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Soil Solution Chemistry and Element Fluxes in Three European Heathlands and Their Responses to Warming and Drought

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Abstract

Soil water chemistry and element budgets were studied at three northwestern European *Calluna vulgaris* heathland sites in Denmark (DK), The Netherlands (NL), and Wales (UK). Responses to experimental nighttime warming and early summer drought were followed during a two-year period. Soil solution chemistry measured below the organic soil layer and below the rooting zone and water fluxes estimated with hydrological models were combined to calculate element budgets. Remarkably high N leaching was observed at the NL heath with 18 and 6.4 kg N ha^{-1} $year^{-1}$ of NO_3–N and NH_4–N leached from the control plots, respectively, indicating that this site is nitrogen saturated. Increased soil temperature of +0.5°C in the heated plots almost doubled the concentrations and losses of NO_3–N and DON at this site. Temperature also increased mobilization of N in the O horizon at the UK and DK heaths in the first year, but, because of high retention of N in the vegetation or mineral soil, there were no significant effects of warming on seepage water NO_3–N and NH_4–N. Retention of P was high at all three sites. In several cases, drought increased concentrations of elements momentarily, but element fluxes decreased because of a lower flux of water. Seepage water DOC and DON was highly significantly correlated at the UK site where losses of N were low, whereas losses of C and N were uncoupled at the NL site where atmospheric N input was greatest. Based on N budgets, calculations of the net change in the C sink or source strength in response to warming suggest no change or an increase in the C sink strength during these early years.

Key words: Soil water chemistry; Warming; Drought; Climate change; Nitrogen leaching; Element budget; Heathland.

Introduction

Heathland ecosystems dominated by evergreen shrubs are characterized by low levels of plant-available nutrients and high turnover time of nutrients in plants and soil (Aerts and Chapin 2000). Heathlands have conservative element cycles

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(Matzner and Ulrich 1980; Nielsen and others 1999). Increased atmospheric input of N is therefore a major threat to heathlands leading to increased production of biomass, N enrichment of litter, and ultimate replacement of evergreen shrubs with grasses and a more rapid N cycle (Heil and Bobbink 1993; Power and others 2001). In the long term, N deposition may lead to N saturation as seen in forest ecosystems (Aber and others 1989, Aber and others 1998; Dise and others 1998), potentially leading to increased N losses and negative effects on soil water quality.

Simultaneously, heathlands are being exposed to climatic changes because the increase in concentration of greenhouse gasses is expected to raise the mean temperature over the next century by 1.4–5.8°C and also to change precipitation patterns (Houghton and others 2001). Such changes will influence virtually all important ecosystem processes because temperature, together with soil moisture and quality of the organic matter, strongly controls the rate of decomposition and nutrient mineralization (Swift and others 1979). Although climate-change experiments on heathland ecosystems in the temperate zone are sparse (Gordon and others 1999), studies from temperate forest ecosystems (Wright 1998; Melillo and others 2002) and tundra ecosystems (Jonasson and others 1993; Shaver and others 1998; Schmidt and others 1999, Schmidt and others 2002) suggest that altered nutrient cycling (for example, increased mineralization and nutrient availability) may be key responses in heathland ecosystems in response to climate perturbations.

Despite nutrient limitation in heathlands, large pools of nutrients are bound in the O horizon, which may potentially be mobilized if climatic conditions change. Consequently, changes in O horizon leachates and seepage water chemistry may be early indicators of changes in soil organic matter turnover and nutrient availability in response to climate change as illustrated in a montane grassland (Ineson and others 1998a, Ineson and others 1998b). Net soil carbon loss, increased DOC leaching losses, and a reduced NO_3–N leaching due to increased plant N uptake after experimental warming were observed. In contrast, Wright (1998) observed increased NO_3–N leaching from 3.2 to 8.1 kg N ha^{-1} $year^{-1}$ after combined warming and CO_2 enrichment of a N-saturated boreal forest. Altered precipitation, amounts or annual distribution, may also affect ecosystem functioning and nutrient cycling, for example, in water-limited ecosystems with very dry soils or in water-logged ecosystems with temporarily anaerobic conditions in the soil. Furthermore, soil water content and temperature may be negatively correlated in soils with high water content (Davidson and others 1998).

We studied element fluxes in three heathland ecosystems in Denmark (DK), The Netherlands (NL), and Wales (UK) placed along gradients in N deposition (factor 4) and precipitation (factor 3). We hypothesized that the N deposition level will be reflected in the leaching losses of NO_3–N, with the NL site having the highest N deposition and also the largest leaching losses of NO_3–N.

Furthermore, we experimentally manipulated temperature by passive nighttime warming and precipitation pattern by applying an extended summer drought. We hypothesized that warming will lead to changes in soil solution chemistry as a result of possible changes in nutrient cycles. We measured solution concentrations in two depths and applied a water balance to all three sites to estimate the water flux. We also measured atmospheric input of elements to the heathlands and calculated annual input and output of DOC and elements. This enabled an evaluation of overall changes in nutrient turnover and storage in the ecosystems.

METHODS

Study Sites

The CLIMOOR project is located at four sites in western Europe. In this study we present data from the three northern sites with comparable vegetation: Mols Bjerge, Denmark (DK) (56°23'N 10°57'E), Oldebroek, The Netherlands (NL) (52°24'N, 5°55'W), and Clocaenog, Wales (UK) (53°03'N 3°28'W). The DK and NL sites are dry lowland heaths, whereas the UK site is a wet upland heath or moorland. The fourth CLIMOOR site, in Spain, was not included in this study because of low rainfall and limited drainage water.

