

Vegetation control on DOC, DON and DIN concentrations in soil water from a montane system, southern Norway

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Soil water concentrations of dissolved organic carbon (DOC) and nitrogen (DON) may depend on vegetation composition. The objective of the present study was to quantify the concentrations of DOC, DON and dissolved inorganic N (DIN) in soil water below vegetation dominated by *Calluna*, *Molinia* or *Sphagnum*. In addition we investigated the difference in concentrations in water collected with macro rhizons (tension lysimeters) and plate (zero tension) lysimeters. The soil water concentrations of DOC, DON and DIN showed high variability. Concentrations of DOC and DON at the 0–10 cm depth increased in the order *Sphagnum* < *Molinia* < *Calluna* in summer, whereas in late autumn the DOC concentrations were at least as high in soil water below *Molinia* as below *Calluna*. The soil water concentrations of DOC and DON at the 20–30 cm depth increased in the order *Calluna* < *Molinia* < *Sphagnum*. The concentrations of nitrate (NO₃⁻) and, to a lesser degree ammonium (NH₄⁺), generally increased in the following order: *Sphagnum* < *Molinia* < *Calluna*. Generally, vegetation was an important control on C and N release in the studied montane system.

Introduction

Nonforested montane heathland landscapes represent an important ecosystem category in Norway, and are important contributors of nitrogen (N) and carbon (C) export to surface waters and marine systems (Kaste *et al.* 1997, Sjøeng *et al.* 2007, Strand *et al.* 2008). The effects of predicted climate scenarios (increased winter temperature, increased summer and autumn precipitation) on C and N leaching from a montane system were investigated in two field manipula-

tion experiments (Austnes *et al.* 2008, Haaland *et al.* 2008, Kaste *et al.* 2008). The results generally demonstrated that this type of a system was relatively robust, with only small to modest effects of the applied changes in climatic factors on production of dissolved C and N species. However, the spatial and temporal variability in C and N concentrations was large (Stuanes *et al.* 2008). The question regarding the contribution of the vegetation in explaining the C and N patterns was raised, since the ground vegetation composition showed great variability within

short distances (Strand *et al.* 2008). This issue is of interest also in the context of predicted changes in vegetation composition due to N deposition, climate change and land use (Hester *et al.* 1996, Britton *et al.* 2003, Tomassen *et al.* 2004, Whinam and Copson 2006).

Different vegetation composition may give rise to different soil water concentrations of C and N due to the link between vegetation, litter, soil organic matter (SOM) and other soil properties (e.g. Kalbitz *et al.* 2000, Neff and Hooper 2002, Michel *et al.* 2006, Rowe *et al.* 2006). *Calluna vulgaris*, *Molinia caerulea* and *Sphagnum* spp. are major species in montane systems. *Calluna* is an evergreen shrub, whereas *Molinia* is a perennial deciduous grass that produces more above- and below-ground litter (van Vuuren *et al.* 1992). Van Vuuren and van der Eerden (1992) reported that *Calluna* litter contained about twice as much lignin as *Molinia* litter, but the decomposition rate was not found to be different for the two litter qualities. Other studies have shown higher decomposition of *Molinia* litter than of *Erica tetralix* (a dwarf shrub like *Calluna*) litter, i.e. a negative relationship between lignin content and decomposition rate (Berendse *et al.* 1989, van Vuuren *et al.* 1993, van Vuuren and Berendse 1993). Moreover, root biomass turnover has been shown to be lower for *Calluna* than *Molinia* (Aerts *et al.* 1992). *Sphagnum* is a peat forming moss with low litter decomposition rate. This is due to the specific chemistry of the *Sphagnum* litter, the acid environment, and the production of sphagnum acid from living *Sphagnum* cells (Verhoeven and Toth 1995, Scheffer *et al.* 2001). An *in situ* decomposition study conducted in the same field location as in the present study, showed much lower decomposition rate for *Sphagnum* litter than for *Molinia* and *Calluna* litter (L. S. Vestgarden unpubl. data). Differences in litter decomposition will also affect the degradability of the SOM (Neff and Hooper 2002).

The importance of litter and SOM quality for dissolved organic C (DOC) and dissolved organic N (DON) production is largely unknown (Kalbitz *et al.* 2000, Michel *et al.* 2006). More degradable material is likely to give higher dissolved organic matter (DOM) production. For instance a low lignin content has been found to have a positive effect on DOC release (Magill

and Aber 2000). However, if the organic material is very easily degradable, the major part will be completely mineralised, giving low DOM production (Tipping *et al.* 2007). Soil water concentration and export of DOC also depend on the extent to which DOM acts as a C source for the micro organisms (Meyer *et al.* 1987, Judd and Kling 2002). Moisture content, hydrology and surface chemistry of the soil particles are other important controls on the release of DOM (Qualls and Haines 1992, Kalbitz *et al.* 2000, Judd and Kling 2002, Cooper *et al.* 2007). These factors may interact with the effects of vegetation cover and composition. Thus, the overall role of different vegetation on C and N release is largely unclear.

Ammonium (NH_4^+) is generally effectively retained in soils, and nitrate (NO_3^-) concentrations often decrease with the increasing organic C content (e.g. Helliwell *et al.* 2007, Strand *et al.* 2008). As for DOM, microbiology, hydrology and surface chemistry are important controls on the release of dissolved inorganic N (DIN). Plant uptake of NH_4^+ and/or NO_3^- is also an important regulator of the DIN concentrations. *Calluna* prefers NH_4^+ as the N source, while *Molinia* and *Sphagnum* utilise both NH_4^+ and NO_3^- (de Graaf *et al.* 1998, Tomassen *et al.* 2003, Herrmann *et al.* 2005).

Soil water is usually collected by lysimeters. Different types of lysimeters give specific information and have advantages and disadvantages with regard to chemical interactions, installation, operating procedures and lifetime (Zabowski and Ugolini 1990, Giesler *et al.* 1996, Ranger *et al.* 2001, Weihermüller *et al.* 2007). The soil solution type of interest is crucial to the choice of lysimeter. Zero tension lysimeters collect water freely percolating in macropores by gravity, while different tension lysimeters also collect soil water held by capillary forces in finer pores (Marques *et al.* 1996, Ranger *et al.* 2001, Reynolds *et al.* 2004). The soil water collected by zero tension lysimeters is a product of rainfall and throughfall, mineralisation in the upper soil layers and displacement of already existing decomposition products in the soil, whereas the soil water collected by tension lysimeters is to a higher degree affected by soil processes, such as microbial production and vegetation uptake

(Berggren 1999, Blodau and Moore 2002, Reynolds *et al.* 2004).

Increased insight in the release of DOC, DON and DIN to soil water below the major vegetation types in montane systems is required to improve the predictions about the overall C and N export from such areas. Hence, the objective of the present study was to quantify the concentrations of DOC, DON and DIN in soil water collected by tension and zero tension lysimeters below vegetation dominated by *Calluna*, *Molinia* or *Sphagnum*. We hypothesised that: (1) Soil water collected by tension lysimeters has higher concentrations of DOC, DON and DIN than soil water from zero tension lysimeters. (2) Concentrations of DOC and DON in upper soil layers with high and fairly similar content of organic matter will reflect the degradability of the litter and SOM of the dominating vegetation and increase in the following order: *Sphagnum* < *Calluna* ≤ *Molinia*. (3) In deeper soil layers the variation in organic matter content is larger. Hence, the concentrations of DOC and DON will depend more on the content than on the quality of SOM, and increase in the following order: *Calluna* < *Molinia* < *Sphagnum*. (4) The concentrations of DIN depend on the surface chemistry of soil particles and N-uptake preferences by plants, thus NO₃⁻ concentrations increase in the order *Sphagnum* < *Molinia* < *Calluna*, whereas NH₄⁺ is effectively retained in all soils.

