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Nitrogen availability in relation to vegetation changes resulting from grass encroachment in Dutch dry dunes

Veer, M.A.C.

Landscape & Environmental Research Group, University of Amsterdam, Nieuwe Prinsengracht 130, NL-1018 VZ Amsterdam, The Netherlands; Tel. +31 20 5257442; Fax +31 20 5257431; e-mail mv@fgb.frw.uva.nl

Abstract. The encroachment of some tall grass species in open dune vegetation, as observed in a Dutch dry dune area, is considered unfavourable from a conservation viewpoint. This paper investigates differences in vegetation and soil properties between grass-dominated and still existing open dune grassland plots at four locations along the coast. Soil properties studied include nitrogen and phosphorus pools and nitrogen availability by mineralization.Vegetation properties included are above and below-ground biomass and nitrogen and phosphorus concentrations in above-ground biomass.

Systematic differences in N-pools between grass-dominated and open dune grassland plots were not observed. However, N-availability by mineralization and its turnover rates are higher in grass-dominated plots than in open dune grassland plots, as well as above and below-ground biomass. In open dune grassland plots, atmospheric N-input is an important source of N, whereas in grass-dominated plots mineralization largely exceeds atmospheric N-input. However, these observations do not explain the mosaic-like vegetation pattern. Grazing intensity is most likely the determinant factor in the dry dune system. It is concluded, that grass encroachment is probably triggered by atmospheric deposition and is enhanced by positive feedbacks in the N-cycle. The relevance of these results for restoration management is briefly discussed.

Keywords: Dune grassland; Nitrogen cycle; Nitrogen mineralization; Nitrogen pool; Phosphorus pool; Succession.

Introduction

During recent decades several Dutch semi-natural ecosystems have been dominated by tall grasses, including chalk grasslands (Bobbink & Willems 1987), heathlands (Aerts 1989; Heil & Diemont 1983), and also dry coastal dunes (Kooijman & van der Meulen 1996). These dunes are of great conservational importance since they harbour almost 70 % of the Dutch flora, of which 15 % are practically exclusive to the dunes (de Molenaar 1986).

The species-rich, open dry dune grasslands have often partly changed into a vegetation dominated by tall grass species. Grass-dominated and open dune grassland plots occur in a mosaic-like pattern. The causes for this grass encroachment are not yet well understood.

Atmospheric nitrogen deposition might play a role, as is the case for heathlands and chalk grasslands (e.g. Berendse & Aerts 1984; Aerts & Berendse 1988; Bobbink et al. 1988; van der Eerden et al. 1991; Prins et al. 1991). Effects of elevated N-deposition are an increased nitrogen availability and, together with S-deposition, an enhanced soil acidification causing imbalanced nutrient availability by deficiencies in magnesium, potassium and phosphorus (Bobbink et al. 1990). Changes in soil chemistry, especially increased N-availability, are assumed to allow grasses to compete more effectively with herbs and cryptogams and thus to promote their dominance.

These theories about the causes for grass encroachment were mainly derived from studies of heathlands and chalk grasslands (e.g. Aerts 1989; van Vuuren 1992; Bobbink & Willems 1987), while knowledge of the vegetation-soil complex in dry dune grasslands is scarce. Earlier experiments in nutrient-poor dune soils (Willis & Yemm 1961; Willis 1963) showed that N-addition resulted in the dominance of some grass species. However, recent experiments in British grasslands (Morecroft et al. 1994; Wilson et al. 1995) and dry coastal dune grasslands (ten Harkel & van der Meulen 1996) showed that N-fertilization does not have effects on species composition any longer. This may be attributed to the prolonged atmospheric deposition of N leading to N-saturation of dry dune ecosystems. Other causes for grass encroachment may be changes in (rabbit) grazing intensity or limited P-availability. As to grazing, it has indeed been shown that a decline in rabbit population leads to a dominance of tall grasses (e.g. Ranwell 1960; Thomas 1963; Westhoff 1985). Furthermore, abandonment of extensive grazing by large herbivores led to grass dominance (e.g. Belsky 1992; Hill et al. 1992). Thus it is likely that several factors are involved in grass encroachment in dry dunes and some of them may interact.

