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Nitrogen deposition and grass encroachment in calcareous and acidic Grey dunes (H2130) in NW-Europe

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ABSTRACT

We present an overview of high nitrogen deposition effects on coastal dune grasslands in NW-Europe (H2130), especially concerning grass encroachment in calcareous and acidic Grey Dunes. The problem is larger than previously assumed, because critical loads are still too high, and extra N-input from the sea may amount to 10 kg ha^{-1} yr^{-1}. Grass encroachment clearly leads to loss of characteristic plant species, from approximately 16 in open dune grassland to 2 in tall-grass vegetation. Dune zones differ in grass encroachment, due to the chemical status of the soil. In calcareous and iron-rich dunes (Renodunal district), grass encroachment showed a clear gradient over the dune area. Grass encroachment is low in calcareous foredunes, due to low P-availability, and large grazers were not needed to counteract grass encroachment after 2001. In partly decalcified middle dunes, P-availability and grass encroachment are high due to dissolution of calcium phosphates, and grazing only partially helped to control this. In acidic, iron-rich hinterdunes, grass encroachment gradually increased between 1990 and 2014, possibly because P-availability increased with time due to increased soil organic matter content. In acidic, iron-poor dunes (Wadden district), grass encroachment is a large problem, because chemical P-fixation with Ca or Fe does not occur. Large grazers may however reduce tall-grass cover. High cumulative N-deposition could theoretically lead to increased N-storage and N-mineralization in the soil. Mineralization indeed increased with N-deposition, but in ^{15}N experiments, most ammonium was converted to nitrate, and storage in soil organic matter was low. Soil N-storage is probably reduced by high nitrate leaching, which will favour dune restoration when N-deposition levels decrease.

1. Introduction

Atmospheric nitrogen deposition is a recognized threat to plant diversity (Bobbink et al., 1998, 2010). Increased atmospheric N-deposition has become a problem in the densely populated parts of Europe and North America, where N-deposition has increased by over an order of magnitude since the start of the industrial revolution (Galloway et al., 2008). In NW-Europe, impacts of high N-deposition can be observed in the United Kingdom, the Netherlands, Germany, Denmark and Sweden (Dupre et al., 2010; Stevens et al., 2010; Field et al., 2014). These authors showed that cumulative N-deposition in semi-natural acidic grasslands was positively correlated with the proportion of monocots like grasses and sedges, and negatively with dicots, which often include characteristic herbs.

From the end of the 1980s, such grass encroachment has also occurred in Dutch coastal dunes (Ten Harkel and Van der Meulen, 1995; Veer and Kooijman, 1997; Kooijman et al., 1998), even though N-deposition in the coastal area was much lower than elsewhere in the country (Houdijk and Roelofs, 1991). Pre-industrial levels of N-deposition were probably between 2 and 6 kg N ha^{-1} yr^{-1} (Fowler et al., 2004). However, in the last decades of the 20th century, total N-deposition in the Dutch coastal dunes probably ranged between 15 and 30 kg ha^{-1} yr^{-1} (Heij and Schneider, 1991; Stuyfzand, 1993; Sival and Strijkstra-Kalk, 1998). The species-rich, open dune grasslands (short-grass) generally changed into vegetation dominated by tall grasses and sedges (tall-grass). Graminoid cover increased from 31% in short-grass to 80% in tall-grass, and mean plant species richness decreased from 17 to 9 species (Veer and Kooijman, 1997). In addition to these results from the Netherlands, evidence for detrimental effects of high N-deposition comes predominantly from Denmark and the UK (Provoost et al., 2011). In the United Kingdom, effects of increased N-deposition in coastal dunes were first noticed by Jones et al. (2004). In this study,

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total N-deposition in coastal dunes ranged from 6 kg ha^{-1} yr^{-1} in the outer Hebrides to 29 kg ha^{-1} yr^{-1} in Norfolk. Over the past 34 years, sand dune vegetation appeared to be highly sensitive to N-deposition, especially in SE Scotland (Pakeman et al., 2016). For Germany, Denmark and Sweden, changes in the vegetation related to higher N-deposition in the coastal dune area were first described by Remke et al. (2009a, b). In the area around the Baltic Sea, wet N-deposition in coastal dune areas ranged between 2 and 8 kg ha^{-1} yr^{-1}, which is comparable to 3–10 kg ha^{-1} yr^{-1} of total N-deposition (Remke et al., 2009a).

Coastal dune grasslands are currently protected by the EU-Habitat directive, and belong to the so-called Grey Dunes (H2130). Nevertheless, >96% of the protected European dune habitats have an unfavourable conservation status (European Environment Agency, 2015). Also, most of these areas remain in unfavourable state or even deteriorate, and improvement occurs in only 3% of them. To improve the situation in Grey Dunes, management measures such as grazing, mowing, sod-cutting and stimulation of aeolian activity have been applied since the early 1990s, in UK, Belgium and France, but especially in the Netherlands (e.g., Ten Harkel and van der Meulen, 1995; Veer, 1998; Kooijman et al., 2005).

For effective management, it is important to have a good overview of the effects of high N-deposition on ecosystem functioning. It is important to know whether critical loads, the N-deposition levels above which changes in the vegetation or ecosystem functioning are observed (Bobbink et al., 2010), are exceeded by the actual N-deposition. Also, the response of Grey dunes to high N-deposition partly depends on the chemical status of the soil and availability of P (Kooijman et al. 1998; Kooijman and Besse, 2002; Kooijman et al., 2009). The effect of grazing, applied to counteract grass encroachment (Ford et al., 2016), may be determined by soil chemistry as well. Furthermore, cumulative N-deposition, i.e., the total N-deposition cumulated over time, may have led to increased N-levels in the soil, as in forest ecosystems (Mulder et al., 2015), or increased net N-mineralization, as in inland dunes (Sparrius and Kooijman, 2012). The objective of this paper is to discuss the effects of high N-deposition in European Grey Dunes (H2130), especially in relation to the uncertainties mentioned above. In this paper, we address the following questions: (1) Are current critical loads in coastal dune grasslands low enough, and estimates of actual N-deposition accurate enough? (2) Are grass encroachment and the effects of grazing on tall-grass vegetation similar in all dune zones? (3) To which extent is the impact of N-deposition mediated by differences in soil chemistry and nutrient availability? (4) Can cumulative N lead to increased N-mineralization and N-storage in the soil?

2. Methods

The methods have been divided in four sections, corresponding to the four research questions. The paper is based on unpublished data and on re-analysis of published data, which will be indicated separately for each section. Nomenclature of vascular plant species is according to van der Meijden (2011), for bryophyte species according to Van Tooren and Sparrius (2007) and for lichen species to NDFF (2016).