The DK site is situated on a southeast-facing end-moraine from the last glaciation at 57-m above sea level. The soil is a relatively nutrient poor sandy podzol with a thin organic layer of 2.0 cm. Sheep grazed the area until 1992. Over the last 30 years *Drschampsia flexuosa* has gained increasing dominance, most likely as a consequence of the low level of management and the increasing atmospheric input of N. A heather beetle attack in the summer of 1999 and especially in 2000 killed *C. vulgaris* in large parts of the area. To promote regrowth of the vegetation, the plots were cut in late September 2000 and the cut biomass was removed.

The NL site is part of a large heathland area, Oldebroekse heide, a flat plain 25-m above sea

Table 1. Vegetation and Soil Properties[a]

	Mols Denmark	Oldebroek Netherlands	Clocaenog Wales
Vegetation	*Calluna vulgaris* *Deschampsia flexuosa*	*Calluna vulgaris* *Deschampsia flexuosa* *Molinia caerulea*	*Calluna vulgaris* *Deschampsia flexuosa* *Vaccinium myrtissil* *Empetrum nigrum*
Soil	Sandy podzol	Sandy podzol	Peaty podzol
Organic layer depth (cm)	2.0	2.5	7
Organic layer C (g C m^{-2})	1190	1680	2348
Organic layer N (g N m^{-2})	63	75	67
Organic layer P (g P m^{-2})	2.3	1.9	2.4
Organic layer C:N	19	22	37
Organic layer C:P	517	884	978
Organic layer pH_{H2O}	4.5	3.7	4.3
Mineral soil pH_{H2O}	4.7	3.8	4.4
Mean annual temperature (°C)	6–8 (9.4)	7–9 (10.1)	8–10 (8.2)
Soil temperature (°C)	8.8	9.5	6.2
Soil temperature warmed plots (°C)	+1.1	+0.5	+0.6
Precipitation (mm)	550 (758)	700 (1042)	2000 (1741)
Precipitation in drought plots (%)	67	87	91
N deposition (kg N ha^{-1} $year^{-1}$)	10–15	30–40	20–25

[a]*Temperature and precipitation are annual means for the last decade with the values for the experimental period in brackets. The effect of warming on soil temperature (in °C increase compared with control) and of drought on precipitation (% of precipitation in control plots) are given. Mean wet N deposition is regional means.*

level. The soil is a well-drained, sandy-to-loamy podzol with an organic layer of 2.5 cm. The vegetation is dominated by *C. vulgaris* of a maximum height of 75 cm with some *D. flexuosa* and *Molinia caerulea*.

The UK site is located in north Wales, within Clocaenog Forest at 490 m altitude. The site is an island of *Calluna* heathland of approximately 15 ha surrounded by plantation forestry. The soil is an acid peaty podzol with a thick organic layer of 7 cm. The vegetation is dominated by mature *C. vulgaris* but with both *Vaccinium myrtillis* and *Empetrum nigrum* present and very sparse *D. flexuosa*. There is no grazing or burning at the site and management is by clipping or turf removal.

The three heathlands are situated along a precipitation (550–2000 mm) and N deposition gradient (10–40 kg N ha^{-1} $year^{-1}$). For more site characteristics, see Table 1.

Experimental Design

Three 4 × 5-m plots in three replicate blocks were assigned to control (C), drought (D), and warming (H) treatments. A passive nighttime warming manipulation was achieved using aluminum curtains covering the vegetation at night to prevent the efflux of infrared radiation from the plots. The curtains were automatically rolled out at night and rolled back at sunrise. Furthermore, the curtains were removed during storms and rain events to maintain the normal hydrology and wind stress. For drought treatment, extended summer drought was achieved using transparent polyethylene curtains, which covered the vegetation during any rain event in the drought period. During periods without precipitation, the curtains were removed to ensure normal light and wind conditions.

The warming treatment was initiated in early spring 1999 and ran continuously to the end of 2000 (Table 1). Drought treatment continued from mid to late May to the end of July (DK), from late May to late July/early August (NL), and from mid June to the end of August (UK) in 1999 and 2000 (Table 1).

A number of background parameters were monitored (for example, air and soil temperature, precipitation, soil moisture at two depths, wind speed). See Beier and others (2004) for details on design and treatment effects.

Soil Water Sampling and Analysis

Soil solution was sampled below the O horizon at DK and UK sites by 10/20 × 20-cm polyethylene zero-tension lysimeters and small tension lysim-

Table 2. Range of Monthly Concentrations (mg L^{-1}) across Two Years in Control Plots in a *Calluna–Deschampsia* Heath in Denmark, The Netherlands, and Wales

