr>
<tr><td></td><td colspan="4"></td><td>Calluna vulgaris, Cladonia chlorophaea s.l.</td><td>Festuca ovina s.l., Polytrichum piliferum †, Cladonia cervicornis, Cladonia crispata, Cladonia gracilis, Cladonia strepsilis, Cladonia verticilata</td><td>Polytrichum piliferum, Agrostis vinealis</td><td>Deschampsia flexuosa, Cladonia arbuscula s.l., Placynthiella icmalea</td><td colspan="2"></td></tr>
</table>

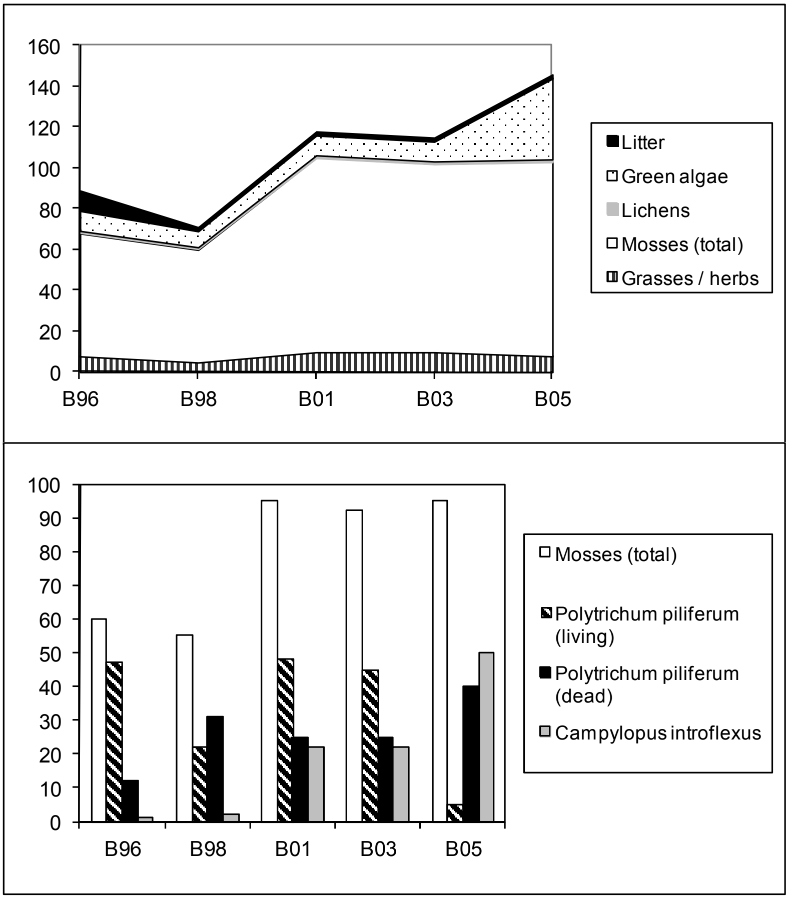


Fig. 5: a. Change in cover % of different vegetation elements between 1996 and 2006 in PQ.B in biotope 1, the pioneer stage (after: KETNER-OOSTRA 2006). b. Change in cover % of *Polytrichum piliferum* (living and dead) and *Campylopus introflexus* between 1996 and 2006 in PQ.B in biotope 1, the pioneer stage.

Abb. 5: a. Veränderung der prozentualen Deckung verschiedener Vegetationselemente zwischen 1996 und 2006 in der Dauerfläche PQ.B im Biotoptyp 1, dem Pionierstadium (nach KETNER-OOSTRA 2006). b. Dieselbe Datenreihe mit genauerer Aufschlüsselung der verschiedenen Moosfraktionen.

and stayed in cluster B1. In 1996 PQ.B started in cluster B1, but it shifted to cluster B2 where it stayed in all successive years. The lichen *Stereocaulon condensatum*, a Red List species, has a high frequency in B2.

Fig. 5a shows the high cover of green algae and the increasing moss cover in PQ.B in the pioneer stage. The cover of grasses and lichens hardly changed. Fig. 5b shows the changes in the moss cover in PQ.B. *Polytrichum piliferum* is gradually dying and replaced by *Campylopus introflexus*.

The third plot in the succession study on drift sand (PQ.C) represented the final succession stage of lichen development on drift sand. We found the cover of the reindeer lichen *Cladonia portentosa* to increase from 60% in 1995 to 75% in 2005, with only small fluctuations, comparable with the increase or decrease of *Deschampsia flexuosa* in that period. In all years studied PQ.C remains in cluster C5.

4.3.2 On gravel-rich depressions

PQ.D, situated on the blown-out gravel-rich depression south of drift sand cell SW, was covered with 25 cm blown-in sand over gravel-rich fluvio-glacial sand. During the total research period, PQ.D stayed in cluster C2, with *Corynephorus canescens*, *Festuca rubra* s.l. and several lichen species typical of the pioneer stage, like *Cetraria aculeata*, *Cladonia cervicornis*, *C. pulvinata*, *C. verticillata*, *C. strepsilis* and *C. zopfii.* In this period, the total number of lichen species fluctuated around 17. However, *Campylopus introflexus* increased from 10% in 1996 to 40% in 2005, and the total lichen cover decreased considerably (Fig. 6).