Material and methods

Site description

The experimental site is located in a montane area, Storgama, in the Telemark county, southern Norway (59°01'N, 8°32'E, 560 m a.s.l.). Annual precipitation at the nearest meteorological station is 994 mm (1961–1990 average). Generally October is the wettest month (128 mm). The mean annual air temperature (1961–1990) is 5.0 °C, with July being the warmest (15.1 °C) and February being the coldest (−4.8 °C) (Strand *et al.* 2008). Average annual wet deposition of NH₄-N and NO₃-N in the period 2001–2005 was 318 mg m⁻² y⁻¹ and 332 mg m⁻² y⁻¹, respectively (Strand *et al.* 2008). The bedrock is mainly gra-

nitic, considerable areas are bare rock (30%), and the soil cover is generally shallow (Seip *et al.* 1979, Strand *et al.* 2008). There are some scattered, small trees (*Pinus sylvestris* and *Betula pubescens*). The ground vegetation is dominated by *Calluna vulgaris* at well-drained sites, *Molinia caerulea* at wetter sites and by *Sphagnum* spp. at poorly drained sites. The soils below *Calluna* are mainly Lithic Haplorthods, whereas soils below *Molinia* and *Sphagnum* are mainly Lithic Udipsamments and Lithic Haplosaprists, respectively (Strand *et al.* 2008). The thickness of the organic layer varies strongly, but is generally in the range 5–15 cm below *Calluna* and 10–25 cm below *Molinia*. Selected soil characteristics are summarised in Table 1. Three locations with either *Calluna*, *Molinia* or *Sphagnum* domination were chosen for soil water sampling.

Soil water sampling by macro rhizons and plate lysimeters

Soil water was collected monthly from upper (0–9 cm) and lower (> 20 cm) soils by use of macro rhizon soil moisture samplers (Eijkkelkamp, Agrisearch Equipment, Netherlands) (tension lysimeters). The rhizons consist of a 9-cm porous component strengthened by a fibreglass epoxy rod coated with acrylonitrile butadiene styrene. The mean pore size is 0.1 μm and the outer diameter is 4.5 mm. The rhizons have polyvinyl chloride (PVC) tubings (internally lined with polyethylene) with the 1 mm internal diameter. For soil water sampling from lower soil depths, extension tubes and PVC protection pipes were connected to the rhizons. The rhizons were installed in the soil at an angle of about 45°, at deeper soil layers in pre-augered holes. Three (in *Calluna* and *Molinia*) or two (in *Sphagnum*) rhizons were installed at the two depths at three randomly chosen places in each vegetation type, giving a total of 18 rhizons below *Calluna* and *Molinia* and 12 in the more homogenous *Sphagnum* soil. All rhizons were installed in August 2005. Water sampling for this study started in May 2006, and was carried out using 50 ml syringes (= combined vacuum pump and sample container). Water from the three (or two) rhizons at the same depth and site was pooled. Thus, on

each sampling date, three samples from each of the two depths were analysed, i.e. six samples for each vegetation type. In June, a dry period (Strand *et al.* 2008) prevented a total analysis program due to small water volumes.

Plate lysimeters (zero tension lysimeters) were also installed, adjacent to the rhizons. Opposite to the snapshot situation indicated by the rhizons, the lysimeters were installed to show the integrated situation between two sampling occasions. Two plate lysimeters were installed next to each other at the 10 and 30 cm depths (20 cm at one *Sphagnum* site and one *Molinia* site due to exposed bedrock and waterlogging, respectively, at the greater depth) at each of the three sites within each vegetation type. The plate lysimeters, 10 × 20 cm with a 2-cm-high rim, were made from plexiglas. Gravitational soil water from the lysimeters was collected through a 7-mm (inner diameter) open tip coupled to a silicon tube (10 mm inner diameter). Water from the two lysimeters at the same depth was converged and one joint tube was connected to a 2-l sealed glass bottle. The bottles were buried in the soil (~30 cm depth). All bottles were emptied once a month through silicon tubes using a portable manual pump. An additional tube from the bottles ensured influx of air while pumping. The water was filtered through 0.45 μm membrane filters (Millipore) and brought to the laboratory. Water collection started in November 2005, but due to soil disturbance when installing the plate lysimeters, water collected before May 2006 was not analysed.

Chemical analyses

Soil water from the rhizons and the plate lysimeters was analysed for DOC, NH₄-N, NO₃-N and total dissolved N (TDN). DOC was analysed using a total organic C analyser (TOC-V, Shimadzu Scientific Instruments, Inc., Kyoto, Japan). NH₄-N was determined colorimetrically at 655 nm after conversion to 5-aminosalicylate (Stasar II, Gilford Instrument laboratories Inc., Oberlin, Ohio). NO₃-N was reduced to NO₂-N, which was determined colorimetrically at 540 nm after conversion to an azo-compound (Tecator FIAstar 5010/5023/5027/5032, Prabin & Co. AB, Sweden). TDN was oxidized to NO₃-N by peroxodisulphate in alkaline solution and determined as NO₃-N above. DON was calculated as TDN minus (NH₄-N + NO₃-N).

Statistics

Effects of vegetation were tested with the General Linear Model (GLM) procedure, compiling all data from each lysimeter type and soil depth. Tukey's multiple comparisons procedure was performed for all analyses that showed significant effects. Effects of vegetation and depth were also tested using GLM for single dates, but due to large spatial variation there were few significant effects. Correlations between selected parameters were tested using Pearson's correlation analysis. Regression analysis was performed to test the relation between rhizon water and

Table 1. Selected soil characteristics for the different vegetation types. Values are based on $n = 3$ profile descriptions (L. T. Strand unpubl. data). Values in parentheses are standard deviations.

Parameter	Depth	<i>Calluna</i>	<i>Molinia</i>	<i>Sphagnum</i>
C concentrations (%)	0–10 cm	44.3 (6.4)	46.8 (7.1)	46.8 (0.7)
	> 20 cm	5.6 (2.8)	30.2 (24.3)	43.3 (7.4)
N concentrations (%)	0–10 cm	1.6 (0.1)	2.3 (0.2)	2.4 (0.5)
	> 20 cm	0.3 (0.2)	1.8 (1.5)	2.5 (0.2)
Mean C/N ratio (from concentrations)	0–10 cm	27.6	20.2	19.8
	> 20 cm	21.8	16.5	17.5
SOC (g kg ⁻¹)	0–10 cm	445 (185)	420 (311)	458 (294)
	> 20 cm	39 (96)	307 (16)	443 (151)
SON (g kg ⁻¹)	0–10 cm	19 (10)	21 (20)	26 (16)
	> 20 cm	2 (5)	19 (1)	26 (9)
pH	0–10 cm	4.2 (0.2)	4.3 (0.1)	4.3 (0.0)
	> 20 cm	4.8 (0.2)	4.8 (0.1)	4.3 (0.1)

