Nitrogen transformations in a forested catchment in southern Norway subjected to elevated temperature and CO_2

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Abstract

Model predictions on the response of soil processes to global warming are mostly inferred from small-scale laboratory studies. In this study, a forested catchment in southern Norway was enclosed by a greenhouse and experimentally manipulated by increasing CO_2 ($+200 \, \mu l \, l^{-1}$ above ambient) and temperature ($+3–5°C$). This paper reports on the effects of the climate manipulation on N mineralization and nitrification. We measured net N mineralization and nitrification in a control and treated part of the greenhouse as well as in an uncovered reference catchment in plots dominated by *Calluna vulgaris* (L.) Hull or *Vaccinium myrtillus* L. Net N mineralization in the 0–10 cm soil layer significantly increased, most likely as a result of increased temperature. The effect was largest in plots dominated by *Calluna*. Nitrification did not significantly increase. Soil moisture inside the incubated cores was not affected by the climate change treatment. Pre-treatment mineralization was similar inside and outside the enclosure whereas nitrification was higher inside the enclosure. The NH_4^+ content was significantly lower inside the chamber due to removal of acidifying components from the precipitation and lower inputs of dry deposition. We found however no differences in pH, %C and %N of the LF and H layer and total C and N in the soil cores between the two catchments. Mineralization was generally higher under *Vaccinium* than under *Calluna* even though measured soil chemical and physical characteristics were similar. Nitrification was higher under *Calluna* than under *Vaccinium*. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Catchment manipulation; Climate change; N mineralization

1. Introduction

Increased emissions of CO_2 and other greenhouse gasses due to combustion of fossil fuels and land use change may lead to a significant increase in global temperature over the next decades (Houghton et al., 1995). An increase in temperature may stimulate decomposition of soil organic matter and mineralization of nutrients. Increased N mineralization in combination with CO_2 fertilization is likely to favor net primary production (NPP) especially in areas where N is limiting NPP. If N mineralization exceeds immobilization by the living biomass, N may leach to ground- or streamwater causing acidification and

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eutrophication of aquatic ecosystems (Hessen and Wright, 1993; Wright and Schindler, 1995).

So far, predictions concerning whole ecosystem responses to climate change have largely been based on modeling in which results from small-scale greenhouse studies and laboratory incubations are extrapolated to the ecosystem level (Overpeck et al., 1990; Rastetter et al., 1992; Schimel et al., 1997). In addition, to date, most large-scale experiments manipulate either CO_2 (e.g. Hendrey et al., 1993; Miglietta and Raschi, 1993) or temperature (e.g. Peterjohn et al., 1993; Mitchell et al., 1994; Rustad et al., 1995). Oechel et al. (1994) observed that in an arctic tundra ecosystem, elevated CO_2 and temperature resulted in a persistent net ecosystem C sequestration due to increased nutrient availability caused by increased mineralization. However, elevated CO_2 alone resulted in a transient response and after 3 years of treatment, net ecosystem C exchange returned to pre-treatment levels stressing the importance of combined CO_2 and temperature manipulations.

CLIMEX (Climate Change Experiment) is an international multidisciplinary project in which temperature and CO_2 are manipulated in a forest catchment ecosystem (Jenkins and Wright, 1995). In this project, measurements on vegetation and soil allow for assessment of future response of a forest ecosystem to climate change. In this paper, we report the effects of elevated CO_2 and temperature on N mineralization.

2. Materials and methods

2.1. Site description

The CLIMEX site is located at Risdalsheia (58°23′N, 8°19′E) near Grimstad, southernmost Norway. The site is 300 m above sea level on a large biotite granite plateau, and is representative for large areas of upland southern Norway. Mean annual precipitation is 1400 mm and mean annual temperature is 5°C (-3°C in January and $+16$°C in July). Depressions in the granite surface are filled with post-glacial soil material in which acid, peaty podsolic soils have developed. Maximum soil depth is 70 cm. About 30–50% of the bedrock is exposed. The vegetation is dominated by dwarfshrubs (*Calluna vulgaris* (L.) Hull, *Vaccinium myrtillus* L., *V. uliginosum* L. and

V. vitis-idaea L.) and scattered trees (*Pinus sylvestris* L. and *Betula pubescens* Ehrh.).

2.2. Experimental design

A natural forested catchment (1400 m^2) was covered by a transparent roof in 1983 as part of the RAIN (Reversing Acidification In Norway) project (Wright et al., 1993). Precipitation was collected from the roof, filtered, and ion-exchanged. Natural levels of sea salt were added before the water was distributed under the roof. In 1993, the catchment was completely enclosed with transparent walls. The greenhouse was separated in two parts by a transparent wall. From June 1994, in the lower 80% of the greenhouse (Roof-T), CO_2 was increased during the growing season by 200 µl l^{-1} compared to the upper 20% (Roof-C). The air temperature was increased by 5°C in January and 3°C in July compared to Roof-C with intermediate temperature increases in the intervening months (Fig. 1). Prior to the treatment, air temperature throughout the greenhouse was homogeneous. An uncovered catchment (Out-C) served as outside control.