PQ.E was situated in the semi-sheltered open *Pinus sylvestris* park landscape (Fig. 4) with gravel-rich fluvio-glacial sand and some blown-in sand. In 1995 the high lichen cover of 70% consisted mainly of *Cladonia portentosa*, *C. gracilis*, *C. crispata*, *C. uncialis*, *C. arbuscula* s.l. and several humicolous species. In 1995 this PQ started in cluster C4, but from 2001 onwards moved to cluster C5 as the result of the decreasing cover of the mentioned lichens (from 70–40%, see Fig. 7) and the loss of *C. arbuscula* s.l. In 1995 in the nearby PQ.F, with the same soil profile as PQ.E but with some charcoal in it, the well-known "after-fire moss" *Ceratodon purpureus* dominated with 75%, but this species had already disappeared in 2001. Gradually other mosses and lichens settled in, but PQ.F was partly turned up by grubbing wild boar in 2002.

4.4. Sites to study the effect of management

Between 1996 and 2006 Ref.G in open sand after management stayed in cluster A1 (bare sand). PQ.I started in cluster B2 and ended in B1 (pioneer stage without *F. ovina* s.l.) in 2005 (Table 3). PQ.H in the pioneer stage with *C. canescens* and *P. piliferum* with some *F. ovina* s.l. started in cluster B2, and stayed there, with *P piliferum* being very vital with only few dead stems. *C. introflexus* was almost absent and here a very vital population of *Stereocaulon condensatum* occurred.

4.5. Successional stages and soil properties in 1996 and 2005

Reference values were measured in biotope 1 in open sand in the NW area (Ref.A) and in biotope 3 (Ref.G) in the eastern area after management. In 1996 pH-H_2O and pH-KCl in the 0–10 cm layer in Ref.A were respectively 6.1 and 4.9; in Ref.G, 5.5 and 4.6 respectively (pH-H_2O from KETNER-OOSTRA 2006). In 2005 the pH-KCl in Ref.A appeared to be the same as in 1996 (4.9), in Ref.G it was 4.8 (see Table 4). This means that the topsoil consisted of more or less sub-neutral sand during the research period.

If we look at the whole 0–10-cm soil layer, the pH-KCl values in 2005 did not differ much from those in 1996 (Table 4). However, in the superficial 0–2-cm layer of PQ.B with *Polytrichum piliferum* pH-KCl clearly decreased from 4.4 in 1996 to 4.0 in 2005. However, in this period in PQ.H with *P. piliferum* (after management) acidification in the 0–2-cm layer was less (pH-KCl from 4.3 to 4.2).

In PQ.C, the succession stage with reindeer lichens, only in 2005 the pH in the 0–2-cm layer and the 0–10-cm layer was clearly different (pH-KCl 3.4 and 4.1 respectively, Table 4). The pH-KCl values of the lichen-rich PQs D, E and F did not change much during the research period, and the differences between the 0–2-cm and 0–10-cm layer stayed in the same order.

In 1996, CEC in the 0–10-cm layer (Table 4) was lowest in Ref.A in biotope 1 (11 mequiv kg^{-1}), and about equal with Ref.G in biotope 3 after management. It increased from open sand to the reindeer lichen-rich vegetation on stabilized drift sand (28 mequiv kg^{-1} in biotope 1). High values for CEC value (55 mequiv kg^{-1}) and for % basic ions (28%) was found for 0–10-cm layer in the research plot PQ.F, with reindeer lichens in biotope 2 with fluvioglacial sand. The 0–2-cm layer of PQ.D in this biotope had the highest CEC value (67 mequiv kg^{-1}).

The oxalate determinations in 1996 (Table 4) were intended to provide information on the buffer capacity of the sand, as the amounts of Al, Fe and P ions are dissociated under

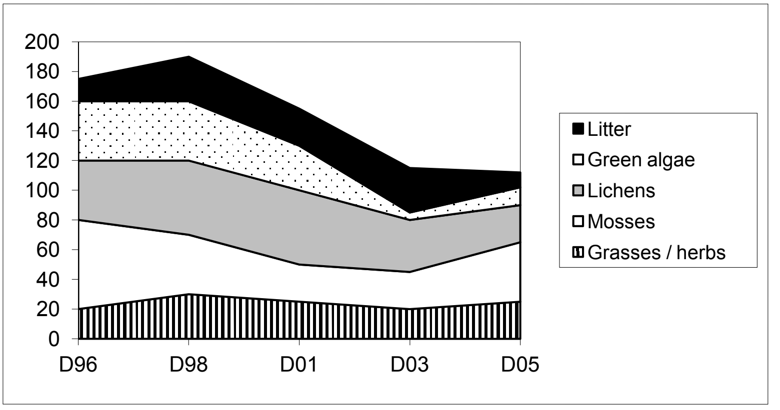


Fig. 6: Change in cover % of different vegetation elements between 1996 and 2006 in PQ.D in biotope 2, the lichen-rich stage of an open blown-out gravel-rich depression (after: KETNER-OOSTRA 2006).

Abb. 6: Veränderung der prozentualen Deckung verschiedener Vegetationselemente zwischen 1996 und 2006 in der Dauerfläche PQ.D im Biotoptyp 2, dem flechtenreichen Stadium ausgeblasener, kiesreicher Senken (nach KETNER-OOSTRA 2006).