The present study focuses on the role of N-cycling in grass encroachment. Specific questions refer to differences in N-mineralization between grass-dominated and open dune grasslands and relations to N and P-pool sizes in soil and vegetation, and to atmospheric deposition patterns.

Fig. 1. Location of the study sites.

Methods

Study sites

Four sites were selected in calcareous dry dunes (Fig. 1), representing vegetation types of the alliance *Galio-Koelerion* (Schaminée et al. 1996). In each vegetation type, grass-dominated and open dune grassland plots were selected. Soils in the dry dunes progress from (A)C profiles to AC-profiles, which in more advanced stages have an endorganic (Ah) horizon. In the decalcified soils of Middelduinen also a B-horizon was present. Ectorganic layers only develop in grass-dominated plots. Some vegetation and site characteristics indicative of the state of acidification are given in Table 1. Diversity was measured with the Shannon-Weaver index:

$$SD = -\sum_{i=1}^{n} (pi) * (\log 10 pi) \qquad (1)$$

where n = number of species; p_i = % cover of species i.

The difference in diversity between grass-dominated and open dune grassland plots illustrates the effect of grass encroachment. At all sites except KV (Table 1) the open dune grasslands have a higher diversity. In TP, ZV and to a lesser extent KV, the soil is neutral and/or neutralized through carbonate weathering. In contrast, the soil of the grass-dominated plots in MD is very acid, while that of the open dune grassland plots is less acid which is due to acid-neutralization through dissolution of amorphous compounds and cation exchange.

Field experiments

A sequential incubation experiment was carried out from April 1993 till June 1994 at two sites, TP and MD. PVC-tubes (length 25 cm; internal ∅ 7 cm) were used to sample intact soil cores. Soil cores were taken at both sites on each sampling date: six in grass-dominated and six in open dune grassland plots. Half of the tubes were taken to the laboratory for analysis. The other half were closed at the top and the bottom and placed back in the soil for incubation during 4 (6) weeks and then analyzed. Aeration of the soil samples during the incubation was ensured through holes in the upper part of the tube.

In the laboratory the upper 5 cm of the mineral soil core was separated; roots were removed. Water content was determined gravimetrically. Samples were extracted with 1M KCl in an 1:10 ratio. The extract was filtered (0.45 µm) and concentrations of NH_4-N and NO_3-N were measured with a continuous flow autoanalyzer.

Differences in inorganic nitrogen concentration (NO_3-N and NH_4-N) were used to calculate mineralization. Differences in NO_3-N were considered to be caused by nitrification during the incubation period. To convert the transformation rates in mg N/kg/ incubation period to an areal estimate, mean dry weight of the sampled horizons in the various plots is used.

The sequential experiment at two sites was extended to all four study sites during the last incubation period.

Biomass and soil sampling

Above-ground biomass including the litter layer of grass-dominated plots was sampled at the end of the

Table 1. Biotic and abiotic characteristics of the study sites.

	Tilanuspad (TP)	Middelduinen (MD)	Zuidervlak (ZV)	Kraansvlak (KV)
Vegetation	*Tortulo-Phleetum*	*Festuco-Galietum agrostietosum*	*Anthyllido-Silenetum*	*Festuco Galietum koelerietosum*
Dominant grass species[1]	*Elymus athericus*	*Carex arenaria*	*Calamagrostis epigejos, Ammophila arenaria, Elymus repens*	*Calamagrostis epigejos*
Diversity index				
Grass-dominated plots	0.40	0.14	0.79	0.69
Open dune grassland plots	0.86	1.25	1.25	0.68
	calcareous	decalcified to 90 cm depth[1]	calcareous	slightly decalcified Ah[1]
pH($CaCl_2$) range Ah horizon				
Grass-dominated plots	6.6-7.0	3.0-3.3	6.7-6.9	5.3-6.7
Open dune grassland plots	6.9-7.0	4.8-6.0	5.6-6.7	6.8-7.2

[1] In grass-dominated plots

summer of 1991 by clipping six plots of 25 cm × 25 cm. Above-ground biomass of open dune grassland plots was sampled at the end of the summer of 1994 by clipping four plots of 50 cm × 50 cm. Samples were dried at 70 °C, sorted into grass species, other species (mainly herbs), mosses, lichens and litter, and weighed.