Element	Denmark	Netherlands	Wales
Soil solution chemistry under organic horizon			
Ca	1.58–7.31	0.39–0.66[a]	0.24–12.0
Mg	0.49–3.40	0.81–0.39[a]	0.21–1.40
Na	1.05–10.23	2.16–3.45[a]	2.20–5.17
K	2.29–18.6	1.94–5.05[a]	0.16–2.50
Al	0.23–1.57	0.16–0.80[a]	0.04–0.28
NH_4–N	0.04–2.30	0.49–1.58[a]	0.01–3.40
NO_3–N	0.03–9.27	0.66–1.36[a]	0.01–0.18
PO_4–P	0.023–1.78	0–0.13[a]	0.005–0.57
Cl	n.d.	1.68–10.42[a]	2.40–10.17
SO_4–S	n.d.	1.14–2.07[a]	0.46–2.90
DON–N	0.47–3.40	0.68–4.99[a]	0.26–2.19
DOC–C	24.5–72.5	11.72–28.6[a]	8.70–42.0
Soil solution chemistry from beneath the rooting zone			
Ca	0.24–6.52	0.37–2.75	0.09–0.38
Mg	0.1–2.36	0.19–0.90	0.29–0.58
Na	1.04–7.89	2.69–6.56	2.40–4.95
K	0.10–4.09	0.72–6.61	0.25–0.96
Al	0.02–1.77	1.11–3.07	0.38–0.89
NH_4–N	0–0.20	0.088–3.76	0.01–0.14
NO_3–N	0–5.19	0.069–11.66	0.01–0.037
PO_4–P	0.02–0.082	0–0.061	0.005–0.021
Cl	7.05–9.50[b]	3.75–9.80	2.75–8.33
SO_4–S	3.88–5.11[b]	1.02–3.69	0.49–2.60
DON–N	0.13–1.74	0.25–3.33	0.081–0.53
DOC–C	3.88–8.08	8.58–29.8	8.10–26.5

n.d. = not determined.
[a]Measured only during the winter and spring of 1999.
[b]From nearby site (Pedersen and others 2002).

eters at the NL site. Below the rooting zone, polytetra fluoroethylene (PTFE) (DK) or ceramic (NL and UK) tension soil water samplers were used (PRENART super quartz, Copenhagen, DK, and Soilmoisture Corp., Goleta, CA, USA). Three soil water samplers were installed in each plot and in each horizon. Each soil solution sample thus was composed of water bulked from three samplers, except for the NL site where all lysimeters were analyzed individually. The tension soil water samplers were installed in 90-cm (DK) and 30-cm (UK, NL) depth. Soil solution was collected in the autumn of 1998, approximately half a year before the manipulations were established in the spring of 1999. Soil solution was collected monthly (DK) and biweekly (NL and UK) and analyzed monthly (DK and UK) and biweekly (NL). Sampling continued to the end of 2000. The lysimeters below the organic horizon at the Dutch site were eaten by soil fauna in the first summer so we have only pretreatment concentrations from this horizon.

Soil solution samples were measured for pH prior to filtration. NO_3^- and NH_4–N were analyzed by an autoanalyzer, Cl and SO_4 by an autoanalyzer (NL) and ICP (UK), TOC by carbon analyzer, and cations (Al, Fe, Ca, Mg, K, Na) were determined on ICP-AES. DON was analyzed by UV digestion (NL) or after perchloric digestion (UK). SO_4 and Cl were not measured at the Danish site and DON was measured campaignwise.

Input by Rain

Precipitation was monitored at each site by two rain gauges collected biweekly (UK and NL) or monthly (DK). The gauges were placed 1–2 m above ground outside the experimental plots. A rain gauge within each plot recorded water input to the different treatments (Beier and others 2004). Analysis of the

