Can management compensate for effects of atmospheric nutrient deposition in heathland ecosystems?

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Summary

1. Atmospheric nutrient deposition has contributed to widespread changes in heathland ecosystems. As a result, management is now considered as a tool that may partly compensate for these nutrient loads. The question thus arises as to what extent management measures have the potential to mitigate or even compensate effects of atmospheric nutrient deposition. We hypothesize that low-intensity management does not compensate atmospheric nutrient loads, particularly with reference to prevailing rates of N deposition.

2. In this study, we evaluated the effectiveness of different management measures in reducing the impact of ongoing atmospheric nutrient loads. We compared the effects of mowing, prescribed burning (low-intensity management) and sod-cutting (high-intensity management) on heathland nutrient budgets (of N, Ca, K, Mg, P) in the Lueneburg Heath nature reserve (NW Germany). Nutrient balances were calculated by analysing the present-day input, the output due to the removal of biomass/humus-horizons, and changes in leaching rates.

3. Nutrient losses by increased leaching following management measures are negligible compared to nutrient losses caused by the removal of above-ground biomass or humus-horizons. The total quantities of nutrients removed by sod-cutting are equivalent to between 37 and 176 years of atmospheric input (for N: 89 years), as the humus-horizons represent huge stores for N, Ca and K.

4. In contrast, the quantities of N removed by mowing and prescribed burning are equivalent to only 5 years of atmospheric input. Heathlands subjected to such treatments will accumulate N in the long term, as these management measures are applied on a 10-15-year cycle. In addition, output/input-ratios for P clearly exceeded those for N for all management measures. It is therefore likely that N/P-ratios will increase in the long term in both the vegetation and soil.

5. *Synthesis and applications*. From a nutrient perspective low-intensity management cannot compensate for accumulation of atmospheric N loads in the long term. Hence, these measures are only effective in combination with high-intensity management measures. If N/P-ratios increase, heathlands currently (co-)limited by N will shift to being more P-limited in the long term. This will promote species which are well adapted to P-limited sites (e.g. *Molinia caerulea*).

Key-words: leaching, mowing, N/P-ratio, nitrogen, nutrient balance, prescribed burning, sod-cutting

Introduction

Atmospheric nutrient deposition has contributed to widespread changes in both the structure and function of many heathland ecosystems throughout Europe (Power et al. 1995, 2001; Alonso, Hartley & Thurlow 2001). Increased N loads, in particular, have been suggested as one possible cause of the replacement of *Calluna vulgaris* (L.) Hull by grasses like

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Deschampsia flexuosa (L.) Trin. (Heil & Bobbink 1993; Power, Ashmore & Cousins 1998). Competition between plants, and hence the vegetation dynamics, may be influenced by elevated nutrient levels in the essentially low-nutrient environment (Mickel, Brunschön & Fangmeier 1991; Berendse, Schmitz & de Visser 1994; Alonso et al. 2001). In addition, N deposition has direct effects on ericaceous species. *Calluna*, for example, shows higher foliar N contents and stimulated shoot growth, an increased sensitivity to late frost events and to drought, and is more subject to damage by heather beetle (*Lochmaea suturalis* (L.) Thompson) outbreaks (Van der Eerden et al. 1991; Power et al. 2004).

Heathland management, primarily aiming at the prevention of scrub and tree establishment, is now considered an important tool for the modification of ecosystem impacts caused by atmospheric nutrient loads. For example, the type and frequency of heathland management measures determines the quantities of nutrients removed from plant and humus compartments (Power et al. 2001). Management practices, therefore, have an impact on the nutritional state of heathland ecosystems and, by reducing nutrient stores, have the potential to affect ecosystem responses to atmospheric nutrient input. Heathland management may thus mitigate or even compensate for effects caused by atmospheric deposition.

However, in the lowlands of north-western Central Europe, high deposition rates for N (Achermann & Bobbink 2003) may raise the question as to whether management regimes currently applied to heathlands are efficient at reducing the impact of atmospheric nutrient loads. If heathlands accumulate nutrients such as N in the long term due to ongoing atmospheric loads, their former function as a source of nutrients will become one of a sink for nutrients. This will question the viability of heathland preservation in the long term, as it is likely that changes in the nutrient budgets will cause persistent changes in species composition.

The objective of our study was to evaluate the effectiveness of different management measures at reducing the quantities of atmospheric nutrient loads and, subsequently, the long-term ability of these measures to preserve the nutrient balance of heathlands. We compared three management measures, two of which may be classified as low-intensity measures (mowing and prescribed burning), and one as a high-intensity measure (sod-cutting; intensity of management measures according to Terry et al. 2004). We hypothesize that nutrient output by means of low-intensity management measures is not sufficient to compensate for the present-day atmospheric nutrient input. As a consequence, low-intensity measures would not prevent nutrient accumulation in heathland ecosystems in the long term. This would result in long-term changes in the nutritional state of heathlands.

The following research questions were addressed in our study: (i) What is the quantity of nutrient elements (N, P, Ca, Mg, K) that can be removed from the different compartments of heathlands (above-ground biomass, O-horizon, A-horizon) by mowing, prescribed burning and sod-cutting? (ii) What are the effects of leaching on the nutrient budgets and how will leaching rates increase after the application of the management measures considered here? (iii) How effective are these measures in the context of current rates of nutrient deposition?