In grass-dominated plots, mean root weights were estimated from six samples of the Ah horizon (to 5 - 10 cm depth), taken with a 12.5 cm × 12.5 cm metal frame at the same time as the above-ground samples. After drying (70 °C) and sieving (2 mm) roots were removed and weighed. For open dune grassland plots mean root weights of the soil samples (described below) were used.

In the grass-dominated plots, soil samples were taken from each horizon to a depth of 1 m in late April and early May 1991. Every horizon was sampled in duplicate; each replicate sample consists of five subsamples. In spring 1994, the topsoil (Ah and/or AC horizon to 5 - 10 cm depth) of the open dune grassland plots and the grass-dominated plots was sampled. At each site two grass-dominated plots and four open dune grassland plots were sampled, each sample consisting of four subsamples. Soils were sampled with a soil monolith sampler (surface 42 cm^2; Wardenaar 1987). Samples were treated as above.

In 1991, mean values for the dry bulk density of every horizon were estimated from undisturbed samples taken in 100-cm^3 steel rings.

Chemical analyses

N and P-contents of the biomass were determined colorimetrically after destruction with HNO_3/H_2O_2 in 1991 and in 1994 after H_2SO_4/H_2O_2 destruction. Loss on ignition (16 h at 500 °C) was used to estimate organic matter and carbon content of the litter layer. Carbon content of organic matter was estimated at 58 % of the ash free material. The P-content of the 1991 soil samples was estimated colorimetrically after destruction with HF and H_2SO_4 (Lim & Jackson in Page et al. 1982). N was determined by means of a salicylic acid-thiosulphate modification of the regular Kjehdahl destruction (Bremner & Mulvaney in Page et al. 1982). In 1994, N and P were determined after destruction with H_2SO_4/H_2O_2. Carbon content was determined by wet oxidation according to Allison (1960). To calculate N and P-pools in the soil (depth of 15 cm), concentrations of the AC and C horizons of the 1991 samples were used.

Destruction methods used in 1991 and 1994 for biomass samples as well as soil samples were different, because in 1991 total element contents were determined and in 1994 only N and P.

Statistical analysis

General linear models and least square means tests were used to investigate differences between grass-dominated plots and open dune grassland plots (Anon. 1988, SAS release 6.03 statistical package).

Results

Nitrogen and phosphorus pools

Nitrogen pools in the upper 15 cm of the soil show significant differences between grass-dominated plots and open dune grassland plots at MD, ZV and KV (Fig. 2). N-pools are largest in the grass-dominated plots of MD and KV and in the open dune grassland plots of ZV. From Table 1 and additional data on the $CaCO_3$-content of the topsoil (van der Meulen et al. 1996) it is apparent that these sites represent older succession stages. Soils of grass-dominated plots of MD are decalcified to a depth of 90 cm and have a slightly developed B-horizon. In grass-dominated plots of KV and open dune grassland plots of ZV, a Ah horizon has developed and decalcification has started. In these plots, N-pools vary from 1500 - 2000 kg/ha. A smaller N-pool (≈ 1000 kg/ha) is found in both types of plots in TP and in the grass-dominated plots of ZV. A small N-pool (300 - 600 kg/ha) is found in the open dune grassland plots of MD and KV.

Differences in P-pools are less pronounced. Differences between locations are more evident than between

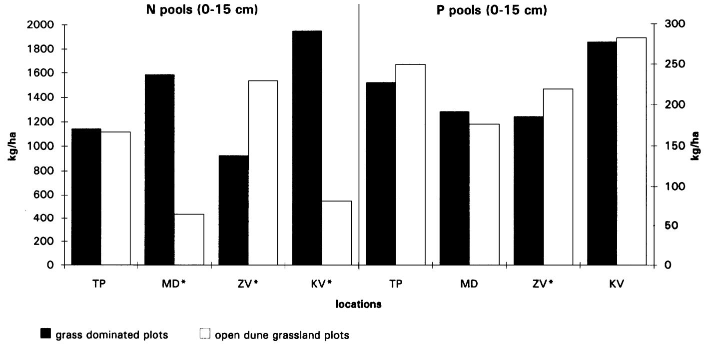

Fig. 2. Nitrogen and phosphorus pools of the upper 15 cm of the soil in kg/ha. *significant difference between grass-dominated and open dune grassland plots ($p < 5$ %).