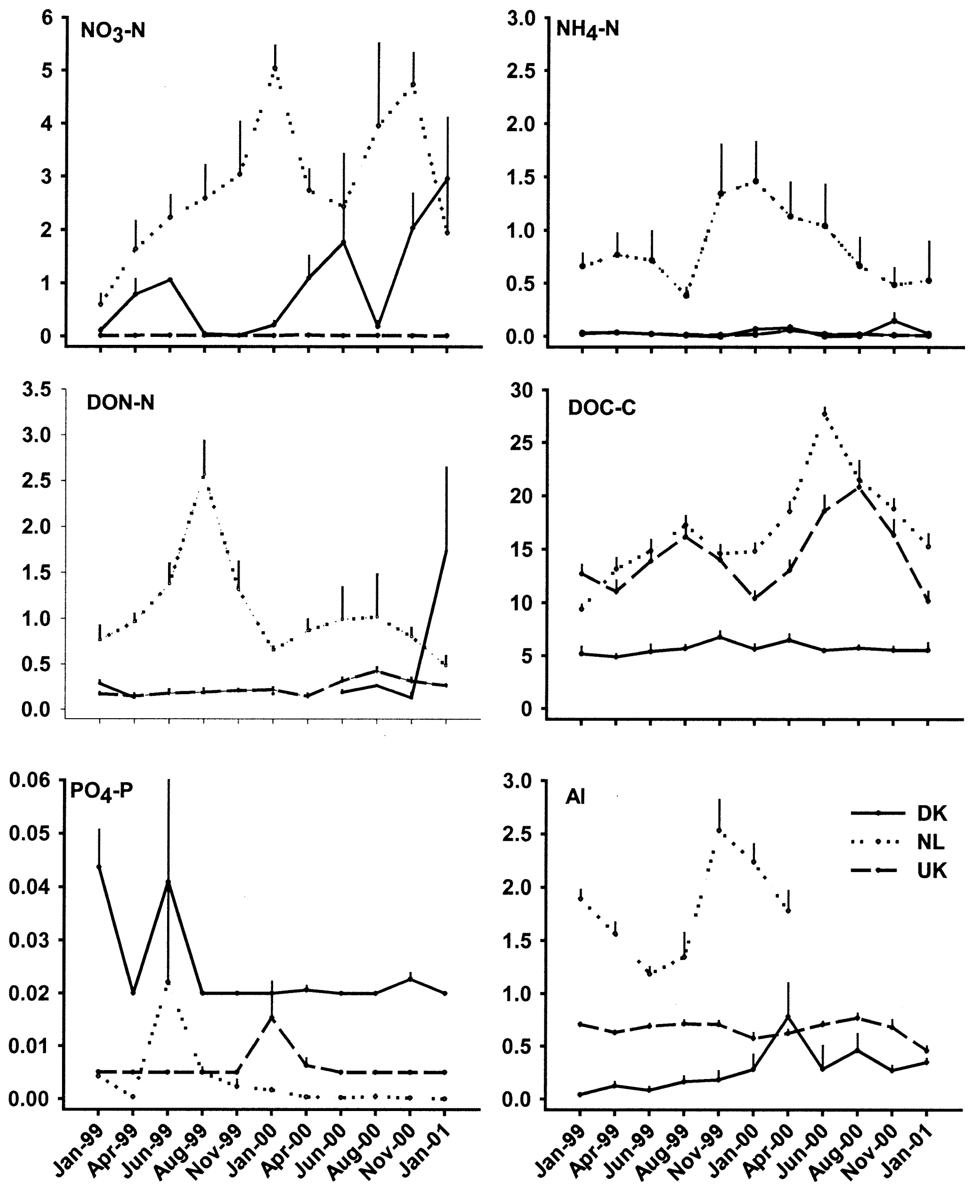

Figure 1. Mean seasonal concentrations of elements (in mg L^{-1}) in the seepage water in three *Calluna* heathland ecosystems in Denmark (DK, unbroken line), The Netherlands (NL, dotted line), and Wales (UK, stippled) from autumn 1998 to the end of the year 2000. *Calluna* at the DK site was attacked by heather beetles. To promote regrowth of *Calluna* plants, the site was cut and biomass removed in September 2000.

elements follows the method used for soil solution samples. The input numbers represent wet deposition and the actual numbers of input may be slightly higher when considering dry deposition (Rode 1999).

Element Fluxes and Nutrient Retention

Water balances in the soil for each site and treatment were estimated with Thornthwaite's equations (UK) (Thornwaite and Mather 1955) and with the water models EVACROP (DK) (Olesen and Heidman 1990) and SWIF (NL) (Tiktak and Bouten 1992) using measured numbers of temperature, precipitation, and soil moisture. The element fluxes were calculated by multiplying the average monthly concentrations in precipitation or soil solution with the average precipitation or drainage in the soil modeled from the water balance.

Mobilization or retention was estimated as the difference between atmospheric input and leaching loss beneath the root zone and the retention (positive values) or mobilization (negative values) relative to the input was calculated [Eq. (1)].

$$\%\text{Retention} = (\text{Input}_{\text{precipitation}} - \text{Output}_{\text{leachate}})/\text{Input}_{\text{precipitation}} \times 100 \quad (1)$$

Statistical Methods

Repeated-measures analyses of variance (ANOVA) with drought or temperature as the main factor was

Table 3. Element Budget (kg ha^{-1} year^{-1}) in Three Heathlands

	Ca	Mg	Na	K	Al	NH_4-N	NO_3-N	PO_4-P	Cl	SO_4-S	DON-N	DOC-C
Denmark												
Input	3.0	3.0	23	1.5	0.4	7.1	5.8	0.4	46[a]	7.7[a]		13
OM leaching	18.7	5.4	19.0	37.4	3.4	1.8	2.9	0.59	n.d.	n.d.	6.8	174
Mineral soil leaching	10.7	3.7	20.5	7.7	0.49	0.14	1.2	0.12	30	15.4	1.1	50
Retention	−7.7	−0.7	2.6	−6.2	−0.09	7.0	4.6	0.28	16	−7.7		−37
% Retention	0	0	11	0	0	98	80	70	33	0		0
Netherlands												
Input	9.4	2.8	21.8	2.0	0.5	8.5	9.3	0.04	42	12	6.2	
Mineral soil leaching	3.1	1.9	19.0	8.1	9.4	6.4	18.1	0.004	36.8	16.1	6.0	135
Retention	6.3	0.9	2.8	−6.1	−8.9	2.1	−8.8	0.036	5.2	−4.1	0.2	
% Retention	67	32.1	12.8	0	0	25	0	90	12	0	3	
Wales												
Input	5.6	7.0	52	5.2	0.50	12.1	4.6	1.5	94	12.4	2.4	41
OM leaching	23.6	7.2	54.7	16.6	2.3	8.1	0.21	1.25	91.2	14.7	8.8	389
Mineral soil leaching	3.59	6.3	56.9	7.2	10.1	0.4	0.19	0.17	79.8	16.5	4.7	237
Retention	2.01	0.68	−5.2	−2.0	−9.6	11.7	4.41	1.33	13.8	−4.1	−2.3	−196
% Retention	36	10	0	0	0	97	96	89	15	0	0	0

n.d. = not determined.
[a]From nearby site (Pedersen and others 2002).

applied to each site to test the effects of the main factors on soil solution chemistry. Input data for all sites were seasonal mean concentrations during the two years of measurement, for example, winter, spring, drought (early summer), late summer, autumn. Furthermore, differences in soil solution chemistry among the control plots across the three sites were tested by repeated-measures ANOVA with site as the main factor, and finally overall effects of the treatments across sites were tested with site and drought or site and temperature as main factors including interactions. All data were analyzed after log (x + 1) transformation to meet assumptions of homogeneous variance. All statistical analyses were performed with SAS (SAS Institute, Cary, NC) using the GLM procedure and type II sum of squares.

