Development of the nitrogen cycle in the soils of a coastal dune succession

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SUMMARY

The development of the soil nitrogen cycle in a coastal dune succession (xerosere) on the East Frisian Island Spiekeroog was investigated. In 13 sites of different successional age the nitrogen pools in the topsoil (0–30 cm) and the organic soil layers were determined. The nitrogen mineralization was studied at the sites during the vegetation period in 1987 (38 weeks) and winter 1990–91 (14 weeks). Turnover rates and nitrification rates were calculated.

The nitrogen pool of the soil was very low in the first stage of the succession (<100 kg N ha^{-1} 30 cm^{-1}) and increased rapidly to more than 1500 kg N ha^{-1} within approx. 200 years. This accumulation rate was strongly exposition-dependent. Mineralization of nitrogen was low in the young sites (15 kg N_{min} ha^{-1} year^{-1} 30 cm^{-1}) and increased to more than 100 kg N_{min} ha^{-1} year^{-1} in sites covered by buckthorn (*Hippophaë rhamnoides*) and in dune forest. Mineralization was also exposition-dependent. The annual nitrogen turnover rate was very high in the young dune sands (up to 18%) and was only 2% in the brown dune sand podsols under *Empetrum* heathland. Nitrification dropped as well in the course of the dune development from 80–90% to 20% nitrate of total mineral nitrogen production over a year. Some hypotheses on nitrogen accumulation and retention during ecosystem and plant cover development are discussed.

Key-words: coastal dunes, nitrogen cycle, primary succession, xerosere.

INTRODUCTION

The substrate for primary succession in terrestrial ecosystems, such as volcanic deposits, glacier retreatment and sand-dune development is extremely low in nitrogen in the beginning of the succession. Olson (1958a,b) studied the accumulation of nitrogen in an inland dune succession. Stevens & Walker (1970) developed the chronosequence concept including the development of nitrogen accumulation in time, when ecosystem succession in coastal dunes occurs. Later, Robertson & Vitousek (1981) and Robertson (1982) pointed out that nitrification in the soils of a primary succession of sand-dunes is controlled by the availability of ammonia. This result was confirmed by Skiba &

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Wainwright (1984). Recently, Kellman & Roulet (1990) investigated the input–output relation of ammonia and nitrate in a tropical sand-dune succession and found remarkable output of nitrate only in a forest ecosystem on recent sand but not in the younger stages. Olff, Huisman & van Tooren (1993) collected evidence for a primary dune succession suggesting that plant competition shifts from being for nutrients in the early stages to being for light in the later stages of succession (see also Tilman 1985, 1986).

Ellenberg (1977) distinguished three aspects of the nitrogen cycle of terrestrial, plant-dominated ecosystems: (i) the plant internal cycle with translocation and allocation of nitrogen compounds between different plant parts, especially to and from storage organs; (ii) the ecosystem-internal cycle, where mineralization of organic nitrogen compounds in soil and uptake of ammonia and nitrate by plants, and returning of organic nitrogen compounds with litter to soil play an important role; and (iii) the ecosystem-external cycle, which describes the input–output balance of the ecosystem.

This paper focuses on the development of the ecosystem-internal nitrogen cycle in the soil of a coastal dune succession. Included are 13 different sites in the order of a chronosequence on the island of Spiekeroog. This chronosequence can be dated from old maps since approximately 1650. Unlike most of the Frisian Islands there are no rabbits on Spiekeroog, and so succession proceeds without the digging, grazing and browsing influence of these small mammals. They became extinct in 1889 (Meyer-Deepen & Meijering 1979), and at that time remarkable changes in vegetation cover presumably took place in the older dunes. Buchenau (1875) found only few specimens of crowberry (*Empetrum nigrum*); today this species covers large areas on the north slopes of the grey and the brown dunes. In 1863, protection of dunes started on Spiekeroog by limiting grazing. As a result of this the vegetation cover became denser and taller. *Hippophaë rhamnoides* is reported to have been introduced to Spiekeroog at the end of the last century (Meyer-Deepen & Meijering 1979), but this rather appears to have been a strong spreading or planting of this species.

MATERIALS AND METHODS

Site description

Spiekeroog is one of the East Frisian Islands in the German Bight (Southern North Sea) and is located at 53°45′N, 7°40′E (Fig. 1). The island covers about 20 km^2 and is 10 km long from the west to the east. The distance to the mainland is about 5 km with a tidal flat area in between. Three landscape elements are found on Spiekeroog (Fig. 1): the beachplain with developing and active dunes, the salt-marsh area in the southern part of the island, and the dunes in the north, which shelter the salt-marshes against storms and high tides. The island was probably formed from sandplates only some 2000 years ago like most of the other West and East Frisian islands. The recent dunes developed in the last centuries in adjacent dune ridges, mainly in a west–southeast direction. Sindowsky (1970, 1973) reconstructed the formation dates of the main dune chains from old maps (Fig. 2).

