Impact of atmospheric nitrogen deposition on lichen-rich, coastal dune grasslands

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door

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Für meine Eltern

Contents

Birds eye view of Hiddensee (D) – in the front the Gellen dune area.

Chapter 1

Introduction

Eva Remke

Introduction

In Europe, sand dunes are covering large areas of the Atlantic, North and Baltic Sea coast. Dune systems are geomorphologically active and very dynamic systems, and hence consist of a fine mosaic of different habitats. At a small scale extremely different conditions occur for plants and animals (van der Maarel, 1997). Critical and limiting factors in dry coastal dunes are the influence of the wind, thus shifting sand and salt spray, and the lack of water and nutrients in these initially bare sands (Kumler, 1997). The level of disturbance determines whether geomorphologic or biological processes dominate the dune system, i.e. periodical sand shifts alternate with less dynamic periods with slow succession (Jungerius and van der Meulen, 1988).

These extreme habitats – extraordinary water deficiency, poor nutrient availability, high disturbance rates and high temperature amplitudes – are home to many specialised and endangered plant and animal species. A range of habitats and species of coastal dunes are protected under the European Habitats Directive (council directive 92/43/EEC of 21 May 1992), for example grey dunes (2130*) with various *Cladonia* spp., dry heaths (2140*, 4030) and wet dune slacks (2190). These habitats and species are of high or even priority community interest and a target of nature conservation in Europe. Additionally, coastal dunes are listed as an Endangered Biotope Complex around the Baltic Sea including grey and brown dunes (dwarf shrubs), wet dune slacks and natural forests as Heavily Endangered Biotopes (Helsinki Commission, 1998).

European coastal dunes are threatened by intensive recreational use and urban development resulting in area loss, degradation and fragmentation (Helsinki Commission, 1998). Furthermore, coastal dunes are negatively influenced by a decrease in sand mobility (due to an increase in coastal protection measures), the cessation of extensive agricultural land use, a decrease in wild herbivore density (van Dijk, 1992; Helsinki Commission, 1998) and sea level rise (Pruszak and Zawadzka, 2005).

Overall, atmospheric pollutants can have a marked influence on these oligotrophic ecosystems (van der Meulen et al., 1996; van Turnhout et al., 2003). Levels of atmospheric nitrogen deposition have increased steadily in central Europe during the 20th century with a steeper increase from the 1960s onwards (Asman and Drukker, 1988). In north-west Europe, this deposition peaked during the 1970-1980s and declined by 10-40% during the decades thereafter (Boxman et al., 1997; Erisman et al., 2001; NEGTAP, 2001). Today, amounts of atmospheric pollution are still high enough to exceed critical loads for various ecosystems (Busch et al., 2001; Craenen et al., 2000; Herman et al., 2001; Nagel and Gregor, 2001). Critical loads are defined as the deposition level of atmospheric pollutants above which negative ecosystem effects occur (Nilsson and Grennfelt, 1988). Critical loads for dry coastal dunes are assumed to be at 10-20 kg N ha^{-1} yr^{-1} in Europe (Acherman and Bobbink, 2003). In the Netherlands, critical loads for lime-poor dune grasslands are presently estimated as 13 kg N ha^{-1} yr^{-1} (van Dobben and van Hinsberg, 2008).

Nutrient-poor and weakly buffered ecosystems are very susceptible – and thus particularly vulnerable – to increased levels of atmospheric nitrogen deposition. In dry ecosystems in north-west and central Europe, effects of atmospheric depositions have been described, for example for forests (Houdijk and Roelofs, 1991; van Dijk et al., 1989, 1990), heathlands (Bobbink et al., 1992; Power et al., 1998; Roelofs, 1986; van den Berg et al., 2005) and partly for coastal dunes (Jones et al., 2004; Kooijman et al., 1998). Lichen-rich, coastal dune grasslands, however, have received less attention, but may even be more

sensitive to atmospheric deposition than other dune vegetations (Kooijman and de Haan, 1995; Kooijman and Besse, 2002). Other habitats dominated by lichens and mosses seem to be highly sensitive to elevated levels of atmospheric deposition, e.g. arctic heath or tundra (Fremstad et al., 2005; Tye et al., 2005) . In order to get a deeper insight into the sensitivity of lichen-rich grasslands, this study focusses on the impact of nitrogen deposition on these lichen-rich grasslands and the succession in dry coastal dunes.

Acidification and eutrophication, major consequences of nitrogen deposition, affect various ecosystem patterns and processes (Bobbink et al., 1992; Heij and Schneider, 1991). Elevated N-loads stimulate plant growth, but lead also to a loss of buffer capacity and to an increased availability of toxic metals (Al^{3+} and Fe^{3+}) within the soil (Aerts and Bobbink, 1999; Heij and Schneider, 1991). Higher soil Al/Ca-ratios are assumed to be toxic for plants growing at intermediate pH levels (de Graaf et al., 1997; Marschner, 1995). High N-deposition may also accelerate succession rates in acid grasslands, heathlands and dune pools (Bobbink et al., 1998; Achermann and Bobbink, 2003). Vegetation becomes dominated by graminoids like *Deschampsia flexuosa* (L.) Trin. or *Molinia caerulea* (L.) Moench (Bobbink et al., 1998). In coastal dunes along the North Sea, large mosses, tall grasses and shrubs have become dominant since the 1970s (Ketner-Oostra and Sykora, 2004; Vertegaal et al., 1991; ten Harkel and van der Meulen, 1996; van der Meulen et al, 1996). Depending on the lime and iron content of sands, different tall graminoids are dominating: the grass *Ammophila arenaria* (L.) Link and the sedge *Carex arenaria* L. under lime and iron-poor conditions (Wadden District) and the grasses *Elymus athericu*s (Link) Kerguelen as well as *Calamagrostis epigejos* (L.) Ruth in calcareous dunes (Renodunaal) (Kooijman et al., 1998). These changes have mainly been attributed to elevated atmospheric nitrogen deposition levels (Kooijman et al., 1998; van der Meulen et al., 1996; van Turnhout et al., 2003). Simultaneously, however, grazing intensity of rabbits and livestock decreased, and confounding effects cannot be totally excluded (Belsky, 1992; Hill et al., 1992; Ranwell, 1960; Thomas, 1963; Westhoff, 1985).

Field research on the impact of atmospheric N-deposition in north-western Europe could only focus on ecosystems with N-loads mainly exceeding the critical loads, whereas field research at less affected or pristine sites is lacking. Comparable ecosystems and climatic conditions occur around the Baltic Sea in north-eastern Europe. According to a coarse network of climate stations and modelled data, the current range of wet N-deposition in the Baltic region is 3-8 kg N ha^{-1} yr^{-1} (Fjæran, 2006; Hjellbrekke, 2001, 2002, 2003, 2004, 2005). As 3 kg N ha^{-1} yr^{-1} is the assumed background deposition for the Baltic region (Søchting et al., 1995), these N-deposition ranges suggest, that pristine, unaffected systems still occur in parts of this area. Atmospheric deposition levels can be very different between coastal and more inland sites. Additionally, modelled data for these coastal areas have an uncertainty as high as 30-80% (Barret 1998; Erisman et al., 1995; Lövblad and Erisman, 1992). Therefore, another focus of this study is to determine N-deposition at various coastal sites.

The vegetation composition and the degree of mosaic pattern for Baltic coastal dunes is rather unknown and a change toward dominance of tall graminoids has not yet been described for coastal dune systems of the Baltic Sea region. Because of the high nature value and the susceptibility of Baltic coastal dry grassland to atmospheric N-deposition, it is of great importance to establish the impact of N-deposition on these ecosystems. Moreover, similar ecosystems exist in sand areas all over the world and many of them also

face rising N-deposition levels. Studying local effects on sand dunes may therefore attribute to a worldwide insight in the impact of N-deposition on dry sand ecosystems.

Main questions:

1. What is the present-day atmospheric nitrogen deposition level on Baltic coastal dunes?

2. What are the effects of atmospheric nitrogen deposition on dry coastal dunes of the Baltic Sea? To what extent do the effects resemble those observed for North Sea dunes?

3. Which processes are affected by elevated nitrogen deposition?

4. What is the difference between highly N-affected and N-unaffected lichen-rich dune grasslands?

In this research, extensive descriptive studies were combined with field experiments. At 19 coastal dune areas around the Kattegat, the southern and central Baltic Sea, stretching from Denmark in the west to Estonia in the east, comparable dunes with different atmospheric N-loads were investigated (figure 1). Because short-term experiments of up to 5-10 years often do not show significant differences between ecosystem features,

Figure 1 Map of field sites along the Kattegat, southern Baltic Sea and Baltic Proper.

possibly due to the relatively short time-span, vegetation change at a few coastal dunes over 70 years has been analysed as well (chapter 2). For vegetation change at various Baltic coastal sites the space-for-time substitution (Pickett, 1989) has been taken as research set-up (chapter 3 and 4). Furthermore, early changes in lichen-rich, dune grasslands due to elevated N-loads were studied in two short term outdoor experiments: once an application of the stable isotope ^{15}N as reduced or oxidised N (two months) and once a two year ammonium-nitrate fertilization (chapter 5 and 6).

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Chapter 2

Site specific factors have an overriding impact on Baltic dune vegetation change under low to moderate N-deposition – a case study from Hiddensee island

Eva Remke and Irmgard Blindow

Abstract

At three coastal dune sites at the island of Hiddensee, north-east Germany, vegetation cover was mapped during 2002 and compared to vegetation surveys from the late 1980s and 1930s. Abiotic and biotic factors, which have been identified as being critical for coastal dunes in former studies such as disturbance, salt spray or nutrient availability, were measured. Grazing and land-use history were reviewed by literature and interviews. Tall graminoid communities, mainly dominated by *Carex arenaria*, are a common vegetation unit today. Development, distribution of these dominances and possible causes for its occurrence have not been analysed.

Generally, older successional vegetation units increased and pioneer stages decreased from the 1930s until 2002. At the geologically youngest site, the southern dunes, grass encroachment by *Carex arenaria* was highest (ca. 50% cover in 2002), and age and density of trees lower than at the older, central dunes. Land-use changes such as decrease in grazing pressure, additional feeding of livestock, increase in coastal protection measures and subsequent decrease in shifting sands as well as varying availability of groundwater and amount of salt spray are relevant factors for vegetation changes in coastal dunes over the past 70 years. Site-specific land-use differences such as livestock density and land-use history have a stronger influence than atmospheric N-pollution on the vegetation composition of these acidic, coastal dunes under low to moderate N-deposition loads of 6-8 kg N ha^{-1} yr^{-1}.

Introduction

Coastal dunes provide a range of habitats with wild flora and fauna species protected under the Habitats Directive, for example, grey dunes (2130*) with various *Cladonia* spp., dry heaths (2140*, 4030) or wet dune slacks (2190) (council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora[1]). These habitats and species are of priority community interest and a target of nature conservation in Europe. At Hiddensee, a German island in the southern Baltic, large parts are under Habitats Directive protection. These areas are mainly semi-natural ecosystems with a long history of agricultural land-use (e.g. Gustavs, 1999). The quality and critical environmental factors of these habitats and species are of primary interest for the local nature conservation authorities such as the National Park (NP) authority. The habitat status and species environment should improve or at least be maintained at its current condition according to the Habitats Directive. Key changes in the coastal dune vegetation and critical environmental factors are of central interest for future management.

Factors threatening the quality and quantity of coastal dunes along the North Sea coast are acidification, eutrophication and dehydration (Aerts and Bobbink, 1999; Heij and Schneider, 1991; Kooijman et al., 1998; van der Meulen et al., 1996) as well as reduced numbers of grazers and browsers (van der Meulen et al., 1996; Veer and Kooijman, 1997). One cause of acidification and eutrophication of oligotrophic and poorly buffered ecosystems is elevated atmospheric nitrogen and sulphur deposition (Bobbink et al., 1998; Ketner-Oostra et al., 2006; Kooijman et al., 1998; Remke et al., 2009/chapter 3). As a result, such semi-natural habitats tend to be dominated by mosses, tall grasses and/or shrubs. Grass dominance may, however, also be a consequence of a decrease in grazing. Rabbit (*Oryctolagus cuniculus* (L.)) activities are an important disturbance factor for coastal

dunes. When rabbits decrease due to epidemics, grasses and shrubs increase their cover (Veer and Kooijman, 1997).

On the island of Hiddensee, initial grass dominance was noticed in the early 1990s (Schubert 1996, 1998), but detailed data of vegetation change and important environmental factors for these dominances are lacking. The aim of this study is to identify relevant environmental factors for vegetation change in the coastal dunes of Hiddensee today and over the past 70 years.

Material and methods

Field sites

The three field sites are all situated on the island Hiddensee, north-east Germany (figure 1) and each have an area of about 4 ha. The ecoregion can be characterised as Baltic (Olson et al., 2004) with a long-term average of 564 mm yr^{-1}, temperature of 8.0°C (world climate data, station Greifswald[2]) and prevailing south-west to westerly winds (Neuber, 1970). Salinity of the surrounding Baltic Sea varies between 8-10 PSU (Möbus, 2000). The central dunes (local name Dünenheide) are ca. 2000-2500 years old, thick aeolian sediments (10-20 m) above Pleistocene deposits of the last glaciation, whereas the southern dunes (local name Gellen) are only 600 years old and rather shallow aeolian sediments (several meters) on top of marine barrier beaches (Möbus, 2000). Since the late 17th century, agricultural land-use can be verified for the research sites at Hiddensee. Heathlands existed in the central dunes and summer meadows existed in the southern
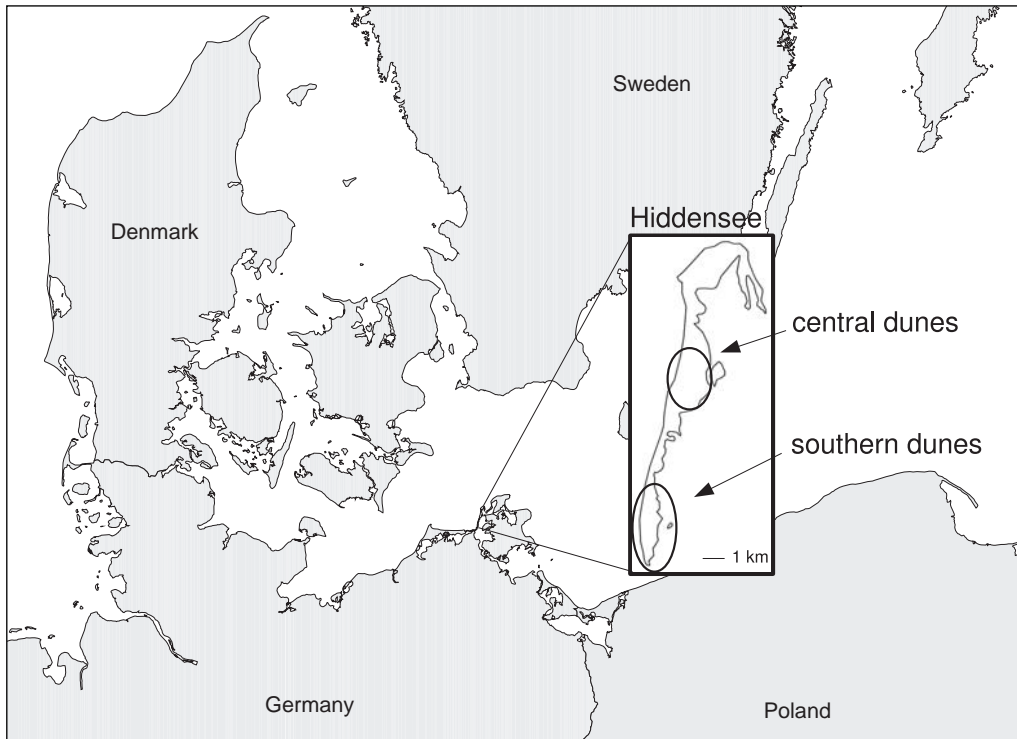

Figure 1 Map of field sites

dunes (Gustavs, 1999). From the middle of the 19th century, coastal protection measures such as groynes along the whole western coastline, stone walls between the open sea and the beach, pine (*Pinus* ssp.) and marram (*Ammophila arenaria* (L.) Link) plantings were carried out to protect parts of the coastline from abrasion, the island from being divided into two, and to reduce the shifting sands on the island. The central dunes were separated into two parts. At the southern half a ca. 20 m broad pine plantation was planted between 1900 and 1960, leeward of the first dune ridge towards the sea (termed central dunes-south hereafter) and the northern half stayed open towards the sea (termed central dunes-north hereafter) (Möbus, 2000).

In 1990 the National Park Vorpommersche Boddenlandschaft was established in this area (Hagge, 1996). The southern tip of the island became a core zone, i.e. all management and land-use is prohibited. In the central dunes of Hiddensee, nature conservation measures can still be undertaken, but livestock grazing stopped with the establishment of the national park.

At a nearby EMEP (Co-operative Programme for Monitoring and Evaluation of the Long-range Transmission of Air Pollutants in Europe) station on the Zingst-peninsula, an average wet deposition of 6.3 kg N ha^{-1} yr^{-1} was measured during 2001-2005 (Remke et al., 2009/chapter 3). During the last two to three decades no major nearby pollution source, such as intensive animal husbandry or power plants, is known.

Field and lab methods

During the 2001 and 2002 growing seasons, vegetation relevees (n=50) after Braun-Blanquet (Pfadenhauer, 1997) were spread over the three field sites to cover all different vegetation units in the dunes. A vegetation map of the three dune areas (ca. 4 ha) was compiled by field mapping (transect walks) supported by geo-referenced aerial photographs. For species determination the following literature was used: for vascular plants Oberdorfer (1994), for mosses Frahm and Frey (1992) and for lichens Wirth (1995).

Browsing intensity of trees was mapped in 20 randomly chosen (random number combined with x-y grid) 5×5 m squares at each field site. The following parameters were noted: tree species, stem diameter at 1.3 m, total height, age (tree-ring count) and browsing intensity after Klötzli (1965).

In 2002, soil samples were taken at the end of the growing season (September) below vegetation relevees from comparable vegetation units in all three sites, i.e. grey dune (n=1), tall grassland (n=1), wet dune slacks (n=2) and dry heath (n=2) (n=18 in total). With a soil core cutter (100 cm^3), three samples were taken from the mineral horizon between 0-20 cm and stored in plastic bags at 4°C. Samples were dried at 105°C for 24 hours and water content (Vol.%) was calculated via fresh-dry weight relation (Schlichting et al., 1995). The pH was determined in 0.01 M CaCl$_2$ extract (Schlichting et al., 1995). C/N-ratios were determined in finely ground soil (5 minutes in a centrifugal ball mill, Fritsch, Idar-Oberstein, Germany) via an elemental analyser (CHNOS element analyser vario EL III, Hanau, Germany Elementar Vario EL, Germany).

In 2005, soil and *Carex arenaria* L. samples were taken in the middle of the growing season (July) from one main succession sequence, going from young short via old short to tall grassland (Heykena, 1965; Jeckel, 1984). The first early successional stage is characterised by short, dry grassland, with at least 30% open sand area, the second stage by older and

lichen-rich, short grassland, with open sand below 5% (Corynephoretum), and the third stage is dominated by tall grasses with at least 50% cover of *C. arenaria* (Caricetum). Below these plots (n=9 for each site), a soil sample mixed from three soil cores (each taken by a 100 cm³ core cutter) was collected from the top 10 cm of the mineral soil layer. All samples were dried at 70°C (plant) and 40°C (soil) for 24 hours. *C. arenaria* samples were ground in a centrifugal mill (rotational speed 18000 for 1-2 minutes, FRITSCH pulverisette 14, Idar-Oberstein, Germany). Total nitrogen of plant material was determined with a C/N-analyser (CHNOS element analyser vario EL III, Hanau, Germany) and total element contents (Al, Ca, Fe, K, Mg, Mn, Na, P and S) were analysed in 200 mg ground material digested in sealed Teflon vessels in a Milestone microwave oven (type Ethos D, Milestone Inc., Sorisole, Italy) after addition of 4 ml HNO_3 (65%) and 1 ml H_2O_2 (30%) (Kingston and Haswell, 1997).

Soil samples from 2005 were sieved with a 2 mm mesh-size before the following analyses. Soil organic matter content was determined as loss on ignition (LOI) at 550°C for 8 h, pH was measured in 0.2 M NaCl, electrical conductivity (EC) was analysed after Rowell and Börsch-Supan (1997) and ortho-P in aqua-dest. extracts colorimetrically with an Auto Analyzer 3 system (Bran+Luebbe, Norderstedt, Germany), using salicylate (Grasshoff and Johannsen, 1977).

Humus and soil profiles were mapped and classified after World Reference Base for Soils (WRB 1994 in Scheffer et al., 1998) and German mapping instructions KA4 (Finnern and Ad-hoc-Arbeitsgruppe Boden der geologischen Landesämter und der Bundesanstalt für Geowissenschaften und Rohstoffe der Bundesrepublik Deutschland, 1994) at each relevee with a Pürckhauer soil core sampler (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands). The percentage of relic ('buried') profiles (i.e. A-horizons overblown by sand) of all profiles was calculated, as a measure of the activity of the site in history and today and as an indicator of whether biological or geomorphological conditions prevailed (Jungerius and van der Meulen, 1988).

At all three field sites, groundwater conductivity (EC; WTW LF 325 with temperature compensation) was measured along a transect from west to east, on three occasions (June, July and August) during the 2002 growing season with piezometers (n=8), which were installed in September 2001 (Schlichting et al., 1995).

Salt spray was measured at the top of the first white dune from the sea, 24 m (first dune foot), 90 m and 140 m inland from the first dune ridge at each field site. Salt spray traps were constructed as described by Sykes and Wilson (1999), and measurements were taken every 4 weeks between October 2002 and October 2003. Conductivity (EC) was measured with a conductometer (WTW LF 325 with temperature compensation) simultaneously with the recording of the amount of captured water.

Data analysis

Plant phytosociological units were classified according to Berg et al. (2001; App.1 and 2). Vegetation field maps from 2002 were digitized with Arc View 3.2 and cover of different vegetation units was calculated. Vegetation maps from Fröde (1957) were compiled between 1935 and 1938, the ones from Schubert (1996, 1998) between 1987-1991 and 1995. These paper maps were geo-referenced with Image Warp for Arc View and digitized within Arc View 3.2. In order to compare vegetation units of the different researchers the synonym lists of Rennwald (2000) and Berg et al. (2001) were used (App. 2).

Statistical analysis was performed using SPSS 11.0. Differences between sites and vegetation units were identified using a one-factorial ANOVA with post-hoc Scheffé tests. If the data were not normally distributed, Mann-Whitney or Kruskal-Wallis tests were conducted. For cross-classified tables Pearson's Chi-squared test for contingency table tests and goodness-of-fit tests were used. For graphical display of data, R was used (R development core team, 2008).

Results
Vegetation change

The cover of the different dune vegetation units changed considerably during the past 70 years. In general, older and more nutrient rich successional stages increased their coverage in all three dune areas, while wet dune heaths (mainly pioneer stages) have diminished from 5-6% to less than 1% today and shifting white dunes (Ammophiletum) have decreased to $\frac{1}{8}$-$\frac{1}{3}$ of their former area (figure 2; App. 3). In the central dunes, the coverage of dry heath was twice as high as in the southern dunes, where minor increases occurred during the past 70 years. At the central dunes-south, stable situations were apparent with ca. 50% dry heath throughout the years. Only at the central dunes-north, was the change stronger. Dry heath decreased from 60% to 40% coverage by 2002, while grey dunes became more dominant (ca. 50% increase). Here, dominance of *Deschampsia flexuosa* P.Beauv. appeared in 2002 as a new unit, covering ca. 20% of the total survey area. Grey dune coverage was more-or-less stable throughout the last 70 years in the central dunes-south and tall grass units covered only very small areas. This is in great contrast to the southern field site. Here grey dunes decreased by 70% after 1990 and tall grass units, dominated by *Carex arenaria*, increased from 1% in 1990 to nearly 50% in 2002. Nardetea, which had small coverages at the southern site in 1936, could not be found in subsequent surveys, and only small numbers of individuals occur today.

In the central dunes (-north and -south), the density of trees has steadily increased, and their species number is twice as high compared to the southern site. Furthermore, trees and shrubs were only $\frac{1}{4}$-$\frac{1}{3}$ as tall in the southern dunes as in the central dunes and only half as old (table 1). Browsing intensity was higher in the southern dunes compared to the central dunes and reaches a value of three (table 1), i.e. the saplings are inhibited in their growth and more than 20 browsing bites are apparent on each plant (Klötzli, 1965). On the southern dunes, nearly all saplings were as small as dwarf shrubs and did not grow higher. On the central dunes-south, browsing intensity was the lowest (below one) and trees the tallest and oldest on average among all sites.

Table 1 Characteristics of woody plants (shrubs and trees apart from chamaephytes) in three dune sites on the island of Hiddensee in 2002. Browsing is measured after Klötzli (1965): the higher the number the higher the browsing intensity. Significant differences between sites (p<0.05) are shown in bold. Results of post-hoc tests in superscript letters, whereby different letters indicate significant differences between single areas.

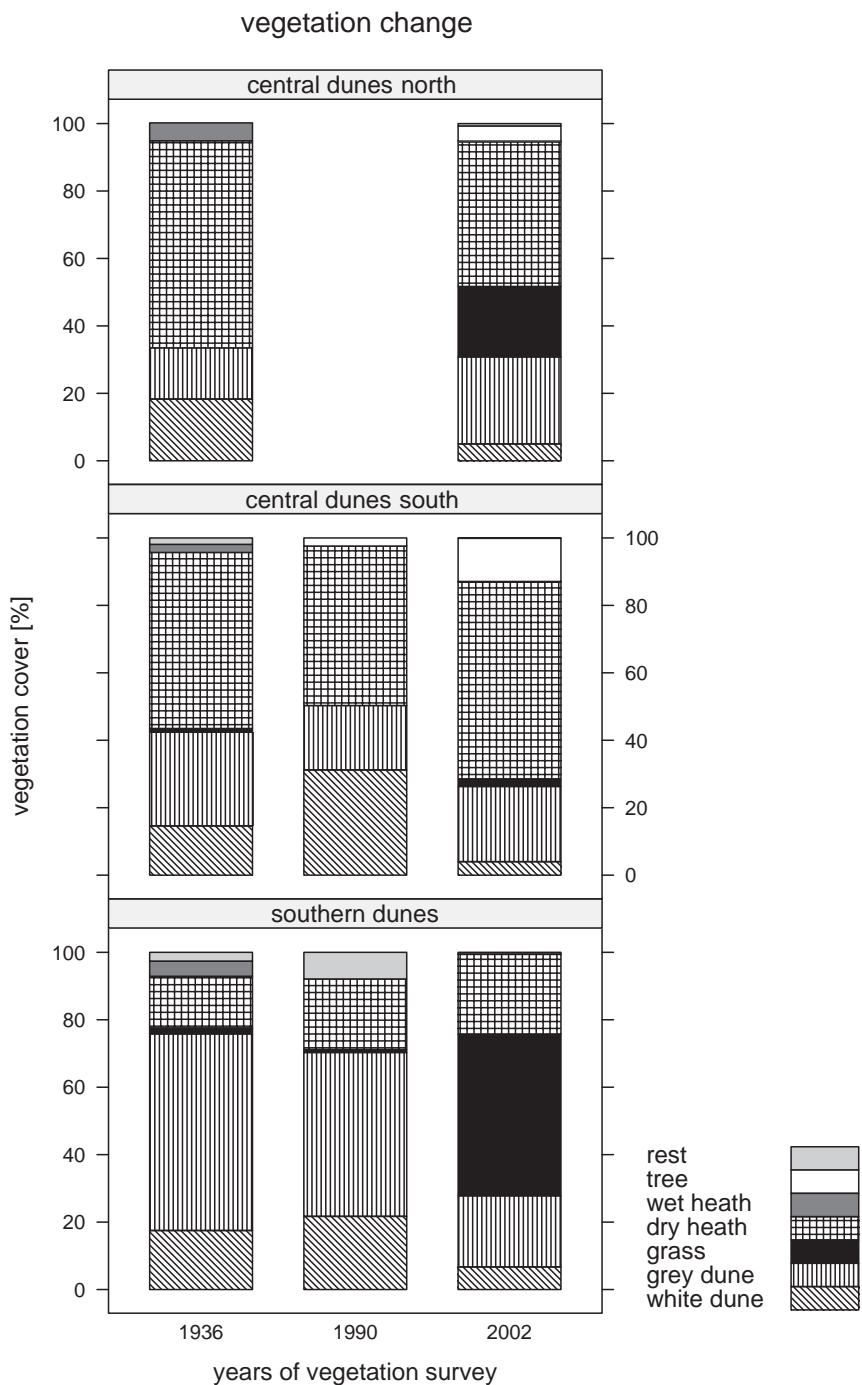| factor	central dunes-north		central dunes-south		southern dunes	
	mean	± SE	mean	± SE	mean	± SE
density [individuals per 100 m²]	1.6	0.6	2.2	0.7	0.7	0.5
height [m]	**1.0**[a]	0.2	**1.3**[a]	0.4	**0.3**[b]	0.03
age [years]	**5.8**[ab]	0.9	**7.0**[a]	1.3	**3.0**[b]	0.41
species number (total per site)	8	-	7	-	4	-
browsing intensity	**2.2**[a]	0.3	**0.8**[b]	0.3	**2.9**[a]	0.29

vegetation change

Figure 2 Vegetation cover in the three coastal dune areas on the island of Hiddensee in 1936, 1990 and 2002.

Table 2 Abiotic factors (means ± 1SE) in the three coastal dune areas on the island of Hiddensee. Significant differences between areas (p<0.05) are shown in bold and results of post-hoc tests in superscript letters, whereby different letters indicate significant differences between single areas. EC-conductivity, LOI-loss on ignition, CEC-cation exchange capacity, salt spray [%] – conductivity of the three inland dune traps as a percentage of the one on the first dune ridge. Salt spray data are only given for months with significant differences among sites.

	factor	central-north		central-south		southern dunes	
		mean	± SE	mean	± SE	mean	± SE
soil profile - classes	arenic umbrisol/ Regosol	**3**	-	**0**	-	**1**	-
	Cambisol/ Braunerde	**1**	-	**0**	-	**0**	-
	Gleysol / Gley	**0**	-	**1**	-	**3**	-
	podzol/ Podsol	**1**	-	**4**	-	**1**	-
buried profiles	[%] of all profiles	20	-	0	-	38	-
ecto-organic layer	Ol [cm]	1.1	0.5	1.5	0.4	1.5	0.9
	Of [cm]	3.1	1.3	5.6	2.4	1.9	0.8
	Oh [cm]	0.7	0.5	0.6	0.4	0.1	0.1
	O total [cm]	4.9	1.8	7.7	2.9	3.5	0.8
groundwater EC	June 2002	**88**[a]	7	**55**[b]	9	**137**[c]	24
[$\mu S\ cm^{-1}$]	July 2002	**102**[ab]	6	**84**[a]	8	**143**[b]	22
	August 2002	**138**[ab]	23	**91**[a]	13	**159**[b]	16
soil samples	pH 2002 [salt]	3.6	0.2	3.7	0.3	3.6	0.1
	EC 2002 [$\mu S\ cm^{-1}$]	197.9	5.3	198.0	6.0	188.5	4.9
	C/N-ratio 2002	20.1	2.5	22.3	1.7	19.3	2.8
	water content 2002 [%]	9.4	3.0	9.1	3.5	8.7	2.9
	LOI 2005 [%]	0.82	0.20	NA	-	1.00	0.31
	pH 2005 [salt]	4.0	0.2	NA	-	3.8	0.5
	CEC 2005 [$\mu mol\ kg^{-1}$]	927.8	397.4	NA	-	829.6	337.6
	ortho-P 2005 [$\mu mol\ kg^{-1}$]	27.5	5.9	NA	-	50.4	14.6
salt spray [%]	January 2002	**55**[ab]	-	**23**[a]	-	**101**[b]	-
	Mai 2002	**35**[a]	-	**19**[a]	-	**119**[b]	-
	June 2002	**22**[ab]	-	**10**[a]	-	**51**[b]	-
	August 2002	**18**[ab]	-	**9**[a]	-	**47**[b]	-

Environmental factors and plant tissue concentrations

None of the soil sample parameters analysed in 2002 and 2006 (organic matter, pH, cation exchange capacity and ortho-P content) differed significantly between the three areas (table 2). Significant differences, however, were found for tissue contents of *Carex arenaria* (above ground tissue). Mg and S contents were ca. 20% (significantly) higher in the central dunes-north than in the southern dunes. There were tendencies in the central dunes for higher contents of K (46% higher), N (20% higher), P (26% higher) and Zn (28% higher) (table 3) and N/P and N/K-ratios were lower but not significantly so (table 3).

The ecto-organic horizon thickness (humus layer) showed an increase from the southern dunes through the central dunes-north to the central dunes-south (table 2). Soil profiles were most differentiated in the central dunes-south as almost only podzols could be mapped and not initial soil developments such as arenic umbrisols (table 2). For the central dunes-north, arenic umbrisol was the most frequent soil class and for the southern dunes, groundwater-affected soils (gleysols) were characteristic. Most sand-buried profiles could be found in the southern dunes with 38% of all mapped profiles (table 2), 20% in the central dunes-north and no buried profiles in the central dunes-south.

Table 3 Element content [%] of *Carex arenaria* (above ground, living tissue) in the central dunes-north and the southern dunes in 2005 (n=9 per site). Significant differences are shown in bold and p-values are given.

factor	central dunes-north		southern dunes		
	mean	± SE	mean	± SE	p-value
Al	0.0051	0.0008	0.0067	0.0012	0.306
Ca	0.1729	0.0147	0.1430	0.0108	0.122
Fe	0.0112	0.0013	0.0138	0.0022	0.396
K	1.1846	0.1468	0.8077	0.1546	0.085
Mg	**0.1577**	0.0087	**0.1283**	0.0081	**0.025**
Mn	0.0187	0.0021	0.0177	0.0035	0.894
Na	0.0698	0.0132	0.0587	0.0141	0.627
N	1.6039	0.1211	1.3884	0.0366	0.075
P	0.1650	0.0133	0.1306	0.0109	0.085
S	**0.1579**	0.0063	**0.1319**	0.0065	**0.015**
N/P-ratio	9.9	0.4	11.1	0.8	0.290
N/K-ratio	1.5	0.2	2.5	0.6	0.160

The groundwater conductivity was different for all three measurements during the 2002 growing season. But only in June did all three areas show a significant difference. In the southern dunes, 2.5-times, and in the central dunes-north, 1.5-times higher conductivity was measured than in the central dunes-south. In July and August, only the southern dunes groundwater had a 2-times significantly higher conductivity than central dunes-south (table 2).

The conductivity of the captured water in the salt traps (mixture of salt spray and rain water) showed a strong dependence to the time of year. The salt concentration of the captured water coming into the dunes was 2-3-times higher during the autumn and winter compared to spring and summer (figure 3). There are remarkable differences between the three areas in the transport inland. In the southern dunes, there was no large difference between the conductivity of the salt trap at the first white dune ridge from the open sea and the three further inland salt traps, in contrast to the pronounced difference for the central dunes (figure 3). In the central dunes-north, 20-50% of the first trap amount was deposited in the inner dune area but in the central dunes-south only 10-20% (table 2). Average conductivity of all salt traps inland was 2-3 times higher in the southern dunes and the central dunes-north compared to central dunes-south.

If one assumes that the captured water has the same ion composition as the open sea water around Hiddensee, then its concentration corresponds on average to only 3-4% of the open sea water salinity of 8-10 PSU. Maxima at the first dune ridge are 10-12%, whereas frequently occurring minima values are less than 1%.

Discussion

A general pattern of vegetation change at all three field sites over the past 70 years is the decrease in shifting white dunes and wet dune heath, mainly pioneer vegetation of dune slacks. This change indicates more stable situations in the late 20th/early 21st century compared to the 1940s and a slowly progressing succession to older vegetation units. Since the late 19th century many different coastal protection measures have been taken at Hiddensee. Most influential for the dunes has been the afforestation with pine. On the leeward side of the first dune ridge *Pinus nigra* J.F. Arnold and *P. mugo* Turra were planted
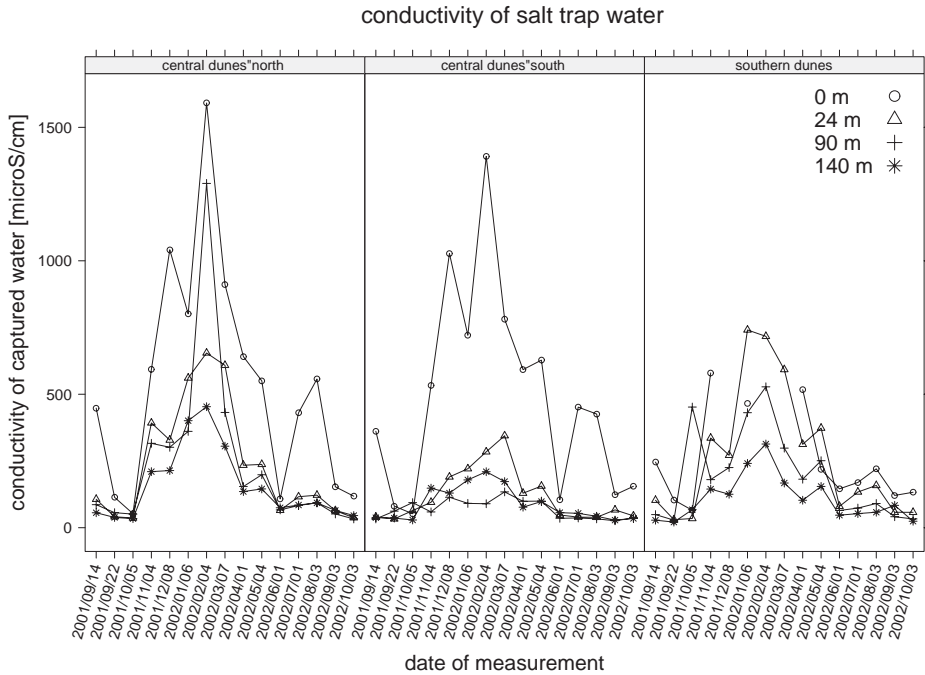
conductivity of salt trap water

Figure 3 Conductivity measured in four salt traps in each of three coastal dune areas on the island of Hiddensee during the course of the year. H0 - trap at the top of the first white dune ridge from the open sea, H24 - trap at the leeward dune-foot of the first white dune (24 m inland from H0 trap), H90 - trap 90 m inland from H0 trap, H140 - trap 140 m inland from H0 trap. Some data are missing for H0 in the southern dunes, as the trap eroded away.

in a ca. 20 m broad coastal protection forest between 1907 and 1960 (Ewe, 1983; Möbus, 2000). Groynes built all along the coastline and stonewalls at the northern part of the western coastline had a large impact as well. The northern part of Hiddensee consists of moraine till which has been the major source material for new land on Hiddensee during the past 5000 to 10000 years (Möbus, 2000). Protection of the western coastline and a reduction in sand supply from the north has resulted in less active dunes in the second half of the 20th century.

Despite the field sites lying geographically close to each other and parent sand material being comparable, the vegetation changes, especially of grass and tree cover, of the three areas differed considerably over the last 70 years. The central dune is approximately 2000-2500 years old (Möbus, 2000) and heathland has existed for at least the past 300 years (Gustavs, 1999). The dune heath is separated into two parts: the southern half is surrounded by forest, with a coastal protection forest (*Pinus* ssp.) towards the open sea and pioneer birch forest towards the hinterland; and the northern half of the dunes is much more open, and most importantly, there is no barrier (forest) towards the open sea. Wind and salt spray can have a strong impact on the whole dune system. In both the north and south central dunes, nearly 50% of the whole area is covered by dry heath; units dominated by *Empetrum nigrum* L. and *Calluna vulgaris* (L.) Hull. In central dunes-south, which are well protected from the impact of wind, sand and salt spray, no major vegetation changes occurred apart from a decrease in pioneer vegetation units (white

dunes, wet dune slacks) and a modest increase in tree/forest cover (2002 only 13%). Tree cover also increased slightly at the central dunes-north (2002 by 5%). This only modest increase in forest cover in the central dunes during the past 70 years can be explained by constant manual shrub and tree removal since the 1960s (H. Hübel 2002, personal communication). Nearby pioneer birch forests on former heathlands (1970s/80s), where no manual shrub removal occurs, are an on-site control for the positive influence of manual shrub and tree removal on open heathland preservation.

In the central dunes-north, a substantial increase in tall grass cover occurred. The tall grass units are mainly dominated by *Deschampsia flexuosa* L. Trin. but also *Carex arenaria*. Former dry-heath areas from the 1930s are covered by tall grass in 2002. The main reason for this conversion is the high grazing intensity by cattle from 1990 onwards with additional feeding on site especially in the late 1990s (H. Hübel and W. Neubauer, personal communications 2002). High nutrient import coupled with high grazing pressure favours grass over heather (e.g. Berendse and Elberse, 1990; Bokdam, 2001; Alonso et al., 2001). Outside the cattle-grazed area, grey dunes increased their coverage in the central dunes-north during the past 70 years. Shifting white dunes are followed by grey dunes in a normal progression of vegetation succession. Additionally, trampling by humans keeps the sand open and gives the wind a working surface. This supports a certain dynamic dune system in the central dunes-north.

The southern dunes are a maximum of 600 years old (Möbus, 2000). They have been an open, shifting dune system since the late 17th century and have been used as summer meadows since then (Gustavs, 1999). The younger age of these dunes explains the reduced cover of dry heath compared to the central parts. During the last 70 years, only 15-25% of the area was covered by *Calluna vulgaris* and *Empetrum nigrum*, and until 1990 the dominant vegetation units were young, open stages such as white and grey dunes. A sign of higher grazing intensities in former times is the occurrence of Nardetum in the 1930s. *Nardus stricta* L. is a highly unpalatable grass which dominates nutrient poor grasslands under high grazing pressure (Klapp and Opitz von Boberfeld, 1990). Today, only single individuals of *Nardus* still occur in the southern dunes.