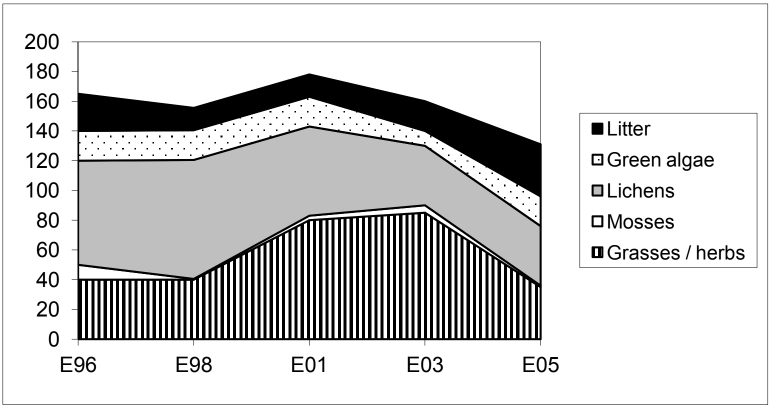


Fig. 7: Change in cover % of different vegetation elements between 1996 and 2005 in PQ.E in biotope 2, the lichen-rich stage (17 species) of a blown-out gravel-rich depression in type B3: open *Pinus* wood (after: KETNER-OOSTRA 2006).

Abb. 7: Veränderung der prozentualen Deckung verschiedener Vegetationselemente zwischen 1996 und 2006 in der Dauerfläche PQ.E im Biotoptyp 2, dem flechtenreichen Stadium (hier mit 17 Arten) ausgeblasener, kiesreicher Senken (Vegetationstyp B3: offener *Pinus*-Bestand) (nach KETNER-OOSTRA 2006).

influence of plant growth. The Al-oxalate values of 10 (±1) mmol kg^{-1} are an indication of the age of these Pleistocene sands; the much younger calcium-poor coastal dunes (on Terschelling) have 2 (± 1) mmol kg^{-1} (KETNER-OOSTRA & SÝKORA 2000). The value of 1 mmol kg^{-1} P-oxalate for the Hulshorst plots was the same as was found at the Kootwijkerzand (KETNER-OOSTRA & SÝKORA 2008) and the calcium-poor dunes (KETNER-OOSTRA & SÝKORA 2000).

4.6. Relation between vegetation and soil

The DCA ordination (Fig. 8) shows the relation between seven external variables and a set of 18 plots, i.e. seven PQs from 1996 (B, C, D, E, F, I and H) and seven PQs from 2005 (B, C, D, E, F, H and K), with Ref.A and Ref.G, both made in 1996 and 2005. From right to

Table 4. Results of the soil analysis of the 0–2-cm and 0–10-cm layers in three biotopes on the Hulshorsterzand in 1996 and 2005 (from KETNER-OOSTRA 2006). The table shows values for pH-KCl, % carbon (C-total), % nitrogen (N-total), % phosphor (P-total), cation exchange capacity (CEC), and Al, Fe and P oxalate. Biotope 1: drift sand with Reference plot A (Ref. A) and three PQs. Biotope 2: blown-out depression with three PQs. Biotope 3: drift sand after management in the early 1990s, with Reference plot G (Ref.G) and two PQs (I and H). All values in italics are in the range below 0.01. Empty cells mean no data available.

[1] Values 0–10 cm were converted from the results of 0–2 cm and 2–10 cm depth.

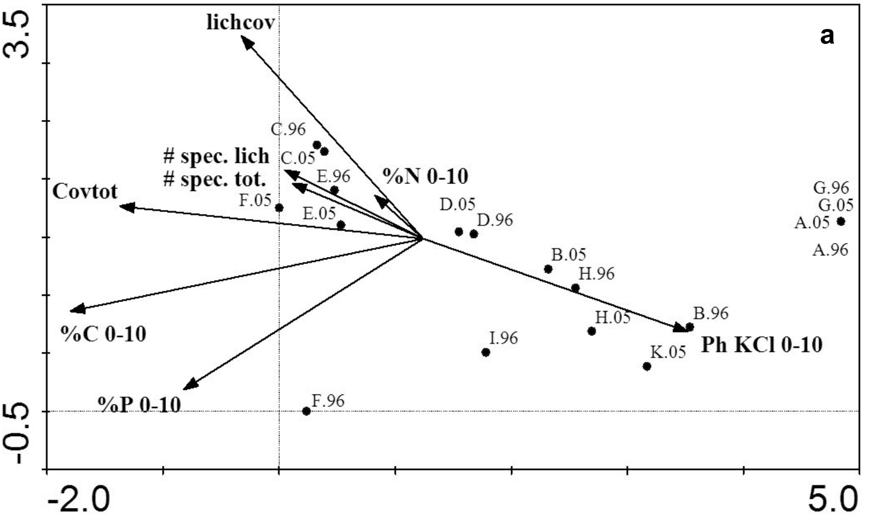
[2] To be divided by 1000.