In addressing these questions, our study aims to provide more information on nutrient budgets and nutrient stores in different compartments of heathland ecosystems. To date there are few, if any, measurements available that quantify impacts of specific management measures on nutrient balances. In addition, empirical studies on nutrient balances are helpful in verifying models simulating vegetation responses to different management regimes (Terry et al. 2004).

Methods

Study area

Our study area is the Lueneburg Heath nature reserve (Lower Saxony, NW Germany; (53°15’N, 9°58’E, 105 m a.s.l.), the site of the largest complex of heathlands (about 5,000 ha) in NW Germany. The study area is characterized by Pleistocene sandy deposits. Prevailing soil types are nutrient-poor podzols or podzolic soils with pH_{H2O} values in the topsoil ranging between 3.3 and 3.5. The climate is of a humid suboceanic type. Mean precipitation is 811 mm $year^{-1}$ and the mean temperature is 8.4 °C (Müller-Westermeier 1996).

Management measures

In this study we compared the management measures mowing, prescribed burning and sod-cutting. All measures in our experiments were carried out during the winter of 2001/2002.

- Mowing is primarily applied to stands dominated by *Calluna vulgaris* in order to initiate its vegetative regeneration. Above-ground biomass was cut with a mower at 10 cm height (Webb 1998; Power et al. 2001). Hence, mowing did not affect the organic layer.
- Prescribed burning procedures in winter are low-intensity measures characterized by “low temperature fires” (Power et al. 2001). They affect the above-ground biomass, whilst the organic layers remain untouched. Periods of fine weather are needed for the burning procedure. Prescribed burning is comparable to mowing in that it is primarily applied to stands dominated by *Calluna vulgaris* in order to initiate regeneration from both seed and root stocks.
- Sod-cutting is a high-intensity measure carried out with a rotary hoe. In this procedure, the above-ground biomass and the organic layers were completely removed and the A-horizon was partially removed. Sod-cutting is applied to stands where

graminoids (mainly *Deschampsia flexuosa*) have partially replaced dwarf shrubs and thus are (co-)dominant.

Sample plots

Within a heathland area of 100 ha in size, 12 sample plots were randomly selected, each 20 x 40 m^2 in size, (4 replicates per management measure). Each sample plot was divided into two subplots (20 x 20 m^2). The management measure was carried out in one subplot and the second subplot served as a control (untreated subplot). The management measure applied to a sample plot was appropriate to its species composition. Therefore, the sample plots selected for mowing and prescribed burning were dominated by *Calluna vulgaris* (mean vegetation cover in the mown subplots: *Calluna* 80%, Poaceae 10%, cryptogams 63%; mean vegetation cover in the burned subplot: *Calluna* 56%, Poaceae 19%, cryptogams 42%), while in the sample plots selected for sod-cutting mean coverage by *Calluna vulgaris* was 46%, by graminoid species 50%, and by cryptogams 59%. The age of *Calluna vulgaris* in all sample plots ranged between 10 and 15 years.

Determination of atmospheric nutrient deposition

Atmospheric nutrient deposition was analysed by means of 12 bulk deposition samplers installed 100 cm above ground in the area where sample plots were situated (Münden 200, Inst. of Forest Hydrology, Han. Münden, Germany). Samples were collected biweekly for a period of 1 year (from winter 2001 to winter 2002; starting immediately after the management measures took place). For the determination of total N, samples were dissolved in a K_2SO_4-NaOH solution according to the Koroleff method (Grasshoff, Ehrhardt & Kremling 1983), and afterwards subjected to microwave digestion (MLS-ETHOS; MLS-GmbH, Leutkirch, Germany). Total N was measured with an ion chromatograph (IC-DX 120 Dionex; Idstein, Germany). Ca-, K-, Mg- and P-concentrations of samples were determined using Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES; Optima 3300 RL; Perkin Elmer, Burladingen, Germany).

In experiments of 6 years duration, Gauger, Köble & Anshelm (2000) compared bulk- and total (i.e. wet and dry)-deposition data. The authors found that bulk deposition samplers underestimate total N-, Ca-, K-, and Mg-deposition by about 23.2%, 35.3%, 25.0%, and 35.7%, respectively. In order to calculate the total deposition, bulk deposition of N, Ca, K, and Mg was corrected by the factors 1.30, 1.54, 1.33, and 1.55 (according to Gauger et al. 2000 and Bleeker et al. 2000).

Determination of nutrient loss by leaching

Nutrient loss by leaching was determined by means of a lysimeter consisting of intact soil cores (100 cm in length and 10 cm in diameter) and tension controlled porous cup soil water samplers (PE-sinter/0.45 µ nylon-membrane; Umwelt-Geräte-Technik, Müncheberg, Germany). Soil water samplers were installed at depths of 100 cm and samples were taken simultaneously and at the same intervals as deposition samples. The analytical procedure corresponds to that of the deposition samples. The mean annual rate of nutrient output was calculated for each management measure and the corresponding controls (3 replicate samples per plot, total n=24).

Nutrient stores in above-ground biomass and soil

Nutrient stores in the above-ground biomass, organic layer and A-horizon were determined in the treated subplots before and immediately after the management measures took place.

