

Shifts in N and P Budgets of Heathland Ecosystems: Effects of Management and Atmospheric Inputs

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ABSTRACT

In the present study we analyzed the combined effects of management (grazing, mowing, prescribed burning, sod-cutting) and atmospheric deposition on N and P budgets of heathland ecosystems (Lüneburger Heide nature reserve; N Germany). We hypothesize that management measures such as grazing and mowing can accelerate a deposition-induced imbalance of N and P pools as a result of a disproportionally high output of P. We analyzed management and deposition affected input–output flows of N and P and related them to changes in the nutritional status of *Calluna vulgaris* 5 years after treatment application. We found that grazing and mowing caused the highest net loss of P due to high P concentrations in the aboveground biomass. In contrast, prescribed burning only slightly affected P pools, as P remained in the system due to ash deposition. Man-

agement-mediated effects on N and P pools were mirrored in the nutritional status of *Calluna vulgaris*: at the grazed and mown sites, the P content of current season's shoots significantly decreased within 5 years after treatments, whereas the N content remained unchanged. We conclude that grazing and mowing can accelerate declining availability of P and, thus, accelerate a deposition-induced shift from N- to P-limited plant growth in the medium term. In the face of ongoing atmospheric N loads management schemes need to combine high- and low-intensity measures to maintain both a diverse structure and balanced nutrient budgets in the long term.

Key words: *Calluna vulgaris*; grazing; leaching; *Molinia caerulea*; mowing; N:P ratio; nutrient limitation; prescribed burning; sod-cutting.

INTRODUCTION

Atmospheric nitrogen loads have contributed to widespread changes in the structure and functioning of many natural and seminatural ecosystems (Power and others 2006). Ecosystem responses to

elevated N inputs range from altered patterns of plant growth, chemistry and phenology to changes in nutrient cycling and, ultimately, shifts in plant community composition and biodiversity loss (Bobbink and others 1998). In heathland ecosystems, atmospheric N deposition is considered responsible for increased aboveground productivity, the accumulation of soil organic matter, and accelerated nutrient cycles (Schmidt and others

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2004). Appreciable impacts of atmospheric N loads on species composition and interspecific competition are attributable to the fact that N is the limiting nutrient for plant growth in many ecosystems (Dise and Stevens 2005). Besides N, P has been proven to limit plant productivity in ecosystems such as wetlands, mires, grasslands, and heaths (Güsewell and others 2003). Given that two nutrients (that is, N and P) are potentially limiting for plant growth in a plant community, the “resource-ratio hypothesis” (Tilman 1985) predicts that fertilization with N will cause P to become relatively scarce and promote species that are strong competitors for P. In the long term, the latter may outcompete species that were the strongest competitors as long as N was scarce (Güsewell and others 2003). Such an imbalance in the N and P supply has been caused by atmospheric nutrient inputs at many sites throughout Europe, because current N deposition rates exceed critical load values for many plant communities, but atmospheric P inputs are very low at almost all sites (Olde Venterink and others 2002). In the long term, atmospheric N deposition may, therefore, cause a shift from N to P limitation of plant growth (Verhoeven and others 1996).

In this context, the employment of management measures to remove nutrients has increased in importance (Dierssen 1996; van Diggelen and Marrs 2003). Management practices have an impact on the nutritional status of heathlands and, by reducing nutrient stores, have the potential to affect ecosystem responses to atmospheric nutrient input (Power and others 2001). However, depending on the management measures applied, different compartments of an ecosystem, such as aboveground biomass or soil horizons, are affected. As a consequence, N and P removal attributable to a focal management measure may vary due to differing N and P stores of the compartments affected (Niemeyer and others 2007). Because atmospheric P inputs and P release due to mineral weathering in sandy soils are low (Nielsen and others 2000), management may cause a net loss of P (Güsewell 2004). Management may, thus, strengthen the effects of N deposition by increasing the relative P shortage and accelerating a shift to P limitation (Verhoeven and others 1996). This may hamper the long-term preservation of seminatural ecosystems (including heaths) and their biodiversity.

Shifts in nutrient stores and nutrient availability often represent a key uncertainty in the assessment of the functioning and conservation perspectives of ecosystems (Lavelle 2000). It is, thus, important to quantify input–output flows and the resulting budgets of key nutrients in relation to ongoing

atmospheric inputs and current management strategies. This may allow for a better understanding and prediction of changes in the structure and species composition of a focal ecosystem. The objective of this study was to quantify short-term (annual) and medium-term (10 years) changes in the N and P budgets of a heathland ecosystem as a function of nutrient deposition and four commonly applied management measures (sheep grazing, mowing, prescribed burning, sod-cutting). In a first step, we aimed to quantify annual input–output flows of N and P as affected by deposition and management (partly based on a reassessment of data published by Härdtle and others 2006). In a second step, we compared net input–output flows with soil N and P pools to assess shifts in the nutrient pools in the medium term (10 years). We hypothesize that management measures only affecting aboveground biomass nutrient stores (that is, grazing and mowing) may cause an excessive output of P, and, thus, will accelerate a deposition-induced imbalance of N and P pools. In addition to nutrient flows, we assessed vegetation responses to shifts in N and P pools by analyzing the nutritional status of *Calluna vulgaris* 5 years after management application. This enabled an evaluation of whether dwarf shrub vegetation mirrors management-induced changes of N and P pools.

METHODS

Study Area and Experimental Set-Up

To calculate N and P flows as affected by management, in the present study we reassessed data gained in previous experiments that focused on management effects on nutrient stores of heathlands (that is, data on N and P stores in the aboveground biomass and humus horizons; see Härdtle and others 2006). These data have been complemented by additional deposition and leachate measurements as well as analyses of the N and P stores in the subsoil.

All experiments have been carried out in the “Lüneburger Heide nature reserve” (NW Germany; 53° 15'N, 9° 58'E, 105 m a.s.l.), an area characterized by nutrient-poor Podzols (diagnostic horizons: albic horizon = A-horizon, spodic horizon = B-horizon), with $\text{pH}_{\text{H}_2\text{O}}$ values in the topsoil ranging between 3.0 and 3.5. The climate is of a humid suboceanic type. Mean precipitation is 811 mm y^{-1} and the mean temperature is 8.4°C (Niemeyer and others 2005).

In the following sections we describe the set-up of the experiments and the analytical procedures

with which the presented data have been obtained. For the original description of the experimental set-up and analytical procedures see Härdtle and others (2006) and Fottner and others (2007).

In an area covering 2,100 ha, management impacts on nutrient budgets were analyzed by means of sheep grazing, mowing, prescribed burning, and sod-cutting experiments (treatments). The grazing experiment began in May 2001 and ended in April 2002. All other treatments (mowing, prescribed burning, sod-cutting) were carried out during the winter of 2001/2002. *Calluna vulgaris* (henceforth referred to as *Calluna*) was the prevailing dwarf shrub at all experimental sites (Table 1). The age of *Calluna* ranged between 10 and 15 years. All sites had been unmanaged for 1 decade prior to the experiments.

