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

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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 *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}.

Keywords *Carex arenaria* · Grass encroachment · Coastal protection · Baltic Sea · Landuse · Grazing · Succession

Abbreviations

CEC	Cation exchange capacity
EC	Electrical conductivity
EMEP	Monitoring and Evaluation of the Long-range Transmission of Air Pollutants in Europe
LOI	Loss on ignition
NP	National park
NP VBL	National Park Vorpommersche Boddenlandschaft
WRB	World Reference Base for Soils

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Nomenclature

Frahm and Frey 1992 (mosses); Oberdorfer 1994 (vascular plants); Wirth 1995 (lichens); World Reference Base for Soils (WRB) 1994 (soil profiles).

Introduction

Coastal dunes provide a range of habitats with wild flora and fauna species protected under the Habitats Directive,

for example, grey dunes (2110*) 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 the 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 local nature conservation authorities such as the National Park (NP). 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). 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 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 the 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 (Fig. 1) and each has an area of about 4 ha. The ecoregion can be characterised as Baltic (Olson et al. 2004) with a long-term precipitation 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 and 10 PSU (Möbus 2000). The central dunes (local name Dünenheide) are ca. 2,000–2,500 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 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*) plantings were carried out to protect parts of the coastline from coastal erosion, 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-peninsular, an average wet deposition of 6.3 kg N ha^{-1} yr^{-1} was measured during 2001–2005 (Remke et al. 2009). 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

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Fig. 1 Map of field sites

dune areas (ca. 4 ha) was compiled by field mapping (transect walks) supported by geo-referenced aerial photographs.

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 cm and 20 cm and stored in plastic bags at 4°C until further analysis. Samples were dried at 105°C for 24 h 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 min 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* 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 *Carex arenaria* L. (Caricetum). Below these plots ($n=9$ for each site), a soil sample mixed from three soil cores (each taken by a 100 cm^3 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 h. *Carex arenaria* samples were ground in a centrifugal mill (rotational speed 18 000 for 1–2 min, 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$_2$O$_2$ (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) 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 and Schachtschabel 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; Online Source 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 (Online Source 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% to 6% to less than 1% today and shifting white dunes (Ammophiletum) have decreased to 1/8 - 1/3 of their former area (Fig. 2; Online Source 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 (L.) Trin. 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 (Online Source 3).

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 1/4 to 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 reached 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

Fig. 2 Vegetation cover in the three coastal dune areas on the island of Hiddensee in 1936, 1990 and 2002
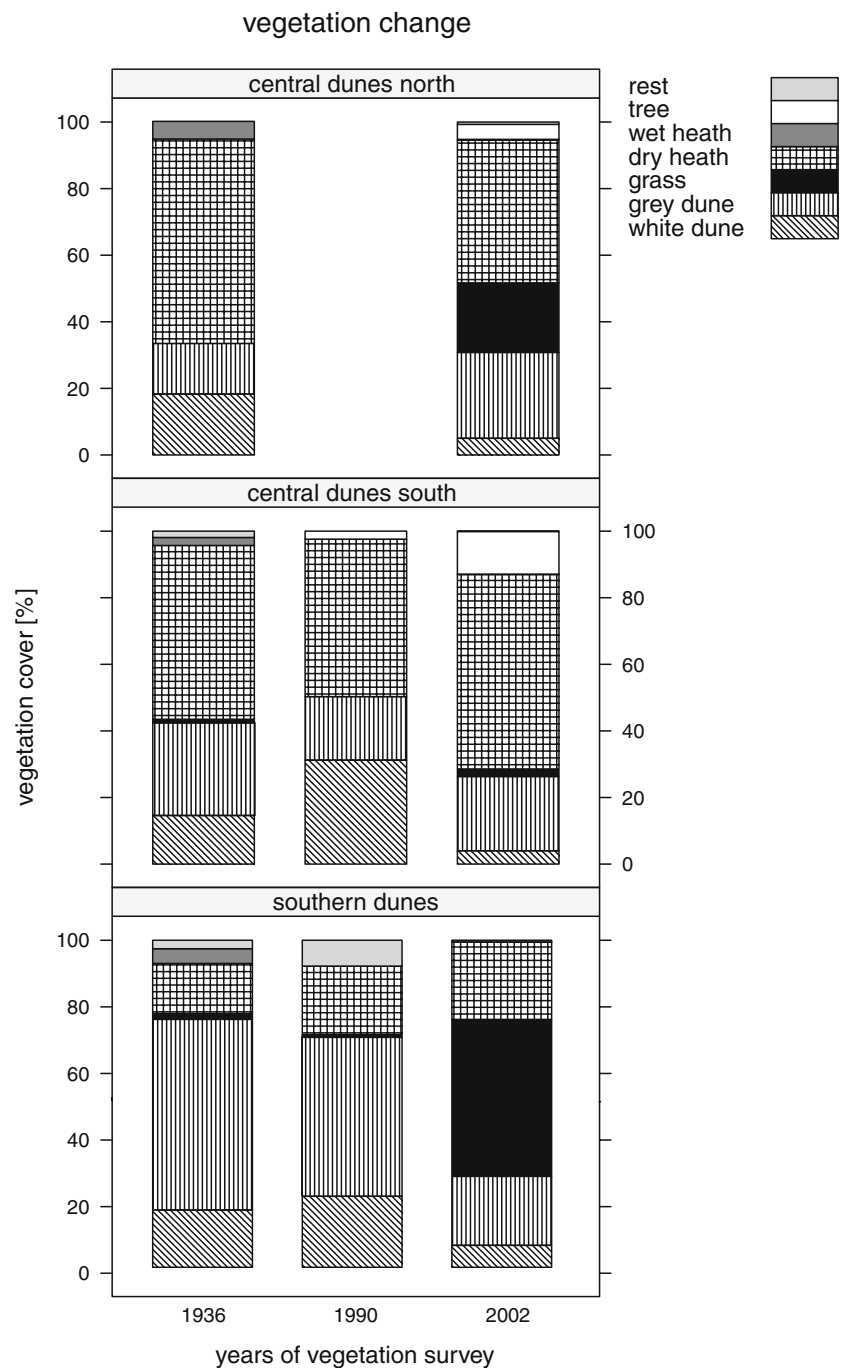
(below one) and trees the tallest and oldest on average among all sites.