In acid, coastal Baltic dunes grass encroachment starts with a N-load of 5 kg N ha^{-1} yr^{-1} (Remke et al., 2009/chapter 3). As Hiddensee receives roughly 6-7 kg N ha^{-1} yr^{-1} (Remke et al., 2009/chapter 3), it seems probable that elevated atmospheric nitrogen deposition caused the prominent vegetation change in the southern dunes between 1990 and 2002, when tall grasslands dominated by *Carex arenaria* increased their cover from 1 to 50% of the research area at the cost of open, species-rich grey dunes. Only 2-3% of the research area in the central dunes, however, is covered by *Carex* and atmospheric N-deposition, which is more-or-less the same for the whole island, can therefore not be the only trigger for this major increase of *Carex* cover at the southern dunes. Additionally, plant nutrition does not seem to be better in the southern dunes as N and other nutrients like K, Mg, P or S in *Carex*-tissue tend to be lower, and N/P- and N/K-ratios are slightly higher than in the central dunes. Periods of nutrient and water shortage, however, probably occur less often in the southern than in the central dunes, and this could trigger a *Carex* expansion. The southern dunes receive more salt via sea-spray that reaches the inner dunes and the conductivity of the groundwater is higher. In coastal dunes, a freshwater cushion lies on top of a saline groundwater layer (Bakker, 1990) and during stormy periods the salty nutrient-rich layer can expand and rise until it is reachable by plants. Additionally, the

dominant soil class mapped in the southern dunes is a gleysol, indicating a higher groundwater table. In times of nutrient or water shortage this higher groundwater supply in the southern compared to the central dunes could be an important factor, but it is not reflected in the total nutrient content of *Carex* shoots during the peak growing season. Salt spray from the open sea can supplement the nutrients leached by precipitation almost completely (Sloet van Oldruitenborgh, 1969). In addition, water is a very important factor in the life history of *Carex*, although it is a typical species of dry habitats (Tidmarsh, 1939; Schütz, 2000). *Carex* has a distinct root-dimorphism with shallow rhizomes and a deep root system up to 3.4 m (Tidmarsh, 1939). Water and nutrients are easily reachable and distributed through its extensive network (D'Hertenfeld and Falkengren-Grerup, 2002).

Of equal importance for the high *Carex* expansion in the southern dunes may be the drastic change in land use since the 1990s. Beginning in the 1980s with diminishing numbers of livestock, grazing stopped totally at the end of the 1990s. With the establishment of the National Park in 1990 the southern dunes became a core zone, which means no direct human action might take place (Haage, 1996). Disturbance by humans either directly by trampling or indirectly by their livestock (grazing, digging and trampling) has been reduced to almost zero. Due to an increase in coastal protection measures along the western coastline, less sand is transported to the dunes and the dunes are subsequently less dynamic. The history of a higher disturbance frequency is well documented by the large number of buried profiles (ca. 40%, table 2). Graminoids like *Carex* can probably take advantage of the decreased grazing pressure and shifting sands. They expand where in former times only small, even more unpalatable grasses like *Nardus stricta* or *Corynephorus canescens* P.Beauv. survived. The Habitats Directive for the preservation of species and habitat-rich dune mosaics makes *Carex* dominances less desirable. The dunes are quite species poor (less than 5 species per 25 m^2) and have a thick litter and root layer. The southern dunes have deteriorated considerably in this respect as species-rich, short dune grasslands (Corynephoretum) turned into *Carex*-dominated grasslands from the mid 1980s onwards, and now cover roughly 50% of the research site.

Other questions we ask are: what are the main characteristics of today's tree cover? And how quickly do the three dune areas afforest naturally? Progressive succession can be a threat to dune habitats depending on the management. The trees on the southern dunes are, on average, only one quarter to one third of the height, half as old and have half the species richness of the central dunes, and most trees do not grow higher than the dwarf shrub layer of *Calluna vulgaris* and *Empetrum nigrum*. This may be explained by the high browsing pressure by roe deer (*Capreolus capreolus* L.), which totally suppresses tree growth.

Another reason for the poor tree establishment in the southern dunes is the low availability of seeds. The only seed source is the coastal protection forest at the northern fringe of the core zone, and the prevailing winds prohibit seed dispersal into the core zone. A good availability of seeds is crucial for recruitment and sapling establishment (Smit and Olff, 1998). On the central dunes, forests are adjacent to the open areas, and within the dunes solitary trees also occur frequently and can serve as seed supply. In the central dunes-south, the coastal protection forest has a high impact on tree establishment. Here, the oldest and tallest trees can be found, and browsing pressure is the lowest and does not reduce tree growth at all. Apart from roe deer, a few mouflon (*Ovis ammon musimon* Pallas) and hares (*Lepus europaeus* Pallas), hardly any wild grazers or browsers exist on Hiddensee. Wild boars (*Sus scrofa* L.) dig primarily in wetter parts, very rarely in the dry

dunes (Simon and Goebel, 1999). Rabbits have been an important grazer and disturbance factor on Hiddensee until the early 1980s when a myxomatosis epidemic eradicated nearly the whole population. But, the previously abundant rabbit populations were located mainly in the northern part, on the sandy grasslands of the moraine hills rather than in the central and southern dunes.

Equally important for tree establishment as seed availability and grazing pressure can be salt stress. On the southern dunes, the concentration of the salt spray across the whole dune area is more-or-less the same, unlike the central dunes-north where most salt spray is deposited on the first dune ridge. This is probably due to the small size of the first dune ridge in the southern dunes compared to the central dunes. The amount of salt spray reaching an area depends not only on wind force and direction but also on the topography of the beach, sea bottom and inland structures (Malloch, 1997). Salinity of the deposited salt-spray is generally rather low: only 3-4% or at maximum 10-12% of the open sea water salinity was measured in the salt traps. In contrast, Sykes and Wilson (1999) measured salt-spray salinity with comparable salt traps and found 65% of the open sea water salinity in their traps on coastal dunes in New Zealand. In the New Zealand dunes, salt spray was identified as a critical environmental factor for the vegetation zonation with salinity of open sea water being approximately 3-4 times higher at New Zealand's shoreline than at the western coast of Hiddensee. Although the total amount of salt deposition is much less at Hiddensee, the higher amount of salt spray reaching the hinterland of the southern dunes might, nevertheless, be an additional stress factor, which hampers sapling establishment and growth.

Significant differences in salt spray in the inner dunes exist between the areas only for the growing season and not for the winter and autumn period. Peak concentrations are more important than average concentrations as stress factors for plant growth (Malloch, 1997). Exposed structures such as young shrubs and trees get an unproportionly high impact from salt spray which can reduce their growth (Parsons, 1981), thus salt concentrations can be critical even at the low concentrations measured in the captured water. Summing up, forest establishment in the southern dunes is likely more suppressed by a combination of higher browsing pressure, higher salt spray stress and fewer seeds than in the central dunes, and will probably take longer than the 30-50 years, which have been assumed for the Darß, an adjacent dune area within the National Park Vorpommersche Boddenlandschaft (Fukarek, 1961).

Conclusions

At Hiddensee, coastal dunes are acid and oligotrophic. The amount of shifting sand, salt spray and groundwater supply seem to be critical factors for the coastal dune vegetation development during the past 70 years. Coastal protection measures and agricultural land use have major site-specific influences and override the impact of low to medium (6-8 kg N ha^{-1} yr^{-1}) levels of atmospheric nitrogen deposition. High browsing intensity by wild herbivores combined with low seed availability and impact from salt spray likely retard progressive succession to a forest in the southern dunes compared to the central dunes.

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1 http://ec.europa.eu/environment/nature/legislation/habitatsdirective
2 www.worldclimate.com, station Greifswald

Keibu, EE. One of nicest dune mosaics of the Baltic.

Even low to medium nitrogen deposition impacts vegetation of dry, coastal dunes around the Baltic Sea

Eva Remke, Emiel Brouwer, Annemieke Kooijman, Irmgard Blindow, Hans Esselink and Jan G.M. Roelofs

Abstract

Coastal dunes around the Baltic Sea have received small amounts of atmospheric nitrogen and are rather pristine ecosystems in this respect. In 19 investigated dune sites the atmospheric wet nitrogen deposition is 3-8 kg N ha^{-1} yr^{-1}. The nitrogen content of *Cladonia portentosa* appeared to be a suitable biomonitor of these low to medium deposition levels. Comparison with EMEP-deposition data showed that *Cladonia* reflects the deposition history of the last 3-6 years. With increasing nitrogen load, we observed a shift from lichen-rich short grass vegetation towards species-poor vegetation dominated by the tall graminoid *Carex arenaria*. Plant species richness per field site, however, does not decrease directly with these low to medium N-deposition loads, but with change in vegetation composition. Critical loads for acidic, dry coastal dunes might be lower than previously thought, in the range of 4-6 kg N ha^{-1} yr^{-1} wet deposition.

Introduction

Atmospheric nitrogen deposition has increased steadily in central Europe during the 20th century with a steeper increase from the 1960s onwards (Asman et al., 1988). The peak for northwest Europe was in the 1970-1980s and declined 10-40% during the decades thereafter (Boxman et al., 1997; Erisman et al., 2001; Larsen et al., 2001; NEGTAP, 2001). Today, amounts of atmospheric pollution are still high enough to exceed critical loads for various ecosystems (Busch et al., 2001; Craenen et al., 2000; Herman et al., 2001; Nagel and Gregor, 2001). Effects of atmospheric deposition are complex. The major consequences of nitrogen deposition in ecosystems are acidification and eutrophication, which both lead to changes in vegetation cover and appearance (Bobbink et al., 1992; Heij and Schneider, 1991). Nutrient-poor and weakly buffered ecosystems are especially vulnerable. In dry ecosystems in northwest and central Europe effects of atmospheric depositions have been described, for example for forests (Houdijk and Roelofs, 1991; van Dijk et al., 1989, 1990), heathlands (Bobbink et al., 1992; Power et al., 1998; Roelofs, 1986; van den Berg et al., 2005) and partly for coastal dunes (Jones et al., 2004; Kooijman et al., 1998).

In coastal dunes along the North Sea, shrubs, tall grasses and mosses have become dominant during the last decades (Ketner-Oostra and Sykora, 2004; Vertegaal et al., 1991). Since the 1970s some tall grass species such as *Ammophila arenaria* (L.) Link, *Calamagrostis epigejos* (L.) Roth, *Elymus athericus* (Link) Kerguelen and *Carex arenaria* L. have become dominant in dry dune grasslands of the Netherlands (ten Harkel and van der Meulen, 1996). In lime- and iron-poor sands, *A. arenaria* and *C. arenaria* are mostly dominant (Kooijman et al.,1998; van der Meulen et al., 1996), and in calcareous dunes *E. athericus* and *C. epigejos* have become dominant, the latter especially in decalcified areas (Kooijman et al., 1998). These changes have mainly been attributed to eutrophication and acidification caused by atmospheric depositions (van der Meulen et al., 1996; van Turnhout et al., 2003). Simultaneously, however, grazing intensity of rabbits and livestock decreased, and confounding effects cannot be totally excluded (e.g. Belsky, 1992; Hill et al., 1992; Ranwell, 1960; Thomas, 1963; Westhoff, 1985).

Comparable vegetation changes within coastal dune systems of the Baltic Sea region have not yet been described. The vegetation composition and the degree of mosaic pattern for coastal dunes is rather unknown. Preliminary results from a coastal dune on the island of

Hiddensee, north-eastern Germany, show a change from species-rich, short dry dune grasslands into grasslands dominated by the tall grass *C. arenaria* within the last 30 years (own unpublished data). In other ecosystems, such as deciduous forests, changes in vascular plant composition and N-availability due to elevated nitrogen deposition have been reported (Falkengren-Grerup and Diekmann, 2003; Falkengren-Grerup and Schöttelndreier, 2004).

Nitrogen deposition loads in coastal dunes in north-west Europe were around 13-15 (20) kg N ha^{-1} yr^{-1} (wet deposition) in the late 1980s/early 1990s (Houdijk and Roelofs, 1991; Sival and Strijkstra-Kalk, 1999) and are estimated to be 10-15 kg N ha^{-1} yr^{-1} today. For coastal Baltic sites, the current range of N wet deposition is 3-8 kg N ha^{-1} yr^{-1} (Fjäran, 2006; Hjellbrekke, 2001, 2002, 2003, 2004, 2005). And 3 kg N ha^{-1} yr^{-1} is the assumed background deposition for the Baltic region (Søchting, 1995), which suggests that pristine, unaffected systems still occur in this region. To understand ecosystem functioning prior to intensive human impact, which is a valuable base for any restoration measure, research in such pristine or nearly pristine sites is essential (Vitousek et al., 1997).

Knowledge about deposition loads originates mainly from climate stations which are part of the EMEP programme, the Cooperative Programme for Monitoring and Evaluation of the Longrange Transmission of Air Pollutants in Europe. The network of climate stations with atmospheric pollution measurements, however, is very coarse, and for most sites, only modelled data are available (Tarrason et al., 2005). For most grid cells (50x50 km^2) modelled data on nitrogen deposition have an uncertainty as high as 30-80% (Barrett,1998; Erisman et al.,1995; Lövblad and Erisman, 1992) and even if there are measurements from nearby climate stations, the amount deposited and measured at climate stations can differ substantially from depositions at local field sites.

Most NO$_x$ originates from stationary and non-stationary burning of fossil fuel, whereas most NH$_x$ is attributed to animal husbandry (Aerts and Bobbink, 1999). Concerning the ratio of wet and dry deposition, most of the dry part is ammonia in open, non-vegetated space in the Netherlands (van Breemen et al., 1982; van Breemen and van Dijk, 1988). Wet N-deposition accounts for ca. 50-80% of the total deposition (Boring et al., 1988; Erisman et al., 2005; Heidam, 1993). Wet deposition can easily and cheaply be measured using open precipitation collectors. In contrast the various dry depositions are hard to quantify as their input into an ecosystem depends on wind exposure, precipitation and vegetation structure (e.g. Boring et al., 1988; NEGTAP, 2001). Many methods quantifying atmospheric deposition are rather expensive and most current methods are unsuitable for remote areas (Pitcairn et al., 2003). An alternative method is the use of a biomonitor, which takes up wet and dry deposition. An ideal biomonitor accumulates the pollutant without being killed by high doses, has a wide geographical distribution, is representative for the collection area, is available all year round and is easy to collect (Carballeira et al., 2000; Conti and Cecchetti, 2001). Advantages of lichens as biomonitors are that they grow slowly. As they lack cuticle and stomata, they absorb different contaminants over the entire surface (Hale, 1969, 1983). *Cladonia portentosa* (Dufour) Coem. could be a suitable biomonitor as it grows acropetally with the old basal parts of the thalli progressively dying off. The intact necromass can also partially isolate the living thalli from the chemical influence of the soil beneath (Crittenden, 1991). Additionally, the lichen mats are efficient accumulators of inorganic N and P in precipitation (Crittenden, 1983, 1989; Hyvärinen and Crittenden, 1998).

In coastal dunes, important abiotic factors are salt spray input and sand mobility (Kumler, 1997). Salt spray is primarily deposited at the most seaward dune ridge and the impact on more inward dunes is small. In contrast, strong winds can mobilize bare sand and spread it over a large dune area. Consequently, sand mobility determines the direction and speed of dune succession, and hence vegetation cover. Depending on the amount of blown sand, less active areas are dominated by biological or highly active areas by geomorphological processes (Jungerius and van der Meulen, 1988). The more intensively the sand is shifting and the more frequently these processes change, the higher the disturbance within the ecosystem. Thus sand mobility is an important cofactor in succession for the total dune area and should not be neglected in research of the vegetation-soil interface.

The aims of the present study are (i) to quantify the local atmospheric nitrogen deposition at Baltic coastal dunes over a large spatial gradient via the biomonitor *Cladonia portentosa*, (ii) to investigate whether the distribution of vegetation dominated by tall graminoids in open, non-calcareous coastal dune systems is correlated with this deposition, (iii) to assess changes in vegetation composition and species number with increasing N-deposition, and (iv) to give recommendations for the critical load of dry, lichen-rich short grasslands of Baltic Dunes.

Figure 1 Map of field sites and EMEP stations (see also table 3).

Field sites

All field sites are coastal dunes spread over a large geographical gradient from the Kattegat in the west, the Southern Baltic to the Baltic proper in the east (figure 1). The research area stretches from the Atlantic over the Central European to the Baltic terrestrial ecoregion (Olson et al., 2004). The annual mean temperature decreases from 8°C in Denmark to 5°C in Estonia (table 1) as the climate gets more continental. Another gradient exists for seawater and therefore sea-spray salinity. The salt gradient decreases steeply in the Kattegat from 24 PSU to ca. 10 PSU and ranges mainly from 7 to 8 PSU in the Southern Baltic and Baltic proper (table 1).

All 19 sites have a pH_{NaCl}<6.5 of the parent sand material and a precipitation of 500-700 mm yr^{-1}. The sites are open dunes with <10% cover of trees and without any physical barrier like a forest towards the sea. The sites have not been intensively managed e.g. by intensive grazing or burning during the last decade.

To find comparable dune sites the available literature was reviewed and site managers, researchers and nature conservationists of each country were contacted. Out of the initial list of ca. 40 sites, 19 sites were chosen during a field visit in early 2005. The criteria for choosing a site were its closeness of fit to parameters such as openness, intensity and type of management, tourism and agricultural activity.

Table 1 Short description of all field sites with synonym used, country, geographical UTM coordinates (from Google Earth), longterm annual mean values for temperature and precipitation, and sea water salinity. Sources for climate data: (1) www.worldclimate.com, station Liepaja; (2) www.worldclimate.com, station Greifswald; (3) temperature: Eggertsson Karlström (2004); precipitation: Raab and Vedin (1995); (4) Ratas and Nilson (1997); (5) Walter and Lieth (1967) in Biermann (1999); (6) temperature: www.dmi.dk, regions København and Nordsjælland; precipitation: Jensen (1986); (7) Anonymus (2004) (8) www.wetter.com, station Kleipeda; (9) www.worldclimate.com, station Duoedde; (10) temperature; www.worldclimate.com, station Łeba; precipitation: Walna et al. (2003). Salinity values are obtained from the mean grid cell values for the period 1900-2005 (Feistel et al., 2008). NP = national park.

name/ synonym	country	longitude UTM	latitude UTM	temp. [°C]	precip. [mm yr-1]	salinity [PSU]
Akmensrags (1)	Latvia	56411065	20989034	6.8	627	7.2
Dünenheide/ Hiddensee (2)	Germany	54550269	13099371	8.0	564	9.0
Gellen/ Hiddensee (2)	Germany	54479486	13064725	8.0	564	9.0
Harilaid (4)	Estonia	58489564	21843912	5.6	703	6.9
Holtemmen/ Laeso (5)	Denmark	57302031	10994222	7.9	576	24.0
Keibu (4)	Estonia	59241349	23739389	5.1	686	7.0
Korshage (6)	Denmark	55974190	11777358	7.3	500	18.4
Nagliu/ Curonian Spit NP (7)	Lithuania	59659837	21083870	7.8	750	7.3
Nida/ Curonian Spit NP(7)	Lithuania	55284024	20958343	7.8	750	7.3
Pajuris (8)	Lithuania	55843364	21062018	7.0	735	7.3
Pape (1)	Latvia	56150317	21027620	6.8	627	7.2
Pärispea (4)	Estonia	59659837	25683665	5.1	686	6.4
Pavilosta (1)	Latvia	56893958	21191670	6.8	627	7.0
Raghammer/ Bornholm (9)	Denmark	55015227	14926422	7.7	572	7.9
Łeba/ Slovinski NP (10)	Poland	54682510	17101320	7.7	575	7.5
Sandhammeren (3)	Sweden	55378837	14180429	7.4	600	7.7
Syrodde/ Laeso (5)	Denmark	57323485	11195125	7.9	576	24.0
Tönnersa (3)	Sweden	56555071	12947505	7.3	700	18.1
Torsö (3)	Sweden	55999030	14657380	7.4	550	7.7

Material and methods

During a field visit in March-April 2005 the vegetation structure was mapped in an ideally 200×200 m open dune area starting at the first dune ridge from the sea. The whole area was divided into grid cells of 10×10 m plots and in each grid cell the borders of the different vegetation structures were delineated on paper in the field. The vegetation structure was divided into six classes: bare sand, short grass, tall grass, dwarf shrub, shrub and tree. The two focal vegetation structure types were defined as follows: 'short grass' is mainly covered by lichens and mosses. Nevertheless typical graminoids for this type are *Corynephorus canescens* (L.) P. Beauv., *Festuca* ssp. (e.g. *Festuca ovina* L., *Festuca rubra* L., F*estuca polesica* Zapał.), with *C. arenaria* occurring only occasionally. 'Tall grass' is dominated by *C. arenaria*, *A. arenaria* or *C. epigejos*, and the sward reaches higher than 30 cm. The vegetation structure maps, compiled on paper in the field, were subsequently scanned. The borders between different vegetation structures were digitized manually with the software ArcView 3.2a, and the percentage coverage for the different vegetation units was calculated for each site.

For all sites, a complete list of vascular plants, bryophytes and lichens (with the exception of liverworts and crustaceous lichens) was compiled in March and July 2005. If necessary, the species were dried and identified by microscope and colouring techniques. For species determination the following literature was used: for vascular plants, Rothmaler et al. (2002), Oberdorfer (1994) and Hegi and Conert (1998), additionally for *Salix* spp., Lautenschlager-Fleury and Lautenschlager (1994), for mosses, Frahm and Frey (1992) and for lichens, Wirth (1995). For all sites, species were separated according to life form.

Field sites range in size from 2.5 to 4 ha (table 5). A 2-ha size limit was chosen as a standard for the area surveyed because previous research showed that 1-2 ha included all relevant open habitats within this ecosystem mosaic (own unpublished data), and species richness therefore can be assumed to have reached total species alpha-diversity.

At six or more points per site, soil horizons were mapped down to groundwater level or at most to 2 m depth, using a Pürckhauer soil core sampler (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands). In order to establish a rough measure for disturbance frequency, the number of relict A-horizons per metre was counted and taken as a proxy for disturbance frequency in further statistical data analysis.

Within each field plot, ten 10 × 10 cm samples of *C. portentosa* were cut with a pair of scissors out of the centre of a lichen patch of ca. 0.4-0.5 m diameter (Søchting, 1995). Only the top 2 cm of the *Cladonia* was collected in order to exclude nutrients taken up from the soil. The samples were cleaned roughly from non-parent material and stored in a paper bag. In the laboratory, all samples were cleaned thoroughly from other material, washed briefly in distilled water and dried at 70ºC for 24 h.

After storage of the *C. portentosa* biomass for 3-4 months the samples were ground in a centrifugal ball mill (rotational speed 18,000 for 1-2 min, FRITSCH pulverisette 14, Idar-Oberstein, Germany). Total nitrogen was determined with a C/N-analyser (CHNOS element analyser vario EL III, elementar Analysensysteme, Hanau, Germany). Lichen-N [%] was compared with measured deposition data from the EMEP programme. Data for measured wet nitrogen deposition of nearby climate stations were extracted from EMEP reports for 1999-2005 (Fjæran, 2006; Hjellbrekke, 2001, 2002, 2003, 2004, 2005, personal communication).

Data were aggregated in spreadsheets and analysed with software packages from the R Project for Statistical Computing (R Development Core Team, 2008). Regression analyses (lm-linear model) were performed followed by model justification procedures. If fitted models were not justified, generalized linear models (glm) with different error structures and distributions were fitted, or data were transformed before regression analysis. Multiple regressions were carried out starting with all environmental factors and subsequently simplified until the least adequate model was reached (stepwise backward deletion). To avoid overdispersion not more than the replicate number divided by three were fitted (Crawley, 2005, 2007).

Results

Relationship between measured wet N-deposition and *Cladonia* N-content

For roughly half of the field sites EMEP data for atmospheric wet N-deposition could be obtained from nearby climate stations. These data were correlated with lichen-N [%] concentration at nearby coastal field sites (see table 3 for details on climate stations).

Between EMEP measurements of wet N-deposition and the lichen N-concentrations a regression was calculated (figure 2, table 2). The best fit was found when data from the last 3 to 6 years of deposition were averaged, with a maximum R^2 at the 5-year average (figure 2, table 2). About 50% of the nitrogen in the *Cladonia* tissue is explained by the N in wet deposition. Using the best fitted regression equation (period 2001-2005), total wet deposition of N for each area was calculated giving estimates for those areas not covered by the EMEP programme. The highest N-deposition load for the Baltic was calculated for Tönnersa (SE) and Pape (LV) with ca. 7.5-7.8 kg N ha^{-1} yr^{-1}, and the lowest for Nagliu (LT) and Keibu (EE) with ca. 2.3-2.5 kg N ha^{-1} yr^{-1} wet deposition (table 3).
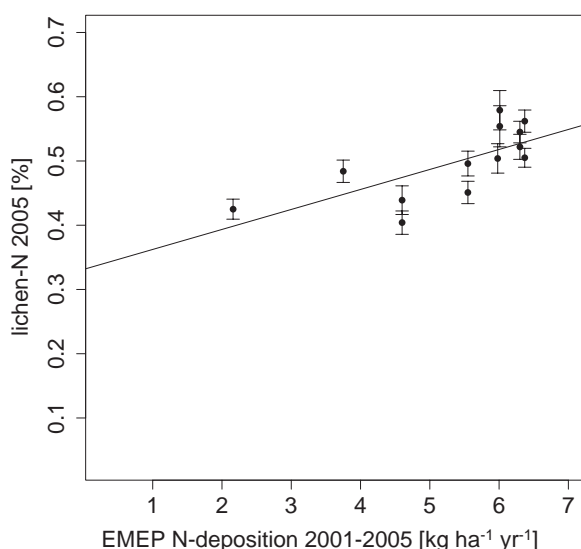

Figure 2 Scatter plot of mean (± 1SE) N in *Cladonia portentosa* lichen tissue [%] for 2005 against the N [kg N ha^{-1} yr^{-1}] in precipitation from nearby EMEP stations averaged for the period from 2001 to 2005 (see table 3). The single regression line and standard error of lichen-N are shown.

Table 2 Regression results between the N-content [%] in *Cladonia portentosa* sampled in 2005 and the total wet N-deposition [kg ha^{-1} yr^{-1}] measured at nearby EMEP stations (table 3).

year of EMEP data	R^2	regression equation	p-value	df
2005	0.3210	y= 0.0780x + 0.1112	0.088	8
2004–2005	0.4465	y= 0.0296x + 0.3436	0.018	10
2003–2005	0.5078	y= 0.0310x + 0.3357	0.009	10
2002–2005	0.4945	y= 0.0286x + 0.3436	0.011	10
2001–2005	0.5223	y= 0.0288x + 0.3385	0.008	10
2000–2005	0.4801	y= 0.0272x + 0.3466	0.012	10
1999–2005	0.4280	y= 0.0257x + 0.3520	0.021	10

The lichen-N [%] content correlates negatively with (increasing) latitude, but not with longitude or any interaction between latitude and longitude (multiple regression result y=-5.578e-08x+5.808, p=0.040, R^2=0.2807, df=17). Therefore, N-deposition – here shown by the N-tissue content in *C. portentosa* – declines significantly towards the east.

Vegetation composition

For nearly all sites (15 in total) tall grass units could be mapped. Exceptions are two sites in Estonia (Keibu and Laheema), one in Poland (Łeba) and one in Denmark (Syrodde) (table 3). The tall grass units were dominated by one of the following graminoids: *A. arenaria*, *C. arenaria*, *C. epigejos*, *Calamophila baltica* (Flügge ex Schrad.) Brand (the hybrid between *C. epigejos* and *A. arenaria*) or *Leymus arenarius* (L.) Hochst. *Ammophila* occurred at nearly every site (95% occurrence). The cover of *Carex*, which also occurred at 95% of all field sites, ranged from 5 to 25%. *Calamagrostis* occurred only in 25% of the field sites and with a cover of only 2-3%. *Calamophila* and *Leymus* were never abundant (5-15% of all sites).

Furthermore, the relation of short grass and tall grass (cover) was related to climate, atmospheric deposition and sand mobility. Single and multiple regressions were calculated between the vegetation units of short grass and tall grass dominated by *C. arenaria* against various abiotic factors. Only the *C. arenaria* dominated tall grass unit was used in the regression as *Carex* units were highly abundant amongst field sites, providing a sufficient sample number. *Ammophila* occurs at a similar abundance, but mainly at its perceived natural position, the first white dune ridge. *Ammophila* thus does not dominate the dunes in contrast to *Carex*.

The coverage of the *Carex* unit over field sites is best explained by the nitrogen lichen tissue content, the buried profiles and precipitation (multiple regression results, table 4), although for the last two factors only a tendency exists (p=0.052 and p=0.053, respectively). All factors are positively correlated and explain about 48% of the total variation (table 4). When a single regression is calculated, *Carex* cover increases significantly only with increasing lichen N-concentration (table 4) and only 23% of the data variation is explained. Sites with *Carex* coverage as high as 40-60% are Pape (LV), Pajuris (LT) and Gellen (DE) (table 3).

Short grass covers mostly 20-50% of the field sites (table 3). Its cover decreases with increasing temperature and salinity. 67% of the data variation is explained by these two factors (multiple regression, table 4). Temperature and salinity overrule the negative effect

Table 3 N-deposition data from EMEP climate stations, *Cladonia portentosa* N-content (mean ± 1SE), the calculated total wet N-deposition based on the regression equation with EMEP data 2001–2005, the percentage of surplus N-deposition in total N-deposition where data from Norway are regarded as background (= 'more N'), cover of the vegetation 'short' = short grass and 'tall' = tall grass (*Carex arenaria*) and number of buried profiles.

field site	climate station	EMEP N [kg ha-1 yr-1]	lichen-N [%] mean	± SE	calc. total N [kg ha-1 yr-1]	more N [%]	short [%]	tall [%]	bur. profile [no.m-1]
Norway		–	0.330	–	–	0	–	–	–
Nagliu	Preila	4.6	0.404	0.018	2.41	22.4	44.4	15.3	5.6
Keibu	–	–	0.409	0.020	2.57	23.9	70.8	0.0	1.7
Pärispea	Lahemaa	2.16	0.425	0.016	3.12	28.7	85.0	0.0	1.7
Akmensrags	–	–	0.428	0.025	3.23	29.8	67.2	6.1	6.7
Nidda	Preila	4.6	0.439	0.022	3.60	33.1	17.3	24.6	6.7
Pavilosta	–	–	0.448	0.016	3.91	35.8	69.4	13.1	8.9
Syrodde	Anholt	5.55	0.451	0.017	4.02	36.8	24.5	0.0	5.6
Sandhammaren	–	–	0.463	0.015	4.39	40.2	18.4	5.5	3.3
Harilaid	Vilsandi	3.75	0.484	0.017	5.10	46.5	62.2	4.2	2.2
Holtemmen	Anholt	5.55	0.496	0.019	5.53	50.4	6.2	0.1	7.8
Korshage	–	–	0.497	0.026	5.54	50.5	13.9	19.5	8.3
Łeba	Łeba	5.98	0.504	0.023	5.81	52.9	48.5	0.0	3.3
Pajuris	Rucava	6.37	0.505	0.015	5.82	53.0	35.2	52.1	5.6
Raghammer	–	–	0.513	0.013	6.10	55.5	36.7	23.3	3.3
Dünenheide	Zingst	6.3	0.522	0.019	6.39	58.1	29.8	5.4	5.6
Torsö	–	–	0.537	0.020	6.89	62.6	49.9	24.9	8.9
Gellen	Zingst	6.3	0.545	0.017	7.19	65.3	24.8	63.8	6.7
Tönnersa	Råö	6.01	0.554	0.032	7.48	67.9	15.6	13.7	1.1
Pape	Rucava	6.37	0.562	0.017	7.76	70.3	26.2	38.4	8.9

of lichen-N, which is apparent in single regression (figure 3, table 4). In single regression, lichen-N explains only 25% whereas salinity explains ca. 40% and temperature ca. 55% of the data variation (table 4). Sites with low coverage of short grass (ca. 15-25%) and high nitrogen deposition load are Tönnersa (SE), Pape (LV) and Gellen (DE) (table 3).

Table 4 Regression results of vegetation and environmental parameters: regression results of vegetation structure types 'short grass' and 'tall grass' *Carex arenaria* and abiotic factors for all field sites. Only significant relationships are shown (***p< 0.001, **p< 0.01, *p< 0.05, °p< 0.1, ns=not significant). For single regression, algebraic sign of the slope of the regression equation, R^2 and significance levels are shown. For multiple regression, the algebraic sign of the slope, overall R^2 and the single/multiple significance levels are given. Interactions between environmental factors are significant only for latitude and therefore other factors are not shown.

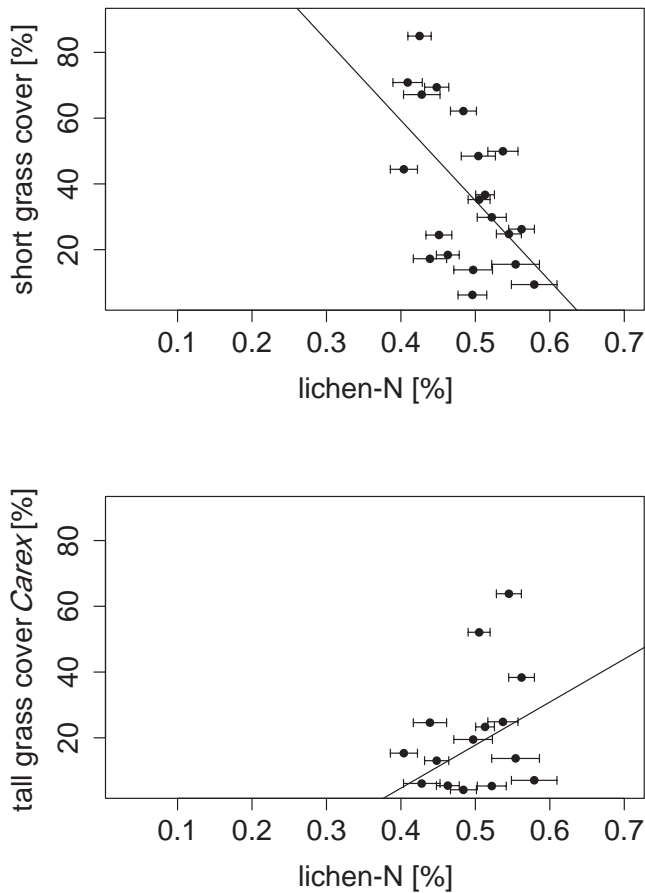| veg. unit	regression	temperature [°C]	precipitation [mm a-1]	salinity [PSU]	lichen-N [%]	bur. profiles [no. m-1]
short grass	single	(-)0.5505***	ns	(-)0.4136**	(-)0.2507*	ns
short grass	multiple	(-)0.6684**/***	ns	(-)0.6684*/***	ns	ns
tall grass	single	ns	ns	ns	(+)0.2252*	ns
tall grass	multiple	ns	(+)0.4770°/*	ns	(+)0.4770*/*	(+)0.4770°/*
latittude	single	(-)0.5545***	(+)0.4999***	(-)0.6481***	(-)0.2807*	ns

Figure 3 Scatter plot of mean plus standard error of N in lichen tissue [%] against the cover of short grass [%] and tall grass *Carex arenaria* [%] at all field sites. The single regression line is shown, regression results can be found in table 4.

Variation in species number

Species richness for the various life forms (lichens, mosses, forbs, graminoids and cryptogams, vascular plants; table 5) did not correlate significantly with lichen-N. The species richness for forbs (p=0.037) and total vascular plants (p=0.007) increased with increasing precipitation and buried profiles. The same is true for grasses, but additionally increasing temperature had a positive effect on the number of grass species (p=0.001).

Moreover, species richness depends on vegetation cover of the field site. Species richness of graminoids decreased with increasing cover of short grass at field sites (p=0.011). Species richness of all other life forms showed no correlation with short grass cover. With increasing tall grass cover the number of grass species tends to rise (p=0.082) and the number of lichens decreases (p=0.011). No other life form showed a significant relationship.

Table 5 Area, species richness of forbs, graminoids, mosses, lichens, vascular plants, cryptogams and total species richness [no.] per field site. The field sites are ordered as in table 3 by increasing lichen-N values.

field site	area [ha]	forbs	graminoids	mosses	lichens	vascular plants	cryptogams	total
Nagliu	3,0	47	19	10	15	84	25	109
Keibu	3,0	16	8	9	19	35	28	63
Pärispea	3,0	10	5	5	15	21	20	41
Akmensrags	2,5	43	14	13	17	68	30	98
Nidda	3,0	28	17	9	8	68	17	85
Pavilosta	4,0	33	11	8	22	52	30	82
Syrodde	4,0	27	14	9	21	50	30	80
Sandhammaren	3,0	15	15	8	17	38	25	63
Harilaid	4,0	43	12	8	19	62	27	89
Holtemmen	4,0	28	14	8	23	54	31	85
Korshage	2,5	34	14	4	7	62	11	73
Łeba	3,0	19	10	9	18	40	27	67
Pajuris	4,0	48	20	8	17	86	25	111
Raghammer	4,0	37	10	7	15	59	22	81
Dünenheide	4,0	21	15	9	12	49	21	70
Torsö	1,0	17	12	8	9	38	17	55
Gellen	4,0	12	14	5	10	35	15	50
Tönnersa	2,5	23	13	8	18	52	26	78
Pape	4,0	50	15	10	15	80	25	105

Discussion

What is the local atmospheric nitrogen deposition at coastal dune sites around the Baltic Sea?

The N-contents of lichens sampled in coastal dunes beside the Kattegat, Southern Baltic and Baltic proper are positively correlated with measured wet deposition at EMEP stations nearby. The best fit is found when the wet N-deposition is averaged for the last 3-6 years. The upper 2 cm of *Cladonia* seems to be a good accumulator for N-deposition and may reflect the deposition and especially the deposition history of a site better than just yearly measurements. Additionally, several years of deposition history fit closer to slow ecosystem changes, which take at least 1-2 years. Hyvärinen and Crittenden (1998) also showed that about 50-60% of data variation in N-content of *C. portentosa* thalli (apex and base) collected from heathlands and moorlands is explained by wet deposition of ammonium and nitrate. The residual N-variation within the *Cladonia* tissue can be explained by various forms of dry and nebulous deposition. Particles can easily attach to the rough surface of the lichens (Hale, 1969, 1983) and be transported deeper into the tissue with subsequent rain. The biomonitor may thus reflect total N-deposition better than wet deposition data from weather stations.

Earlier studies show considerable differences in modelled and measured N-deposition data. Correlations between measured nitrate deposition and lichen-N in *Hypogymnia physodes* (L.) Nyl. were markedly stronger within a subset of 13 sites than within 179 sites for which deposition was modelled (Brutteig, 1993). One reason might be the high uncertainty (30-80%) for most grid cell values in modelled deposition data, especially when the measuring station density is not very high, as is the case in the Baltic Sea region (Barrett, 1998; Erisman et al., 1995; Lövblad and Erisman, 1992). Therefore modelled data have not been used in this study.

In *C. portentosa* thalli 0.20-0.30 N [%] seems to be a natural background level, while a content of 1.30 N [%] is suggested as lethal to reindeer lichens (Søchting, 1995). Around the Baltic Sea, lichen values ranged between 0.40 and 0.56 N [%]. The approximate amount of wet N-deposition calculated for each site gives low to medium values (2.3-2.5 kg N ha^{-1} yr^{-1} to 7.5-7.8 kg N ha^{-1} yr^{-1}) in a European context. In north-west Europe, which is one of the hot spots of anthropogenic N-deposition (Vitousek et al., 1997), 13-20 kg N ha^{-1} yr^{-1} wet deposition was measured in open dune areas at two Dutch West-Frisian islands, Terschelling and Schiermonnikoog, in the late 1980s/early 1990s (Houdijk and Roelofs, 1991; Sival and Strijkstra-Kalk, 1999), i.e. about 2-6 times more than in the Baltic dunes. Even if one accounts for missing dry and wet deposition forms – bulk precipitation underestimates atmospheric deposition by 20-50% (Boring et al., 1988; Erisman et al., 2005; Heidam,1993) – the N-deposition within the Baltic Sea region is still low. Within the Baltic Sea area, the N-lichen concentrations are lower in the eastern coastal sites and higher in the western sites (Denmark and Sweden). This trend is generally supported by EMEP maps from recent years (e.g. Tarrason et al., 2005). The cause of this pattern is probably the lower intensity of agriculture and industry in the Baltic States compared to Denmark and Sweden.

Do tall graminoids like *A. arenaria*, *C. arenaria* and *C. epigejos* dominate the dunes?

C. epigejos only occurs at a quarter of all field sites and at a low coverage. *A. arenaria* and *C. arenaria*, however, are widespread and abundant grasses within the acidic, coastal sites in the Baltic. *Ammophila* grows mainly at the first white dune towards the beach. It occurs in its perceived natural position. In contrast, *Carex* covers larger areas in the central and hinterdunes. This pattern differs from comparable sites along the North Sea. In lime- and iron-poor sands, *A. arenaria* and *C. arenaria* both dominate the hinterdunes (Kooijman et al.,1998; van der Meulen et al., 1996). Tall grasses like *Ammophila* can intercept more than 50% (average of 19-84%) of the bulk ammonium deposition, which will not directly reach the undergrowth anymore (Heil et al., 1988). *Ammophila* may therefore have a competitive advantage under conditions of increased nutrient input from the air, as it grows taller than *C. arenaria* and can probably scavenge more nitrogen. One reason that *Ammophila* does not encroach onto the Baltic dunes may be because it is at its eastern biogeographical distribution limit in the Baltic States (Meusel et al., 1965). It has been planted in the 20th century in Estonia (personal communication U. Ratas) and is probably only naturalized in those dunes. Also *C. arenaria* has its eastern distribution limit in the Baltic States, but it can grow further east, nearly up to the Russian border (Meusel et al., 1965; Tietema, 1981).

Can vegetation change and species loss be linked to a higher nitrogen load?

With increasing nitrogen deposition (estimated from lichen-N), increasing precipitation and frequent (historical) sand mobility, the cover of *C. arenaria* increases. *C. arenaria* cover showed a significant positive response to atmospheric N-deposition in fixed dunes, dune grasslands and dune slacks in Great Britain (Jones et al., 2004). Average temperature and salinity are negatively correlated with short grass cover. These two factors overshadow the negative impact of nitrogen deposition, which is apparent in single regression analysis.

The lichen-rich, short grassland might decrease more due to competitive disadvantage than damage to ecosystem processes at these low nitrogen deposition loads. *C. arenaria* has an advantage over *Corynephorus* and *Festuca* spp. as it can better exploit temporally and spatially patchy distributed nutrients (N, P, K) and water (D'Hertenfeld and Falkengren-Grerup, 2002; D'Hertenfeld and Jónsdóttir, 1999; Jónsdóttir and Watson, 1997; Noble and Marshall, 1983; Tietema, 1981). Nevertheless, *Carex* might be nitrogen limited under natural conditions and prospers with an additional N-load as other nutrients are not limiting. Noble and Marshall (1983) found the pattern of plant growth of *Carex* closely related with the gradient of N-concentration within the clone. Its relative competitive strength increases and thus vegetation composition changes. Other investigations from different ecosystems show that vegetation changes after increased nitrogen deposition are caused by changes in competitive relationships (Aerts et al., 1990; Berendse and Aerts, 1984; Heil and Bruggink, 1987; Kellner and Redbo-Torstensson, 1995).