- In the mowing experiment the aboveground biomass was cut with a mower at 10 cm height. Thus, mowing did not affect the organic layer (low-intensity mow). In the study area mowing is applied in a 10-year cycle.

- Prescribed burning was applied in winter (low temperature fire). Winter burning affects the aboveground biomass, while leaving the organic layer untouched. Prescribed burning is applied in a 10-year cycle.
- Sod-cutting is a high-intensity measure carried out with a rotary hoe. In this procedure, the aboveground biomass and the organic layers were completely removed and the albic horizon was partially removed. Sod-cutting is applied approximately in a 30-year cycle.
- For the grazing experiment, a flock with 541 ewes ("German heath sheep" breed) was used (grazed area: 486 ha; stocking rate: 1.1 sheep ha⁻¹). Grazing took place throughout the year and also continued after the end of the sampling procedure in April 2002. The flock was tended by a shepherd and on average remained in the heath 8 h day⁻¹. The flock spent the remainder of the time in the sheepfold or moving on the pathways between the sheepfold and grazing area. The sheep received no additional fodder, except at lambing time.

Table 1. Pre-Management Vegetation and Nutrient Pools

Vegetation/species cover (%)		Grazing	Mowing	Prescribed burning	Sod-cutting
<i>Calluna vulgaris</i>		89	80	56	46
Other Ericaceae		3	<1	1	<1
Poaceae		3	10	19	50
Cyperaceae		1	<1	1	<1
Cryptogams		97	63	42	59
Aboveground biomass	Biomass	8885 (1512)	19083 (1683)	17956 (797)	10876 (1405)
	N	119.2 (27.1)	221.5 (7.5)	196.9 (28.3)	121.6 (24.4)
	P	9.0 (2.0)	14.4 (3.2)	12.9 (1.4)	7.4 (1.6)
	N:P ratio	13.3 (2.9)	15.4 (2.0)	15.3 (1.8)	16.4 (3.4)
Organic layer (O-horizon)	N	756.4 (35.5)	839.8 (122.8)	736.1 (95.4)	934.5 (93.3)
	P	27.2 (1.3)	29.6 (4.1)	23.5 (5.1)	38.1 (3.0)
Thickness: 3.9 cm (0.5)	N:P ratio	27.9 (1.7)	28.4 (1.7)	31.3 (2.6)	24.5 (1.1)
Albic horizon (A-horizon)	N	769.8 (317.1)	932.0 (260.5)	1782.3 (196.0)	1728.8 (197.0)
	P	77.0 (15.9)	82.7 (5.8)	114.0 (12.0)	100.4 (8.0)
Thickness: 10.2 cm (2.4)	N:P ratio	9.7 (2.6)	11.3 (2.6)	15.6 (2.4)	17.2 (0.7)
Spodic horizon (B-horizon)	N	654.1 (116.0)	451.1 (66.7)	2008.5 (713.9)	1469.8 (352.4)
	P	159.7 (49.8)	94.6 (14.5)	194.6 (67.0)	166.4 (36.3)
Thickness: 8.3 cm (1.9)	N:P ratio	4.3 (0.7)	4.8 (0.8)	10.3 (1.7)	8.8 (0.6)
Total pools (biomass + O + A + B)	N	2299.5 (526.0)	2444.4 (374.5)	4723.8 (603.5)	4254.7 (587.8)
	P	272.9 (57.9)	221.3 (42.3)	345.0 (68.4)	312.3 (47.2)
	N:P ratio	8.4 (2.3)	11.0 (2.4)	13.7 (2.6)	13.6 (2.6)

Means of $n = 40$ for the aboveground biomass (grazing experiment), and $n = 4$ for all remaining values. Pre-management vegetation/species cover (means of 8 relevés per experimental site), total aboveground biomass (in kg ha⁻¹), pools of N and P (in kg ha⁻¹), and N:P ratios of different heathland compartments (biomass, organic layer, albic horizon, spodic horizon, total pools). In addition, the thickness of the organic layer, albic horizon, and spodic horizon is given (SD in brackets; according to data from Härdtle and others 2006, Fottner and others 2007).

Design of the Mowing, Burning, and Sod-Cutting Experiments

Within the experimental area 12 sample plots were randomly selected, each $20 \times 40 \text{ m}^2$ in size (four replicates per management measure). Each sample plot was divided into two subplots (one treatment and one control; $20 \times 20 \text{ m}^2$). Nutrient stores in the aboveground biomass, organic layer, albic horizon, and spodic horizon were determined in the treated subplots before and immediately after the management measures took place.

Aboveground Biomass

Aboveground plant material was harvested from 1 m^2 patches (randomly selected) in each of the treated subplots ($n = 4$ per management measure), air dried, and weighed. The procedure was repeated immediately after treatment to determine the quantities of N and P in the remaining aboveground biomass (mown and burned subplots).

Organic Layer

In the treatments the thickness of the organic layer was determined at the intersections of a $10 \times 10 \text{ m}^2$ grid (points spaced 2 m apart), and 100 cm^3 of the organic layer was sampled at each intersection point (short core sampler, Ehlert, Niederkassel, Germany). A total of 36 samples were obtained and thoroughly mixed. Organic material was treated in the same way as the aboveground biomass. The procedure was repeated in the burned subplot (immediately after burning) 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).

Albic Horizon

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

Spodic Horizon

The spodic horizon was drilled at the 36 intersections with a soil auger (Pürckhauer, Ehlert, Niederkassel, Germany), the thickness of the spodic horizon measured and 20 cm^3 of the drilled soil material sampled. Samples were treated according to the procedure described for the organic layer. The spodic horizon was not affected

by management measures. Samples were used for the determination of N and P stores of the spodic horizon (Table 1).

Design of the Grazing Experiment

Biomass removal by sheep grazing was analyzed separately for *Calluna* and *Deschampsia*. Biomass output of *Calluna* was studied by means of 40 sample plots ($2 \times 1 \text{ m}^2$) randomly placed in the grazed area at the beginning of the grazing experiment in May 2001. Each sample plot was divided into two subplots ($1 \times 1 \text{ m}^2$). One of the subplots was fenced (exclosure = control), whereas sheep had open access to the second subplot (treatment). At the end of April 2002 biomass was harvested 3 cm above ground in the center of both subplots on an area of $50 \times 50 \text{ cm}^2$ (to avoid edge effects). Biomass output of *Deschampsia* was analyzed by means of a second set of 40 sample plots randomly placed in the grazed area (designed as described above). Between June and September 10 sample plots (that is, pairs of grazed and ungrazed subplots) were randomly selected and harvested monthly to analyze mean biomass output of *Deschampsia* during summer. The harvested plant material was air dried and weighed. Grazing was quantified as difference in biomass weight between grazed and ungrazed subplots.

Because the N and P contents of *Calluna* and *Deschampsia* may change within the course of the year (Aerts 1993), we also collected plant material monthly over the period of 1 year (*Calluna*: five current season's shoots of 20 randomly selected plants; *Deschampsia*: 50 g of aboveground biomass of 20 randomly selected tufts). The mean nutrient content for the entire year and that for the period June through September was used to calculate the nutrient output due to *Calluna* and *Deschampsia* biomass removal, respectively.