Above-ground biomass: Above-ground plant material was harvested from 1 m² patches (randomly selected) in each of the treated subplots (n = 4 per management measure). Harvested plant material was separated into three groups: dwarf shrubs (primarily consisting of *Calluna vulgaris*), graminoids (primarily consisting of *Deschampsia flexuosa* and *Molinia caerulea* (L.) Moench), cryptogams (mainly consisting of bryophytes, but also with a few lichens). The air dried plant material was weighed for each group and ground with a ball mill (Pulverisette 7; Fritsch, Idar-Oberstein, Germany). The procedure was repeated after the management measures had been carried out in order to determine the quantities of nutrients in the remaining above-ground biomass (mown and burned subplots).

Organic layer: In the treated subplots the thickness of the organic layer (O_L, O_f, and O_h horizons) was determined at the intersection points of a 10 x 10 m^2 grid (points spaced 2 m apart) and 100 cm^3 of the O-material (including below-ground biomass) was sampled at each intersection point. A total of 36 samples were obtained and thoroughly mixed. O-material was treated in the same way as the above-ground biomass. The procedure was repeated in the burned subplot (immediately after burning) in order to determine the level of nutrient input due to the deposition of ash (in the mown subplot, the organic layer was not affected, and in the sod-cut subplot the organic layer was completely removed).

A-horizon: The A-horizon was sampled according to the procedure described for the organic layer, and was treated in the same way as the above-ground biomass. After sod-cutting, the thickness of the remaining A-horizon was determined using the 36 intersection points of the grid.

Chemical analyses: Prior to the chemical analyses, samples of the three compartments (above-ground biomass, organic layer, A-horizon) were dried at 105 °C. N and C contents were analysed with a C/N-analyser (Vario EL; Elementar, Hanau, Germany). Samples for Ca-, K-, Mg-, and P-determination were dissolved in an HNO_3-HCl-H_2O_2 solution (Wong, Gu & Ng 1997; Lamble & Hill 1998) and digested using a microwave (see above). Digests were analysed by means of ICP-OES (see treatment of deposition samples).

Calculation of increased leaching rates

After the application of the management measures it is to be expected that leaching rates will have increased in comparison to the controls (untreated subplots). This is mainly due to the removal of the vegetation, which leads to increases in both the amount of percolating water (as a consequence of reduced evapotranspiration rates in the treated sites), and in the quantities of leached nutrients (as a consequence of a reduced nutrient uptake by the remaining vegetation; Sedláková & Chytrý 1999). Compared to mown and burned sites, leaching rates are expected to be particularly high in sites subjected to sod-cutting. This is due to the complete removal of the vegetation and partial removal of the humus-horizons (Gimingham, Hobbs & Mallik 1981; Sedláková & Chytrý 1999). It is likely that leaching rates will decrease in step with the recovery of the vegetation in the treated subplots (with increasing evapotranspiration and nutrient uptake rates of the regenerating vegetation; Gimingham et al. 1981; Forgeard 1990; Sedláková & Chytrý 1999). According to Forgeard (1990), Maltby, Legg & Proctor (1990) and Sedláková & Chytrý (1999), vegetation cover in mown and burned sites will achieve the *status quo ante* after about 5 years, whilst in sod-cut sites vegetation recovery will take about 15 years. In order to calculate an approximate value for the quantities of increased nutrient loss by leaching due to the application of the management measures considered here, we assume a linear decrease of leaching rates (due to the development of the vegetation) until the *status quo ante* is achieved (mown and burned subplots after 5 years, sod-cut subplot after 15 years). We therefore assume that leaching rates will decrease by 1/5 per year on the mown and burned subplots and by 1/15 per year on the sod-cut subplots.

Calculation of nutrient balances

In order to test our hypothesis regarding the low-intensity management measures, we calculated the ratio of the net output of nutrients (as a result of the management measures applied) and the annual net input. This ratio provides a term of reference that describes the period of time (in years) in which the quantities of nutrients removed due to a particular management measure are equivalent to atmospheric nutrient inputs (Table 2; cf. Britton et al. 2000; Mitchell et al. 2000). We call this the “Theoretical Effective Period (=TEP)“.

The TEP (unit: years) is calculated for each nutrient element according to the following formula:

TEP = net output (kg ha^{-1}) / annual net input (kg ha^{-1} yr^{-1}); where:
net output = nutrients removed by means of a particular management measure + increased leaching (in: kg ha^{-1}); and
annual net input = annual nutrient deposition - annual leaching under the control subplots (in: kg ha^{-1} yr^{-1}).

For the calculation of the TEP we assumed that deposition rates remain unchanged for the subsequent years.

In the Results and Discussion sections we focus in particular on the effects of management on the budget of N and P, as heathland ecosystems are considered to be limited primarily by these nutrients (Kirkham 2001).

Statistics

Comparisons of nutrient measurements for atmospheric deposition, leaching rates, above-ground biomass and soils were carried out using one-way ANOVA (SPSS 11.5). Leaching data were log-transformed, and the remaining data arcsin-transformed prior to ANOVA and the calculation of means and SD.

Results

Atmospheric deposition

A comparison of the atmospheric nutrient deposition revealed no significant differences ($p > 0.05$) between the 12 open top deposition samplers. Atmospheric nutrient deposition was therefore considered to be equal for all of the sample plots. N input amounted to 22.8 kg ha^{-1} year^{-1} (Fig. 1). P deposition rates were below the analytically detectable threshold value (0.0326 mg l^{-1}). Therefore, deposition rates were below 0.5 kg ha^{-1} year^{-1}.