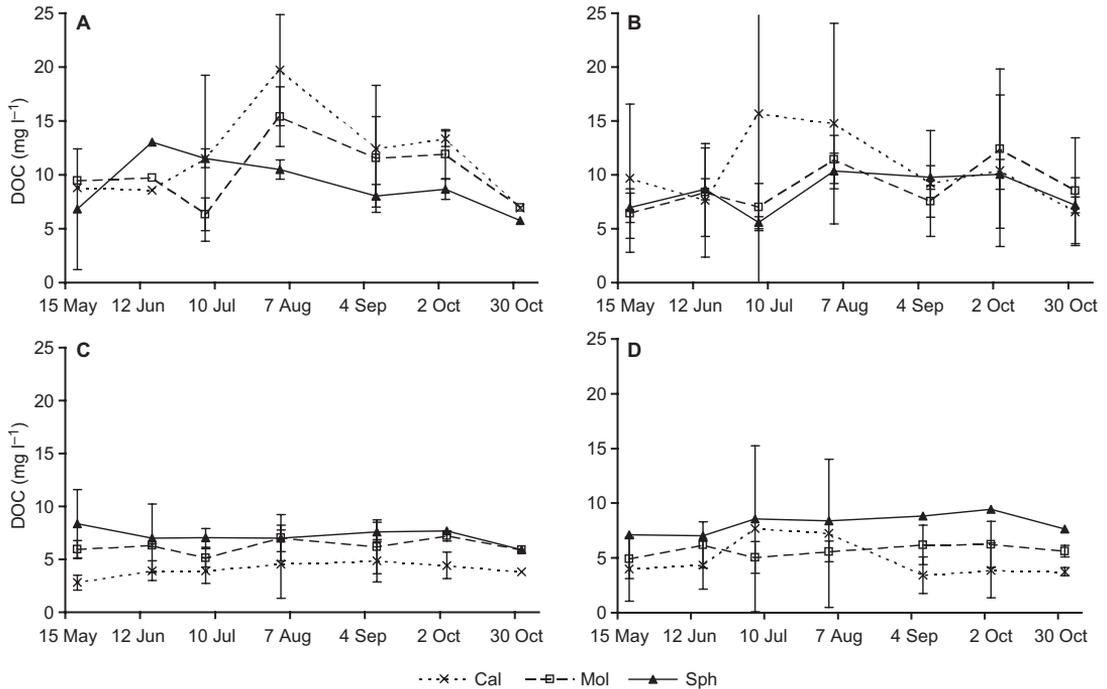


Fig. 1. Mean dissolved organic carbon (DOC) concentrations in soil water collected with (A) rhizons at 0–9 cm depth, (B) plate lysimeters at 0–10 cm depth, (C) rhizons at > 20 cm depth, and (D) plate lysimeters at 20/30 cm depth from May to November 2006. Error bars indicate ± 1 SD. Cal = *Calluna*, Mol = *Molinia*, Sph = *Sphagnum*.

plate lysimeter water for selected parameters. Results were considered significant at $p \leq 0.05$. Minitab Release 14 was used as statistical software.

Results

DOC, DON and DIN

Concentrations of DOC in water of the upper soil layers tended to increase in summer below *Calluna*, and in August the concentrations were significantly higher than below *Sphagnum* (Fig. 1A and B). In autumn, the DOC concentrations in soil water below *Molinia* were at least as high as below *Calluna*. For DON there was also a tendency of increased concentrations during summer, in this case below both *Calluna* and *Molinia* (Fig. 2A and B). Generally, DOC and DON concentrations in the upper soil layers below *Sphagnum* were slightly lower than those below *Calluna* and *Molinia*, and they showed the smallest variation with time. Concentrations of

DOC and DON declined significantly with depth below *Calluna*, and to a lesser extent below *Molinia* (Figs. 1, 2A and C). There was little variation with depth below *Sphagnum*, so that in the deeper soil layers, *Sphagnum* soil water had significantly higher DOC concentrations than *Calluna* soil water (all data compiled; Fig. 1C and D). For the rhizon samples from the deeper soil layers, DOC concentrations below *Sphagnum* were also significantly higher as compared with those below *Molinia* (Fig. 1C), and both DOC and DON concentrations were significantly higher below *Molinia* than below *Calluna* (Figs. 1C and 2C). There was less temporal variation in DOC and DON concentrations at this depth. The DOC/DON ratio increased in late autumn below all vegetation types (Fig. 3). DOC/DON declined with depth in rhizon soil water below *Calluna* (Fig. 3C). The DOC and DON concentrations showed a similar pattern in rhizon and plate lysimeter water, whereas NH_4^+ and NO_3^- concentrations were considerably higher and showed much more variation in water from the plate lysimeters as compared with that from

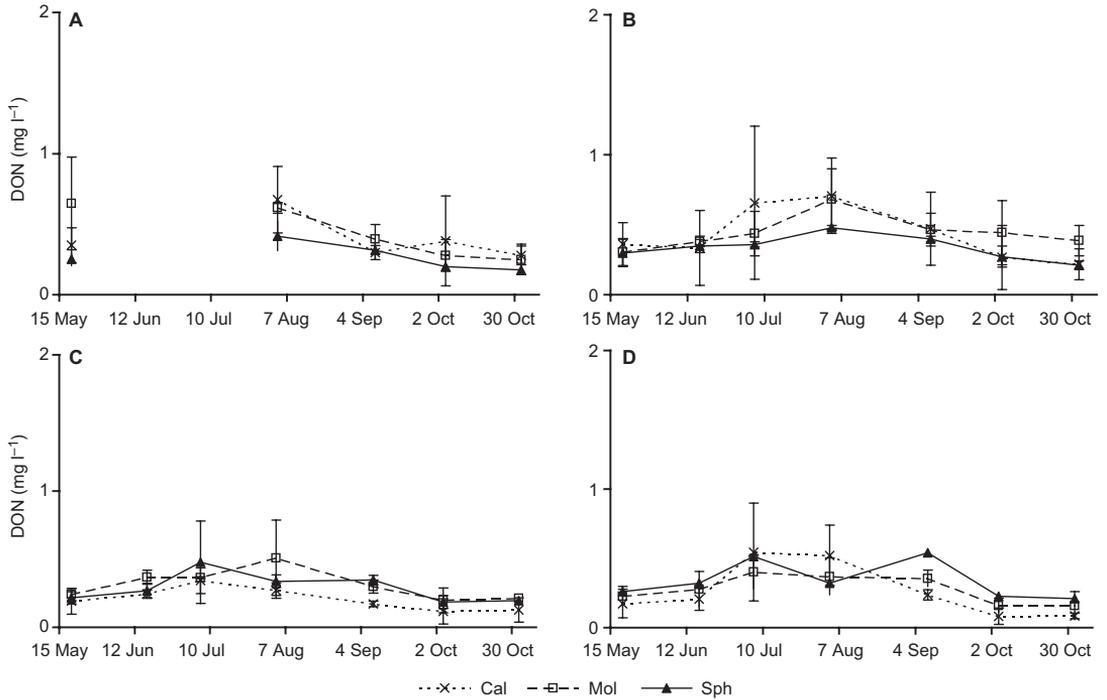


Fig. 2. Mean dissolved organic nitrogen (DON) concentrations in soil water collected with (A) rhizons at 0–9 cm depth, (B) plate lysimeters at 0–10 cm depth, (C) rhizons at > 20 cm depth, and (D) plate lysimeters at 20/30 cm depth from May to November 2006. Error bars indicate ± 1 SD. Cal = *Calluna*, Mol = *Molinia*, Sph = *Sphagnum*.