2.1. Critical loads and actual N-deposition in Grey dunes

The section on extra N-input from the sea in coastal dunes in the Netherlands has not been published before. To calculate actual N-deposition in the Dutch coastal dunes, the OPS model was used, based on spatial patterns in emissions, meteorology and deposition velocity of NO_x and NH_y (Van Jaarsveld, 2004). The model calculations have been calibrated by measurements in the field. For NO_x, model simulations were generally rather good, due to relatively slow deposition rates of NO_x, which result in a homogeneous distribution pattern. For NH_3, however, with fast deposition rates due to its rapid reactivity, distribution patterns were much more variable. Ammonia measurements were obtained with the MAN-measurement network (Meetnet Ammoniak in Natuurgebieden), which started in 2005 (Stolk et al., 2009), and included 240 sites in 70 nature reserves in 2015, with 50 sites in 11 coastal dune areas. Ammonia concentrations were measured monthly with Gradko ammonia diffusion tube samplers, filled with H_2SO_4 to trap the NH_3 present in the air entering the tube, and located on tree stems or branches in relatively open areas (Stolk et al., 2009). In the coastal dune area, measured ammonia concentrations were on average 2 times higher than modelled values, varying from 4 times higher on the Wadden islands, 2 times higher in the dunes of the mainland, and 0.5 times higher in the southern delta area. The measurements indicated that ammonia is evaporating from the sea, especially during spring and summer. The extra N-deposition could partly derive from ships, but the amount was especially proportional to the amount of chlorophyll-a, which is an indicator for algae (Van der Woerd and Pasterkamp 2008). For the coastal area, an additional module on the model was developed, with ammonia emission based on satellite data on the chlorophyll-a distribution over the North Sea. The total amount of seaborne emission is calibrated on the gap between model prediction and MAN-measurements. This amount is in agreement with earlier emission estimates reported in the literature (Asman et al., 1994). With the emission module included, the model results are now in good agreement with the measurements.

The section on grass encroachment in relation to N-deposition along the Baltic Sea is a re-analysis of data provided by Remke et al. (2009a). Nineteen different coastal dune areas were studied in Germany, Denmark, Sweden, Estonia, Latvia, Lithuania and Poland, all with soil pH < 6.5, precipitation of 500–700 mm yr^{-1}, and N-deposition below 10 kg ha^{-1} yr^{-1}. Atmospheric N-deposition was derived from lichen N-concentrations and sampling of wet N-deposition. In all sites, vegetation structure was mapped in a 200 × 200 m open dune area, starting at the first dune ridge from the sea. Two structurally defined vegetation types were studied especially: short-grass and tall-grass. Short-grass was mainly covered by lichens and mosses, and small graminoids such as *Corynephorus canescens*, *Festuca* spp., and *Carex arenaria* in low abundance. Tall-grass was dominated by *C. arenaria*, *Ammophila arenaria* or *Calamagrostis epigejos* and the sward reached higher than 30 cm. The borders between different vegetation structures were digitized manually with the software ArcView 3.2a. Tall-grass ratio was calculated as tall-grass cover divided by the total of short-grass and tall-grass combined. To analyze changes in tall-grass ratio, stepwise multiple linear regression was applied with atmospheric N-deposition, temperature, precipitation and salinity as explanatory factors (Cody and Smith, 1987).

2.2. Grass encroachment and grazing effects in different dune zones

The data on grass encroachment in different dune zones have not been published before. For the calcareous and iron-rich dunes of the Renodunal district, which starts halfway in the Netherlands, and extends towards Belgium and France (Eisma, 1968), the Amsterdamse Waterleidingduinen (AWD) were selected. In AWD, a distinct zonation is present with calcareous foredunes from the 18th century, partly decalcified middle dunes from the 15th century, and acidic hinterdunes from the 9–11th century (Van Til and Mourik, 1999). In all three dune zones, grazed and ungrazed areas of approximately 15 ha were selected, in the same areas where net mineralization of N and P was studied (see Section 2.3). In the Dutch coastal dunes, grass encroachment became apparent in the 1990s (Ten Harkel and van der Meulen, 1995; Veer and Kooijman, 1997), and has been followed since that time. False colour 1:5000 aerial photographs of 1990, 2001, 2008 and 2014 were used to analyze changes in the area of dune grassland, and the cover of short-grass and tall-grass vegetation within them over the years. This was done in areas where grazing with cattle (foredunes: 0.09–0.13 animals per ha; middle dunes: 0.13–0.22 animals per ha) or sheep (hinterdunes: 0.91 animals per ha) was applied since 1990, but also in ungrazed control areas, although in the hinterdune control area sheep grazing was applied after 2008. In all photographs, the borders between different vegetation structures were digitized manually with the software ArcGIS 10.1, applying the previous boundary method (Janssen, 2004). The area of dune grassland, as well as the areas with short-grass and tall-grass in them, were calculated for each site. Differences between years were tested for each dune area separately with chi-square tests (Mason et al., 1994). Differences were significant ($p < 0.05$) with χ^2 values above 3.841.

The relationship between plant species richness and tall-grass cover has also not been published before. This relationship was studied in 63 plots of 6 m^2 in the same three dune zones over a gradient in grass encroachment, with 21 plots in foredunes, 25 in middle dunes and 17 in hinterdunes. The plots were installed as permanent plots, mostly in 2004, and monitored every two to three years. For all vascular plant species, mosses and lichens, cover values were recorded. Tall-grass cover was based on the combined cover of *Ammophila arenaria*, *Elymus repens* subsp. *arenosa*, *Calamagrostis epigejos* and *Carex arenaria*. Characteristic Grey dune species (Van Til and Mourik, 1999) were grouped together as well. We tested relationships between tall-grass cover and number of Grey dune species with regression analysis for the three dune zones combined, based on the first record of each permanent plot. The best fit was found with an exponential model. In addition, for each dune zone, Grey dune species which disappeared or showed a clear decrease with increasing tall-grass cover (>20–30%) were listed.

2.3. Nutrient availability in different dune zones

To link the changes in vegetation in different dune zones to differences in soil characteristics and nutrient availability, field and laboratory experiments were conducted in 1998 and 2005. Part of the field experiment has been published in Kooijman and Besse (2002), but only for ungrazed sites. The laboratory study has not been published before. For the calcareous and iron-rich Renodunal district, net mineralization of N and P was studied in AWD, in areas with and without large grazers in calcareous foredunes, partly decalcified middle dunes and acidic, iron-rich hinterdunes. For the acidic and iron-poor Wadden district, Zwanenwater was included, with both ungrazed areas and areas with cattle and horses, with 0.07 animals per ha.

In the field experiment of 1998, in each of four grazed and ungrazed areas, four 1.5×1.5 m exclosures were constructed in tall-grass vegetation to keep out cattle, sheep and/or rabbits. Net mineralization of N and P was measured in situ in pvc cores with resin bags according to Kjönaas (1999), from April to October. In the laboratory experiment of spring 2005, the organic layer was analyzed separately from the mineral topsoil. Also, microbial biomass was taken into account. Samples were collected in the same four dune zones with ungrazed and grazed areas, in five replicate plots. In each plot, the organic layer was sampled in 25×25 cm squares, and the mineral topsoil in three metal rings of 5 cm depth and a volume of 100 cm^3. Soil pH was measured in deionized water. Soil organic matter content was determined with loss on ignition at 550 °C. For incubation, fresh, homogenized samples of organic layer or mineral topsoil were put into petri dishes and stored at optimal moisture levels at 20 °C in the dark for six weeks (Tietema, 1992). Ammonium, nitrate and phosphate concentrations of fresh and incubated samples were extracted with 50 ml 0.5 M K_2SO_4 solution, and measured on a continuous-flow analyzer. Net mineralization was calculated from differences between incubated and fresh samples. Microbial C was measured in fresh and incubated samples with the chloroform fumigation and extraction procedure (Jenkinson and Powlson, 1976). In both mineralization experiments, differences between the four sites and the two grazing treatments were tested with two factor general linear models, and post-hoc LSMeans tests (Cody and Smith, 1987).

The section on P-availability in iron-rich dunes is a re-analysis of data published in Kooijman et al. (2009). In the acidic, iron-rich hinterdunes of the AWD, 60 soil samples were collected over a range of soil organic matter content. Phosphate concentrations, total Fe and organic Fe were measured according to Kooijman et al. (1998 and 2009). Amorphous mineral Fe was calculated as the difference between total amorphous and organic Fe. Relationships between soil C-content, mineral Fe and plant-available P were analyzed with regression analysis (Cody and Smith, 1987). The section on distribution of Fe in iron-rich and iron-poor soils is a re-analysis of data published in Kooijman et al. (1998). Soil samples ($n = 4$) were collected in four sites in the Wadden district, and in three calcareous and two acidic sites in the Renodunal district. The transition site between Renodunal and Wadden district is included in the latter, based on iron and iron-bound P. Differences between the three dune zones were tested with one-way general linear models and post-hoc LSMeans tests (Cody and Smith, 1987).