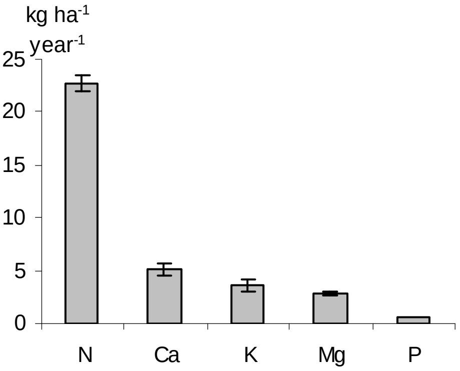

Fig. 1. Annual quantities of total nutrient deposition (wet and dry deposition; means ± SD, n = 12) in the sample plots. Deposition rates for P were less than 0.5 kg ha^{-1} year^{-1}.

Pre-management above-ground biomass

Based on the criteria underlying the application of the management measures, dwarf shrub biomass achieved the highest values in the subplots designated for mowing and prescribed burning (Fig. 2). Poaceae achieved the highest biomass values in the sod-cut subplots. Mowing and prescribed burning had little or no effect on the biomass of Poaceae and cryptogams. Nutrient removal by means of these measures was therefore mainly due to the removal of *Calluna vulgaris*-biomass. Sod-cutting removed the entire above-ground biomass.

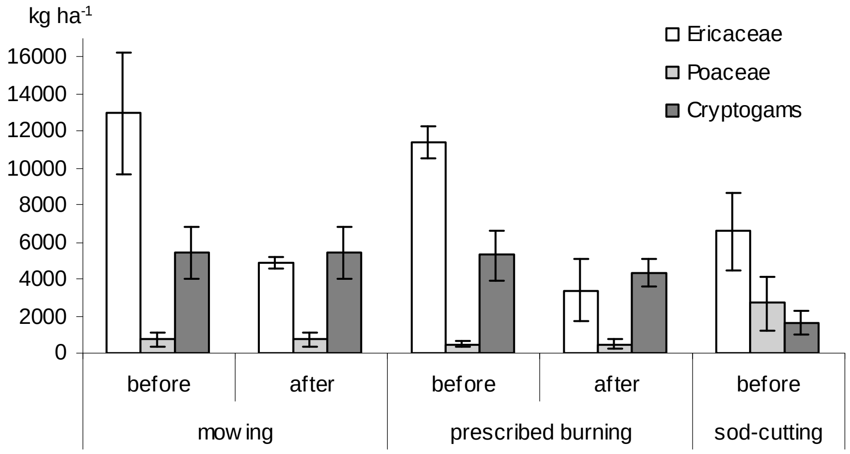

Fig. 2. Above-ground biomass of Ericaceae, Poaceae and cryptogams in the subplots before and after the application of management measures (means ± SD; n = 4). Sod-cutting removed the entire above-ground biomass.

Nutrient stores in the above-ground biomass and soils

Table 1 gives an overview of the nutrient stores in the above-ground biomass, the organic layer and the A-horizon (pre- and post-management stores). Stores of N in the above-ground biomass were highest in the mown subplots (221.5 kg ha^{-1}) and lowest in the sod-cut subplots (121.6 kg ha^{-1}; pre-management stores). Regarding the dominant species in the above-ground biomass (*Calluna vulgaris* and *Deschampsia flexuosa*), we found N and P contents for *Calluna vulgaris* of 1.03% and 0.07%, respectively and of 2.11% and 0.13% respectively for *Deschampsia flexuosa* (data not shown in Table 1).

Mowing reduced the N store in the above-ground biomass by about 44%, and prescribed burning by about 53%. Ca, Mg, K and P stores in the organic layer of the burned subplots increased significantly as a result of ash deposition.

As expected, nutrient removal was highest in the sod-cut subplots. The N store in the organic layer (which had been completely removed) amounted to 935 kg ha^{-1}. In the A-horizon, where the N store exceeded even the value of the organic layer, 627 kg N ha^{-1} were removed by sod-cutting. In our experiment this corresponded to 36% of the total N store in the A-horizon.

Nutrient output by leaching in the treated and untreated subplots

Leaching rates for N were significantly increased in the burned and the sod-cut subplots (Fig. 3 a-c). The N output during the first year after sod-cutting increased by about 4 kg ha^{-1}. The differences in leaching rates (of N) between the burned subplots and the corresponding controls were 2.2 kg ha^{-1} year^{-1}, and for the mown subplots and the corresponding controls 1.0 kg ha^{-1} year^{-1}. The quantities of leached P for all subplots were close to the analytically detectable threshold value. Leaching rates for this element were thus below 0.5 kg ha^{-1} year^{-1} in all subplots.

Table 1. Nutrient stores in the above-ground biomass, organic layer and A-horizon before and after the subplots were subjected to the management measures; mean values (n = 4) and SD (in brackets); %: percentage of the pre-management nutrient store. Nutrient stores increased in the organic layer in the burned subplots as a result of ash deposition.