2.3. Soil nitrogen mineralization and nitrification

We measured net soil N mineralization and nitrification prior to the start of the climate change treatment (June 1993–June 1994) and during the first two treatment years using the sequential core incubation method (Raison et al., 1987; Berendse et al., 1987, 1989; Berendse, 1990). In Roof-C, Roof-T and Out-C, five plots of 4–5 m^2 were established both in *Calluna* and *Vaccinium*-dominated areas to measure vegetation growth. In each vegetation plot total C, N and pH-KCl of the LF and H layer were measured. Total C and N were measured by dry combustion on a Carlo Erba CHN element analyzer. The pH-KCl (1 M KCl) was measured in a suspension having a 1 : 20 soil–solution ratio (w/w) after shaking for 2 h. In each vegetation plot, we measured net N mineralization and nitrification in two plots of 0.1 m^2. Each year was divided in four incubation periods: April–June, June–August, August–October, and October–April. At the start of each incubation period, two samples were taken 5–10 cm apart using PVC tubes (length 15 cm, diameter 2.8 cm, wall thickness 2 mm). Soil was sampled to a depth of 10 cm unless bedrock was shallower. One
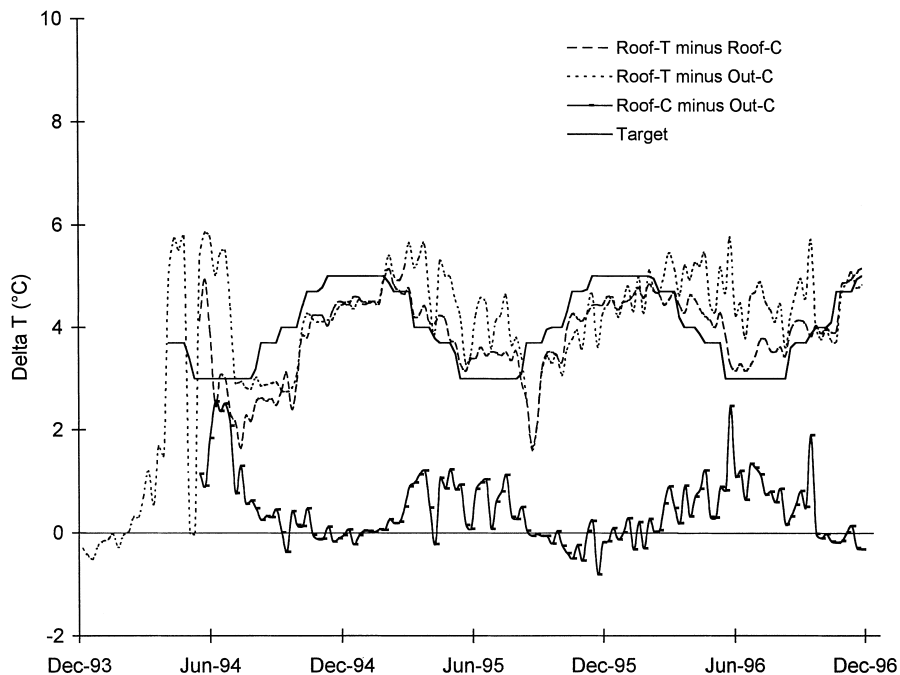
Fig. 1. Differences in air temperature between manipulated (Roof-T) and control sites (Roof-C, and Out-C).

sample was collected from the field and analyzed for N compounds whereas the second sample was closed on both ends with polyethylene caps and put back into the soil. The incubated PVC tubes had four 4 mm holes to allow for gas diffusion. At the end of the incubation period, the cores were collected from the field. The samples were weighed and stored overnight at $4°C$. The next day, 20 g of field moist soil was extracted with 50 ml 1 M KCl by shaking for 1 h. The KCl extracts were filtered and analyzed for NH_4–N and NO_3–N by colorimetry on a Technicon auto analyzer. Net N mineralization was calculated as the difference in NO_3–N + NH_4–N between the paired incubated and reference samples. Nitrification was calculated as the increase in NO_3–N.