2.4. Increased N-mineralization and N-storage in the soil?

The section on net N-mineralization in relation to N-deposition is a re-analysis of data published in Remke et al. (2009b). The 19 sites along the Baltic Sea were divided in 9 sites with acidic and 10 with slightly calcareous parent material, and further separated in sites with wet N-deposition lower and higher than 5 kg N ha^{-1} yr^{-1}. In each site, a 2×2 m plot was selected in pioneer, short-grass and tall-grass vegetation, the latter mostly with *C. arenaria*. In each plot, soil samples (0–10 cm) were collected for analysis of pH, soil organic matter and potential net N-mineralization, and living aboveground biomass of *C. arenaria* for chemical analysis. Differences between parent materials and N-deposition were tested with linear and linear mixed effect models (R development core team, 2008). Tests between two classes were performed by Student's *t*-test if data were normally distributed, and otherwise Kruskal-Wallis tests.

The data on storage of N in the soil have not been published before. In AWD, ^{15}N storage in the soil was studied in a laboratory experiment with samples from calcareous and acidic dune zones, both with low and high organic matter content (OM). The pH_{H2O} ranged from 7.0–8.3 in the calcareous and 3.8–5.3 in the acidic site (Kooijman et al., 2014). Soil organic matter content ranged from 8 to 12 g kg^{-1} soil at low OM, and from 16 to 25 g kg^{-1} soil at high OM. In each of the four sites, five mineral soil samples (0–5 cm) were collected in October 2010. The organic layer was negligible in all sampling sites. In the laboratory, soil samples were put in incubation bags, with three replicate subsamples for all 20 sampling points, and for all seven time series from the start of the experiment to sampling after 1, 2, 4, 8, 16 and 32 weeks. The duration of the experiment was long enough to see changes in SOM (Sjöberg and Persson, 1998). Labeled N was applied as ammonium sulphate, as 5 mg ^{15}N kg^{-1} soil, to avoid fertilization effects. All samples were incubated in the dark at 20 °C until analysis. Labeled and unlabeled N in ammonium, nitrate and dissolved organic N were extracted with 0.05 M K_2SO_4 solution, and measured with a Skalar autoanalyzer (all N) and with the SPINMAS-technique (labeled N; Stange et al., 2007). Microbial N was analyzed with chloroform fumigation-extraction (Jenkinson and Powlson, 1976), and measured in the same way. The amount of labeled and unlabeled N in soil organic matter was analyzed with density dependent fractionation (Cerli et al., 2012), after 16 and 32 weeks. For each fraction and time series, mean values of the three samples per sampling point were used as input value for statistical analysis. Differences between time series, lime content (calcareous and acidic), and OM (low and high) were tested with three-way general linear models and posthoc LSMeans tests (Cody and Smith, 1987).

3. Results

3.1. Critical loads and actual N-deposition

In the Netherlands, N-deposition in the coastal dunes is relatively low, compared to more inland parts of the country. However, N-deposition from the sea, due to ammonia emission on beaches and tidal flats, may account for an extra 3 kg N ha^{-1} yr^{-1} on the dunes of the mainland, and 10 kg N ha^{-1} yr^{-1} on the Wadden islands (Fig. 1). Based on the OPS-model including the emissions from the sea, total N-deposition is now calculated to be around 15 kg ha^{-1} yr^{-1} in large parts of the coastal dunes. The modelled and measured contribution from the sea shows a spatial pattern more or less opposite of the anthropogenic contribution: low in the densely populated part of the west coast, and high on the Wadden Islands. As a consequence, the variability in total N-deposition in coastal dunes is limited, and only few small and remote areas receive a deposition of < 14 kg ha^{-1} yr^{-1}.

In the Baltic Sea area, tall-grass cover in the dune grassland vegetation significantly increased over the gradient in wet deposition from 2 to 8 kg N ha^{-1} yr^{-1} (Fig. 2; $R^2 = 0.28$). On average, tall-grass ratio increased from 0 to 50%. The increase in tall-grass was mostly due to high N-deposition, as N-deposition explained 28% of the variance. Temperature, precipitation and salinity only showed additional contributions of 3–8%, which were not significant. The response to higher N-deposition was especially apparent in dunes with acidic parent material. In the nine acidic sites, tall-grass ratio clearly increased with N-deposition from 0 to 50% around a wet N-deposition of 8 kg N ha^{-1} yr^{-1} ($R^2 = 0.70$), while the relationship was insignificant in the ten sites with more calcareous parent material ($R^2 = 0.07$).

3.2. Grass encroachment and grazing effects in different dune zones

The number of characteristic Grey dune species significantly decreased with tall-grass cover from approximately 16 in open dune grassland to 2 in tall-grass vegetation (Fig. 3; $R^2 = 0.43$). In calcareous foredunes, 11 characteristic herb and lichen species disappeared or strongly decreased at higher tall-grass cover, among which *Arenaria serpyllifolia* and *Sedum acre*. In partly decalcified middle dunes, 27 species were negatively affected by high tall-grass cover, among which *Polygala vulgaris* and *Thymus pulegioides*. Acidic hinterdunes showed a strong decrease in especially lichen species such as *Cetraria aculeata* and *Cladonia ciliata*, which form an important part of plant biodiversity.

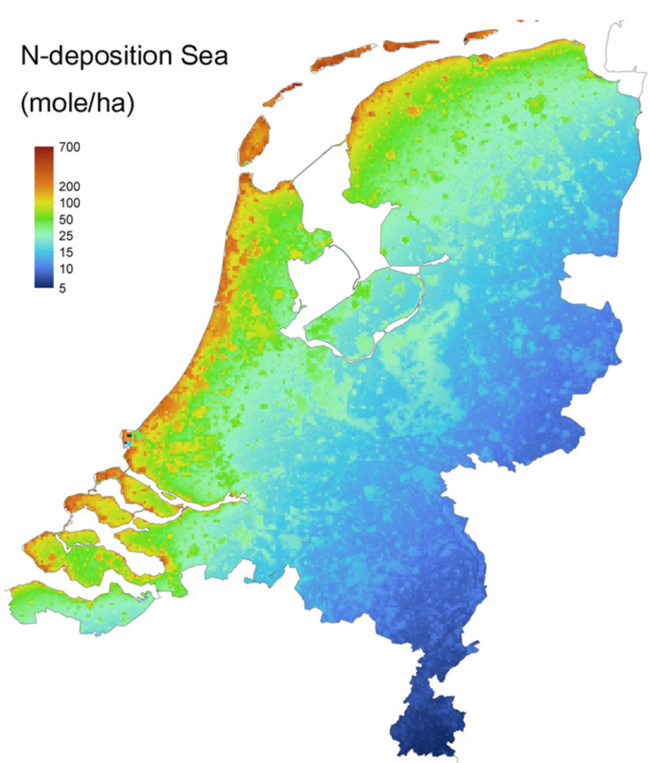

Fig. 1. Extra N-deposition from the coast in the Netherlands, derived from ammonia emission on the beach and tidal flats.