Table 2. N and P-pools (kg/ha) and C/N ratio of the litter layer in the study sites (For abbreviations, see Table 1). Means and standard deviations based on $n = 6$ in grass-dominated plots (GD) and $n = 4$ in open dune grassland plots (OD). *significant difference between GD and OD plots ($p < 5\%$).

	N-pools (kg/ha)				P-pools (kg/ha)				C/N ratio			
Site	GD		OD		GD		OD		GD		OD	
TP	77	(± 21)	-		4.7	(± 1.1)	-		28	(± 3)	-	
MD	58	(± 28)	-		3.0	(± 1.3)	-		25	(± 2)	-	
ZV	15	(± 13)	-		0.7	(± 0.7)	-		34	(± 6)	-	
KV	75*	(± 61)	2.4	(± 1.5)	4.3*	(± 2.5)	0.1	(±0.1)	28*	(± 4)	45	(± 7)

grass-dominated and open dune grassland plots at a specific location. Only ZV shows a significant difference. P-pools are largest in KV (≈ 280 kg/ha) and smallest in the decalcified MD (≈ 180 kg/ha).

Litter pools are given in Table 2. A litter layer is present in all grass-dominated plots and in the open dune grassland plots of KV. N and P-pools in the litter layer are much larger in grass-dominated plots than in open dune grassland plots, but are low in proportion to the above mentioned soil pools. Intermediate C/N ratios point to a moderate decomposition.

N-mineralization in the field

N-mineralization is higher in grass-dominated plots. In the calcareous TP site (Fig. 3a), however, this difference is less pronounced than in MD (Fig. 3b). In spite of the high standard deviations, a general seasonal trend can be seen, especially in the grass-dominated plots of both locations. Mineralization is highest in the period May-September and lowest in winter. In the open dune grassland plots, this seasonal variation is less obvious. Results of the extended experiment (four locations) at the end of the research period (Table 3) support the conclusion that mineralization is higher in grass-dominated plots. The sites which represent older stages of succession, the grass-dominated plots of MD and KV, show the highest mineralization.

Annual mineralization rate is highest (196 kg ha^{-1} yr^{-1}) in the grass-dominated plots of MD (Table 4). Grass-dominated plots in TP are noticeably lower in mineralization (74 kg ha^{-1} yr^{-1}), followed by the open dune grassland plots of TP and MD (41 and 11 kg ha^{-1} yr^{-1} respectively). Turnover rates drop in the same sequence from 26 to 2%.

Nitrification in the calcareous areas is very high. In both plots of TP almost 100 % of the mineral nitrogen is available as nitrate. In the open dune grassland plots of MD relative nitrification is also high. In the grass-dominated plots with a very acid topsoil, nitrification is strongly inhibited and NH_4 is the dominant N-form.

Biomass and nutrient concentrations

The amount of above and below-ground biomass is much higher in grass-dominated plots than in open dune