Soil moisture content was measured after drying the samples at $105°C$ for 24 h. Moisture content expressed as g H_2O per g dry soil sampled at any one time showed a large variation due to the large variation in soil organic C content (6.7 to 53.0%). We normalized water content to total pore space rather than to dry soil, and expressed moisture as relative water content (RWC = volume fraction water/total pore space;

Skopp et al., 1990). Total pore space was calculated from volume fractions of organic (ϕ_{om}) and mineral (ϕ_{om}) material as $1 - \phi_{om} - \phi_m$. Carbon content measured on 160 cores correlated well ($r^2 = 0.93$) with bulk density which justified conversion of mass fraction to volume fraction (Marnette and Stein, 1993). We calculated organic matter content by multiplying C content by 1.7 (Schachtschabel et al., 1984). ϕ_{om} and ϕ_m were calculated by assuming a bulk density of 1.4 g cm^{-3} for organic matter and 2.65 g cm^{-3} for mineral matter (Koorevaar et al., 1983). Volumetric water content was calculated by multiplying gravimetric water content with bulk density.

2.4. Statistical methods

Presence of time trends in N mineralization and nitrification for each vegetation type was tested using paired T-tests for Out-C, Roof-C and Roof-T separately comparing pre-treatment with post-treatment data. Data on relative water content were analyzed for each site by repeated measures 4-way MANOVA

using year, vegetation, season and initial versus final moisture content as factors. Tests for differences between locations were carried out using *T*-tests. Statistical analysis was carried out using DataDesk version 6.0. Effects were considered significant if $p < 0.05$.

3. Results and discussion

3.1. Climate treatment

In Roof-T, annual N mineralization significantly increased during the first treatment year from 2.9 to 4.4 g N m^{-2} under *Calluna* and from 4.1 to 5.8 g N m^{-2} under *Vaccinium* (Fig. 2). In the second treatment year, mineralization in *Calluna* plots continued to increase to 6 g N m^{-2} whereas under *Vaccinium*, mineralization dropped to 5.4 g N m^{-2} and was not significantly ($P = 0.059$) different from pre-treatment mineralization. In the control sites Out-C and

Roof-C, mineralization was constant throughout the three measurement years. However, in *Vaccinium* plots in Roof-C mineralization increased in the first treatment year followed by a decrease in the second treatment year. In several *Vaccinium* plots in Roof-C, presence of a very loose litter layer often prevented sampling 10 cm soil. Consequently, mineralization rates in Roof-C expressed per m^2 soil were lower than in the other plots. Since measurements under *Calluna* and *Vaccinium* in Out-C and under *Calluna* in Roof-C showed no temporal variation we conclude that the increase in mineralization as measured in Roof-T must have been caused by the climate manipulation. Nitrification appeared to increase in Roof-T during the treatment years as opposed to Out-C and Roof-C under both vegetation types but the increases were not significant (Fig. 3).

Moisture content in the 0–10 cm soil layer under both vegetation types in control and treated plots was
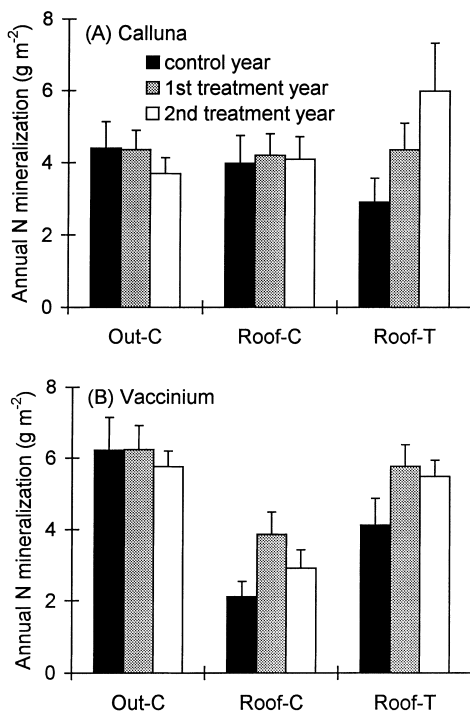