Dune formation was not a continuous process (Ehlers 1986, 1988). Different dune formation phases resulted in large dune areas. There are areas of homogenous height and form, such as the brown dune complex. The oldest part of the island was formed before 1650, but cannot be dated further back. The western part of it has become
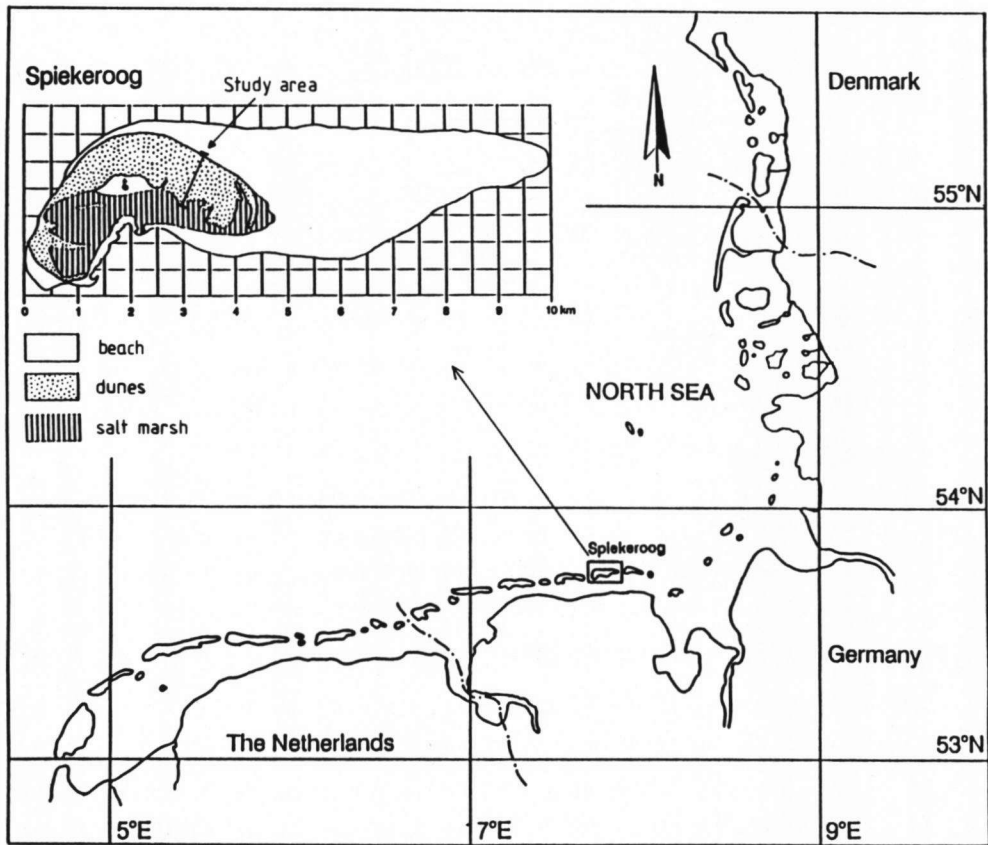
Fig. 1. Location of Spiekeroog in the German Bight and of the study area.

eroded. The main dune area in the east of the old island developed between 1650 and 1960. Today only small new dune fields are developing in the north-eastern area (Hempel 1980).

We investigated 11 different sites along a north-east–south-west transect (marked line, Fig. 1), all of which are part of a typical dune xerosere on lime-poor sand. We further included two more sites lying in the oldest part of the island covered with deciduous tree forests (Fig. 3). These two sites (12 and 13) do not fully correspond to the dune succession of the other sites, because they developed on an old beachplain, which was separated from the sea by dunes in the south. So they are situated lower than the other sites. Nevertheless, they are included here because their vegetation is very typical and consists of near-natural deciduous forests. Soil types, plant communities and dominating species are listed in Table 1 (soil types after Avery 1973; plant communities after Pott 1992).

The beachplain and the foredunes have pH values (H_2O) of c. 8·0 due to the carbonate content and sea spray. However, the primary lime content of the sand on the beach of Spiekeroog is very low and does not exceed 0·4–0·5% (Schuba 1990; Eis 1990). So decalcification takes place within 50–100 years and the pH drops very quickly (Fig. 4).
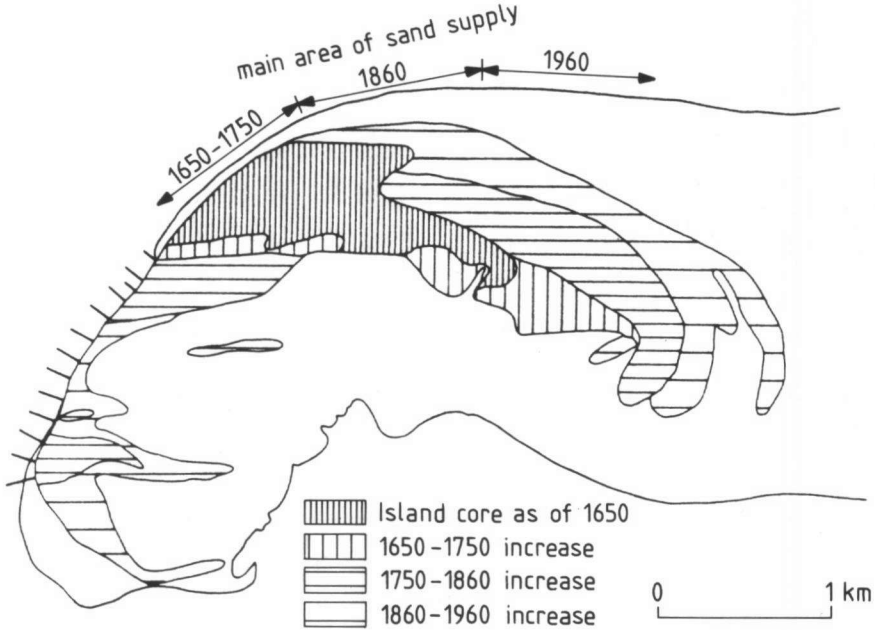
Fig. 2. Development of dune ridges after about 1650 (after Sidowsky 1973) and location of the dune transect.
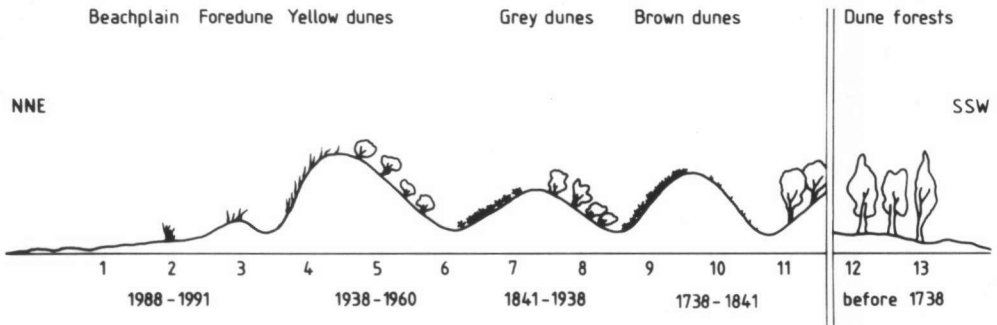