Result and Discussion

Soil Solution Chemistry Along Natural Gradients

Across sites, there was a highly significant effect of site on element concentrations for most solutes in both O horizon leachates (Table 2; $p < 0.05$ for NH_4–N and $p < 0.001$ for other elements) and seepage water (Table 2 and Figure 1; $p < 0.01$–0.001 for all elements). NH_4–N and NO_3–N and Al concentrations (Figure 1) and fluxes (Table 3) were high in seepage water at the NL site. N deposition has exceeded critical loads of 15–20 kg N ha^{-1} year^{-1} for half a century (Heil and Bobbink 1993). Therefore, plant growth is probably limited by other nutrients than N and the soil may be saturated with N; thus, it is not surprising that N concentration and fluxes were high. The DK site has higher concentrations and fluxes of Ca and P and plant growth may be more N limited resulting in low concentrations and fluxes of inorganic N (Figure 1 and Table 3). At the UK site, plant production may be colimited by N and P indicated by low seepage water concentrations and fluxes of inorganic N and P (Figure 1 and Table 3). N leaching data are reflected by the NL site having the highest aboveground biomass production of the three sites, three times higher than the DK site, whereas the production at the UK site was negligible (Peñuelas and others 2004).

N losses were negatively correlated with pH across the three sites, similar to observations in forest soils where N transformation and leaching have been suggested as a driving force in soil acidification (Verstraten and others 1990).

Soil Solution Chemistry—Responses to Warming and Drought

In a number of studies in arctic or temperate forest soils, elevated temperature increased net mineralization (Chapman and others 2001; Emmer and Tietema 1990; Nadelhoffer and others 1991; Reich

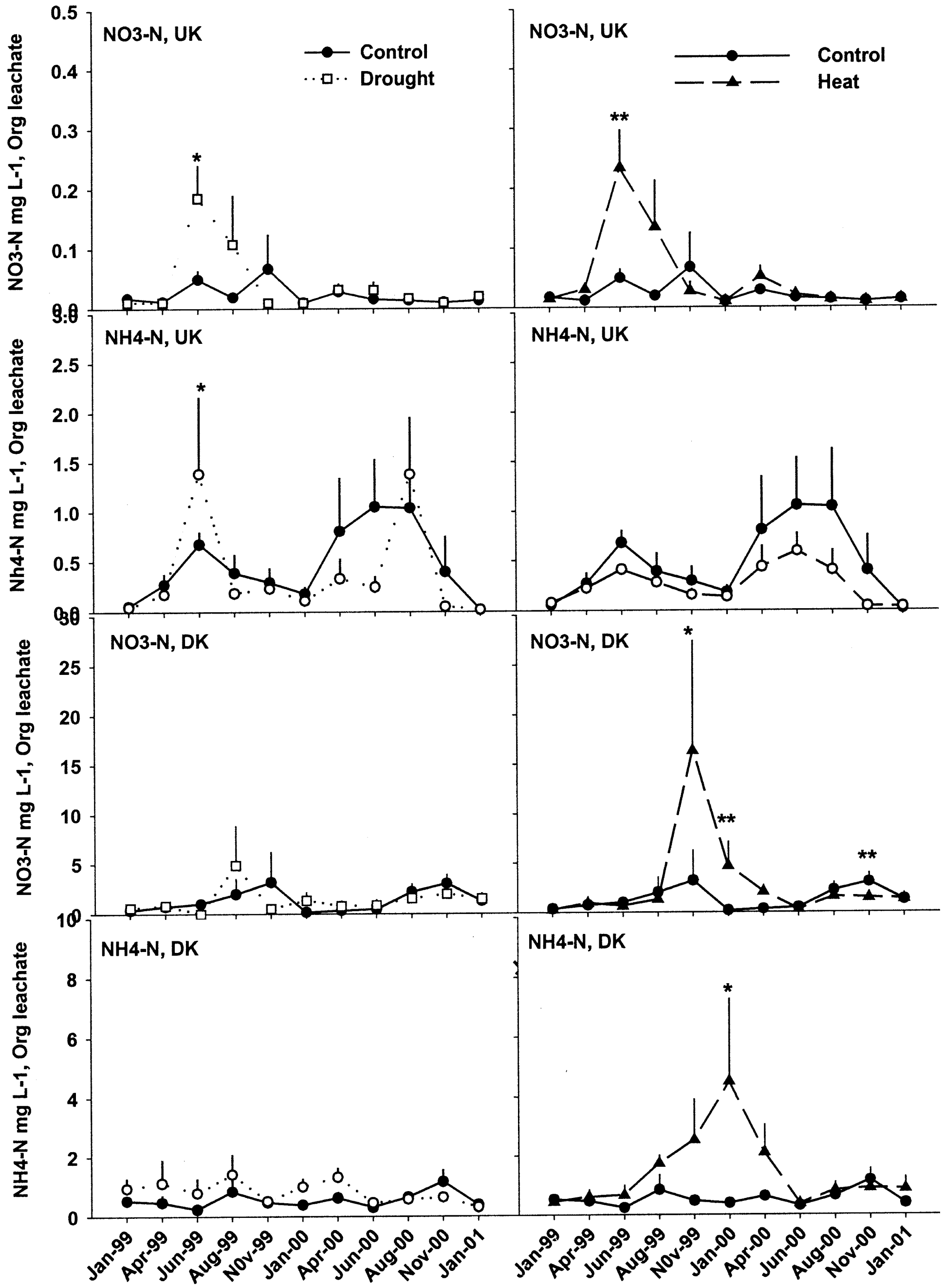

Figure 2. Mean seasonal NO_3–N and NH_4–N (in mg NL^{-1}) in O horizon leachates at the UK and DK sites during the first two years of treatments with extended summer drought and nighttime warming. O horizon leachate was not measured at the NL site. The effects of applied summer drought or nighttime warming were tested by two-way repeated- measures ANOVA (DK) with the main factors being drought (D) or warming (W) and block (B) and one-way (UK) repeated-measures ANOVA. The results are given for each country. No overall significant effects were found. Seasonal effects are given for each time. Significance levels of *, **, and *** indicate $p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$, respectively.