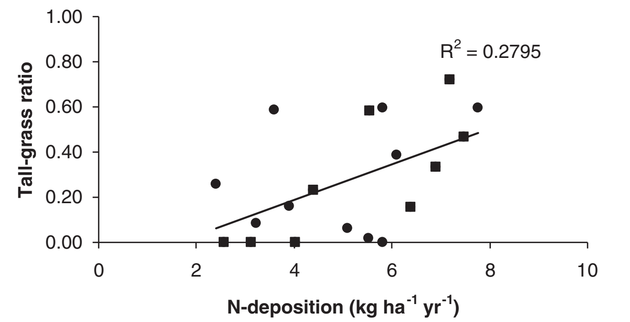

Fig. 2. Relationship between wet N-deposition, based on EMEP wet deposition data and correlations with Lichen-N concentrations, and tall-grass ratio (% tall-grass of total dune grassland cover) in 19 coastal dune areas along the Baltic Sea. The correlation is significant ($p < 0.05$). Circles = dune areas with slightly calcareous parent material; squares = dune areas with acidic parent material.

Grass encroachment significantly differed between dune zones (Fig. 4). In calcareous foredunes, grass encroachment was never a major problem between 1990 and 2014. In this dune zone, dune grasslands accounted for 67–84% of the area throughout this period. Also, even in dune grasslands of the control area without cattle grazing, tall-grass is currently not a major problem. In this area, tall-grass cover significantly increased from 36% to 52% between 1990 and 2001 ($\chi^2 = 7.1$), but significantly decreased to 8% in 2008 and 2014 ($\chi^2 = 37.2$) without management. In grazed areas, tall-grass cover was 30% in 1990, and significantly decreased to 14–19% in later years ($\chi^2 = 8.5$ and 7.0 respectively). In partly decalcified middle dunes, dune grasslands are however less common. Dune grasslands accounted for 47–60% of the area in 1990, and 34–41% in 2008. Also, within dune grasslands, tall-grass cover significantly increased in control areas from 23% in 1990 to 90% in 2001 ($\chi^2 = 195.2$), and remained high after that. Cattle grazing helped to reduce tall-grass, but only after a while, as tall-grass further increased until 2001. Also, even with grazing, tall-grass cover remained relatively high, with values around 40% of the area. In the acidic hinterdunes, dune grassland is again more common. In the period 1990–2014, 81–89% of the area consisted of dune grassland. In ungrazed areas, grass encroachment had a slower start than in the middle dunes, but in 2008, 78% of the dune grasslands also consisted of tall-grass. Grazing with sheep, however, appeared to counteract grass encroachment very well. In grazed areas, tall-grass cover in dune grasslands significantly decreased from 43% in 1990 to 11% in 2014 ($\chi^2 = 23.8$). For this reason, sheep were introduced after 2008 in the former control area, which led to a rapid and significant decrease in tall-grass cover from 78% in 2008 to 16% in 2014 ($\chi^2 = 49.2$).

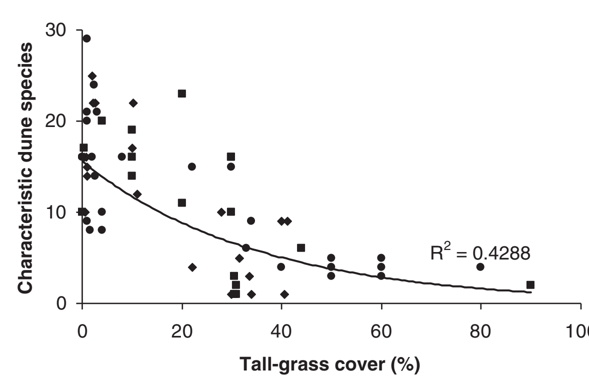

Fig. 3. Relationship between tall-grass cover and number of characteristic Grey dune species in 6 m^2 plots in different dune zones in Amsterdamse Waterleidingduinen (AWD), based on 21 plots in Foredunes (triangles), 25 plots in Middle dunes (circles) and 17 plots in Hinterdunes (squares). Regression analysis was based on all 63 records combined. The correlation is significant ($p < 0.05$).

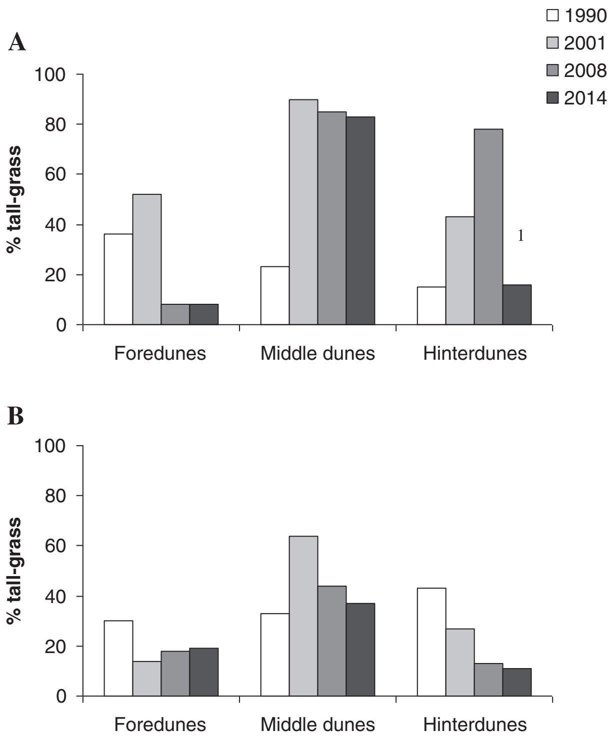

Fig. 4. Tall-grass cover (%) in Grey dunes in Amsterdamse Waterleidingduinen (AWD) in calcareous foredunes, partly decalcified middle dunes and acidic hinterdunes in 1990, 2001, 2008 and 2014. A = ungrazed control areas; B = areas grazed with large herbivores. [1] = in the control area in the hinterdunes, grazing was applied after 2008.

3.3. Nutrient availability in different dune zones

In the abovementioned dune areas, the patterns in aboveground biomass correspond to some extent with those in grass encroachment. In AWD, aboveground biomass production and standing dead, measured in rabbit and cattle-proof exclosures, did not differ between dunes zones when compared together with Zwanenwater (Table 1). However, for ungrazed sites, biomass production showed a significant second order correlation with pH ($R^2 = 0.37$), with values of 179 g m^{-2} at pH 7, a clear peak of 283 g m^{-2} at pH 5, and again lower values of 91 g m^{-2} at pH 3 (Kooijman and Besse, 2002). In the Wadden site Zwanenwater, where grass encroachment was very severe, biomass production reached values of 397 g m^{-2}.

These patterns in biomass production and grass encroachment were in turn reflected in the availability of N and especially P (Table 1, Fig. 5). Grazing significantly affected net mineralization of N in both field and laboratory experiment, and of P during laboratory incubation ($p < 0.05$). Differences between dune zones were significant for both nutrients in both experiments. In calcareous foredunes, availability of N and P was relatively low in both ungrazed and grazed areas, as indicated by low net mineralization of the two nutrients in both field and laboratory studies. The organic layer played no role in net mineralization yet, although micro-organisms were present. In partly decalcified middle dunes, however, mineralization of N and especially P significantly increased, especially under ungrazed conditions. The organic layer also contributed more to nutrient supply than in calcareous foredunes. With grazing, nutrient supply generally decreased, probably especially due to lower contribution of the organic layer. In acidic, iron-rich hinterdunes, net N-mineralization did not differ from partly decalcified middle dunes in the field experiment and was lower in the laboratory experiment. However, net P-mineralization was significantly lower than in partly decalcified middle dunes in both field and laboratory. Grazing reduced net N-mineralization in the field experiment, but net P-mineralization was unaffected by grazing and remained low. In acidic, iron-rich soils, P-availability increased with soil organic matter content, associated with a shift from mineral to organic Fe (Fig. 6). In soils with low C-content, iron was mainly present in mineral form, and plant available P was low, probably due to P-fixation in iron phosphates. In soils with high C-content, however, mineral Fe was transformed in organic Fe, and plant available P increased, probably due to weaker binding to Fe–OM complexes.