At N-unaffected sites, i.e. sites with only a quarter more N-deposition than background, lichen-rich short grasslands cover 45-80% whereas taller graminoids are restricted to 5-15%. N-affected sites, however, are characterized by only 15-25% short grasslands, but 40-60% cover of taller graminoids. A coverage of more than 50% of lichen-rich grasslands seems to be common for pristine sites. Taller graminoids occur, but do not dominate.

Species richness was positively influenced by climate (temperature and precipitation) and disturbance intensity (buried profiles), but unaffected by nitrogen load (lichen N-content). The impact of low to medium nitrogen loads seems not to be high enough to override the site-specific and climatic-induced variation in species richness.But the species richness is dependent on vegetation cover. With higher short grass cover fewer graminoids occur, and with higher tall grass cover more graminoids and fewer lichens occur. At higher nutrient availability, and warmer and wetter climate, tall graminoids have a higher competitive strength and might outcompete lichens. Within grass dominated plots, therophytes and lichens decrease strongly and the results are species-poor stands (Veer and Kooijman, 1997). At higher nitrogen deposition loads in north-west Europe – today and historically – species loss is directly attributed to airborne pollutants and its effects on ecosystem processes like acidification, eutrophication or susceptibility to secondary stress factors (Bobbink et al., 1998; Ketner-Oostra and Sykora, 2004). The lowest current wet nitrogen depositions along the North Sea, estimated at 10-15 kg N ha^{-1} yr^{-1}, are still >20% higher than the quantities deposited on the Baltic dunes. Other studies reported a decrease in plant diversity at ambient or artificial total N-deposition of 10 kg N ha^{-1} yr^{-1} (Clark and Tilman, 2008; Falkengren-Grerup and Diekmann, 2003; Stevens et al., 2006). Direct effects of N-deposition on species richness in acid systems probably occur only from deposition loads of 10 kg N ha^{-1} yr^{-1} upwards.

What is the critical load for Baltic coastal dunes?

In this study an impact of atmospheric nitrogen deposition on vegetation composition and subsequent loss of cryptogams, as suitable habitat decreases, in acid coastal dunes of the Baltic Sea has been shown. The vegetation change from short lichen-rich grasslands to grassland dominated by taller graminoids and species loss is gradual, making it hard to set a threshold for a critical load for these ecosystems. Values apparent in this research area are all below or just at the edge of today's estimates of critical loads. Critical loads

for species-rich lowland heathlands, acidic grasslands and coastal dunes are considered to be 10-20 kg N ha^{-1} yr^{-1} (Acherman and Bobbink, 2003; Bobbink et al., 1992; Bobbink and Roelofs, 1995; Jones et al., 2004). When setting a critical load for acidic, coastal dunes in the Baltic, it should be borne in mind that from up to 4 kg N ha^{-1} yr^{-1} wet deposition, or a total of 5-8 kg N ha^{-1} yr^{-1}, vegetation change and subsequent species loss occur. Thus a long-term low load of this magnitude alters these ecosystems.

Conclusions

At remote coastal sites *C. portentosa* seems to be a good biomonitor for the N-deposition history for the last 3-6 years. Even at medium loads of 3-8 kg N ha^{-1} yr^{-1} wet deposition, vegetation dominance of taller graminoids could be detected. The critical load for these acidic, dry coastal ecosystems is estimated as 4-6 kg N ha^{-1} yr^{-1} wet deposition or a total of 5-8 kg N ha^{-1} yr^{-1}, i.e. lower than previously thought.

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Harilaid, EE. In species-rich dune grasslands lichens are the first to disappear.

Low atmospheric nitrogen loads lead to grass encroachment in coastal dunes, but only on acid soils

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Abstract

The impact of atmospheric N-deposition on succession from open sand to dry, lichen-rich, short grassland and tall grass vegetation dominated by *Carex arenaria* was surveyed in 19 coastal dune sites along the Baltic Sea. Coastal dunes with acid or slightly calcareous sand reacted differently to atmospheric wet deposition of 5-8 kg N ha^{-1} yr^{-1}. Accelerated acidification, as well as increased growth of *Carex* and accumulation of organic matter, was observed only at acid sites with pH_{NaCl} of the parent material below 6.0. At sites with slightly calcareous parent material, increased N-deposition had no effect. A trigger for grass encroachment seems to be high acidification in early successional stages to below pH_{NaCl} 4.0. Metals like Al or Fe become freely available and may hamper intolerant species. At acid sites, N-mineralisation increases with elevated N-deposition, which may further stimulate *Carex arenaria*. Due to high growth plasticity, efficient resource allocation and tolerance of high metal concentrations, *C. arenaria* is a superior competitor under these conditions and can start to dominate the dune system. *Carex*-dominated vegetation is species-poor. Even at the moderate N-loads in this study, foliose lichens, forbs, and grasses were reduced in short grass vegetation at acid sites. Species indicating these first effects of atmospheric deposition on dry, lichen-rich, short grasslands are identified and recommendations for restoration of grass-encroached sites given.

Introduction

Effects of atmospheric nitrogen deposition on semi-natural ecosystems have been intensively studied in the last three decades. Nutrient-poor and weakly buffered ecosystems are particularly vulnerable. In dry ecosystems in north-western and central Europe, negative impacts of high atmospheric deposition (15-30 kg N ha^{-1} yr^{-1}) have been described for forests (Houdijk et al., 1993; van Dijk et al., 1989, 1990), heathlands (Bobbink et al., 1992; Power et al., 1998; Roelofs, 1986; van den Berg et al., 2005) and some types of coastal dunes (Jones et al., 2004; Kooijman et al., 1998). However, even low levels of nitrogen deposition may have negative effects. For coastal dunes of the Baltic Sea, which only receive 3-8 kg N ha^{-1} yr^{-1}, critical loads for dry, acid, lichen-rich grasslands as low as 4-6 kg N ha^{-1} yr^{-1} have been suggested (Remke et al., 2009/chapter 3).

Increased atmospheric N-deposition may affect various ecosystem patterns and processes. Elevated N-loads stimulate eutrophication and plant growth, but also lead to acidification and loss of buffer capacity, increasing the availability of toxic metals (Al^{3+} and Fe^{3+}) within the soil (Aerts and Bobbink, 1999; Heij and Schneider, 1991). Al and Fe concentrations of 50-100 ppm in plant tissue can harm acid intolerant species and disturb the P-metabolism (Fink, 2007). Higher soil Al/Ca-ratios are assumed to be toxic for plants growing at intermediate pH levels (de Graaf et al., 1997) as Ca^{2+} inhibits the uptake of Al^{3+} (Marschner, 1995).

High N-deposition may also accelerate succession rates in acid grasslands, heathlands and dune pools (Bobbink et al., 1998; Achermann and Bobbink, 2003). Vegetation becomes dominated by tall graminoids like *Deschampsia flexuosa* (L.) Trin., *Molinia caerulea* (L.) Moench, *Carex arenaria* L. and *Calamagrostis epigejos* (L.) Roth (Bobbink et al., 1998; Kooijman et al., 1998; Remke et al., 2009/chapter 3). Processes behind this species change are a switch from competition for nutrients to a competition for light and space, and resistance of plant species to toxicity such as high metal concentrations or a very low pH

(Bobbink et al., 1998; de Graaf et al., 1997; Kleijn et al., 2008). In the Baltic region, dry, lichen-rich dune grasslands are reduced as N-affected dunes become dominated by *Carex arenaria* (Remke et al., 2009/chapter 3). Under unpolluted conditions, the succession pathway starts with bare sand, which is then slowly colonised by a few pioneer graminoids like *Corynephorus canescens* P. Beauv. and *Carex arenaria*, by lichens like *Cetraria muricata* (Ach.) Eckfeldt and mosses like *Ceratodon purpureus* (Hedw.) Brid. With time, the bare soil is totally covered by low, but highly characteristic vegetation. These short grasslands contain about 20-25 plant species (per relevee of 16-25 m²), mostly lichens and mosses (Ellenberg, 1996). Grey dunes and wet dune slacks add an essential part to the species diversity of coastal dunes and habitats. Species diversity of coastal habitats comprises 40-70% of the total diversity in Flanders and The Netherlands (Kooijman, 2004; Provoost and Bonte, 2004), about 25% on the West Frisian islands (Niedringhaus et al., 2008), and forms therefore an essential part of total biodiversity.

Succession from bare sand to fully developed lichen-rich dune grassland may take 50-70 years, and is accompanied by a moderate decrease in soil pH (0.5-1 pH units) and accumulation of organic matter (Ellenberg, 1996). Eventually taller graminoids, dwarf shrubs or trees become dominant. The sequence from young short via old to tall grassland is one of the major succession lines for Baltic coastal dunes and has been described for the Vistula Spit (Steffen, 1931), the Łeba bar (Hueck, 1932) as well as the Curonian spit

Figure 1 Map of field sites along the Kattegat, southern Baltic Sea and Baltic Proper.

(Paul, 1953). However, with increased levels of atmospheric N-deposition, crucial soil processes may change, and lead to dominances of dense, tall grass stands.

The aim of this study is to determine, (i) which soil processes promote the shift from lichen-rich, short, dry grasslands to a dominance of *Carex arenaria*, (ii) which process changes can be linked to atmospheric N-deposition, (iii) to specify characteristics of *Carex arenaria* stands under different atmospheric N-loads, and (iv) to describe the effects of elevated deposition loads on species composition and richness. Finally, early indicators for the influence of low atmospheric N-deposition levels are listed, and recommendations for restoration of dry, coastal dunes dominated by tall graminoids are given.

Field sites

The 19 coastal dune sites are spread over a large geographical gradient from the Kattegat in the west of the Southern Baltic to the Baltic proper in the east (figure 1; Remke et al., 2009/chapter 3). The research area therefore stretches from the Atlantic through Central Europe to the Baltic terrestrial ecoregion (Olson et al., 2004). The average annual temperature decreases from 8°C in Denmark to 5°C in Estonia (table 1) as the climate

Table 1 Short description of all field sites with synonym used, country, geographical UTM coordinates (from Google Earth), longterm annual mean values for temperature and precipitation, and sea water salinity. Sources for climate data: (1) www.worldclimate.com, station Liepaja; (2) www.worldclimate.com, station Greifswald; (3) temperature: Eggertsson Karlström (2004); precipitation: Raab and Vedin (1995); (4) Ratas and Nilson (1997); (5) Walter and Lieth (1967) in Biermann (1999); (6) temperature: www.dmi.dk, regions København and Nordsjælland; precipitation: Jensen (1986); (7) Anonymus (2004) (8) www.wetter.com, station Kleipeda; (9) www.worldclimate.com, station Duoedde; (10) temperature; www.worldclimate.com, station Łeba; precipitation: Walna et al. (2003). Salinity values are obtained from the mean grid cell values for the period 1900-2005 (Feistel et al., 2008). NP = national park.

name/ synonym	country	longitude UTM	latitude UTM	temp. [°C]	precip. [mm yr^{-1}]	salinity [PSU]
Akmensrags (1)	Latvia	56411065	20989034	6.8	627	7.2
Dünenheide/ Hiddensee (2)	Germany	54550269	13099371	8.0	564	9.0
Gellen/ Hiddensee (2)	Germany	54479486	13064725	8.0	564	9.0
Harilaid (4)	Estonia	58489564	21843912	5.6	703	6.9
Holtemmen/ Laeso (5)	Denmark	57302031	10994222	7.9	576	24.0
Keibu (4)	Estonia	59241349	23739389	5.1	686	7.0
Korshage (6)	Denmark	55974190	11777358	7.3	500	18.4
Nagliu/ Curonian Spit NP (7)	Lithuania	59659837	21083870	7.8	750	7.3
Nida/ Curonian Spit NP(7)	Lithuania	55284024	20958343	7.8	750	7.3
Pajuris (8)	Lithuania	55843364	21062018	7.0	735	7.3
Pape (1)	Latvia	56150317	21027620	6.8	627	7.2
Pärispea (4)	Estonia	59659837	25683665	5.1	686	6.4
Pavilosta (1)	Latvia	56893958	21191670	6.8	627	7.0
Raghammer/ Bornholm (9)	Denmark	55015227	14926422	7.7	572	7.9
Łeba/ Slovinski NP (10)	Poland	54682510	17101320	7.7	575	7.5
Sandhammeren (3)	Sweden	55378837	14180429	7.4	600	7.7
Syrodde/ Laeso (5)	Denmark	57323485	11195125	7.9	576	24.0
Tönnersa (3)	Sweden	56555071	12947505	7.3	700	18.1
Torsö (3)	Sweden	55999030	14657380	7.4	550	7.7

gets more continental. Another gradient exists for sea water salinity and therefore salt-spray. Salinity decreases steeply within in the Kattegat from 24 to ca. 10 PSU and ranges mainly between 7-8 PSU in the Southern Baltic and Baltic proper (table 1). All 19 sites have parent sand material with pH_{NaCl} below 6.5 and receive precipitation of 500-700 mm yr^{-1} (table 1). All sites are open dunes without any physical barrier like a forest towards the sea, and have less than 10% cover of trees. During the last decade, management impacts such as grazing or burning have not been intensive.

The data set was separated into two main groups, with pH of the parent material below ('acid') or above ('slightly calcareous') 6.0 (table 2), i.e., below or within the carbonate buffer range. Above pH 6.5-6.2, the system is buffered by dissolution of calcium carbonate, below pH 6.0 by cation exchange, and below pH 5.0 by aluminium and iron buffer systems (Scheffer and Schachtschabel, 1998). In addition, both pH-groups were separated into two N-deposition classes below and above a total wet N-deposition of 5 kg N ha^{-1} yr^{-1}, estimated by N content of the biomonitor *Cladonia portentosa* (Remke et al., 2009/chapter 3; table 2). The calculated total wet N-deposition ranged from 2.6-7.8 total N kg ha^{-1} yr^{-1}, but critical loads were estimated as 4-6 kg N ha^{-1} yr^{-1} (Remke et al., 2009/chapter 3). The N-content in *C. portentosa* proved to be a suitable biomonitor of N-deposition in remote areas as it explained ca. 50% of the variation in wet N-deposition measured at nearby EMEP stations (regression equation: *C. portentosa* tissue N[%]=0.0228×N-deposition[kg ha^{-1} yr^{-1}]+0.3385, R^2=0.5223, p=0.008; further discussion see Remke et al., 2009/chapter 3).

Table 2 Classification of field sites. Sites with pH_{NaCl}>6.0 of the parent sand material are classified as 'slightly calcareous' sites with pH_{NaCl}<6.0 as 'acid'. Sites with calculated total wet N-deposition <5 kg N ha^{-1} yr^{-1} are classified as N-unaffected or 'low' N-deposition sites, sites with calculated total wet N-deposition >5 kg N ha^{-1} yr^{-1} as N-affected or 'high' N-deposition sites (dep. class). Total deposition of N was calculated using the lichen biomonitor (calc. total N; method see Remke et al., 2009/chapter 3).

field site	parent sand pH	pH class	lichen-N [%]		calc. total N	dep. class
			mean	± SE	[kg ha^{-1} yr^{-1}]	
Keibu	5.64	acid	0.409	0.020	2.57	low
Pärispea	5.82	acid	0.425	0.016	3.12	low
Syrodde	5.30	acid	0.451	0.017	4.02	low
Sandhammaren	5.27	acid	0.463	0.015	4.39	low
Korshage	5.43	acid	0.497	0.026	5.54	high
Dünenheide	5.63	acid	0.522	0.019	6.39	high
Torsö	5.09	acid	0.537	0.020	6.89	high
Gellen	5.02	acid	0.545	0.017	7.19	high
Tönnersa	5.50	acid	0.554	0.032	7.48	high
Nagliu	6.82	slightly calcareous	0.404	0.018	2.41	low
Akmensrags	6.98	slightly calcareous	0.428	0.025	3.23	low
Nidda	6.87	slightly calcareous	0.439	0.022	3.60	low
Pavilosta	6.85	slightly calcareous	0.448	0.016	3.91	low
Harilaid	6.59	slightly calcareous	0.484	0.017	5.10	high
Holtemmen	6.15	slightly calcareous	0.496	0.019	5.53	high
Łeba	6.79	slightly calcareous	0.504	0.023	5.81	high
Pajuris	6.42	slightly calcareous	0.505	0.015	5.82	high
Raghammer	6.63	slightly calcareous	0.513	0.013	6.10	high
Pape	6.54	slightly calcareous	0.562	0.017	7.76	high

Material and methods

In each of the 19 dune sites, three 2×2 m plots were selected in June-July 2005, in a sequence from young short via old short to tall grassland. The 1st, early successional stage is characterised by short, dry grassland, with at least 30% open sand area, the 2nd stage by older and lichen-rich, short grassland, with open sand below 5%, and the 3rd stage is dominated by tall grasses with least ca. 50% cover of sand sedge (*Carex arenaria*). In each plot, species cover was estimated. If necessary, species were dried and identified using a microscope and colouring techniques. For species determination the following literature was used: for vascular plants Rothmaler et al., (2002), Oberdorfer (1994) and Hegi and Conert (1998), additionally for *Salix* spp. Lautenschlager-Fleury and Lautenschlager (1994), for mosses Frahm and Frey (1992) and for lichens Wirth (1995). Within each plot, above-ground biomass was sampled in a circle with a diameter of 29.5 cm. Within each circle, thickness of the humus horizon (Ol, Of, Oh) was measured (Finnern et al., 1994). Below this, a soil sample mixed out of three soil cores (each core cutter 100 cm³) was collected from the top 10 cm of the mineral soil layer. In addition, at each site, three soil samples (top 2-3 cm) were taken along the first dune ridge towards the open sea to determine the pH of the parent sand material. All samples were dried at 70°C (plant) and 40°C (soil) for 24 hours.

The lichen, *Cladonia portentosa* (Dufour) Coem., was used as biomonitor for atmospheric nitrogen deposition (Remke et al., 2009/chapter 3). Within each plot, ten 10x10 cm samples of *C. portentosa* were cut with a pair of scissors out of the centre of a lichen patch of ca. 0.4-0.5 m diameter (Søchting, 1995). Only the top 2 cm of the *Cladonia* were collected in order to exclude nutrient uptake from the soil. The samples were cleaned roughly and stored in a paper bag. In the laboratory, all samples were cleaned thoroughly, washed briefly in distilled water and dried at 70°C for 24 h.

Fresh biomass was separated into cryptogams (lichens and mosses), vascular plants and litter, and weighed after drying at 70°C for 24 h. A subsample of *Carex arenaria* was taken for further analysis. *Carex* and *Cladonia portentosa* samples were ground in a centrifugal mill (rotational speed 18000 for 1-2 minutes, FRITSCH pulverisette 14, Idar-Oberstein, Germany). Total nitrogen and CN-ratio of plant and soil material (finely ground in a centrifugal ball mill, Fritsch, Idar-Oberstein, Germany) were determined with a C/N-analyser (CHNOS element analyser vario EL III, elementar Analysensysteme, Hanau, Germany). Total P was analysed for sand sedge only, with 200 mg ground material digested in sealed Teflon vessels in a Milestone microwave oven (type Ethos D, Milestone Inc., Sorisole, Italy) after addition of 4 ml HNO_3 (65%) and 1 ml H_2O_2 (30%) (Kingston and Haswell, 1997).

Soil samples were sieved with a 2 mm mesh-size before the following analyses. Soil organic matter content was determined as loss on ignition (LOI) at 550°C for 8 h, and pH was measured in 0.2 M NaCl. Total extractable amounts of Al, Ca, Fe, Mg, Mn, P, S and Zn were measured in these 0.2 M NaCl extracts, and Na in a double deionised water extract with inductively-coupled plasma emission spectrophotometry (ICP-OES: IRIS Intrepid II XDL, Thermo Fisher Electric, Breda, The Netherlands). Nitrogen mineralisation was measured in a laboratory incubation experiment of 26 days, with 60 g of sieved soil in glass beakers sealed with parafilm kept at 40% water holding capacity and 25°C in total darkness. NO_3^- and NH_4^+ were measured at the start and end of the incubation period, using extractions with double deionised water and 0.2 M NaCl,

respectively. Ortho-P was measured in double deionised water extracts at the start of the incubation period. Nitrate, ammonium and phosphate were measured colorimetrically with an Auto Analyzer 3 system (Bran+Luebbe, Norderstedt, Germany), using ammonium molybdate (Henriksen, 1965), hydrazine sulphate (Technicon, 1969) and salicylate (Grasshoff and Johannsen, 1977), respectively.

Linear models and linear mixed effect models were fitted using R (R development core team, 2008), followed by model justification procedures. Mixed effect models were applied to overcome spatial pseudo-replication within the data set (field site as random factor). If fitted models were not justified, generalised linear models (glm) with gamma error distributions were fitted or data were transformed by log or (double) square root before regression analysis. Multiple regressions were carried out starting with all environmental factors and subsequently simplified using stepwise backward deletion until the minimal adequate model was reached. To avoid over-dispersion no more variables than the replicate number divided by three were fitted (Crawley, 2005, 2007). Tests between 2 classes were performed by Student's t-test, if the data were normally distributed, otherwise the non-parametric Kruskal-Wallis test was performed.

Results
Acidification

Acidification rates differed between early and later successional stages. Initial acidification, i.e. differences in pH between parent material and the 1st succession stage, was negatively correlated with acidification during subsequent succession (figure 2). At sites with small
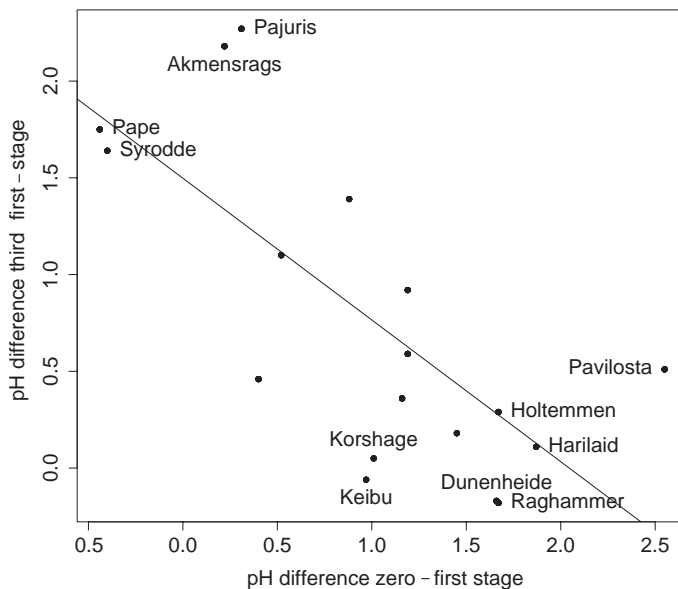

Figure 2 Relationship between the pH difference of the parent sand material and the 1st vegetation succession stage and the pH difference within succession i.e. 1st and the 3rd succession stage. Every point is a site and extreme sites are labelled. For example, Pajuris or Akmensrags have a low pH decrease between the parent sand material and the 1st succession stage, and Pavilosta and Harilaid have a high pH difference within later succession. (regression equation: y=-0.74x+1.45, R^2=0.5166, p=0.001)

pH differences between parent material and the 1st stage of succession, the pH decreased by nearly 2 units during the succession from the 1st to the 3rd stage. Sites following this pattern were Akmensrags, Nagliu, Pajuris, Syrodde, Pape and Gellen (figure 2). Sites with high pH differences (~2 units) between parent material and initial succession stage, showed minimal pH decrease with further succession. Dünenheide, Harilaid, Pavilosta, Holtemmen, Keibu and Korshage were examples for this pattern. The early acidification, i.e. the high pH-decrease between the parent sand material and the first stage, shows no link to N-deposition levels. The early decrease in pH (parent sand – 1st stage) cannot be linked to N-deposition (regression results: acid p=0.595; slightly calcareous p=0.845; all p=0.660). Only the pH differed with N-deposition. Especially at acid sites and later successional stages the pH was significantly lower (0.3-0.5 units) at N-affected sites (table 3).

Eutrophication

Soil pH and organic matter (LOI) were closely related and changed during succession, but were also affected by N-deposition (figure 3). Organic matter increased exponentially with decreasing pH, but only in areas with high N-deposition. Plots with more than 1.0-1.5% soil organic matter and a pH<4.0 belonged mainly to the 3rd succession stage at N-affected sites, which are densely covered by *Carex arenaria*. A significant increase in organic matter with N-deposition occurred only at sites with acid parent material (table 3). At these sites, organic matter concentration was 2-4 times higher at N-affected than at N-unaffected sites. At sites with slightly calcareous parent material, however, organic matter increased during succession, but did not differ between low and high N-deposition areas (table 3).
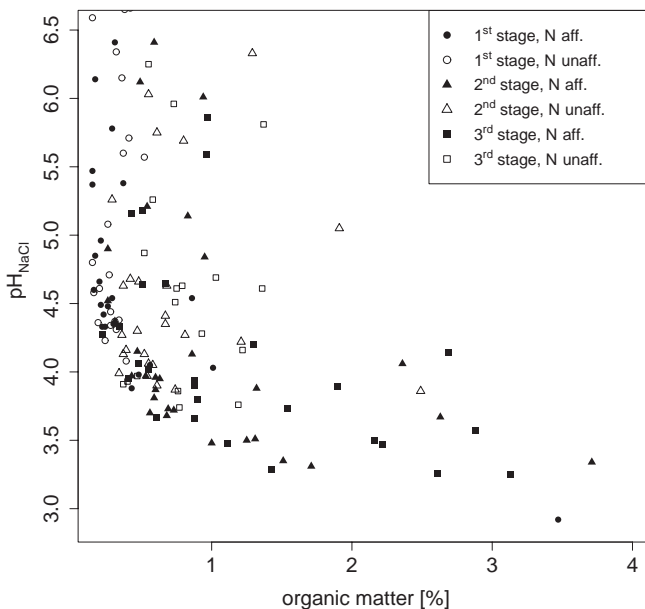
Figure 3 Organic matter content (LOI) versus pH of all vegetation units.

Table 3 Arithmetic mean values (± 1SE) of soil and plant data for all sites, separated for pH classes (acid, slightly calcareous), deposition classes (N-unaffected and N-affected) and vegetation succession stages (1st, 2nd and 3rd stage). Significant differences (p<0.05) between deposition classes (N-affected and N-unaffected) are shown in bold. LOI = loss on ignition, Ol = thickness of litter layer, CEC = cation exchange capacity.

acid sites

deposition	N-unaffected			N-affected		
succession stage	1st	2nd	3rd	1st	2nd	3rd
lichen-N [%]	**0.428 (0.06)**	**0.437 (0.06)**	**0.463 (0.00)**	**0.541 (0.03)**	**0.531 (0.06)**	**0.533 (0.05)**
LOI [%]	0.28 (0.03)	**0.50 (0.05)**	**0.41 (0.03)**	0.38 (0.07)	**1.15 (0.19)**	**1.46 (0.26)**
Ol [cm]	**0.1 (0.04)**	**0.3 (0.05)**	0.4 (0.10)	**0.0 (0.00)**	**0.10 (0.04)**	0.8 (0.10)
pH [NaCl]	4.91 (0.31)	**4.25 (0.11)**	**3.94 (0.02)**	4.27 (0.08)	**3.74 (0.06)**	**3.67 (0.09)**
C/N-ratio soil	10.9 (1.2)	**11.6 (0.6)**	11.8 (1.6)	8.7 (0.9)	**14.2 (0.7)**	13.5 (0.9)
N-miner. [g/m^3]	**0.69 (0.12)**	**0.84 (0.12)**	**0.87 (0.19)**	**1.27 (0.16)**	**1.69 (0.21)**	**2.65 (0.36)**
N-NH$_4$ [g/m^3]	0.56 (0.11)	0.78 (0.11)	0.81 (0.22)	0.91 (0.13)	0.93 (0.06)	1.22 (0.12)
N-NO$_3$ [g/m^3]	**1.20 (0.30)**	2.29 (0.70)	**0.99 (0.28)**	**2.41 (0.63)**	3.84 (0.86)	**5.41 (1.08)**
NH$_4$/NO$_3$-ratio	0.57 (0.1)	0.74 (0.2)	0.92 (0.3)	0.54 (0.1)	0.49 (0.1)	0.36 (0.1)
Al/Ca-ratio soil	1.27 (0.41)	**0.40 (0.13)**	0.42 (0.1)	1.19 (0.2)	**1.04 (0.2)**	0.98 (0.39)
Fe [µmol/kg]	9.03 (1.96)	20.56 (3.26)	**40.28 (2.12)**	13.00 (1.97)	**65.73 (11.32)**	**74.42 (14.54)**
CEC [µmol/kg]	1190 (504)	1276 (270)	**662 (106)**	624 (142)	1250 (431)	**1781 (317)**
ortho-P [µmol/kg]	**9.98 (2.05)**	24.70 (5.14)	42.49 (5.08)	**27.53 (7.17)**	31.22 (8.13)	63.18 (8.69)
N/P-ratio *Carex*	**7.8 (1.1)**	**7.1 (0.4)**	**8.1 (0.1)**	**11.5 (0.5)**	**9.6 (0.5)**	**9.6 (0.5)**
N *Carex* [%]	**11.43 (0.54)**	**11.72 (0.99)**	12.95 (1.05)	**17.48 (1.44)**	**14.61 (0.54)**	15.29 (0.63)
P *Carex* [%]	1.71 (0.35)	1.67 (0.12)	1.62 (0.15)	1.59 (0.18)	1.56 (0.09)	1.62 (0.08)
Carex cover per plot [%]	2.9 (1.1)	**6.2 (2.0)**	47.7 (10.2)	5.6 (1.4)	**12.3 (2.1)**	77.1 (4.7)
vascular plant biomass [g/m^2]	66.8 (14.1)	219.4 (63.4)	954.8 (107.8)	78.7 (10.4)	539.5 (164.6)	1066.4 (94.9)
lichen & moss biomass [g/m^2]	16.7 (11.1)	768.3 (120.4)	51.8 (32.9)	13.1 (5.6)	868.3 (173.3)	371.2 (170.7)

slightly calcareous sites

deposition	N-unaffected			N-affected		
succession stage	1st	2nd	3rd	1st	2nd	3rd
lichen-N [%]	**0.441 (0.07)**	**0.442 (0.08)**	**0.441 (0.07)**	**0.516 (0.06)**	**0.516 (0.06)**	**0.519 (0.08)**
LOI [%]	0.31 (0.03)	0.74 (0.11)	0.89 (0.07)	0.26 (0.05)	0.64 (0.08)	0.84 (0.14)
Ol [cm]	0.05 (0.02)	0.80 (0.18)	1.28 (0.22)	0.07 (0.04)	0.59 (0.11)	1.25 (0.23)
pH [NaCl]	5.58 (0.26)	4.90 (0.24)	4.73 (0.2)	5.70 (0.3)	4.74 (0.2)	4.57 (0.21)
C/N-ratio soil	16.0 (3.4)	12.0 (0.7)	12.0 (0.62)	12.0 (0.87)	12.7 (0.93)	13.5 (0.72)
N-miner. [g/m^3]	1.19 (0.11)	1.38 (0.36)	3.00 (0.37)	1.10 (0.15)	1.81 (0.27)	3.33 (0.64)
N-NH$_4$ [g/m^3]	0.35 (0.08)	0.65 (0.12)	1.05 (0.09)	0.42 (0.06)	0.52 (0.11)	0.90 (0.17)
N-NO$_3$ [g/m^3]	1.19 (1.08)	5.17 (1.30)	4.08 (0.88)	1.02 (0.69)	4.24 (0.63)	3.20 (1.33)
NH$_4$/NO$_3$-ratio	0.25 (0.1)	2.00 (0.8)	0.35 (0.05)	0.16 (0.03)	1.02 (0.44)	0.42 (0.14)
Al/Ca-ratio soil	0.74 (0.4)	0.12 (0.1)	0.71 (0.6)	0.07 (0.03)	0.19 (0.11)	0.08 (0.02)
Fe [µmol/kg]	4.86 (0.66)	13.24 (2.69)	24.81 (5.64)	5.46 (1.08)	18.32 (4.79)	22.04 (4.81)
CEC [µmol/kg]	1353 (224)	2600 (342)	2663 (342)	1141 (127)	1915 (274)	2356 (320)
ortho-P [µmol/kg]	12.20 (1.60)	49.68 (13.57)	54.52 (9.84)	22.78 (7.37)	64.37 (12.71)	70.39 (14.83)
N/P-ratio *Carex*	9.9 (0.7)	7.9 (0.5)	7.9 (0.4)	9.3 (0.6)	7.8 (0.4)	7.0 (0.28)
N *Carex* [%]	**13.02 (0.42)**	12.41 (0.46)	13.27 (0.77)	**14.91 (0.65)**	12.76 (0.38)	13.71 (0.61)
P *Carex* [%]	1.40 (0.09)	1.62 (0.08)	1.73 (0.13)	1.76 (0.20)	1.73 (0.09)	1.99 (0.12)
Carex cover per plot [%]	4.3 (0.7)	5.8 (0.8)	60.6 (2.5)	4.9 (1.1)	7.0 (1.2)	65.1 (3.29)
vascular plant biomass [g/m^2]	86.3 (9.0)	233.7 (41.0)	905.0 (68.0)	84.4 (10.2)	238.5 (30.4)	897.9 (78.7)
lichen & moss biomass [g/m^2]	18.6 (11.6)	893.0 (80.6)	180.8 (72.0)	29.3 (19.0)	844.1 (97.3)	147.1 (68.5)

During succession, net N-mineralisation generally increased from the 1st to the 3rd stage (table 3). The amount of N-mineralisation per unit soil organic matter was positively correlated with pH (figure 4) and furthermore related to N-deposition. The increase of N-mineralisation/ LOI with increasing pH was 3 times steeper at N-affected than at N-unaffected sites (figure 4), and N-mineralisation in total was elevated 2-3 times at sites with high N deposition (table 3).
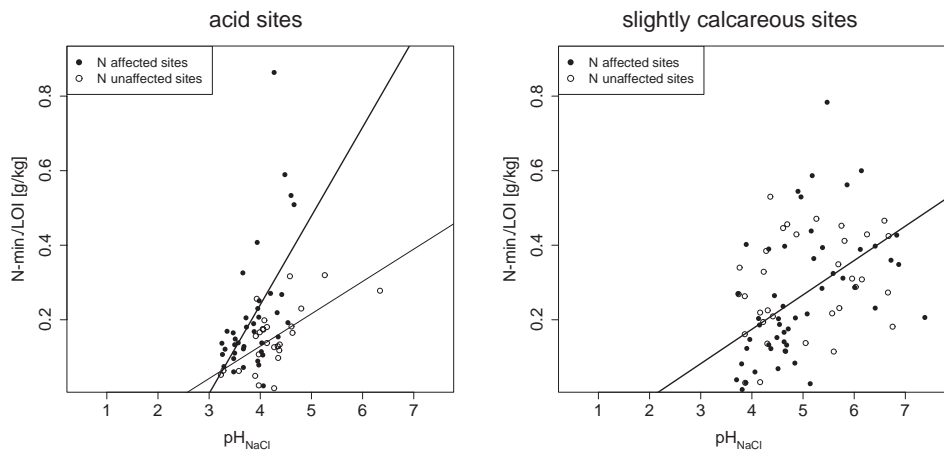
Figure 4 N-mineralisation per day per LOI [g kg^{-1}] against the pH$_{NaCl}$ for acid and slightly calcareous sites separately. (Regression results: acid sites: N-affected y=0.238×-0.712 (p=0.000), N-unaffected y=0.087×-0.218 (p=0.001); slightly calcareous sites: N-affected y=0.092×-0.194 (p=0.005), N-unaffected no regression equation as p=0.104.)

Toxicity

The Al/Ca-ratio increased with increasing N-deposition only at sites with acid parent material (2nd stage, table 4), and was twice as high at N-affected than at N-unaffected sites (2nd stage, table 3). At acid sites, the Al/Ca-ratio exceeded the values of 1 in all succession stages. At sites with slightly calcareous parent material, Al/Ca-ratios were 5-10 times lower. Salt-extractable Fe soil concentrations were at least 2 times higher at acid than at slightly calcareous sites. At acid sites, the Fe content was 1.5 to 3 times higher under high compared to low N-deposition.

Table 4 Regression results of various factors (depending factor) with atmospheric N-deposition (measured as lichen-N; independent factor). Climatic factors (temperature, precipitation), salinity and UTM coordinates had no significant impact in multiple regression. Regression results of the listed factors were not significant in other successional stages and are not shown.

depending factor	acid sites		slightly calcareous	all sites	
pH-difference parent sand and 1st stage		p=0.595	p=0.845		p=0.660
Al/Ca-ratio (2nd stage)	y=0.85x-3.34	p=0.034	p=0.807		p=0.179
Carex tissue N (1st stage)		p=0.137	p=0.196	y=3.45x-2.10	p=0.021
Carex tissue N (2nd stage)	y=2.79x-0.73	p=0.040	p=0.446	y=1.74x+4.35	p=0.013
Carex tissue N/P-ratio (1st stage)	y=3.86x8.95	p=0.013	p=0.919	y=1.93x-0.48	p=0.058
Carex tissue N/P-ratio (2nd stage)	y=2.53x-4.10	p=0.012	p=0.331	y=1.83x-0.84	p=0.009
Carex tissue N/P-ratio (3rd stage)	y=3.23x-7.53	p=0.047	p=0.778		p=0.122
Carex cover [%] (3rd stage)	y=7.90x-29.07	p=0.039	p=0.806	y=4.72x-14.92	p=0.040

Characteristics of *Carex arenaria* plants and vegetation stands

Increased atmospheric N-deposition (measured as lichen-N) was positively correlated to the N-content of *Carex* tissue, but only in early succession stages at acid sites and all sites pooled (table 4). N/P-ratios (*Carex*) were positively correlated to N-deposition in all three succession stages at acid sites (table 4). Tissue P-concentrations of *Carex arenaria* did not differ among sites or succession stages, and ranged between 51.2 and 56.6 µmol P g^{-1}. There was no significant relationship between tissue-N of *Carex* and total N, NH_4^+ or NO_3^- in the soil.

At acid sites, cover of *Carex arenaria* significantly increased under N-affected conditions in later stages of succession (table 3 and 4, figure 5). *Carex*-cover was 1.5-2 times higher under N-affected conditions. In early stages, or slightly calcareous sites, *Carex*-cover was
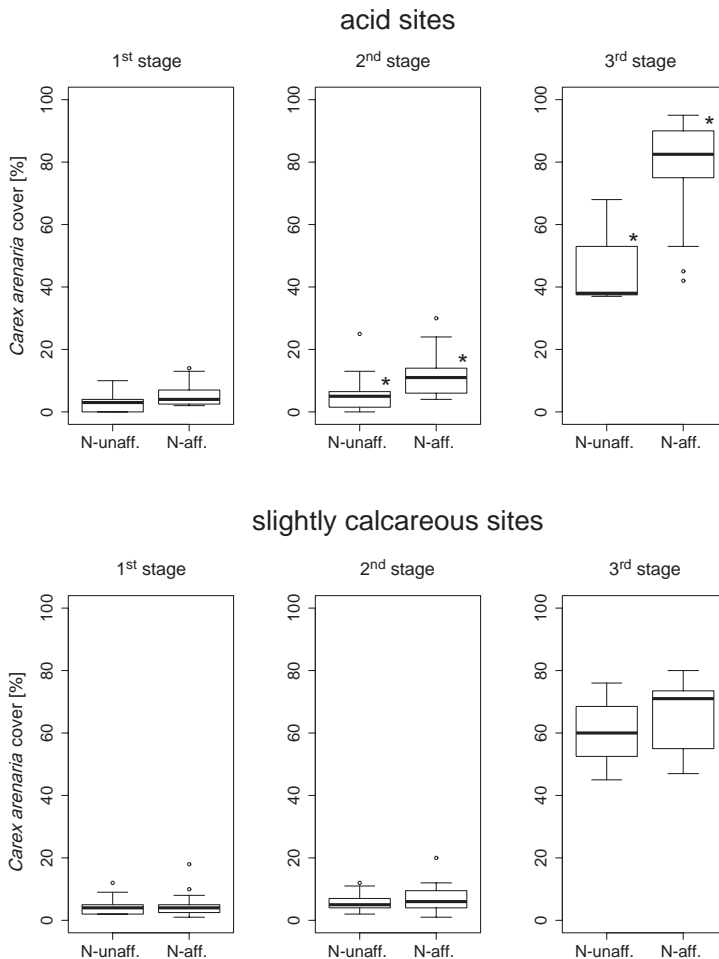
Figure 5 Box and whisker plots for the cover of *Carex arenaria* per plot at acid and slightly calcareous and N-unaffected versus N-affected sites for the three different vegetation succession stages. Significant differences (p<0.05) between N-unaffected and N-affected sites are shown with an asterisk *.

not affected by N-deposition. In the 3rd succession stage, *Carex*-cover was negatively correlated to species numbers of lichens and mosses (y=-0.09×+8.48, p=0.000) and positively to total biomass of vascular plants (y=0.47×+33.70, p=0.027). *Carex* cover was not significantly correlated to soil organic matter. Furthermore, longitude, latitude, climate data (temperature, precipitation) and salinity were not significantly correlated to *Carex*-cover in multiple regression.