		Mowing					Prescribed burning					Sod-cutting				
Nutrient stores in the		N	Ca	K	Mg	P	N	Ca	K	Mg	P	N	Ca	K	Mg	P
Above-ground biomass (kg ha^{-1})	before	221.5 (7.5)	61.7 (0.9)	61.8 (19.7)	17.0 (1.6)	14.4 (3.2)	196.9 (28.3)	67.4 (7.5)	56.3 (10.3)	18.2 (1.2)	12.9 (1.4)	121.6 (24.4)	34.8 (8.2)	35.8 (6.6)	10.8 (2.4)	7.4 (1.6)
	after	124.7* (20.8)	32.3* (5.8)	24.7* (6.8)	8.5* (1.6)	7.3* (1.6)	92.7* (10.5)	28.2* (5.2)	13.0* (5.3)	6.2* (1.2)	4.9* (0.7)	removed				
	%	56.3	52.4	40.0	50.0	50.7	47.1	41.8	23.1	34.1	38.0					
Organic layer (kg ha^{-1})	before (thickness: 3.9cm**)	839.8 (122.8)	80.9 (13.6)	41.6 (4.6)	20.1 (1.1)	29.6 (4.1)	736.1 (95.4)	56.1 (11.1)	31.2 (5.1)	16.9 (3.4)	23.5 (5.1)	934.5 (93.3)	104.7 (40.3)	51.2 (2.2)	27.1 (6.9)	38.1 (3.0)
	after	not affected (before = after)					741.3 (139.0)	91.6* (13.1)	49.3* (13.4)	27.8* (6.4)	29.9* (4.5)	removed				
	%						100.7	163.3	158.0	164.5	127.3					
A-horizon (kg ha^{-1})	before (thickness: 10.8cm**)	932.0 (260.5)	168.9 (48.0)	312.5 (104.9)	130.3 (49.4)	82.7 (5.8)	1782.3 (196.0)	156.8 (22.6)	298.2 (18.2)	70.6 (14.0)	114.0 (12.0)	1728.8 (197.0)	198.5 (34.7)	380.6 (50.1)	71.9 (15.9)	100.4 (8.0)
	after (thickness: 7.7cm**)	not affected (before = after)					not affected (before = after)					1102.3* (98.1)	115.4* (14.4)	215.0* (4.8)	45.0* (4.7)	69.8* (2.5)
	%											63.8	58.1	56.5	62.6	69.5

*) differences (before-after) are significant at the level of $p < 0.05$
**) values for the sod-cutting experiment

Nutrient balances and TEP

Table 2 summarizes output-input flows and gives the TEP for a particular nutrient element (last row in Table 2). With reference to N, for example, the application of mowing and prescribed burning removed quantities that corresponded to about 5 years of atmospheric input (TEP = 5.0 and 5.1 years, respectively). The TEP (for N) for sod-cutting was 89.8 years.

The TEP for P was calculated for two different scenarios as P-concentrations in deposition and leaching rates fell below the analytically detectable threshold value (Table 2): (i) maximal accumulation rates of P (assumptions: deposition = 0.5 kg ha^{-1} year^{-1}, leaching control/increased leaching = 0 kg ha^{-1} year^{-1}/0 kg ha^{-1}) and (ii) “balanced” accumulation rates of P (assumptions: annual net input = output by increased leaching within the first year after management = 0.1 kg ha^{-1} year^{-1}, i.e. 0.3 kg ha^{-1} over 5 years in the mown and burned subplots, and 0.8 kg ha^{-1} over 15 years in the sod-cut subplot). For both scenarios the TEP for P was highest for sod-cutting and lowest for prescribed burning.

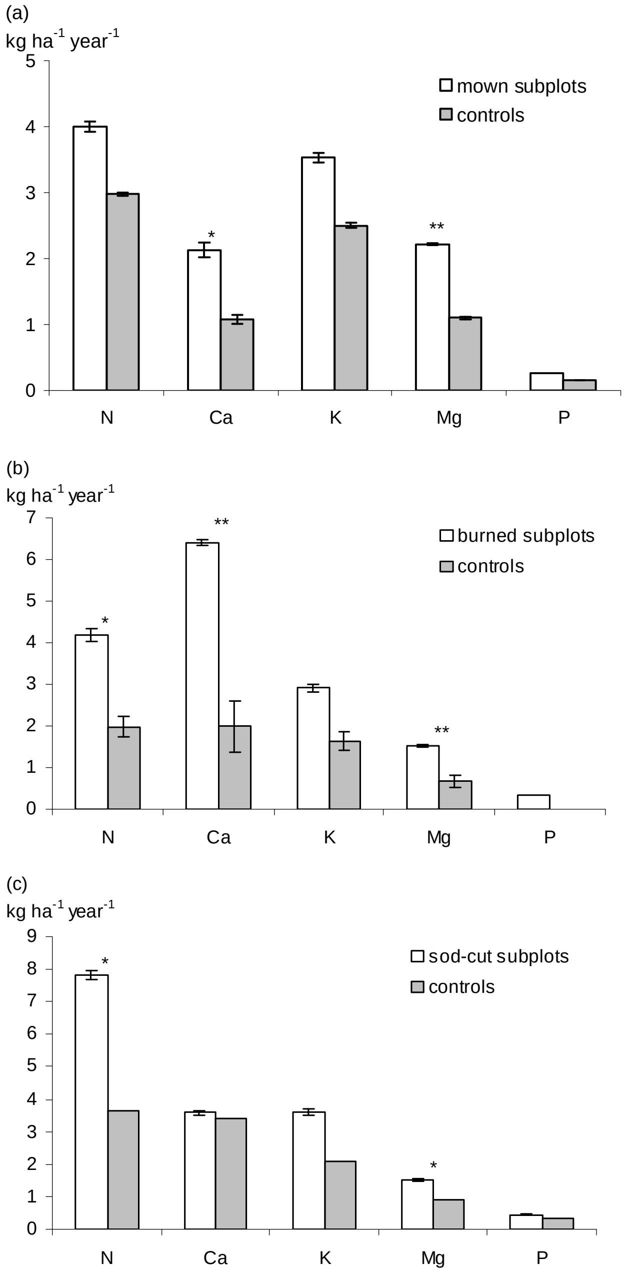

Fig. 3. Leaching in the treated subplots and the corresponding controls (means ± SD; n = 4) within one year after the application of a management measure (a: mowing, b: prescribed burning, c: sod-cutting). Asterisks indicate significant differences between treated subplots and the corresponding controls: * = $p < 0.05$, ** = $p < 0.01$.