In the Wadden district, with acidic and iron-poor soils, net N-mineralization was higher than in the acidic iron-rich Renodunal soil in the field experiment. However, net P-mineralization was higher than in the iron-rich soil for both field and laboratory, especially in areas without grazing. High P-availability was probably partly caused by the dense organic layer. However, iron contents in the soil are low, and mainly present in organic form, which implies relatively weak binding of P to Fe–OM complexes (Table 2). Grazing significantly reduced availability of both N and P, probably due to reduction of the organic layer.

3.4. Increased net N-mineralization and storage of N in the soil?

Cumulative N-deposition may lead to higher net N-mineralization. In the Baltic Sea area, net N-mineralization indeed increased from low to high N-deposition in pioneer, short-grass and tall-grass vegetation, although mainly in dunes with acidic parent material (Table 3). Also, N:P ratio of aboveground parts of *C. arenaria* showed

Table 1
Vegetation and soil characteristics and net mineralization of N and P in the field (from April to October) in rabbit exclosures with tall-grass vegetation in four different dune zones in Renodunal and Wadden district. Mean values ($n = 4$) and standard deviations. [1] = significant differences between dune zones; [2] = significant differences between ungrazed and grazed treatments ($p < 0.05$); [ns] = not significant. Different letters indicate significant differences for a particular parameter between individual mean values.

		Renodunal calcareous soil	Renodunal decalcified soil	Renodunal acidic soil	Wadden acidic soil
pH^{1}_{H2O}	Ungrazed	6.9 (0.9)^{c}	4.8 (0.4)^{b}	4.1 (0.4)^{a}	3.9 (0.2)^{a}
	Grazed	6.8 (0.4)^{c}	4.7 (0.3)^{b}	3.9 (0.2)^{a}	4.5 (0.1)^{a,b}
Soil organic matter (%)^{ns}	Ungrazed	3.3 (1.4)^{a}	5.3 (2.9)^{b}	4.2 (0.9)^{a,b}	3.9 (2.2)^{a,b}
	Grazed	6.1 (2.7)^{b}	3.9 (1.8)^{a,b}	3.4 (0.9)^{a,b}	1.4 (0.4)^{a}
Aboveground biomass (g m^{-2})^{1}	Ungrazed	254 (115)^{a}	193 (61)^{a}	142 (65)^{a}	397 (130)^{b}
	Grazed	222 (85)^{a}	214 (84)^{a}	163 (65)^{a}	228 (99)^{a}
Standing dead (g m^{-2})^{1,2}	Ungrazed	350 (295)^{a}	140 (85)^{a}	89 (48)^{a}	1504 (1086)^{b}
	Grazed	32 (23)^{a}	51 (29)^{a}	87 (114)^{a}	510 (498)^{a}
Net N-mineralization (g m^{-2})^{1,2}	Ungrazed	2.3 (0.7)^{a,b}	4.5 (2.4)^{b}	4.3 (0.6)^{b}	10.9 (3.8)^{c}
	Grazed	2.7 (0.6)^{a,b}	2.3 (0.5)^{a,b}	1.2 (0.7)^{a}	5.4 (3.5)^{b}
Nitrification^{1,2} (%)	Ungrazed	106 (27)^{c}	112 (28)^{c}	87 (5)^{bc}	56 (26)^{b}
	Grazed	85 (7)^{b,c}	88 (11)^{c}	56 (35)^{b}	21 (16)^{a}
Net P-mineralization (mg m^{-2})^{1}	Ungrazed	−45 (79)^{a}	153 (97)^{b,c}	13 (15)^{a,b}	225 (26)^{c}
	Grazed	−23 (91)^{a,b}	33 (156)^{a,b}	25 (37)^{a,b}	85 (142)^{a,b,c}

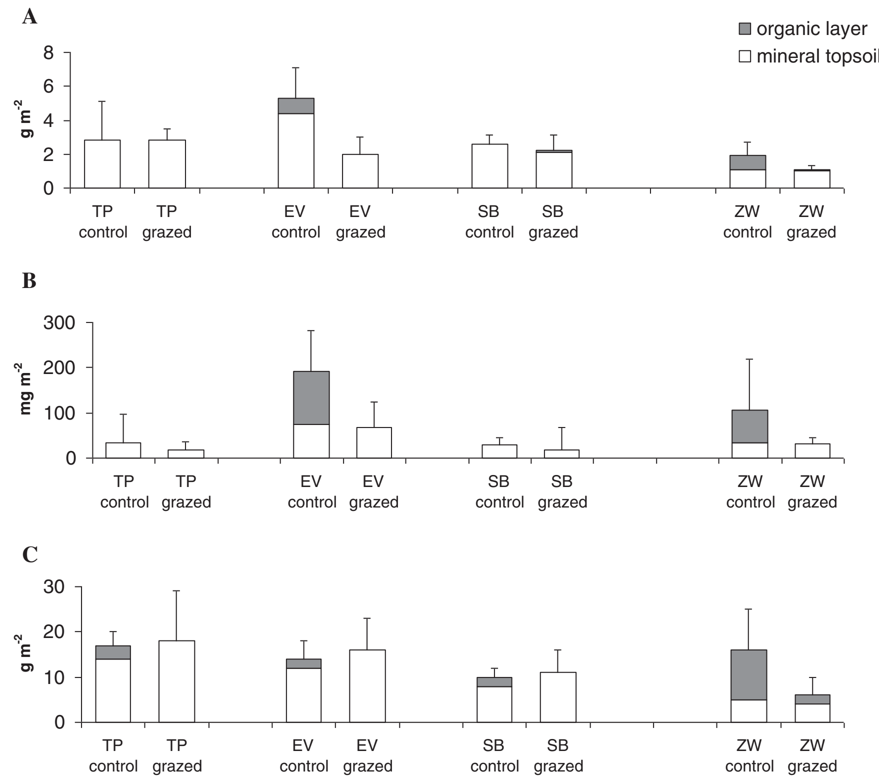

Fig. 5. Net mineralization of N and P in a six-week laboratory experiment, and microbial C in fresh samples of the organic layer and mineral topsoil from control and grazed tall-grass vegetation in four different dune zones in Renodunal and Wadden district. TP = Renodunal district, calcareous soil; EV = Renodunal district, partly decalcified soil; SB = Renodunal district, acidic soil; ZW = Wadden district, acidic soil. A = net N-mineralization; B = net P-mineralization; C = microbial C. Mean values and standard deviations ($n = 5$). The sites are the same as in Table 1.

a clear increase with high N-deposition. In dune soils with slightly calcareous, more neutral parent material, net N-mineralization and foliar N:P ratio did not differ between areas with low and high N-deposition.

Cumulative N-deposition may also lead to increased storage of N in the soil. In the ^{15}N experiment with calcareous and acidic dunes soils with low and high organic matter content. Total recovery differed between time series, but was relatively high in general, with mean values varying between 73% and 105%. It was expected that labelled ammonium would be assimilated by micro-organisms and then converted to soil organic matter. However, within a few hours after application, a large part of the labeled ammonium had been converted to nitrate, especially in calcareous soil (Fig. 7). In acidic soil, nitrification significantly lagged behind, but after one week, nitrification had occurred here as well, although at lower values than in calcareous soil. After 16 weeks, recovery of ^{15}N in nitrate was higher than 50% in all soil types.