Fig. 2. Annual net N mineralization in Out-C, Roof-C and Roof-T during control and two treatment years under *Calluna* (A) and *Vaccinium* (B). Error bars represent standard errors of the mean.
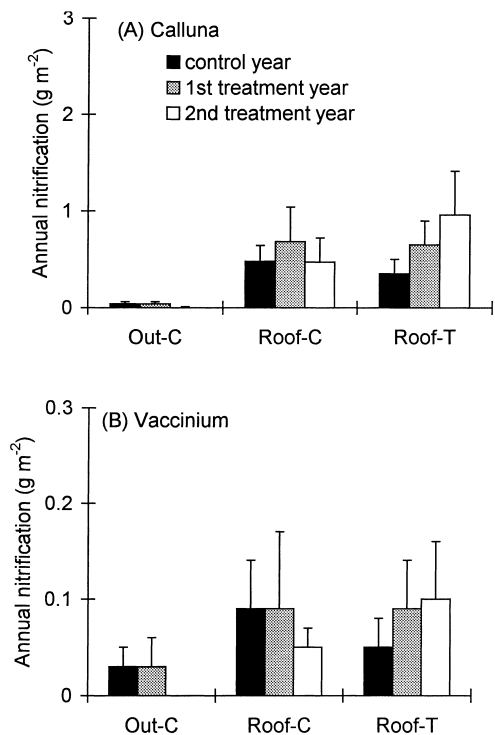

Fig. 3. Annual nitrification in Out-C, Roof-C and Roof-T during control and two treatment years under *Calluna* (A) and *Vaccinium* (B). Error bars represent standard errors of the mean. Note the factor 10 scale difference between *Calluna* and *Vaccinium*.
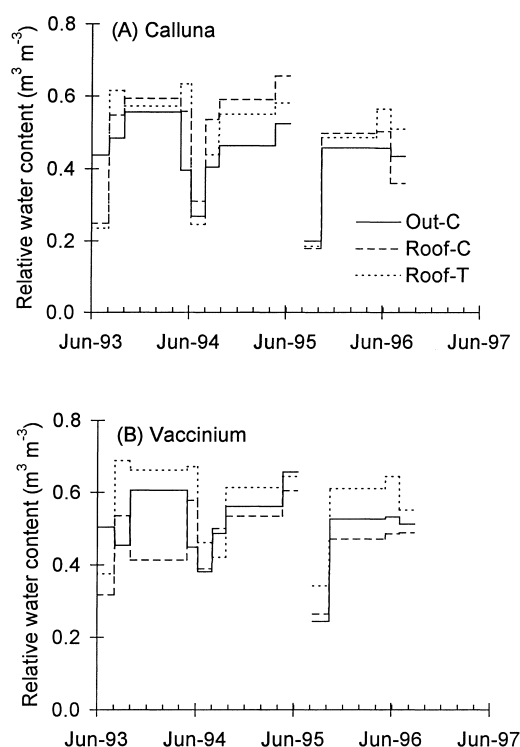
Fig. 4. Relative water content (=volume water divided by total pore space) of soil inside mineralization tubes under *Calluna* (A) and *Vaccinium* (B) during pre-treatment and treatment period. Values are averages of reference and incubated cores for each incubation period. The climate manipulation started in June 1994.

Table 1
MANOVA results on relative water content in mineralization tubes in control (Out-C, Roof-C) and treated (Roof-T) plots

Factor	Out-C	Root-C	Root-T
Vegetation (V)	***[a]	ns	***
Season (S)	***	***	***
Year (Y)	**	***	*
Initial vs. final (I)	***	***	***
V × S[b]	ns	**	ns
V × Y	ns	ns	ns
V × I	ns	ns	ns
S × Y	***	ns	***
S × I	*	**	ns
Y × I	**	ns	ns

[a] $*P < 0.05$; $**P < 0.01$; $***P < 0.001$; ns = not significant.
[b] Higher order interactions were calculated but not included in the table. Higher order interactions were not significant.

3.2. Chamber effects

The construction of the enclosure affected environmental conditions such as windspeed, precipitation regime and may have caused introduction of artifacts. The KCl-extractable NH_4^+ content of the reference samples during the pre-treatment year was significantly higher ($P < 0.001$) in Out-C (25.0 ± 27.5 mg kg^{-1}; $n = 80$) than in Roof-C (7.3 ± 7.6 mg kg^{-1}; $n = 80$) and Roof-T (8.0 ± 10.1 mg kg^{-1}; $n = 80$; Table 2). This lower NH_4^+ content inside the greenhouse was most likely a result of removal of NH_4^+ and NO_3^- from the precipitation as well as a reduction of N inputs in dry deposition in the greenhouse. The reduction in N inputs inside the