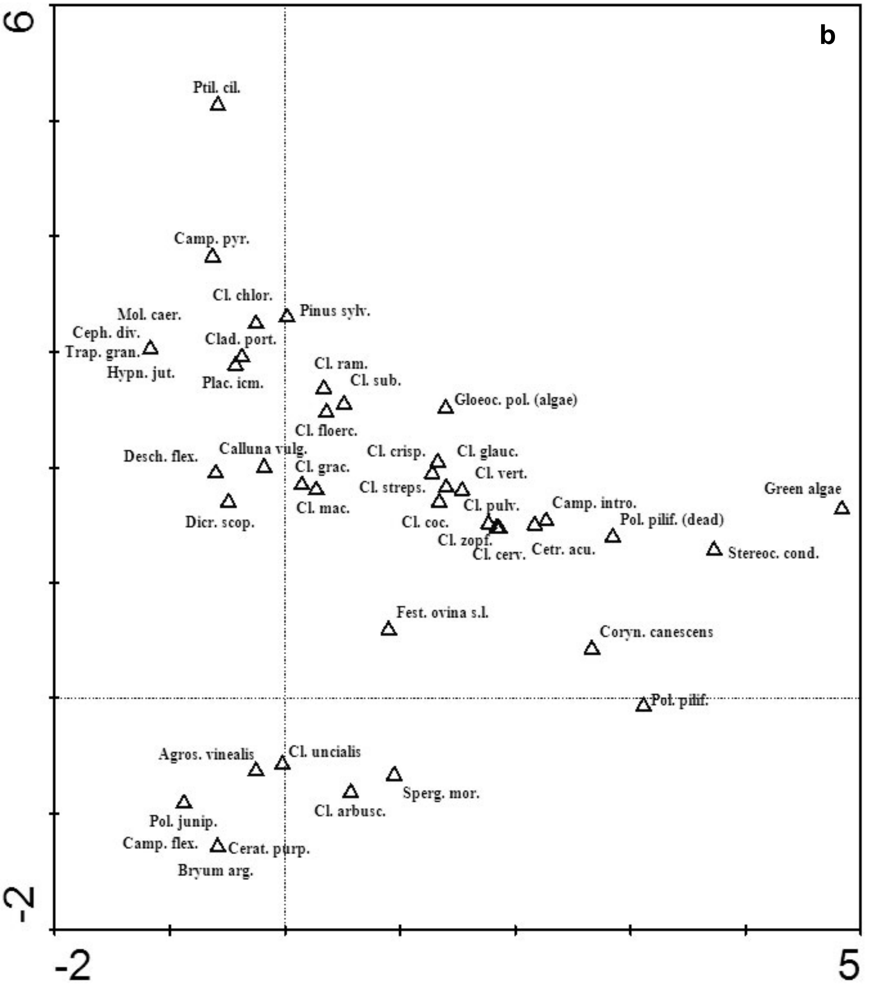
Tabelle 4: Ergebnisse der Bodenanalysen der obersten 2 bzw. der obersten 10 cm in den drei Biotoptypen des Hulshorsterzandes 1996 und 2005 (aus KETNER-OOSTRA 2006). Angegeben sind pH-KCl, Konzentration von Gesamt-C, Gesamt-N, und Gesamt-P (Letzerer geteilt durch 1000), Kationenaustauschkapazität (CEC), Basensättigung (% basic ions), sowie mit Oxalat gemessene Al-, Fe-, und P-Gehalte.

Biotope	PQ		pH-KCl 0–2	pH-KCl 0–10[1]	% C 0–2	% C 0–10[1]	% N 0–2	% N 0–10[1]	% P 0–2[2]	% P 0–10[2]
1.	Ref. A	1996	4.9	4.9	0.2	0.2	*0.01*	*0.01*	**7**	**7**
		2005	4.9	4.9	0.2	0.2	*0.01*	*0.01*	7	7
	K	1996	4.6		0.2	-	*0.01*		8	
		2005	4.7	4.7	0.2	0.2	*0.01*	*0.01*	11	10
	B	1996	4.4	4.4	0.4	0.3	0.03	0.01	8	7
		2005	4.0	4.4	0.5	0.3	0.04	0.02	7	8
	C	1996		4.1		0.5		0.04		6
		2005	3.4	4.1	1.6	0.6	0.11	0.04	21	12
2.	D	1996	3.6	3.9	1.2	0.6	0.24	0.17	10	7
		2005	3.7	4.0	1.7	0.6	0.10	0.05	16	11
	E	1996	3.3	3.8	2.3	0.9	0.15	0.06	17	9
		2005	3.4	3.9	2.4	1.0	0.11	0.05	19	11
	F	1996		4.2		1.0		0.05		14
		2005		3.8		0.9		0.03		13
3.	Ref. G	1996	4.6	4.6	0.2	0.2	*0.01*	*0.01*	7	7
		2005	4.8	4.8	0.2	0.2	*0.01*	*0.01*	10	10
	I	1996	4.9		0.2		*0.01*		7	
		2005								
	H	1996	4.3	4.4	0.6	0.3	0.05	*0.01*	9	7
		2005	4.2	4.5	0.4	0.2	0.02	*0.01*	10	10

	PQs in 1996	CEC (mequiv kg^{-1})	% basic ions	Al oxalate (mmol kg^{-1})	Fe oxalate (mmol kg^{-1})	P oxalate (mmol kg^{-1})
1.	Ref.A (0–10 cm)	12	20	11	1	1
	C (0–10 cm)	28	15	9	4	1
2.	D (0–2 cm)	67	7			
	F (0–10 cm)	55	28			
3.	Ref.G (0–10 cm)	11	7			
	H (0–2 cm)	22	13			

left, the first axis corresponds to a vegetation change from open sand to lichen-rich vegetation and is clearly related to a decrease in pH, an increase in organic matter, in % total N and in % total P. From 1996 to 2005 some PQs shifted from the right-hand side of the DCA (Fig. 8a) to the left-hand side, indicating changes to more organic and acid conditions with PQ.B as a clear example (B.96–B.05). The differences between 1996 and 2005 are quite small in PQ.C, PQ.D, PQ.E and in PQ.H (after management).