N and P Stores in Aboveground Biomass and Soil

Prior to the chemical analyses, all samples were ground with a ball mill (Pulverisette 7; Fritsch, Idar-Oberstein, Germany), dried at 105°C , and subsequently weighed (determination of oven dry weight). The N content of the samples was analyzed with a C/N-analyzer (Vario EL; Elementar, Hanau, Germany). For P determination, samples were dissolved in an $\text{HNO}_3\text{-HCl-H}_2\text{O}_2$ solution (Lamble and Hill 1998) and digested using a microwave (MLS-ETHOS; MLS-GmbH, Leutkirch, Germany). Digests were analyzed by means of an inductively coupled

plasma optical emission spectrometer (Optima 3300 RL; Perkin Elmer, Burladingen, Germany).

Determination of Atmospheric Nutrient Deposition

Atmospheric nutrient deposition was analyzed by means of 16 bulk deposition samplers installed 100 cm above ground in the area where experiments were carried out (four samplers per experiment; Münden 200, Inst. of Forest Hydrology, Han. Münden, Germany). Samples were collected fortnightly for a period of 1 year (grazing experiment: from May 2001 through April 2002; all the other experiments: immediately after treatment). For the determination of total N, samples were dissolved in a K_2SO_4 -NaOH solution according to the Koroleff method (Grasshoff and others 2002), and afterwards subjected to microwave digestion (see above). Total N was measured with an ion chromatograph (IC-DX 120 Dionex; Idstein, Germany). P concentrations of samples were determined using an ICP-OES (see above).

In experiments of 6 years duration Gauger and others (2000) compared bulk and total (that is, wet and dry) deposition data. The authors found that bulk deposition samplers underestimate total N-deposition by about 23.2% (see also Bobbink and others 1992). To calculate the total deposition, bulk deposition of N was corrected by the factors 1.30 (according to Gauger and others 2000 and Niemeyer and others 2005).

Nutrient Input from Excrements (Grazing Experiment)

Nutrient input via excrement (that is, feces and urine) was calculated according to Fottner and others (2007). In these experiments, excrement input (per ewe) was analyzed by means of feces bags and by stable experiments.

Determination of Nutrient Loss by Leaching

Nutrient loss by leaching was determined by means of lysimeters consisting of intact soil cores (100 cm in length and 10 cm in diameter) and tension controlled suction cups (PE-sinter/0.45 μ nylon-membrane; Umwelt-Geräte-Technik, Müncheberg, Germany). Suction cups were installed at depths of 100 cm and samples were taken simultaneously and at the same intervals as deposition samples. To avoid effects of soil disturbance on nutrient measurements, samplers were installed 4 months prior to treatments. The analytical procedure corresponded

to that of the deposition samples. The mean annual rate of nutrient output was calculated for each treatment and the corresponding control (four replicates per management measure; total n of samplers = 32). Post-management leaching rates were measured for 1 year. The quantity of increased post-management nutrient loss by leaching was approximated according to Härdtle and others (2006). The authors assumed that the status quo ante of leaching (that is, pre-treatment leaching) will be achieved after 5 years in the mown and burned subplots, and after 15 years in the sod-cut subplots. During that time (that is, during the recovery of vegetation and humus horizons) a continuous decrease of post-management leaching rates was assumed.

Post-Management Nutritional Status of *Calluna*

To assess dwarf shrub responses to management-induced shifts in N and P pools, N and P contents of current season's shoots of *Calluna* were analyzed 5 years after treatment application (for grazing: 5 years after continuous grazing). In October 2006 we collected five current season's shoots of 20 randomly selected *Calluna* plants in each subplot (that is, treatments and corresponding controls; four replicates per treatment). The collected plant material was treated and analyzed as described for the aboveground biomass (see above).

Grazing effects on the nutritional status of *Calluna* were analyzed by means of four separate sample plots (20 \times 10 m²) selected at random in four different heath areas (each about 500 ha in size and grazed by one flock from 2001 to 2006). Sample plots were divided into two subplots (10 \times 10 m²), one of which was fenced (see above). In addition, sample plots served for the collection of *Calluna* shoots in 2006 and for the determination of leaching, as well as for the determination of N and P stores in the organic layer, albic and spodic horizon (see above).

Annual Net Input-Output Flows of N and P

To balance nutrient input-output flows, we calculated the annual net input and the annual net output of N and P. This approach allows for a comparison of the four management measures, despite different management cycles. The annual net input and output was defined as follows:

Annual net input (kg ha⁻¹ y⁻¹) = atmospheric nutrient deposition (+excrement input in the grazed heaths) – leaching control.

Table 2. Input/Output Flows of N and P

Nutrient	Grazing		Mowing		Prescribed burning		Sod-cutting	
	N	P	N	P	N	P	N	P
Annual input: atmospheric deposition (kg ha ⁻¹ y ⁻¹)	22.8	0.3	22.8	0.3	22.8	0.3	22.8	0.3
Annual input: excrement (kg ha ⁻¹ y ⁻¹)	3.5	0.2	No excrement input		No excrement input		No excrement input	
Annual output: leaching control (kg ha ⁻¹ y ⁻¹)	2.2	0.2	3.0	0.2	2.0	0.2	3.7	0.2
Annual net input: (kg ha ⁻¹ y ⁻¹)	24.1	0.3	19.8	0.1	20.8	0.1	19.1	0.1
Output: removal aboveground biomass (kg ha ⁻¹)	25.6	1.9	96.8	7.1	104.2	8.0	121.6	7.4
Input: ash deposition on the org. layer (kg ha ⁻¹)	No ash deposition		No ash deposition		5.2	6.4	No ash deposition	
Output: removal organic layer (kg ha ⁻¹)	Not affected		Not affected		Not affected		934.5	38.1
Output: removal albic horizon (kg ha ⁻¹)	Not affected		Not affected		Not affected		626.5	30.6
Output: increased leaching* (kg ha ⁻¹)	0.0	0.0	3.1	0.3	6.6	0.3	33.4	0.8
Net output/annual net output (kg ha ⁻¹ y ⁻¹)**	25.6/ 25.6	1.9/ 1.9	99.9/ 9.9	7.4/ 0.7	105.6/ 10.6	1.9/ 0.2	1716.0/ 57.2	76.9/ 2.6
Annual (net) input – output (kg ha ⁻¹ y ⁻¹) = balances	–1.5	–1.6	9.9	–0.6	10.2	–0.1	–38.1	–2.5

*Increase in leaching rates (compared to the controls) following management measures (that is, removal of biomass and humus horizons; calculation of increased leaching rates, see text).

**Calculated by dividing the net output by the duration of the management cycle (grazing: 1 year, mowing and prescribed burning: 10 years, sod cutting: 30 years).

Mean values (n = 16 for atmospheric nutrient deposition, n = 40 for aboveground biomass values of the grazing experiment, n = 4 for all remaining values).

Input/output flows of N and P due to atmospheric deposition, excrement input (grazing experiment), deposition of ash (burning experiment), leaching, and the removal of biomass/humus horizons due to treatments (for the sake of clarity in this table, SDs are not repeated here as these values have already been mentioned in the text and in Figures 1 and 2; data on N flows from Härdle and others 2006, Fottner and others 2007).