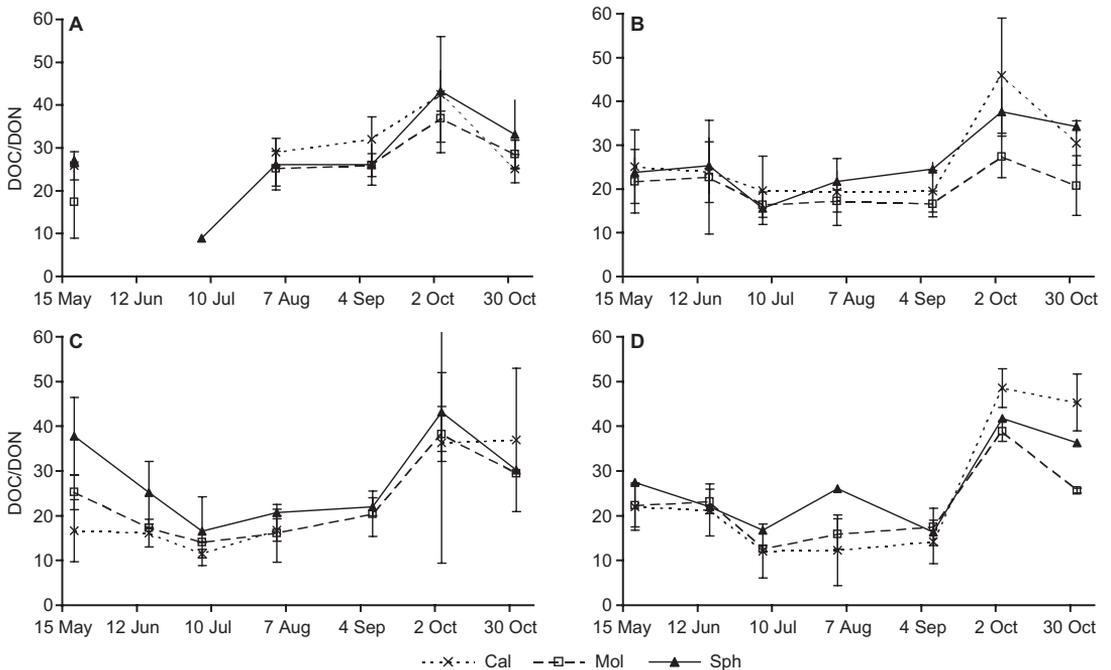


Fig. 3. Mean DOC/DON ratio in soil water collected with (A) rhizons at 0–9 cm depth, (B) plate lysimeters at 0–10 cm depth, (C) rhizons at > 20 cm depth, and (D) plate lysimeters at 20/30 cm depth from May to November 2006. Error bars indicate ± 1 SD. Cal = *Calluna*, Mol = *Molinia*, Sph = *Sphagnum*.

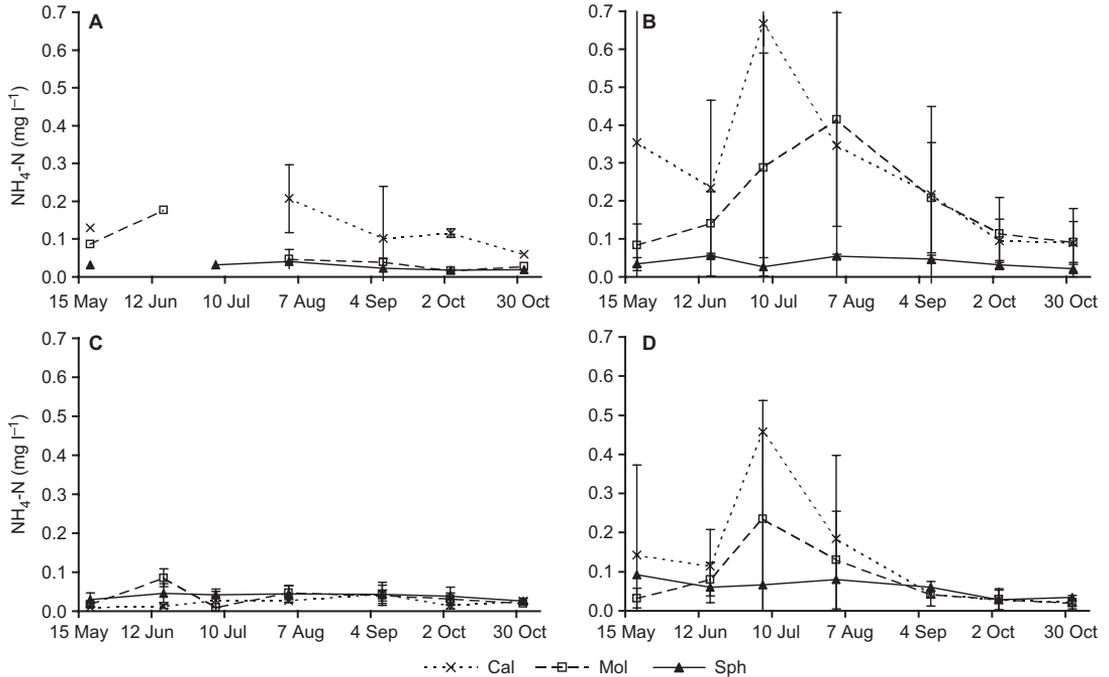


Fig. 4. Mean ammonium ($\text{NH}_4\text{-N}$) concentrations in soil water collected with (A) rhizons at 0–9 cm depth, (B) plate lysimeters at 0–10 cm depth, (C) rhizons at > 20 cm depth, and (D) plate lysimeters at 20/30 cm depth from May to November 2006. Error bars indicate ± 1 SD. Cal = *Calluna*, Mol = *Molinia*, Sph = *Sphagnum*.

the rhizons (Figs. 4 and 5). This pattern was evident throughout the sampling period, but was especially clear during summer. Compiling all data, concentrations of NO_3^- in plate lysimeter soil water were significantly higher below *Calluna* than below the other two vegetation types, at both depths (Fig. 5B and D). The same trend was shown for the rhizons, but differences were significant in May, July and August at > 20 cm only (Fig. 5A and C). Soil water NH_4^+ concentrations below *Calluna* were higher than below *Sphagnum* in the upper soil layers. This was only significant for the rhizon water (Fig. 4A). At the deeper soil layers, the NH_4^+ concentrations in rhizon water were significantly lower below *Calluna* than below *Sphagnum* (all data compiled; Fig. 4C). For the rhizon water, the DIN concentrations below *Molinia* and *Sphagnum* were relatively similar (Figs. 4A and C, 5A and C), whereas for the plate lysimeter water there was a tendency towards higher DIN concentrations below *Molinia* than below *Sphagnum* (Figs. 4B and D, 5B and D). In the same way as for DOC and DON concentrations, the difference in DIN

concentrations in soil water below *Calluna* and *Molinia* decreased in the autumn, at both depths (Figs. 4 and 5).

Correlations

Figure 6 shows the linear relationship between chemistry in soil water sampled by rhizons and plate lysimeters. For DOC and DON concentration, results for the two different water types were significantly correlated ($R^2 = 0.53$ and 0.51 , respectively) (Fig. 6A and B). By contrast, there were poor correlations between results from the two lysimeter types for NH_4^+ and NO_3^- concentration (Fig. 6C and D).

Correlations between different parameters for soil water sampled by either rhizons or plate lysimeters, are summarised in Table 2. The DOC concentration was significantly and positively correlated with the DON and NH_4^+ concentrations. For the plate lysimeters, the DOC concentration was also significantly positively correlated with the NO_3^- concentration, but the