highest in winter and early spring and lowest during summer (Fig. 4). In all sites, moisture content significantly varied between years (Table 1) and was lowest in the second year of treatment compared to the pre-treatment year. Consequently, the lower moisture content in Roof-T in the second year of treatment must be ascribed to interannual weather variability and not to the climate change treatment. Although mineralization tubes were closed at both ends, soil moisture significantly increased during the incubations even when the unconfined soil dried out (Fig. 5). This increase in moisture was generally largest when initial soil moisture was low such as in summer. Consequently, moisture conditions inside the tubes were different from the unconfined soil. Still, the moisture pattern in the closed cores was similar for all sites and therefore does not affect conclusions regarding effects of the climate manipulation.
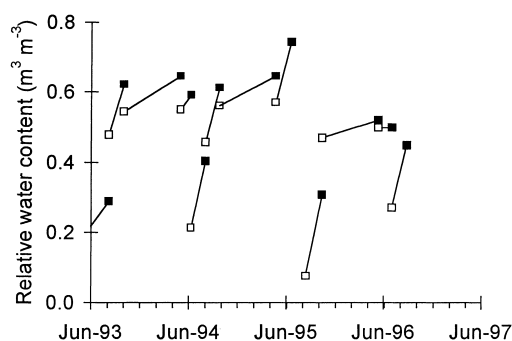

Fig. 5. Relative water content under *Calluna* in Out-C in reference samples (open squares) and incubated samples (closed symbols). The lines connect reference and incubated samples for each incubation period. The climate manipulation started in June 1994.

Table 2
Chemical characteristics of soils in control (Out-C, Roof-C) and treated (Roof-T) areas[a]

	N	Out-C		Roof-C		Roof-T	
		Calluna	*Vaccinium*	*Calluna*	*Vaccinium*	*Calluna*	*Vaccinium*
%C-LF	5	56.7 (1.9)	53.1 (2.1)	49.4 (2.7)	54.6 (0.6)	53.8 (1.0)	54.7 (0.5)
%N-LF	5	1.8 (0.3)	1.9 (0.1)	1.6 (0.3)	1.6 (0.1)	1.8 (0.1)	2.0 (0.3)
C/N-LF	5	32.5 (4.1)	28.1 (2.3)	32.0 (4.4)	35.0 (2.5)	30.9 (2.5)	28.5 (4.8)
pH-LF	5	3.49 (0.21)	3.85 (0.5)	3.94 (0.39)	3.61 (0.29)	3.68 (0.27)	3.60 (0.14)
%C-H	5	55.4 (1.4)	56.2 (0.4)	47.0 (2.6)	51.5 (2.9)	52.3 (3.0)	54.0 (0.7)
%N-H	5	1.9 (0.1)	2.0 (0.1)	1.9 (0.2)	1.6 (0.3)	2.2 (0.1)	2.2 (0.2)
C/N-H	5	29.6 (2.3)	27.5 (1.1)	24.9 (2.0)	32.6 (4.5)	24.2 (0.8)	24.7 (2.6)
pH-H	5	2.96 (0.08)	3.30 (0.3)	3.47 (0.24)	3.11 (0.22)	3.27 (0.08)	3.24 (0.12)
C ($kg\ m^{-2}$)	20	6.20 (1.62)	6.56 (1.93)	6.22 (2.71)	5.04 (1.95)	5.60 (2.78)	5.70 (2.12)
N ($kg\ m^{-2}$)	20	0.23 (0.08)	0.24 (0.08)	0.26 (0.15)	0.17 (0.08)	0.27 (0.16)	0.23 (0.12)
NH_4^+ ($mg\ kg^{-1}$)	40	22.6 (23.3)	27.3 (31.0)	9.0 (9.1)	5.5 (5.3)	7.8 (13.0)	8.2 (5.9)
NO_3^- ($mg\ kg^{-1}$)	40	0.8 (1.4)	0.5 (0.5)	0.8 (1.9)	0.2 (0.5)	0.6 (1.0)	0.3 (0.5)

[a] The standard deviation of each mean is given in parenthesis.

greenhouse did not result in changes in initial NO_3^- content and pH in the LF and H layer (Table 2). Although NH_4^+ content inside and outside the greenhouse differed, pre-treatment mineralization was similar. Inside the chamber nitrification rates under *Calluna* were higher than outside even though NH_4^+ availability was lower. Presence of a snowpack during winter in Out-C may have reduced aeration and thus development of a population of nitrifying bacteria in Out-C compared to Roof-C and Roof-T. Still, moisture content in the mineralization tubes did not differ between the covered and uncovered catchment.