Species richness

At acid sites, the species number of foliose lichens, as well as number of all lichen species together (2nd and 3rd stage; figure 6), and grasses and forbs (3rd stage) were significantly lower (2-3 species) under high N-deposition (table 5). Foliose lichens such as *Cladonia glauca* Flörke, *Cl. macilenta* (Leighton) Arnold, *Cl. coccifera* (L.) Willd. and *Cetraria aculeata* (Schreber) Fr./*muricata* (Ach.) Eckfeldt, grasses such as *Festuca polesica* Zapał and *Ammophila arenaria* (L.). Link, and forbs such as *Hypochaeris radicata* L., *Thymus serpyllum* L. and *Hieracium umbellatum* L. were absent or had lower cover at N-affected sites. In contrast, *Carex arenaria* and *Corynephorus canescens* were more abundant at acid sites with high N-deposition, and *Rumex acetosella* L. was exclusively found at these sites.
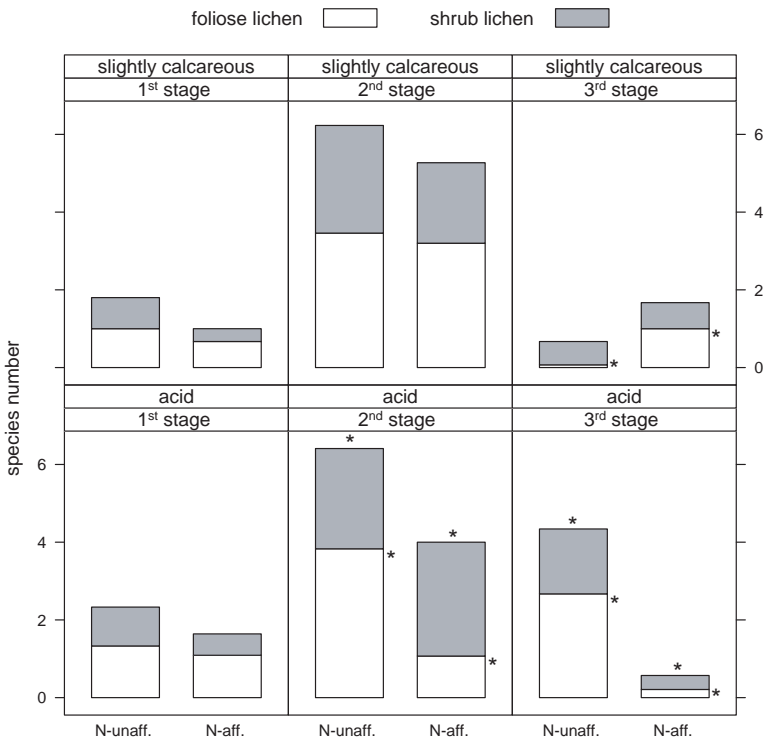
Figure 6 Species number of foliose, shrub and total lichen [per 4 m² plot] at acid and slightly calcareous and N-unaffected versus N-affected sites for the three different vegetation succession stages. Significant differences (p<0.05) between N-unaffected and N-affected sites are shown with an asterisk * beside each bar for different lichen groups and on the top of the bar for total lichen species number (foliose and shrub lichen data pooled).

Table 5 Species richness (mean ± 1SE in brackets; per 4 m² plot) for different life forms separated for deposition classes, pH classes and succession stages. Significant differences (p<0.05) between deposition classes (N-affected and N-unaffected) are shown in bold. Foliose lichens are lichens with basal thalli mainly flat on the ground like *Cetraria* ssp., *Cladonia glauca* or *Cl. foliacea*, *Hypogymnia physodes* and *Peltigera* ssp. Shrub lichens are *Cladonia* spp. with no substantial basal thalli and only upwards growing structures e.g. *Cl. arbuscula*, *Cl. furcata*, or *Cl. uncialis*.

acid sites

deposition	N-unaffected			N-affected		
succession stage	1st	2nd	3rd	1st	2nd	3rd
foliose lichens	1.3 (0.5)	**3.8 (0.8)**	**2.7 (1.2)**	1.1 (0.4)	**1.1 (0.3)**	**0.2 (0.2)**
shrub lichens	1.0 (0.4)	2.6 (0.4)	1.7 (0.9)	0.5 (0.3)	2.9 (0.4)	0.4 (0.2)
all lichens	2.3 (0.9)	**6.4 (0.7)**	**4.3 (1.5)**	1.6 (0.5)	**4.0 (0.5)**	**0.6 (0.2)**
mosses	0.8 (0.2)	1.8 (0.3)	1.3 (0.3)	1.0 (0.3)	1.4 (0.3)	0.6 (0.3)
grasses	2.6 (0.4)	3.0 (0.4)	**3.7 (0.3)**	2.9 (0.4)	3.4 (0.3)	**2.0 (0.2)**
forbs	1.6 (0.6)	3.1 (0.4)	**2.3 (0.7)**	0.2 (0.1)	3.7 (0.6)	**0.9 (0.3)**
total	7.2 (1.2)	14.2 (1.1)	**11.7 (2.4)**	5.7 (0.9)	12.5 (0.7)	**4.1 (0.7)**

slightly calcareous sites

deposition	N-unaffected			N-affected		
succession stage	1st	2nd	3rd	1st	2nd	3rd
foliose lichens	1.0 (0.5)	3.5 (0.8)	**0.1 (0.1)**	0.7 (0.3)	3.2 (0.7)	**1.0 (0.5)**
shrub lichens	0.8 (0.3)	2.8 (0.5)	0.6 (0.2)	0.3 (0.2)	2.1 (0.4)	0.7 (0.3)
all lichens	1.8 (0.7)	6.2 (1.0)	0.7 (0.2)	1.0 (0.4)	5.3 (0.8)	1.7 (0.8)
mosses	1.0 (0.3)	**3.4 (0.4)**	1.9 (0.4)	0.9 (0.2)	**2.1 (0.2)**	1.5 (0.3)
grasses	2.5 (0.2)	**3.7 (0.3)**	2.9 (0.4)	3.3 (0.3)	**4.1 (0.3)**	2.9 (0.2)
forbs	**1.7 (0.4)**	6.3 (0.7)	3.5 (0.5)	**2.1 (0.4)**	5.3 (0.3)	3.3 (0.4)
total	6.9 (0.8)	19.6 (1.3)	8.9 (1.0)	7.3 (0.7)	16.7 (1.1)	9.4 (1.1)

The most important predictors for the decrease in species numbers at acid sites were selected with multiple regression. For the 2nd succession stage, the model explained 20-50% of the variance, with Al/Ca-ratio and its (statistical) interaction with pH and N-deposition as most important factors. For the 3rd stage, only N-deposition was a significant predictor for species richness and explained 30-60% of the variance (table 6). Species with preference for low Al/Ca-ratios were *Hieracium umbellatum* (higher coverage), *Cladonia glauca* (higher coverage and occurrence), and *Jasione montana* L., *Cladonia coccifera* and *Cladonia floerkeana* (Fr.) V.Wirth (higher occurrence). Species excluded from sites with high Al/Ca ratios were *Cladonia glauca*, *Viola* ssp. and *Luzula* ssp. However, *Rumex acetosella*, *Anthoxanthum odoratum* L. and *Corynephorus canescens* were more abundant at high Al/Ca-ratios.

At sites with slightly calcareous parent material, the effect of N-deposition was less pronounced than at acid sites, and even slightly positive for overall species richness (table 5). In multiple regression, Al/Ca-ratio and pH mainly determined species richness (table 6). N-affected sites had one species of foliose lichen (3rd stage), grass (2nd stage) and forb (1st stage) more, but one moss species less (2nd stage). *Cladonia coniocrea* auct. (foliose lichen), *Hypochaeris radicata* (forb), *Anthoxanthum odoratum* and *Festuca rubra* L. (grasses) were more abundant at high N-deposition. *Dicranum scoparium* Hedw. (2nd stage) had exceptionally high coverages (30-40%) at high N-deposition. However, *Pleurozium schreberi* (Brid.) Mitt. (moss), *Cetraria aculeata/muricata* and *C. islandica* (L.) Ach. (1st and 2nd stage) occurred only at N-unaffected sites.

Table 6 Multiple regression results of species groups with the factors lichen-N, Al/Ca-ratio and pH. Significant factors with algebraic sign of the slope, R^2 and p-level are given (p<0.0001 ***, p<0.001 **, p<0.01 *, p<0.05 #, not significant ns) for the different succession stages at acid and slightly calcareous sites separately.

acid sites

species group	1st stage		2nd stage		3rd stage	
	sig. factor (slope)	R², p-level	sig. factor (slope)	R², p-level	sig. factor (slope)	R², p-level
foliose lichens	ns		Al/Ca-ratio (-) interaction with pH interaction with lichen-N	0.4765*	lichen N (-)	0.2809#
all lichens	ns		Al/Ca-ratio (-) interaction with pH interaction with lichen-N	0.4138#	ns	
grass	ns		ns		lichen-N (-)	0.5860***
forbs	lichen-N (+) pH (+) interaction of both	0.8907***	ns		ns	
total	ns		pH (+)	0.1952#	lichen-N (-)	0.3143#

slightly calcareous sites

species group	1st stage		2nd stage		3rd stage	
	sig. factor (slope)	R², p-level	sig. factor (slope)	R², p-level	sig. factor (slope)	R², p-level
foliose lichens	ns		ns		Al/Ca-ratio (-) interaction with lichen-N	0.2416#
all lichens	ns		pH (-)	0.3708***	ns	
moss	ns		lichen-N (-) Al/Ca-ratio (-)	0.3567*	ns	
grass	ns		pH (-)	0.1784#	ns	
forbs	Al/Ca-ratio (-)	0.1722#	lichen-N (-) Al/Ca-ratio (-) interaction of both	0.5313***	ns	
total	ns		pH (-)	0.2554*	ns	

Discussion
Which processes change during grass encroachment?

At these 19 coastal dune sites within the Baltic Sea region even medium loads of wet N-deposition (5-8 kg N ha^{-1} yr^{-1}) have an impact on soil and vegetation factors. At these medium N-loads factors are changing significantly only at acid sites (parent sand pH<6.0) not at slightly calcareous sites (parent sand pH>6.0). The pH of the parent sand material is a main factor responsible for the reaction of the system to these low to medium N-loads. Although pH-differences are small between acid and slightly calcareous sites, they determine which buffer range is acting and how quickly the buffering capacity of cations is depleted, if toxic levels of soluble metals can occur or if mineralisation processes are hampered.

The acidity of the soil has a major influence on soil processes. Some field sites show the expected pattern of acidification during vegetation succession in coastal dunes. The pH remains almost constant during the transition from parent sand material to 1st stage, but decreases with increasing successional age (Ellenberg, 1996). In contrast to these are sites

where the pH decreases already between the parent sand material and the 1st succession stage, after which it remains stable. This pH reduction during the early successional stages was not correlated to N deposition, but may instead be caused by anthropogenic sulphur deposition, e.g. ship traffic. Sulphur generally generates two times more protons than reduced or oxidised nitrogen (NEGTAP, 2001). Pure chemical reactions might prevail in the pure sands at initial successional stages, whereas biological transformations of N such as nitrification may dominate the acidifying processes in later succession stages with higher soil organic matter contents. This is supported by the lower pH values of later successional stages at higher N-deposition in this study.

As soil pH decreases, organic matter (LOI) accumulates exponentially (this chapter; Stützer, 1998; Scheffer and Schachtschabel, 1998). In these dry, oligotrophic systems, organic matter retains moisture and stabilises the soil micro-climate. Most typical dry dune plant species are adapted to fluctuating, extreme temperatures, drought and frequent soil moisture changes. The more stabilised conditions, which prevail during organic matter accumulation, support the growth of ruderal, nitrophilous species at the cost of typical dry dune species like *Jasione montana*. Graminoids like *Carex arenaria*, *Calamagrostis epigejos* and *Festuca rubra* become dominant, where a sufficient layer of organic matter is available or the top sand layer is nutrient rich (Boorman and Van der Maarel, 1997). This observation is supported by the current data set. At acid sites, the total standing vascular plant biomass and the cover of *C. arenaria* are 1.5-3 times higher at N-affected than at N-unaffected sites.

At older successional stages, the higher N-content and N/P-ratio in *Carex* tissue at N-affected sites is in contrast with the higher C/N-ratio in the soil. Different explanations are possible. One is that surplus mineralised N is taken up directly by *Carex*. In addition, in acid soils more N might be available for vascular plants in competition with microbes as microbial communities seem to have a lower demand for N (Kooijman and Besse, 2002; Kooijman et al., 2008). Another possible explanation is, that NO_3^-, which is not taken up, is readily leached. Furthermore, the immobilised N can be bound in structures with higher C/N-ratios like fungi in these acid soils, which might then result in a higher C/N-ratio for the total soil.

Although nitrification is hampered at a pH<4.2 (Aerts and Bobbink, 1999; Roelofs et al., 1985), the higher amount of organic matter at acid, N-affected sites nevertheless increases N-mineralisation to the same level as at slightly calcareous sites (table 3). At acid sites, microbes have a lower demand for N, and therefore the net availability of N for vascular plants, e.g. *Carex*, seems to be higher.

Al/Ca-ratios as well as available Fe concentrations are higher at N-affected, acid sites compared to N-unaffected sites. *Carex*, which is more abundant at these sites seems not to be hampered by these high metal concentrations, though metal toxicity might inhibit the growth of many typical plants of dry, lichen-rich dune grasslands. In addition, *Carex* can grow taller and has greater growth plasticity (Tietema, 1981) than typical dry dune grassland species, and can thus dominate the system.

A N/P-ratio of 7-12 indicates that *Carex* is far from being P-limited and still N-limited (Koerselman and Meuleman, 1996). This is supported by the total tissue concentration of P in *Carex*. P-limitation and critical values depend on plant species and plant tissue part, but a tissue concentration of 50-60 µmol P g^{-1} dw, which is the range for *Carex* at these 19 sites, is critical but not severely limiting (Troelstra et al., 2001).

Carex arenaria is therefore assumed to find optimal growth conditions in Baltic dune sites with high N deposition as it is not hampered by low pH conditions, but is favoured by increased availability of its limiting nutrient, nitrogen. With its larger structure, *C. arenaria* can probably comb out more atmospheric N via its leaves as *Ammophila arenaria* does (Heil et al., 1988). The N-content and N/P-ratio of *Carex* increase with rising N-deposition mainly at older successional stages, but no correlation was apparent between different soil N-forms and *Carex* tissue N. At older successional stages, atmospheric N may therefore contribute more to the nutrition of *Carex* than soil-derived N. With its extensive rhizome network, *C. arenaria* can exploit and transport temporally and spatially widespread resources nearly all year round (Noble and Marshall, 1983; D'Hertenfeld and Falkengren-Grerup, 2002; D'Hertenfeld and Jónsdóttir, 1999) and thereby efficiently use the surplus nitrogen supply. *C. arenaria* finally wins the competition under higher N-loads. Organic matter content >1.0-1.5% and pH<4.0 might be the threshold condition for a system shift to a vegetation dominated by *Carex*. Similar shifts in competitive relationships at increasing N-levels have been reported from heathlands and coniferous forests (Aerts et al., 1990; Berendse and Aerts, 1984; Heil and Bruggink, 1987; Kellner and Redbo-Torstensson, 1995). Another possible reason for grass encroachment is lack of (rabbit – *Oryctolagus cuniculus* (L.)) grazing (Veer and Kooijman, 1997), but rabbits have not been important grazers according to local sites managers and nature conservationists within the 19 dune sites around the Baltic Sea during the last 1-2 decades, and no other herbivores like elk (*Alces alces* (L.)), red deer (*Cervus elaphus* L.), roe deer (*Capreolus capreolus* L.) or hare (*Lepus capensis* L.) have been reported to have a major impact on these dry grassland dune systems. Thus, grazing can be excluded as an important factor for grass encroachment by *Carex arenaria* in Baltic dunes.

Character of *Carex* dominated vegetation units

Dominance by *C. arenaria* can vary considerably. Such vegetation units sometimes are species-rich and open (Harilaid or Pavilosta), but sometimes a species-poor, thick grass sward (Korshage or Gellen). The species-rich, more open *Carex* dominated vegetation is a community known from Baltic dunes since the 1920s (Steffen, 1931; Hueck, 1932; Paul, 1953). At the Curonian Spit, a slightly calcareous and N-unaffected site today, Paul (1953) recorded during the late 1930s an average of 12 species in the optimal phase of a *C. arenaria* community (*Cladonia* spp. excluded). This number is still the same today, and, quite remarkably, species assemblages have not changed during the last seven decades. A decreased number of species (9) at slightly calcareous, N-affected Baltic dunes is comparable to Dutch dunes (Veer and Kooijman, 1997).

At higher N loadings, *Carex* dominance is characterised by a dense grass sward. With increasing biomass the light availability decreases, and a dense root network is established (Veer and Kooijman, 1997). These types of *Carex* units are probably quite persistent. Once a thick grass sward is set up, it is difficult for other plants and even trees to germinate and establish. Most of the few species that are still occurring in this vegetation unit (three on average) are relics of former, more open stages.

The effects of N-deposition on species richness

In acid dune systems, even N-loads less than 8 kg N ha^{-1} yr^{-1} can have a negative impact, while slightly calcareous sites are still well enough buffered by the carbonate system (Scheffer and Schachtschabel, 1998; Blum, 2007), and thus no acidifying impact of this moderate atmospheric N-deposition is occurring. As the three factors soil Al/Ca-ratio, N-deposition and soil pH are strongly intercorrelated, their impact cannot be separated totally, but their importance can be ranked. Kleijn et al., (2008) could not observe any systematic difference between Al/Ca-ratio at growth sites of common and rare species, but rare species occurred at a restricted pH-range. In this study, Al/Ca-ratio and N-deposition (measured as lichen N), showed the largest impact on dry coastal dunes.

Foliose lichens, which have their thalli directly flat on the ground, disappear along with two to three forb and grass species. *Cladonia glauca* and *Festuca polesica* do not grow at all at N-affected sites. Also in other habitats, coverage and species richness of lichens and mosses decrease at higher atmospheric deposition (Boorman and Fuller 1982; Heil and Diemont, 1983; Ketner-Oostra and Sykora, 2004; Lee and Carpon, 1998; Van Tooren et al., 1990). At ambient or artificial total N-deposition of 10 kg N ha^{-1} yr^{-1} total plant species diversity was reduced in American prairie grasslands (Clark and Tilman 2008), Swedish deciduous forests (Falkengren-Grerup and Diekmann, 2003) and British grasslands (Stevens et al., 2004, 2006). Particular to Baltic dunes, there seems to be a decrease in foliose lichens even at moderate deposition loads of <8 kg N ha^{-1} yr^{-1} wet deposition, whereas shrub-thalli lichens do not change their coverage under these conditions. At N-affected field sites, soil pH is lower and Al and Fe are more available than under pristine conditions, and hence, lichen species not adapted to these high concentrations might take up more metals, which may affect their vitality (Hauk et al., 2002, 2007).

Recommendations for coastal dune management

Ecological thresholds and early indicators for ecosystem changes are well used tools in nature conservation and management, though research of their practical application to various ecosystems is still needed (Groffman et al., 2006). This study elucidates the impact of low to medium loads of nitrogen deposition on coastal dunes. An early indicator for a dune system change due to N-loads of 5-8 kg N ha^{-1} yr^{-1} may be an increased drop in soil pH between freshly deposited sand (parent material) and the 1st successional stage. If the total organic matter content (LOI) in the upper mineral soil horizon of lichen-rich, short grasslands (2nd stage) is above 1-1.5% and the pH is below 4.0-4.5, the system is about to change. Heavy metals become freely available, e.g Al/Ca-ratios >1 occur and short grasslands are no longer suitable for slow-growing lichen species. In particular *Cladonia* species growing with their thalli flat on the ground decrease their cover. *Cladonia glauca* and *Cl. macilenta* agg. Hoffm. might be good indicator species of an intact system; higher coverages of *Rumex acetosella* or *Dicranum scoparium* in short grasslands indicate the opposite. Slightly calcareous sites are only marginally affected by these relatively low N-loads as the calcium buffer capacity is not completely depleted yet.

Stands of *C. arenaria* are a natural part of the Baltic coastal ecosystem (Steffen, 1931; Hueck, 1932; Paul, 1953). If the coverage of *C. arenaria* per field site does not exceed 30-40% (Remke et al., 2009/chapter 3), these stands can be species rich (12-16 species per 4 m² plot). However, *C. arenaria* stands have become more widespread and more dense.

At many sites, a dense, species poor (4-6 species per 4 m² plot) grass sward has established over about 60-70% of the area (Remke et al., 2009/chapter 3). Because soil conditions have been irrevocably altered, restoration of dune grasslands on such sites should include turf stripping, removal of soil enriched with organic matter (Ah-layer) and addition of low doses of lime (Dorland et al., 2004; Symes and Day, 2003).

Acknowledgements

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Kleipeda - http://www.worldclimate.com/cgi-bin/grid.pl?gr=N55E021
Łeba - http://www.worldclimate.com/cgi-bin/grid.pl?gr=N54E017
Liepaja - http://www.worldclimate.com/cgi-bin/grid.pl?gr=N56E021
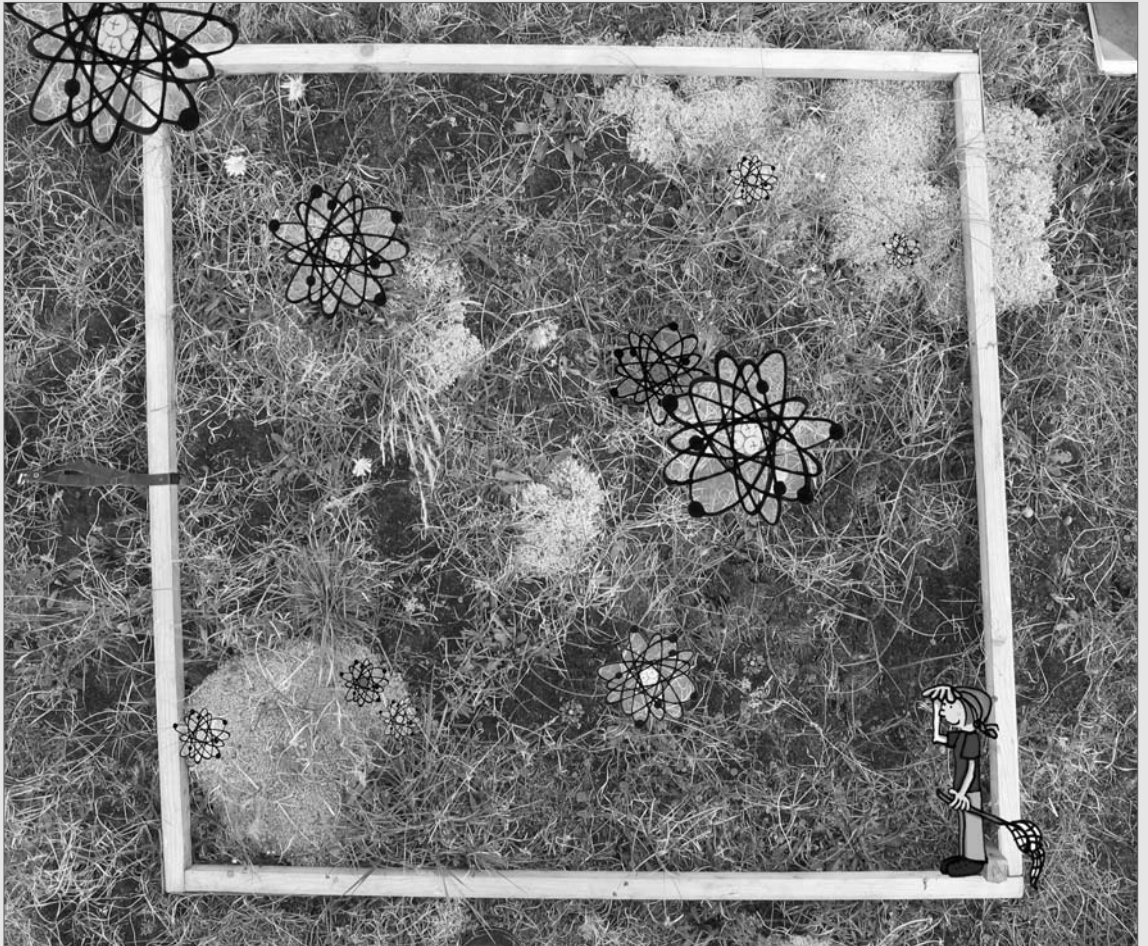regions København and Nordsjælland - www.dmi.dk/dmi/index/danmark/vejrarkiv.htm

Hiddensee, D. Experimental field plot – where have the atoms gone to?

Effects of simulated N-deposition on dry, lichen-rich coastal grasslands – a short-term experiment with ^{15}N enriched nitrate and ammonium

Eva Remke, Emiel Brouwer, Annemieke Kooijman, Irmgard Blindow and Jan G. M. Roelofs

Abstract

Two dry, lichen-rich coastal dune grasslands with a current atmospheric wet N-deposition of 7-8 kg N ha^{-1} yr^{-1}, were compared with respect to vegetation and soil response to a single dose of ^{15}N-enriched NH_4^+ (10% $^{15}NH_4Cl$) or NO_3^- (5% Na$^{15}NO_3$) in July 2006. Soil and plant samples were taken two months after application. The two field sites were Terschelling(NL), where nitrogen deposition has gradually declined after a peak deposition of 15-20 kg N ha^{-1} yr^{-1} in the early 1990s, and Hiddensee (D), where deposition levels have gradually increased to the current level.

The higher historical N-deposition at Terschelling is still indicated by the higher N-content in the lichen *Cladonia portentosa*, higher grass and dead biomass and a different species assemblage. Uptake and recovery of ^{15}N is still higher at Hiddensee. Total recovery of applied ^{15}N in biomass was rather low and varied between 6-13% for both sites, but leaching losses can account for further 30-60%. Nearly all of the recovered ^{15}N (90-98%) was found in lichen and moss tissue. Only 0.6% and 1.5% were found in forbs and grasses respectively.

It thus appears, that high atmospheric N-uptake and storage in lichens and mosses, the dominant life forms, as well as slow nutrient cycling plus high leaching losses tends to keep the ecosystem in its oligotrophic state. The high uptake of preferably reduced nitrogen by lichens might explain the fast disappearance of sensitive lichen species in Dutch, coastal dunes at higher N-loads of especially reduced N during the 1980s. Apart from the actual atmospheric N-deposition, site history of atmospheric deposition is of great importance, if one wants to judge the overall impact of N-loads on N-uptake and cycling.

Introduction

Atmospheric N-deposition can have a strong effect on nutrient poor, semi-natural ecosystems (Bobbink et al., 1998). The sensitivity and resilience of ecosystems to N-deposition depends on site factors like soil pH and buffering capacity, total N-budget and cycling, but also total amount, concentration, duration and molecular form of N-deposition (Bobbink et al., 1998; Pearce and van der Wal, 2008; Remke et al., 2009b/ chapter 4; van den Berg et al., 2008).

Lichen-rich grasslands occur on extremely nutrient poor and dry sands. When circumstances become less extreme, they are readily invaded by tall graminoid species. In particular under acid conditions, a transition to tall grass stands, e.g. *Carex arenaria* L., occurs (Remke et al., 2009b/chapter 4). Probably important processes, which lead to grass encroachment are accelerated acidification and accumulation of organic matter (Remke et al., 2009b/chapter 4). Research on N-deposition in other ecosystems reveals changes such as accelerated acidification, eutrophication (e.g. increased N-mineralisation), increased availability of toxic elements (e.g. Al, Fe) in the soil, elevated N/P-ratios and shift from N- to P-limitation (Bobbink et al., 1998; Matson et al., 2002, Kooijman et al., 1998; Remke et al., 2009b/chapter 4). Knowledge about the history of N-deposition and the N-cycling in dry, coastal dunes might be of importance for restoration actions and other management measures. Experimental work under field conditions in ecosystems with a well-known history leads to a better understanding of the impact of changing environmental factors (Haag and Matschonat, 2001).

Atmospheric N mainly deposits in two forms, in its oxidised (NO_x) or reduced (NH_x) form. In north-western Europe the main N-form has been reduced N in atmospheric deposition during the 1980s (de Haan et al., 2008). This has changed to the oxidised form at the begin of the 21st century when NH_x input by agriculture had been reduced (de Haan et al., 2008). In heathlands, reduced nitrogen has a stronger negative impact than oxidised nitrogen (van den Berg et al., 2008). Plants differ in their preferred form of N-uptake, nitrate or ammonium (Kronzucker et al, 1997; Marscher, 1995; Miller and Cramer, 2008). In general plants adapted to low pH and reducing soil conditions tend to uptake NH_4^+ and at higher pH and in more aerobic soils, NO_3^- is the predominant form (Matthuis, 2009). Species preferring nitrate tend to be fast growing, pioneer species at calcareous sites (Pearson and Stewart, 1993; Marschner, 1995) and species of low productive vegetation on mineral nutrient poor, neutral or slightly acidic soils or waters (de Graaf et al., 1998; Schuurkes et al., 1986). Whereas species preferring ammonium/ ammonia tend to be slow growing, climax species of acid soils (Pearson and Stewart, 1993; Marschner, 1995). For acid dunes, effects of different N-forms and preferences of typical dry dune plants for molecular N-forms are largely unknown.

In this study, a field experiment with labeled nitrogen (^{15}N) has been conducted at two coastal dune sites with contrasting N-deposition history. Historical data are completed with actual measurements of atmospheric deposition and supported by further field observations. It is tested, whether (i) the ^{15}N uptake and recovery differs between sites and (ii) the uptake of ^{15}N-NH_4^+ and ^{15}N-NO_3^- differs between life forms and plants.

Study sites

The two field sites are located in open, dry, coastal dunes at two different islands, Terschelling, The Netherlands and Hiddensee, Germany. Terschelling is a West-Frisian island in the North Sea, where the sea water has a salinity of ca. 35 PSU (Swertz et al, 1999). It has an Atlantic climate (Olson et al., 2004) with an average temperature of 9.5°C and a precipitation of 775.5 mm yr^{-1} (www.worldclimate.com, station Leeuwarden and Groningen). The experiment was conducted in a dry, lichen-rich, short dune grasslands north of Horn (UTM: 53413915, 5373309). Hiddensee is situated in the German part of the southern Baltic Sea, where the salinity is ca. 8-10 PSU (Feistel et al., 2008). The climate is characterized as Baltic (Olson et al., 2004) with an average temperature of 8.0°C and 564 mm yr^{-1} precipitation (www.worldclimate.com, station Greifswald). The experimental site is located at an open dune system at the southern tip of Hiddensee, an area called Gellen (UTM: 54479486, 13064725). Wet N-deposition has been 13-20 kg N ha^{-1} yr^{-1} in open dune areas at Terschelling in early 1990s (Houdijk and Roelofs, 1991; Sival and Strijkstra-Kalk, 1999). At Hiddensee no long records are known. But a nearby EMEP station at Zingst had an average of 6.3 kg N ha^{-1} yr^{-1} during 2001-2005 (Remke et al., 2009a/chapter 3), and no major nearby pollution sources like intensive animal husbandry or power plants are known for at least the past two to three decades. The nitrogen input in the last two decades stayed the same (Tarrasón and Schaug, 1999).

During the two months, that the experiment was running, a total of 171 mm precipitation (average 2.6 mm day^{-1}) was measured at Hiddensee and 229 mm (average 3.1 mm day^{-1}) at Terschelling (www.wetteronline.de). At Hiddensee 6 mm and at Terschelling 5 mm rain fell during the first week after fertilization.

Material and methods

At each field site, Terschelling and Hiddensee, a ^{15}N-NH_4^+ (10% ^{15}N enriched NH_4Cl) or ^{15}N-NO_3^- (5% ^{15}N enriched $NaNO_3$) solution was applied once in the middle of the vegetation period (mid-July) of 2006. The applied amounts were the equivalents of one month wet N-deposition of 0.5, 8, 16, 40 kg N ha^{-1} yr^{-1} dissolved in 3 L m^{-2} deionised water. The 0.5 kg N ha^{-1} yr^{-1} dose was not expected to cause any treatment effect and was applied to trace the partitioning of N-uptake. The plots (n=6; in total n=48 per site) were 1 m², and 5-7 m apart from each other in order to avoid exchange of nutrients by rhizomatic plants.

In each plot the coverage of plant life form (lichens, mosses, grass, forbs, litter, open sand) was estimated, a species list of all vascular plants, lichens and mosses was compiled, and the microrelief, orientation, inclination and number of animal droppings was noted. Plant species were identified with the following literature: for vascular plants, Rothmaler et al. (2002) and Oberdorfer (1994), for mosses, Frahm and Frey (1992) and for lichens, Wirth (1995).

All biomass samples, single plant species and soil samples were taken two months after N-application. For vascular plants (*Carex arenaria*, *Corynephorus canescens* P. Beauv.) roots and shoots were collected, and for the moss *Dicranum scoparium* Hedw. the green parts of the above ground plant material was collected. For the lichen *Cladonia portentosa* (Dufour) Coem. the top few cm's of the thalli were sampled in order to exclude tissue with nutrients taken up from the soil. The samples were cleaned roughly in the field and stored in a paper bag at 4°C. At each plot, a total aboveground biomass sample (circle with a diameter of 29.5 cm) was taken. Below this biomass circle, three soil samples were taken between 0-10 cm depth, using a core cutter (100 cm³). The three soil samples were mixed together, stored in one paper bag, and dried at 40°C for 24 hours before further analysis.

Background wet deposition of nitrogen was measured at both field sites by collecting bulk precipitation between July 2006 and July 2008. Two rainwater collectors, consisting of a black polyethylene bottle (2 L) connected to a funnel with a plastic filter on top, and containing 2 ml of a 200 mg L^{-1} $HgCl_2$ solution to inhibit microbial activity, were placed several meters apart from each other in an open dune area. Each collector was placed in a PVC pipe dug into the sand, and rainwater was collected 10 cm above ground level in open habitat. Six times per year, samples were collected, precipitation volume was measured in the field and samples were stored at -20°C until further analysis.

For the lichen biomonitor, ten 10x10 cm samples of *Cladonia portentosa* were cut with a pair of scissors out of the centre of a lichen patch of ca. 0.4-0.5 m diameter at field site (Søchting, 1995). Only the top 2 cm of *Cladonia* were collected. Samples were cleaned and analysed like other plant material.

Biomass samples were sorted into cryptogams (lichens and mosses), forbs, grasses and dead biomass. Separately collected plant species (*Carex*, *Corynephorus*, *Dicranum* and *Cladonia*) were thoroughly cleaned, and only the living (green) tissue was taken for further analysis. It was briefly rinsed in deionised water and dried at 70°C for 24 hours. All plant and soil samples were ground in a centrifugal mill (rotational speed 18000, FRITSCH pulverisette 14, Idar-Oberstein, Germany) for 1-2 minutes. For plant and soil material, stable isotope ratios of nitrogen $\delta^{15/14}N$, atom.% ^{15}N and total N were determined with an elemental analyzer (EA 1110 Elemental Analyzer, Carlo Erba/ Thermo Fisher

Scientifique) coupled through a Conflo III to an IRMS (DeltaPlus, ThermoFinnigan, Bremen, Germany).

For the total amounts of other elements (Al, Ca, K, Mg, Na, P and S) 200 mg of the ground (plant and soil) material was digested in sealed Teflon vessels in a Milestone microwave oven (type Ethos D, Milestone Inc., Sorisole, Italy) after addition of 4 ml HNO_3 (65 %) and 1 ml H_2O_2 (30 %) (Kingston and Haswell, 1997).

Dried soil samples were sieved (2 mm diameter), bulk density and total root biomass determined. Within the soil > 2 mm, pH (0.2 M NaCl and double deionised water) and organic weight were determined (Loss on Ignition (LOI), 550 °C for 8 hours). Total extractable amount of Al, Ca, K, Mg, P and S were analysed in a 0.2 M NaCl and Na in a deionised water extract. Elements in acid destructions of plant material and extracts of soil were analysed with inductively-coupled plasma emission spectrophotometry (ICP-OES: IRIS Intrepid II XDL, Thermo Fisher Electric, Breda, The Netherlands).

For calculation of nitrogen mineralization (and nitrification) 60 g of sieved soil was kept in sealed (parafilm) glass beakers at 40% water holding capacity for 28 days at 25°C in total darkness. NO_3^- and NH_4^+ were measured at start and end of the incubation period. The concentrations of ortho-P, NO_3^- (deionised water extract), and NH_4^+ (0.2 M NaCl extract) of the samples from deposition collectors and of the various soils were measured colorimetrically with an Auto Analyzer 3 system (Bran+Luebbe, Norderstedt, Germany), using ammonium molybdate (Henriksen, 1965), hydrazine sulphate (Technicon, 1969) and salicylate (Grasshoff and Johannsen, 1977) respectively.

The ^{15}N atom.% was corrected for different enrichments by dividing the incorporated ^{15}N-NH_4^+ by two (equation 1 and 2).

(1) ^{15}N [%] treatment - ^{15}N [%] control = ^{15}N [%] uptake

(2) for ^{15}N-NH_4^+ : ^{15}N [%] uptake / 2 = corrected ^{15}N [%] uptake

For the total recovery of applied ^{15}N the amount of ^{15}N in the biomass (and soil) per relevee was calculated:

(3) total N [g] × (corrected ^{15}N [%] uptake / 100) = ^{15}N [g]

(4) ^{15}N [g] × (biomass part [g DW m^{-2}] × relevee cover [%] / 100) = ^{15}N biomass part [g DW m^{-2}]

Hereafter, for the term 'corrected ^{15}N [%] taken up' the simplified term '^{15}N atom.%' is used.

Before fertilization of the plots, at each plot one rhizon soil moisture sampler (5 cm porous polymer, Eijkelkamp, Giesbeck, The Netherlands), coupled to a syringe under vacuum, was installed vertically in the top 5 cm mineral soil. In each syringe 2 ml of a 200 mg L^{-1} $HgCl_2$ solution was added to inhibit microbial activity in captured soil pore water. One week after fertilization all syringes were brought to the laboratory and collected water was frozen until further analysis. Less than ca. 10% of all rhizon samplers functioned properly due to vacuum loss in the syringes at dry soil conditions. Thus, only a rough estimate of N-leaching via the soil pore water can be given (table 5). Due to small sample amounts , only total, not ^{15}N, NH_4^+ and NO_3^- in captured water could be analysed

(Auto Analyzer 3 system, Bran+Luebbe, Norderstedt, Germany). During the first week after fertilization 5-6 mm of rain fell at both field sites at one instance. At least half of the rain will be taken up by the vegetation. This can be supported by own observations during the fertilization with the same amount of water. Rain showers can be comparable intense and short as sprinkling with a spraying can, but are normally less intense. The rest, ca. 3 L, might rinse to deeper soil layers and as the organic matter content is really low, probably leached further down in the soil profile. A rough estimate for the total amount of leached N per plot is therefore calculated as:

(5) amount '^{15}N' = (concentration of NH_4^+ or NO_3^- in captured water per treatment [µmol L^{-1}] - concentration of NH_4^+ or NO_3^- respectively in control treatment [µmol L^{-1}]) × 3 L

Further on, the percentage of N in leachate of total applied ^{15}N-NH_4^+ and ^{15}N-NO_3^- was calculated (table 5).

Data were analysed statistically with software packages from the R-Project for Statistical Computing (R development core team, 2008). Effect of treatments and differences between plant types were analysed with an ANOVA and a Tukey-HSD post-hoc test. Factors not normally distributed were transformed (log, (double) square root) before subsequent analysis (Crawley, 2005, 2007). Tests between two classes were performed by students t-test, when normally distributed. Otherwise a non- parametric Kruskal-Wallis test was performed (Crawley, 2005, 2007).

Results
Difference between the two field sites

The measured, total wet N-deposition for Hiddensee is 8.3 kg N ha^{-1} yr^{-1} and for Terschelling 7.3 kg N ha^{-1} yr^{-1} in 2006-2008. However, the lichen-N [%] of the biomonitor *Cladonia portentosa* gave contrasting results to the wet deposition measurements for Terschelling and coherent results for Hiddensee. At Terschelling, the lichen biomonitor had an N-content of 0.76%, which is equivalent to the wet deposition of

Table 1 Means (± 1SE) for different soil factors at the two field sites. All elements were salt extracted apart from NO_3^-, ortho-P and sodium (Na), which were water extracted. Significant differences between sites are shown in bold (p<0.05).

	Hiddensee		Terschelling	
	mean	± SE	mean	± SE
pH [NaCl]	4.0	0.1	3.9	0.0
pH [H$_2$O]	5.5	0.1	5.4	0.1
LOI [%]	0.82	0.10	0.83	0.06
N-NO_3^- [g m^{-3}]	0.46	0.06	0.47	0.03
N-NH_4^+ [g m^{-3} d^{-1}]	2.36	0.11	2.18	0.12
N-min. [g m^{-3}]	1.7	0.2	2.1	0.2
ortho-P [µmol kg^{-1}]	32.3	4.5	29.3	8.0
Al [µmol kg^{-1}]	142.6	13.9	155.4	9.3
Ca [µmol kg^{-1}]	589.9	55.0	546.5	28.8
K [µmol kg^{-1}]	**229.7**	14.6	**363.3**	16.5
Mg [µmol kg^{-1}]	**289.5**	28.4	**504.1**	23.0
Na [µmol kg^{-1}]	**22.2**	13.3	**75.1**	12.1
P [µmol kg^{-1}]	**32.1**	2.1	**15.9**	1.2
S [µmol kg^{-1}]	33.8	1.8	32.7	1.2

Table 2 Means (± 1SE) of different vegetation and relevee factors for each site. Significant differences are shown in bold (p<0.05).