Annual net output (kg ha⁻¹ y⁻¹) = [nutrient removal due to biomass and soil removal (–ash deposition in the burning experiment) + increased leaching]/management cycle (grazing: 1 year, mowing and prescribed burning: 10 years, sod-cutting: 30 years).

Medium-Term Management Impacts on N and P Pools

To assess management impacts on nutrient pools in the medium term, we calculated the “relative net input/output flow” of N and P (according to Olde Venterink and others 2002), expressed as the 10-year net input/output flow of N and P (see Table 2) in percentage of the sizes of (i) the N and P pools of the topsoil (that is, humus horizons = organic layer + albic horizon) and (ii) the total N and P pools (that is, humus horizons + spodic horizon; see Table 1). Results of the first calculation are helpful to interpret short-term

changes of the nutritional status of *Calluna* due to changes in nutrient pools, because *Calluna* roots are mainly located in the humus horizons (Genney and others 2002). The second calculation may help to assess medium-term ecosystem responses to unbalanced N and P budgets. In the calculation of total nutrient pools we omitted the pools of the sandy bedrock due to the absence of plant roots in this horizon. In addition, nutrients leached into the bedrock were considered as ecosystem loss (Schmidt and others 2004). For the calculation of nutrient balances (Table 2) we assumed that deposition rates remain unchanged for the subsequent years.

Statistics

Comparisons of nutrient measurements for atmospheric deposition, leaching rates, aboveground biomass and soils were carried out using one-way ANOVA (SPSS 15.0; SPSS Inc., Chicago, IL).

Leaching data were log-transformed, and the remaining data arcsin-transformed prior to ANOVA and the calculation of means and SD.

RESULTS

Pre-Management N and P Pools

Aboveground biomass N and P pools were low compared to soil N and P pools (Table 1). They were highest in the spodic horizon of plots destined for burning (up to 2008.5 kg ha⁻¹ for N and 194.6 kg ha⁻¹ for P; Table 1). N:P ratios were highest in the organic layer (24.5–31.3) and amounted to 13.3–16.4 in the aboveground biomass (pre-treatment values).

Nutrient Inputs (Atmospheric Deposition and Excrement)

Deposition rates for N and P did not differ significantly between the 16 bulk deposition samplers (that is, $P > 0.05$). Atmospheric deposition was therefore considered to be equal for all of the experimental sites. N input amounted to 22.8 kg ha⁻¹ y⁻¹ (SD = 0.8; Table 2). P deposition was 0.3 kg ha⁻¹ y⁻¹ (SD = 0.1).

In the grazing experiment total N and P inputs from excrement (consisting of feces and urine) were 3.5 kg ha⁻¹ y⁻¹ and 0.2 kg ha⁻¹ y⁻¹, respectively (Table 2).

Management Effects on N and P Pools in Aboveground Biomass and Soil

The annual N and P output from sheep grazing was 25.6 kg ha⁻¹ y⁻¹ and 1.9 kg ha⁻¹ y⁻¹, respectively (Figure 1; Table 2). Aboveground biomass-N removed as a result of the other treatments ranged from 96.8 kg ha⁻¹ (mown subplots) to 121.6 kg ha⁻¹ (sod-cut subplots). P output ranged between 7.1 kg ha⁻¹ and 8.0 kg ha⁻¹.

Total nutrient removal was highest in the sod-cut subplots. The N store in the organic layer amounted to 934.5 kg ha⁻¹. In the albic horizon, where the N store exceeded the value of the organic layer, 626.5 kg N ha⁻¹ were removed by sod-cutting. In our experiment, this corresponded to 36% of the total N store in the albic horizon. In the burning experiment, N and P stores of the organic layer increased (by 5.2 kg ha⁻¹ and 6.4 kg ha⁻¹, respectively) due to the deposition of ash.

N and P Loss by Leaching

N and P loss attributable to leaching significantly increased in the burned and the sod-cut subplots

(Figure 2). Post-treatment output of N increased by about 2.2 kg ha⁻¹ y⁻¹ and 4 kg ha⁻¹ (first year after burning and sod-cutting, respectively). For neither of the management measures was a significant increase in P leaching found. P leaching ranged between 0.2 kg ha⁻¹ y⁻¹ and 0.4 kg ha⁻¹ y⁻¹ for the controls and 0.2 kg ha⁻¹ y⁻¹ and 0.5 kg ha⁻¹ y⁻¹ for the treatments (Figure 2).

Post-Management Nutritional Status of *Calluna*

Current season's shoots of *Calluna* showed significantly increased N and P contents in the burned subplots (compared to the corresponding controls; $P < 0.001$) 5 years after treatment (Figure 3). In the grazed and mown subplots, the P content of current season's shoots was significantly lower compared to the controls ($P < 0.05$ and $P < 0.01$, respectively). No significant differences were found between the nutritional status of *Calluna* plants that had re-established in the sod-cut subplots compared to plants in the corresponding controls. The N:P ratios of current season's shoots significantly increased in the grazed and mown subplots, and decreased in the subplots subjected to prescribed burning.

Annual Net Input–Output Flows of N and P

Based on the underlying management cycles, annual balances for N and P were negative in the grazed subplots (−1.5 kg ha⁻¹ y⁻¹ and −1.6 kg ha⁻¹ y⁻¹, respectively) and the sod-cut subplots (−38.1 kg ha⁻¹ y⁻¹ and −2.5 kg ha⁻¹ y⁻¹, respectively; Table 2). In the mown and the burned subplots, balances were positive for N, but negative for P. Annual net P loss was lowest in the burned subplots (−0.1 kg ha⁻¹ y⁻¹).

Medium-Term Management Impacts on N and P Pools

Sod-cutting had the strongest effects on both the N and P pools (Table 3). In the sod-cut subplots the total N pool decreased by 9%, and the total P pool by 8%. Sod-cutting, thus, affected total N and P pools at a similar order of magnitude. By contrast, grazing and mowing strongly impacted the P pools (reduction of topsoil pools by 14.1% and 4.7%, respectively), whereas N pools only slightly decreased or even increased (grazed and mown subplots, respectively). Prescribed burning hardly affected both total and topsoil P pools (reduction by 0.3% and 0.7%, respectively), and N pools increased in a similar range as in the mown subplots.