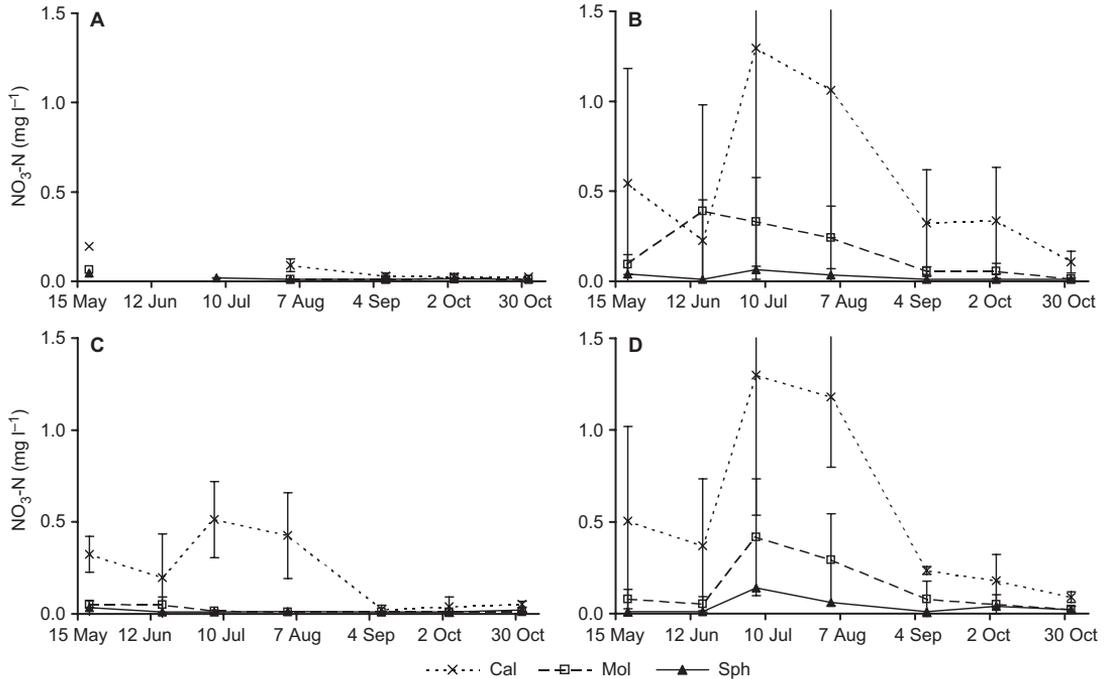


Fig. 5. Mean nitrate ($\text{NO}_3\text{-N}$) concentrations in soil water collected by (A) rhizons at 0–9 cm depth, (B) plate lysimeters at 0–10 cm depth, (C) rhizons at > 20 cm depth, and (D) plate lysimeters at 20/30 cm depth from May to November 2006. Error bars indicate ± 1 SD. Cal = *Calluna*, Mol = *Molinia*, Sph = *Sphagnum*.

correlation between the DON and NO_3^- concentrations was stronger. NH_4^+ and NO_3^- were significantly positively correlated in both types of water.

Discussion

Lysimeter type and the chemistry of the collected water

Comparisons of the zero tension and tension lysimeters most often show higher concentrations of solutes in solution collected by tension lysimeters, since the water is assumed to have more time

to react with the soil in finer pores as compared with the freely draining water (Simmons and Baker 1993, Fernandez *et al.* 1995, Marques *et al.* 1996, Reynolds *et al.* 2004). In the present study, we have to take into account that the two different lysimeter types reflect two different situations regarding time resolution. However, the slightly lower DOC and DON concentrations in rhizon water than in plate lysimeter water corresponded to results reported by Geibe *et al.* (2006), and may be a result of larger residence time and a higher possibility of retention of DOM in the finer pores, from where the rhizons collect water.

The several times greater DIN concentrations in plate lysimeter water than in rhizon water, and

Table 2. Pearson correlations for different soil water results sampled by zero tension lysimeters and macro rhizons (in boldface). $n = 75\text{--}100$, $p \leq 0.05$, ns = not significant.

	DOC	DON	DOC/DON	$\text{NH}_4\text{-N}$
DON	0.77/ 0.75	–	–	–
DOC/DON	ns/ 0.26	–0.37/– 0.32	–	–
$\text{NH}_4\text{-N}$	0.52/ 0.70	0.75/ 0.63	ns/ns	–
$\text{NO}_3\text{-N}$	0.36/ns	0.64/ 0.79	ns/ns	0.80/ 0.34

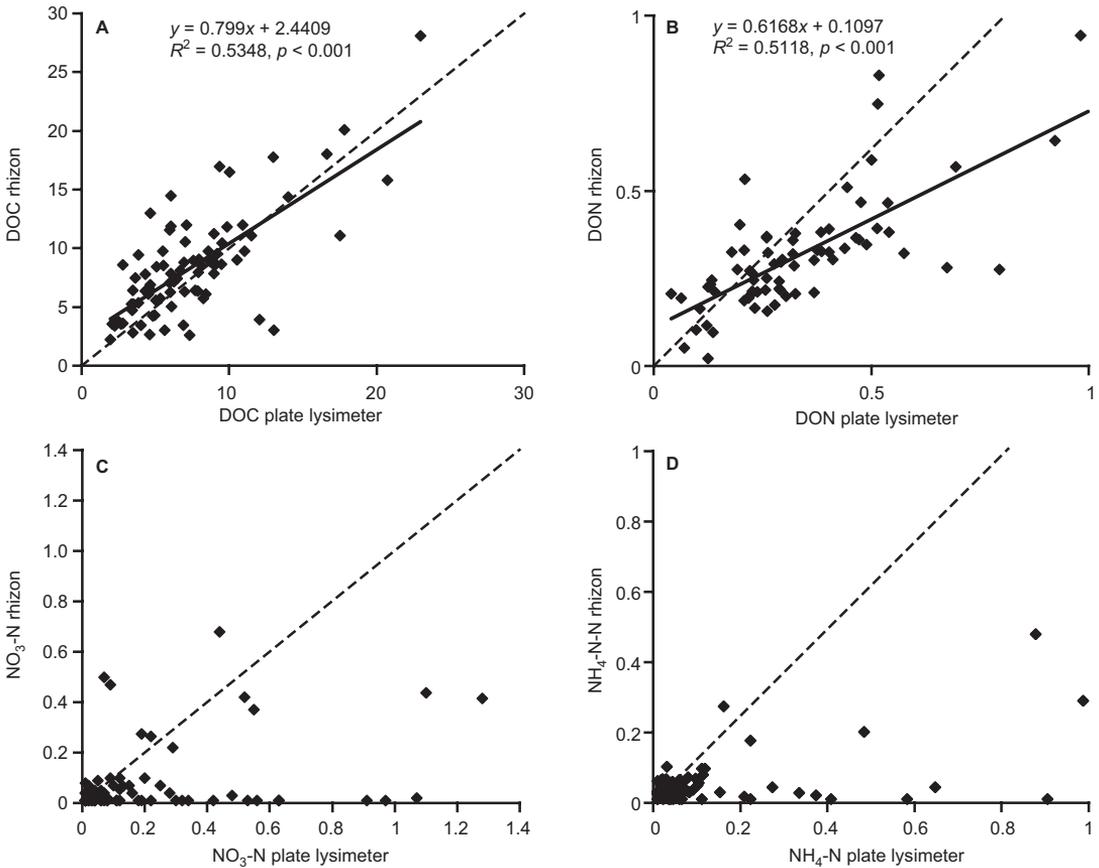


Fig. 6. Correlations between macro rhizon (tension) lysimeter results and plate (zero tension) lysimeter results for (A) DOC, (B) DON, (C) NO₃-N and (D) NH₄-N concentrations. Linear regressions lines and coefficients of determination (R^2) are given. The dashed lines indicate the 1:1 ratio.

the poor correlations between the two types of soil water for *Calluna* and *Molinia* sites, contradicted what we hypothesised (hypothesis 1). Our initial explanation was that mineralisation occurred before the glass containers were emptied and the water filtered. Both NH₄⁺ and NO₃⁻ concentrations are known to be easily altered by biological processes (Ross and Bartlett 1990, Weihermüller *et al.* 2007), and especially at high temperatures during summer it is possible that this could occur. However, DON did not show any corresponding decrease as compared with that in rhizon water. On the contrary, it showed a slight increase, and DON was positively correlated with NO₃⁻. Even though the differences between the two solution types were considerable, the concentrations in water from plate lysimeters were not unrealistically high as compared

with those of the precipitation in the area (Strand *et al.* 2008). Thus the most plausible explanation for the high concentrations of DIN in the zero tension water as compared with that in the rhizon water is that the freely percolating water was less affected by soil processes, due to short residence time and the fact that the root systems and associated mycorrhiza only to a low degree develop in macropores (Ranger *et al.* 2001).