	Hiddensee		Terschelling	
	mean	± SE	mean	± SE
inclination [°]	**0.6**	0.1	**3.0**	0.3
rabbit pellets [no. m⁻²]	**0**	0	**78**	6
forb cover [%]	**10.0**	0.7	**12.4**	0.8
grass cover [%]	25.1	1.2	23.1	0.8
moss cover [%]	24.7	2.3	25.0	1.8
lichen cover [%]	39.2	2.4	40.6	2.8
litter cover [%]	12.7	0.8	12.6	0.7
open sand cover [%]	**5.3**	0.8	**6.7**	0.5
grass [g m⁻²]	**38.6**	9.1	**67.0**	12.7
forb [g m⁻²]	14.3	6.2	27.4	9.7
lichen and moss [g m⁻²]	884.6	209.6	889.4	105.8
dead biomass [g m⁻²]	**174.4**	41.3	**297.8**	38.6
root biomass [g cm⁻² and 10 cm depth]	410.3	64.1	379.2	35.8

Table 3 Species occurrence [%] at Hiddensee and Terschelling in all relevees. (*Viola reichenbachiana/ riviana*: these two species could not be differentiated as only vegetative parts were available. *Cetraria aculeata/ muricata* and *Cladonia coccifera/ pleurota* could not be differentiated reliably and were therefore grouped.)

	species occurrence [%]			species occurrence [%]	
species	Hiddensee	Terschelling	*species*	Hiddensee	Terschelling
vascular plants			lichens		
Agrostis capillaris	4	10	*Cetraria islandica*	2	-
Aira parecox	-	94	*Cetrariaaculeata/ muricata*	38	29
Ammophila arenaria	13	98	*Cladonia arbuscula*	29	6
Anthoxantum odoratum	56	2	*Cladonia cervicornis*	-	15
Arenaria serpyllifolia	-	2	*Cladonia ciliata*	4	6
Calamagrostis epigejos	-	2	*Cladonia coccifera/ pleurota*	4	56
Calluna vulgaris	8	-	*Cladonia coniocrea*	17	2
Carex arenaria	98	100	*Cladonia fimbriata*	17	35
Cerastium fontanum	-	4	*Cladonia floerkeana*	15	-
Cerastium semidecandrum	-	25	*Cladonia foliacea*	35	83
Corynephorus canescens	100	96	*Cladonia furcata*	27	23
Crataegus spec.	2	-	*Cladonia rangiformis*	38	69
Empetrum nigrum	2	35	*Cladonia glauca*	4	-
Festuca ovina agg.	38	17	*Cladonia gracilis*	42	10
Festuca rubra	8	6	*Cladonia macilenta*	6	-
Galium verum	10	-	*Cladonia portentosa*	100	98
Hieracium pilosella	17	13	*Cladonia pyxidata*	25	42
Hieracium umbellatum	60	92	*Cladonia ramulosa*	42	42
Holcus lanatus	-	8	*Cladonia rangiformis*	38	69
Hypocheris radicata	63	100	*Cladonia subulata*	23	-
Jasione montana	79	98	*Cladonia uncialis*	13	-
Leontodon autumnalis	-	15	*Hypogymnia physodes*	8	-
Lonicera periclymenum	-	6			
Lotus corniculatus	-	6	mosses		
Luzula campestris	10	88	*Brachythecium albicans*	-	2
Polypodium vulgare	-	44	*Campylopus introflexus*	6	46
Rumex acetosella	69	88	*Ceratodon purpureus*	31	2
Teesdalia nudicaulis	2	-	*Dicranum scoparium*	98	100
Veronica officinalis	-	10	*Hypnum cupressiforme agg.*	-	21
Viola canina	4	17	*Polytrichum piliferum*	2	10
Viola reichenbachiana/ riviana	6	-	*Rhythidiadelphus squarrosus*	-	2
Viola tricolor agg.	4	-			

14.1 kg N ha^{-1} yr^{-1}. At Hiddensee, these numbers were 0.57% and 8.0 kg N ha^{-1} yr^{-1} respectively (calculation see Remke et al., 2009a/chapter 3). Furthermore, at Hiddensee the total wet deposition was more dominated by NH_4^+ with 61% versus 53% at Terschelling.

The two sites showed no difference in soil-pH, organic matter content of the mineral soil, available nitrate, ammonium or N-mineralisation (table 1). But salt extractable mineral soil constituents gave higher results at Terschelling compared to Hiddensee for K (1.5x), Mg (2x) and Na (3x) (table 1) and only P (2x) is higher at Hiddensee.

Aboveground biomass for grass and dead biomass was ca. 2x higher at Terschelling than at Hiddensee (table 2). Differences in vegetation cover were apparent only for forbs and

Table 4 Element tissue concentration [mg g^{-1}] for single species at control treatments. Significant differences (p<0.05) between sites are shown in bold.

	Carex (s)				Carex (r)			
	Hiddensee		Terschelling		Hiddensee		Terschelling	
	mean	SE	mean	SE	mean	SE	mean	SE
Al	**0.07**	0.009	**0.04**	0.004	0.07	0.014	0.06	0.006
Ca	2.64	0.317	2.28	0.126	0.80	0.154	0.88	0.042
K	**9.00**	0.915	**14.47**	0.557	6.02	0.629	7.10	0.387
Mg	1.60	0.171	1.40	0.029	0.71	0.144	0.69	0.019
Na	**0.96**	0.037	**1.80**	0.155	**0.67**	0.058	**0.99**	0.029
P	1.39	0.099	1.55	0.042	1.43	0.095	1.45	0.091
S	1.33	0.045	1.37	0.041	**0.71**	0.066	**0.78**	0.020
N	11.95	1.064	11.41	0.305	4.89	0.696	4.94	0.188
N/P-ratio	9.0	1.40	7.4	0.28	3.5	0.48	3.5	0.15
	Corynephorus (s)				Corynephorus (r)			
	Hiddensee		Terschelling		Hiddensee		Terschelling	
	mean	SE	mean	SE	mean	SE	mean	SE
Al	0.03	0.004	0.03	0.003	NA		0.06	0.016
Ca	2.01	0.173	2.10	0.444	NA		1.88	0.294
K	6.80	0.858	6.96	0.214	NA		3.48	0.616
Mg	0.84	0.137	0.70	0.029	NA		0.62	0.089
Na	0.57	0.102	0.84	0.154	NA		1.67	0.374
P	1.25	0.109	1.22	0.138	NA		1.63	0.382
S	0.90	0.063	0.90	0.214	NA		1.26	0.189
N	9.38	0.542	7.90	0.700	NA		8.60	0.406
N/P-ratio	7.8	0.88	6.5	0.15	NA		7.3	1.00
	Cladonia				Dicranum			
	Hiddensee		Terschelling		Hiddensee		Terschelling	
	mean	SE	mean	SE	mean	SE	mean	SE
Al	0.15	0.013	0.18	0.021	**0.19**	0.014	**0.38**	0.052
Ca	**0.38**	0.031	**0.54**	0.019	**1.88**	0.157	**2.24**	0.169
K	1.37	0.053	1.57	0.086	3.47	0.147	5.05	1.035
Mg	**0.29**	0.017	**0.46**	0.013	1.07	0.036	1.33	0.124
Na	**0.34**	0.026	**0.45**	0.026	0.53	0.047	0.67	0.079
P	0.44	0.024	0.45	0.028	1.15	0.030	1.13	0.095
S	**0.66**	0.033	**0.85**	0.031	0.83	0.036	0.89	0.052
N	**6.23**	0.294	**7.60**	0.292	**10.33**	0.482	**8.46**	0.415
N/P-ratio	14.9	1.21	16.9	0.93	9.0	0.47	7.7	0.47

open sand with a slightly higher cover at Terschelling (table 2). Species composition between the two sites was remarkably different (table 3). Various reindeer lichens occurred only at Hiddensee e.g. *Cladonia macilenta* agg. Hoffm., *Cl. glauca* Flörke, *Cl. subulata* (L.) Weber ex F.H. Wigg. and *Cl. uncialis* (L.) Weber ex F.H. Wigg. and other lichens like *Hypogymnia physodes* (L.) Nyl. and *Cetraria islandica* Ach. still grew on bare sand. At Terschelling these species were absent, but grasses like *Calamagrostis epigejos* (L.) Rothor, *Holcus lanatus* L. as well as the moss *Hypnum cupressiforme* Hedw. or *Rhythidiadelphus squarrosus* (Hedw.) Warnst. occurred.

The total N-control treatment tissue concentration was for *Cladonia* (20%) higher at Terschelling than at Hiddensee, but for *Dicranum* (20%) higher at Hiddensee (table 4). No other life form or species showed significant differences. Compared to *Corynephorus*, *Carex* had 30% more N in its shoot tissue and 50% less N in its root tissue (table 4).

Site differences in soil mineral concentration were only reflected in plant background tissue of *Carex arenaria*, not of *Corynephorus canescens*. *Carex* had 1.5-2x higher K- and Na-shoot (and root) tissue concentration at Terschelling than at Hiddensee. (table 4). *Cladonia portentosa* incorporated 30-60% more Mg, Na and S at Terschelling in its tissue and *Dicranum* had 2x higher Al-tissue concentration at Terschelling.

Nitrate and ammonium recovery in plant and soil

The total recovery of the applied N in biomass was for ^{15}N-NH_4^+ 13% at Hiddensee and 9% at Terschelling and for ^{15}N-NO_3^- ca. 7% at each site (table 5). In the soil pore water roughly 20-30% of the applied ^{15}N-NO_3^- and 50-70% of the applied ^{15}N-NH_4^+ could be collected at both sites during the first week after fertilization (table 5).

Table 5 Percentage recovery for each biomass part within the totally recovered ^{15}N and the total recovery of applied ^{15}N in biomass ('cryptogams' = lichens and mosses, 'dead' = dead biomass) and soil pore water are given. Soil and root biomass had zero recovery rates and are therefore not listed in this table. Treatment levels of NH_4^+ or NO_3^- 8, 16 and 40 resemble one month equivalents for 8, 16 or 40 kg N ha^{-1} yr^{-1} (^{15}N enriched).

| | | biomass parts | | | | total recovery of appl. ^{15}N [%] | | | |
| | | ^{15}N in total recovered [%] | | | | total biomass | soil pore water | | |
treat	field site	cryptogams	dead	forbs	grass		NO_3^-	NH_4^+	total N
NH_4^+ 8	Hiddensee	94.6	3.1	0.8	1.6	12.1	5.1	61.6	66.7
NH_4^+ 16	Hiddensee	95.9	3.1	0.1	0.7	18.5	0.9	43.9	44.9
NH_4^+ 40	Hiddensee	93.6	4.5	0.6	1.3	7.5	1.6	92.7	94.4
NO_3^- 8	Hiddensee	98.0	1.5	0.0	1.8	6.6	-3.6	-7.7	-11.4
NO_3^- 16	Hiddensee	94.6	3.9	0.7	1.5	6.2	NA	NA	NA
NO_3^- 40	Hiddensee	95.8	1.8	0.9	1.6	8.0	62.7	0.8	63.5
NH_4^+ 8	Terschelling	94.3	4.6	0.7	0.3	7.4	0.8	62.2	63.1
NH_4^+ 16	Terschelling	92.8	5.7	0.5	1.0	8.9	1.2	63.5	64.7
NH_4^+ 40	Terschelling	89.8	7.4	0.6	2.2	10.3	1.4	33.2	34.7
NO_3^- 8	Terschelling	94.7	3.5	0.3	1.6	5.4	4.7	0.4	5.1
NO_3^- 16	Terschelling	93.8	3.1	0.6	2.5	8.2	37.5	2.4	39.9
NO_3^- 40	Terschelling	91.1	5.8	0.7	2.3	5.7	23.1	1.2	24.3
average NH_4^+	Hiddensee	94.7	3.6	0.5	1.2	12.7	2.5	66.1	68.7
average NO_3^-	Hiddensee	96.2	2.4	0.5	1.6	7.0	29.5	-3.4	26.1
average total	Hiddensee	95.4	3.0	0.5	1.4	9.8	-	-	-
average NH_4^+	Terschelling	92.3	5.9	0.6	1.2	8.9	1.1	53.0	54.1
average NO_3^-	Terschelling	93.2	4.2	0.6	2.1	6.5	21.8	1.3	23.1
average total	Terschelling	93.6	4.3	0.6	1.6	8.4	-	-	-

In root biomass and soil nearly no ^{15}N could be detected (data not shown) and the total amount of N in soil was ca. 0.2 [mg g^{-1}] at both sites. Most of the ^{15}N was taken up by lichens and mosses, 95% at Hiddensee and 93% at Terschelling of the total ^{15}N found in the biomass. Forbs only took up ca. 0.5% at both sites, the dead biomass incorporated 3% at Hiddensee and 5% at Terschelling.

Lichens and mosses as well as the dead biomass took up more ^{15}N-NH$_4^+$ than ^{15}N-NO$_3^-$, whereas forbs preferentially took up ^{15}N-NO$_3^-$ (only at Terschelling a tendency, figure 1). With respect to grass biomass (life form sample), no significant difference between N-forms was apparent. Though looking at *Carex* and *Corynephorus* separately, at the high treatment dose *Carex* incorporated more ^{15}N-NO$_3^-$ than ^{15}N-NH$_4^+$, while *Corynephorus* took up equal amounts of ^{15}N-NH$_4^+$ and ^{15}N-NO$_3^-$ (figure 2). Within the tissue (shoot and root) of *Corynephorus* 2x more ^{15}N could be analysed compared to *Carex*. In contrast to *Carex* and *Corynephorus*, *Cladonia* (1.5x) and *Dicranum* (2x) took up more ^{15}N-NH$_4^+$ than ^{15}N-NO$_3^-$ (figure 3).

Generally, more ^{15}N was taken up at Hiddensee than at Terschelling (table 6). Within the total biomass sample, lichens and mosses (cryptogams) took up ca. 30% more ^{15}N-NH$_4^+$ and ^{15}N-NO$_3^-$ and forbs 30% more ^{15}N-NO$_3^-$ at Hiddensee than at Terschelling. *Corynephorus* (shoot) took up 50% more ^{15}N-NO$_3^-$ and *Cladonia* took up 30-60% more ^{15}N-NH$_4^+$ and ^{15}N-NO$_3^-$ at Hiddensee. *Carex* (shoot) and dead biomass were an exception of this pattern, ca. 50% more ^{15}N-NO$_3^-$ was taken up at Terschelling than at Hiddensee.
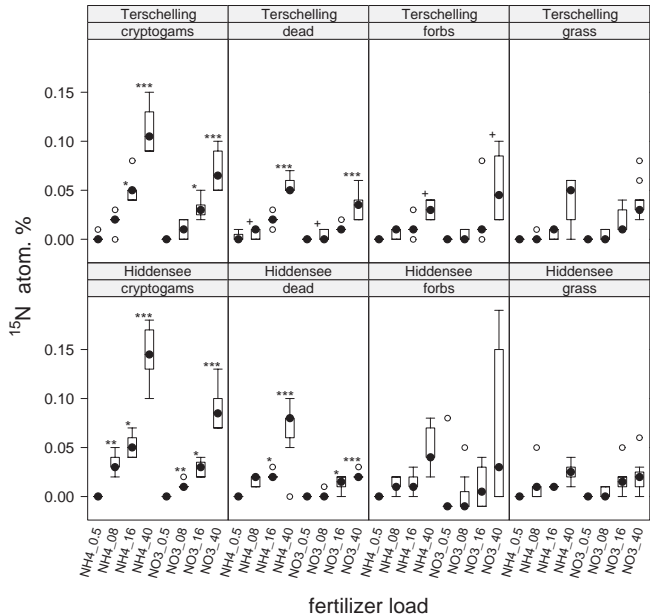
Figure 1 Boxplots for ^{15}N atom.% of different biomass compartments ('cryptogams' = lichens and mosses, 'dead' = dead biomass) for all fertilizer applications and the two field sites. NH$_4^+$ 0.5 and NO$_3^-$ 0.5 are control treatments with 0.5 kg N ha^{-1} yr^{-1} (^{15}N enriched), NH$_4^+$ or NO$_3^-$ 8, 16 and 40 resemble one month equivalents for 8, 16 or 40 kg N ha^{-1} yr^{-1} (^{15}N enriched). Significant differences between same level of NH$_4^+$ and NO$_3^-$ treatment for one field site and plant life form are shown, e.g. Terschelling cryptogams NH$_4^+$ 40 kg N ha^{-1} yr^{-1} against NO$_3^-$ 40 kg N ha^{-1} yr^{-1}, NH$_4^+$ 8 kg N ha^{-1} yr^{-1} against NO$_3^-$ 8 kg N ha^{-1} yr^{-1} etc. (***<0.001, **<0.01, *<0.05, +<0.1).
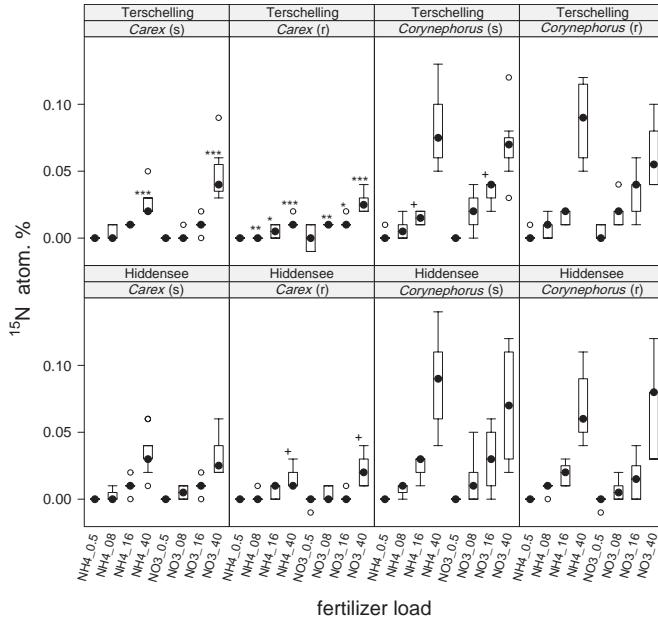
Figure 2 Boxplots for ^{15}N atom.% of *Carex arenaria* and *Corynephorus canescens* ('s' = shoot i.e. above ground living biomass and 'r' = root i.e. below ground biomass) for all fertilizer applications and the two field sites. NH_4^+ 0.5 and NO_3^- 0.5 are control treatments with 0.5 kg N ha^{-1} yr^{-1} (^{15}N enriched), NH_4^+ or NO_3^- 8, 16 and 40 resemble one month equivalents for 8, 16 or 40 kg N ha^{-1} yr^{-1} (^{15}N enriched). Significant differences between the same level of NH_4^+ and NO_3^- at each field site are shown (***<0.001, **<0.01, *<0.05, +<0.1).

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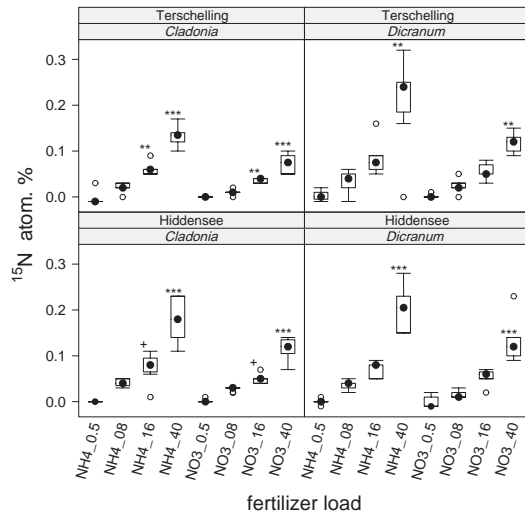
Figure 3 Boxplots for ^{15}N atom.% of *Cladonia* and *Dicranum* for all fertilizer applications and the two field sites. NH_4^+ 0.5 and NO_3^- 0.5 are control treatments with 0.5 kg N ha^{-1} yr^{-1} (^{15}N enriched), NH_4^+ or NO_3^- 8, 16 and 40 resemble one month equivalents for 8, 16 or 40 kg N ha^{-1} yr^{-1} (^{15}N enriched). Significant differences between same level of NH_4^+ and NO_3^- and field site are shown (***<0.001, **<0.01, *<0.05, +<0.1).

Table 6 ^{15}N atom.% (mean ± 1SE) of different biomass compartments ('cryptogams' = lichens and mosses, 'dead' = dead biomass) and single species ('r' = roots i.e. below ground roots and rhizomes and 's' = shoot i.e. aboveground living biomass) at the highest fertilizer applications ^{15}N-NH$_4$$^+$ and NO$_3$$^-$ 40 kg ha^{-1} yr^{-1}. Significant differences between sites for each treatment shown in bold of total ANOVA (site comparison by treatment and type). For each significant difference the site which has the higher mean of ^{15}N atom% are given ('H' = Hiddensee and 'T' = Terschelling).

| | treat ^{15}N-NH$_4$$^+$ 40 | | | | | | treat ^{15}N-NO$_3$$^-$ 40 | | | | | |
| | Hiddensee | | Terschelling | | | higher site | Hiddensee | | Terschelling | | | higher site |
	mean	± SE	mean	± SE	p-value		mean	± SE	mean	± SE	p-value	
biomass												
cryptogams	**0.143**	0.010	**0.112**	0.011	0.0426	H	**0.090**	0.009	**0.070**	0.009	0.0024	H
dead	0.063	0.012	0.054	0.003	0.1697		**0.022**	0.002	**0.035**	0.006	0.0258	T
forbs	0.044	0.009	0.028	0.006	0.1089		**0.071**	0.040	**0.053**	0.020	0.0005	H
grass	0.023	0.004	0.038	0.010	0.3049		0.021	0.007	0.039	0.006	0.0523	
single species												
Carex (s)	0.031	0.006	0.023	0.005	0.1404		**0.032**	0.007	**0.049**	0.008	0.0335	T
Carex (r)	0.014	0.004	0.010	0.002	0.0901		**0.023**	0.005	**0.022**	0.003	0.0078	H
Corynephorus (s)	0.087	0.012	0.083	0.013	0.1686		**0.104**	0.039	**0.070**	0.010	0.0024	H
Corynephorus (r)	0.067	0.013	0.088	0.010	0.4321		**0.069**	0.017	**0.057**	0.008	0.0037	H
Cladonia	**0.183**	0.015	**0.136**	0.009	0.0175	H	**0.114**	0.009	**0.073**	0.008	0.0009	H
Dicranum	0.204	0.021	0.202	0.039	0.3820		**0.135**	0.021	**0.117**	0.009	0.0040	H

Discussion

Difference between the two field sites

The short term application of labelled nitrogen has been done at two sites with contrasting N-deposition history, one low site at the Baltic Sea, Hiddensee, and one high site at the North Sea, Terschelling. At Hiddensee, measured wet atmospheric N-deposition and the value given by the lichen biomonitor both result in a value of 7-8 kg N ha^{-1} yr^{-1}. At Terschelling, the wet deposition measured in 2006-2008 is only ca. 7 kg N ha^{-1} yr^{-1} and the one measured with the biomonitor is calculated to be 14 kg N ha^{-1} yr^{-1}, which goes also inline with recorded, historical values (13-20 kg N ha^{-1} yr^{-1}) in the late 1980s/ early 1990s (Houdijk and Roelofs, 1991; Sival and Strijkstra-Kalk, 1999). At Hiddensee the N-deposition has probably not changed for a long time and is in the same range for at least the last two decades (Tarrasón and Schaug, 1999). But at Terschelling the N-deposition, and in particular the amount of NHx might have decreased during the last two decades, in agreement with the whole Netherlands (de Haan et al., 2008). The lichen biomonitor shows the history of N-deposition and not only the actual deposition (compare Remke et al., 2009a/chapter 3). On top, it might capture higher quantities of dry deposition, which is less captured in bulk precipitation.

Dry deposition of NHx might be, despite a reduction during the last decades, higher at Terschelling than at Hiddensee due to nearby, intensively used meadows. The higher N-deposition history at Terschelling is also supported by species assemblages at both sites. Higher reindeer lichen diversity occurs at Hiddensee and nitrophilous species like *Calamagrostis epigejos*, *Holcus lanatus* and *Rhythidiadelphus squarrosus* grow only at Terschelling. And although rabbits (*Oryctolagus cuniculus* (L.)), important grazers in dunes along the North Sea, occur at Terschelling and none in the research area at Hiddensee, the standing living grass and dead biomass and forb cover is higher at Terschelling than at Hiddensee.

Rabbits shape their environment by creating a grass-dominated, short vegetation with a certain cover of open soil and a decreased standing living and dead biomass (Bakker et al., 2004). Additionally, it is known that rabbit pellets can fertilize vegetation locally via latrines with high numbers of pellets, but little is known about the effect on fertilization and nutrient cycling of pellets that are scattered during foraging (Bakker et al., 2004). No latrines were apparent in experimental plots at Terschelling, therefore high levels of nutrient input via pellets at plots is not probable. It is thus more likely, that the higher grass and dead biomass can be linked to the higher N-deposition history at Terschelling than to internal fertilization by rabbits.

No difference is apparent for N-related soil factors between sites. Looking at the total N-content in plant tissue no vascular plants showed a difference. Only *Cladonia portentosa* has a higher N-content (ca. 20%) at Terschelling. *Cladonia* can store N for a certain range of years (Remke et al., 2009a/chapter 3). Vascular plants can control the uptake and redistribution of N actively, former difference in N-deposition is not reflected anymore in actual plant tissue.

Site differences in available soil mineral elements are not reflected in *Corynephorus* but in *Carex. Corynephorus* is known to have arbuscular mycorrhiza (AM) like nearly all Poaceae (Sitte et al., 2002). Whereas only some sedges are known to form AM (Muthukumar et al., 2004), but this has not been reported for *C. arenaria*. In this study *Carex* takes up mineral elements following the availabilities in soil, which supports non-mycorrhizal root structure with more-or-less unfiltered element uptake.

Cladonia portentosa efficiently takes up nutrients from the air and precipitation (Crittenden 1983, 1989; Hyvärinen and Crittenden, 1998), and therefore, under coastal conditions major nutrient input comes from the sea spray. The salinity of the sea near Terschelling is 3.5x higher than at Hiddensee, which explains the higher concentrations of Ca, Mg, Na and S in *Cladonia* at Terschelling.

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Total recovery and differential uptake of ^{15}N-NH$_4^+$ and ^{15}N-NO$_3^-$

The total recovery of applied N was very low with 9-13% for ^{15}N-NH$_4^+$ and 7% for ^{15}N-NO$_3^-$ within biomass and none recovered in the soil. Leaching losses via soil pore water were estimated to be very high, around 30-60% during the first week. Recoveries in literature are most often higher. In a sub-artic heath, 48% of the applied ^{15}N is recovered (Andresen et al, 2008), for a *Deschampsia* dominated heathland 63% if vegetated and 11% for the barren soil (Troelstra et al., 2001). However, all these ecosystems have a higher organic matter and N-content in the soil, and probably also a higher root density. Evans et al. (2008) found that about 80% of applied nitrate has been immobilised by microbial activity and only 6% leached in a peaty, organo-mineral soil in UK uplands. The coastal dry grasslands in this study have only 0.8% organic matter and 0.2 N [mg g^{-1}] in the top 10 cm soil layer. Thus, most of the applied N leaches through the coarse sand without being attached to any ligand or taken up and immobilized by microbes, fungi or plant roots. Low recovery rates though, might also be slightly underestimated as dry deposited N or N of low-intensity rain events are likely to be more efficiently retained than experimentally high-intensity one-shot applications (Evans et al., 2008).

Nearly all of the ^{15}N recovered could be found in lichens and mosses (93-95%). These two groups together are the most abundant life forms and dominate the short, dry, coastal

dune grasslands. Effects on this part of the system are a driving factor for the whole ecosystem. Whereas vascular plants are of minor importance for the N-uptake of the whole ecosystem - only 0.5% of the total sum of ^{15}N is recovered. One reason might also be that forbs take up less nutrients via leaves more via roots and not as lichens and mosses over the total surface (Crittenden, 1991; Hale, 1969,1983). Lichens and mosses have a more permeable surface, and less developed systems for nutrient transport and nutrient uptake as vascular plants (Sitte et al., 2002). Nevertheless, larger growing vascular plants may intercept areal N, which is subsequently accumulating at the lower growing lichen and moss layer. The high recovery of ^{15}N in dead biomass is probably due to a higher percentage of dead lichens and mosses in the litter, which incorporated ^{15}N passively.

Most species took up more ^{15}N at Hiddensee than at Terschelling (table 6). This is especially so for *Cladonia portentosa* and the total cryptogam biomass (lichens and mosses). Coastal dry dunes are probably still more N-limited and more likely to take up atmospheric N-deposition at Hiddensee than at Terschelling. The difference between the two sites in N-limitation is nevertheless not high enough to be revealed in significant site differences in total plant tissue N-concentration. But biomass growth might be higher at Terschelling and therefore total N per m² in biomass higher at Terschelling than at Hiddensee. For *Carex* (shoot) this is the other way around. More ^{15}N is taken up at Terschelling than at Hiddensee. This, however, might be due to the fact that the availability of important macro-nutrients e.g. Mg, Na or K in the soil is by several factors higher at Terschelling than at Hiddensee, and thus the incorporation of extra available N can be higher. This is supported by the fact, that *Carex* also shows a higher background element concentration for these elements at Terschelling.

When one compares the uptake of nitrate versus the one of ammonium separately at each field site *Carex* takes up more ^{15}N-NO_3^- than ^{15}N-NH_4^+. It behaves thus more like a calcicole plant and not as a calcifuge, which prefers ammonium. The usage of preferably NO_3^- as N-source might be a reason for the strong competitiveness and fast growth of *Carex* (Pearson and Stewart, 1993). *Corynephorus cancescens* is more balanced in this respect and shows no preference for either N-form. It behaves more like a calcifuge, but as *Corynephorus* can also thrive under calcareous soil conditions this balanced uptake does not surprise.

Furthermore, the amount of ^{15}N found in *Corynephorus* was 2x higher than the one found in *Carex* tissue. And in general, *Corynephorus* had ca. 20% higher N tissue concentration than *Carex*: ca. 30% less in is shoot tissue but ca. 50% more in its root tissue. The tussock structure of *Corynephorus* might act like a funnel, and although not much N might be taken up via the waxy, small leaves, the run off gathers at the base and is then taken up via the roots and distributed in the whole plant. *Corynephorus* seems to be more efficient in N-uptake than *Carex*, but not as plastic as *Carex* in its growth. The N-tissue concentration (plant dry weight) might be less for *Carex*, but total growth higher and therefore the N-tissue concentration diluted. Additionally, parts of the taken-up N in *Carex* might have been redistributed outside of the experimental plot via the long rhizomes and therefore not found in plant tissue analysis. *Carex arenaria* can transport elements via rhizomes over long distances (Noble and Marshall, 1983; D'Hertenfeld and Falkengren-Grerup, 2002; D'Hertenfeld and Jónsdóttir, 1999).

Lichens and mosses in total biomass as well as the single samples of *Cladonia portentosa* and *Dicranum scoparium* took up more ^{15}N-NH$_4^+$ than ^{15}N-NO$_3^-$ (figure 1 and 3). Generally, green algae lichens have a preference for NH$_4^+$ before NO$_3^-$ (Crittenden, 1996; Dahlmann et al., 2004). Also lichens in this study seem to have a higher affinity to atmospheric deposition of reduced N, the more toxic N-form. This combined with their high uptake of applied ^{15}N might makes these lichen species especially vulnerable to increased NH$_4^+$ deposition. In order to detoxify NH$_4^+$ in tissue as well as to maintain cellular pH during NH$_4^+$ assimilation, which produces an excess of protons in plant tissue, lichens synthesise polyamines (Pirintsos et al., 2009). More sensitive species seem to be less able to produce such polyamines than more tolerant lichen species (Pirintsos et al., 2009). This could explain why several lichens were the first species that disappeared from coastal dunes at higher atmospheric N-loads in the 1980/ 90s (Ketner-Oostra and Sykora, 2004). The dominant N-form was at that time reduced and not oxidized nitrogen (de Haan et al, 2008).

Conclusions

The historical wet N-deposition was two times higher at Terschelling than at Hiddensee, but during the last two years the wet N-deposition has been nearly the same, 7-8 kg N ha^{-1} yr^{-1}, for both islands. Nevertheless, the additional amount of dry deposition might still be higher at Terschelling than at Hiddensee today. The species assemblage and standing biomass shows the higher deposition history at Terschelling. The uptake of ^{15}N for various single plants and life forms and total recovery of ^{15}N-NH$_4^+$ is higher at Hiddensee. Total recovery of applied ^{15}N is very low and this is probably due to high leaching losses.

High leaching losses and small nutrient recoveries in biomass and soil tend to keep the system oligotrophic. The long-lived and slow-growing lichens and mosses, that catch nearly all of the recovered ^{15}N, preferably ^{15}N-NH$_4^+$, recycle nutrients rather slow within the system, and therefore support oligotrophic situations and a long persistence of lichen-rich, short dry grasslands. The impact of atmospheric N-deposition on these systems might be comparatively low, when it comes to nutrient accumulation. But the high uptake of preferably reduced nitrogen by lichens might explain the fast disappearance of sensitive lichen species in Dutch, coastal dunes at higher N-loads of especially reduced N during the 1980s. Grass encroachment of *Carex arenaria* in acid, dry coastal dunes cannot be explained by more efficient uptake of N and preferred uptake of NH$_4^+$ compared to *Corynephorus*, but is probably due to a higher growth plasticity of *Carex*.

Acknowledgements

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Terschelling, NL. Sampling the fertilized experimental plots.

Chapter 6

Positive feedbacks accelerate N-deposition induced grass encroachment in dry dunes

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Abstract

Two dry dune grasslands were monthly fertilized with artificial N-deposition during two years: Terschelling (The Netherlands) with a historical deposition of about 15-20 kg N ha^{-1} yr^{-1} and Hiddensee (Germany) with 8-10 kg N ha^{-1} yr^{-1}. Actual N-deposition on both sides was between 8-14 kg N ha^{-1} yr^{-1}. The sites slightly differ in soil properties and species assemblage. At Terschelling the pH is slightly lower (approx. 0.2-0.4 units), the mineral and ecto-organic layer thicker, organic matter content higher and about 25% less species, mainly lichens, occur.

N-fertilisation treatments at both sites did not result in a change in soil properties apart from a tendency to higher Al/Ca-ratios at higher N-loads. The lichen *Cladonia portentosa* and the moss *Dicranum scoparium* reacted faster to N-fertilisation with elevated nitrogen tissue content and a higher free amino acid concentration than the grass *Corynephorus canescens*. *Carex arenaria* showed only minor increases in nitrogen and free amino acids. N/P- and N/Mg-ratios increased and C/N-ratios of plants decreased 2- to 3-fold at Hiddensee and less so, 1.5-2 times, at Terschelling. *Carex* showed a marked increase in height after two years of fertilisation. Mortality was very high for *C. canescens* (85% at highest N-load) and *Cladonia* (approx. 20% at highest N-load) after two years of fertilisation. *Dicranum* and *Carex* showed no or only slightly increased mortality at higher N-loads.

With higher external N-load, the dominant vegetation of dry dunes changes from slow growing plants adapted to oligotrophic conditions and a slow nutrient cycling, towards a dominance of plants with higher nitrogen level tolerance, higher biomass increments and turnover such as *Carex*. Furthermore, the amount of dead biomass increases. Species growing at sites receiving for a longer time period to higher atmospheric N-depositions might be faster damaged at additionally elevated N-loads, their ecological resilience seems to be lower. Higher living and dead biomass results in the accumulation of soil organic matter, faster nutrient cycling and a more constant water content of the soil. These positive feedbacks might explain the recently observed invasion by grasses, shrubs and trees in dry dunes along the north-west European coast.

Introduction

Atmospheric N-deposition can have a strong effect on nutrient-poor, semi-natural ecosystems (Bobbink et al., 1998). The sensitivity and resilience of ecosystems to N-deposition depends on site factors like soil-pH and buffering capacity, total N-budget and cycling, but also total amount, concentration, duration and molecular form of N-deposition (Bobbink et al., 1998; Pearce and van der Wal, 2008; Remke et al., 2009b/ chapter 4; van den Berg et al., 2008).

Lichen-rich grasslands occur on extremely nutrient-poor and dry sands. When circumstances become less extreme, they are readily invaded by tall graminoid species. A transition to tall grass stands, e.g. *Carex arenaria* L., occurs especially under acid conditions (Remke et al., 2009b/chapter 4). Important processes, which lead to grass encroachment are probably accelerated acidification and organic matter accumulation (Remke et al., 2009b/ chapter 4). Research on N-deposition in other ecosystems reveals changes such as accelerated acidification, eutrophication (e.g. increased N-mineralisation), increased availability of toxic elements (e.g. Al, Fe) in the soil, elevated N/P-ratios and shift from

N- to P-limitation in plants (Bobbink et al., 1998; Matson et al., 2002; Kooijman et al., 1998). Shifts in the nutrient availability, nutrient imbalances and thus limitation are well documented for dry heathlands or forest ecosystems, but less well known for coastal dunes. An increased Al/Ca-ratio was hypothesized to occur at increased N-loads in acid coastal dunes, but not tested experimentally (Remke et al., 2009b/chapter 4).

Lichens and mosses are not only the dominant life forms in dry coastal dune grasslands, they also intercept wet N-deposition far more efficient than forbs and grasses (chapter 5). It is apparent, that those species play a dominant role also in nutrient storage and cycling. Lichens and mosses have a long and slow life cycle, and impose therefore a slow nutrient cycling on the whole ecosystem. This slow recycling of nutrients plus high leaching losses tends to keep the ecosystem in an oligotrophic state (chapter 5). The question is, whether nitrogen deposition has an additional influence on the quality of plant tissue, e.g. the mineral element content, especially on lichens and mosses but also on other vascular plants, and if it causes nutritional imbalances like in *Pinus* ssp. (van Dijk et al., 1990). Assimilated N can have primary effects on plants. Among these effects are higher N-content, higher stomatal conductance and N-storage in the form of free amino acids. Secondary effects comprise increased growth and shoot/root-ratio, a decreased mycorrhizal infection or higher mortality (Krupa, 2003). The question arises, how different life forms in a dry coastal system can cope with higher loads of external N and if there are more or less sensitive species. Within this reserach the following hypotheses were stated:

1. At the historically higher deposition site and higher N-treatments, soil will be more acidified, the cation and anion pool will be more depleted, and consequently the Al/Ca-ratio will be higher than at the historically low deposition site.

2. Lichens and mosses take up nutrients more directly than vascular plants. The N-content of lichens and mosses will respond to N-fertilization earlier than of vascular plants.

3. Foliar N-content of vascular plants, lichens and mosses will be higher at the historical high deposition site than at the low deposition site. Additional taken up N will be stored in free amino acids and therefore content of free amino acids is higher at high N-loads.

4. At higher N-loads vascular plants shift from N- to P-limitation and get depleted in cations.

Study sites

The two field sites are located in open, dry, coastal dunes at two different islands, Terschelling, The Netherlands, and Hiddensee, Germany. Terschelling is a West-Frisian island in the North Sea, which has a salinity of approx. 35 PSU in open sea water (Swertz et al., 1999). It has an Atlantic climate (Olson et al., 2004) with an average temperature of 9.5°C and a precipitation of 775.5 mm yr-1 (www.worldclimate.com, station Leeuwarden and Groningen). The experiment was conducted in a dry, lichen-rich, short dune grasslands south-west of Midsland aan Zee (UTM: 53394764, 5250006). Hiddensee is situated in the German part of the Southern Baltic Sea, where the salinity is approx. 8-10 PSU (Feistel et al., 2008). The climate is characterized as Baltic (Olson et al., 2004)

with an average temperature of 8.0°C and 564 mm yr^{-1} precipitation (www.worldclimate.com, station Greifswald). The experimental site is located at an open dune system at the southern tip of Hiddensee, an area called Gellen (UTM: 54479486, 13064725).

Wet N-deposition has been 13-20 kg N ha^{-1} yr^{-1} in open dune areas at Terschelling in the early 1990s (Houdijk and Roelofs, 1991; Sival and Strijkstra-Kalk, 1999). At Hiddensee no long-term recordings are known, but a close-by EMEP station at Zingst recorded an average of 6.3 kg N ha^{-1} yr^{-1} wet deposition during 2001-2005 (Remke et al., 2009a/ chapter 3). The nitrogen input stayed the same throughout the last two decades (Tarrasón and Schaug, 1999). At both sites approx. 7-8 kg N ha^{-1} yr^{-1} bulk deposition were measured between 2006 and 2008 (chapter 5). However, the biomonitor *Cladonia portentosa* (Dufour) Coem. resulted in approx. 8 kg N ha^{-1} yr^{-1} for Hiddensee and approx. 14 kg N ha^{-1} yr^{-1} for Terschelling. The difference in N-loads derived from the biomonitor might be explained by higher amounts of historical N-deposition as well as higher levels of dry (gaseous and particular) depositions at Terschelling compared to Hiddensee (chapter 5).

Material and methods

At both field sites, Terschelling and Hiddensee, a NH$_4$NO$_3$ solution was added monthly between October 2006 until July 2008. The assumed total atmospheric N-deposition was 8 kg N ha^{-1} yr^{-1} for Hiddensee and 20 kg N ha^{-1} yr^{-1} for Terschelling as definite numbers were only available at the end of the experiment. The total N-deposition load aims for each site were background condition (control), 20, 40 and 80 kg N ha^{-1} yr^{-1}. In order to reach these levels the additions were the monthly equivalents of 0, 12, 32 and 72 kg N ha^{-1} yr^{-1} for Hiddensee and 0, 20 and 60 kg N ha^{-1} yr^{-1} wet N-deposition for Terschelling dissolved in 3 L m^{-2} deionised water. After sprinkling the N-solution onto the vegetation, the vegetation was sprinkled with 1 L of deionised water per plot after 24 h to avoid salt burn on plant tissue, unless it had been raining within this time period. The plots (3 for each treatment) were 1 m² in size and 5-7 m separated from each other in order to avoid interchange of nutrients by rhizomatic plants.

In each plot the coverage of plant life form (lichens, mosses, grass, forbs, litter), open sand and species (vascular plants, lichens and mosses) was estimated before the start of the experiment (2006) and after one year (2007) of fertilisation. After two years (2008) of fertilisation, a species list of all vascular plants, lichens and mosses was compiled. Additionally the microrelief, orientation, inclination and counts of animal droppings were noted. Plant species were identified using the following literature: Rothmaler et al. (2002) as well as Oberdorfer (1994) for vascular plants, Frahm and Frey (1992) for mosses, and Wirth (1995) for lichens.

All biomass samples, single plant species and soil samples were taken one and two years after the start of N-fertilisation at the beginning of October 2007 (one year) and the end of July 2008 (two years). In both cases, soil and plant sampling took place three weeks after fertilisation. For vascular plants shoots (the sedge *Carex arenaria* and the grass *Corynephorus canescens* P. Beauv.), and for the moss *Dicranum scoparium* Hedw. the green parts of the above ground plant material were collected. For the lichen *Cladonia portentosa* the top few cm of the thalli were sampled in order to exclude tissue with nutrients taken up from the soil. The samples were immediately stored at 4°C. In 2007, one year after fertilization, samples were stored at 4°C until further analysis, and in 2008, two years after fertilization, samples were frozen at -20°C until further processing for amino acid analysis.

Additionally, a total aboveground biomass sample (29.5 cm diameter circle) was taken at each plot. In this circle three soil samples were taken from the upper 10 cm with a core cutter (100 cm³). The three soil samples were stored together in one paper bag, mixed and dried at 40°C for 24 hours before further analysis.

Biomass samples were sorted into the compartments cryptogams (lichens and mosses), forbs, grasses and dead biomass during winter. Single plant species taken for amino acid analysis (*Carex*, *Corynephorus*, *Dicranum* and *Cladonia*) were thoroughly cleaned with deionised water on a cooled surface, and only living (green) tissue was taken for further analysis.

Part of the plant tissues was taken for free amino acid analysis. Free amino acids were extracted according to van Dijk and Roelofs (1988). They were quantified by measuring fluorescence after precolumn derivation with 9-Fluoroenylmethyl-Chloroformate (FMOC-Cl) and measured using HPLC (with a Star 9050 variable wavelength UV-VIS and Star 9070 fluorescence detector; Varian Liquid Chromatography, Palo Alto, USA) with norleucine as the internal standard. Twenty-two amino acids were detected (alanine, anserine, arginine, asparagine, aspartic acid, cysteine, glutamine, glutamic acid, glycine, histidine, isoleucine, leucine, lysine, methionine, ornithine, phenylalanine, proline, serine, taurine, threonine, tyrosine and valine) and are expressed on a dry weight basis.