Fig. 3. Schematic representation of the dune succession investigated on Spiekeroog and presumable age of the different dune stages from old maps. Sites 1–11 represent the complete xerosere development of the dunes, sites 12 and 13 developed on a lower lying old beachplain, which has been separated from the sea by dune ridges.

The topsoil of the grey dunes is free of carbonate (Eis 1990) and pH (H_2O) has fallen to values between 5 and 6. The brown dunes, which are more than 200 years old, and sites on the dune forest have pH values between 3·6 and 3·8 in the topsoil and these values may even be 0·5–1·0 unit lower in KCl or $CaCl_2$ solution. The minimum and maximum values of the annual change are also given in Fig. 4. They are about one pH unit for most sites (see also Schuba 1990). The highest values are found in spring. During the summer there is a tendency for values to drop resulting in the lowest pH in autumn. The dune succession described here gives a typical example of quick acidification of carbonate-poor sands of coastal dunes.

Table 1. Soils and vegetation of sites

Site no.	Situation	Soil type	Plant community	Approx. age (years)	Dominating plant species
1	Beachplain	raw soil	No vegetation	1	No vegetation
2	Beachplain	raw soil	Elymo–Agropyretum juncei	<5	Elymus farctus
3	Young yellow dune (<4 m high)	raw soil	Elymo–Ammophiletum typicum	5	Ammophila arenaria
4	Yellow dune, north slope	raw soil	Elymo–Amm. festucetosum arenariae	30–50	Ammophila arenaria
5	Yellow dune, south slope	sand ranker	Elymo–Amm. festucetosum arenariae with Hippophaë rhamnoides	30–50	Hippophaë rhamnoides
6	Yellow dune, dry dune valley, south slope	sand ranker	Tortulo-Pleetum arenarii	30–50	Corynephorus canescens
7	Grey dune, north slope	podsolic ranker	Carici-Empetretum festucetosum* with Polypodium vulgaris	50–120	Empetrum nigrum
8	Grey dune,	podsolic ranker	Hippophao–Sambucetum nigrae	50–120	Sambucus nigra, Sorbus aucuparia
9	Brown dune, north slope	podsolic brown soil	Carici-Empetretum typicum polypodietosum	150–250	Empetrum nigrum
10	Brown dune, south slope	sandy ranker, slightly podsolic	Violo-Corynephoretum canescensis with Campylopus introflexus	150–250	Corynephorus canescens, Campylopus introflexus
11	Brown dune, north slope	podsolic brown soil forest	Carici arenariae-Betuletum* pubescentis (natural forest)	150–250	Betula pubescens spp. carpatica
12	Dune valley	gleyic podsol	Carici arenariae-Betuletum* pubescentis dominated by Betula pubescens	>250	Betula pubescens ssp. carpatica
13	Dune valley	gleyic podsol	Carici arenariae-Betuletum* pubescentis dominated by Alnus glutinosa	>250	Alnus glutinosa

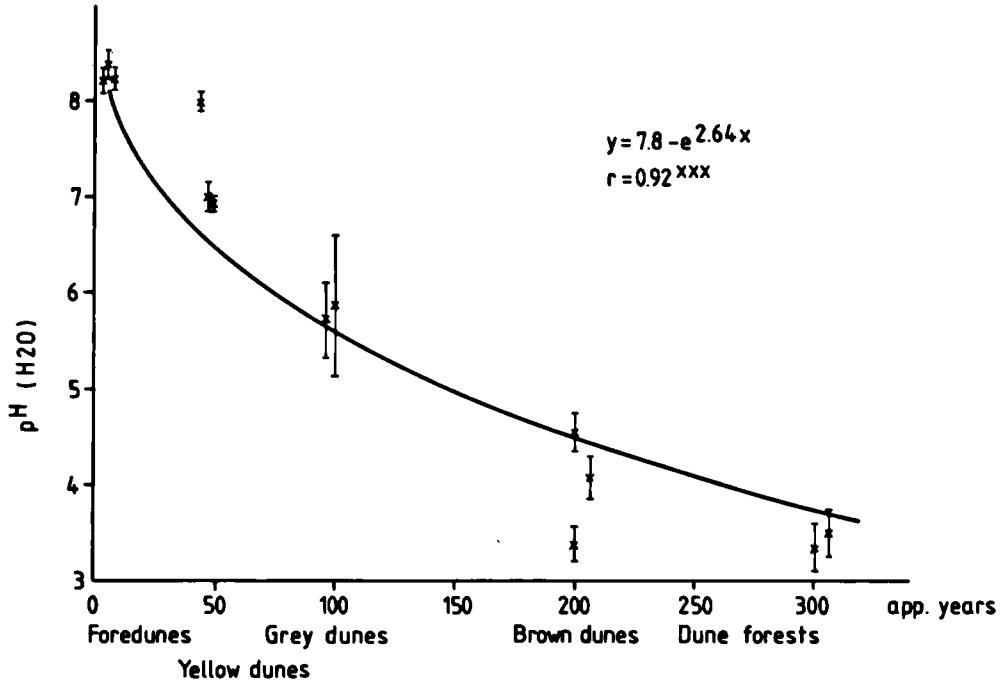*Named after H. von Glahn (personal communication)