Table 2. Summary of the effects of mowing, prescribed burning and sod-cutting on the nutrient balances (input-output-comparison) of the heathland studied here. Mean values (n = 4) are given in the table (for the sake of clarity in this table, SDs of all measurements are not repeated here as these values have already been shown in Table 1, Fig. 1 and Fig. 3). The TEP for P was calculated for two different scenarios: (i) maximal accumulation rates of P (assumptions: deposition = 0.5 kg ha^{-1} year^{-1}, leaching control/increased leaching = 0 kg ha^{-1} year^{-1}/0 kg ha^{-1}) and (ii) "balanced" accumulation rates of P (assumptions: annual net input of P = 0.1 kg ha^{-1} year^{-1}, output by increased leaching after the first year = 0.1 kg ha^{-1} year^{-1}, i.e. 0.3 kg ha^{-1} over 5 years in the mown and burned subplots, and 0.8 kg ha^{-1} over 15 years in the sod-cut subplot).

	Mowing					**Prescribed burning**					**Sod-cutting**				
	N	Ca	K	Mg	P	N	Ca	K	Mg	P	N	Ca	K	Mg	P
Annual input: **atmospheric deposition** (kg ha^{-1} yr^{-1})	22.8	5.1	3.6	2.8	< 0.5	22.8	5.1	3.6	2.8	< 0.5	22.8	5.1	3.6	2.8	< 0.5
Annual output: **leaching control** (kg ha^{-1} yr^{-1})	3.0	1.1	2.5	1.1	< 0.5	2.0	2.0	1.6	0.7	< 0.5	3.7	3.4	2.1	0.9	< 0.5
Annual net input: (kg ha^{-1} yr^{-1})	19.8	4.0	1.1	1.7	< 0.5	20.8	3.1	2.0	2.1	< 0.5	19.1	1.7	1.5	1.9	< 0.5
Output: **removal above-ground biomass** (kg ha^{-1})	96.8	29.4	37.1	8.5	7.1	104.2	39.2	43.3	12.0	8.0	121.6	34.8	35.8	10.8	7.4
Input: **ash deposition on the org. layer** (kg ha^{-1})	no ash deposition					5.2	35.5	18.1	10.9	6.4	no ash deposition				
Output: **removal organic layer** (kg ha^{-1})	not affected					not affected					934.5	104.7	51.2	27.1	38.1
Output: **removal A-horizon** (kg ha^{-1})	not affected					not affected					626.5	83.1	165.6	26.9	30.6
Output: **increased leaching** (5 / 15 years) (kg ha^{-1})	3.1	3.2	3.1	3.4	< 1.5	6.6	13.3	3.9	2.6	< 1.5	33.4	1.5	12.2	5.0	< 4.0
Net output: (kg ha^{-1})	99.9	32.6	40.2	11.9	< 8.6	105.6	17.0	29.1	3.7	< 3.1	1716.0	224.1	264.8	69.8	< 80.1
Theoretical Effective Period (years)	5.0	8.2	36.5	7.0	i) >14 ii) 74	5.1	5.5	14.6	1.8	i)>3.2 ii) 19	89.8	131.8	176.5	36.7	i)>152 ii) 764

Discussion

Atmospheric deposition, leaching, and nutrient stores

The rates of atmospheric nutrient deposition found in our study area are in agreement with other records for NW Germany (Bleeker et al. 2000; Herrmann, Pust & Pott 2005). They are also in the range reported by studies conducted in the British Isles (Power et al. 1998, 2001; Kirkham 2001), and are somewhat lower than deposition rates in many regions in the Netherlands (Bakema et al 1994; Erisman & de Vries 2000). However, N deposition in the study area exceeded critical load values for dry heathlands (Achermann & Bobbink 2003), which emphasizes the need for an increase in the output of nutrients by means of an appropriate long-term management strategy.

Comparisons of both leaching data and nutrient stores (organic layer, A-horizon) are difficult, due to the lack of corresponding analyses in north-western Central Europe. Leaching values given for N for heaths in NW Germany are in a comparable range to our findings (Matzner & Ulrich 1980; Engel 1988), but are based on rough calculation rather than on direct measurements. Quantities of leached nutrients must also be interpreted in the context of precipitation rates prevailing during a field experiment. During our study the annual precipitation values exceeded the long-term average value by about 300 mm. However, as shown by Sieber et al. (2004), effects on the total quantities of leached nutrients are comparatively low: Increased precipitation increases the quantities of percolating water, but simultaneously leads to decreased concentrations of dissolved ions. Hence, rates of leached nutrients are only slightly affected by varying precipitation rates (provided that emission rates remain constant; Sieber et al. 2004).