The remaining plant material was dried at 70°C for 24 hours. All plant and soil samples were ground in a centrifugal mill (rotational speed 18 000 for 1-2 minutes, FRITSCH pulverisette 14, Idar-Oberstein, Germany). Total N was determined (for plant and soil material) with an elemental analyzer (EA 1110 Elemental Analyzer, Carlo Erba/ Thermo Fisher Scientific).

For the total amounts of other elements (Ca, Mg, P and S) 200 mg of the ground (plant and soil) material was digested in sealed Teflon vessels in a Milestone microwave oven (type Ethos D, Milestone Inc., Sorisole, Italy) after addition of 4 ml HNO_3 (65 %) and 1 ml H_2O_2 (30 %) (Kingston and Haswell, 1997).

Dried soil samples (at 40°C for 24 hours) were sieved (2 mm diameter), bulk density and total root biomass was determined. The pH was measured in 0.2 M NaCl and deionised water, and organic weight was determined as Loss on Ignition (LOI) (550 °C for 8 hours). Total extractable amounts of Al, Ca, K, Mg, P and S were analysed in a 0.2 M NaCl and Na in a double deionised water extract. Elements in acid destructions of plant material, salt and water extracts of soil were analysed with inductively-coupled plasma emission spectrophotometry (ICP-OES: IRIS Intrepid II XDL, Thermo Fisher Electric, Breda, The Netherlands).

For calculation of nitrogen mineralisation (and nitrification) a 60 g sieved soil sample was kept in sealed (parafilm) glass beakers at 40% water holding capacity for 28 days at 25°C in total darkness. NO_3^- and NH_4^+ were measured at start and end of the incubation period. The concentrations of ortho-P, NO_3^- (deionised water extract), and NH_4^+ (0.2 M NaCl extract) of soil samples were measured colorimetrically with an Auto Analyzer 3 system (Bran+Luebbe, Norderstedt, Germany), using ammonium molybdate (Henriksen, 1965), hydrazine sulphate (Technicon, 1969) and salicylate (Grasshoff and Johannsen, 1977), respectively.

In July 2007 three whole plants of *Corynephorus canescens* with roots (and partly soil surrounded) were taken per field plot and stored at 4°C immediately. In the laboratory, the roots were cut off and rinsed with deionised water. Arbuscular mycorrhiza (AM) structures were coloured with trypan-blue after Philipps and Haymann (1970).

Mycorrhizal infection (vesicles, arbuscules and hyphae) were counted on two plates with a mixture of the three plants per plot with the magnified line intersect method after Mc Gonigle et al. (1990).

Data were analysed statistically with software packages from the R-Project for Statistical Computing (R development core team, 2008). Effects of treatments and differences between plant types were analysed with an ANOVA and a Tukey-HSD post-hoc test. Data not normally distributed were transformed (log, (double) square root) before subsequent analysis (Crawley, 2005, 2007). Tests between two classes were performed by students t-test, when normally distributed. Otherwise a non-parametric Kruskal-Wallis test was performed (Crawley, 2005, 2007).

Results
Site differences

At Terschelling, both litter layer (Of) and mineral horizon (Ah) are two times thicker than at Hiddensee, and also dead biomass shows a tendency to be two times higher at Terschelling than at Hiddensee (table 1). Grass cover is the same for both sites, but moss and forb cover is approx. 2-5 times higher at Hiddensee (table 1). Lichen cover is higher at Terschelling, but lichen species numbers per m^2 are twice as high at Hiddensee than at Terschelling (table 1). Also forb species numbers are two times and total species numbers

Table 1 Site differences for relevee background data (average of 2006, 2007 and 2008), ecto-organic soil horizon and Ah-layer thickness (average of 2007 and 2008), life form cover (average of 2006, 2007 and 2008) and biomass (2008) as well as species number (average of 2006, 2007 and 2008) per plot are given (mean ± 1SE).

	Hiddensee		Terschelling		p-value
	mean	± SE	mean	± SE	
inclination [%]	**0.7**	0.3	**4.6**	0.9	0.043
rabbit pellets [no. m^{-2}]	**0**	0	**91**	15	0.000
Ol [cm]	0.83	0.25	1.29	0.21	0.129
Of [cm]	**2.17**	0.02	**4.50**	0.20	0.002
Oh [cm]	0.32	0.12	0.42	0.08	0.500
Ah [cm]	**3.17**	0.31	**5.50**	0.22	0.029
bulk density [g cm^{-3}]	1.29	0.02	1.24	0.03	0.089
grass cover [%]	25.0	5.5	25.3	5.2	0.940
forb cover [%]	**14.8**	3.0	**3.2**	0.9	0.000
moss cover [%]	**31.6**	10.4	**14.9**	5.1	0.024
lichen cover [%]	**43.0**	8.1	**61.0**	10.5	0.034
dead biomass cover [%]	16.7	3.4	14.7	2.3	0.434
open sand cover [%]	7.2	2.7	3.1	1.4	0.057
grass biomass [g m^{-2}]	34.7	7.3	39.1	6.1	0.513
forb biomass [g m^{-2}]	27.9	11.0	12.7	6.2	0.275
lichen and moss biomass [g m^{-2}]	381.3	49.0	372.7	51.8	0.827
dead biomass [g m^{-2}]	268.8	43.7	685.5	191.8	0.080
root biomass [g m^{-2} and 10 cm depth]	400.2	59.8	489.8	94.8	0.275
total species [no. species m^{-2}]	**16.3**	1.5	**11.9**	1.6	0.029
grass [no. species m^{-2}]	2.9	0.2	3.9	0.4	0.080
forbs [no. species m^{-2}]	**3.3**	0.5	**1.8**	0.4	0.023
moss [no. species m^{-2}]	1.9	0.5	2.1	0.1	0.596
lichen [no. species m^{-2}]	**8.2**	1.6	**4.1**	1.1	0.037

Table 2 Species occurrence [% of all relevees per site and all treatments pooled] per year and site. No significant differences between years or treatments were apparent.

	Hiddensee			Terschelling		
	2006	2007	2008	2006	2007	2008
grasses						
Carex arenaria	100	100	100	100	100	100
Corynephorus canescens	100	100	92	100	100	89
Festuca ovina	0	0	0	0	0	22
Festuca rubra	25	17	25	0	22	33
Luzula campestris	25	42	42	33	44	33
Ammophila arenaria	0	0	0	100	89	100
Anthoxantum odoratum	0	50	83	0	0	0
Agrostios capillaris	17	25	0	0	0	0
Holcus lanatus	8	0	0	0	0	0
Aira praecox	0	0	0	0	0	33
forbs and (dwarf) shrubs						
Jasione montana	75	83	75	0	0	0
Hypocheris radicata	92	83	75	56	56	56
Hieracium pilosella	17	0	0	11	0	0
Hieracium umbellatum	50	50	50	11	0	11
Rumex acetosella	50	42	58	89	100	100
Viola canina	0	0	0	11	22	22
Polypodium vulgare	0	0	0	11	22	11
Empetrum nigrum	0	0	0	22	22	22
Calluna vulgaris	0	0	0	0	11	11
Rosa spec.	0	0	0	0	22	11
mosses						
Dicranum scoparium	100	100	100	100	100	100
Ceratodon purpureus	42	50	50	0	0	0
Campylopus introflexus	25	25	42	89	89	100
Polytrichum piliferum	0	0	0	33	33	44
Pleurozium schreberi	0	0	0	0	11	0
lichens						
Cetraria aculeata/muricata	50	58	33	0	11	0
Cladonia arbuscula	8	0	17	0	0	0
Cladonia ciliata	25	16	25	0	0	0
Cladonia cervicornis	0	8	8	0	0	11
Cladonia coniocrea	75	50	92	33	56	56
Cladonia fimbriata	83	83	67	56	78	89
Cladonia floerkeana	58	42	42	11	11	22
Cladonia foliacea	50	58	67	56	67	78
Cladonia furcata	67	67	75	22	22	11
Cladonia glauca	42	42	50	0	0	0
Cladonia gracilis	33	42	33	44	33	33
Cladonia macilenta	42	42	58	0	0	0
Cladonia pleurota/coccifera	25	33	42	56	56	56
Cladonia portentosa	92	92	92	100	100	100
Cladonia pyxidata	50	75	75	67	67	56
Cladonia ramulosa	100	100	100	44	33	56
Cladonia ranigformis	8	8	8	0	0	0
Cladonia subulata	58	33	50	0	0	0
Cladonia uncialis	17	17	17	0	0	0
Hypogymnia physodes	17	17	8	0	0	0

one third higher at Hiddensee, with an average of approx. 16 species per m² (table 1). Species only occurring in field plots at Terschelling were mainly vascular plants such as *Ammophila arenaria* (L.) Link, *Viola canina* L., *Polypodium vulgare* L., *Empetrum nigrum* L. and *Calluna vulgaris* L. (table 2). Typical for Hiddensee is the higher species diversity of lichens: *Cetraria* spec. *Hypogymnia physodes* (L.) Nyl., *Cladonia glauca* Flörke, *Cl. subulata* (L.) Weber ex F.H. Wigg., *Cl. uncialis* (L.) Weber ex F.H. Wigg., *Cl. arbuscula* (Wallr.) Flot. and *Cl. macilenta* agg. Hoffm. only occur at Hiddensee (table 2). At field sites, rabbits (*Oryctolagus cuniculus* (L.)) occurred only at Terschelling and none at Hiddensee and inclination at plots was higher at Terschelling (table 1).

Impact of N-treatments on the soil

After one year of fertilisation, in July 2007, soil factors mainly differed between sites and did not show a treatment effect. The total organic matter of the mineral soil layer (LOI) was slightly lower, the pH_{NaCl} slightly higher and ortho-P two times higher at Hiddensee than at Terschelling (table 1 and 3). After two years of fertilisation, the Al/Ca-ratios increased with higher N-treatments at both experimental sites (table 3).

Impact of N treatments on plants – primary effects

After one year of fertilisation, only the N-tissue concentration of *Cladonia portentosa* and *Dicranum scoparium* have increased significantly with higher N-load. This increase was steeper at Hiddensee than at Terschelling (table 4, figure 1).

Table 3 Mean soil factors and mean root biomass per treatment after one (2007) and two (2008) years of fertilisation (LOI - loss on ignition, CEC - cation exchange capacity). Significant differences (p<0.05) are shown in bold and differences between treatments are given with different letters.

after one year of fertilisation (2007)	Hiddensee				Terschelling		
	G0	G20	G40	G80	TS0	TS40	TS80
LOI [%]	**0.42 a**	**0.43 ab**	**0.36 a**	**0.38 a**	**1.03 b**	**0.56 ab**	**0.49 a**
pH -salt	**4.48 ab**	**4.62 a**	**4.59 ab**	**4.48 ab**	**4.09 b**	**4.19 ab**	**4.37 ab**
pH -water	6.91	6.76	6.72	6.77	6.72	6.89	6.81
C/N	16.1	15.6	12.5	13.1	14.8	11.3	12.0
N [%]	0.02	0.02	0.03	0.02	0.04	0.03	0.02
nitrification [g cm⁻³ d⁻¹]	1.26	1.00	1.29	2.15	2.51	1.82	1.24
N-mineralisation [g cm⁻³ d⁻¹]	1.53	1.22	1.64	2.45	2.61	1.89	1.41
ortho-P [µmol kg⁻¹]	**38.4 a**	**37.5 a**	**23.1 ac**	**29.0 ac**	**15.8 abc**	**9.8 b**	**14.7 bc**
CEC [µmol kg⁻¹]	774.5	732.5	923.9	387.5	440.2	348.5	526.1
Al/Ca	NA	0.60	0.70	1.43	0.33	0.62	0.89

after two years of fertilisation (2008)	Hiddensee				Terschelling		
	G0	G20	G40	G80	TS0	TS40	TS80
LOI [%]	0.37	0.50	0.50	0.39	0.63	0.54	0.52
pH -salt	4.27	4.33	4.32	4.27	4.00	4.09	4.10
pH -water	5.59	5.64	5.60	5.53	5.42	5.52	5.54
C/N	22.9	20.2	22.1	25.2	21.5	19.7	18.9
N [%]	0.02	0.02	0.02	0.01	0.01	0.01	0.01
nitrification [g cm⁻³ d⁻¹]	0.85	1.38	1.62	2.70	2.49	1.93	2.21
N-mineralisation [g cm⁻³ d⁻¹]	1.17	1.38	2.23	2.90	2.11	1.94	1.94
ortho-P [µmol kg⁻¹]	51.9	33.6	36.9	45.0	21.4	16.1	30.5
CEC [µmol kg⁻¹]	914.5	1272.3	1314.5	468.3	1095.1	918.1	1129.1
Al/Ca	**0.27 ab**	**0.16 ac**	**0.16 a**	**0.60 ab**	**0.69 bc**	**0.67 ab**	**0.92 b**

After two years of fertilisation, apart from *Cladonia* and *Dicranum* also *Corynephorus canescens* showed significant increase in N-tissue content (table 4, figure 1). For *Corynephorus* the N-tissue content was about 2 times higher at the highest N-treatment at Hiddensee and Terschelling compared to the control treatment at Hiddensee (table 4). N/P- and N/Mg-ratios of plant tissue increased only at Hiddensee with higher N-treatment and were already quite high at all treatment levels at Terschelling (table 4).

Table 4 Mean element content [mg g^{-1}] in above ground plant tissue per treatment after one (2007) and two (2008) years of fertilisation. Significant differences of ANOVA (p<0.05) are shown in bold and differences between treatments (HSD-Tukey post-hoc) are given with different letters.

|		Hiddensee				Terschelling		
		G0	G20	G40	G80	TS0	TS40	TS80
Carex								
2007	N	11.25	12.07	12.85	11.39	10.26	9.89	9.07
2008	N	12.96	13.19	14.16	17.22	15.98	16.89	17.99
2008	Ca	1.78	1.81	1.98	1.89	1.21	1.45	1.36
2008	Mg	1.41	1.45	1.64	1.50	1.79	1.78	1.85
2008	P	**2.14** [a]	**1.98** [a]	**1.84** [ac]	**1.73** [abc]	**1.18** [bc]	**1.15** [b]	**1.14** [b]
2008	S	**1.42** [ab]	**1.34** [ab]	**1.32** [a]	**1.40** [ab]	**1.61** [b]	**1.63** [b]	**1.65** [b]
2008	C/N	36.32	35.16	33.34	27.63	29.23	27.47	25.83
2008	N/P	**6.06** [a]	**6.16** [a]	**7.67** [a]	**9.91** [ab]	**14.26** [b]	**15.09** [b]	**16.49** [b]
2008	N/Mg	9.13	11.61	8.66	11.94	8.91	9.57	9.74
Corynephorus								
2007	N	7.10	7.02	6.82	8.29	7.84	8.97	7.78
2008	N	**6.84** [a]	**9.10** [ab]	**11.88** [ab]	**12.88** [ab]	**13.88** [b]	**12.90** [ab]	**11.36** [ab]
2008	Ca	1.77	2.30	2.21	1.70	1.85	1.56	1.93
2008	Mg	0.74	0.90	1.04	0.99	0.66	0.66	0.94
2008	P	1.11	1.24	1.35	1.07	1.30	1.25	1.30
2008	S	0.74	0.78	0.82	0.81	1.15	1.04	0.91
2008	C/N	**70.88** [a]	**51.84** [ab]	**42.54** [ab]	**37.50** [b]	**34.45** [b]	**37.03** [b]	**37.19** [b]
2008	N/P	**6.31** [a]	**7.43** [ac]	**8.78** [ab]	**12.07** [b]	**10.78** [bc]	**10.78** [bc]	**8.57** [abc]
2008	N/Mg	**9.34** [a]	**10.24** [ab]	**11.34** [ab]	**13.05** [ab]	**21.44** [ab]	**22.58** [b]	**11.70** [ab]
Cladonia								
2007	N	**5.29** [a]	**6.21** [ab]	**6.37** [ab]	**8.35** [b]	**6.13** [ab]	**6.77** [ab]	**8.44** [ab]
2008	N	**6.32** [a]	**8.40** [a]	**7.89** [a]	**12.16** [b]	**6.42** [a]	**8.43** [ab]	**9.96** [b]
2008	Ca	**0.32** [ac]	**0.40** [abc]	**0.40** [abc]	**0.29** [ac]	**0.52** [b]	**0.54** [b]	**0.34** [c]
2008	Mg	**0.35** [a]	**0.35** [a]	**0.36** [a]	**0.32** [a]	**0.46** [b]	**0.50** [b]	**0.35** [a]
2008	P	0.38	0.39	0.36	0.36	0.32	0.35	0.35
2008	S	**0.64** [a]	**0.87** [ab]	**0.73** [ab]	**1.00** [b]	**0.69** [ab]	**0.92** [ab]	**0.99** [b]
2008	C/N	**71.74** [a]	**53.28** [ab]	**56.57** [a]	**37.30** [b]	**65.75** [a]	**51.08** [ab]	**41.70** [b]
2008	N/P	**16.51** [ac]	**15.65** [a]	**22.40** [abcd]	**33.67** [bd]	**19.99** [abcd]	**24.46** [abcd]	**29.40** [cd]
2008	N/Mg	**18.03** [ac]	**17.42** [ac]	**22.01** [ac]	**38.55** [b]	**14.09** [a]	**16.98** [ab]	**28.08** [ab]
Dicranum								
2007	N	**8.05** [a]	**9.92** [a]	**9.85** [a]	**14.45** [b]	**10.37** [ab]	**10.31** [ab]	**11.49** [ab]
2008	N	**8.91** [ad]	**10.65** [ad]	**11.29** [abcd]	**15.77** [bc]	**8.62** [ab]	**11.94** [abcd]	**13.91** [cd]
2008	Ca	**1.68** [ab]	**1.57** [ab]	**1.28** [a]	**1.20** [a]	**2.44** [b]	**2.45** [b]	**1.83** [ab]
2008	Mg	**1.24** [ab]	**1.00** [a]	**1.05** [a]	**0.88** [a]	**1.67** [b]	**1.64** [b]	**1.21** [ab]
2008	P	**1.03** [a]	**1.07** [a]	**0.88** [ab]	**0.83** [abc]	**0.83** [abc]	**0.71** [b]	**0.57** [c]
2008	S	0.70	0.77	0.72	0.93	0.87	1.05	0.98
2008	C/N	**47.28** [a]	**42.03** [a]	**38.60** [ab]	**26.52** [b]	**46.07** [a]	**35.61** [ab]	**28.93** [b]
2008	N/P	**8.18** [a]	**9.89** [a]	**13.14** [bf]	**19.03** [c]	**10.34** [adf]	**16.99** [bc]	**24.42** [e]
2008	N/Mg	**6.83** [ac]	**10.70** [a]	**10.96** [a]	**18.05** [be]	**5.24** [c]	**7.50** [cd]	**11.55** [ade]
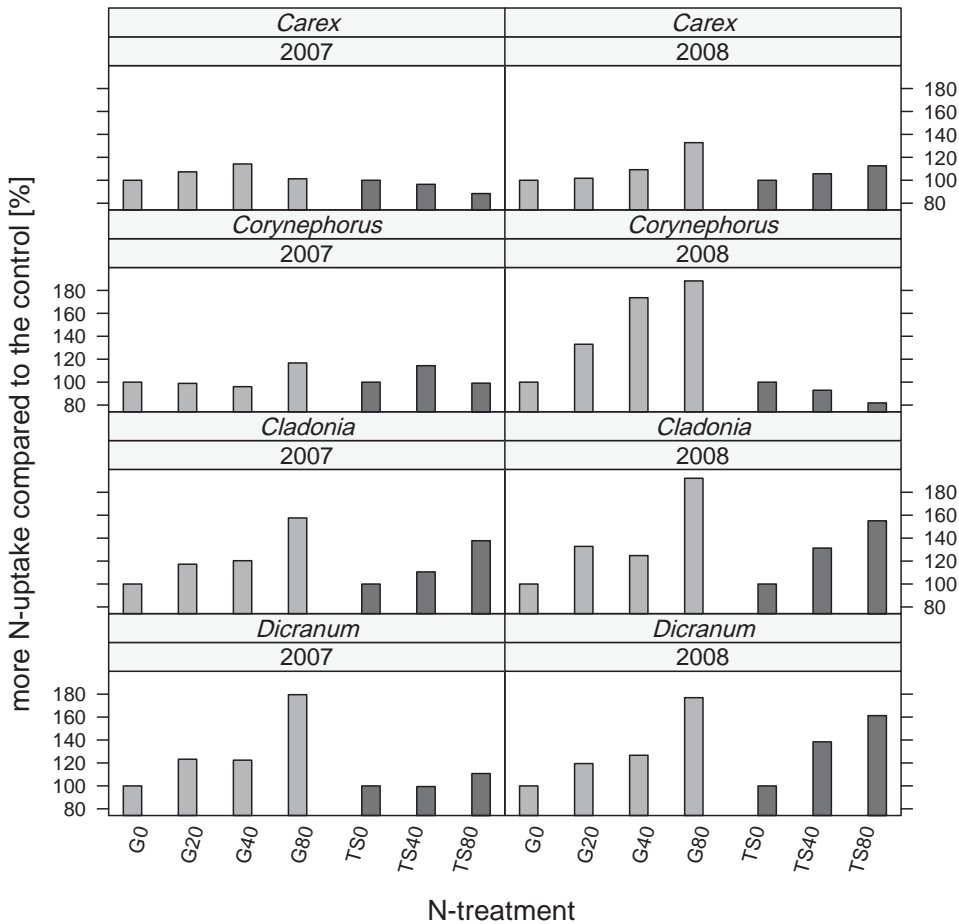
Figure 1 Uptake of N [%] with control plots set as base for different plants and one year (2007) and two years (2008) of N-treatment.

Carex arenaria did not show a significant increase in N-tissue concentration, though a tendency was apparent, but P-tissue content decreased significantly with higher treatment level and was higher at Terschelling than at Hiddensee (table 4). At the highest treatment load at Terschelling, N/P-ratios of *Carex* were around 17, which is nearly three times as high as the control treatment at Hiddensee (table 4). The Mg- and S-tissue concentrations were comparatively higher at Terschelling than at Hiddensee for *Cladonia*, *Dicranum* and *Carex*.

Free amino acids showed a pronounced reaction to N-treatment in all four analysed species and at both sites. At the highest N-treatment, asparagine or arginine accumulated up to 20 times more compared to the control in *Corynephorus* and *Dicranum*, while there was a 10-fold increase in *Cladonia* and no increase at all for these free amino acids in *Carex* (table 5). *Carex* showed only modest increases in alanine, glutamic acid and aspartic acid (1.5-4 times). Glutamine increased only for the cryptogams, i.e. *Dicranum* and

Table 5 Mean free amino acid concentration [µmol g^{-1} dw] in *Carex arenaria* (shoot), *Corynephorus canescens* (shoot), *Cladonia portentosa* and *Dicranum scoparium* tissue per treatment after two years of fertilisation (2008). Amino acids are sorted per plant with increasing C/N-ratio of the respective amino acid. Significant differences ($p < 0.05$) between treatments are given with different letters (ANOVA with HSD-Tukey post-hoc). Only free amino acids with significant differences between treatments are shown.

	C/N-ratio	Hiddensee				Terschelling		
		G0	G20	G40	G80	TS0	TS40	TS80
Carex								
anserine	2.5	0.00 a	0.18 a	0.28 a	0.00 a	0.69 ab	0.50 ab	1.75 b
alanine	3.0	1.25 a	1.43 ab	1.26 a	1.50 ab	2.07 ab	2.34 ab	2.54 b
aspartic acid	4.0	0.61 ab	0.00 a	0.23 ab	0.29 ab	1.66 ab	2.60 b	2.15 ab
glutamic acid	5.0	1.91 a	1.94 a	2.11 ab	2.29 ab	3.02 ab	3.75 b	3.10 ab
leucine	6.0	0.34 ac	0.37 a	0.23 abc	0.35 ac	0.14 bc	0.18 abc	0.00 b
Corynephorus								
asparagine	2.0	0.97 a	2.98 ab	10.62 ab	18.62 ab	14.04 b	7.72 ab	15.29 b
taurine	2.0	0.12 ab	0.05 ab	0.14 ab	0.46 a	0.00 b	0.26 ab	0.00 ab
anserine	2.5	0.00 a	0.00 a	0.00 a	0.03 a	0.49 b	0.36 b	0.71 b
lysine	3.0	0.32 ab	0.36 ab	0.66 ab	0.90 a	0.12 ab	0.13 b	0.09 ab
isoleucine	6.0	0.24 a	0.32 ab	0.46 ab	0.68 b	0.45 ab	0.33 ab	0.42 ab
leucine	6.0	0.37 a	0.46 ab	0.67 ab	0.88 b	0.33 a	0.27 a	0.19 a
Cladonia								
arginine	1.5	2.74 ad	6.27 ae	7.54 afg	23.55 b	2.53 def	8.03 cdef	21.14 bcg
taurine	2.0	3.17 a	8.36 ab	6.86 ab	8.98 ab	3.27 a	5.21 ab	11.55 b
glutamine	2.5	5.30 af	11.83 bg	9.61 aeg	23.48 bd	3.30 cf	5.77 ace	19.19 dg
proline	5.0	1.65 ab	4.33 a	2.07 ab	4.21 a	0.56 b	1.33 ab	2.73 ab
valine	5.0	0.25 ab	0.32 ab	0.26 ab	0.35 a	0.19 b	0.21 ab	0.20 b
leucine	6.0	0.26 a	0.28 a	0.22 a	0.13 ab	0.16 ab	0.15 ab	0.03 b
Dicranum								
arginine	1.5	1.03 a	2.58 abd	6.63 bf	23.47 cg	1.48 a	6.44 df	18.48 efg
asparagine	2.0	2.10 ac	2.55 ac	4.73 ab	7.30 b	1.64 c	2.58 ac	2.84 c
glycine	2.0	0.42 a	0.71 ab	0.82 ab	1.26 ab	0.72 ab	1.58 b	1.44 b
taurine	2.0	0.12 a	0.09 a	0.09 a	0.18 a	0.28 ab	0.23 ab	0.67 b
glutamine	2.5	1.04 a	1.59 a	1.80 abc	3.62 b	1.05 abc	1.53 ac	2.07 bc
lysine	3.0	0.07 ab	0.12 ab	0.17 ab	0.26 a	0.05 ab	0.00 b	0.00 b
glutamic acid	5.0	0.40 a	0.55 ac	0.64 abc	1.02 b	0.63 abc	0.87 bc	1.12 b

Cladonia 2-3 times and 4-6 times respectively at both sites. Some amino acids showed a slight increase at Hiddensee, but nearly no change with N-treatment at Terschelling. Lysine (and leucine) showed a 3-fold increase for *Corynephorus* and *Dicranum* at Hiddensee and remained at a lower level at Terschelling. Leucine remained constant in *Carex* tissue at Hiddensee and decreased to zero at the highest treatment level at Terschelling.

The total amount of free amino acids and free amino acids with a low C/N-ratio were strongly positively correlated with increasing N-tissue content of plants (table 6, figure 2). Amino acids with a low C/N-ratio were defined as having a C/N-ratio ≤ 2.5 and show significant differences for any analysed plant tissue (table 5; anserine, arginine, asparagine, glutamine, glycine and taurine). Additionally, these low C/N-ratio amino acids comprised the main part of all free amino acids analysed (figure 2). Free amino acid content in *Cladonia portentosa* tissue increased 2.5 times steeper with its increasing tissue N-content compared to the other three analysed plants, *Carex arenaria*, *Corynephorus canescens* and *Dicranum scoparium* (table 6).
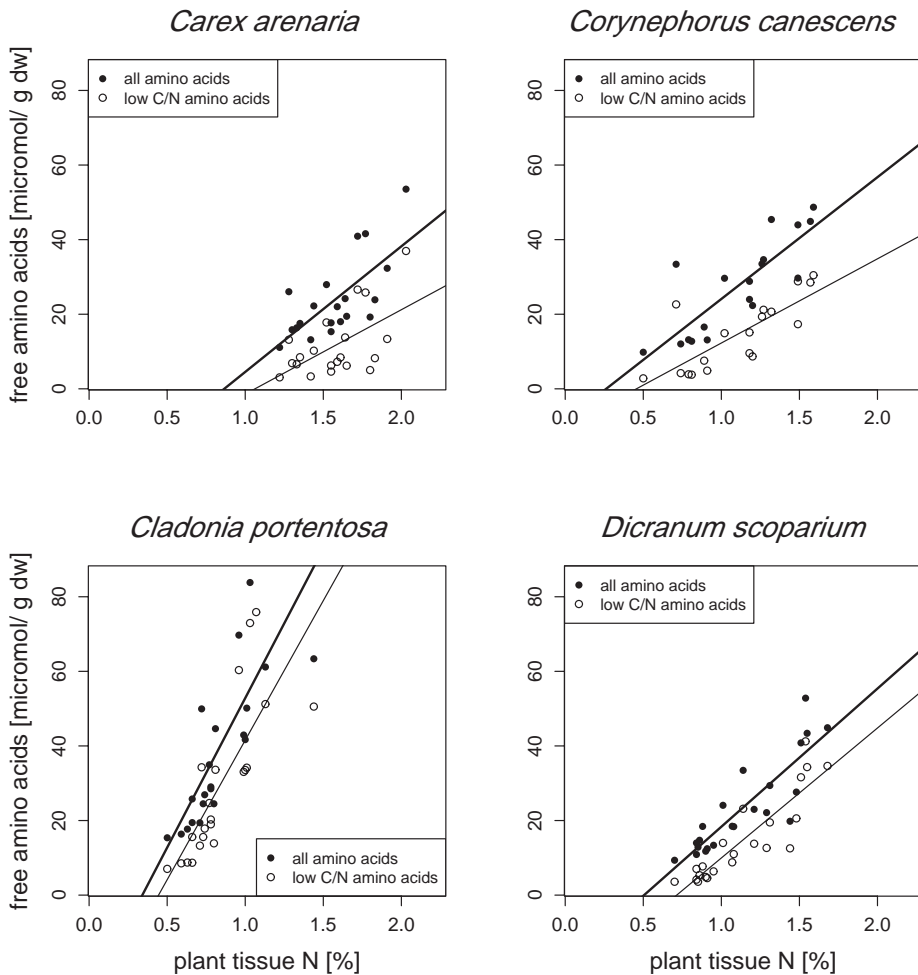
Figure 2 Scatter plot of the free amino acid tissue content against the tissue N-concentration of *Carex arenaria*, *Corynephorus canescens*, *Cladonia portentosa* and *Dicranum scoparium* after two years of fertilisation (in 2008). In filled circles, data for all free amino acids added are shown. Open circles show only the amino acids with a C/N-ratio ≤ 2.5 and giving significant differences for any analysed plant tissue (table 5), i.e. anserine, arginine, asparagine, glutamine, glycine and taurine. Regression lines are shown and regression results are given in table 6.

Impact of N treatments on plants – secondary effects

The height of *Carex arenaria* did not show a treatment effect after one year, but after two years shoots were approximately one quarter to one third taller at the highest treatment load compared to the control (figure 3) This difference, however was only visible at Hiddensee. The horizontal cover of *Carex* as well as of *Anthoxantum odoratum* L. only showed a trend to increase at higher N-loads. At Hiddensee, *Anthoxantum* did not occur at all in experimental plots one year after fertilisation, but after two years of fertilisation 3-4% coverage of *Anthoxantum* occurred at higher treatment loads.

Table 6 Statistical results of linear regression (lm) between the free amino acid tissue content and the tissue N-concentration of *Carex arenaria*, *Corynephorus canescens*, *Cladonia portentosa* and *Dicranum scoparium* after two years of fertilisation (in 2008). Once all free amino acids were added, and once only the amino acids with a C/N-ratio ≤ 2.5 and giving significant differences for any analysed plant tissue (table 5), i.e. anserine, arginine, asparagine, glutamine, glycine and taurine.

		equation	R²	F	df	p-value
Carex	all amino acids	y=33.7×-29.2	0.4890	17.23	18	<0.001
	low C/N amino acids	y=22.6×-24.0	0.3222	8.56	18	0.009
Corynephorus	all amino acids	y=32.7×-8.6	0.6804	34.07	16	<0.001
	low C/N amino acids	y=30.3×-16.4	0.3850	10.64	17	0.005
Cladonia	all amino acids	y=80.2×-27.3	0.6021	30.26	20	<0.001
	low C/N amino acids	y=74.8×-33.3	0.6057	30.73	20	<0.001
Dicranum	all amino acids	y=37.0×-18.7	0.7559	61.95	20	<0.001
	low C/N amino acids	y=34.8×-24.9	0.7824	71.93	20	<0.001
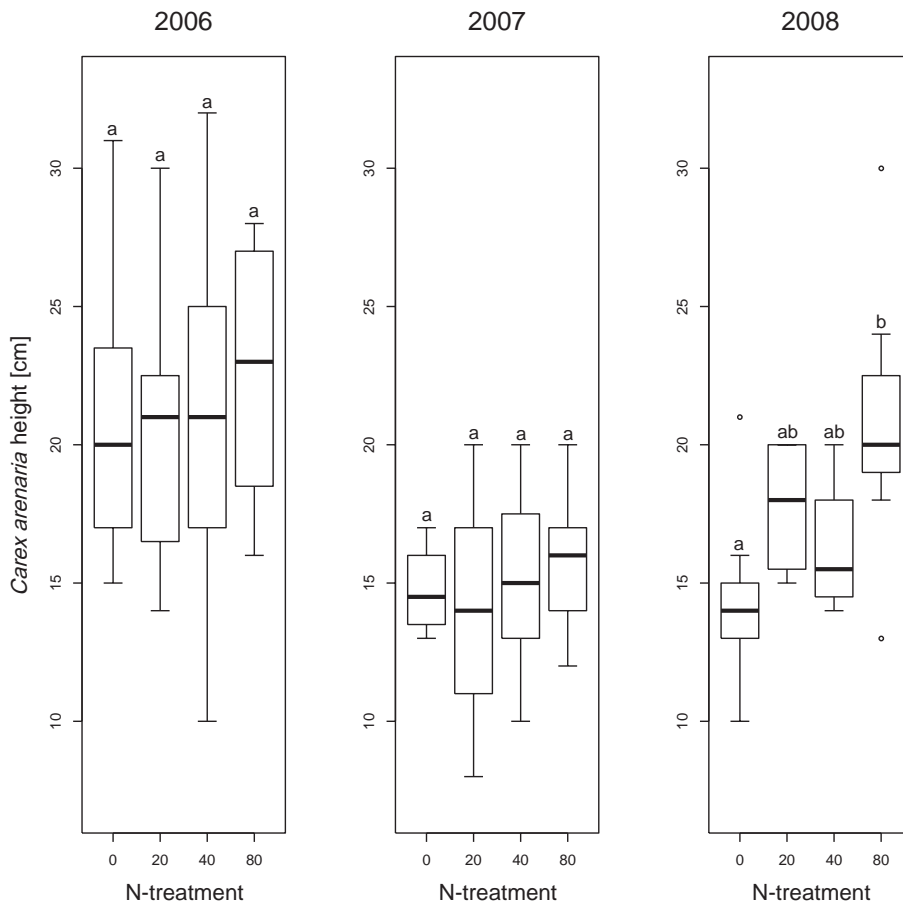
Figure 3 Height of *Carex arenaria* [cm] at Hiddensee for the different years and treatments. Significant differences (ANOVA with HSD-Tukey as post-hoc) between treatments within each year are shown with letters. For Terschelling no significant differences occurred, hence data is not shown.

Mortality of plant parts increased with increasing N-treatment and was higher at Terschelling than at Hiddensee (table 7). *Cladonia* showed an increasing percentage of dead tissue, i.e. destroyed, whitish to yellow surface structure, especially at Terschelling (20% at highest N-treatment), but appeared healthy at Hiddensee (0-2% of dead tissue). *Carex* showed larger parts of yellow and brownish plant tissue at higher N-loads. The percentage of dead tissue of *Corynephorus* increased with N-load and was generally higher at Terschelling than at Hiddensee. It ranged from 13% at the Hiddensee control treatment to 88% at the highest Terschelling N-load (only statistical tendency with only $p<0.1$). *Dicranum* showed no trend for sites and N-treatments.

The infection rate with arbuscular mycorrhiza (AM) of *Corynephorus canescens* roots was not significantly different after one year of N-fertilisation between N-treatments or between sites (test results for pooled AM-structures and treatment effect: Kruskal-Wallis chi-squared = 2.4622, df = 6, p-value = 0.8727; infection rates on average: hypha 42-46 %, vesicle 0.2-0.8%, arbuscle 0.1-0.3%).

Table 7 Mean dying and mean dead parts [%] of *Cladonia portentosa*, *Dicranum scoparium*, *Carex arenaria* and *Corynephorus canescens* per treatment and plot for 2008. Significant differences between treatments of ANOVA (HSD-Tukey as post hoc) are shown with letters and p-value for ANOVA is given.

		Hiddensee				Terschelling			
		G0	G20	G40	G80	TS0	TS40	TS80	p-value
Carex	dying	**4.0 ab**	**3.7 ab**	**2.7 a**	**6.7 ab**	**5.0 ab**	**5.0 ab**	**8.3 b**	**0.031**
	dead	38.3	43.3	40.0	56.7	58.3	56.7	58.3	0.535
Corynephorus	dying	1.5	1.7	0.5	2.0	4.0	4.0	5.5	0.173
	dead	12.5	30.0	25.0	28.3	56.7	56.7	87.5	0.062
Cladonia	dying	7.5	15.7	19.3	8.3	21.7	46.7	41.7	0.102
	dead	**1.0 ab**	**0.0 a**	**0.0 a**	**1.7 ab**	**7.3 ab**	**13.3 ab**	**20.0 b**	**0.009**
Dicranum	dying	68.3	61.7	40.0	61.7	63.3	43.3	65.0	0.467
	dead	18.3	8.3	15.3	26.0	15.0	40.0	20.0	0.526

Discussion
Site differences

The two field sites, Terschelling (NL) with a deposition of 15-20 kg N ha^{-1} yr^{-1} in the mid 1990s and Hiddensee (D) with lower depositions of around 7-8 kg N ha^{-1} yr^{-1}, have an actual total deposition of around 8-12 (14) kg N ha^{-1} yr^{-1} with Hiddensee at the lower end and Terschelling at the higher end of the range (chapter 5). The higher historical and actual N-deposition are for soil factors only visible if they are directly related to dead plant biomass. At Terschelling, two times higher amounts of dead biomass result in thicker ecto-organic (litter) layers (Of), and organic matter is consequently incorporated into the soil, a thicker organic horizon (Ah) occurs.

Total and lichen species number per m^2 were up to 2 times higher at Hiddensee. Lichens like *Cetraria* spp., *Hypogymnia physodes* or *Cladonia glauca* still grow at Hiddensee, but disappeared nearly completely from Terschelling. This higher diversity at Hiddensee is most probably due to lower former and current N-depositions at Hiddensee compared to Terschelling. Similarly, Ketner-Oostra and Sykora (2004) reported a loss in lichen species diversity in Dutch dunes, and attributed this mainly to increased levels of

atmospheric pollution. Lichens seem to be one of the most sensitive life-forms to detect impacts of nitrogen deposition (Fremstad et al., 2005). At comparable low N-deposition loads, at ambient or artificial total N-deposition of 10 kg N ha^{-1} yr^{-1} species diversity decreased also e.g. in prairie grasslands (Clark and Tilman, 2008), deciduous forests (Falkengren-Grerup and Diekmann, 2003) or acid grasslands (Stevens et al., 2006).

The living biomass of grasses is the same for both sites, though one would expect higher grass cover at Terschelling because of its higher N-load. Most probably, rabbits forage large amounts of the standing biomass and equalize the N-deposition induced site differences. Higher biomass of forbs at Hiddensee (5 times) than at Terschelling might mainly be due to rabbit grazing and not N-deposition. With rabbit grazing primarily taller growing species such as *Hieracium umbellatum* L. or *Jasione montana* L. are foraged, while small, in flat rosettes growing forbs (Bakker, 2003) such as *Hypochaeris radicata* L. remain.

Impact of N-fertilisation on the soil

There are nearly no N-treatment effects on the analysed soil features apparent at each site separately. Looking at the two sites and the N-treatment - lowest N-load at the control treatment at Hiddensee, the low N-deposition site, and highest N-load the highest N-treatment at Terschelling - as a continuous row, however, a tendency to an increase in the Al/Ca-ratio with higher N-load is apparent. These elevated Al/Ca-ratios at higher N-loads go inline with earlier findings of a comparison of 19 dunes sites around the Baltic Sea (Remke et al., 2009b/chapter 4). They show a trend to soil acidification and soil depletion in base cations at higher N-depositions. A comparable depletion in base cations and increased availability of aluminium has been found in other ecosystems such as chalk grasslands, heathlands (Bobbink et al., 1998; de Graaf et al., 1997), acid grasslands (Stevens et al., 2009) and forests (van Dijk et al., 1989). Effects of N-deposition on the mineral soil in dry coastal dunes are probably quite slow. High amounts of wet deposited N are probably leached (chapter 5), and therefore quickly unavailable to plants. But over time, a system that is highly affected by atmospheric N-pollution has higher amounts of soil organic matter. More binding options for N-forms, mainly NH_4^+, exist and N is not leached at high rates any longer. The process of nutrient accumulation is positively reinforced. A positive feedback of established grass encroachments has already been assumed for Dutch dunes (Veer and Kooijman, 1997, Kooijman et al., 2009).