Fig. 4. Change of pH(H₂O) in the topsoil (0–5 cm depth) of dunes of different age on Spiekeroog. Values are mean values of the annual change in 1987.

Bulk density

All soils were sampled at every 5 cm layer situated adjacent vertically for the whole profile to 30 cm depth. Organic soil layers were sampled additionally, if present, and separately. Bulk density was measured by taking 100 cm^3 of undisturbed soil of every layer (five replicates). Organic soil layers were taken by cutting 1000 cm^2 samples (three replicates) down to the mineral soil surface. Bulk density and mass were calculated on an oven-dry (105°C) basis.

pH

pH was determined by adding demineralized water to a soil/water suspension of 2·5:1 of fresh soil. The suspension was stored overnight and stirred before measurement with a glass electrode. pH was determined every 4 weeks according to the sampling times of nitrogen net mineralization.

Total nitrogen

The samples for determination of bulk density were ground after drying and N-concentration was determined by using a Carlo-Erba-Element-Analyzer.

Nitrogen net mineralization

The net mineralization of nitrogen was determined in the vegetation period from March to November 1987 for 38 weeks for all sites except number 11 (dry dune forest). Here the corresponding incubation period was 1990. A second measurement period lasted from November 1990 to March 1991, according to the winter period. On each sampling
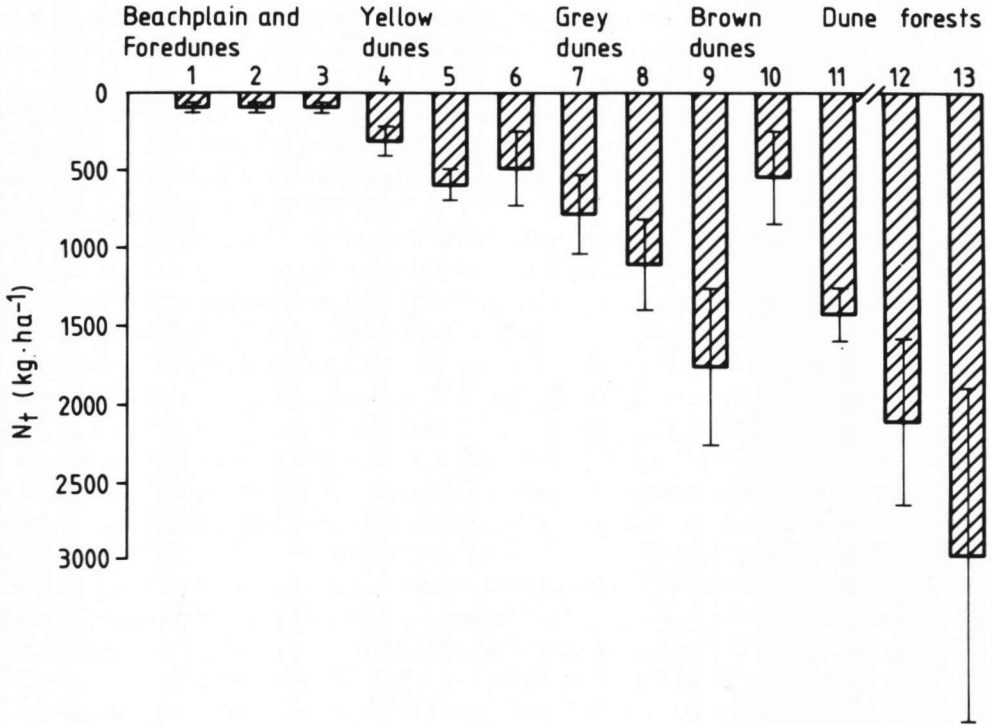
Fig. 5. Total nitrogen (N_t) pool in the topsoil of the dune succession. Sites and presumed age as described in Fig. 3. N_t-values are given in kg ha^{-1} for the upper 30 cm. Values for organic soil layers are included for sites where they occur. Vertical bars indicate the standard error of the means.

date (every 4 weeks) three samples of fresh soil from every soil layer (approximately 200–300 g) and from 10 different places on the site were taken after mixing the material thoroughly. One sample was analysed for NH_4-N and NO_3-N after transport to the laboratory in an isolated box. The other samples were stored in polyethylene bags at the depth of sampling for an incubation period of 8 weeks, resulting in overlapping incubation periods (Gerlach 1973; see also Raison *et al.* 1987). The sum of NH_4-N and NO_3-N was calculated and is termed mineral nitrogen (N_{min}). All chemical analyses for mineral nitrogen were carried out by micro-kjeldahl distillation after extraction with 1% KAl $(SO_4)_2$-solution described by Bremner & Keeney (1965) and Page *et al.* (1982). All results are calculated on an oven-dry (105°C) soil material basis.