DISCUSSION

Input Flows of N and P

In the study area, deposition rates found for N and P may be considered representative for many landscapes in Europe (Olde Venterink and others

2002; Galloway and others 2004). Our findings confirmed that deposition rates for P are generally low, whereas N deposition may exceed critical load values for many seminatural ecosystems (Bobbink and others 2003). Besides atmospheric nutrient loads, excrement input from animals may consti-

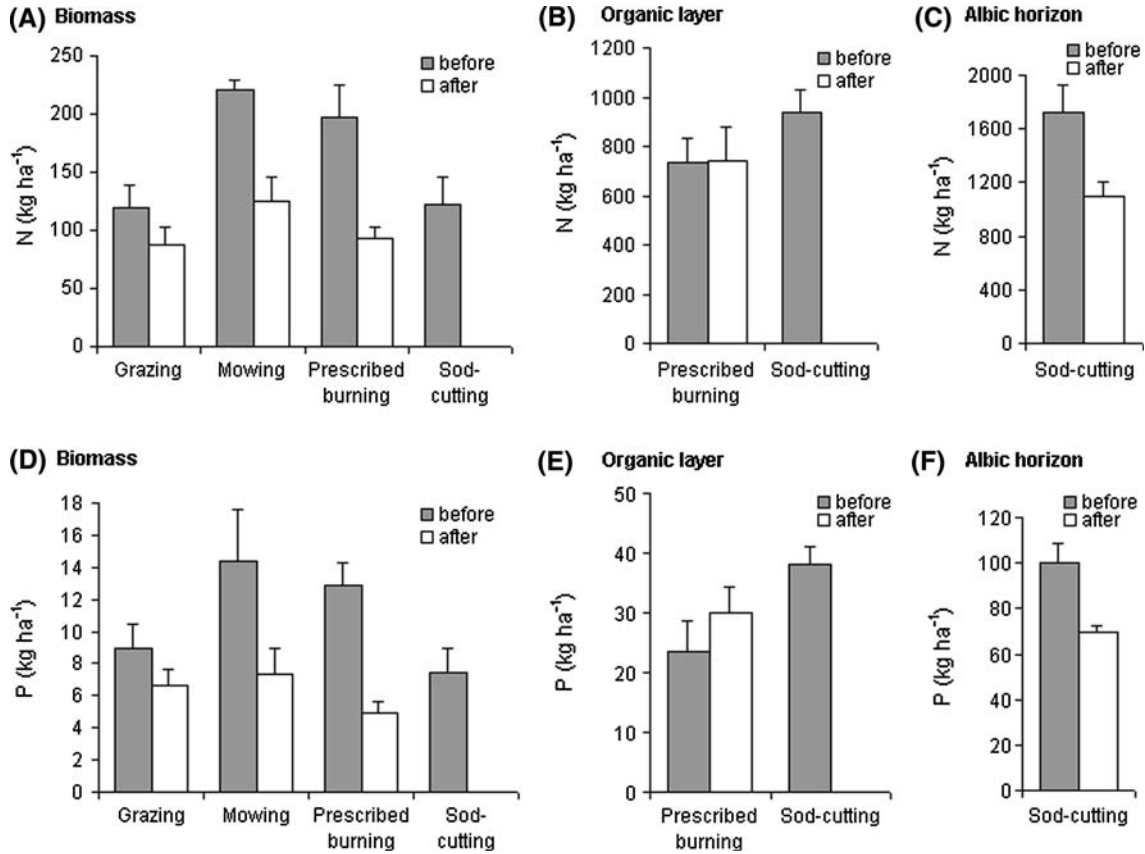


Figure 1. N stores (A–C) and P stores (D–F) in the aboveground biomass, the organic layer, and the albic horizon prior to and after treatments (means + 1 SD; $n = 40$ for the grazing experiment, for all the other experiments $n = 4$). In the burning experiment N and P stores in the organic layer increased due to ash deposition. Sod-cutting removed the entire aboveground biomass and the organic layer. All values refer to the dry weight of samples. With the exception of the increase of the N content in the organic layer after burning (B) all differences (before–after) are significant at the level of $P < 0.05$ (data on N and P stores in the aboveground biomass and humus horizons from Härdtle and others 2006, Fottner and others 2007).

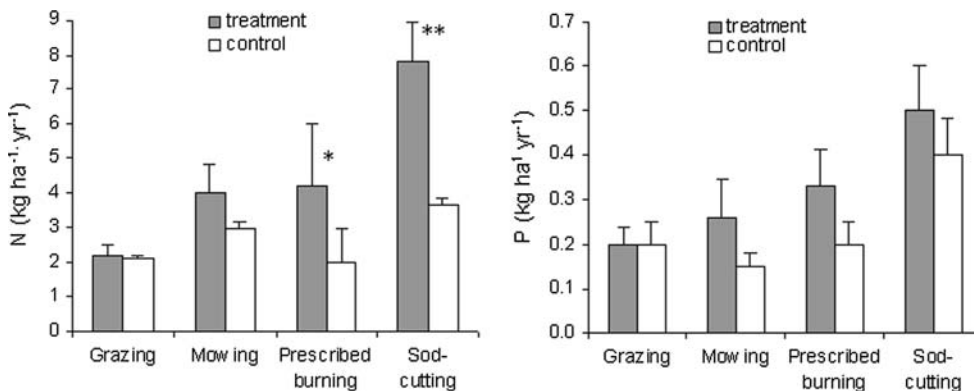


Figure 2. Leaching of N and P in the treated subplots and the corresponding controls (means + 1 SD; $n = 4$; within 1 year after treatment). Asterisks indicate significant differences between treated subplots and the corresponding controls ($*P < 0.05$, $**P < 0.01$).

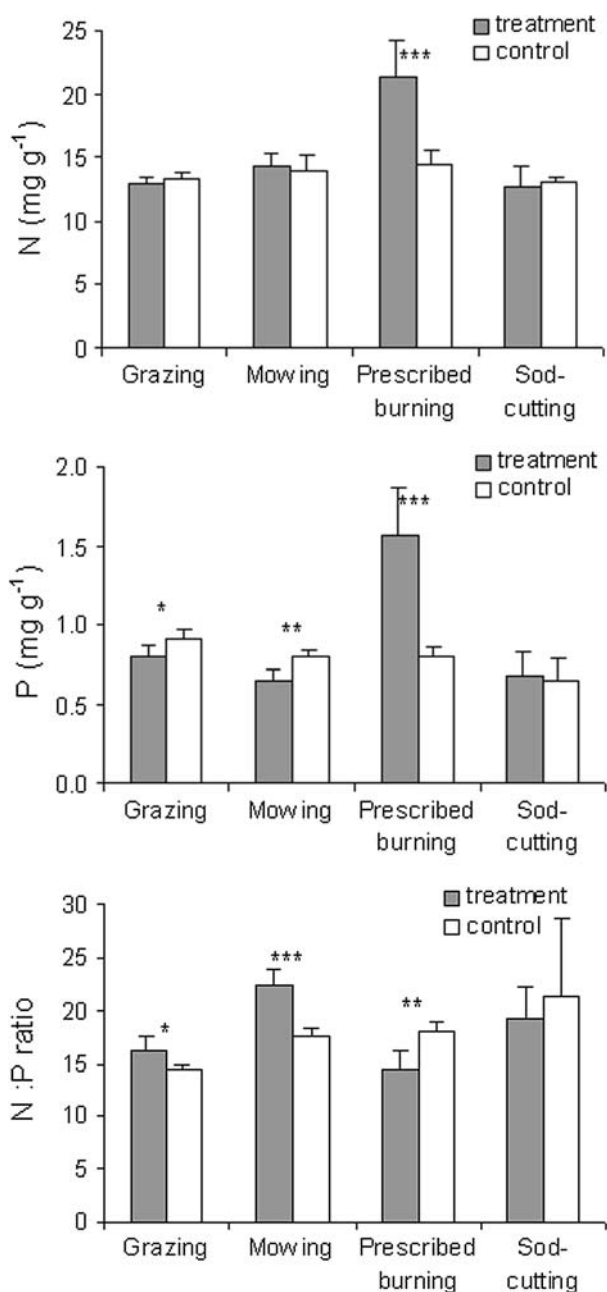


Figure 3. N content, P content, and N:P ratios of current season's shoots of *Calluna vulgaris* in the controls and the treatments (5 years after treatments took place, in the grazing experiment 5 years after continuous grazing); means + 1 SD; $n = 4$; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