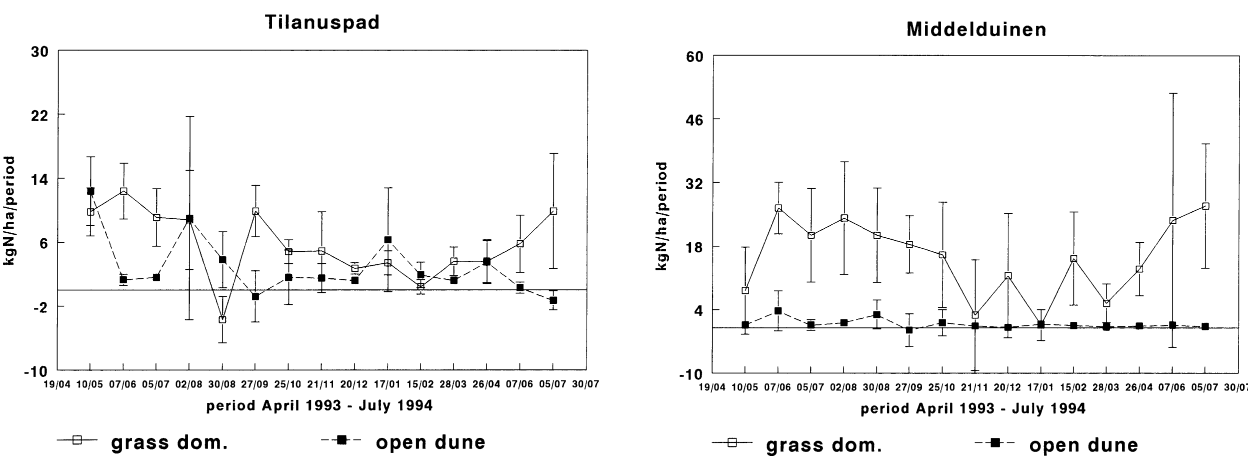

Fig. 3. Nitrogen mineralization in kg N ha^{-1} $period^{-1}$ in grass-dominated and open dune grassland plots in Tilanuspad (a) and Middelduinen (b) from April 1993 till July 1994. Period is incubation period of 4 (6) weeks.

Table 3. Nitrogen mineralization (kg/ha/period) in grass-dominated (GD) and open dune grassland plots (OD) (7 June - 5 July 1994) at sites Tilanuspad (TP), Middelduinen (MD), Zuidervlak (ZV) and Kraansvlak (KV).

	TP	MD	ZV	KV
GD	10 ± 7	36 ± 14	10 ± 8	15 ± 3
OD	–1 ± 1	0.3 ± 1	6 ± 7	1 ± 1

Table 4. Annual rates of mineralization (kg ha^{-1} yr^{-1}), turnover and nitrification (kg ha^{-1} yr^{-1}) in grass-dominated (GD) and open dune grassland (OD) at sites Tilanuspad (TP) and Middelduinen (MD).

	TP		MD	
	GD	OD	GD	OD
Mineralization[1]	74	41	196	11
N turnover rate[2]	9.2%	5.3%	26%	2.6%
Nitrification	78	38	34	8
Relative nitrification[3]	100%	93%	17%	72%

[1]Potential maximum annual mineralization (0-5 cm); [2]Annual mineralization rate/soil N-pool (0-5 cm); [3] % mineralization.

grassland plots (Fig. 4). Mean above-ground biomass in grass dominated plots is ca. 1000 g/m^2, while in open dune grassland plots it ranges from 100 - 400 g/m^2. In grass-dominated plots, differences in below-ground biomass among the sites were much greater than differences in above-ground biomass. Above-ground biomass varies from ca. 800 g/m^2 (TP and KV) to 1100 g/m^2 (MD and ZV), whereas below-ground biomass varies from 550 g/m^2 (TP) to more than 1500 g/m^2 (MD). In open dune grassland plots, below-ground biomass varies from 350 - 550 g/m^2. In all open dune grassland plots except TP and grass-dominated plots of MD and KV, the percentage root biomass of the total biomass is relatively high. Open dune grassland plots of ZV form the most striking examples.

N/P ratios of the above-ground biomass, which are considered to be a reflection of N and P-availability in the soil, are given in Table 5. A clear trend can be detected. At all sites the N/P ratio is higher in the biomass of grass-dominated plots, only in KV the difference is not significant. Trends in N and P-concentrations separately are not so obvious.

Discussion

Nitrogen cycling in dune soils

Comparing the results with the findings of Gerlach (1993) and Gerlach et al. (1994), who investigated the nitrogen cycle in a primary dune succession in non to slightly calcareous sands, it appeared that most nitrogen pools fit into their succession-related range of pools, although pools measured in this study on mainly calcareous sands are somewhat larger. Especially pool sizes of grass-dominated plots of KV and MD are considerably larger. Mineralization rates of grass-dominated plots are much higher than those measured by Gerlach et al. (1994) and consequently turnover rates are also higher. In contrast, open dune grassland plots do not have exceptionally high mineralization and turnover rates.