RESULTS

Total nitrogen (N_t) pools

The change in total nitrogen pool sizes in the topsoil is given in Fig. 5. The young foredunes and beachplain show remarkably low nitrogen contents, which result in low pools of 102, 97 and 98 kg ha^{-1} 30 cm^{-1}, respectively. With increasing age and a more dense vegetation in the yellow dunes the N-pool reaches values of between 310 (north slope), 598 (southern slope) and 489 kg ha^{-1} 30 cm^{-1} (dry yellow dune valley). So, within *c.* 50 years the N-storage of the topsoil increased about 3–6-fold compared to the

original substratum. Sand drift is still relatively important in these sites; the litter is easily buried, resulting in quick mineralization. This means that a distinct organic soil layer cannot be distinguished here.

The grey dune ridge is about 100 years old, consisting of almost fixed dunes, and is covered with a very dense vegetation of shrubs (Table 1). A distinct organic soil layer has developed, so the N-pools in the topsoil of these dunes are very high and amount to 790 (site 7) and 1120 kg ha^{-1} 30 cm^{-1} (site 8), respectively. Nitrogen accumulation in the brown dunes is extremely dependent on the exposition of the site. The north slope (site 9) shows a very high nitrogen pool with 1780 kg ha^{-1} 30 cm^{-1}. This is mostly due to the thick layer of humus on the mineral soil, which consists mainly of the litter from *Empetrum nigrum*. Under the *Empetrum*-heath the N storage has increased from approximately 310 (north slope of yellow dune) to 1780 kg ha^{-1} 30 cm^{-1} within 120 years. This is a total increase of 1470 kg ha^{-1} or an annual increase of 12·25 kg ha^{-1}. It remains open to debate whether this decrease resulted from biological N-fixation by separate and/or symbiontic N-fixing micro-organisms or also from input by wet or dry deposition (e.g. bird droppings). The southern slope is covered with scattered vegetation of *Corynephorus canescens* and some cryptograms with very low productivity. So the N-pool of 546 kg ha^{-1} 30 cm^{-1} reaches only a third of the amount of the northern slope. Site 11 is as old as sites 9 and 10, but represents a natural forest. Initially, the trees were growing in small dry dune valleys; *Betula pubescens*, in particular, spread up the hill, covering the north slopes of the brown dunes and outcompeting *Empetrum nigrum*. Here the nitrogen pool in the podsolic brown earth reaches 144 kg ha^{-1} 30 cm^{-1} (including $O_{L,F,H}$-horizons), which is still similar to the value of the *Empetrum*-heath.

Sites 12 and 13 represent birch and alder forests growing on gleyic podsols. These sites lie in former dune slacks and therefore do not correspond to the xerosere described. The groundwater table changes between 10 and 40 cm below ground over the course of a year. The gleyic podsol under the old birch forest contains 2141 kg ha^{-1} in the upper 30 cm of the soil (organic layer included) and the highest amount of nitrogen is found under the cover of alder (*Alnus glutinosa*) with 2995 kg ha^{-1} 30 cm^{-1}, probably due to the high nitrogen content of the alder litter.

Nitrogen mineralization and turnover

The annual nitrogen net mineralization is given in Fig. 6. The bottom parts of the columns give the amount of mineralized nitrogen for the vegetation period 1987 (March–November, 38 weeks). The upper parts of the columns give the values for the winter time 1990–91 (November 1990–March 1991, 14 weeks). The total amount of annually mineralized nitrogen (N_{min}) results from the total height of the column. (The partitioning of N_{min} to ammonia and nitrate is given in Fig. 8.)

On the beachplain and in the sand of the primary dunes (sites 1–3) the net nitrogen mineralization is estimated to be 18, 14·4, and 18 kg N_{min} ha^{-1} year^{-1} 30 cm^{-1}, respectively. These values for methodical reasons may have a wide variance due to the influence of the high instability of the sand. Sometimes the incubated polyethylene bags were buried under a sand layer more than 80 cm thick and sometimes the covering sand was blown away, so that the uppermost bags were exposed to the sun during incubation. Nevertheless, the mineralization is apparently high and reaches 15–19% of the total nitrogen pool (Fig. 7). The sand of the yellow dune shows an annual mineralization of 28·3 kg ha^{-1} 30 cm^{-1} on the north slope and of 114 kg on the south slope. This
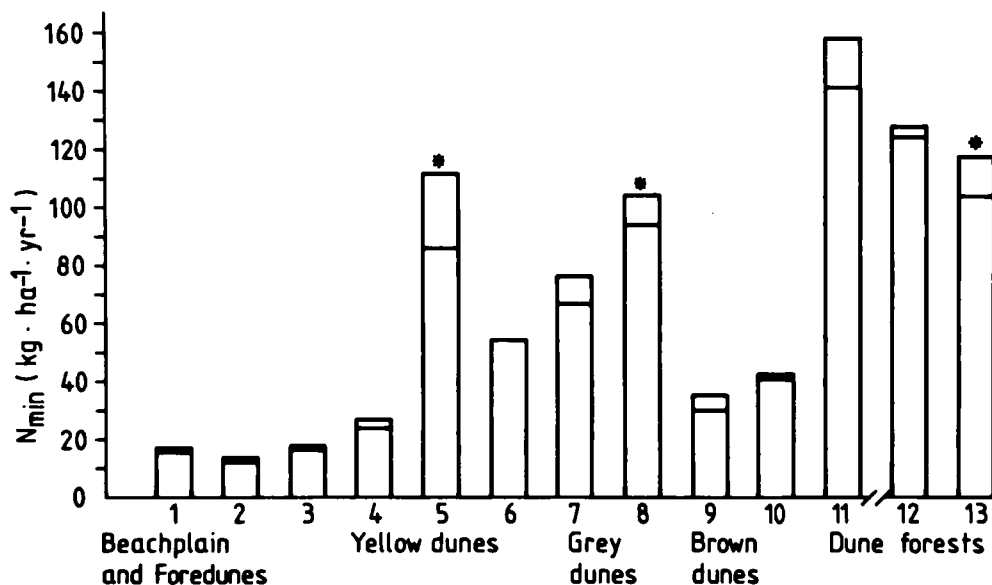
Fig. 6. Mean annual net mineralization of nitrogen in the topsoils (30 cm) of the dune succession. The lower parts of the columns represent the incubation period of 38 weeks during the growing season. The upper part of the columns represent the incubation period of 14 weeks during the winter season. Values are given in kg N_{min} ha^{-1} for the above-mentioned time periods, which correspond in total to the net mineralization per year. Asterisks mark sites with dominating vegetation of N-fixing plants: sites 4 and 8 with *Hippophaë rhamnoides*, site 13 with *Alnus glutinosa*.