tute a source of N and P in grazed seminatural ecosystems (Grant and Armstrong 1993). In our experiment, N and P input from sheep defecation was low due to the low stocking rate (1.1 sheep ha⁻¹; Fottner and others 2007), but inputs may achieve fivefold values in intensively grazed grasslands (Orr

and others 1995). Moreover, excrement input was reduced in our experiment because sheep stayed in a sheepfold at night. This may have lowered input rates up to 50% (compared to an all-day stay of a flock in a heath) due to the defecation behavior of sheep (high defecation rates during the night; Fottner and others 2007).

Output Flows of N and P

Despite the spatial variability in aboveground biomass stores of N and P inherent in heathland ecosystems, our findings are within the ranges given by other authors (Armstrong and others 1997; Terry and others 2004). Net N and P outputs were highest in the sod-cut subplots, because organic layers and the albic horizon were completely or partially removed, respectively. In these humus horizons, N and P stores were about 20 times higher than in the aboveground biomass (see Table 1). The quantities of N removed from the aboveground biomass by burning were similar to the effects obtained by (low-intensity) mowing and sod-cutting. However, high-temperature burns may considerably increase the quantities of burned organic material (Diemont 1996; Nilsen and others 2005). Mowing may result in a greater range of nutrient loss than burning. Because mowing is carried out at different levels of intensity (by varying the cutting height), the quantities of nutrients removed will vary accordingly (Power and others 2001). Thus, nutrient outputs resulting from high-intensity mowing may exceed values found in our study (Terry and others 2004).

Leaching of N and P was elevated within the first year after treatment application (with the exception of the grazed subplots), particularly for N in stands subjected to prescribed burning and sod-cutting. This increase may be due to increasing amounts of percolating soil water, decreased post-management nutrient uptake by plants, and enhanced mineralization rates in the organic layer and the albic horizon (Berendse 1990; Dorland and others 2003). In contrast to N, post-treatment leaching of P was low at all subplots (Table 2). This may be attributable to low deposition rates, generally low concentrations of plant-available P in heath soils, as well as to the sorption behavior of ortho-phosphate in the albic and spodic horizon of podzols (Nielsen and others 2000).

Our calculation of increased post-management leaching rates (Table 2) was based on the simplifying assumption that post-management leaching will decrease linearly in step with vegetation and soil recovery (Niemeyer and others 2007). Despite

Table 3. Relative Net Input/Output Flow of N and P (in %)

Management measure	Grazing	Mowing	Prescribed burning	Sod-cutting
<i>N</i>				
Input/output flows in % of the topsoil pool	−0.9	5.0	3.8	−13.7
Input/output flows in % of the total pool	−0.7	4.1	2.2	−9.0
<i>P</i>				
Input/output flows in % of the topsoil pool	−14.1	−4.7	−0.7	−17.1
Input/output flows in % of the total pool	−5.9	−2.7	−0.3	−8.0

Relative net losses (negative values) or gains (positive values) of N and P within 10 years in % of (i) pre-treatment pools of N and P in topsoil (that is, humus horizons = organic layer + albic horizon) and (ii) the total pre-treatment pools of N and P (that is, of humus horizons + spodic horizon; calculated according to data presented in Tables 1 and 2).

an approximate calculation of increased leaching following management, the total amount of nutrient loss due to leaching was very low compared to output flows caused by the removal of biomass or humus horizons (Table 2). Thus, post-management leaching rates have only minor effects on total N and P outputs, even at sites subjected to high-intensity management. We conclude that the management measures considered here will cause increased nutrient losses by leaching, but overall effects of leaching on N and P budgets are negligible.

Management-Specific Effects on N and P Budgets

As well as management-specific changes in total N and P stores, we found that the ratios of N and P removed were not the same for all measures. Both N:P net input–output ratios and P net-loss were highest in the grazed and mown subplots, and the annual P net-output even exceeded the annual net-output of N under grazing (Table 2). Grazing in particular may severely affect P pools in the long term, as about 14% of the topsoil P pool will be removed within 10 years (Table 3). These findings are attributable to the fact that grazing and mowing only impact the aboveground biomass with its comparatively high P stores. In heaths the vegetation acts as an accumulator for P (Mohamed and others 2007), as expressed by low N:P ratios for the aboveground biomass (13.3–16.4) compared with high ratios in the organic layer (24.5–31.3; Table 1) where most of the fine and coarse roots of *Calluna* are located (Genney and others 2002). As sheep mainly feed on current season's shoots with high P tissue, P output was highest in the grazing experiment (Grant and Hunter 1966). Prescribed burning, in contrast, hardly affected P budgets, because P remained in the system due to ash deposition (Niemeyer and others 2005). Sod-cutting has the

potential to affect N and P stores in particular, because this measure removes organic layers with high stores of these elements. Thus, sod-cutting may also aggravate the availability of P, but this effect may be moderated by P liberation processes from the A- and B-horizon in the long term.

In the face of ongoing atmospheric N loads, only grazing and sod-cutting have the potential to preserve a low-nutrient environment, whereas measures such as mowing and burning cannot prevent a continuous accumulation of N in the long term. However, relative N and P output flows indicate that grazing and mowing may cause an increasing P shortage. This finding corroborates the hypothesis that grazing and mowing can strengthen effects of atmospheric N loads by aggravating the relative availability of P (compare Güsewell 2004).

Calluna Responses to Changes in Nutrient Pools

Management-related shifts in N and P pools were reflected in the nutritional status of *Calluna*. In the grazed and mown subplots, N:P ratios of current season's shoots were significantly increased 5 years after treatment application. This increase was attributable to decreasing P content of shoots, as their N content remained unchanged (Figure 3). It is likely that P losses caused by these measures aggravated the P supply of *Calluna*, resulting in increased shoot N:P ratios. Both N:P ratios (>22) and P contents (<0.7 mg g^{−1}) of shoots indicate that *Calluna* has shifted to P limitation at least at the mown sites, whereas N or N–P co-limitation is likely for the controls (according to data from Güsewell 2004). Increased N and P contents of *Calluna*-shoots at burned sites reflected an improved nutrient supply due to ash deposition and enhanced mineralization rates (Ward and others 2007). For example, significantly lower N:P ratios

of plants at burned sites coincide with high amounts of P in the ash (6.4 kg ha^{-1} ; Table 2). Surprisingly, *Calluna* plants that re-established in the sod-cut subplots showed a similar nutritional status to plants grown in the controls. We assume that mineralization rates increased in the albic horizon after sod-cutting, enabling a sufficient N and P supply of young *Calluna* plants (Dorland and others 2003).