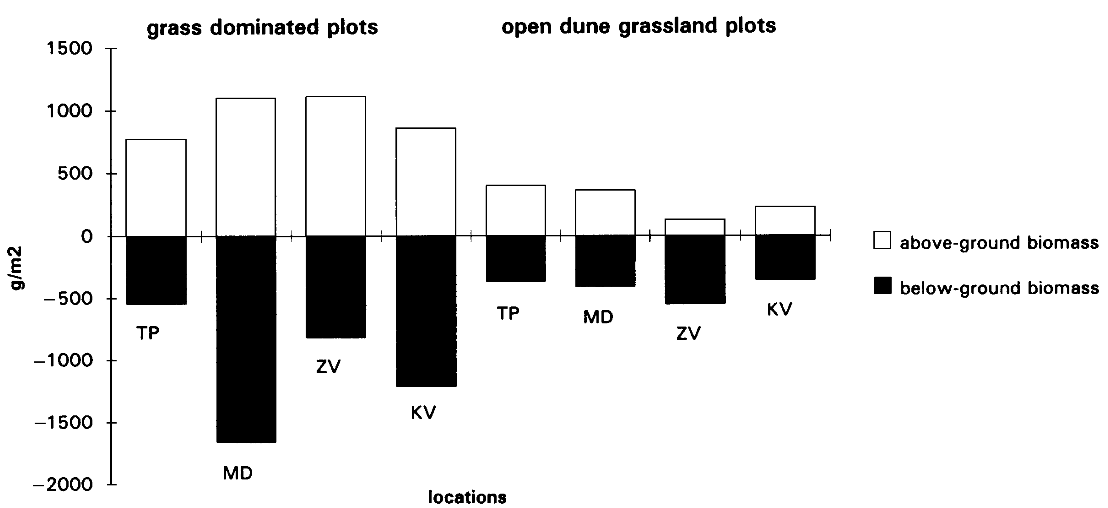

Fig. 4. Above and below-ground biomass (g/m^2) in grass-dominated and open dune grassland plots at four sites. Above-ground biomass is including standing dead. Below-ground biomass is restricted to the topsoil (to 5 - 10 cm depth).

In grass-dominated plots relatively large below and above-ground biomass values were found, pointing to a large input of litter. The presence of a litter layer supports this conclusion. Gerlach et al. (1994) found that turnover rates drop during the course of succession. Combining this with the knowledge that in grasslands with increasing succession below-ground biomass increased (Gleeson & Tilman 1990) it can be concluded that N-turnover will not increase and may even be lowered upon succession. This was indeed observed by Wedin & Tilman (1990), who found that a large amount of especially below-ground biomass was accompanied by low mineralization rates. In contrast with the foregoing, results from this study indicate that biomass, mineralization rates and turnover rates are positively correlated. Synthesizing this information, it can be concluded that the grass-dominated plots do not represent a natural successional stage of the dry dune succession and they do have an elevated nitrogen cycle compared to the open dune grassland plots.

Atmospheric N-input is supposed to be a main source of N in the dune ecosystem. Morecroft et al. (1994) and Gerlach (1993) both emphasized the contribution of atmospheric input to N-supply for plants in grasslands respectively parts of the dune succession. This atmospheric N-input was measured at a dry dune site near The Hague (ten Harkel 1997) during the same period as the field incubation experiment was carried out. For open dune grassland plots, the N-input (≈ 35 kg ha^{-1} yr^{-1}) is in the same order as the mineralization rates, whereas in grass-dominated plots mineralization exceeds atmospheric N-input. Present atmospheric N-input thus cannot account for the high N-mineralization in the latter plots.

It can be concluded that grass-dominated plots in comparison with open dune grassland plots do have some specific characteristics. N-availability by mineralization and turnover rates are high as well as above and below-ground biomass.