extremely high mineralization on the south slope may be due to the nitrogen-rich litter of the *Hippophaë* shrubs. Root nodules in buckthorn are rare and, if present, were not included in the incubated bags.

The relatively high amplitude of temperature changes in the topsoil and the higher average temperature on the south side compared to the north side may play an important role as well. This becomes clear by comparison of the mineralization values for the winter period. They are 3·5 on the north and 26·8 on the south side. The lower part of the southern yellow dune slope, which is free of *Hippophaë* shrubs but covered with grassland vegetation (*Tortulo–Phleetum*) is noticeably lower in nitrogen mineralization (56 kg ha^{-1} year^{-1} 30 cm^{-1}). Here we found no net mineralization during the winter but immobilization of $-0·5$ kg ha^{-1} 30 cm^{-1}. North and south slopes of the grey dunes (sites 7 and 8) are not as different in mineralization as the corresponding slopes of the yellow dunes: 77·8 and 107 kg ha^{-1} 30 cm^{-1}, respectively. *Hippophaë rhamnoides* is present on the south slope as well but does not grow well, perhaps because of the impact of low pH and nematodes (Oremus 1982; Zoon 1986). The brown dune slopes (sites 9 and 10) show much lower values: 36·1 on the north and 34·2 on the south slopes. The dry dune forest (site 11) which develops spontaneously on the north slopes of the brown dunes, shows the highest mineralization values in the different successional stages with 162·3 kg ha^{-1} 30 cm^{-1}. In the gley soils (sites 12 and 13) the mineralization is lower, probably due to the high groundwater table during most of the year. The nitrogen turnover rates (Fig. 7) drop during the course of succession from more than 18% of the pool in the foredunes to only 2% in the brown dunes and 4 and 6% in the dune forest (except site 11 with 11%).
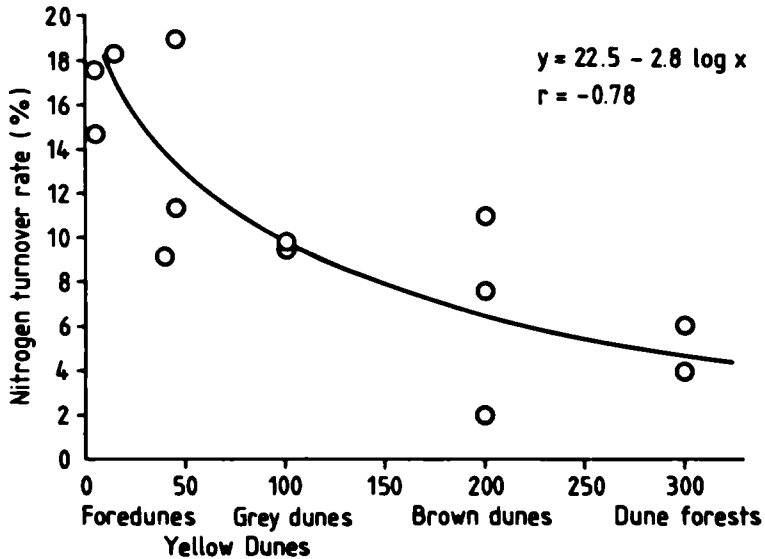
Fig. 7. Nitrogen turnover rate in the soils of the dune succession. Values give the relative nitrogen net mineralization rate as percentages of the total nitrogen pool for the corresponding soil profile depth of 30 cm. The graph corresponds with the logarithmic regression equation $y = 22.5 - 2.8 \log x$, the correlation coefficient is $r = -0.78$.

Generally, the annual turnover rates are unexpectedly high. This may be due to nitrogen-rich organic matter on the beachplain and in the foredunes, where the organic matter mainly comes from marine debris and litter. The N-fixing plants buckthorn (*Hippophaë rhamnoides*) and alder (*Alnus glutinosa*) in sites 5, 6, and 13, respectively (see asterisks in Fig. 7) produce litter with a high N-content and a low C/N-value and so the litter can easily be mineralized by micro-organisms.