Impact of N-fertilisation on plants – primary effects

The various types of species showed a quite remarkable difference in N-uptake and their N/ion-ratio. Lichen (*Cladonia*) and moss (*Dicranum*) increased their tissue N-content after one year of fertilisation already, while graminoids showed a reaction to N-fertilisation only after two years (significantly only for *Corynephorus*). *Corynephorus* seems to have reached a saturation N-level at roughly 12-14 mg N g^{-1} plant dry weight, and even with a higher N-fertilisation this did not increase anymore. *Carex*, however, still increased its N-tissue content at the highest N-load at the higher N-deposition site Terschelling to about 18 mg N g^{-1} plant dry weight. Additionally, *Carex* stored N only from a tissue concentration of approx. 10 mg N g^{-1} onwards in free amino acids, whereas the other analysed plant species already started to produce free amino acids at 3-5 mg N g^{-1} (figure 2). Six mechanisms influence plant nitrogen use or acquisition and predict their

competitive strength: photosynthetic tissue allocation, photosynthetic nitrogen use efficiency, nitrogen fixation, nitrogen leaching losses, gross nitrogen mineralisation as well as plant nitrogen residence time (Laungani and Knops, 2009). Laungani and Knops (2009) showed, that the key mechanism allowing invasion of *Pinus strobus* L. into nitrogen limited grasslands was its higher nitrogen residence time. This positive feedback allowed P. *strobus* to accumulate twice as much nitrogen in its tissues and four times as much nitrogen to photosynthetic tissues as compared to other plant species. Higher tissue N-concentrations of *Carex arenaria* and its effectiveness in invading coastal grasslands indicate that the same mechanisms might also be valid for *Carex arenaria*.

Parallel to the increase of N-tissue content in *Carex* tissue, its amount of tissue P-content decreases. Carex reaches a N/P-ratio of 16-17, which indicates starting P- instead of N-limitation (Koerselman and Meuleman, 1996). Apart from Carex, C/N- and N/Mg-ratio change with N-treatment in all species. This change is mainly due to an elevated uptake of N and not a decrease in e.g. Mg-tissue concentration. Nutritional imbalances at higher N-deposition loads can thus pose a problem for these species (*Cladonia*, *Corynephorus* and *Dicranum*). Higher amounts of elements such as Ca, Mg or S at Terschelling compared to Hiddensee in *Cladonia* and *Dicranum* tissue can be explained by the approx. 3 times higher salinity of the open sea water and thus higher deposition of these elements with the sea spray.

The uptake of N showed the tendency to be lower at Terschelling than at Hiddensee. For *Corynephorus* after two years even no change in N-content occurred anymore. Additionally the ratio change for N/P, N/Mg or C/N with N-treatment were stronger for the low deposition site Hiddensee than for the high N-deposition site Terschelling. Although N-deposition might have decreased at Terschelling in the last decades to levels between 10-15 kg N ha^{-1} yr^{-1} or even lower, vegetation might still be more N-saturated. *Corynephorus* seem to have reached its nitrogen saturation level.

The amount of N-uptake by the different plants corresponds well with the concentration of free amino acids in plant tissue. *Dicranum*, *Cladonia* and *Corynephorus* showed a 10- to 20-fold increase in free amino acids with mainly a low C/N-ratio like asparagine (C/N-ratio of 2), arginine (C/N-ratio of 1.5) or glutamine (C/N-ratio of 2.5). This transformation of NH_4^+ to amino acids and amines enables the plant to detoxify high levels of NH_4^+ in plant tissue and store N with a minimal amount of other elements like carbon, which might get limiting otherwise (Marschner, 1995). Such an increase in free amino acids with higher availability of NHy has also been detected in other studies (Thomassen et al., 2003; van Dijk and Roelofs, 1988). Especially *Cladonia* has a very high free amino acid content per N-tissue content, which might explains its quite large tolerance to high deposition loads. *Carex*, however, did not show such a marked increase in free amino acids, especially not in these low carbon forms. Additionally, the N-tissue increase is not as steep as in the other three species, only 30% in *Carex* compared to 50-100% for the other three species. *Carex* either seems to take up less nitrogen than e.g. *Corynephorus* or, more plausibly, takes up comparable amounts, but invests nitrogen in additive growth and transports excessively taken up nitrogen within its extensive rhizome network to other places, which are less well supplied and which serve as a storage place for nutrients. Elements and water are transported within the rhizomes of *Carex* over long distances of at least 1-2 m (D'Hertenfeld and Falkengren-Grerup, 2002; D'Hertenfeld and Jónsdóttir, 1999). *Carex* therefore has probably no need to detoxify N and store it in free

amino acids, it transports N to other places within its network instead. *Corynephorus*, in contrast, grows in tussocks. Ingested N cannot be relocated to other plants and has to be used or stored within the individual. Additionally, *Corynephorus* is not as plastic in growth as *Carex* and cannot use excessively incorporated N as much as *Carex* for extended growth. One efficient way is to transfer unused N into free amino acids. The accumulation of specific free amino acids such as asparagine can probably be considered as an early warning sign for N-stress in still healthy-looking *Corynephorus* stands, comparable to *Stratiotes aloides* L. in NH_4^+ enriched waters (Smolders et al., 2000).

One remarkable reaction was found with lysine and leucine. At Hiddensee, these amino acids slightly increased in *Dicranum* and *Corynephorus*, while both decreased in *Cladonia*. At Terschelling, however, lysine and leucine concentration in all four species (*Carex*, *Corynephorus*, *Cladonia* and *Carex*) decreased or were already at a low level. Both amino acids are essential and cannot be synthesized by animals or humans (Marschner, 1995; Harrison, 1995). A N-load above 15 kg N ha^{-1} yr^{-1} over a longer period such as 1-2 decades seems to deplete typical dune grassland species in essential free amino acids such as lysine or leucine. Dune invertebrates such as grasshoppers are known to forage on species such as Corynephorus. They can search for plants particularly rich in amino acids (Harrison, 1995), but if nearly all available plants have diminished essential amino acids, this decrease might create a bottleneck in grasshoppers' life cycle.

Impact of N-fertilisation on plants – secondary effects

Only a few indications of higher N-loads on secondary effects in plants could be validated. The growth height of *Carex* increased by a quarter to a third after two years of fertilisation comparing control with the highest N-treatment. The horizontal cover of *Carex* as well as of *Anthoxantum odoratum* L. only showed a trend to increase at higher N-loads. Two years is a short time period for vegetation changes in these oligotrophic and dry ecosystems with a slow nutrient cycle and high leaching losses. But the trend of increasing height and cover of grass species supports the hypothesis that higher loads of atmospheric N-deposition lead to an increase in grasses in dry, coastal dunes. A species change in these systems will probably need at least a couple of years depending on site preconditions like load and level of historical N-depositions or buffering capacity of the soil. In lichen-dominated alpine vegetation, lichen species started to decrease their cover and species richness after 2-4 years within 10 years of fertilisation (Fremstad et al., 2005). Vascular plants showed only minor reactions in cover or richness (Fremstad et al., 2005).

Very important, the amount of dead biomass increased manifold in typical dune grassland species adapted to oligotrophic conditions such as *Corynephorus* (7 times) and *Cladonia* (20 times). *Corynephorus* reached levels of 88% dead parts of standing shoots at the highest N-treatment at Terschelling, *Cladonia* levels of approx. 20% dead parts. Contrastingly, *Carex* increased its dying or dead biomass only slightly. *Corynephorus* and *Cladonia* can probably not cope with too high levels of excessive nitrogen, whereas *Carex* can easily relocate it to other plant-network sites and can probably tolerate more nutrient-rich conditions. Nevertheless, arbuscular mycorrhizal (AM) infection seems to be unaffected by higher N-loads. The AM-infection rate of *Corynephorus* showed no treatment or site effect after one year of fertilisation. Consistently, *Corynephorus* shows no strong nutrient depletion for phosphorus after neither one nor two years of fertilisation.

Conclusion

Short, dry dune grasslands are self-sustained oligotrophic ecosystems. Lichens and mosses act like a sponge for atmospherically deposited elements: they take up elements, like nitrogen, very efficiently, store them in their tissue (some have a wide tolerance of nutrient uptake), their growth and biomass turnover is rather low, and ecosystem nutrient cycling is slow. In sandy soils with low organic matter content high leaching are probable. With higher N-deposition loads, the organic matter content is elevated to a critical level, which changes the system from being highly limited in water and nutrient to more modest soil conditions. Standing biomass of more competitive grasses and dead biomass of more sensitive species increase, organic matter input into the soil is accelerated. Graminoids like *Carex arenaria* seem to facilitate their own environment. At historically higher deposition sites, quite healthy looking species in lichen-rich grasslands might be less resilient to elevated nitrogen deposition than at pristine sites. Indications are the occurrence of nutrient imbalances, limitation by other nutrients than nitrogen and accelerated death of typical plant species.

Early warning signs for a healthy looking ecosystem could be a thicker ecto-organic layer, an Al/Ca-ratio close to 1 in the mineral soil, higher levels of standing dead biomass (especially *Corynephorus* above 50%), a high amount of free amino acids - especially those low in C/N-ratio such as arginine, asparagine or glutamine - or a less rich lichen assemblage. To oligotrophic conditions adapted, slow growing species like *Corynephorus* or *Cladonia* react most sensitively to elevated N-depositions. They are likely to be overgrown by faster growing grasses and possibly also mosses.

Acknowledgements

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Chapter 7

Synthesis

Eva Remke

Status quo of coastal dunes around the Baltic Sea

Around the Baltic Sea, comparable coastal dune sites were chosen by literature review, questionnaire and site visits. All 19 sites chosen have a $pH_{H_2O} < 6.5$ of the parent sand material and a precipitation of 500-700 mm yr^{-1}. The sites are open dunes with < 10% cover of trees and without any physical barrier like a forest towards the sea. These sites have not been intensively managed e.g. by intensive grazing or burning during the last decade.

At each of these sites, atmospheric nitrogen deposition has been measured using a biomonitor, the lichen *Cladonia portentosa* (Dufour) Coem. Many methods quantifying atmospheric deposition are rather expensive and most current methods are unsuitable for remote areas (Pitcairn et al., 2003). An alternative method is the use of a biomonitor, which takes up wet and dry deposition. An ideal biomonitor accumulates the pollutant without being killed by high doses, has a wide geographical distribution, is representative for the collection area, available all year round and easy to collect (Carballeira et al., 2000; Conti and Cecchetti, 2001). Lichens are suitable as biomonitor, because of their slow growth. As they lack cuticle and stomata, they absorb different contaminants over the entire surface (Hale, 1969, 1983). The N-content of lichens sampled in coastal dunes beside the Kattegat, Southern Baltic and Baltic proper is positively correlated with measured wet deposition at nearby EMEP stations (European Monitoring and Evaluation Program, a co-operative programme for monitoring and evaluation of the long-range transmission of air pollutants in Europe). The best fit is found when wet N-deposition is averaged for the last 3-6 years. This time span, covering several years of deposition history, fits closer to slow ecosystem changes, which take at least 1-2 years (chapter 3), and might therefore fit better to ecosystem changes than just yearly measurements. The approximate amount of wet N-deposition calculated for each site is low to medium, 2.3-7.8 kg N ha^{-1} yr^{-1}, in a European context. Even if one accounts for missing dry and wet deposition forms – bulk precipitation underestimates total atmospheric deposition by 20-50% (Boring et al., 1988; Erisman et al., 2005; Heidam, 1993) – the N-deposition within the Baltic Sea region is still low.

Of the four tall graminoid species encroaching coastal dunes of the North Sea, *Ammophila arenaria* (L.) Link, *Calamagrostis epigejos* (L.) Roth, *Carex arenaria* L. and *Elymus athericus* (Link) Kerguelen, only *C. arenaria* covers larger areas in the central and hinter dunes of the Baltic Sea (chapter 3). These *C. arenaria* stands expand at higher atmospheric N-depositions, whereas the area of lichen-rich short grasslands declines. At N-unaffected sites, i.e. sites with maximally 25% more N-deposition compared to background, lichen-rich short grasslands cover 45-80% of the dry sand dunes, whereas taller graminoids are restricted to 5-15% of the area. N-affected sites, however, are characterized by only 15-25% cover of short grasslands, but 40-60% cover of taller graminoids. A coverage of more than 50% of lichen-rich grasslands seems to be common for pristine sites. Taller graminoids occur, but do not dominate (chapter 3).

Apart from N-deposition, a dominance of *C. arenaria* is promoted by higher availability of water – ground water or precipitation – and a relatively low disturbance rate (chapter 2 and 3). Disturbance in coastal dunes primarily consists of shifting sands due to wind activity or trampling by large herbivores, game or livestock. Site specific characteristics such as the level of disturbance or groundwater table can therefore support or diminish a dominance of *C. arenaria* (chapter 2 and 3; figure 1). At the Curonian Spit (LT), Paul
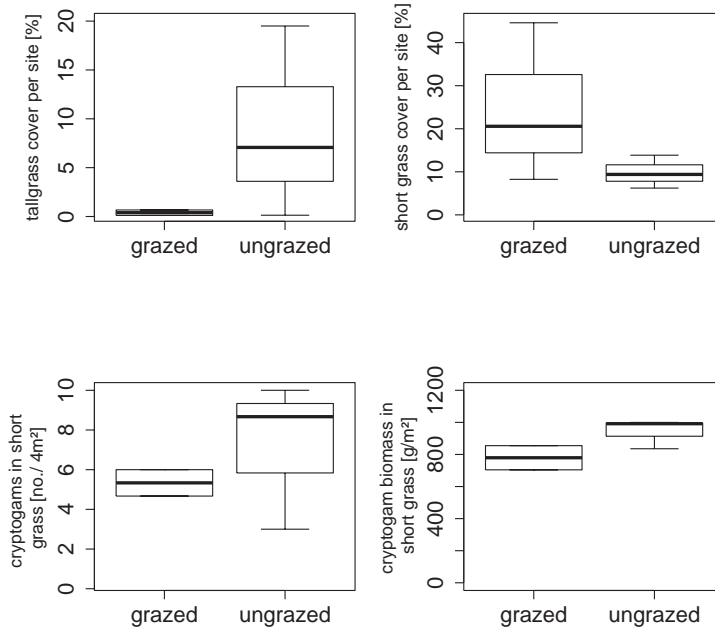
Figure 1 Impact of livestock grazing at three Baltic coastal dunes (Hagön, SE, Holtemmen, DK, and Korshage, DK) on different vegetation characteristics. Tall grass vegetation mainly consits out of *Carex arenaria*, short grasses are species like *Corynephorus canescens* or *Festuca ovina*. With cryptogams only mosses and lichens are meant.

(1944) found that growth of *C. arenaria*, *Calamagrostis epigejos* and *Festuca ovina* L. was stimulated by a rise of the ground water table and reduction in sand mobility due to coastal protection measures. At Baltic coastal dunes, with low to medium levels of N-deposition, livestock can keep tall grasses in check as long as grazing (and potential additional feeding) results in a net nutrient loss (chapter 2). At three Baltic coastal dunes grazed and ungrazed sites were adjacent. Although grazing intensities and herbivore composition differed between sites (various goat, cattle and horse breeds), there were common trends. In grazed dunes the cover of *C. arenaria* decreased, short grassland cover increased, and number and biomass of cryptogams decreased (figure 1). So, livestock grazing can keep a dune grassland short, but characteristic species, in particular lichens, will decline.

The species composition of vegetation dominated by *C. arenaria* can vary considerably. At pristine sites, this vegetation is sometimes species rich and open (Harilaid, EE, or Pavilosta, LT), but at higher N-loads, it forms a species-poor, thick grass sward (Korshage, DK, or Tönnersa, SE) (chapter 4). The species-rich, more open *C. arenaria* dominated vegetation has been described in Baltic dunes since the 1920s (Steffen, 1931; Hueck, 1932; Paul, 1953). At the Curonian Spit, such rather N-unaffected dunes still exist. At these slightly calcareous dunes, Paul (1953) recorded an average of 12 species in the optimal phase of a *C. arenaria* community (*Cladonia* species excluded) during the late 1930s. This number is still the same today, and, quite remarkably, species assemblage has not changed during the last seven decades. A similar decreased number of species (9) of N-affected, slightly calcareous Baltic dunes is also observed in comparable Dutch dunes (Veer and

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Kooijman, 1997), which have received higher N-loads of about 15-20 kg N ha^{-1} yr^{-1} during the past decades. With increasing biomass light availability decreases, and a dense root network establishes (Veer and Kooijman, 1997). This type of *C. arenaria* vegetation is probably quite persistent. Once a thick grass sward has developed, it is difficult for other plants and even trees to germinate and establish. Most of the few species that are still occurring in this vegetation unit (on average 4 in acid dunes) are relics of former, more open stages (chapter 4).

Processes and patterns in dry dune grassland succession – the influence of N-deposition

Under pristine conditions, one of the major succession lines in dry coastal dunes is the slow colonization of the bare sand by lichens, mosses and pioneer grasses, leading to the formation of a lichen-rich short grassland with nearly 100% vegetation cover (figure 2a). Further succession leads to a vegetation dominated by tall grasses or dwarf shrubs such as *Empetrum nigrum* L. or *Calluna vulgaris* L. (e.g. Paul, 1953). The thick carpet of lichens and mosses in short dune grasslands is like a sponge, which efficiently takes up atmospheric depositions (chapter 5 and 6). At bare patches, deposited nitrogen quickly leaches through the coarse sand and is lost for plant or microbial uptake. In a short-term (two months) experiment, only 6-13% of applied ^{15}N was intercepted by the vegetation, and interception was practically restricted to lichens and mosses. Leaching losses were estimated to be around 30-60% (chapter 5), and missing losses might be due to volatilisation of nitrogen. Lichens have a slow biomass turnover (Ahmadjian, 1993; Nash,

pristine conditions

initial stage   short grass   tall grass

slow colonization

long persistence
slow succession

- bare sand
- high drainage
- well buffered

- OM < 1%
- species (lichen) rich
- cryptogams as sponge
- slow nutrient cycling
- high leaching losses
- Al/Ca < 1

- thicker humus, Ah
- high biomass
- fast nutrient cycling
- high nutrient recovery
- Al/Ca < 1

legend
moss   lichen   forb   grass
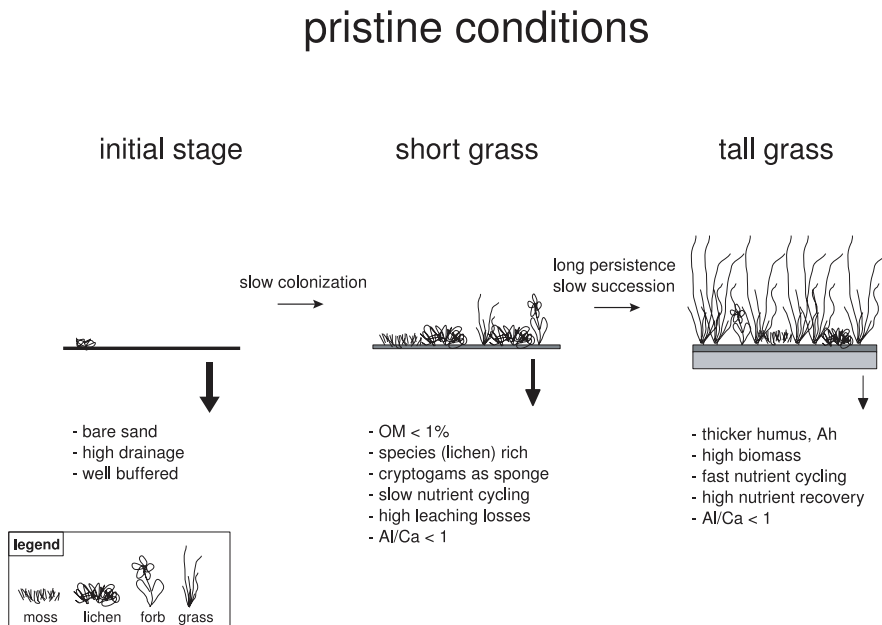
Figure 2a Succession series in dry coastal dunes under pristine conditions, i.e. without elevated atmospheric depositions.

2008), storing atmospheric deposition for a long time period. Tolerated amounts largely depend on species-specific sensitivity to atmospheric depositions. Lichen-rich dry dune grasslands seem to sustain oligotrophic conditions because of high uptake capacity of lichens and mosses, slow nutrient turnover and high leaching losses (figure 2a).

At elevated N-deposition loads, lichen species diversity and cover decreases, while dead biomass (standing biomass and litter) and nutrient input into the soil increases (chapter 6). Soil organic matter accumulates to a larger extent, resulting in higher and more constant soil moisture compared to pristine conditions (figure 2b). Opposite to N-unaffected sites, thicker litter layers, humic soils and an increased interception and evaporation of the standing biomass inhibit leaching of water and nutrients to deeper soil layers. Floristic and faunistic specialists, who are well adapted to highly fluctuating soil moisture and extreme temperature changes, are out-competed by species, which are well adapted to less extreme environmental conditions and have a higher growth plasticity, hence are highly competitive when space and light get limiting. Tall graminoids such as *C. arenaria* can flourish. They facilitate their establishment and persistence by fast nutrient turnover, thick litter and root sward and high standing biomass (chapter 6; figure 2b). Graminoids like *C. arenaria* or *C. epigejos* become dominant, where a sufficient layer of organic matter is available or the top sand layer is nutrient rich (Boorman and van der Maarel, 1997). Additionally, evaporation of dense tall grasslands and water storage will be higher than in lichen-rich short grasslands, and will probably result in less water infiltration.

At which atmospheric nitrogen deposition load dry coastal dunes are affected depends very much on the lime content of the soil. Although pH-differences are small between acid and slightly calcareous Baltic dune sites, they determine which buffer range is acting

polluted conditions
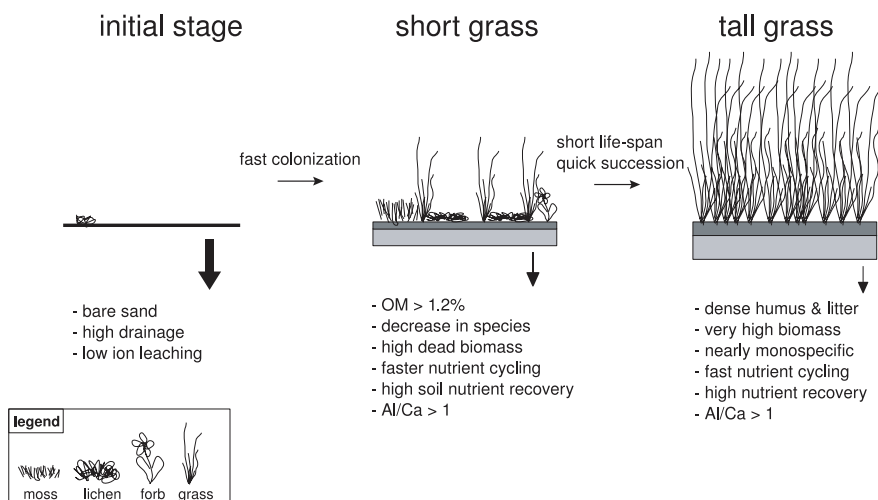
Figure 2b Succession series in dry coastal dunes under polluted conditions, i.e. at elevated atmospheric nitrogen depositions.

(Scheffer and Schachtschabel, 1998; Blum, 2007), how quickly the buffering capacity of cations is depleted, if toxic levels of soluble metals can occur or if mineralisation processes are hampered (chapter 4), if phosphorus is available or bound (Kooijman et al., 1998), how high the N-demand of soil microorganisms is, and consequently how much nitrogen is left for vascular plants (Kooijman and Besse, 2002). At these rather low to medium atmospheric total N-loads of 5-8 kg N ha^{-1} yr^{-1}, effects on soil, plant and vegetation could only be found at acid sites: pH dropped, organic matter accumulated, nitrogen mineralisation was hampered – probably microorganisms have a lower N-demand, more N is left for vascular plants – , water availability rose, *C. arenaria* showed a strong growth response and species diversity, in particular (foliose) lichens, decreased. Organic matter accumulates exponentially from a certain pH downwards (Stützer, 1998; Scheffer and Schachtschabel, 1998; chapter 4), probably around pH$_{NaCl}$<4.0 in dry dune grasslands. At these low pH-ranges, elements like aluminium or iron reach toxic levels for plant species adapted to slightly or well buffered soils (de Graaf et al., 1997; Kleijn et al., 2008), but apparently not so for *C. arenaria*. Lichen species not adapted to these high concentrations of aluminium or iron might take up more metals, which may affect their vitality (Hauck et al., 2002, 2007). Graminoids such as *C. arenaria* facilitate their own environment by several positive feedbacks (figure 3). Once the pH has dropped to a critical level, sufficient organic matter, nutrients and water are available, growth is extended, a taller and higher amount of biomass and litter builds up, organic matter input into the soil is accelerated. The circle starts again. Additionally, taller and dense vegetation
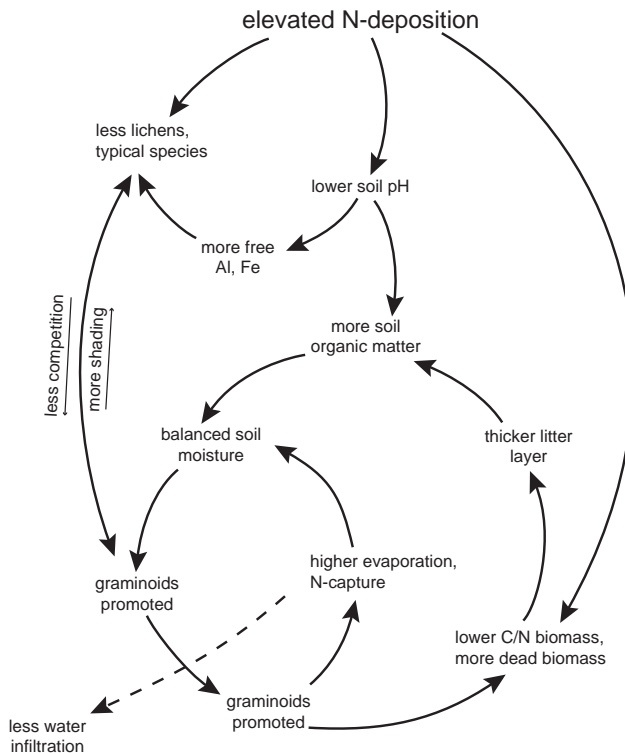
Figure 3 Positive feedbacks at elevated atmospheric N-deposition in lichen-rich, dry short dune grasslands.

intercepts higher amounts of also gaseous and nebulous atmospheric nitrogen, evapotranspiration is elevated, and water loss to deeper soil layers decreases. Moisture conditions at the soil/ ecto-organic horizon interface are more balanced and circumstances more favourable for taller graminoids.

Some Baltic field sites show the expected pattern of acidification during vegetation succession in coastal dunes. The pH remains almost constant during the transition from parent sand material to the 1st stage, the initial stage with mainly bare sand, but decreases with successional age (Ellenberg, 1996; figure 4). During succession, respiration of roots and microbes leads to increased carbonic acid production, dissolution of lime and subsequent leaching of calcium occurs. In contrast to these are Baltic dunes where the pH decreases already between the parent sand material and the 1st successional stage, after which it remains stable (figure 4). This acidification during the early successional stages was not correlated to parent sand material pH or N-deposition, but may instead be caused by anthropogenic sulphur deposition like ship traffic. Sulphur generally generates two times more protons than reduced or oxidised nitrogen (NEGTAP, 2001). Pure chemical reactions might prevail in the bare sands at initial successional stages, whereas biological transformations of nitrogen such as nitrification may dominate the acidifying processes in later successional stages with higher soil organic matter contents. This is supported by the lower pH values of later successional stages, which could be linked to higher N-deposition among Baltic dune sites (chapter 4; figure 4). Atmospheric nitrogen deposition can probably only affect later successional stages on organic-rich sands, whereas at initial stages on almost purely mineral sands are stronger influenced by sulphur deposition.
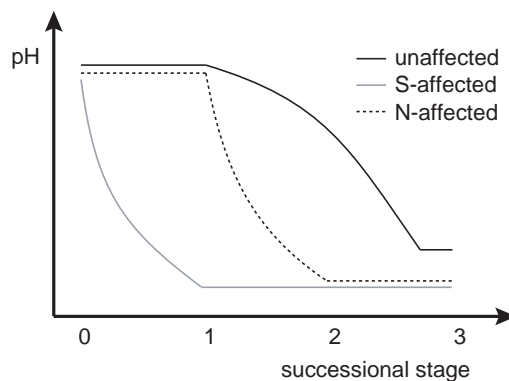
Figure 4 Impact of atmospheric sulphur and nitrogen deposition on the pH of the different succession stages in dry coastal dunes (xerosere): from parent sand material pH (stage 0) to initial colonization of the bare sand by pioneer cryptogams and grasses (stage 1), and then lichen-rich short grasslands with nearly 100% cover (stage 2) to finally tall grasslands covered with taller graminoids such as *Carex arenaria* (stage 3).

However, it takes probably a long time until atmospheric N-deposition affects the soil of dry sand dunes. After two years of monthly N-fertilization with up to 80 kg N ha^{-1} yr^{-1} no significant differences were detected in various soil characteristics, whereas plants, in particular lichens and mosses, showed a quicker, marked response (chapter 6). Lichens and mosses increased their N-tissue concentration already after one year, and far more

pronounced after two years. Luxuriously taken up nitrogen is stored in free amino acids with a low C/N-ratio. Sensitive species such as *Cl. portentosa* and *Corynephorus canescens* P. Beauv. also increased their percentage of damaged/ dead biomass (chapter 6). Dry coastal dune grasslands might be, however, quite susceptible to rather low, but longterm atmospheric N-loads. Nitrogen that enters the system as dry deposition or via low-intensity rain events is likely to be more efficiently retained than experimentally high-intensity one-shot applications (Evans et al., 2008). Most of the nitrogen that was added as a monthly fertilization solution, will probably leach quickly to deeper soil layers in the bare, coarse dune sand (chapter 5). A more gradual application would enable the plants to take up a greater part of the applied nitrogen. N-fertilization experiments therefore most probably underestimate the critical load of nitrogen deposition in sand dunes.

Lichens seem to prefer reduced above oxidised nitrogen (chapter 5). Generally, green algae lichens have a preference for NH_4^+ before NO_3^- (Crittenden, 1996; Dahlmann et al., 2004). Combined with their high uptake of applied ^{15}N, this might make these lichen species especially vulnerable to increased NH_4^+ deposition. In order to detoxify NH_4^+ in their tissue as well as to maintain cellular pH during NH_4^+ assimilation, lichens synthesise e.g. polyamines (Pirintsos et al., 2009). More sensitive species seem to be less able to produce such polyamines than more tolerant lichen species (Pirintsos et al., 2009). This could explain why several lichens were the first species that disappeared from coastal dunes at higher atmospheric N-loads in the 1980/ 90ies (Ketner-Oostra and Sykora, 2004). The dominant N-form at that time was reduced and not oxidized nitrogen (de Haan et al, 2008).

Also in other habitats around the world, coverage and species richness of lichens and mosses decrease at elevated atmospheric N-deposition levels (Boorman and Fuller, 1982; Heil and Diemont, 1983; Lee and Caporn, 1998; van Tooren et al., 1990). Already at ambient or artificial total N-deposition of 10 kg N ha^{-1} yr^{-1} total plant species diversity was reduced in American prairie grasslands (Clark and Tilman, 2008), Swedish deciduous forests (Falkengren-Grerup and Diekmann, 2003) and British grasslands (Stevens et al., 2004, 2006).

C. canescens and *C. arenaria* have different growth forms, tussock versus rhizom network, and growth plasticity, low versus high. Nutrients and water can be transported over long distances within the rhizom network of *C. arenaria* (Noble and Marshall, 1983; D'Hertenfeld and Falkengren-Grerup, 2002; D'Hertenfeld and Jónsdóttir, 1999), and thus high element loads can be transported to plant parts where a deficiency is apparent. *C. canescens*, however, has to cope with higher amounts of consumed nitrogen within one tussock and has to detoxify high levels of NHy by metabolism, investment of luxurious taken up nitrogen in extended growth or transformation to non-toxic storage forms like free amino acids. This, however, might be more limited for *C. canescens* than for *C. arenaria*, and *C. canescens* plants die as toxic tissue nitrogen concentrations occur. *C. canescens* seems to have reached a N-level saturation at roughly 12-14 mg N g^{-1} plant dry weight, and even with a higher N-fertilization this does not increase any further (chapter 6). *C. arenaria*, however, still increases its N-tissue content at the highest N-load at a higher N-deposition site (Terschelling, NL) to about 18 mg N g^{-1} plant dry weight (chapter 6). Plant species adapted to oligotrophic environments such as *C. canescens* might have a shorter life-cycle under N-affected than under pristine conditions. At historically higher deposition sites, quite healthy looking plants in lichen-rich grasslands might be less resilient to elevated

nitrogen deposition than at pristine sites. Indications are the occurrence of nutrient imbalances, limitation by other nutrients than nitrogen and accelerated death of typical, to oligotrophic conditions adapted plant species.

Recommendations for restoration ecology and environmental policy

Early signs of an impact of atmospheric N-depositions are not easy to detect. Only once a system has experienced longer periods of elevated N-loads and has already swapped to more nutrient rich conditions, a dense vegetation has established, the impact is obvious. Early indicators of nitrogen deposition impact might therefore be a valuable tool in nature conservation and restoration ecology to be aware of changed environmental impacts. An early indicator of the influence of low to medium N-loads such as 5-8 kg N ha^{-1} yr^{-1} on acid to slightly calcareous dune ecosystems may be the total organic matter content (LOI). If the LOI in the upper mineral soil horizon of lichen-rich, short grasslands is above 1-1.5% and the pH is below 4.0-4.5, the system is about to change to nutrient-richer, less extreme soil conditions. Furthermore, at pristine sites the pH during the succession from bare sand over lichen rich short grasslands to tall grasslands slowly decreases, whereas at affected sites the pH stays the same at a lower level (figure 4). At a low pH (pH$_{salt}$<4.0), metals become freely available, e.g Al/Ca-ratios >1 occur, and living conditions in short grasslands are no longer suitable for slow-growing species adapted to nutrient-poor conditions. The ecto-organic layer gets thicker and higher levels of standing dead biomass occur (e.g. *C. canescens* above ca. 50%). If species are adapted to oligotrophic conditions such as *Cl. portentosa* or *C. canescens*, a high amount of free amino acids, especially those low in C/N-ratio such as arginine, asparagine or glutamine, might be a good early warning sign comparable to *Stratiotes aloides* L. in ammonium enriched waters (Smolders et al., 2000). Species diversity decreases, in particular *Cladonia* species with thalli growing flat on the ground such as *Cl. glauca* Flörke and *Cl. macilenta* agg. Hoffm., decrease their cover at higher N-loads. Furthermore, the occurrence of lichens such as *Hypogymnia physodes* (L.) Nyl. on the ground and *Cetraria* spp. or the vital occurrence of *Jasione montana* L., *Hypochaeris radicata* L., *Luzula* ssp., *Thymus serpyllum* L. and *Viola* spp. might be a good indicator of an intact system. Higher coverages of *C. arenaria* (above 10%), *Rumex acetosella* L. or *Dicranum scoparium* Hedw. and the presence of species with a higher nutrient demand such as *Anthoxantum odoratum* L., *C. epigejos* or *Holcus lanatus* L. in short grasslands may indicate the opposite. In general, lichens and mosses seem to be an earlier indicator of atmospheric depositions than vascular plants as their nutrient supply comes mainly via the atmosphere and not the soil, they grow year round and have a higher permeability of their outer surface (Nash, 2008; Hale, 1969, 1983). But one has to bear in mind that not only one singular feature standing alone can give a proper indication of an elevated atmospheric nitrogen deposition influence. Only a certain array and combination of features will give a sound judgement.

Looking at the whole dune site, stands of the tall grassland unit *C. arenaria* are a natural part of the Baltic coastal ecosystem (Steffen, 1931; Hueck, 1932; Paul, 1953). Under pristine conditions, *C. arenaria* units do not cover more than 30-40% per field site (chapter 3), and stands are species rich (12-16 species per 4 m² plot). At N-affected sites, however, *C. arenaria* stands can be quite dense and species poor (4-6 species per 4 m² plot

at acid dunes), its thick grass sward covering over 60-70% of the area (chapter 3). While the total number of species is not a good indicator of an impact of low to medium N-depositions in lichen-rich short grasslands, the number and occurrence of certain lichen species are suitable indicators (chapter 3, 4).

Critical loads for species-rich coastal dune grasslands, which have an acidic to slightly calcareous parent sand material, are probably lower than previously thought. In Europe, critical loads for species-rich lowland heathlands, acidic grasslands and coastal dunes are considered to be 10-20 kg N ha^{-1} yr^{-1} (Acherman and Bobbink, 2003; Bobbink et al., 1992; Bobbink and Roelofs, 1995; Jones et al., 2004, van Dobben and van Hinsberg, 2008). When setting a critical load for acid to acidic coastal dunes in the Baltic, it should be borne in mind that from up to 4 kg N ha^{-1} yr^{-1} wet deposition, or a total of 5-8 kg N ha^{-1} yr^{-1}, vegetation change from short grasslands to tall grasslands and subsequent species loss occurs (chapter 3). Especially dry coastal dunes with acid parent sand material seem to be negatively impacted already by these low nitrogen loads (chapter 4). Similar critical load ranges, 5-10 kg N ha^{-1} yr^{-1}, are assumed for comparable ecosystems, like weakly buffered soft water lakes or lichen and moss dominated habitats such as mountain summits and tundra (Achermann and Bobbink, 2003).

Key processes to look at in restoration of lichen-rich short dune grasslands are acidification and accumulation of organic matter. As soil conditions have been irrevocably altered, restoration of dune grasslands with dense *C. arenaria* swards should include turf stripping, removal of soil enriched with organic matter (Ah-layer) and restoration of original pH by addition of a certain dose of lime (Dorland et al., 2004; Jentsch et al., 2009). Restoration measures such as liming are today more successful than 20 years ago as acid load dropped strongly during the last decades. In short grasslands, which are still quite species rich and soil properties are not intensively changed, less intensive measures might be sufficient. A new layer of freshly deposited, more calcareous-rich sand might be enough to re-establish more oligotrophic, dry and fluctuating environmental circumstances and a higher soil-pH. If low or high intensity measures are appropriate to take and in which frequency, very much depends on the input of (atmospheric) nitrogen and sulphur into the system. At a heathland in north-western Germany, which receives ca. 20 kg N ha^{-1} yr^{-1} (bulk deposition), low intensity measures such as mowing cannot compensate for atmospheric N-loads in the long run. High intensity measures such as sod-cutting are needed for a long-term balanced N-budget (Härdtle et al., 2006).

The best measure, however, remains the prevention of increased atmospheric sulphur and nitrogen deposition loads. Although there are improvements in legal regulations for establishment of intensive animal husbandry in factories and energy power plants, the later control of required filter systems is less well implied. In Germany, filter systems are only controlled by the owner and not automatically by unbiased, external institutions (§ 26, 27, 28 and 29, Elfte Verordnung zur Durchführung des Bundes-Immissionsschutzgesetzes (Verordnung über Emissionserklärungen – 11. BImSchV), in der Fassung der Bekanntmachung vom 5. März 2007, BGBl. I S. 289). Correctness of emission declarations by companies and properly running, sufficiently controlled filter systems cannot be guaranteed. Furthermore, marine vessels consume sulphur rich bunker oil (up to 5% sulphur by weight), mainly without filter systems, and have been recognized as significant sources of sulphur in the atmosphere (Capaldo et al., 1999; Collins et al., 2009; Corbett and Fischbeck, 1997). On land, only fuels with sulphur contents in the

ppm range (50-350 ppm) are allowed (Greening, 2001). Between 1960 and 1990 high amounts of atmospheric sulphur depositions caused acidification, hence degradation of various ecosystems (NEGTAP, 2001). Subsequently, various measures were taken to decrease sulphur deposits on the main land (Vestreng et al., 2007). But shipping today still rather resembles a waste-to-energy plant than clean energy supply for ship traffic. International legislation clearly needs further improvements to prevent ongoing degradation of habitats due to atmospheric depositions.

Main questions and hypotheses

1. What is the present-day atmospheric nitrogen deposition level on Baltic coastal dunes?

   Atmospheric nitrogen deposition loads are low to moderate, 5-8 kg N ha^{-1} yr^{-1}, in a European perspective within coastal regions of the Baltic Sea. There are even sites which are close to background deposition e.g. at the Estonian or Lithuanian coast.

2. What are the effects of atmospheric nitrogen deposition on dry coastal dunes of the Baltic Sea? To what extent do the effects resemble those observed for North Sea dunes?

   At moderate loads of nitrogen depositions (5-8 kg N ha^{-1} yr^{-1}), dry coastal dunes become dominated by a dense sward of only *Carex arenaria*, that leaves almost no room for other species. Critical loads for these acid dunes are probably lower than previously derived from studies along the North Sea, about 5-10 kg N ha^{-1} yr^{-1}.

3. Which processes are affected by elevated nitrogen deposition?

   Moderate nitrogen loads (5-8 kg N ha^{-1} yr^{-1}) showed a marked effect only at acid dune systems, as pH decreased, organic matter accumulated, and toxic metals reached critical levels. In short-term experiments (two months; two years) no effect on the soil was detected, but species adapted to oligotrophic, dry conditions showed increased investment in free amino acids and dead biomass. Even under these moderate nitrogen loads, competition for nitrogen and water swaps to competition for other nutrients, light and space.

4. What is the difference between highly N-affected and N-unaffected lichen-rich dune grasslands?

   Under pristine conditions, lichen-rich dune grasslands are self-sustained oligotrophic systems: slow growing lichens (and mosses) take up and store most of atmospheric nitrogen deposition, but only ca. 10% is taken up by soil and vegetation. The remaining part of atmospheric deposition is probably lost via leaching losses through the bare sand and volatilisation. Under polluted conditions, the pH is decreased, organic mater accumulated and extreme conditions are smoothed out. Taller graminoids are favoured and facilitate their growth by several positive feedbacks. Typical short grassland species are likely to be less resilient.

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Harilaid, EE. The leaning lighthouse as an evidence of constant coastal change. (Ute Eulitz)

Zusammenfassung

Dünengebiete erstrecken sich in Europa über große Strecken entlang der Küsten des Atlantiks, der Nord- und Ostsee. Charakteristisch für Dünen ist ihre hohe Dynamik und dem daraus resultierendem, feinen Mosaik aus unterschiedlichen Habitaten. Sehr nahe beieinander kann man extrem unterschiedliche Bedingungen für Pflanzen und Tiere vorfinden. Kritische und limitierende Faktoren werden unter anderem durch den starken Einfluss des Windes hervorgerufen: die Stärke des Sandgebläses und der Eintrag von Gischt sind Stressfaktoren für Flora und Fauna. Durch die ständige Umlagerung der reinen Sande findet man in grundwasserfernen Dünen zumeist keine ausreichende Versorung mit Wasser und Nährstoffen. Der permanente Angriff des Windes schichtet die Dünensande vielfach um und erst wenn sich eine gewisse Pflanzendecke entwickelt hat, kann sich Humus anreichern, die Böden setzten sich und ausgeglichenere Umstände entstehen.