Causes of grass encroachment

Since there is lack of evidence for any spatial variability in atmospheric deposition which could explain the observed mosaic-like pattern of grass-dominated and open dune grassland plots, it must be concluded that grass-encroachment in the dry dunes cannot be simply due to atmospheric N-deposition. Thus, other factors must be involved. Ten Harkel & van der Meulen (1996), for example, showed that dry dune grasslands did not become grass-dominated as long as the vegetation was grazed, not even when fertilized. Boorman & Fuller (1982) found that under fertilization perennial grasses did not dominate the sward, because of intensive rabbit grazing. Other studies showed that a decrease in grazing intensity, for instance after an outbreak of myxomatosis or when domestic grazing animals are excluded, may lead to an increase in biomass and dominance of tall grasses (e.g. Ranwell 1960; Zeevalking & Fresco 1977; Belsky 1992; Hill et al. 1992). Only when grazing is absent, the relatively high nitrogen availability allows grasses to become dominant. The foregoing strongly indicates that grass encroachment may have been triggered by atmospheric deposition and subsequently was enhanced as a result of enhanced N-mineralization. This type of feedback has been described by Wedin & Tilman (1990), who discussed positive feedbacks between species composition of vegetation and N-cycling. They showed that such feedback can lead to alternative stable states of the vegetation/soil complex. Feedbacks in the N-cycle were also described by Morecroft et al. (1994), who found an increasing mineralization rate with increasing N-input. Other types of positive feedbacks were described by Wilson & Agnew (1992), who, among others, paid attention to the role of grazing, NPK and light-mediated switches in ecosystem functioning.

According to Bobbink (1991) the high N/P ratio in the shoots of *Brachypodium pinnatum* in chalk grasslands points to stimulation of growth by an efficient use of increased N and to the capability to cope with an increasing shortage of P. Probably, the dominant grass

Table 5. N and P concentrations (g/kg) and N/P ratio of the above-ground biomass. Mean values and standard deviations based on n = 6 (grass-dominated plots) and n = 4 (open dune grassland plots). * = significant difference between grass-dominated and open dune grassland plots (p < 5%). For abbreviations, see Table 1.

	N(g/kg)				P(g/kg)				N/P ratio			
Site	grass-dominated plots		open dune grassland plots		grass-dominated plots		open dune grassland plots		grass-dominated plots		open dune grassland plots	
TP	11.4*	(± 0.9)	14.2	(± 2.0)	0.6*	(± 0)	1.0	(±0.3)	21*	(± 3)	15	(± 4)
MD	16.6*	(± 1.5)	12.5	(± 1.7)	1.0	(± 0.2)	1.3	(±0.2)	17*	(± 2)	10	(± 1)
ZV	11.7*	(± 1.2)	21.3	(± 1.4)	0.6*	(± 0.1)	1.5	(±0.2)	21*	(± 2)	15	(± 1)
KV	13.4*	(± 1.3)	8.9	(± 0.5)	0.8*	(± 0.1)	0.6	(±0.1)	17	(± 2)	15	(± 1)

species in dry dunes also have such adaptations, resulting in the observed higher N/P ratio of the above-ground biomass in grass-dominated plots. However, more detailed data on shoot and root turnover rates and nutrient concentrations are required for a better insight into growing strategies and competitive abilities of dry dune grass species in relation to P-availability.

Though P-availability may differ, this cannot be the basic cause for the observed mosaic of tall grass-dominated and open dry dune grasslands, since primary differences in soil P-content at a site are small. It is therefore suggested, that the observed mosaic-like patterns in grass-encroachment are best explained by the interaction of grazing and N-availability, which is controlled by feedback mechanisms.

Implications for management

It can be concluded that grass-dominated plots in comparison with open dune grassland plots do have some specific characteristics. N-availability by mineralization and turnover rate are high as well as above and below-ground biomass. Therefore management measures to restore dry dune grasslands should be focused on these characteristics. Mowing removes the biomass, opens the vegetation and thus improves the conditions for small species to compete with grasses. In addition, mowing removes the dense litter layer, which may inhibit species to germinate (Tilman 1993) and exposes the ground surface promoting the colonisation of new species. Results of mowing experiments on sand dunes (Anderson & Romeril 1992) and in grasslands (Bakker 1989) showed positive effects. Apart from a higher diversity, mowing also encouraged rabbit activity. Also grazing by large herbivores results in a reduction of standing crop and a more open vegetation structure (e.g. Bakker 1989; Kooijman & de Haan 1995; ten Harkel & van der Meulen 1996). Mowing and grazing not only cause a changed light regime, but also a decrease in biomass and litter input, and thus have a strong impact on N-cycling. Eventually, these measures may lead to a decrease in nitrogen availability.

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