3.3. Vegetation

In Out-C and Roof-T, mineralization was lower under *Calluna* than under *Vaccinium* (Fig. 2). In Roof-C and Roof-T, nitrification was significantly ($P < 0.001$) higher under *Calluna* than under *Vaccinium* (Fig. 3). Both in Out-C and Roof-T we found no significant differences in total C and N content of the 0–10 cm soil layer between *Calluna* and *Vaccinium* plots prior to the start of the treatment (Table 2). In Roof-C, total N was significantly lower and total C tended to be lower ($P = 0.067$) under *Vaccinium* than under *Calluna* which was caused by the smaller amount of soil sampled under *Vaccinium*. We also found no significant differences in initial NH_4^+ content, %C, %N, C/N ratio and pH in the LF and H layer

between the vegetation types. Only initial NO_3^- content was significantly ($P = 0.008$) higher under *Calluna* (0.7 ± 1.5 $mg\ kg^{-1}$; $n = 120$) than under *Vaccinium* (0.4 ± 0.5 $mg\ kg^{-1}$; $n = 120$). It is however unlikely that this relatively small difference in NO_3^- content explains the differences in mineralization and nitrification observed between the two vegetation types. Although litter production may vary in quality and quantity between *Vaccinium* and *Calluna*, bulk soil chemical parameters were very similar. However, a significant amount of litter is produced by the overstory vegetation and will be mixed with the *Calluna* or *Vaccinium* litter. Beier and Rasmussen (1997) estimated that annual overstory leaf litterfall at the site varied between 100–200 $g\ m^{-2}$ soil whereas annual litterfall for the understory vegetation was estimated to be around 200 $g\ m^{-2}$ soil for *Vaccinium* plots and 200-400 $g\ m^{-2}$ for *Calluna* plots with around 50% being leaf litter (Arp, pers. comm.). Consequently at least 50% of the leaf litter inputs originate from overstory vegetation.

In all sites except Roof-C, MANOVA analysis showed significant effects of vegetation on RWC with RWC being lower in *Calluna* than *Vaccinium* plots (Fig. 4). *Calluna* is largely confined to the fringes of soil pockets or other shallow areas having lower moisture supply from the subsoil. In Roof-C, the loose litter layer under *Vaccinium* may have decreased water holding capacity of the soil resulting in a relatively

lower moisture content compared to the *Vaccinium* soils in Out-C and Roof-T. Tietema et al. (1992) showed that mineralization in the organic surface horizon of a Douglas fir and mixed Douglas fir/Scots pine stand increased linearly between moisture contents of 0 and 1.5 g H_2O g dry soil^{-1} being equivalent to a RWC of approximately 0.25. Above this value no effects of moisture on mineralization were found. In our study RWC was generally higher than 0.25 (Fig. 4) so it is questionable whether differences in moisture content between *Calluna* and *Vaccinium* soils explain observed differences in mineralization. Whether differences in moisture content explain patterns in nitrification rates remains difficult to assess. Van Vuuren et al. (1992) observed lower nitrification rates under *Erica tetralix* and *Molinia* on wet sites than under *Molinia*, *Deschampsia flexuosa* and *Calluna* on dry sites most likely as a result of lower oxygen availability on the wet sites. Tietema et al. (1992) observed that nitrification increased with increasing moisture content in a Douglas fir forest whereas it was not affected by moisture in a mixed stand of Scots pine and Douglas fir. Other factors that affecting nitrification such as pH or NH_4^+ content were similar for both vegetation types.

Our data suggest that measured bulk soil chemical and physical parameters could not explain differences in mineralization and nitrification observed between *Calluna* and *Vaccinium* dominated areas. We did not have information on contents of lignin or other secondary metabolites but it is likely that *Vaccinium* leaves contain less lignin than the more woody *Calluna* leaves which may have affected N mineralization/nitrification rates.

4. Conclusions

While differences in temporal patterns in moisture between the confined and unconfined soil may have resulted in a different mineralization rates inside and outside the tubes, the measured increase in net N mineralization must be ascribed to the treatment. This is corroborated by the observations that total N uptake of *Calluna* and total inorganic N in runoff from Roof increased as a result of elevated CO_2 and temperature (Wright, 1998; Van Breemen et al., 1998). The increase in mineralization may help to sustain

increased NPP due to CO_2 fertilization as observed by Oechel et al. (1994). The increase in mineralization exceeded plant demand resulting in increased leaching of N. Wright (1998) calculated that the increase in NH_4 release during the first three treatment years in Roof-T must have been 70 mg N m^{-2} soil per year whereas NO_3 release increased by 140 mg N m^{-2} soil per year to sustain the measured increase in N runoff. The observed increase in N mineralization during the first two treatment years in Roof-T was approximately 800 mg N m^{-2} soil per year whereas nitrification increased (non significantly) by approximately 80 mg N m^{-2} soil per year taking into account the surface area covered by *Calluna* and *Vaccinium*.