Storage of ^{15}N in soil organic matter of the AWD was measured after 16 and 32 weeks. After 16 weeks, 7–24% of the ^{15}N applied had been recovered in the light floating fraction, i.e. in particulate soil organic matter not bound to mineral soil surfaces, a rather labile pool of SOM. In the heavy fraction, ^{15}N was not present at all. After 32 weeks, values were slightly lower, and mean values for the two periods combined were 7% ($\pm$2%) recovery in calcareous soil with low organic matter content (OM), 14% ($\pm$4%) in calcareous soil with high OM, 9% ($\pm$2%) in acidic soil with low OM and 19% ($\pm$8%) in acidic soil with high OM. Storage in soil organic matter was significantly higher in soils with high OM, but also in acidic soil, perhaps due to slightly lower nitrification. However, with maximum values of 20%, N-storage in soil organic matter was not very large.

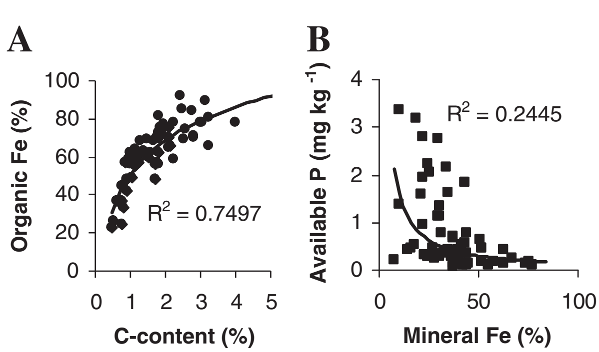

Fig. 6. Relationships between (A) soil C-content and amorphous organic Fe, and (B) between mineral Fe and plant-available P in iron-rich acidic dune soils in the Amsterdamse Waterleidingduinen. Both correlations were significant ($p < 0.05$).

Table 2
Soil variables related to Fe in calcareous and acidic dune soils. Values given are means (n = 8–21) and standard deviations. [1] = significant differences between dune soils in general linear models ($p < 0.05$); different letters indicate significant differences between particular mean values.

	Renodunal calcareous soil	Renodunal decalcified soil	Wadden acidic soil
pH[1]	6.5 (0.9)[c]	5.2 (1.2)[b]	3.5 (0.2)[a]
SOM (%)	4.5 (3.2)[a]	4.5 (2.7)[a]	3.1 (2.6)[a]
Total extractable Fe (mmol kg^{-1})[1]	8.5 (2.4)[b]	11.7 (2.3)[c]	4.1 (2.0)[a]
Organic Fe (%)[1]	24 (12)[a]	48 (31)[b]	84 (11)[c]
Mineral Fe (%)[1]	76 (12)[c]	52 (31)[b]	16 (11)[a]

Table 3
Net N-mineralization in areas with low and high atmospheric deposition (n = 4–6) around the Baltic Sea in dunes with acidic and slightly calcareous, more neutral parent material. N-deposition = wet atmospheric deposition in kg ha^{-1} yr^{-1}; Net Nmin = net N-mineralization (g m^{-3} in 26 days under laboratory conditions); N:P Carex = ratio of N- and P-concentrations in living biomass of *Carex arenaria* * = significant differences ($p < 0.05$) between low and high N-deposition for a particular vegetation type. Data are based on Remke et al. (2009b).

		Acidic pioneer	Acidic short-grass	Acidic tall-grass	Neutral pioneer	Neutral short-grass	Neutral tall-grass
N-deposition	Low N	3.5 (0.8)	3.5 (0.8)	3.5 (0.8)	3.3 (0.6)	3.3 (0.6)	3.3 (0.6)
	High N	6.7 (0.8)	6.7 (0.8)	6.7 (0.8)	6.0 (0.9)	6.0 (0.9)	6.0 (0.9)
pH	Low N	4.9 (0.3)	4.3 (0.1)	3.9 (0.0)	5.6 (0.3)	4.9 (0.2)	4.7 (0.2)
	High N	4.3 (0.1)	3.7 (0.1)	3.7 (0.1)	5.7 (0.3)	4.7 (0.2)	4.6 (0.2)
Net Nmin	Low N	0.7 (0.1)	0.8 (0.1)	0.9 (0.2)	1.2 (0.1)	1.4 (0.4)	3.0 (3.3)
	High N	1.3 (0.2)*	1.7 (0.2)*	2.7 (0.4)*	1.1 (0.2)	1.8 (0.3)	3.3 (0.6)
N:P Carex	Low N	7.8 (1.1)	7.1 (0.4)	8.1 (0.1)	9.9 (0.7)	7.9 (0.5)	7.9 (0.4)
	High N	11.5 (0.5)*	9.6 (0.5)*	9.6 (0.5)*	9.3 (0.6)	7.8 (0.4)	7.0 (0.3)

4. Discussion

4.1. Critical loads and actual N-deposition

Atmospheric N-deposition has been high in large parts of NW-Europe (Galloway et al., 2008), but highest levels were found in the Netherlands, especially in the 1990s, when total N-deposition reached levels of 50 kg N ha^{-1} yr^{-1} (de Haan et al. 2008). Since then, N-deposition has decreased, and currently reaches levels of 25 kg N ha^{-1} yr^{-1}. In coastal dunes, total N-deposition is lower than in the mainland, but these receive extra ammonium from the sea, up to values of 10 kg ha^{-1} yr^{-1}. The extra input means that N-deposition is approximately 15 kg ha^{-1} yr^{-1} in almost all dune areas. This amount equals the current Dutch critical load for calcareous Grey dunes, which implies that calcareous Grey dunes are still endangered. For acidic Grey dunes, with official critical loads of 10 kg N ha^{-1} yr^{-1}, actual N-deposition is considerably exceeded. Until 2030, N-deposition levels in the Netherlands are expected to decrease further (PAS, 2015). However, as this decrease will be mostly due to reduced ammonium deposition in agricultural areas, the coastal dunes may not really benefit, and N-deposition levels remain too high for acidic Grey dunes in the coming decades. Other NW-European countries may have lower N-deposition in coastal dune areas than the Netherlands, although perhaps not in the UK (Jones et al. 2004; Field et al., 2014; Pakeman et al., 2016). However, many countries may not be aware of the extra ammonium deposition originating from the sea, especially on wide and nutrient-rich beaches and coastal flats, which may increase total N-deposition. The knowledge gap may be solved by measuring actual ammonium concentrations with ammonium diffusion samplers, and compare them with modelled values in N-deposition models.

Compared to the Dutch situation, tall-grass ratios of 50% in the Baltic Sea area are relatively low. In AWD, tall-grass cover in dune grasslands could increase to 80–90%, and in Zwanenwater, tall-grass cover increased to 75% already in 1992 (Kooijman and de Haan, 1995). Lower tall-grass cover in the Baltic is probably due to the lower N-deposition, which ranged from 2 to 8 kg ha^{-1} yr^{-1}. In the Netherlands, N-deposition in coastal areas is currently 15 kg ha^{-1} yr^{-1}, and values amounted to 30 kg ha^{-1} yr^{-1} in the past (Heij and Schneider, 1991; Stuyfzand, 1993; Sival and Strijkstra-Kalk, 1998). Nevertheless, the clear increase in tall-grass and decrease in short-grass already at low N-deposition in the Baltic imply that the current critical loads are too high. Significant negative effects start around 4–6 kg N ha^{-1} yr^{-1} wet deposition, or 5–8 kg N ha^{-1} yr^{-1} total deposition, especially in dunes with acidic parent material. This is supported by Pakeman et al. (2016), who found functional changes in acidic fixed dunes above 4.1 kg N ha^{-1} yr^{-1}, or above 5.9 kg N ha^{-1} yr^{-1} if the lower 95% confidence interval was applied. In the past decades, international critical loads for species-rich coastal dune grasslands have been lowered from 10 to 20 kg N ha^{-1} yr^{-1} (Achermann and Bobbink, 2003; Jones et al., 2004) to 8–15 kg N ha^{-1} yr^{-1} (Bobbink and Hettelingh, 2011). In the Netherlands, official critical loads differ between calcareous and acidic Grey dunes (van Dobben and van Hinsberg, 2008), and are currently 15 kg N ha^{-1} yr^{-1} for the first and 10 kg N ha^{-1} yr^{-1} for the latter. However, the above results suggest that, at least for acidic dunes, 10 kg N ha^{-1} yr^{-1} is still too high.