Vegetation control on DOC and DON

The higher DOM production in the upper soil layers below *Calluna* than below *Molinia* during summer contradicted what we hypothesised (hypothesis 2). However, it corresponds with Strand *et al.* (2002), who reported higher soil

water concentrations of DOC below *Calluna* than below *Molinia* in a lysimeter experiment with soil from the same area as in the present study. Generally, one could expect higher DOM production below *Molinia* due to the lower lignin content of the litter (van Vuuren and van der Eerden 1992, Magill and Aber 2000) and the possibly higher degradability (Berendse *et al.* 1989, Aerts *et al.* 1992, van Vuuren *et al.* 1993, van Vuuren and Berendse 1993). However, if litter and SOM below *Molinia* is more degradable, the lower DOM production in summer may be due to a higher degree of complete mineralisation (Gödde *et al.* 1996, Tipping *et al.* 2007). A higher degradability of the *Molinia* soil may be supported by the lower C/N ratio as compared with that in the *Calluna* soil (Table 1), as a low C/N ratio is commonly associated with higher decomposition rates (Gödde *et al.* 1996, Kalbitz *et al.* 2000). However, a low C/N ratio can also be associated with low decomposition rates, if it is an indication of highly decomposed material (Gödde *et al.* 1996).

The similar or higher DOC and DON concentrations in the upper soil layers below *Molinia* as compared with those below *Calluna* in late autumn (Oct.–Nov.) were in line with hypothesis 2. It also corresponds with results from a freezing–thawing laboratory study on soil cores (upper 15 cm) from the same area. In that study, the *Molinia* soil gave higher concentrations and fluxes of DOC and DON than the *Calluna* and *Sphagnum* soils (Vestgarden and Austnes 2009). These results are more in line with what could be expected if SOM and litter below *Molinia* is more degradable (*see above*). It is possible that the higher degradability is more strongly reflected in DOM production in late autumn and winter, as the relative contribution of DOM (compared with CO₂) to the C released during decomposition has been found to be higher at lower temperatures (Gödde *et al.* 1996).

The decline in DOC and DON concentrations with depth below *Calluna*, can be related to the marked decrease in organic matter content with depth in this soil (Table 1) (Tipping *et al.* 1999). The decreased DOC/DON ratio with depth could be due to older and more decomposed organic matter in the deeper than the upper soil layers (Schlesinger 1997) or a weaker adsorption of

DOM with low DOC/DON ratio (Kalbitz *et al.* 2000).

Sphagnum was an important source for DOC and DON release. At the 10 cm depth the C content was ~45% for all vegetations. Given the special properties and slower decomposition of organic matter derived from *Sphagnum* (Verhoeven and Toth 1995, Scheffer *et al.* 2001, L. S. Vestgarden unpubl. data), one could expect markedly lower DOC and DON concentrations below *Sphagnum* than below *Calluna* and *Molinia* at this depth. However, the concentrations were only slightly lower below *Sphagnum*. The higher DON, and particularly DOC, concentrations at the > 20 cm depth below *Sphagnum* as compared with those below the other vegetations, supported hypothesis 3 and was probably due to the higher C and N contents below *Sphagnum* (Table 1).

The summer peaks of DOC and DON in our study correspond to the seasonal pattern of total organic carbon and nitrogen in the runoff from small headwater catchments in the same area (Strand *et al.* 2008). DOC and DON are often found to be higher in summer than winter, due to enhanced microbial activity and/or low water fluxes (Cronan and Aiken 1985, Currie *et al.* 1996, Scott *et al.* 1998, Kalbitz *et al.* 2000). The increase in DOC/DON ratio in late autumn may be a result of the DOM being less decomposed than in summer, when the temperature is higher, or a result of increased input of fresh litter (Currie *et al.* 1996).

Vegetation control on concentrations of NH₄⁺ and NO₃⁻

The higher concentrations of inorganic N for *Calluna* as compared with those for *Molinia* were most evident for NO₃⁻. Since this vegetation effect was not significant for rhizon water, hypothesis 4 was only partly supported. A similar vegetation effect on NO₃⁻ concentrations was found in the above-described freezing–thawing incubation experiment by Vestgarden and Austnes (2009). Hence a higher NO₃⁻ retention, a lower nitrification and/or a more extensive denitrification may have occurred below *Molinia* and *Sphagnum* as compared with that below *Calluna*. Moreover, *Calluna* prefers NH₄⁺ as the N

source, whereas *Molinia* and *Sphagnum* utilise/absorb both NH_4^+ and NO_3^- (de Graaf *et al.* 1998, Tomassen *et al.* 2003, Herrmann *et al.* 2005). This may also contribute to a higher NO_3^- concentration below *Calluna* than below *Molinia* and *Sphagnum*.

To get rough estimates of N fluxes, we combined the plate lysimeter NO_3^- , NH_4^+ and DON concentrations with the runoff data (continuously logged) from an adjacent small (48 m²) and shallow (mean depth 12 cm, max. depth 34 cm) headwater catchment (Strand *et al.* 2008). Since detailed water fluxes for the different vegetation spots are lacking, the estimates only indicate potential fluxes, and the differences between vegetations are results of differences in concentration only. The TDN flux estimates from the 10 cm depth for the period May–November were 467, 362 and 194 mg N m⁻² for *Calluna*, *Molinia* and *Sphagnum*, respectively. From the 20 cm depth, corresponding values were 313, 204 and 222 mg N m⁻². NO_3^- -N contributed 54% to the TDN loss below *Calluna* (20 cm). Thus, with an annual wet deposition of 332 mg NO_3^- -N m⁻² in the area (average for the period 2001–2005) (Strand *et al.* 2008), the NO_3^- -N export from the 20 cm depth below *Calluna* (May to November) corresponded to 50% of the deposition input. Summing NO_3^- and NH_4^+ gives an output equal to 32% of the annual wet deposition of inorganic N (650 mg m⁻²) (Strand *et al.* 2008) during summer and autumn. Corresponding values for *Molinia* and *Sphagnum* based on the same approach are 10% and 6%. In addition to the already-mentioned limitations of the flux estimates, our results include neither winter nor spring, which may be important contributors, and also to some degree may give different patterns concerning the vegetation control of the concentrations and fluxes of N (Vestgarden and Austnes 2009).

Possible consequences of vegetation changes on DOM and DIN release from montane areas

During the last decades, a replacement of vegetation adapted to low N-input with more nitrophilous species has been driven by increased N

deposition and nutrient availability (Milne and Hartley 2001). This has been especially evident for nutrient-poor heathlands, where *Calluna vulgaris* to a large extent has been replaced by grasses such as *Molinia caerulea* and *Deschampsia flexuosa* (Heil and Bruggink 1987, Chambers *et al.* 1999, Britton *et al.* 2003). Increased nutrient availability and higher sensitivity to frost and damage by the heather beetle *Lochmaea suturalis* (Thompson) is probably the key to these specific changes (Aerts 1989, Lee 1998, Carroll *et al.* 1999, Sæbø *et al.* 2001, Roem *et al.* 2002). Increased grazing may also give replacement of *Calluna* moorland with *Molinia*-dominated grassland (Hester *et al.* 1996).

Increased N-deposition has also changed species composition in ombrotrophic bogs with invasion of grasses as *Molinia* when the *Sphagnum* layer has reached a maximum N content and started leaching of N to the roots of vascular plants (Tomassen *et al.* 2004). Declined size of *Sphagnum* beds may also be due to higher temperatures and lower precipitation (Whinam and Copson 2006).

Our results indicate that a shift of *Calluna* to *Molinia* will have greater effects on DIN production than on DOM production, since the soil water NO_3^- concentrations in soil water were 60%–70% higher below *Calluna* than *Molinia* during summer/autumn. Hydrology and possible hydrologic changes will play an important role for the effects of a change from *Calluna* towards *Molinia* domination. Where the water flows at shallow depths, our results indicate no change, or a slight reduction of DOM concentrations with the given vegetation shift, whereas at sites with the main water flow occurring deeper than 20–30 cm, DOM, and especially DOC concentrations may increase if *Molinia* replaces *Calluna*.