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) and P (26% 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-

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 m^2]	1.6	0.6	2.2	0.7	0.7	0.5
height [m]	**1.0a**	0.2	**1.3a**	0.4	**0.3b**	0.03
age [years]	**5.8ab**	0.9	**7.0a**	1.3	**3.0b**	0.41
species number (total per site)	8	–	7	–	4	–
browsing intensity	**2.2a**	0.3	**0.8b**	0.3	**2.9a**	0.29

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.

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

Table 2 Abiotic factors (means +/− 1 SE) 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 dunes-north		Central dunes-south	
		Mean	+/− SE	Mean	+/− SE
soil profile—classes	arenic umbrisol/Regosol	**3**	–	**0**	–
	Cambisol/Braunerde	**1**	–	**0**	–
	Gleysol/Gley	**0**	–	**1**	–
	podzol/Podsol	**1**	–	**4**	–
buried profiles	[%] of all profiles	20	–	0	–
ecto-organic layer	Ol [cm]	1.1	0.5	1.5	0.4
	Of [cm]	3.1	1.3	5.6	2.4
	Oh [cm]	0.7	0.5	0.6	0.4
	O total [cm]	4.9	1.8	7.7	2.9
groundwater EC [μS cm-1]	June 2002	**88a**	7	**55b**	9
	July 2002	**102ab**	6	**84a**	8
	August 2002	**138ab**	23	**91a**	13
soil samples	pH 2002 [salt]	3.6	0.2	3.7	0.3
	EC 2002 [μS cm^{-1}]	197.9	5.3	198.0	6.0
	C/N-ratio 2002	20.1	2.5	22.3	1.7
	water content 2002 [%]	9.4	3.0	9.1	3.5
	LOI 2005 [%]	0.82	0.20	NA	–
	pH 2005 [salt]	4.0	0.2	NA	–
	CEC 2005 [μmol kg^{-1}]	927.8	397.4	NA	–
	ortho-P 2005 [μmol kg^{-1}]	27.5	5.9	NA	–
salt spray [%]	January 2002	**55ab**	–	**23a**	–
	Mai 2002	**35a**	–	**19a**	–
	June 2002	**22ab**	–	**10a**	–
	August 2002	**18ab**	–	**9a**	–

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		P-value
	Mean	+/− SE	Mean	+/− SE	
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