Possible Effects of the Species Composition and Unquantified Nutrient Flows

N and P balances are also affected by the (pre-treatment) species composition and soil chemical processes that have not been quantified in this study. In the mown and burned plots, differences in the nutrient stores of the aboveground biomass and output flows due to biomass removal were low, despite differences in the species composition of mown and burned plots (compare Tables 1 and 2). This indicates that differences in the species cover of these plots only had a slight impact on total output flows. This may apply in particular to plots subjected to sod-cutting, where the removal of aboveground biomass only contributed to about 7% of the total output flows (due to the huge nutrient stores in the soil). Additional sources of uncertainty are N losses caused by denitrification, volatilization of NH_3 , and leaching of particulate organic N. However, these flows may be negligible compared to N losses caused by biomass and soil removal, particularly as regards dry and acid heathland soils (Galloway and others 2004). Interpretation of data must also take into account the fact that small amounts of P may be released from soils due to weathering of minerals (Brady and Weil 2001). However, we assume calculation inaccuracies due to P release by mineral weathering to be low, because our extraction and digestion method of total P embraced inorganic P components released by mineral weathering at least in the short- and medium term (Lamble and Hill 1998). Moreover, the P content of minerals of sandy podzols is low (P content $<0.05\%$; Brady and Weil 2001).

Possible Implications of Unbalanced N–P Budgets in the Long Term

According to a recent overview of heathland fertilization experiments with N or P, in more than 75% of the studies dry heathland vegetation proved to be limited by N (Bobbink and others

2003). It is likely that increasing N availability and P shortage will cause a shift from currently N-limited to more P-limited plant growth (Verhoeven and others 1996). This, in turn, may change the competitive balance between heathland species, because these differ with regard to their N and P requirements (Roem and others 2002). Atmospheric N loads have been suggested as one possible cause of the encroachment of graminoids in many NW European heathlands (Dierssen 1996; Alonso and others 2001; Brys and others 2005). However, there is no evidence to what extent an imbalance of N and P pools caused by the long-term application of grazing or mowing may have contributed to shifts in the species composition. As long as heaths are grazed or mown, the immediate effects of (for example) browsing or cutting may delay an encroachment of grasses, as such effects are superior to those resulting from changing soil chemical properties (Grant and others 1996; Calvo and others 2005). But the latter become apparent when management measures change or are ceased.

Increasing shortage of plant-available P may favor graminoids such as *Molinia caerulea*, because the competitive performance of this species increases with the extent of P limitation, due to its low P requirements (Roem and others 2002). In fertilization experiments with N, for example, *Molinia caerulea* was able to allocate about twice as much biomass to its root systems as *Calluna* (Aerts and others 1991). Arbuscular mycorrhizae, typical of most graminoids, significantly improve the P supply of its host plant, making graminoids more competitive at P-limited sites (Grimoldi and others 2005). In contrast, ericoid mycorrhiza have been shown to improve the N supply of host plants (for example, *Calluna*), thus, providing a competitive advantage at N-limited sites (Sokolovski and others 2002). In addition, *Calluna* concentrates its roots in the organic layer (in contrast to *Molinia caerulea*) and is, thus, restricted in its ability to utilize P stores of the albic and spodic horizon. This low flexibility in root allocation, mainly attributable to the requirements of the ericoid mycorrhizae, makes *Calluna* more susceptible to invasion by grasses (Genney and others 2002).

We assume that our findings also apply to other landscapes of high conservation value, because comparable effects of grazing and mowing on P pools at a focal site have also been documented for grasslands, fens, and mires (Koerselman and others 1990). For example, deleterious effects of grazing on the P supply of plants have also been reported by Vare and others ((1996); understorey of pine forests), Owens and others ((2003); grasslands),

and Moss and others ((1981); heaths). Management effects on N stores mainly depend on grazing pressure and the degree of litter or soil removal through mowing, burning, or sod-cutting (Terry and others 2004). In the study area only grazing and sod-cutting had the potential to compensate for atmospheric N loads. Thus, the maintenance of both a diverse structure and balanced nutrient budgets on a long-term basis requires management schemes that combine high-intensity measures with low-intensity measures.