Both organic matter and nutrient content in the organic layer and A-horizon are in good agreement with results reported by Engel (1988). According to Chapman, Hibble & Rafarel (1975) the humus accumulation (organic layer) in a 25 year old British heath amounted to 30 t ha^{-1}. This is about 55% of the value we found in the sod-cut subplot (organic layer: 54.5 t ha^{-1}). The amounts of organic matter in the organic layer of three Dutch heathlands investigated by Diemont (1996) ranged between 25 t ha^{-1} and 65 t ha^{-1}. Comparable values were found by Mitchell et al. (2000) for the quantities of nutrients located in the organic layer, although their study focused on successional sites mostly dominated by shrubs and trees.

The quantities of nutrients removed from a heathland ecosystem primarily depend on the nutrient stores which have accumulated during heathland succession in the two compartments, above-ground biomass and soil. Although the above-ground biomass within the subplots may be highly variable (e.g. biomass of *Calluna vulgaris* in the mown subplots; cf. Diemont 1996), our findings are within the ranges given by other authors (Matzner & Ulrich 1980; Diemont 1996; Terry et al. 2004). In the subplots destined for mowing, pre-management above-ground biomass for *Calluna vulgaris* (mean biomass 12,958 kg ha^{-1}) may mark the upper threshold value found in *Calluna vulgaris*-dominated stands in the Lueneburg Heath (Engel 1988). Our values are also within the range given by other authors for mean nutrient content (for N and P) in the two main species representing the above-ground biomass in our subplots (*Calluna vulgaris* and *Deschampsia flexuosa*; Aerts 1993; Alonso et al. 2001; Kirkham 2001). Our results for nutrient output via the removal of above-ground biomass may thus be considered representative for most heaths in NW Central Europe.

Nutrient output from above-ground biomass and soil

As expected, net nutrient output is highest in the sod-cut subplots, even though pre-management nutrient stores in the above-ground biomass were lower than in the other plots. The removal of the organic layer caused very high nutrient losses, particularly for N and Ca. In the O-layer, the N store was about five times higher than in the above-ground biomass. Furthermore, the A-horizon of heathlands must also be considered a huge nutrient store, particularly with reference to the K content. The K output from the A-horizon was three times the amount located in the organic layer, even though only one-third of the A-horizon was removed by sod-cutting. Therefore, the the greater the amount of the A-horizon removed by sod-cutting, the greater the effect on the K balance of the system.

In contrast, prescribed burning removes only small amounts of K, Ca and Mg. This is due to the high concentrations of these elements in the ash deposited on the organic layers after burning. Nevertheless, the quantities of N removed by burning from the above-ground biomass in our study are similar to the effects obtained by mowing and sod-cutting, but low compared with findings of other heathland burning experiments (Diemont 1996). These differences are mainly related to the impact of the temperature of the fire, which strongly affects the amount of burned organic matter in the above-ground biomass and the organic layer (Forgeard & Frenot 1996; Power et al. 2001). In addition, nutrient loss increases with increasing organic matter available for combustion (Diemont 1996). In our study, the low-intensity measures primarily affected the dwarf shrub layer, whilst Poaceae and cryptogams generally remained untouched. This can be explained by the fact that both graminoid species and cryptogams formed a separate understorey layer beneath the dwarf shrub layer. This layer is only slightly affected by low-intensity mowing, as its vegetation height is generally lower than the cut-height. Low-temperature burns also only partially remove the above-ground biomass, mainly affecting the dwarf shrubs and to a lesser extent the grasses and mosses (Diemont 1996; Terry et al. 2004).

The removal of nutrients in the mown subplots is comparatively high due to high above-ground biomass values. However, as mowing may be carried out at different levels of intensity (variability of the cut height), the quantities of nutrients removed will vary accordingly (Power et al. 2001). Therefore, nutrient outputs resulting from low- or high-intensity mowing may vary over a wide range (Terry et al. 2004). Compared to the effects of prescribed burning, mowing has a higher efficiency of removal for the elements Ca, Mg, K and P.

Increase in leaching rates

Post-management leaching rates differed distinctly for the five nutrient elements considered here. This is mainly due to their different sorption behaviour and to changes in their availability in the soil solution (Olff & Pegtel 1994). Quantities of leached N under the sod-cut subplots are particularly high. This may be attributed to several factors, such as the absence of N-uptake by plants and increased mineralization rates of roots and organic material in the remaining A-horizon (Mitchell et al. 1999; Dorland et al. 2003). Elevated mineralization rates are induced by increased soil temperatures and soil moisture levels, both affected by the removal of the vegetation (Mallik & FitzPatrik 1996; Anderson & Hetherington 1999; Schmidt et al. 2002). Elevated nutrient levels and leaching rates have also been documented for heath subjected to prescribed burning (Foregeard & Frenot 1996; Mallik & FitzPatrik 1996). In burned heath, leaching rates were particularly high for N, which is in agreement with our findings. In contrast, the quantities of leached P in all subplots fell below the analytically detectable threshold value. The reason for this may be the generally low concentrations of phosphate available to plants in heathland soils, but also the sorption of ortho-phosphate in the A- and B-horizons (Olff & Pegtel 1994).