a
lichcov
C.96
spec. lich
C.05
spec. tot.
E.96
%N 0-10
Covtot
F.05
E.05
D.05
D.96
G.96
G.05
A.05
A.96
B.05
H.96
B.96
H.05
Ph KCl 0-10
I.96
K.05
%C 0-10
%P 0-10
F.96
3.5
-0.5
-2.0
5.0


b
6
-2
-2
5
Ptil. cil.
Camp. pyr.
Cl. chlor.
Pinus sylv.
Mol. caer.
Ceph. div.
Clad. port.
Trap. gran.
Hypn. jut.
Plac. icm.
Cl. ram.
Cl. sub.
Gloeoc. pol. (algae)
Cl. floerc.
Calluna vulg.
Desch. flex.
Cl. crisp.
Cl. glauc.
Cl. grac.
Cl. vert.
Cl. streps.
Green algae
Cl. mac.
Camp. intro.
Dicr. scop.
Cl. pulv.
Pol. pilif. (dead)
Cl. coc.
Cl. zopf.
Cetr. acu.
Stereoc. cond.
Cl. cerv.
Fest. ovina s.l.
Coryn. canescens
Pol. pilif.
Agros. vinealis
Cl. uncialis
Sperg. mor.
Cl. arbusc.
Pol. junip.
Camp. flex.
Cerat. purp.
Bryum arg.

On the right-hand side of the DCA species diagram (Fig. 8b), with the least acid sand (Fig. 8a), *Stereocaulon condensatum*, a lichen characteristic of pioneer conditions is plotted. More to the centre of the diagram the pioneer species *Cetraria aculeata*, *Cladonia cervicornis*, *C. zopfii*, *C. pulvinata* and *C. verticillata* are visible. These species were not only found on bare sand but also on mats with dead *Polytrichum piliferum* and *Campylopus introflexus*.

In the centre of the DCA, mostly humicolous species are present, *Cladonia coccifera, C. glauca, C. crispata* and *C. strepsilis*. *C. macilenta*, *C. floerkeana* and *C. gracilis* are plotted more to the left, where *Calluna vulgaris* and *Deschampsia flexuosa* are situated. *Cladonia ramulosa* and *C. subulata* occur in the top of the diagram, the area with a higher % N. Here *C. chlorophaea* s.l. and the aero-hygrophyte *C. portentosa* are plotted in the highest position, quite near to *Pinus sylvestris* seedlings and the grass *Molinia caerulea*. The liverwort *Ptilidium ciliare* is found in the topmost position.

The aero-hygrophytic lichens *Cladonia arbuscula* s.l. and *C. uncialis* occur at the base of the diagram, in the higher % C and % P area. Moss-rich and lichen-rich PQ.F in the open *Pinus* wood was partly turned up by grubbing wild boar in 2002. In 2005 PQ.F moved to the centre of the DCA (Fig. 8a) with less aero-hygropytic lichens and more humicolous species (Fig. 8b).

The parameter, that after forward selection and Monte-Carlo permutation test appeared to be significant, pH-KCl in the 0-10 cm layer (p = 0.004) and the next important parameter % C (not significant p = 0.15) are displayed in a CCA (Fig. 9). The first axis appears to be positively related to pH-KCl in the 0–10-cm layer (r = 0.75) and negatively to % C (r = –0.90) in this layer.

The reference plot Ref.A in cell NW (with spontaneous succession) remained in the least acid area of the CCA. (A.05–A.96), while reference plot Ref.G in cell SW (after management), moved to a slightly higher pH-KCl (G.96–G05). PQ.B (in cell NW) with *Polytrichum piliferum* and *Campylopus introflxus* kept the same pH-KCl (B.96–B05), while PQ.H (in cell SW after management) with more or less the same vegetation, but without *C. introflexus*, was slightly less acid in 2005 (H.96–H.05). PQ.C with *Deschampsia flexuosa* and reindeer lichens seemed more acid in 2005 by the production of more humus (C.96–C05). PQ.D was rather stable in % C and pH-KCl (D.96–D.05). In PQ.E % C increased and a more acid pH-KCl was the result (E.96–E.05), just as in PQ.F (F.96–F.05).

Fig. 8: Biplots of a relevé (PQ) ordination (a) and a species ordination (b) showing the first two axes of DCA ordination on seven PQs and two reference plots from 1996 and 2005 (18 relevés in total).

In 8a, the relation between species composition of these relevés and seven parameters (in the 0–10-cm soil layer, significant after Monte Carlo Permutation test without forward selection) is indicated by arrows. Covtot = total vegetation cover; lichcov = lichen cover; %N = % N-total; Ph KCl = pH; %P = % P-total; %C = % Carbon-elementary; # spec. tot. = total number of plant species; # spec. lich = total number of lichen species. 0–10 cm = depth of soil layer.