4.2. Grass encroachment and grazing effects in different dune zones

The clear decrease in the number of characteristic Grey dune species with tall-grass cover suggests that high N-deposition is a real problem to biodiversity in the coastal dunes. This further supports the strong

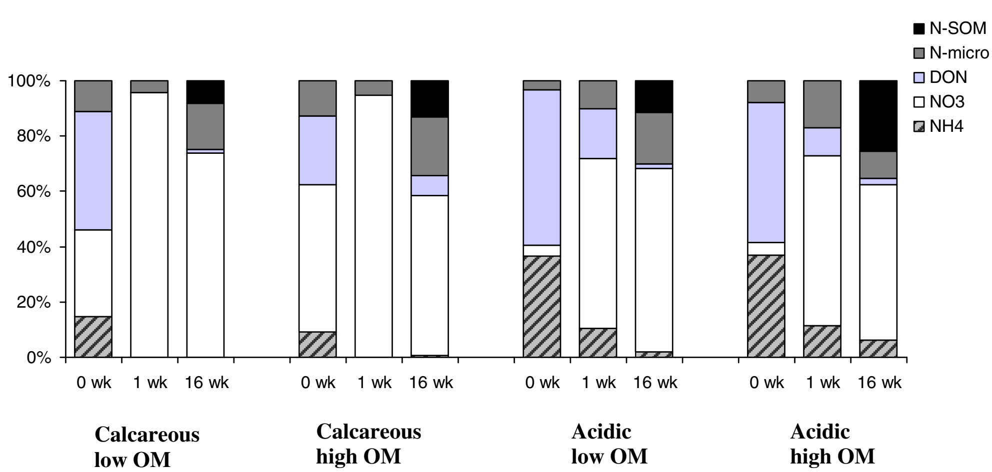

Fig. 7. Recovery of ^{15}N in different soil fractions at the start of the experiment and after one and sixteen weeks of soil incubation in the laboratory of calcareous and acidic dune soils with low or high organic matter content (OM). N-SOM is N in soil organic matter; N-micro = N in microbial biomass. Mean values (n = 5, each based on three experimental replicates).

decline in plant diversity with increased N-deposition and grass encroachment (Veer and Kooijman, 1997; Bird and Choi, 2017), and is consistent with changes in semi-natural inland grasslands (Dupre et al., 2010; Stevens et al., 2010). Grass encroachment may also negatively affect characteristic animals (Van Til et al., 2014; Nijssen et al., 2017).

Despite these general patterns, the responses to high N-deposition differed between dune zones. In calcareous foredunes, the relatively small amount of tall-grass, even in areas without cattle grazing, suggest that grass encroachment is only a minor problem. In the ungrazed area, tall-grass cover even spontaneously decreased after 2001. Also, in areas with cattle grazing, the number of animals was strongly reduced between 2001 and 2008, which suggests that grazing is currently not even needed. The decrease of tall-grass vegetation was probably partly due to the decrease in N-deposition since the 1990s. Also, increase of rabbit populations played a role, which had collapsed in the coastal dunes since 1990 due to Rabbit Haemorrhagic Disease, but increased again after 2003 (Drees et al., 2009). In partly decalcified middle dunes, grass encroachment is a much larger problem, and grazing could counteract this only to a limited extent. The middle dunes are also prone to shrub-encroachment, especially with invasive species such as *Prunus serotina* (Ehrenburg et al., 2008), which may explain why the actual dune grassland area is much smaller than in calcareous foredunes and acidic hinterdunes. Grass encroachment was also lower in acidic hinterdunes, although this had increased in 2008, after which sheep grazing was applied. Grazing appeared to be very effective, and reduced tall-grass cover to approximately 10% in both grazed and formerly ungrazed areas.

In the lime-poor and iron-poor Wadden district, grass encroachment seems to be a major problem, in contrast to the Renodunal district, where high tall-grass cover mainly occurs in partly decalcified middle dunes. In the Wadden area Zwanenwater, tall-grass vegetation increased between 1986 and 1992 from 5% to more than 75% of the area, although grazing could be effective (Kooijman and de Haan, 1995). The present situation is slightly better, but in an analysis of Grey dunes in the Wadden district in the period 2005–2012, in most areas, only 2–18% of the dune grasslands was in good state, even though in the majority cattle grazing was applied (Everts et al., 2013). High grass encroachment in acidic, iron-poor dunes was also found along the Danish coast (Ovesen, 2001). Also, on the German Wadden island Spiekeroog, south slopes were dominated by lichen-rich *Violo-Corynephoretum* short-grass in 1990 (Isermann and Corder, 1992), but currently are mostly covered with *C. arenaria*, which is often dominant in tall-grass vegetation in acidic dunes.

4.3. Nutrient availability in different dune zones

The gradient in grass encroachment in the Renodunal dunes from calcareous foredunes to partly decalcified middle dunes and acidic, iron-rich hinterdunes can be partly explained by differences in nutrient availability. As N-deposition does not really differ between dunes zones, and differences in net N-mineralization were less prominent than for P, P-availability is probably the most important factor.

In calcareous foredunes, both grass encroachment and P-availability were low, probably due to chemical fixation of P in calcium phosphates (Lindsay and Moreno, 1966). Calcium phosphates (co)precipitate with calcium carbonates in lime-rich soil, and are insoluble as long as pH is high. In many calcicole dune plants, arbuscular mycorrhiza may help with P-nutrition (Ernst et al., 1984). However, foliar N:P ratio of the nonmycorrhizal *Carex arenaria* showed that P-availability in calcareous dunes is actually very low. In calcareous foredunes, N:P ratios ranged from 22 to 25 (Kooijman et al., 2014), which clearly point to P-limitation (Koerselman and Meuleman, 1996; Güsewell, 2004). If P is a limiting factor, atmospheric N-deposition cannot be used for extra plant growth, and biomass production remains low. As a result, litter input, net N-mineralization and grass encroachment will probably also be relatively low. Low P-availability in calcareous dunes is to some extent supported by N-fertilization experiments. In a field study in the Netherlands, vegetation did not respond to N-fertilization at all (Ten Harkel and van der Meulen, 1995). In a field study in Wales, biomass first increased with N-fertilization (Plassmann et al., 2009), but after six years, only with N and P combined (Ford et al., 2016).