and others 1997). Thus, we expected higher element concentrations and fluxes in the heated plots. Seepage water concentrations of most elements were similar in control and warmed plots and fluxes were the same or slightly lower as a result of a slightly lower water flux in the warmed plots. In the O horizon leachate, a short-term increase in NO_3–N (DK, UK) and NH_4–N (DK) concentrations (Figure 2) were observed, whereas inorganic N fluxes from this horizon increased only at the DK site (Table 4). In the seepage water beneath the root zone, warming had no effect on inorganic N concentrations at the DK and UK sites (Figure 3), except after the attack by heather beetles at the DK site in the summer of 2000. In contrast, a highly significant increase in seepage water NO_3–N concentration (Figure 3) and fluxes (Table 4) was seen at the NL site with elevated temperature. Simultaneously, increased plant growth in the warmed plots at the Dutch site (Peñuelas and others 2004) indicated increased nutrient availability as also reported from arctic heathlands (Hartley and others 1999;

Table 4. N fluxes (kg N ha^{-1} $year^{-1}$) at Two *Calluna* Heath Sites in Denmark (DK), The Netherlands (NL), and Wales (UK) in Response to Extended Summer Drought and Nighttime Warming

	Control			Drought			Warming		
Treatment	NO_3–N	NH_4–N	DON	NO_3–N	NH_4–N	DON	NO_3–N	NH_4–N	DON
DK									
Input	5.8	7.1		4.2	4.9		5.3	6.5	
OM leaching	2.9	1.8	6.8[a]	2.7	2.6	4.9	11	5.3	8.9[a]
Output	1.2	0.1	1.1[a]	0.8	0.09	1.0	0.5	0.2	0.8[a]
Retention	4.6	7.0		3.5	4.8		4.8	6.3	
% Retention	80	98		82	98		91	97	
NL									
Input	9.3	8.5	6.2	6.4	6.5	4.3	7.4	6.8	4.9
OM leaching									
Output	18	6.4	6.0	16	6.8	5.7	35	7.0	11
Retention	−8.8	2.1	0.2	−9.4	−0.30	−1.4	−28	−0.16	−5.8
% Retention	0	25	3	0	0	0	0	0	0
UK									
Input	4.6	12	2.4	3.6	9.7	1.8	4.1	11	2.2
OM leaching	0.2	8.1	8.8	0.2	6.0	8.1	0.2	5.0	9.1
Output	0.20	0.4	4.7	0.2	0.2	3.8	0.2	0.2	4.2
Retention	4.4	12	−2.3	3.4	9.5	−2.0	3.9	10	−2.0
% Retention	96	97	0	95	98	0	95	98	0

Fluxes are calculated for the first treatment year at the Danish site because of a heather beetle attack in the second year. Thus, data represent only 9 months of warming treatment. The Dutch and Welsh numbers are based on the second year with treatments.
[a]DON was not measured routinely at the Danish sites and the values in precipitation and soil solution are an estimate based on campaign measurements.

Schmidt and others 1999), upland grassland (Ineson and others 1998a), and forested catchments (Lukewille and Wright 1997; Melillo and others 2002).

At all sites, concentrations of some elements increased during and after the drought treatment, but due to the reduced water flow element fluxes were generally reduced (Table 4). At the relatively wet UK site, microbial activity was potentially limited by the wet conditions as indicated by low mineralization rates (Emmett and others 2004), but concentrations and fluxes of solutes in the soil water did not indicate any major responses to drought.

The response in leaching of NO_3–N to warming from the O horizon (UK and DK) and in seepage water (NL) shows the relative magnitude of the response among the sites as NL is much greater than DK which is greater than UK. This order of magnitude was not correlated with the soil temperature at the sites or with the degree of warming, and the responses could not be predicted from variation in temperature and precipitation across sites. Instead, data suggested that the N status rather than the degree of warming primarily drove the magnitude of response to warming. This may be explained by the higher natural variability in key drivers (for example, temperature and precipitation) between sites compared with the treatment effects (Table 1; Beier and others 2004). A similar pattern of greater differences across sites than observed in response to climate manipulations within a single site has also been observed in a number of warming experiments in arctic tundra ecosystems (Jonasson and others 1999; Schmidt and others 2002; Shaver and others 2000).

Mobilization or Retention of Elements

The input of elements was very similar in the NL and DK sites except for NO_3–N and Ca, whereas the input of many elements was higher at the UK site mainly because of the 2–3 times higher input of precipitation.

Most of the N and P deposited at the UK and DK sites apparently was retained within the ecosystem (Table 3). In contrast, at the NL site P retention was high while only 25% of the input of NH_4–N was retained and significant amounts of NO_3–N were leached resulting in a negligible overall retention of N. High retention of N has often been reported from heathlands (for example, Kristensen 2001; Matzner and Ulrich 1980; Nielsen and others 1999; Power and others 1998), but the high NO_3–N loss from the