Invasion of *Molinia* on *Sphagnum* beds is not likely to cause major changes in soil water DOM and DIN concentrations. However, where water flows in deeper soil layers, one could expect decreased DOM concentrations.

Conclusions

Soil water collected by tension (rhizons) had lower concentrations of DOC, DON and DIN

than water collected by zero tension (plate) lysimeters. This was opposite to what we hypothesised (hypothesis 1). The explanation was probably that the rhizons collect water from the finer soil pores, where the residence time is longer and the possibility of retention is higher. The concentrations of DOC and DON in upper soil layers with high and fairly similar content of organic matter was lower below *Sphagnum* than below *Calluna* and *Molinia*. This was probably due to lower degradability of *Sphagnum* litter and SOM, but the difference was not as marked as expected. Higher concentrations were observed below *Calluna* than *Molinia*, especially during summer, most likely due to a higher degree of complete mineralisation to CO₂ below *Molinia*. Hypothesis 2, that the concentrations would increase in the order *Sphagnum* < *Calluna* ≤ *Molinia* was thus only partly supported. The concentrations of DOC and DON in deeper soil layers increased in the order *Calluna* < *Molinia* < *Sphagnum*. This corresponds to the variation in organic content, and the results are thus in line with hypothesis 3. Soil water concentrations of inorganic N increased in the order *Sphagnum* < *Molinia* < *Calluna* for the plate lysimeters. This was most evident for NO₃⁻. Generally NO₃⁻ concentrations were higher than the concentrations of NH₄⁺, indicating that NH₄⁺ was more effectively retained in the soils. Thus, hypothesis 4 was partly supported.

The vegetation composition, as well as possible changes in this, seem to be important controls on the present and future C and N release in our and other similar heterogeneous montane systems.

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References

- Aerts R. 1989. Above-ground biomass and nutrient dynamics of *Calluna vulgaris* and *Molinia caerulea* in a dry heathland. *Oikos* 56: 31–38.
- Aerts R., Bakker C. & de Caluwe H. 1992. Root turnover as determinant of the cycling of C, N, and P in a dry heathland ecosystem. *Biogeochemistry* 15: 175–190.
- Austnes K., Kaste Ø., Vestgarden L.S. & Mulder J. 2008. Manipulation of snow in small headwater catchments at Storgama, Norway: effects on leaching of total organic carbon and total organic nitrogen. *Ambio* 37: 38–47.
- Berendse F., Bobbink R. & Rouwenhorst G. 1989. A comparative study on nutrient cycling in wet heathland ecosystems. II. Litter decomposition and nutrient mineralization. *Oecologia* 78: 338–348.
- Berggren D. 1999. The solubility of aluminium in two Swedish acidified forest soils: an evaluation of lysimeter measurements using batch titration data. *Water Air Soil Pollut.* 114: 137–153.
- Blodau C. & Moore T.R. 2002. Macroporosity affects water movement and pore water sampling in peat soils. *Soil Sci.* 167: 98–109.
- Britton A., Marrs R., Pakeman R. & Carey P. 2003. The influence of soil type, drought and nitrogen addition on interactions between *Calluna vulgaris* and *Deschampsia flexuosa*: implications for heathland regeneration. *Plant Ecol.* 166: 93–105.
- Carroll J.A., Caporn S.J.M., Cawley L., Read D.J. & Lee J.A. 1999. The effect of increased deposition of atmospheric nitrogen on *Calluna vulgaris* in upland Britain. *New Phytol.* 141: 423–431.
- Chambers F.M., Mauquoy D. & Todd P.A. 1999. Recent rise to dominance of *Molinia caerulea* in environmentally sensitive areas: new perspectives from palaeoecological data. *J. Appl. Ecol.* 36: 719–733.
- Cooper R., Thoss V. & Watson H. 2007. Factors influencing the release of dissolved organic carbon and dissolved forms of nitrogen from a small upland headwater during autumn runoff events. *Hydrol. Proc.* 21: 622–633.
- Cronan C.S. & Aiken G.R. 1985. Chemistry and transport of soluble humic substances in forested watersheds of the Adirondack Park, New York. *Geochim. Cosmochim. Acta* 49: 1697–1705.
- Currie W.S., Aber J.D., McDowell W., Boone R.D. & Magill A.H. 1996. Vertical transport of dissolved organic C and N under long-term N amendments in pine and hardwood forests. *Biogeochemistry* 35: 471–505.
- de Graaf M.C.C., Bobbink R., Roelofs J.G.M. & Verbeek P.J.M. 1998. Differential effects of ammonium and nitrate on three heathland species. *Plant Ecol.* 135: 185–196.
- Fernandez I.J., Lawrence G.B. & Son Y.H. 1995. Soil-solution chemistry in a low-elevation spruce–fir ecosystem, Howland, Maine. *Water Air Soil Pollut.* 84: 129–145.
- Geibe C.E., Danielsson R., van Hees P.A.W. & Lundström U.S. 2006. Comparison of soil solution chemistry sampled by centrifugation, two types of suction lysimeters and zero-tension lysimeters. *Appl. Geochem.* 21: 2096–2111.
- Giesler R., Lundström U.S. & Grip H. 1996. Comparison of soil solution chemistry assessment using zero-tension lysimeters or centrifugation. *Eur. J. Soil Sci.* 47: 395–405.
- Gödde M., David M.B., Christ M.J., Kaupenjohann M. & Vance G.F. 1996. Carbon mobilization from the forest floor under red spruce in the northeastern USA. *Soil Biol. Biochem.* 28: 1181–1189.
- Haaland S., Austnes K., Kaste Ø., Mulder J., Riise G., Vest-