Our data do not provide conclusive evidence whether the increased mineralization will be permanent or transient. For *Calluna*, mineralization continued to increase during the second year of treatment but for *Vaccinium*, the increase in mineralization was only significant in the first year of treatment. The measured increase in N mineralization may diminish with time when labile N pools are exhausted. Changes in substrate quality of litter produced under elevated CO_2 may also provide a negative feedback on N mineralization. Still, studies dealing with effects of elevated CO_2 on litter chemistry and decomposition rates (e.g. Norby et al., 1986; Cotrufo et al., 1994; Cotrufo and Ineson, 1995; Franck et al., 1997; Norby and Cotrufo, 1998) are inconclusive as to whether elevated CO_2 favors or depresses litter decomposition. Zak et al. (1993) hypothesized that increased belowground microbial activity caused by higher root exudation may stimulate net N mineralization suggesting that elevated temperature and CO_2 will both enhance each other. With the closed core incubation method used in this study no living plant roots were present so the increase in mineralization was most likely a due to higher soil temperatures rather than higher atmospheric CO_2 concentrations.

One important feature of many large-scale manipulation experiments (including ours) is that the manipulations are being implemented in a step-wise fashion whereas most environmental perturbations occur gradually. Luo and Reynolds (in press) showed that extrapolation of short-term measurement from step-wise manipulation experiments have to be interpreted with caution since many feedback mechanisms may operate on different time scales. In order to correctly

results from these studies, long-term measurements are crucial for obtaining a better understanding of the impact of environmental change on natural ecosystems.

References

Beier, C., Rasmussen, L., 1997. Tree responses. In: Jenkins, A. (Ed.), CLIMEX project: Results from the third year of treatment. Climate Change Research Report 9/1997 Norwegian Institute for Water Research, pp. 36–44.

Berendse, F., 1990. Organic matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems. J. Ecol. 78, 413–427.

Berendse, F., Beltman, B., Bobbink, R., Kwant, R., Schmitz, M., 1987. Primary production and nutrient availability in wet heathland ecosystems. Oecol. Plant. 8, 265–279.

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.

Cotrufo, M., Ineson, P., Rowland, A.P., 1994. Decomposition of tree leaf litters grown under elevated CO_2: effect of litter quality. Plant Soil 163, 121–130.

Cotrufo, M.F., Ineson, P., 1995. Effects of enhanced atmospheric CO_2 and nutrient supply on the quality and subsequent decomposition of fine roots of *Betula pendula* Roth. and *Picea sitchensis* (Bong) Carr. Plant Soil 170, 267–277.

Franck, V.M., Hungate, B.A., Chapin, F.S., Field, C.S., 1997. Decomposition of litter produced under elevated CO_2: dependence on plant species and nutrient supply. Biogeochemistry 36, 223–237.

Hendrey, G.R., Lewin, K.F., Nagy, J., 1993. Free air carbon dioxide enrichment: development, progress, results. Vegetatio 104/105, 17–32.

Hessen, D.O., Wright, R.F., 1993. Climatic effects on fresh water: nutrient loading, eutrophication and acidification. In: Holten, J.I., Paulsen, G., Oechel, W.C. (Eds.), Impacts of Climatic Change on Natural Ecosystems with Emphasis on Boreal and Arctic/alpine areas. Norwegian Institute for Nature Research, Trondheim, pp. 154–167.

Houghton, J.T., Meira Filho, L.G., Bruce, J., Hoesung, L., Callander, B.A., Haites, E., Harris, N., Maskell, K., 1995. Climate Change 1994. Cambridge University Press, Cambridge, UK

Jenkins, A., Wright, R.F., 1995. The CLIMEX project: Performance of the experimental facility during the first year of treatment. In: Jenkins, A., Ferrier, R.C., Kirby, C. (Eds.), Ecosystem Manipulation Experiments. Commission of European Communities, Brussels, pp. 323–328.

Koorevaar, P., Menelik, G., Dirksen, C., 1983. Elements of Soil Physics. Developments in Soil Science 13. Elsevier, Amsterdam, 230 pp.

Luo, Y., Reynolds, J.F., in press. Validity of extrapolating field CO_2 experiments to predict carbon sequestration in natural ecosystems. Ecology.

Marnette, E.C.L., Stein, A., 1993. Spatial variability of chemical compounds related to S-cycling in two moorland pools. Water Res. 27, 1003–1012.