8b: *Agros. vinealis = Agrostis vinealis; Bryum arg. = Bryum argenteum; Calluna vulg. = Calluna vulgaris; Camp. intro. = Campylopus introflexus; Camp. pyr. = Campylopus pyriformis; Cerat. purp. = Ceratodon purpureus; Cetr. acu. = Cetraria aculeata; Ceph. div = Cephaloziella divaricata; Cl. arbusc. = Cladonia arbuscula; Cl. cer. = Cladonia cervicornis; Cl. chlor. = Cladonia chlorophaea* s.l.*; Cl. coc. = Cladonia coccifera; Cl. crisp. = Cladonia crispata; Cl. floerc. = Cladonia floerkeana; Cl. glauc. = Cladonia glauca; Cl. mac. = Cladonia macilenta; Cl. port. = Cladonia portentosa; Cl. pulv. = Cladonia pulvinata; Cl. ram. = Cladonia ramulosa; Clad. streps. = Cladonia strepsilis; Cl. sub. = Cladonia subulata; Cl. uncialis = Cladonia uncialis; Cl. vert. = Cladonia verticillata; Cl. zopf. = Cladonia zopfii; Coryn. canescens = Corynephorus canescens; Desch. flex. = Deschampsia flexuosa; Dicr. scop. = Dicranum scoparium; Fest. ovina* s.l. *= Festuca ovina* s.l.; *Gloeoc. pol. = Gloeocystis polydermatica; Hypn. jut. = Hypnum jutlandicum; Pinus sylv. = Pinus sylvestris; Plac. icm. = Placynthiella icmalea; Pol. junip. = Polytrichum juniperinum; Pol. pilif. = Polytrichum piliferum; Ptil. cil. = Ptilidium ciliare; Sperg. mor. = Spergula morisonii; Stereoc. cond. = Stereocaulon condensatum.*

Abb. 8: Biplots der DCA-Ordination mit sieben Dauerquadraten aus den Jahren 1996 und 2005 sowie zwei Referenzplots (d. h. 18 Aufnahmen insgesamt). Dargestellt ist die Ebene der ersten beiden Achsen mit (a) die Lage der Aufnahmeflächen und die Vektoren der korrelierten Umwelt- und Strukturparameter und (b) die Lage wichtiger Arten im Ordinationsraum. Für die verwendeten Abkürzungen siehe die englische Legende.

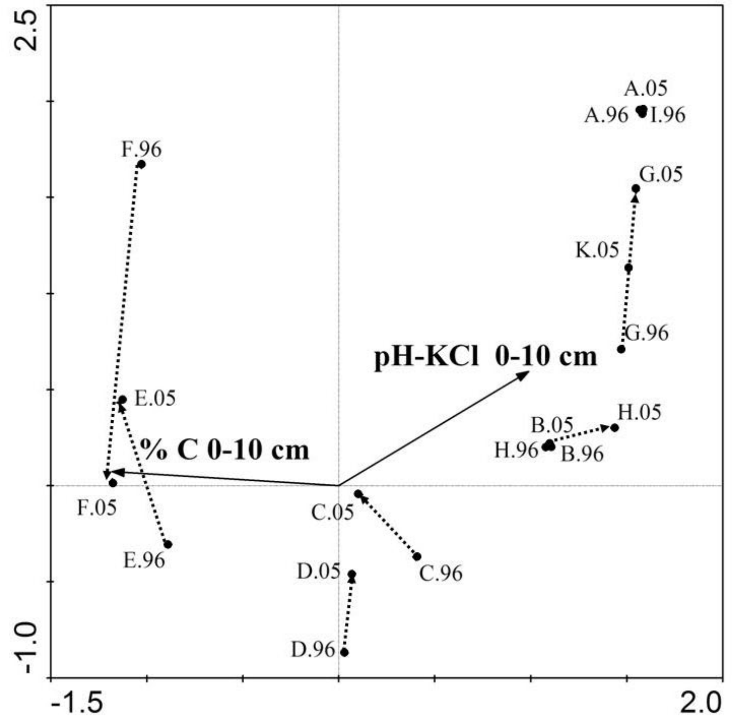


Fig. 9: Biplot of a relevé (PQ) ordination showing the first two axes of CCA on seven PQs and two Reference plots from 1996 and 2005 (18 relevés in total). The arrows indicate the relation between two parameters (in the 0–10-cm soil layer), that proved to be significant after forward selection and Monte-Carlo permutation test, and the first two axes of a CCA. Shifts in species composition of PQs from 1996 to 2005 are indicated by dotted arrows. Ref.A and PQ.B did not change and consequently remained on the same place in the ordination diagram.

Abb. 9: Biplot der CCA-Ordination mit sieben Dauerquadraten aus den Jahren 1996 und 2005 sowie zwei Referenzplots (d. h. 18 Aufnahmen insgesamt). Dargestellt sind die beiden Umweltparameter, die sich nach Vorwärtsselektion und Monte-Carlo Permutationstest als signifikant erwiesen haben. Die Vegetationsveränderungen zwischen 1996 und 2005 sind durch Vektoren dargestellt, wobei sich Ref.A und PQ.B nicht merklich verändert haben.

5. Discussion

5.1. Succession and lichen diversity

In drifting sand with a sub-neutral pH-KCl of about 5 the succession appears to start with green algae, followed by *Polytrichum piliferum* and *Corynephorus canescens (*Fig. 8). Only one lichen species, viz. *Stereocaulon condensatum*, can stand the harsh environmental circumstances of actively drifting sand. This species from the Red List (APTROOT et al. 2012) is doing rather well between *P. piliferum* plants in areas where sand has been blown out. This both applies for the NW area with spontaneous succession and for the eastern area, as an effect of management.