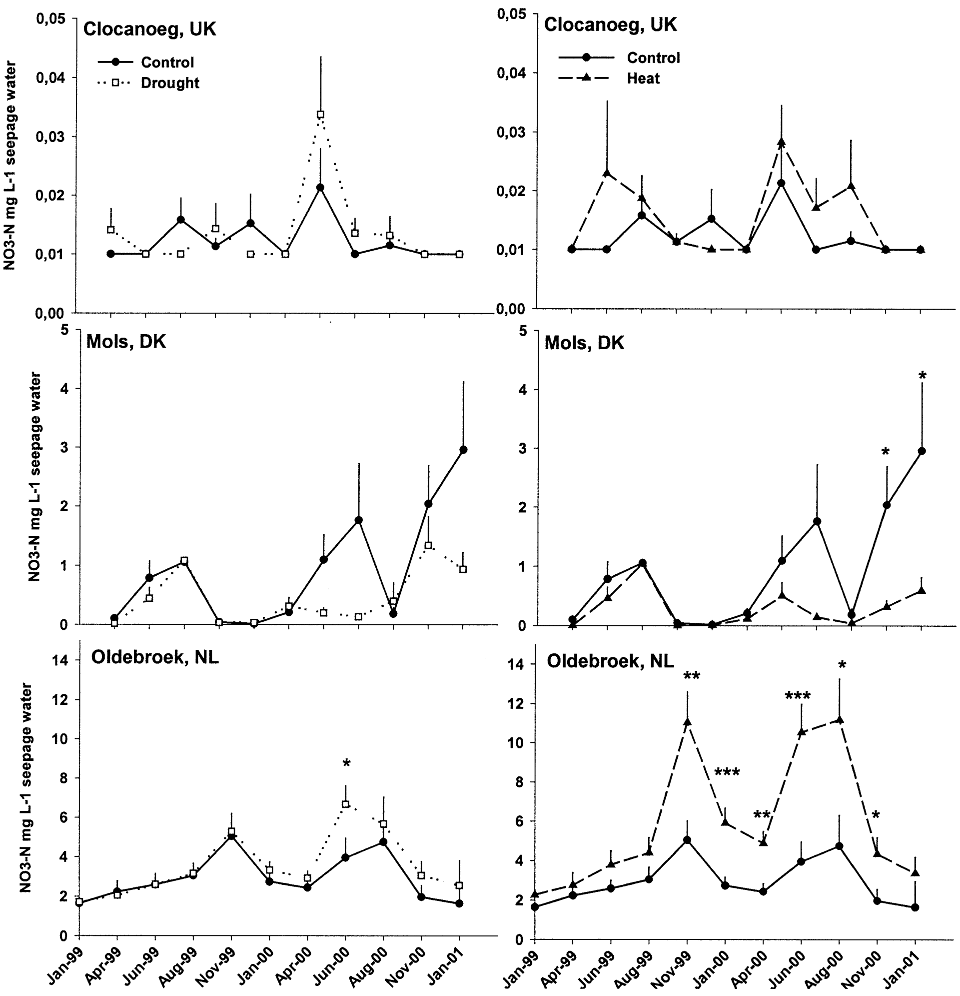

Figure 3. Mean seasonal NO_3–N (mg L^{-1}) in seepage water at the UK, DK, and NL sites during the first two years of treatments with extended summer drought and nighttime warming. The effects of applied summer drought or nighttime warming were tested by two-way repeated-measures ANOVA (DK and NL) with the main factors being drought (D) or warming (W) and block (B) and one-way (UK) repeated-measures ANOVA. The results are given for each country. No overall significant effects were found. Seasonal effects are given for each time. Significance levels of *, **, and *** indicate $p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$, respectively.

NL site to our knowledge is the first such reported case from heathlands (Table 4 and Figure 3), suggesting that the system may be N-saturated as has been reported from forested ecosystems (Aber and others 1998; Dise and others 1998).

Precipitation contained Mg and Na in similar amounts to losses from the O horizon at the DK and UK sites where O horizon leachate was sampled. In contrast, Ca and K in wet deposition were highly enriched (Table 3). The source of these cations may be a result of leaching from the vegetation as reported by Bobbink and Heil (1993), Matzner and Ulrich (1980) and Rode (1999).

High mobilization of base cations in the vegetation–upper soil layer but strong retention in the mineral soil is a common feature in heathlands (Matzner and Ulrich 1980; Nielsen and others 1999, Nielsen and others 2000). Despite high retention of cations in the mineral soil, we observed a net loss of Ca and K of 7.7 and 6.2 kg ha^{-1} $year^{-1}$ at the DK site. In contrast, Ca was retained at both UK and NL sites, and instead large amounts of K and Al were leached (2 kg K and 9.6 kg Al ha^{-1} $year^{-1}$ at the UK site and 6.1 kg K and 8.9 kg ha^{-1} $year^{-1}$ from the NL site). There was a high correlation between seepage water Al and NO_3–N ($r^2 = 0.82$; $y = 0.22x + 22.8$, where y is Al and x is NO_3–N) as found in acid forest soils (Verstraten and others 1990; Dise and others 2001). This is further supported by data from the heated plots at the NL site where the doubling of NO_3–N leaching below the rooting zone was accompanied by a similar doubling of Al and K fluxes to 16 and 14 kg ha^{-1} $year^{-1}$, respectively.