REFERENCES

- Aerts R. 1993. Biomass and nutrient dynamics of dominant plant species from heathlands. *Geobotany* 20:51–84.
- Aerts R, Boot RGA, van der Aart PJM. 1991. The relation between above- and belowground biomass allocation patterns and competitive ability. *Oecologia* 87:551–9.
- Alonso I, Hartley SE, Thurlow M. 2001. Competition between heather and grasses on Scottish moorlands: interacting effects of nutrient enrichment and grazing regime. *J Veg Sci* 12:249–60.
- Armstrong HM, Gordon IJ, Hutchings NJ, Illius AW, Milne JA, Sibbald AR. 1997. A model of the grazing of hill vegetation by sheep in the UK.2. The prediction of offtake by sheep. *J Appl Ecol* 34:186–207.
- Berendse F. 1990. Organic-matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems. *J Ecol* 78:413–27.
- Bobbink R, Heil GW, Raessen M. 1992. Atmospheric deposition and canopy exchange processes in heathland ecosystems. *Environ Pollut* 75:29–37.
- Bobbink R, Hornung M, Roelofs JGM. 1998. The effects of airborne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *J Ecol* 86:717–38.
- Bobbink R, Ashmore M, Braun S, Fluckiger W, Van den Wyngaert IJJ. 2003. Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update. Achermann B, Bobbink R, Eds. Empirical critical loads for nitrogen. Swiss Agency for the Environment, Forest and Landscape: Environmental Documentation No. 164. pp 43–170.
- Brady NC, Weil RR. 2001. The nature and properties of soils. London: Prentice-Hall. 960 p.
- Brys R, Jacquemyn H, De Blust G. 2005. Fire increases above-ground biomass, seed production and recruitment success of *Molinia caerulea* in dry heathland. *Acta Oecol* 28:299–305.
- Calvo L, Alonso I, Fernandez AJ, De Luis E. 2005. Short-term study of effects of fertilisation and cutting treatments on the vegetation dynamics of mountain heathlands in Spain. *Plant Ecol* 179:181–91.
- Diemont WH. 1996. Survival of Dutch heathlands. IBN Scientific Contribution 1. Wageningen, The Netherlands: IBN-DLO.
- Dierssen K. 1996. Vegetation Nordeuropas. Stuttgart: Ulmer, p 838.
- Dise NB, Stevens CJ. 2005. Nitrogen deposition and reduction of terrestrial biodiversity: evidence from temperate grasslands. *Sci China C Life Sci* 48:720–8.
- Dorland E, Bobbink R, Messelink JH, Verhoeven JTA. 2003. Soil ammonium accumulation after sod cutting hampers the restoration of degraded wet heathlands. *J Appl Ecol* 40:804–14.
- Fottner S, Härdtle W, Niemeyer M, Niemeyer T, von Oheimb G, Meyer H, Mockenhaupt M. 2007. Impact of sheep grazing on nutrient budgets of dry heathlands. *Appl Veg Sci* 10:391–8.
- Galloway JN, Dentener FJ, Capone DG, Boyer EW, Howarth RW, Seitzinger SP, Asner GP, Cleveland CC, Green PA, Holland EA, Karl DM, Michaels AF, Porter JH, Townsend AR, Vorosmarty CJ. 2004. Nitrogen cycles: past, present, and future. *Biogeochemistry* 70:153–226.
- Gauger T, Köble R, Anshelm F. 2000. Kritische Luftschadstoff-Konzentrationen und Eintragsraten sowie ihre Überschreitung für Wald und Agrarökosysteme sowie naturnahe waldfreie Ökosysteme. Studie Umweltbundesamt Berlin, Bericht No. 29785079, Berlin. pp 1–140.
- Genney DR, Alexander IJ, Hartley SE. 2002. Soil organic matter distribution and below-ground competition between *Calluna vulgaris* and *Nardus stricta*. *Funct Ecol* 16:664–70.
- Grant SA, Armstrong HM. 1993. Grazing ecology and the conservation of heather moorland: the development of models as aids to management. *Biodivers Conserv* 2:79–94.
- Grant SA, Hunter RF. 1966. The effects of frequency and season of clipping on the morphology productivity and chemical composition of *Calluna vulgaris*. *L. Hull. New Phytol* 65:125–33.
- Grant SA, Torvell L, Common TG, Sim EM, Small JL. 1996. Controlled grazing studies on *Molinia* grassland: effects of different seasonal patterns and levels of defoliation on *Molinia* growth and responses of swards to controlled grazing by cattle. *J Appl Ecol* 33:1267–80.
- Grasshoff H, Ehrhardt M, Kremling K, Eds. 2002. Methods of seawater analysis. Weinheim: Wiley-VHC.
- Grimoldi AA, Kavanova M, Lattanzi FA, Schnyder H. 2005. Phosphorus nutrition-mediated effects of arbuscular mycorrhiza on leaf morphology and carbon allocation in perennial ryegrass. *New Phytol* 168:435–44.
- Güsewell S. 2004. N:P ratios in terrestrial plants: variation and functional significance. *New Phytol* 164:243–66.
- Güsewell S, Koerselman W, Verhoeven JTA. 2003. Biomass N:P ratios as indicators of nutrient limitation for plant populations in wetlands. *Ecol Appl* 13:372–84.
- Härdtle W, Niemeyer M, Niemeyer T, Assmann T, Fottner S. 2006. Can management compensate for atmospheric nutrient deposition in heathland ecosystems? *J Appl Ecol* 43:759–69.
- Koerselman W, Bakker SA, Blom M. 1990. Nitrogen, phosphorus and potassium budgets for two small fens surrounded by heavily fertilized pastures. *J Ecol* 78:428–42.
- Lamble KJ, Hill SJ. 1998. Microwave digestion procedures for environmental matrices. *Analyst* 123:103–33.
- Lavelle P. 2000. Ecological challenges for soil science. *Soil Sci* 165:73–86.
- Mohamed A, Härdtle W, Jirjahn B, Niemeyer T, von Oheimb G. 2007. Effects of prescribed burning on plant available nutrients in dry heathland ecosystems. *Plant Ecol* 189:279–89.
- Moss R, Welch D, Rothery P. 1981. Effects of grazing by mountain hares and red deer on the production and chemical composition of heather. *J Appl Ecol* 18:487–96.
- Nielsen KE, Hansen B, Ladekarl UL, Nørnberg P. 2000. Effects of N-deposition on ion trapping by B-horizons of Danish heathlands. *Plant Soil* 223:265–76.
- Niemeyer T, Niemeyer M, Mohamed A, Fottner S, Härdtle W. 2005. Impact of prescribed burning on the nutrient balance of heathlands with particular reference to nitrogen and phosphorus. *Appl Veg Sci* 8:183–92.

- Niemeyer M, Niemeyer T, Fottner S, Härdtle W, Mohamed A. 2007. Impact of sod-cutting and choppering on nutrient budgets of dry heathlands. *Biol Conserv* 134:344–53.
- Nilsen LS, Johansen L, Velle LG. 2005. Early stages of *Calluna vulgaris* regeneration after burning of coastal heath in central Norway. *Appl Veg Sci* 8:57–64.
- Olde Venterink H, Pieterse NM, Belgers JDM, Wassen MJ, de Ruiter OD. 2002. N, P and K budgets along nutrient availability and productivity gradients in wetlands. *Ecol Appl* 12:1010–26.
- Orr RJ, Penning PD, Parsons AJ, Champion RA. 1995. Herbage intake and N excretion by sheep grazing monocultures or a mixture of grass and white clover. *Grass Forage Sci* 50:31–40.
- Owens LB, Van Keuren RW, Edwards WM. 2003. Non-nitrogen nutrient inputs and outputs for fertilized pastures in silt loam soils in four small Ohio watersheds. *Agric Ecosyst Environ* 97:117–30.
- Power SA, Barker CG, Allchin EA, Ashmore MR, Bell JNB. 2001. Habitat management: a tool to modify ecosystem impacts of nitrogen deposition? *ScientificWorldJournal* 1:714–21.
- Power SA, Green ER, Barker CG, Bell JNB, Ashmore MR. 2006. Ecosystem recovery: heathland response to a reduction in nitrogen deposition. *Glob Chang Biol* 12:1241–52.
- Roem WJ, Klees H, Berendse F. 2002. Effects of nutrient addition and acidification on plant species diversity and seed germination in heathland. *J Appl Ecol* 39:937–48.
- Schmidt IK, Tietema A, Williams D, Gundersen P, Beier C, Emmett BA, Estiarte M. 2004. Soil solution chemistry and element fluxes in three European heathlands and their responses to warming and drought. *Ecosystems* 7:638–49.
- Sokolovski SG, Meharg AA, Maathuis FJM. 2002. *Calluna vulgaris* root cells show increased capacity for amino acid uptake when colonized with the mycorrhizal fungus *Hymenoscyphus ericae*. *New Phytol* 155:525–30.
- Terry AC, Ashmore MR, Power SA, Allchin EA, Heil GW. 2004. Modelling the impacts of atmospheric nitrogen deposition on *Calluna*-dominated ecosystems in the UK. *J Appl Ecol* 41:897–909.
- Tilman D. 1985. The resource-ratio hypothesis of plant succession. *Am Nat* 125:827–52.
- van Diggelen R, Marrs RH. 2003. Restoring plant communities – introduction. *Appl Veg Sci* 6:106–110.
- Vare H, Ohtonen R, Mikkola K. 1996. The effect and extent of heavy grazing by reindeer in oligotrophic pine heaths in northeastern Fennoscandia. *Ecography* 19:245–53.
- Verhoeven JTA, Koerselman W, Meuleman AFM. 1996. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. *Trends Ecol Evol* 11:494–7.
- Ward SE, Bardgett RD, McNamara NP, Adamson JK, Ostle NJ. 2007. Long-term consequences of grazing and burning on northern peatland carbon dynamics. *Ecosystems* 10:1069–83.