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 (Fig. 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 (Fig. 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 seawater around Hiddensee, then its concentration corresponds on average to only 3–4% of the open seawater 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 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 5 000 to 10 000 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 2,000–2,500 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; *Empetrum nigrum* L. and *Calluna vulgaris* (L.) Hull. dominated units. 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 dune, 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). Adjacent to these heathlands, pioneer birch forests exits. These birch forest have been heathlands in 1970s/80s, but no manual shrub removal occurred during the past decades and therefore succession to pioneer forests took place. These sites therefore can serve as an on-site control for the positive influence of manual shrub and tree removal on open heathland preservation.
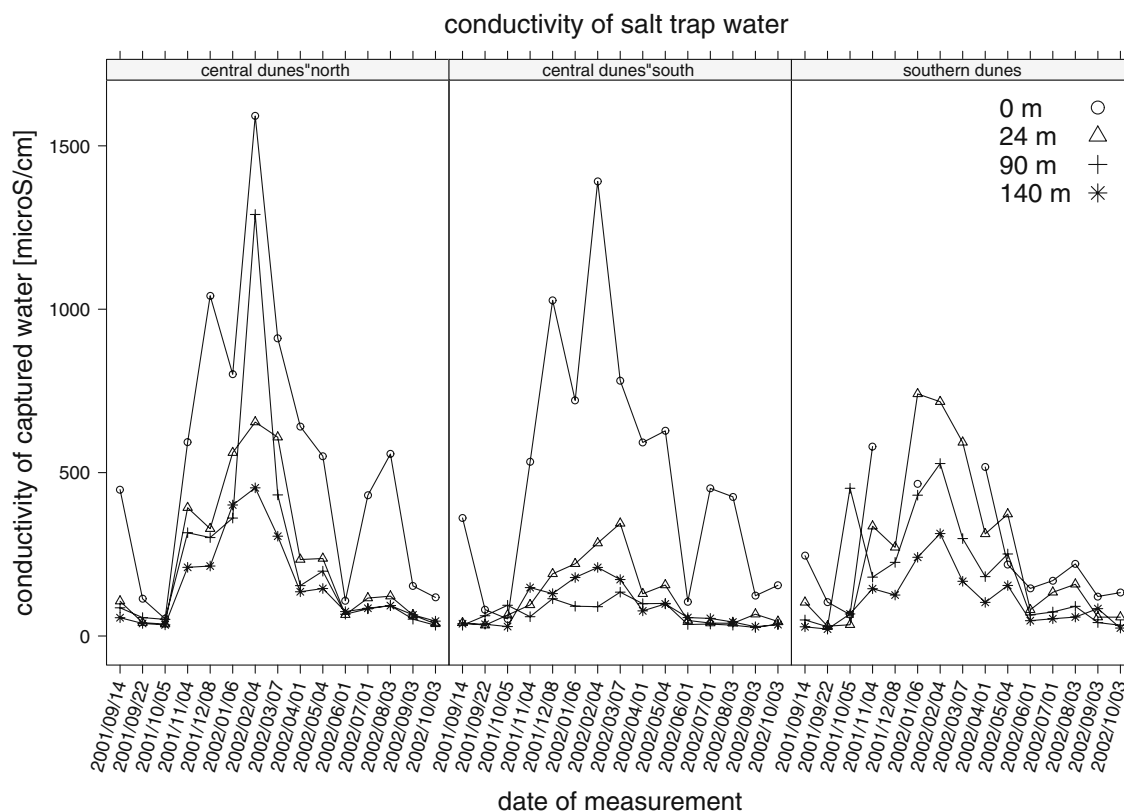
conductivity of salt trap water

Fig. 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 the central dunes-north, a substantial increase in tall grass cover occurred. The tall grass units are mainly dominated by *Deschampsia flexuosa* 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 deposition of 5 kg N ha^{-1} yr^{-1} (Remke et al. 2009). As Hiddensee receives roughly 6–8 kg N ha^{-1} yr^{-1} wet deposition (Remke et al. 2009), it seems probable that elevated atmospheric nitrogen deposition caused the prominent vegetation change in the southern dunes between 1990 and 2002. During this period 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. Opposite to the steep increase in tall grasslands in the southern dunes only 2–3% of the research area in the central dunes, however, is covered by *Carex*. 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 arenaria* 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 arenaria* 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 arenaria,* although it is a typical species of dry habitats (Tidmarsh 1939; Schütz 2000). *Carex arenaria* 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 arenaria* 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 (Hagge 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 arenaria* 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 arenaria* dominances less desirable. The

dunes are quite species poor (less than five 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 arenaria* dominated grasslands from the mid 1980s onwards, and now cover roughly 50% of the research site.

Furthermore, the characteristics and development of forest cover were of central interest. Progressive succession can be a threat to open 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 strongly 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; a mouflon is a European wild sheep breed) 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 (personal communication B. Blase, H. Hübel).

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 seawater 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 is more suppressed in the southern dunes than in the central ones. This is probably due to a combination of higher browsing pressure, higher salt spray stress and fewer seed availability in the southern dunes. Succession in the southern dunes will therefore take longer than the 30–50 years. This is the time period, which has been assumed for forest succession at the Darß, an adjacent dune area within the National Park VBL (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} y^{r-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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