Some other pioneer lichens are rather rare on the Hulshorsterzand, like *Cladonia foliacea* (not present in the tables in KETNER-OOSTRA 2006). Other pioneers are specific of open gravel-rich sand, with some inblowing sand, which we studied in the 'lichen steppe' in the central part of the Hulshorsterzand (*Cladonia cervicornis*, *C. verticillata* and the related rarer *C. pulvinata*, *C. zopfii, C. uncialis* and *C. arbuscula* s.l. (the latter two VU in the Red List). Between 1996 and 2006, pH-KCl had dropped to 4.0 with a much higher % C, % N and % P, especially in the 0–2-cm layer (Table 4). GÜNZL (2005) mentions almost the same lichen species for acidic soils in Northern Hesse (Germany), all on their Red List, but includes some other *Cladonia* species and *Cetraria aculeata* not red-listed in the Netherlands.

The pioneer lichen species *Cladonia strepsilis* (VU in the Red List) is typical for gravel-rich sand, but here grows together with species like *C. crispata*, *C. gracilis* and the group of humicolous species mentioned below. Their constancy in the monitoring tables in KETNER-OOSTRA (2006) reveals that these species-rich settlements probably are of rather old age and remained stable by the constant influx of mobile sand (BÜLTMANN 2005).

Most humicolous lichen species like *Cladonia coccifera*, *C. ramulosa*, *C. floerkeana* and *C. macilenta* were doing well in the research area. In the managed area, these species occurred on litter remaining from pines removed in 1991 (Table 1, relevés 3a, 3b and 3c). *Festuca ovina*, the grass species that marks this succession stage, is only treated as *F. ovina* s.l. in the monitoring, while *F. ovina* subsp. *hirtula* (VAN DER MEIJDEN 2005) was recorded in 2006. This subspecies with Red List status is of national importance, as its occurrence on the Hulshorsterzand is unique, while CR for the Netherlands.

Like on other acidic soils (GÜNZL 2005), the terminal stages of lichen succession at the Hulshorsterzand are reached when aero-hygrophylous reindeer lichens like *Cladonia portentosa*, *C. arbuscula* s.l. and the podetia of *C. uncialis* have settled in. The related vegetation types on drift sand are characterized by several grasses, like *Festuca ovina* s.l., *Deschampsia flexuosa* and *Agrostis vinealis*, and proved to be rather stable. The same grass species but with *F. ovina* s.l. increasingly dominating, occurred in the 'lichen desserts' on flat gravel-rich locations. Without sand blowing-in, a decreasing lichen cover and the loss of some red-listed lichens was found. In general, in this grass-rich vegetation *Calluna vulgaris* will germinate and gradually a dry heath might develop, initially in a mosaic with the lichen-rich grass vegetation (STORTELDER et al. 1996).

This succession from initial species-poor *Corynephorus canescens* vegetation into lichen-rich stages might take 10–15 years, as was found in a historical study of aerial photographs of other inland sand dune complexes on the Veluwe (SPARRIUS 2011). On such a photograph of 1960 it was observed that places on the Hulshorsterzand with over 10 lichen species at present, were already covered with such vegetation at that time.

5.2. Lichen diversity in the past and in the present

Already in 1968 *Cladonia cornuta*, *C. phyllophora* and *C. squamosa* were probably scarce in drift sands on the Veluwe (APTROOT et al. 2012) and they were not found during our research. *Cladonia digitata*, *C. fimbriata*, *C. squamosa* and *C. polydactyla* still occur on rotting wood, mainly inside the forest (Table 2). The aero-hygrophyte *Cladonia rangiferina* has become extinct in the Netherlands and *C. ciliata* is rated in the Red List as EN (both not found on the Hulshorsterzand after 1959). In the Netherlands, some of these species occur at the southern border of their mainly boreo-alpine distribution area, and their extinction has been linked to climatic change (VAN HERK et al. 2002). The decrease of *Hypogymnia tubulosa* in epiphytic and terrestrial habitats is probably mainly because of the SO_2 pollution before the 1970s or of the NH_3 pollution since then. However, detailed inventories revealed that many lichens were still present, and in addition, certain terrestrial growing crustose species were found in 2006, which make up for the total of 34 terrestrial growing species between 1996 and 2006.

5.3. The neophyte *Campylopus introflexus* as a threat

Before the 1970s, *Polytrichum piliferum* appeared to be the only pioneer moss species on bare sand, as was found on the Kootwijkerzand (also at the Veluwe) at that time (KETNER-OOSTRA & SÝKORA 2008). In the life cycle of *P. piliferum* some of the shoots from the rhizomes may form male and female plants, with antheridia and archegonia, respectively. 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 blown-in. In wet and probably eutrophic circumstances (with high 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.

Since the 1970s the neophyte *Campylopus introflexus* (VAN DER MEULEN et al. 1987) thwarted the rejuvenation of *P. piliferum*. *C. introflexus* is quickly colonizing mainly by means of vegetative propagation from leaves or stem tops but also by means of spores. This intrusion into the *P. piliferum* carpets, when these are less vital, became very clear in our succession study in the NW area between 1996 and 2006 (see Fig. 5).