- garden L.S. & Stuanes A. 2008. Manipulation of precipitation in small headwater catchments at Storgama, Norway: effects on leaching of organic carbon and nitrogen species. *Ambio* 37: 48–55.
- Heil G.W. & Bruggink M. 1987. Competition for nutrients between *Calluna vulgaris* (L.) Hull and *Molinia caerulea* (L.) Moench. *Oecologia* 73: 105–108.
- Helliwell R.C., Coull M.C., Davies J.J.L., Evans C.D., Norris D., Ferrier R.C., Jenkins A. & Reynolds B. 2007. The role of catchment characteristics in determining surface water nitrogen in four upland regions in the UK. *Hydrol. Earth Sys. Sci.* 11: 356–371.
- Herrmann M., Pust J. & Pott R. 2005. Leaching of nitrate and ammonium in heathland and forest ecosystems in north-west Germany under the influence of enhanced nitrogen deposition. *Plant Soil* 273: 129–137.
- Hester A.J., Miller D.R. & Towers W. 1996. Landscape scale vegetation change in the Cairngorms, Scotland, 1946–1988: implications for land management. *Biol. Cons.* 77: 41–51.
- Judd K.E. & Kling G.W. 2002. Production and export of dissolved C in arctic tundra mesocosms: the role of vegetation and water flow. *Biogeochemistry* 60: 213–234.
- Kalbitz K., Solinger S., Park J.H., Michalzik B. & Matzner E. 2000. Controls on the dynamics of dissolved organic matter in soils: a review. *Soil Sci.* 165: 277–304.
- Kaste Ø., Austnes K., Vestgarden L.S. & Wright R.F. 2008. Manipulation of snow in small headwater catchments at Storgama, Norway: effects on leaching of inorganic nitrogen. *Ambio* 37: 29–37.
- Kaste O., Henriksen A. & Hindar A. 1997. Retention of atmospherically-derived nitrogen in subcatchments of the Bjerkreim river in southwestern Norway. *Ambio* 26: 296–303.
- Lee J.A. 1998. Unintentional experiments with terrestrial ecosystems: ecological effects of sulphur and nitrogen pollutants. *J. Ecol.* 86: 1–12.
- Magill A.H. & Aber J.D. 2000. Dissolved organic carbon and nitrogen relationships in forest litter as affected by nitrogen deposition. *Soil Biol. Biochem.* 32: 603–613.
- Marques R., Ranger J., Gelhaye D., Pollier B., Ponette Q. & Goedert O. 1996. Comparison of chemical composition of soil solutions collected by zero-tension plate lysimeters with those from ceramic-cup lysimeters in a forest soil. *Eur. J. Soil Sci.* 47: 407–417.
- Meyer J.T., Edwards R.T. & Risley R. 1987. Bacterial growth on dissolved organic carbon from a blackwater river. *Microb. Ecol.* 13: 13–29.
- Michel K., Matzner E., Dignac M.F. & Kögel-Knabner I. 2006. Properties of dissolved organic matter related to soil organic matter quality and nitrogen additions in Norway spruce forest floors. *Geoderma* 130: 250–264.
- Milne J.A. & Hartley S.E. 2001. Upland plant communities — sensitivity to change. *Catena* 42: 333–343.
- Neff J.C. & Hooper D.U. 2002. Vegetation and climate controls on potential CO₂, DOC and DON production in northern latitude soils. *Global Change Biol.* 8: 872–884.
- Qualls R.G. & Haines B.L. 1992. Biodegradability of dissolved organic-matter in forest throughfall, soil solution, and stream water. *Soil Sci. Soc. Am. J.* 56: 578–586.
- Ranger J., Marques R. & Jussy J.H. 2001. Forest soil dynamics during stand development assessed by lysimeter and centrifuge solutions. *For. Ecol. Manage.* 144: 129–145.
- Reynolds B., Stevens P.A., Hughes S. & Brittain S.A. 2004. Comparison of field techniques for sampling soil solution in an upland peatland. *Soil Use Manage.* 20: 454–456.
- Roem W.J., Klees H. & Berendse F. 2002. Effects of nutrient addition and acidification on plant species diversity and seed germination in heathland. *J. Appl. Ecol.* 39: 937–948.
- Ross D.S. & Bartlett R.J. 1990. Effects of extraction methods and sample storage on properties of solutions obtained from forested podosols. *J. Environ. Qual.* 19: 108–113.
- Rowe E.C., Evans C.D., Emmett B.A., Reynolds B., Helliwell R.C., Coull M.C. & Curtis C.J. 2006. Vegetation type affects the relationship between soil carbon to nitrogen ratio and nitrogen leaching. *Water Air Soil Pollut.* 177: 335–347.
- Sæbø A., Håland Å., Skre O. & Mortensen L.M. 2001. Influence of nitrogen and winter climate stresses on *Calluna vulgaris* (L.) Hull. *Ann. Bot.* 88: 823–828.
- Scheffer R.A., van Logtestijn R.S.P. & Verhoeven J.T.A. 2001. Decomposition of *Carex* and *Sphagnum* litter in two mesotrophic fens differing in dominant plant species. *Oikos* 92: 44–54.
- Schlesinger W.H. 1997. *Biogeochemistry: an analysis of global change*, 2nd ed. Academic Press, San Diego.
- Scott M.J., Jones M.N., Woof C. & Tipping E. 1998. Concentrations and fluxes of dissolved organic carbon in drainage water from an upland peat system. *Environ. Int.* 24: 537–546.
- Seip H.M., Abrahamson G., Gjessing E.T. & Stuanes A. 1979. *Studies of soil-, precipitation- and run-off chemistry in six small natural plots (“mini-catchments”)*. SNSF-project, IR 46/79, Oslo.
- Sjøeng A.M.S., Kaste Ø., Tørseth K. & Mulder J. 2007. N leaching from small upland headwater catchments in southwestern Norway. *Water Air Soil Pollut.* 179: 323–340.
- Simmons K.E. & Baker D.E. 1993. A zero-tension sampler for the collection of soil-water in macropore systems. *J. Environ. Qual.* 22: 207–212.
- Strand L.T., Abrahamson G. & Stuanes A.O. 2002. Leaching from organic matter-rich soils by rain of different qualities: I. Concentrations. *J. Environ. Qual.* 31: 547–556.
- Strand L.T., Haaland S., Kaste Ø. & Stuanes A. 2008. Natural variability in soil and runoff from small headwater catchments at Storgama, Southern Norway. *Ambio* 37: 18–28.
- Stuanes A.O., de Wit H.A., Hole L.R., Kaste Ø., Mulder J., Riise G. & Wright R.F. 2008. Effect of climate change on flux of N and C: air-land-freshwater-marine links: synthesis. *Ambio* 37: 2–7.
- Tipping E., Woof C., Rigg E., Harrison A.F., Ineson P., Taylor K., Benham D., Poskitt J., Rowland A.P., Bol R. & Harkness D.D. 1999. Climatic influences on the leaching of dissolved organic matter from upland UK Moorland soils, investigated by a field manipulation experiment. *Environ. Int.* 25: 83–95.
- Tipping E., Smith E., Bryant C.L. & Adamson J.K. 2007.

- The organic carbon dynamics of a moorland catchment in NW England. *Biogeochemistry* 84: 171–189.
- Tomassen H.B.M., Smolders A.J.P., Lamers L.P.M. & Roelofs J.G.M. 2003. Stimulated growth of *Betula pubescens* and *Molinia caerulea* on ombrotrophic bogs: role of high levels of atmospheric nitrogen deposition. *J. Ecol.* 91: 357–370.
- Tomassen H.B.M., Smolders A.J.P., Limpens J., Lamers L.P.M. & Roelofs J.G.M. 2004. Expansion of invasive species on ombrotrophic bogs: desiccation or high N deposition? *J. Appl. Ecol.* 41: 139–150.
- van Vuuren M.M.I. & van der Eerden L.J. 1992. Effects of three rates of atmospheric nitrogen deposition enriched with ¹⁵N on litter decomposition in a heathland. *Soil Biol. Biochem.* 24: 527–532.
- van Vuuren M.M.I., Aerts R., Berendse F. & Devisser W. 1992. Nitrogen mineralization in heathland ecosystems dominated by different plant species. *Biogeochemistry* 16: 151–166.
- van Vuuren M.M.I. & Berendse F. 1993. Changes in soil organic matter and net nitrogen mineralization in heathland soils, after removal, addition or replacement of litter from *Erica tetralix* or *Molinia caerulea*. *Biol. Fertil. Soil* 15: 268–274.
- van Vuuren M.M.I., Berendse F. & Devisser W. 1993. Species and site differences in the decomposition of litters and roots from wet heathlands. *Can. J. Bot.* 71: 167–173.
- Verhoeven J.T.A. & Toth E. 1995. Decomposition of *Carex* and *Sphagnum* litter in fens: effect of litter quality and inhibition by living tissue homogenates. *Soil Biol. Biochem.* 27: 271–275.
- Vestgarden L.S. & Austnes K. 2009. Effects of freeze-thaw on C and N release from soils below different vegetation in a montane system: a laboratory experiment. *Global Change Biol.* 15: 876–887.
- Weihermüller L., Siemens J., Deurer M., Knoblauch S., Rupp H., Gottlein A. & Putz I. 2007. In situ soil water extraction: a review. *J. Environ. Qual.* 36: 1735–1748.
- Whinam J. & Copson G. 2006. *Sphagnum* moss: an indicator of climate change in the sub-Antarctic. *Polar Rec.* 42: 43–49.
- Zabowski D. & Ugolini F.C. 1990. Lysimeter and centrifuge soil solutions — seasonal differences between methods. *Soil Sci. Soc. Am. J.* 54: 1130–1135.