Carbon and Nitrogen and Their Interactions

N retention was high at the UK site and DON constituted 85% of the N loss (Table 4), similar to observations from forest ecosystems with low N losses (Hedin and others 1995; Campbell and others 2000; Perakis and Hedin 2002). At the NL site, where N loss was high, the contribution from NO_3–N increased and DON accounted for less than 25%. However, even in the control plots, we observed high background concentrations of NH_4–N

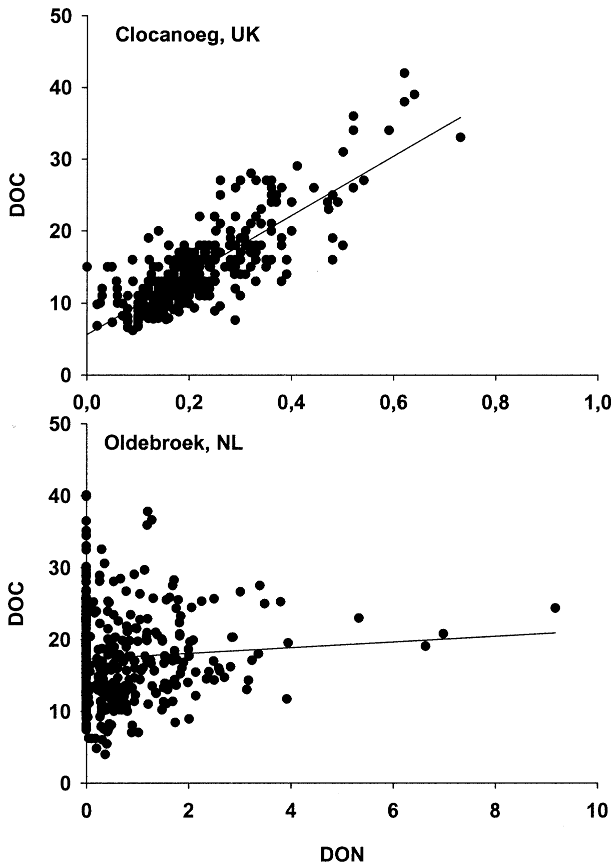

Figure 4. The relationship between dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) concentrations in seepage water at *Calluna* heathlands at the UK and NL sites during 1999–2000.

and DON at the NL site compared with the other sites (Figure 1).

DOC leaching from the plots was related to soil organic matter content at the sites, with the highest fluxes at the UK site (237 kg C ha^{-1} year^{-1}), compared with 135 and 50 kg ha^{-1} year^{-1} at the NL and DK sites (Table 3). Seepage water DON and DOC concentrations were significantly correlated ($F = 599$, $p < 0.0001$) at the UK site (Figure 4) whereas no correlations were observed at the NL site suggesting a breakdown between the codependence on the C and N cycles at this N-polluted site. The lowest amounts of DOC were leached from the DK site, possibly because of the sampling depth. Corresponding to observations of high DOC retention throughout the soil profile in similar heathlands, probably because of precipitation of organic compounds (Nielsen and others 1999), DON increased more than DOC at the NL site with warming, resulting in decreased DOC:DON ratios from 22 in the control to 12. These ratios are lower than the DOC:DON ratios (25–30) reported from North American forests fertilized with high N (McDowell and others 1998). In contrast, a trend of a small increase in DOC leaching losses but not DON losses with warming was observed at the UK site but not at the NL and DK sites. Previously, both a positive effect of warming on DOC losses (Freeman and others 2001) and no effect (Michalzik and others 1998) have been reported. The reason for this variability between sites is not well understood.

Earlier studies have suggested that N mobilization from soils will regulate the C sink or source strength within ecosystems (Shaver and others 1992). At the NL site, N leaching increased by about 2.2 g N m^{-2} year^{-1} in response to warming, while carbon accumulation in plant biomass increased by 15% or 90 g C m^{-2} year^{-1} during the first two years of warming (Peñuelas and others 2004) resulting in approximately 1.8 g N m^{-2} year^{-1} of additional plant uptake of N. Consequently, the NL site mobilized an extra 4.0 g N m^{-2} year^{-1} from the soil in response to warming. The C:N ratio in the soil is 22.5, which suggests mobilization and losses of a total of 90 g C m^{-2} year^{-1} from the soil compared with the increase in plant C of 90 g C m^{-2} year^{-1} caused by warming, indicating that there are no net losses or gains of carbon at the NL site. Instead, N is redistributed from the soil to the plants as also observed after warming in a number of arctic and temperate ecosystems (Jonasson and others 1999; Shaver and others 2000; Schmidt and others 2002). In the UK site, NPP increased by 16% or 72 g C m^{-2} year^{-1} (Peñuelas and others 2004), corresponding to an extra plant uptake of approximately 1.4 g N m^{-2} year^{-1}. N retention was approximately the same in the control (1.3 g N m^{-2} year^{-1}) and the warmed plots (1.2 g N m^{-2} year^{-1}) suggesting an extra mobilization of 1.4 g N m^{-2} year^{-1} from the soil and transferred to the plants in response to warming. The C:N ratio in the soil is 37 compared with 53 in the plants; thus, the soil may lose 52.0 g C m^{-2} year^{-1}, whereas plants may gain 72.0 g C m^{-2} year^{-1}. This suggests that the UK site may increase C storage in the initial years of warming. Carbon balances cannot be calculated for the DK site because a heather beetle attack impeded the estimation of plant productivity and the status as a source or sink of carbon cannot be stated.

CONCLUSIONS

In general, responses in soil solution chemistry and element fluxes to experimental drought and warming were small compared to those from the natural variability across sites and seasons. Initially, warming apparently increased the mobilization of N at all sites, with the most pronounced effect at the NL site, where NO_3–N leaching increased by 100%. Drought increased soil solution concentrations of several elements during and after the drought, but it generally decreased the flux of elements because of lower water flow. None of these responses could be related to the natural gradient in temperature and rainfall across sites but were mainly related to pretreatment soil characteristics and differences in atmospheric N deposition.

The alteration in soil solution chemistry combined with plant productivity data gives no evidence for changes in overall carbon storage in the NL site but a small increase in C storage in the UK site. Furthermore, it suggests that N moves from the soil to plant biomass and that carbon storage patterns change within the ecosystem in the initial years of warming.

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