Miglietta, F., Raschi, A., 1993. Studying the effect of elevated CO_2 in the open in a naturally enriched environment in Central Italy. Vegetatio 104/105, 391–402.

Mitchell, M.J., Raynal, D.J., White, E.H., Stehman, V.S., Driscoll, C.T., David, M.B., McHale, P.J., Bowles, F.P., 1994. Increasing soil temperature in a northern hardwood forest: effects on elemental dynamics and primary productivity. USDA Forest Service.

Norby, R.J., O'Neill, E.G., Luxmoore, R.J., 1986. Effects of atmospheric CO_2-enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient-poor soil. Plant Physiol. 82, 83–89.

Norby, R.J., Cotrufo, M.F., 1998. A question of litter quality. Nature 396, 17–18.

Oechel, W.C., Cowles, S., Grulke, N., Hastings, S.J., Lawrence, B., Prudhomme, T., Riechers, G., Strain, B., Tissue, D., Vourlitis, G., 1994. Transient nature of CO_2 fertilization in Arctic tundra. Nature 371, 500–503.

Overpeck, J.T., Rind, D., Goldberg, R., 1990. Climate-induced changes in forest disturbance and vegetation. Nature 343, 51–53.

Peterjohn, W.T., Melillo, J.M., Bowles, F.P., Steudler, P.A., 1993. Soil warming and trace gas fluxes: experimental design and preliminary flux results. Oecologia 93, 18–24.

Raison, R.J., Connell, M.J., Khanna, P.K., 1987. Methodology for studying fluxes of soil mineral-N in situ. Soil Biol. Biochem. 19, 521–530.

Rastetter, E.B., McKane, R.B., Shaver, G.R., Melillo, J.M., 1992. Changes in C storage by terrestrial ecosystems: how C–N

interactions restrict responses to CO_2 and temperature. Water Air Soil. Pol. 64, 327–344.

Rustad, L.E., Fernandez, I.J., Arnold, S., 1995. Experimental soil warming effects on C, N and major element cycling in a low elevation spruce-fir forest soil. In: Hom, J., Birdsey, R., O'Brien, K. (Eds.), Gen. Tech. Rep. NE Radnor USDA Forest Service, PA, pp. 1–7.

Schachtschabel, P., Blume, H.P., Hartge, K.H., Schwertmann, U., 1984. Lehrbuch der Bodenkunde. Ferdinand Enke Verlag, Stuttgart.

Schimel, D.S., Braswell, B.H., McKeown, R., Ojima, D.S., Parton, W.J., Pulliam, W., 1997. Climate and nitrogen controls on the geography and timescales of terrestrial biogeochemical cycling. Global Biogeochemical Cycles 10, 677–692.

Skopp, J., Jawson, M.D., Doran, J.W., 1990. Steady-state aerobic microbial activity as a function of soil water content. Soil Sci. Soc. Am. J. 54, 1619–1625.

Tietema, A., Warmerdam, B., Lenting, E., Riemer, L., 1992. Abiotic factors regulating nitrogen transformations in the organic of acid forest soils: moisture and pH. Plant Soil 147, 67–78.

Van Breemen, N., Jenkins, A., Wright, R.F., Arp, W.J., Beerling, D.J., Berendse, F., Beier, C., Collins, R., Van Dam, D., Rasmussen, L., Verburg, P.S.J., Wills, M.A., 1998. Impacts of elevated carbon dioxide and temperature on a boreal forest ecosystem (CLIMEX project). Ecosystems 1, 345–351.

Van Vuuren, M.M., Aerts, R., Berendse, F., De Visser, W., 1992. Nitrogen mineralization in heathland ecosystems dominated by different plant species. Biogeochemistry 16, 151–166.

Wright, R.F., 1998. Effect of increased CO_2 and temperature on runoff chemistry at a forested catchment in southern Norway (CLIMEX project). Ecosystems 1, 216–225.

Wright, R.F., Lotse, E., Semb, A., 1993. RAIN project: Results after 8 years of experimentally reduced acid deposition to a whole catchment. Can. J. Fish. Aquat. Sci. 50, 1–11.

Wright, R.F., Schindler, D.W., 1995. Interaction of acid rain and global changes: effects on terrestrial and aquatic ecosystems. Water Air Soil. Pol. 85, 89–99.

Zak, D.R., Pregitzer, K.S., Curtis, P.S., Teeri, J.A., Fogel, R., Randlett, D.L., 1993. Elevated atmospheric CO_2 and feedback between carbon and nitrogen cycles. Plant Soil 151, 105–117.