Diese sehr unterschiedlichen Habitate mit ihren extremen Randbedingungen – starker Wassermangel, arme Böden, hohe Störungsintensitäten und stark fluktuierende Temperaturen – beherbergen eine Reihe von spezialisierten und gefährdeten Pflanzen- und Tierarten. Unterschiedlichste Habitate und Arten wie z.B. die Graudünen (2130*) mit ihren Rentierflechten (*Cladonia* sp.) oder auch nasse Dünentäler sind sowohl unter der FFH-Richtlinie (Council Directive 92/43/EEC of 21st of May 1992) geschützt als auch von der Helsinki Komission als gefährdete Biotope aufgeführt. Gefährdungsursachen für europäische Dünengebiete sind eine intensive Freizeitnutzung, Gebietsverluste durch Bebauung, und die Degradation und Fragmetierung von Habitaten. Die Mobilität des Sandes und der Dünen wird vermindert durch verstärkten Küstenschutz, die Einstellung landwirtschaftlicher Nutzung, geringere Wildtieredichten (v.a. Kaninchen *Oryctolagus cuniculus* (L.)) und durch die Meeresspiegelerhöhung. Abgesehen von diesen Faktoren übt Luftverschmutzung einen starken Einfluss auf diese nährstoffarmen Ökosysteme aus. Vor allem Stickstoff- und Schwefeleinträge sind seit Mitte des 20. Jahrhunderts angestiegen. Der Höhepunkt wurde um 1970-1990 erreicht und sank in den Jahrzehnten danach wieder um ca. 10-40 %. Heutzutage ist der Stickstoffeintrag immer noch zu hoch für viele nährstoffarme Ökosysteme eingetragen. In trockenen Dünensytemen in Europa liegen die Grenzwerte (critical load) von Stickstoffeinträgen bei ca. 10-20 kg N ha^{-1} a^{-1}. Ab diesem Grenzwert verändern sich Prozesse und Systemeigenschaften eines Ökosytems fundamental.

Die von Natur aus nährstoffarmen Dünenlandschaften sind eines der empfindlichsten Ökosysteme der Erde, wenn man den Einfluss von Luftverschmutzung, v.a. Stickstoffeintrag, betrachtet. Andere nährstoffarme Systeme, in denen zudem intensiv geforscht wurde und viel Fachwissen dokumentiert wurde, sind z.B. Kalkmagerrasen oder Heiden. Sehr starke Luftverschmutzungen (Stickstoff und Schwefel) in den 1970 und 1980er werden als eine der Hauptursachen für eine Vergrasung, Zunahme an Moosen und Gebüschen, eine insgesamt dichtere Vegetationsdecke in nährstoffarmen Ökosystemen angesehen. Flechtenreiche Kurzgrasfluren der Dünen sind bisher hingegen vernachlässigt worden. Von anderen flechten- und moosdominierten Ökosystemen wie. z.B. arktischen Tundren oder Heiden ist bekannt, dass sie sehr sensibel auf Luftverschmutzungen reagieren. Um einen besseren Einblick in die Funktionsweise von flechtenreichen Grasländern (Kurzgrasländer wie z.B. Silbergrasfluren) der Dünen zu bekommen und den Einflussbereich von Luftverschmutzung einschätzen zu können, wurde diese Studie in relativ unberührten, europäischen Dünengebieten durchgeführt.

Beinahe natürliche, pristine Referenzgebiete im Vergleich zu schon stark veränderten Gebieten in Nord-West Europa wurden in Ostseeraum vermutet, da dort die gemessenen und modellierten Werte von Stickstoffeinträgen im Binnenland unterhalb des bisher angenommenen, kritischen Grenzwertes (critical load) für Dünengebiete liegen.

Dieser Eindruck hat sich bestätigt. Die Spannweite der Stickstoffeinträge liegt bei 2,3-7,8 kg N ha^{-1} a^{-1} (nasse Deposition), was einem totalen Stickstoffeintrag von ca. 3-12 kg N ha^{-1} a^{-1} entspricht. Gemessen wurden diese Einträge mit Hilfe eines Biomonitors, der Ebenästigen Rentierflechte *Cladonia portentosa* (Dufour) Coem. Ein geeigneter Biomonitor zur Messung von Luftverschmutzung besitzt gegen diese eine hohe Toleranz, stirbt nicht sofort bei hohen Konzentrationen ab, hat eine weite geographische Verbreitung, ist representativ für die untersuchten Gebiete, ist ferner das ganze Jahr über vorhanden und einfach zu sammeln. Flechten sind zusätzlich ein geeigneter Biomonitor, weil sie sehr langsam wachsen. Der Stickstoffgehalt in der Ebenästigen Rentierflechte wurde mit den gemessenen, nassen Depositionen in der Nähe gelegener Wetterstationen korreliert. Die beste Korrelation ergab sich, wenn die nasse Deposition der letzten drei bis sechs Jahre gemittelt verwendet wurde. Dieser lange Zeitraum passt auch besser zu Vegetationsveränderungen, die selten schnell von statten gehen, sondern in den meisten Ökosystemen mindestens ein bis zwei Jahre dauern.

Schon ab 5-8 kg N ha^{-1} a^{-1} (totale Deposition) konnten Vergrasungserscheinungen und Dominanzen der Sandsegge (*Carex arenaria* L.) gefunden werden. In gleichem Maße wie mit steigendem Stickstoffeintrag Sandseggen zunehmen und eine Dominanz (>50% Bedeckung) im Dünengebiet ausbilden, verschwinden flechten- und moosreiche Kurzgrasrasen. Beachtlich ist, dass in diesen eher sauren, nährstoffarmen Dünen der kritische Wert für Luftverschmutzung anscheinend viel niederiger liegt als bisher angenommen wird. Der kritische Wert liegt nicht bei 10-20 kg N ha^{-1} a^{-1} sondern bei 5-10 kg N ha^{-1} a^{-1}.

In pristinen Gebieten, d.h. bei weniger als 5 kg N ha^{-1} a^{-1} Eintrag, haben langsam wachsende Flechten genügend Zeit die Rohböden, d.h. die offenen Sande, zu besiedeln. Die Sande sind nicht entkalkt durch saure Einträge (Stickstoff und Schwefel), und Metalle wie Aluminium und Eisen sind kaum im Boden gelöst und damit nicht pflanzenverfügbar. Mit zunehmender Dauer und voranschreitender Besiedlung durch Pflanzen entsteht eine dichte Flechten- und Moosdecke. Diese Kryptogamen agieren beinahe wie ein Schwamm, wenn es darum geht Wasser und Nährstoffe aufzunehmen und zu binden. Relativ wenig ist für Gefäßpflanzen oder Bodenorganismen verfügbar. Zudem ist der Biomasseumsatz (turnover) dieser Arten, die an nährstoff- und wasserarme Standorte mit stark schwankenden und extremen Temperaturen angepasst sind, sehr gering und darausfolgend die Anreicherung organischer Masse sehr gernig. Die Arten erhalten sich dadurch selber ihren Lebensraum und verzögern die Sukzession.

In durch Stickstoff und auch Schwefel stark beeinflussten Dünen hingegen, nimmt die Artenvielfalt und Biomasse der Flechten ab. Der Sandboden wird zunehmend durch saure Einträge entkalkt. Ab einem pH-Wert im Salzextrakt von ca. 4 nimmt der Anteil an gelösten Metallen stark zu. Al/Ca-Verhältnisse größer als eins weisen auf toxische Konzentrationen von Aluminium hin. Zudem schwankt die Zusamensetzung der Bodenorganismem von bakerien- zu pilzdominiert. Biomasse wird im Boden mehr angereichert und der einst arme Boden wird immer humusreicher. Dadurch ist die Fähigkeit Nährstoffe und Wasser zu binden erhöht. Die Bedingungen werden und

weniger extrem. Konkurrenzstärkere Arten sind im Vorteil, können die höhere Verfügbarkeit von Wasser und Nährstoffen bessern nutzen, und dominieren letzlich die Vegetation. Diese Arten haben zudem eine höhere Biomasseproduktion und -umsatz. Es ensteht eine dichte Humus-, Streu- und Vegetationsdecke. An extreme Standorten angepasste Arten sind wenig konkurrenzfähig und werden zusehens verdrängt. Zusätzlich scheinen aber noch interne, physiologische Prozesse eine Rolle zu spielen. Typische Arten wie z.B. das Silbergras (*Corynephorus canescens* P. Beauv.) oder die Ebenästige Rentierflechte speichern bei höheren Stickstoffgaben den Stickstoff in freie Aminosäuren. Bei höheren, experimentellen Stickstoffgaben im Feld (40-80 kg N ha^{-1} a^{-1} über 2 Jahre) und im schon vorbelasteten Gebiet (Terschelling) stirbt das Silbergras zunehmend ab.

Frühe Warnzeichen von erhöhtem Stickstoffeintrag im Bereich des Bodens sind ein Gehalt an organischer Masse über 1-1,5 % (LOI) und pH-Werte von ca. 4-4,5. Es sind kaum pH-Wert Veränderungen im Sukzessionsverlauf von offenen Sanden, über flechten- und moosreiche zu grasdominierten Beständen zu verzeichnen. Der saure Regen wäscht schon aus den Anfangsstadien der Dünensukzession, die kahlen Sanden, Kalke und andere Puffersubstanzen aus. Der Boden-pH ist zu diesem Zeitpunkt schon niedriger und nimmt im Zuge fortschreitender Sukzession kaum noch durch die Atmung von Wurzeln und Mikroben und damit verstärkter Kohlensäureproduktion ab. Besonders Gebiete mit schwach abgepufferten Sanden sind gefährdet und zeigen diese Veränderungen schon bei niedrigen bis mittelhohen Stickstoffeinträgen.

Im Bereich der Artenvielfalt sind erste Anzeichen von Luftverschmutzung v.a. im Artenspektrum und Zustand der Flechten zu erkennen. Wenn *Hypogymnia physodes* (L.) Nyl. oder *Stereocaulon* Arten auf dem Boden wachsen, ist dies zumeist ein Zeichen von noch stets relativ gut abgepufferten Sanden. Flechtenarten, die mit ihren Strukturen (Thalli) vornehmlich auf dem Boden ausgebreitet wachsen, sind vor allem in Dünen mit Stickstoffeinträgen unter 5 kg N ha^{-1} a^{-1} zu finden und nehmen an Artenanzahl und Bedeckung bei einer höheren Luftverschutzung ab. Beispiele sind *Cl. macilenta* agg. Hoffm. oder *Cladonia glauca* Flörke. Ein großes und vitales Vorkommen von Gefäßpflanzen wie z.B. dem Bergsandglöcken (*Jasione montana* L.), dem Ferkelkraut (*Hypochaeris radicata* L.), Simsen (*Luzula* spp.), Thymian (*Thymus serphyllum* L.) oder Veilchen (*Viola* spp.) deutet auf eher geringeren Einfluss von Luftverschmutzung hin. Generell sind Flechten und Moose besser geeignet als frühe Warnzeichen für Luftverschmutzung als Gefäßpflanzen, weil sie ihre Hauptnährstoffversorgung über die Luft beziehen und nicht über den Boden aufgenommen wird, sie das ganze Jahr über wachsen und ihre Oberfläche eine höhere Durchlässigkeit hat.

In pristinen Gebieten scheint eine Bedeckung von 45-80 % mit flechtenreichen Kurzgrasrasen und 5-14 % mit höher wachsenden Gräsern wie z.B. der Sandsegge kennzeichnend zu sein. In stark durch Luftverschmutzung beeinflussenten Gebieten werden die Kurzgrasrasen auf ca. 15-25 % Bedeckung zurückgedrängt und eine Vegetation von höher wachsenden Gräsern dominiert die Dünen. Es ist zu beachten, dass nicht nur eines dieser Kennzeichen ausreicht, um den Einfluss von Luftverschmutzung einschätzen zu können. Nur eine Kombination verschiedener früher Warnzeichen zusammen kann eine verläßliche Indikation liefern.

Schlüsselprozesse, die bei Management- oder Restaurierungsmaßnahmen im Hinterkopf behalten werden sollten, sind die Versauerung der Böden, die Akkumulation von organischer Masse in diesen reinen Sandböden, und toxische Mengen von Metallen wie

z.B. Aluminium. Wenn Böden unwiederruflich stark verändert sind, sollte zur Wiederherstellung von artenreichen Dünengrasländern aus dichten Sandseggenbeständen der Oberboden komplett entfernt werden. Bei zukünftig anhaltend hoher Luftverschmutung oder auch zu stark versauerten Sanden, sollte die Fläche ferner gekalkt werden. So denn Dünengebiete nur geringe Anzeichen von Luftverschmutzung erkennen lassen und die Böden weniger stark verändert sind, reichen weniger intensive Maßnahmen. Ein neue Decke kalkreicherer Sande reicht in vielen Fällen vollkommen aus, um wieder nährstoffarme, trockene und stark fluktuierende Umweltbedingungen herzustellen. Die beste aller Maßnahmen ist und bleibt aber die Vermeidung von einer Luftverschmutzung. Um von Natur aus nährstoffarme Dünen in ihrer vollkommen Ausprägung und Funktionsweise langfristig erhalten zu können, werden wir nicht umhin kommen, momentane Einträge weiter zu veringern.

Curonian Spit, RU. Huge shifting dunes along the coast.

Samenvatting

Grote delen van de kustlijn van de Atlantische Oceaan, de Noordzee en de Oostzee worden gevormd door duingebieden. Karakteristiek voor deze duinen is hun hoge dynamiek en het daaruit resulterende, fijne mozaïek van verschillende habitats. De condities voor planten en dieren kunnen over zeer kleine afstanden sterk verschillen. De sterke wind speelt een belangrijke rol in deze systemen: stuivend zand en het inwaaien van 'saltspray' zijn stressfactoren voor flora en fauna. Verder zorgt de stevige wind ervoor, dat het duinzand regelmatig wordt omgewoeld en er geen organische stof in de bodem kan ophopen. In zandige duinen die buiten het bereik van grondwater liggen, zijn voor veel plantensoorten daarom te weinig water en nutriënten beschikbaar.

Pas bij voldoende plantengroei kan zich een humuslaag vormen die zorgt voor een stabieler systeem met meer constante omstandigheden. In de diverse duinhabitats met hun extreme condities - sterk tekort aan water, arme bodem, hoge mate van verstoring en sterk fluctuerende temperaturen - zijn een groot aantal gespecialiseerde en bedreigde planten- en diersoorten te vinden. Verschillende habitats en soorten, zoals Grijze duinen (2130*) met hun rendiermossen (*Cladonia* sp.) en natte duinvalleien (2190) zijn zowel onder de Europese Habitatrichtlijn (Council Directive 92/43/EEC of 21st of May 1992) beschermd en tevens in de Helsinki Conventie als bedreigd biotoop opgenomen.

Europese duingebieden worden bedreigd door intensief gebruik door recreanten, areaalverlies door uitbreiding van bebouwing en degradatie en fragmentatie van leefgebieden. De mobiliteit van het zand en de duinen is sterk verminderd door intensieve kustbescherming, afname van het agrarische gebruik, de teruggang van het aantal wilde dieren – vooral konijnen (*Orytolagus cuniculus* (L.)) – en door de zeespiegelstijging. Naast deze factoren heeft ook de luchtvervuiling een sterke invloed op deze nutriëntenarme ecosystemen. Met name de stikstof- en zwaveldepositie is sinds het midden van de twintigste eeuw toegenomen. De depositiewaardes waren het hoogst rond 1970-1990 en zijn sindsdien weer met 10-40 % afgenomen.

Ook nu nog lijden veel nutriëntenarme ecosystemen onder een te hoge stikstofdepositie. Voor droge duinen in Europa geldt een 'critical load' voor stikstofdepositie van ongeveer 10-20 kg N ha^{-1} j^{-1}. Bij hogere depositiewaardes verlopen processen beduidend anders en vinden fundamentele veranderingen in het functioneren van het duinecosysteem plaats.

De van nature nutriëntenarme duinlandschappen zijn een van de gevoeligste ecosystemen op aarde als het gaat om de invloed van luchtvervuiling, met name stikstof. Van andere nutriëntenarme systemen, zoals kalkgraslanden en heide, die uitgebreid zijn onderzocht, is bekend dat sterke luchtvervuiling (stikstof en zwavel) in de jaren '70 en '80 van de vorige eeuw leidde tot het dichter worden van de vegetatie door vergrassing, vermossing en verbossing. Tot nu toe is er over korstmosrijke duingraslanden op dit gebied weinig bekend. Van andere, korstmosrijke ecosystemen zoals Arctische toendra en heidegebieden is echter bekend, dat zij erg gevoelig zijn voor luchtvervuiling. De huidige studie heeft tot doel beter inzicht te verschaffen in het functioneren van korstmosrijke duingraslanden en de invloed van luchtvervuiling op dit systeem. Hiervoor is onderzoek verricht in de relatief onaangetaste duingebieden langs de Oostzee. Op basis van gemeten en gemodelleerde stikstofdeposities uit het binnenland werd aangenomen dat de stikstofdepositie in deze gebieden onder de tot nu toe aangenomen 'critical load' voor duingebieden ligt. De duingraslanden langs de Oostzee kunnen daardoor dienen als relatief weinig aangetaste referentiegebieden die vergeleken kunnen worden met de sterk aangetaste duingebieden in Noord-West Europa.

De onderzoeksresultaten bevestigden dat de stikstofdepositie langs de Oostzeekust onder de aangenomen 'critcal load' voor duinsystemen ligt. De bandbreedte van stikstofdepositie in de onderzochte kustgebieden bedraagt 2,3-7,8 kg N ha^{-1} j^{-1} (natte depositie), wat overeenkomt met een totale stikstofdepositie van ongeveer 3-12 kg N ha^{-1} j^{-1}. Deze waarden zijn gemeten met behulp van een biomonitor, Open rendiermos (*Cladonia portentosa* (Dufour) Coem.). Een geschikte bioindicator voor het meten van luchtvervuiling heeft een hoge tolerantie voor de betreffende stof, sterft niet bij hoge concentraties, heeft een grote geografische verspreiding, is representatief voor de onderzochte gebieden, is het hele jaar beschikbaar en makkelijk te verzamelen. Korstmossen zijn geschikte bioindicatoren, omdat ze erg langzaam groeien. Het stikstofgehalte in Open rendiermos is vergeleken met de natte depositiewaarden die gemeten werden in nabijgelegen weerstations. De beste correlatie werd gevonden wanneer een vergelijking werd gemaakt met de gemiddelde natte depositie over de laatste drie tot zes jaar. Deze langere tijdspanne komt goed overeen met de snelheid van veranderingen in de vegetatie, die ten minste een tot twee jaar duren.

Al vanaf 5-8 kg N ha^{-1} j^{-1} (totale depositie) treedt er vergrassing op, waarbij Zandzegge (*Carex arenaria* L.) dominant wordt. Toename van de bedekking van Zandzegge en het optreden van dominantie van deze soort (> 50% bedekking) gaat gepaard met het verdwijnen van korstmos- en mosrijk duingrasland. Deze resultaten laten zien dat de 'critical load' voor luchtvervuiling in deze zure, nutriëntenarme duinen blijkbaar veel lager ligt dan tot nu toe werd aangenomen. De 'critcal load' ligt niet bij 10-20 kg N ha^{-1} j^{-1} maar bij 5-10 kg N ha^{-1} j^{-1}.

In onaangetaste gebieden, dus bij minder dan 5 kg N ha^{-1} j^{-1} depositie, hebben langzaam groeiende korstmossen voldoende tijd zich op de kale zandbodem te vestigen. In deze gebieden is het zand niet ontkalkt door zure depositie (stikstof en zwavel), en zijn metalen zoals aluminium en ijzer in de bodem bijna nooit beschikbaar voor planten. Bij voortschrijdende successie ontstaat een dichte korstmos- en mosbedekking. De korstmossen zijn in staat als een spons water en nutriënten op te nemen en vast te houden waardoor deze slechts in geringe mate beschikbaar zijn voor vaatplanten en bodemorganismen. De soorten die aan deze nutriëntenarme en droge standplaatsen en hun extreme temperaturen zijn aangepast hebben een geringe omzetting van biomassa (turnover) waardoor de accumulatie van organisch materiaal zeer gering is. Hierdoor houden deze soorten hun leefomstandigheden in stand en vertragen zij de successie.

In duinen met een hoge stikstof- en zwaveldepositie is de soortenrijkdom en biomassa van korstmossen beperkt. In deze gebieden wordt de zandbodem voortdurend ontkalkt door de zure depositie. Bij een pH waarde van 4,0 of minder (in zout extractie gemeten) neemt het aandeel opgeloste metalen sterk toe. Een Al/Ca-ratio groter dan één wijst op toxische concentraties van aluminium. Bovendien verandert de samenstelling van de bodemorganismen van een dominantie van bacteriën naar een dominantie van schimmels. De biomassa in de bodem accumuleert en de eens arme bodem wordt steeds humusrijker. Door de toegenomen humuslaag houdt de bodem meer nutriënten en water vast, waardoor de omstandigheden minder extreem worden. Concurrentiekrachtige soorten zijn beter in staat te profiteren van de hogere beschikbaarheid van water en nutriënten, waardoor deze op den duur de vegetatie gaan domineren. Deze concurrentiekrachtige soorten hebben bovendien een hogere biomassaproductie en -omzet, waardoor een dichte humus-, strooisel- en vegetatielaag ontstaat. Plantensoorten die zijn aangepast aan

extreme standplaatsen zijn veel minder concurrentiekrachtig en worden meer en meer verdrongen. Het onderzoek heeft aangetoond dat daarnaast ook interne, fysiologische processen een belangrijke rol spelen. Karakteristieke soorten zoal Buntgras (*Corynephorus canescens* P. Beauv.) en Open rendiermos slaan de extra beschikbare stikstof op in de vorm van vrije aminozuren. Bij hoge, experimentele stikstofgiften in het veld (40-80 kg N ha^{-1} j^{-1} in twee jaar) en in al aangetaste gebieden sterft het Buntgras hierdoor in toenemende mate.

Vroege waarschuwingstekens van verhoogde stikstofdepositie zijn een in de bodemlaag aanwezige organische massa van meer dan 1-1,5 % (LOI) en een pH waarde van ongeveer 4-4,5. De zure regen zorgt ervoor dat kalk en andere bufferstoffen al in het beginstadium van de successie uitspoelen. Hierdoor blijft de pH gedurende de verdere normale successiereeks van open zandbodem, via korstmos- en mosrijke vegetaties naar een door gras gedomineerde vegetatie nagenoeg constant. Verdere verlaging van de pH door respiratie van wortels en micro-organismen en daarmee sterkere koolzuur productie vindt nagenoeg niet plaats. Vooral gebieden met een zwak gebufferde zandbodem zijn gevoelig en vertonen deze veranderingen al bij lage stikstofdepositiewaardes.

Met betrekking tot soortenrijkdom zijn eerste tekenen van luchtvervuiling het sterkst zichtbaar in het soortenspectrum en de kwaliteit van korstmossen. Aanwezigheid van soorten als *Hypogymnia physodes* (L.) Nyl. en *Stereocaulon* soorten wijst op een nog relatief goed gebufferde bodem. Korstmossoorten, die met hun thalli met name op de grond uitgebreid groeien, worden vooral aangetroffen in duingebieden met een lage stikstofdepositie (minder dan 5 kg N ha^{-1} j^{-1}). Bij toenemende depositiewaarden neemt zowel het aantal als de bedekking van deze korstmossoorten sterk af. Voorbeelden zijn *Cladonia macilenta* agg. Hoffm. of *Cl. glauca* Flörke. Het veelvuldig voorkomen van vaatplanten zoals Zandblauwtje (*Jasione montana* L.), Gewoon biggekruid (*Hypochaeris radicata* L.), veldbiezen (*Luzula* spp.), Tijm (*Thymus serphyllum* L.) of viooltjes (*Viola* spp.) wijst op een geringe invloed van luchtverontreiniging. Over het algemeen zijn korstmossen en mossen beter geschikt als vroege indicatoren voor luchtverontreiniging dan vaatplanten, omdat ze de meeste nutriënten direct uit de lucht opnemen en niet uit de bodem halen. Bovendien groeien ze het hele jaar door en is de oppervlakte van de thalli sterk doorlatend.

Het is gebleken dat relatief onaangetaste duingebieden worden gekenmerkt door een bedekking van 45-80 % korstmosrijk duingrasland en 5-14 % hoger groeiend gras zoals Zandzegge. In sterk door luchtvervuiling aangetaste gebieden worden de korstmosrijke duingraslanden teruggedrongen tot een bedekking van slechts 15-25 % en domineert een vegetatie met hoog groeiende grassen. Opgemerkt dient te worden dat geen van de genoemde vroege alarmsignalen van luchtvervuiling in duinsystemen op zichzelf daadwerkelijk wijst op dergelijke vervuiling. Slechts een combinatie van de genoemde kenmerken geeft een betrouwbare indicatie.

Samenvattend zijn de sleutelprocessen waaraan bij het beheer en het herstel van duingebieden moet worden gedacht de verzuring van de bodem, de accumulatie van organische massa in de minerale zandbodem en de hoeveelheid metaal – zoals aluminium – in de bodem. Als een bodem onherstelbaar sterk is veranderd, is herstel van soortenrijk duingrasland vanuit een dichte zandzeggevegetatie alleen mogelijk door het volledig verwijderen van de bovenste bodemlaag. Bij aanhoudende luchtvervuiling en sterk verzuurde zandbodems is het raadzaam aanvullend te bekalken. In duingebieden die

slechts in beperkte mate te lijden hebben gehad onder luchtvervuiling en waar de bodem minder sterk is veranderd, volstaan minder intensieve maatregelen. Een nieuw dek van kalkrijk zand is in de meeste gevallen voldoende om nutriëntenarme, droge en sterk fluctuerende condities te herstellen. Echter, het verkomen van luchtvervuiling blijft de beste maatregel. Op lange termijn is behoud van karakteristieke nutriëntenarme duinsystemen alleen mogelijk indien de atmosferische zwavel- en stikstofdepositie in de toekomst verder afneemt.
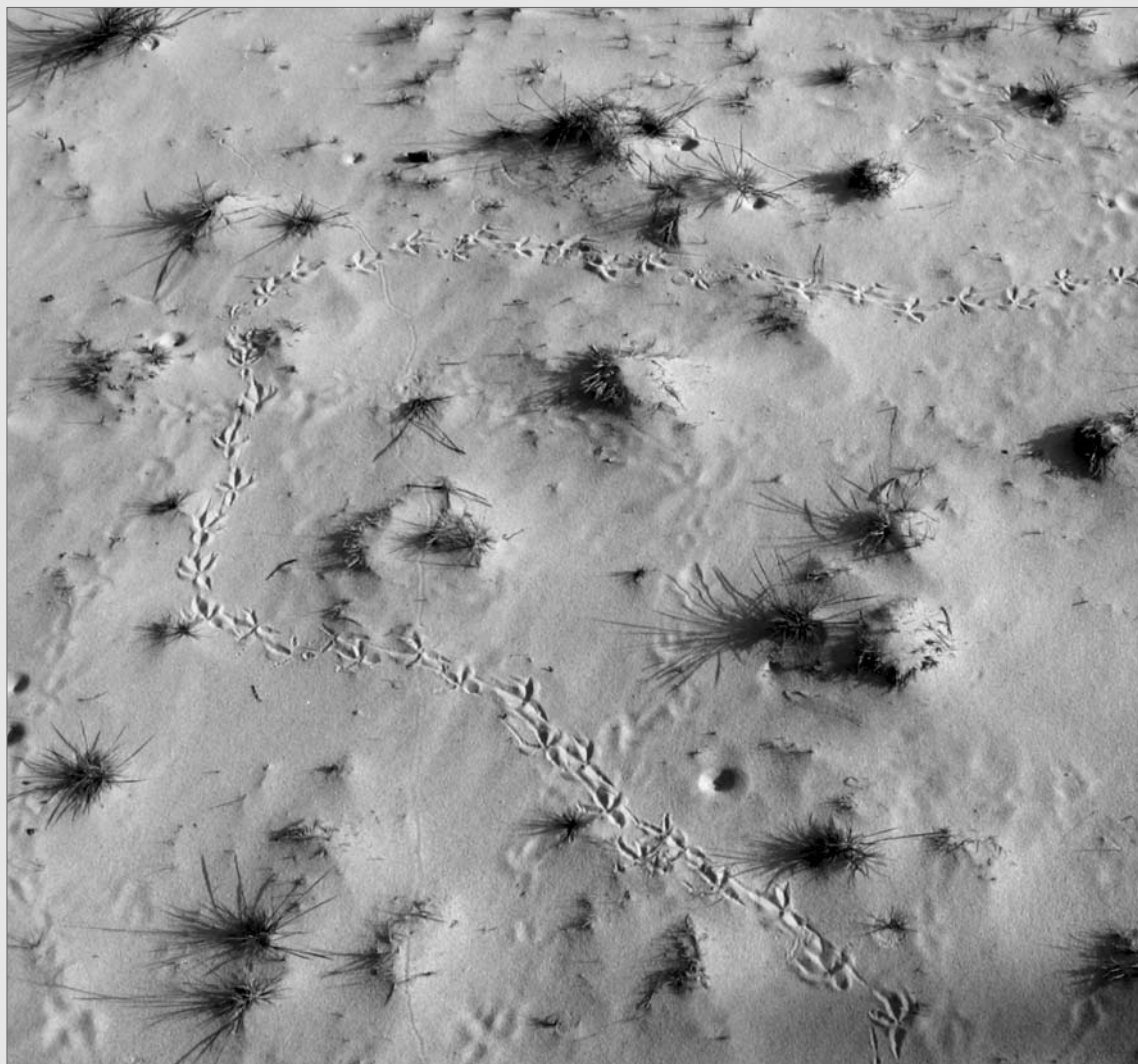
Torsö, SE. Fauna tracks.

A big thank you to …

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Gellen, D. Sand sedge (*Carex arenaria*) waves. (Sabine Hilt)

Appendix

Appendix 1 Species occurrences per vegetation unit [%] (chapter 2)

community	*Corynephorus*	*Jasione*	*Ammophila*	*Carex*	*Avenella*	*Empetrum*	*Calluna*	*Erica*	*Polytrichum*
number of relevees	9	7	4	5	3	4	8	3	8
cover forbs, grass and dwarf shrubs	41	70	93	99	100	91	94	93	37
cover moss and lichen	62	42	23	6	0	48	41	28	74
cover shrub	0	0	0	3	5	3	7	5	0
cover litter	6	5	33	15	0	8	3	5	2
cover open soil	11	7	4	0	0	3	1	3	3
species number on average per relevee	14	17	10	5	10	13	12	13	10
species									
Campylopus introflexus	56	14	0	0	0	0	13	0	13
Cladonia coccifera s.l.	56	0	0	0	0	0	0	0	13
Cladonia ramulosa	44	0	0	0	0	0	13	0	0
Cladonia uncialis	67	14	0	0	0	0	0	0	0
Cetraria aculeata	67	29	0	0	0	0	0	0	0
Cladonia fimbriata	56	0	0	20	0	50	63	67	0
Cladonia pyxidata	78	14	0	0	0	100	88	67	25
Cladonia macilenta ssp. *floerkeana*	89	0	0	0	0	0	13	0	0
Cladonia gracilis	89	43	0	0	0	25	0	0	0
Cladonia foliacea	67	0	0	0	0	0	0	0	0
Corynephorus canescens	100	100	50	0	0	0	0	0	0
Dicranum scoparium	78	57	25	40	0	100	88	33	13
Cladonia portentosa	89	71	0	20	0	100	75	33	0
Cladonia furcata	67	29	0	0	0	0	0	0	0
Cladonia ciliata var. *tenuis*	33	43	0	0	0	0	0	0	0
Rumex acetosella	44	43	0	0	0	0	0	0	0
Hypocheris radicata	22	57	25	0	0	0	0	0	0
Anthoxantum odoratum	0	57	0	0	0	0	0	0	0
Jasione montana	0	71	25	0	0	0	0	0	0
Hieracium umbellatum	11	57	50	0	0	0	0	0	0
Gallium verum x mollugo	0	86	75	20	0	0	0	0	0
Festuca ovina agg.	0	100	0	20	0	0	0	0	0
Festuca rubra	0	86	75	20	0	0	0	0	0
Ceratodon purpureus	0	57	75	0	0	0	0	67	0
Ammophila arenaria	0	71	100	0	0	0	0	0	0
Carex arenaria	100	100	100	100	100	75	88	67	75
Avenella flexuosa	0	14	0	60	100	0	50	67	0
Empetrum nigrum	0	0	0	20	33	100	63	0	13
Hypnum lacunosum	0	29	0	0	0	50	50	33	0
Pleurozium schreberi	0	0	0	0	0	50	38	67	0
Cladonia coniocrea	11	14	0	20	0	50	38	67	13
Hypnum cupressiforme	0	14	100	40	33	100	88	33	13
Lophocolea heterophylla	0	0	25	20	0	75	50	67	25
Hypogymnea physodes	11	0	50	0	0	100	75	0	0
Calluna vulgaris	0	0	0	40	100	100	100	100	75
Erica tetralix	0	0	0	0	0	75	38	100	50
Salix repens	0	43	0	20	67	25	50	100	88
Carex nigra	0	0	0	0	0	0	13	33	38
Juncus squarrosus	0	0	0	0	0	0	0	0	63
Polytrichum commune	0	0	0	0	0	0	0	0	100
Cetraria muricata	11	0	0	0	0	0	0	0	0
Spergula morisonii	11	0	0	0	0	0	0	0	0
Cladonia pleurota	33	0	0	0	0	0	0	0	0
Cephaloziella hampeana	0	0	0	0	0	25	0	0	0
Cladonia cervicornis	11	0	0	0	0	0	0	0	0

Appendix 1 (continued)

community	Corynephorus	Jasione	Ammophila	Carex	Avenella	Empetrum	Calluna	Erica	Polytrichum
Cladonia cariosa	11	0	0	0	0	0	0	0	0
Cladonia macilenta ssp. *macilenta*	11	0	0	0	0	0	0	0	0
Cladonia glauca	22	0	0	0	0	0	13	0	0
Cladonia arbuscula	22	29	0	0	0	0	0	0	0
Hieracium pilosella	0	57	0	0	0	0	0	0	0
Cladonia rangiformis	0	29	0	0	0	0	0	0	0
Brachythecium albicans	0	29	0	0	0	0	0	0	0
Teesdalia nudicaulis	0	14	0	0	0	0	0	0	0
Trifolium arvense	0	14	0	0	0	0	0	0	0
Vicia hirsuta	0	14	0	0	0	0	0	0	0
Vicia lathyroides	0	14	0	0	0	0	0	0	0
Artemisia campestris	0	14	0	0	0	0	0	0	0
Ameria maritima	0	14	0	0	0	0	0	0	0
Viola riviniana	0	14	0	0	0	0	0	0	0
Cerastium semidecandrum	0	29	0	0	0	0	0	0	0
Agrostis capillaris	0	29	25	0	0	0	0	0	13
Luzula campestris	0	14	0	0	0	0	0	0	0
Viola tricolor (ssp. curtisii)	0	14	50	0	0	0	0	0	0
Viola canina	0	14	50	0	0	0	0	0	0
Dryopteris filix-mas	0	0	25	0	0	0	0	0	0
Sclerepodium purum	0	0	25	0	0	25	0	0	0
Cephaloziella divaricata	11	0	0	20	0	0	0	0	0
Sorbus x *hybrida* s.l.	0	0	0	20	0	0	0	0	0
Senecio sylvaticus	0	0	0	20	0	0	0	0	0
Epilobium angustifolium	0	0	0	20	33	0	0	0	0
Betula pendula	0	0	0	0	33	25	13	33	38
Rubus caesius agg.	0	0	0	0	67	0	0	0	0
Padus serotina	0	0	0	0	100	0	0	0	0
Molinia caerulea	0	0	0	0	67	0	0	0	0
Sorbus aucuparia	0	0	0	0	100	0	0	0	0
Betula pubescens	0	0	0	0	67	25	0	0	0
Dryopteris carthusiana	0	0	0	0	33	0	0	0	0
Ceratium holosteoides	0	0	0	0	33	0	0	0	0
Cladonia squamosa	0	0	0	0	0	0	13	0	0
Plagiothecium laetum	0	0	0	0	0	0	13	0	0
Dicranum undulatum	0	0	0	0	0	25	13	67	0
Populus tremula	0	0	0	0	0	0	25	67	13
Sphagnum molle	0	0	0	0	0	0	0	33	13
Salix aurita	0	0	0	0	0	0	13	0	0
Gymnocolea inflata	0	0	0	0	0	0	0	33	13
Drosera rotundifolia	0	0	0	0	0	0	0	0	25
Sphagnum magellanicum	0	0	0	0	0	0	0	0	13
Juncus effusus	0	0	0	0	0	0	0	0	50
Lophozia capitata	0	0	0	0	0	0	0	0	25
Holcus lanatus	0	0	0	0	0	0	0	0	25
Pinus sylvestris	0	0	0	0	0	0	0	33	25
Agrostis stolonifera	0	0	0	0	0	0	0	0	50
Sphagnum fimbriatum	0	0	0	0	0	0	0	0	13
Sphagnum centrale	0	0	0	0	0	0	0	0	13
Juncus articulatus	0	0	0	0	0	0	0	0	13
Juncus conglomeratus	0	0	0	0	0	0	0	0	13
Juncus balticus	0	0	0	0	0	0	0	0	13

Appendix 2 Synonymlist of the phytosociological units in the different years (chapter 2)

vegetation unit nr.	phytosociological community names of different vegetation mappings	abbreviation for vegetation unit	vegetation class figure 2
Remke 2002			
1	Corniculario aculeatae-Corynephoretum canescentis Steffen 1931 nom. Inv. Prop.	*Corynephorus*	grey dune
2	Helichryso-arenarii-Jasionetum litoralis Libbert 1940	*Jasione*	grey dune
3	Festucetum arenariae (with restrictions)	*Ammophila*	white dune
4	Caricetum arenariae Steffen 1931	*Carex*	grass
5	Galio harcynici- Deschampsietosum flexuosae Passarge 1979	*Avenella*	grass
6	Salici repentis-Empetretum nigri Fukarek 1961	*Calluna*	dry heather
6	Hieracio umbellati-Empetretum nigri Libbert et Passarge 1964	*Empetrum*	dry heather
7	Empetro-Ericetum (Tüxen 1937) Westhoff ex de Smidt 1975	*Erica*	wet heather
8	Polytrichetum perigionale Hueck 1932	*Polytrichum*	wet heather
Schubert 1987-1991, 1995			
1	Spergulo morisonii-Corynephoretum canescentis (R. Tx. 1928) Libb. 1933	*Corynephorus*	grey dune
2	Helichryso-Jasionetum Libb. 1940	*Jasione*	grey dune
3	Elymo-Ammophiletum arenariae Br. Bl. Et de Leeuw 1936	*Ammophila*	white dune
4	Caricetum arenariae R. Schub.	*Carex*	grass
5	Hieracio-Avenelletum flexuosae (Bräut. 1972) Pass. 1979	*Avenella*	grass
6	Hieracio Empetretum Libb. 1940 em Schub. 1995	*Empetrum*	dry heather
7	Salici repentis-Ericetum R. Tx et Buchw. 1942	*Erica*	wet heather
8	Polytrichetum perigionale Hueck 1932	*Polytrichum*	wet heather
Fröde 1935-1938			
1	Corynephoretum cladonietosum Tüxen 1937	*Corynephorus*	grey dune
2	Festuca ovina-Plantago dubia community – subassoziation of *Hypocheris radicata* and *Rumex acetosella*	*Jasione*	grey dune
3	Elymo-Ammophiletum Br Bl et de Leeuw 1936	*Ammophila*	white dune
4	nothing comparable mapped	*Carex*	grass
5	nothing comparable mapped	*Avenella*	grass
6	Calluno-Genistetum typicum Tüxen 1937	*Calluna*	dry heather
6	Calluno-Genistetum empetretosum Tüxen 1937	*Empetrum*	dry heather
7	Ericetum tetralicis sphagnetosum Allorge 1926, Ericetum tetralicis typicum Tüxen 1937	*Erica*	wet heather
8	Polytrichetum perigionale Hueck 1932	*Polytrichum*	wet heather

Appendix 3 Percentage of the vegetation units at the the three field sites and different years (chapter 2)

abbreviation for vegetation units	central dunes-north			central dunes-south			southern dunes			vegetation class of figure 2
	1930s	1980s	2002	1930s	1980s	2002	1930s	1980s	2002	
Agropyron[1]	-	-	-	1.6	-	-	1.9	7.9	-	rest
Ammophila	18.3	5	-	14.6	31.2	4.1	17.5	21.7	6.7	white dune
Avenella	-	17.7	-	-	-	-	-	-	-	grass
Carex	-	3.2	-	-	-	2.1	-	0.9	48	grass
Corynephorus	15.2	23.5	-	27.8	17	21.6	58.3	48.6	17.6	grey dune
Jasione	-	2.3	-	-	2.1	0.7	-	-	3.5	grey dune
Lotus-Cynosurus[2]	-	-	-	-	-	-	0	-	-	grass
Nardus[3]	-	-	-	1.1	-	-	1.8	-	-	grass
Calluna	-	0.8	-	38	-	-	-	-	19.8	dry heath
Empetrum	59.1	42.1	-	14.2	47.3	58.5	15.3	20.9	3.8	dry heath
Empetrum-Ammophila[4]	2.3	-	-	-	-	-	-	-	-	dry heath
Empetrum-total	61.4	42.9	-	52.2	47.3	58.5	15.3	20.9	23.6	dry heath
Erica	1.4	0.2	-	1	-	0.1	4.5	-	-	wet heath
Polytrichum	3.9	0	-	1.4	-	0.1	-	-	0.1	wet heath
Rhynchospora[5]	-	-	-	0.3	-	-	-	-	-	wet heath
Pinus[6]	-	4.5	-	-	2.4	12.8	-	-	-	trees
buildings[7]	0.1	0.6	-	-	-	-	-	-	-	rest

phytosociological unit if not named in synonym list and other unit descriptions

1 Elymo-Agropyretum juncei Br.Bl. et de Leeuw 1936 emend R.Tx. 1957

2 Cynosuretum cristati R. Tx. 1940 ap. Brücker 1942

3 Polygalo-Nardetum strictae Oberd. 1957

4 transition vegetation community of Fröde between *Empetrum* and *Ammophila*

5 Rhynchosporetum albae Osv. 1923 em. W. Koch 1926

6 coastal protection forest (*Pinus* spp. afforestation) and natural rejuvenation of single individuals in the dunes

7 private houses and surrounding premises