Nitrification

Figure 8 gives an impression of the relative nitrification rate which is defined as

$$\frac{NO_3 - N}{N_{min} - N} \times 100 \text{ given in \% (see Gehu \& Ghestem 1965).}$$

Sites 12 and 13 are omitted in Fig. 8 due to temporarily high groundwater level resulting in anaerobic environment in the soil. Nitrification is very high in the soils of sites 1–8, where about 80–100% of the mineral nitrogen is available as nitrate for plants. The podzol and podsolic brown earths from sites 9–11 show lower values but even in these acid substrates, especially in the A_h-horizons, remarkably high fractions of mineral nitrogen are oxidized to nitrate.

DISCUSSION

Acidification of the dunes on Spiekeroog is more rapid than described by Salisbury (1925) for the dunes of Blakeney Point (Great Britain). He found a decrease from 8·2 in the original sand to 5·5 in 280-year-old dune ridges covered with heathland vegetation.
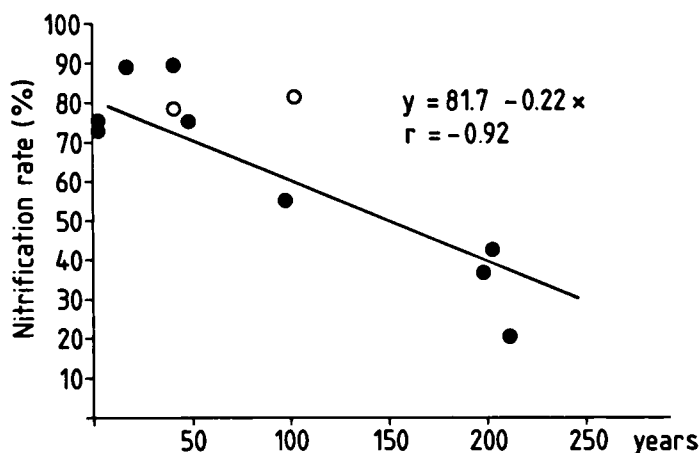
Fig. 8. Nitrification rate in the topsoil of 11 sites of the dune succession. Closed circles indicate the relative amount of nitrate of total annual mineralized nitrogen for each soil. Rates are calculated from the sum of all soil layers up to 30 cm depth. The line gives the linear regression equation with a correlation coefficient of $r=0.92$. Open circles represent sites with *Hippophaë rhamnoides*. Sites 12 and 13 are omitted here due to temporarily high groundwater level resulting in anaerobic environment of the soil.

The primary $CaCO_3$-content in his dune succession was about 6·3%. Wilson (1960) found a decrease in pH from near 7 in the initial stages of a dune succession (primary lime content 0·015%) to 3·8–4·4 within 240 years, which corresponds very well with our results.

Accumulation of nitrogen

In the inland dunes of Lake Michigan, Olson (1958a,b) found the strongest changes in nitrogen pools in the very beginning of an 8000-year-old dune succession. The accumulation rate in those dune sands for the upper 10 cm of soil can be calculated to be about 0.004 g dm^{-3} $year^{-1}$ corresponding to 4.03 kg N ha^{-1} $year^{-1}$ in the first 1000 years. Additionally, little further accumulation was observed between 1000 and 8000 years, so he established a steady state concerning input–output rates for the older dunes. Syers *et al.* (1970) investigated the accumulation of organic matter and, amongst other things, the accumulation of nitrogen in a more than 10 000-year-old dune succession. They found a rapid increase in the first 1000 years in the soil. Subsequently the rates were lower but did not reach a steady state. The annual accumulation rate can be calculated as 1 kg ha^{-1} $year^{-1}$ m^{-1} soil depth for the 10 000 years succession and 4 kg ha^{-1} $year^{-1}$ m^{-1} for the first 1000 years, respectively. In our dune succession the annual accumulation rate varies between 7.1 kg ha^{-1} (site 9) for the brown dune north slope and 5.8 kg ha^{-1} (site 11) in the natural dune forest on the one hand, and only 2.2 kg ha^{-1} (site 10) for the brown dune south slope (all calculated for 30 cm soil depth). So it can be concluded that these accumulation rates from a 250-year-old dune succession are in good agreement with the data from Olson (1958a,b) and Syers *et al.* (1970). There is no decrease in the accumulation rate (Fig. 5) in the first 250 years but a remarkable diversification between the differently exposed slopes of the dunes. This diversification may be due to microclimatic conditions on north and south slopes (Gerlach 1993) and effects of different dominant plant species which produce litter of different decomposability. In

particular, the litter of crowberry (*Empetretum nigrum*), which dominates sites 7 and 9, is very acid and has a variable C/N-ratio. So mineralization is suppressed in these sites, only reaching low values (see also Berendse *et al.* 1987).

Nitrogen mineralization, turnover rates and nitrification

The nitrogen net mineralization and the nitrogen turnover rate (% annually produced ammonia and nitrate of total nitrogen) in dune ecosystems have only scarcely been investigated. Among salt-marsh soils, Gehu & Ghestem (1965) tested the mineralization capacity in the soils of a dune succession of *Elymo–Agropyretum* (corresponding to sites 1 and 2 in this study), to *Euphorbio–Ammophiletum*, which is the vicarious plant association in northern France to the *Elymo–Ammophiletum* in this study (corresponding to sites 3 and 4), *Tortulo–Phleetum* (site 6) and *Hippophaë* shrub communities (sites 5 and 8) to *Calluno–Genistetum* and *Corynephoretum canescensis* in the acid soil series, which may correspond to the *Carici–Empetretum* and *Violo–Corynephoretum*, respectively, in this study. Using a laboratory incubation technique (25°C), Gehu & Ghestem (1965) found a very similar order of mineralization intensity (which is given in concentration values and not in kg ha^{-1}).