In some cases, the recovery of vegetation on sites subjected to prescribed burning and sod-cutting may be retarded for two or more years (Diemont & Linthorst Homan 1989; Dorland et al. 2003), and leaching rates thus remain increased for more than one year. In this case, our model will underestimate the nutrient losses due to leaching. In our approach, the linear decrease of leaching rates associated with a linear increase of vegetation cover must be considered as an approximation. However, as Table 2 shows, the total amount of nutrient loss due to leaching is always very low compared to the nutrient output caused by the removal of the above-ground biomass or humus-horizons. For example, if the increase in leaching rates is underestimated by 100% (3.1 instead of 6.2 kg ha^{-1} within 5 years) in the mown plots, TEP will increase only by about 3.7% (from 5.0 to 5.2 years). Thus, leaching rates caused by different patterns of post-management vegetation recovery have only minor effects on the outcome of the TEP. In summary, the management measures considered here will cause increased nutrient losses by leaching, but the overall effect of leaching on the nutrient budget of heathlands is low.

Nutrient balances and TEP

The quantities of N removed by mowing and prescribed burning are equivalent to 5 years of atmospheric input (Table 2). In most cases, these measures are not applied over a shorter cycle than 10-15 years due to the period of time that the vegetation needs for recovery (Terry et al. 2004). As a consequence, stands will accumulate N in the long term. Thus, our hypothesis is supported with regard to N: in view of the present-day deposition rates, mowing and prescribed burning are insufficient to prevent N-accumulation in heathland ecosystems in the long term. A comparable finding applies to the nutrients Mg and Ca, which have a TEP of 1.8 and 5.5 years, respectively, when prescribed burning is employed. By contrast, sod-cutting TEP values are several decades or even more than a century, due to the nutrient losses from the organic layer and A-horizon. It remains unclear to what extent atmospheric nutrient loads (particularly for N) accelerate vegetation growth (Berendse et al. 1994, Power et al. 1998), a process which would permit the shortening of management cycles (Diemont 1996). This would increase the nutrient output arising from management measures.

In the study by Mitchell et al. (2000), the quantities of nutrients removed by management were also related to atmospheric inputs. The authors found TEPs for Ca, Mg and N ranging between 41 and 197 years. These findings are in agreement with our results for the sod-cut subplots, although both litter and trees were removed from successional sites in order to restore heathland vegetation.

Outcomes of TEP are affected by some other soil chemical processes that have not been quantified in this study, but need to be considered when interpreting TEP outcomes. One source of uncertainty in our calculation of the TEPs for N are losses caused by denitrification. Such losses would increase the output rate and thus the TEP. However, the underestimation of the TEP in our study may be low for this process as denitrification takes place primarily in wet heathlands (Troelsta, Wagenaar & Smant 1997; Galloway et al. 2004). Further uncalculated N losses are leaching of particular organic N and volatilisation of NH_3, which also may increase TEP values. In our study, effects of N losses due to these processes may be negligible (Galloway et al. 2004) compared to N losses caused by biomass and soil removal. Interpretation of TEP outcomes must also allow for the fact that small amounts of K, Ca and Mg may be released from soils due to weathering of minerals (Brady & Weil 1996). In sandy podzols of the study area, Ca, Mg, and K contents of the C-horizons are below 0.1%, 0.1%, and 1.1% respectively (Scheffer & Schachtschabel 2002). These stores are very low compared with stores in the above-ground biomass and humus-horizons. Weathering of minerals thus may have slight effects on the TEP calculated for K, but are negligible for Ca and Mg (as regards podzols). In contrast, TEPs calculated for N and P are not affected by mineral weathering due to the very low N and P contents of minerals of sandy podzols (for $P < 0.05\%$; Brady & Weil 1996).

For the interpretation of our results it is important to mention that the sample plots had not been managed for about one decade prior to this study. Therefore, organic material had accumulated in the O- and the A-horizons. This may have increased the TEP, particularly for the sod-cut subplots. By contrast, age of stands in sod-cut plots only slightly affects the TEP, because nutrient stores in the above-ground biomass are very low compared to the stores in the O- and A-horizons.

As P-concentrations fell below the analytically detectable threshold value, TEPs are calculated for two different scenarios in Table 2. If the second scenario is assumed (“balanced accumulation rates for P”), it is likely that TEPs for P are many times higher than those for N. Consequently, output/input-ratios for P exceed those for N for all management measures. Thus, N/P-ratios in the vegetation and humus-horizons will increase in the long term and P will become an increasingly (co-)limiting factor for vegetation growth (Koerselman & Meuleman 1996). This conclusion is supported by studies by Verhoeven, Koerselman & Meuleman (1996) and Kirkham (2001). It is likely that N/P-ratios rise particularly in those compartments in which N accumulation takes place. According to Power et al. (1998) and Nielsen et al. (2000), these are primarily the A- and B-horizons, but to a lesser extent also the organic layer (Kristensen 2001).

In summary, our study provides evidence that low-intensity management measures (mowing, prescribed burning) are not sufficient to compensate for present-day atmospheric N deposition. In order to preserve a balanced N budget in the long term, high-intensity measures (like sod-cutting) will be an indispensable instrument in heathland preservation (Barker et al. 2004), possibly applied in combination with low-intensity measures (e.g. two 10-15 year-cycles of mowing followed by sod-cutting). In this context it may be important to note that effects of nitrogen on shoot growth of *Calluna vulgaris* are lower in the heaths which had undergone more intensive management treatments (Barker et al. 2004). However, as output/input-ratios for P exceed those for N for all management measures, we assume that heathland ecosystems currently (co-)limited by N may shift to being more P-limited in the long term. This will change the competitive performance between heathland species since these differ with regard to their N- and P-requirements (Roem, Klees & Berendse 2002). Increasing N- and limited P-availability may favour *Molinia caerulea* in particular, as this species is well adapted to P-limited sites (Kirkham 2001).

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