New research between 2006 and 2010 made clear that this intrusion of *C. introflexus* in *P. piliferum* carpets is favoured by the high N-deposition in this central area of the Netherlands: > 30 kg ha^{1} yr^{-1} compared with < 30 kg ha^{-1} yr^{-1} in the period 1950–1980; see SPARRIUS & KOOIJMAN (2011).

However, *Campylopus introflexus* is not growing well where sand is continuously blown in. This was apparent in biotope 3, the management site. Here *P. piliferum* was thriving, while between 1996 and 2006 the cover of *C. introflexus* was only < 1%.

Already in the past, the blown-out gravel-rich depressions were covered with a layer of drifting sand, even the species-rich plot PQ.D had 20 cm drift sand on top of the gravel-rich fluvioglacial sand, while still some sand was blown in from the nearby footpath. Here the lichen richness remained around 17 species, but the lichen cover decreased considerably in the research period (Fig. 6). In the same period, *C. introflexus* increased from 10 to 40 %, which might prove to be a real danger for this 'lichen steppe' in the future.

5.4. The danger of grass encroachment and encroachment of self-sown trees

In the gravel-rich depressions in the semi-sheltered park landscape with only little blown-in sand some aero-hygrophytic species disappeared and the total lichen-cover diminished substantially. From the monitoring reports it is clear that this was mainly the result of several years with a high production of grasses, mainly *Festuca ovina* s.l. (covering 40% in 1996 to 85% in 2003; see Fig. 7), resulting in much litter. This might be the effect of untypical weather in those years, with much rain in autumn and spring, probably the result of 'climatic change'. Grass-encroachment is also partly linked to N-deposition, having a fertilizing effect on these sandy soils.

After stabilisation of the soil, often *Pinus sylvestris* seedlings established and the succession to a young forest started, resulting in the decrease of lichen diversity and cover.

5.5. Acidification in calcium-poor dunes and depressions

Vegetation change from open sand to lichen-rich vegetation is clearly followed by a decrease in pH, an increase in organic matter, in % total N and in % total P. The lichen composition is clearly related to this gradient.

In pioneer vegetation, CEC is gradually increasing during succession from open sand to the reindeer lichen-rich grass vegetation on stabilized drift sand (biotope 1). The highest amount of cathions was found in the lichen-rich PQs in blown-out depressions with perifluvioglacial sand, which might be the result of the longevity of this vegetation. Both inland and coastal dune areas appear to be rather poor in phosphorus ions.

5.6. Positive effect of large-scale management

It appeared to be possible to maintain or revitalize lichen-rich dune vegetation by large scale management. After the intervention in 1991 in drift sand cell SW, there was still much active sand in 2006. The gradually sloping dune was influenced by the prevailing southwesterly wind, but probably also by the northeastern wind (JUNGERIUS & KETNER-OOSTRA 2006). Grasses and the neophytic moss *C. introflexus* did not increase in our research site on this dune slope. The low cover of the pioneer moss *P. piliferum* combined with that of *Stereocaulon condensatum*, the lichen from deflation locations. Other lichens, such as the common humicolous *Cladonia* species only established on litter near the former stands of pine trees. Our positive results on the southwesterly exposed slope agreed with those of RIKSEN

Fig. 10: Management measures carried out. a: topsoil removal at the borderline between dry heath and drift sand in 2009. b: sieving machine in action with piles of sand left after the sieving.
Abb. 10: Durchgeführte Managementmaßnahmen. a. Oberbodenabtrag an der Grenze zwischen Trockenheide und mobiler Binnendüne. b. Sandhaufen nach der Einsatz der Siebmaschine.

& GOOSSENS (2007), who found that the wind erosion activity was higher in bare sand at the surface on a dune slope than on a deflation plane.

The effects of different techniques (applied in the 1970s) for cutting trees in order to reactivate aeolian erosion at the Kootwijkerzand, were evaluated with PQs by DANIËLS (1990). In the same nature reserve long-term effects of management (applied 1960–1980) were evaluated in 2005 (KETNER-OOSTRA & RIKSEN 2005). The effect of the removal of trees on wind erosion and sand drifting was greatest in the southern and central parts of the area, where the mainly southwestern wind could increase in force. The removal of the humus layer appeared to be very crucial.

6. Conclusion and management perspective

The succession from initial species-poor *Corynephorus canescens* vegetation into lichen-rich stages, with 34 species in the study area, and followed by mosaic vegetation with heath, is endangered by the present relative high aerial N deposition. The habitat quality in inland sand dunes is negatively influenced by encroachment of grasses and the invasive moss *Campylopus introflexus*. However, *C. introflexus* is not growing well where sand is continuously blown in, as appeared after monitoring of the restoration measures from 1991. The sand kept drifting and the pioneer community thriving.

The negative effect of encroachment of woody species on lichen diversity and cover can be prevented by removing their seedlings at a regular basis.

We cannot predict how much longer than 15 years the positive effects of the large-scale management from 1991 will last for the Hulshorsterzand, when there is still a high N emission in this central part of the Netherlands (around 30 kg ha^{-1} yr^{-1}; see SPARRIUS 2011). The advice given in JUNGERIUS & KETNER-OOSTRA (2006) for new restoration measures in other parts of this nature reserve was partly followed. In the winter of 2009 trees were cut and several hectare of topsoil in cell NW were removed (Fig. 10), financed by OBN (Overlevingsplan Bos & Natuur; the National Survival plan for Forests and Nature).

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