By far the highest amount of mineralization was found under the *Hippophaë* shrubs, due to the N-fixing capacity of this plant species. The N-fixing capacity of this species is estimated to be 27–179 kg ha^{-1} year^{-1} (Becking 1970; Oremus 1982). Simon (1991) obtained values between 16·3 and 148·6 kg ha^{-1} year^{-1} for different places at site 5 on Spiekeroog in 1990. This indicates a high input of nitrogen compounds. The chemical composition of the *Hippophaë* litter and the relatively high pH favours nitrification. So all sites with *Hippophaë* have a high nitrification rate near 100% (Fig. 8). As a result of the high mineralization rate and of leaching the high input does not result in exceptionally high N_t-accumulation (Fig. 5). The N_t-values are in the same order of magnitude as the adjacent sites. The high overall nitrification in the younger dune stages was also stated by Skiba & Wainwright (1984) in British dune sands (under cover of *Ammophila* and *Hippophaë*) and also by Kachi & Hirose (1983) in Japanese dune sands under *Carex kobomugi*. Both results were obtained from laboratory incubation experiments, the former authors further added $(NH_4)SO_4$, and so their results give only an estimation of the potential mineralization capacity.

According to our results from mineralization investigations in the course of the year, the amount of nitrate formation at the site seems to be remarkably lower in the older stages of succession. This trend seems to be in agreement with Rice & Pancholy (1972), who stated an inhibition of nitrification in climax ecosystems (forest). On the other hand, in all sites of succession and even in the soils of mature forest ecosystems remarkable amounts of nitrate are formed if there is a sufficient source of oxygen (Runge 1974). We assume that the classic nitrite- and nitrate-forming bacteria, like *Nitrosomonas* and *Nitrobacter* play a dominant role in the nitrification in young stages of succession with sufficient calcium supply and high pH-values. With increasing hydrogen ion activity and lower pH-values in older parts of the succession the microbial flora changes and heterotrophic micro-organisms (actinomycetes and fungi) may produce nitrite and nitrate as well (e.g. Hirsch *et al.* 1961; Focht & Verstraete 1977; Kuenen & Robertson 1988). The mineralization of nitrogen is very high even in the dune forest, so limitation of nitrate production by ammonium availability, as could be

assumed for the first eight sites of the succession (see also Robertson 1982), is not very plausible.

Odum's (1969) hypothesis for nitrogen cycling seems valid, i.e. that the ecosystem's ability to conserve nutrients increases during the course of succession (see Vitousek & Reiners 1975; Gorham *et al.* 1979; Reiners 1981). The order of magnitude of mature ecosystems, such as deciduous forest soils in our climate, is reached within some 100 years compared to the data of Melillo (1981). A steady state, as Olson hypothesized for his dune succession, does not seem to have been reached yet in our succession on Spiekeroog. On the other hand, we doubt that there is such a steady state in primary dune successions, because the site exposure is so important for vegetation development (Gerlach 1993) and cyclic patterns of growth (accumulation phase) and destruction (nutrient loss phase) occur even in natural forests (Sprugel 1984). The young dune ecosystems are 'open' ecosystems concerning nitrogen cycling. They have low pools, high turnover rates and must have high losses of nitrate by leaching, especially under *Hippophaë* vegetation. Older dune ecosystems are of a more 'closed' type (especially heathland dunes like site 9) with high pools, low turnover rates and low nitrification.

The impact of special dominating plants like *Hippophaë rhamnoides* or *Empetrum nigrum* on the soil nitrogen cycle as an ecosystem succession process consists not only in fixation of N (*Hippophaë*) or preventing losses of nitrogen by leaching in the case of *Empetrum* (acid litter accumulation), but also in accelerating and reducing nitrogen mineralization, respectively. The fixation of nitrogen and the acceleration of nitrogen cycling by *Hippophaë rhamnoides* enhances plant growth and plant biomass. Additionally, this biologically increased nitrogen supply facilitates the establishment of nitrophilous species like *Epilobium angustifolium*, shrubs like *Sambucus nigra* and others already in the grey dunes. Van Andel *et al.*(1993) describe this facilitation as one of the main vegetation succession mechanisms. This is not a direct beneficial effect, but rather an indirect one via mineralizing and nitrifying micro-organisms. The special role of *Empetrum nigrum* is mainly to prevent the mineralization and to reduce the nitrogen supply of other plants. The acid litter accumulates on the soil surface and nitrogen is recycled mainly (and exclusively) for *Empetrum nigrum* itself by mycorrhiza. So vegetation succession velocity is reduced, and the brown dune stage can be stable for many years. We do not believe that the brown dunes on Spiekeroog ever had a vegetation cover of *Hippophaë*, because there are no trunks left and the distribution and cycling of nitrogen make this implausible. The woody species occurring in the brown dunes are mainly *Betula pubescens* and *Sorbus aucuparia* starting on the dry dune valleys. Here they reach the groundwater table soon after establishment, changing nutrient cycling by transporting basic cations (Ca, Mg) to the soil surface with litter and so accelerating the nitrogen cycle (compare sites 9 and 11 in Fig. 6). The impact of trees on vegetation succession seems to be competition for light rather than facilitation of the establishment of nitrophilous species in the herb layer, as could be stated for *Hippophaë rhamnoides*.

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