In partly decalcified middle dunes, the much larger grass encroachment than in calcareous dunes may also be related to P-availability, as suggested by high net P-mineralization in both field and laboratory. In partly decalcified soil, when calcium carbonates in the topsoil have dissolved, calcium phosphates dissolve as well (Lindsay and Moreno, 1966; Syers and Walkers, 1969). Mineral P, which mainly consists of calcium phosphates, indeed decreased from calcareous to decalcified dune soils (Kooijman et al., 1998). Solubility of phosphate is highest in middle dunes with pH 5, which is low enough for dissolution of calcium phosphates, but not yet low enough for formation of iron and aluminium phosphates (Lindsay and Moreno, 1966). In addition, formation of organic layers, due to higher litter input and lower decomposition than in calcareous soil, may play a role. Organic layers mainly consist of organic material, which reduces sorption of P to mineral components. Relatively high P-availability in the partly decalcified middle dunes is supported by low foliar N:P ratios, which showed values around 11–12 (Kooijman and Besse, 2002).

In acidic, iron-rich hinterdunes, grass encroachment had a slower start than in partly decalcified hinterdunes, but reached 80% tall-grass cover in ungrazed areas in 2008. These patterns may also be related to P-availability. In acidic, iron-rich hinterdunes, P-mineralization may be low due to high iron concentrations, which increase at low pH, and strongly contribute to P-sorption (Lindsay and Moreno, 1966; Gu et al., 1994). However, P-availability in iron-rich soils is also dependent on soil organic matter. In soils with low C-content, P-availability was reduced by mineral amorphous Fe, which can bind P to iron (hydr)oxides and in iron phosphates. In soils with high C-content, where organic Fe predominates, P is probably weakly sorbed to Fe–OM complexes (Gu et al., 1994), which means that P-availability to the vegetation is higher. As soil organic matter content may reach a maximum within 50 years, especially in young successional stages (Aggenbach et al., 2017), it is possible that soil organic matter content and P-availability have increased over the period 1990–2014, which has resulted in higher grass encroachment. Uptake of P from Fe–OM complexes may be further enhanced in nonmycorrhizal species such as *C. arenaria*, which have generally higher root exudation of carboxylates than mycorrhizal plants, which increases phosphate uptake by ligand exchange (Lambers et al., 2006).

In the acidic, iron-poor Wadden district, high grass encroachment is probably also related to high P-availability, as suggested by the high net P-mineralization in both field and laboratory studies. High P-availability may be partly due to lack of chemical P-fixation mechanisms. Both Ca and Fe content of the parent material are low (Eisma, 1968). As a result, soils were acidic, and iron content was not only lower than in Renodunal district soils, but also mainly organic, which means that P is mainly weakly sorbed to Fe–OM complexes. However, the organic layer also plays a role. The organic layer is generally rather extensive in the Wadden district, due to high biomass and litter production, and low rates of decomposition (Kooijman and Besse, 2002). In the organic layer, mineral content is low, and sorption of P to mineral particles reduced. Relatively high P-availability in acidic, iron-poor soils is supported by low foliar N:P ratios, with values around 10 (Kooijman et al., 1998; Remke et al., 2009b). This further supports that dunes without chemical P-fixation, such as in the Wadden district or around the Baltic Sea, are very sensitive to high atmospheric N-deposition and grass encroachment.

4.4. Increased net N-mineralization and storage of N in the soil?

In this study, cumulative N-deposition indeed led to increased net N-mineralization, especially in acidic soils. This is in accordance with

Sparrius and Kooijman (2012), who found a similar result for inland drift sands. However, cumulative N-deposition does probably not lead to increased storage of N in the soil. In coniferous forest floor samples, storage in soil organic matter ranged from 36 to 74% after 21 weeks (Sjöberg and Persson, 1998). However, in the dune soils of our study, maximum N-storage after 16 and 32 weeks was only approximately 20% of the labelled N applied. Also, in the forest study, recovery of ^{15}N in nitrate was very low, while our study showed rapid conversion of ^{15}N-ammonium to nitrate, even in acidic soil. Nitrification was slightly higher in calcareous than acidic soil, because nitrifying bacteria are relatively weak competitors, which only increase when ammonium demand of other micro-organisms has been satisfied (Hart et al., 1994; Kowalchuk et al., 1997). However, in both soil types a major part of the ^{15}N was found back in nitrate. Nitrate was not reabsorbed by micro-organisms and lost via denitrification, probably because oxygen is not a limiting factor in dry soils, and alternative redox acceptors are not needed. High nitrate levels can be taken up by plant roots (if present), but can also leach to the groundwater. Ten Harkel et al. (1998) estimated that 70% of added ammonium fertilizer was leached as nitrate in a calcareous foredune site. High leaching and low storage in coastal dunes were supported by Remke (2010), who found high leaching and low ^{15}N storage in the soil in a field experiment in acidic dune grasslands on Terschelling. High leaching and low storage of N in the soil may imply that high N-deposition does not lead to increased accumulation of N in the soil. In a sister study on soil succession in calcareous dunes with high and low N-deposition, accumulation of soil N was indeed not larger in the AWD dunes of the Netherlands than in the dunes of Newborough Warren in Wales (Aggenbach et al., 2017).

4.5. Concluding remarks

In the NW-European coastal dunes, N-deposition will probably remain higher than the critical loads in the coming decades, especially in acidic Grey dunes. Also, at least in the Netherlands, not only actual, but also critical loads for acidic dunes are still too high. This is important especially if cash flow for habitat restoration depends on whether, or to which extent, critical loads are exceeded by actual N-deposition.

Different dune zones differ in response to high N-deposition, and calcareous dunes are less sensitive than acidic dunes. In calcareous dunes, grass encroachment is generally lower, due to low P-availability, absence of thick organic layers and high rabbit activity. In calcareous dunes, N-accumulation in the soil seems unaffected by high N-deposition, possibly due to high nitrification and nitrate leaching to the groundwater. The real danger in calcareous dunes is decalcification of the topsoil, which is higher in areas with high N-deposition (Aggenbach et al., 2017). Apart from changes in plant species composition, acidification also leads to dissolution of calcium phosphates, higher biomass production, lower pH and more extensive organic layers, which further contribute to high P-availability.

In partly decalcified and acidic dunes, high N-deposition leads to much stronger grass encroachment than in calcareous dunes. In acidic dunes, net N-mineralization increased with N-deposition. In addition, most partly decalcified and acidic dunes are characterized by high P-availability, because chemical P-fixation only occurs in iron-rich soils with low organic matter content. Many acidic dunes have low N:P ratios in the vegetation, which points to N-limitation, but also to excess P, and means that both the functioning and species richness in acidic dunes are very sensitive to high N-deposition.

4.6. Implications for management

The most important measure to improve Grey dune habitats would evidently be lower N-deposition, although recovery can take a long time (Stevens, 2016). If this is not possible, local management measures can help, although it is not clear whether ecosystems and plant communities can be restored completely (Jones et al., 2017). In calcareous dunes, light grazing by large herbivores may be applied to counteract grass encroachment, but if rabbit populations are large enough, this may not even be necessary. The most important threat in calcareous dunes is acidification of the topsoil, which leads to increased P-availability and higher biomass production. However, acidification can be counteracted by aeolian activity, which brings calcareous sand back to the surface, especially in areas with high wind velocities close to the sea.

In partly decalcified and acidic dunes, grazing is needed to counteract grass encroachment at least to some extent. Grazing reduces aboveground biomass, improves light conditions for small plant species, and slows down development of organic layers with high mineralization of N and especially P. Low P-availability is only possible in iron-rich soils with low organic matter content, which is a reason to increase aeolian activity especially in hinterdunes with iron-rich parent material. In partly decalcified soils, removal of topsoil may lead to return of characteristic plant and animal species (van Til et al. 2014). On the acidic, iron-poor Wadden islands it is perhaps better to opt for a completely different approach, such as an increase of large scale dynamics (Oost et al., 2012). This may not help the present Grey dunes, but lead to their development in the future.

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The authors declare that they have no conflict of interests.

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