Oecologia (1993) 95:179–186

Oecologia

In situ mineralization of nitrogen and phosphorus of arctic soils after perturbations simulating climate change

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Received: 10 October 1992 / Accepted: 5 April 1993

Abstract. Seasonal net nitrogen (N) and phosphorus (P) mineralization was investigated at Abisko, Swedish Lapland in soils of a subarctic heath and in soils of a colder (by about 4° C), high altitude fellfield by (a) using *in situ* soil incubation in soils which had been shaded or subjected to two levels of increased temperature, combined with (b) reciprocal transplantation of soils between the two sites. Proportionally large and significant net seasonal mineralization of N, in contrast to non-significant P mineralization, was found in untransplanted and transplanted fellfield soil. In contrast, P was mineralized in proportionally large amounts, in contrast to low N mineralization, in the transplanted and untransplanted heath soil. The differences indicate that P was strongly immobilized in relation to N at the fellfield and that N was more strongly immobilized than P in the heath soil. The immobilization in both soils remained high even after a temperature change of 4–5° C experienced by transplanted soils. Air temperature increases of up to 4–5° C in greenhouses resulted in a soil temperature increase of 1–2° C and did not cause any extra increase of net N and P mineralization. The results suggest that soil temperature increases of up to 2° C, which are likely to occur by the end of the next century as an effect of a predicted 4–5° C rise in air temperature, have only small effects on net mineralization in at least two characteristic tundra soils. These effects are probably smaller than the natural fluctuation of plant available nutrients from site to site, even within the same plant community. A further soil temperature increase of up to 4–5° C may enhance decomposition and gross mineralization, but the rate of net mineralization, and hence the change of nutrient availability to the plants, depends on the extent of microbial immobilization of the extra nutrients released.

Key words: Arctic-Alpine – Climate change – N and P mineralization – Nutrient immobilization – Soils

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The large organic deposits in northern taiga and tundra ecosystems contain about one-third of the world's pool of soil carbon (Oechel and Billings 1992 and references therein). In these ecosystems, at least 95% of organically bound plant nutrients are incorporated in the soil pool (Marion et al. 1982; Jonasson 1983). The availability to the plants of this nutrient pool depends largely on the biological processes of microbial decomposition and immobilization.

The rate of microbial decomposition, defined here as the degradation of organic matter to CO_2, H_2O and other inorganic compounds, is strongly regulated in northern ecosystems by substrate quality, temperature and soil moisture (Flanagan and Veum 1974; Heal and French 1974; Heal et al. 1981). This process controls the carbon flow from soil to atmosphere and also controls the release of plant available inorganic nutrients from the organically bound, and usually plant unavailable, state in the soil organic matter (the gross mineralization). The decomposition rate is, however, not a good predictor of the rate at which nutrients are made available to the plants, because nutrients which are released are withdrawn to varying degrees from the pool available to plants by immobilization in the microbiota and by non-biological fixation to the soil (Marion et al. 1982; Jonasson and Chapin 1991; Nadelhoffer et al. 1991). Also, an unknown amount of nutrients is released from the organic matter and transported directly to the plants by mycorrhizal fungi (Read 1991), and some plant species can even use organic nitrogen by absorption of amino acids (Chapin et al. 1993). Due to the immobilization and fixation processes, the net nutrient mineralization, i.e. the net release of inorganic nutrients after gross mineralization, microbial immobilization and non-biological fixation, is often much lower than the gross mineralization, and negative net mineralization during a growing season, i.e. a loss of nutrients from the initially available pool, is not uncommon (Chapin et al. 1988; Nadelhoffer et al. 1991; Giblin et al. 1991). The trade-off of soil nutrients between uptake by microorganisms and plants should be particularly significant in arctic ecosystems because low

nutrient availability is a major factor regulating primary production and community composition there (Haag 1974; Ulrich and Gersper 1978; Shaver and Chapin 1980; Jonasson 1992).

For the next century, it has been predicted that the global mean air temperature will increase by 4–5° C as an effect of the emission of greenhouse gases (Mitchell et al. 1990), with an above-average increase in polar areas. Such a rise could have large effects on nutrient and carbon turnover in the Arctic due to the strong regulating effect of temperature on decomposition and nutrient mineralization (Nadelhoffer et al. 1992). On a global scale, the possible enhancement of decomposition in arctic soils could increase the net carbon flux to the atmosphere and create a globally significant positive feedback to climate change (Chapin et al. 1992).

In this study we explore the possible effects of predicted global warming on nutrient mobilization by analysing temperature effects on net nutrient mineralization. Firstly, we report our measurements of the seasonal net nutrient release from soils of two similar vegetation types at a low and a high altitude site, both in the subarctic, with different soil temperature regimes. Secondly, we demonstrate how net nutrient mineralization responds to experimental manipulations of the environment simulating various aspects of climate change.

Methods

Environmental perturbations

The study took place during the summer of 1991 in two plant communities dominated by the circumpolar dwarf shrub *Cassiope tetragona* at Abisko in northern Swedish Lapland. One community was located within a subalpine heath close to the tree limit at 450 m above sea level, and the other was at a fellfield at 1150 m a.s.l. The vegetation and other site characteristics are described in Havström et al. (1993).

Temperature and light were manipulated at each site within six blocks of 400 m^2 by erecting dome-shaped plastic greenhouses and shading screens (both about 50 cm high and with 1.2×1.2 m surface area) just after snow melt. Two types of greenhouses were built, one with a 5–10 cm gap above the ground on two sides, and the other with the plastic tightly fixed to the ground. Both types had a ventilation vent at the top, and gave a low and a high temperature increase, respectively (see Havström et al. 1993). The plastic was a 0.05-mm thick polyethylene film supported by PVC tubes. The shading treatment, which reduced light by about 60%, consisted of a similar construction, but covered by hessian (sack-cloth) instead of polyethylene film. The manipulations were initiated in the summer of 1989 for a related research project, i.e. 2 years before this study. That project also included a combination of nutrient addition treatments with each of the temperature and light manipulations. Each block contained, therefore, one unfertilized and one fertilized set of shading, low- and high-temperature enhancement treatments, and fertilized and unfertilized controls; i.e. eight treatments altogether, replicated over the six blocks.

Hourly air and soil mean temperature responses to the manipulations were measured during three periods between 29 June and 6 September (see Table 1) using a Delta Logger (Delta-t devices Ltd., Cambridge, UK). The total lengths of the recording periods were 503 h at the heath site and 583 h at the fellfield site. We measured air temperature in the plant canopy by connecting copper-constantan thermocouples to the shoots of *Cassiope* at about 10 cm above ground, and soil temperature by inserting similar thermocouples into the soil at 3–5 cm depth, corresponding to the depth of the bulk of the root mass. Temperatures were recorded in three plots of each treatment every 10 s and were later integrated into hourly means. The installation was calibrated on a day when the plastic and shading screens had been removed.

In addition, we measured the integrated air temperature over the whole growing season in three replicates of the different treatments using plastic cells filled with a water-absorbing resin. These cells are permeable to water and increase their weight by humidity absorption in a manner proportional to ambient temperature (Ambrose 1980). The cells were immersed in distilled water in a small glass container and hung by nylon threads inside miniature Stevenson screens built of opaque plexiglass at 0.3 m above ground surface. They were left in the field during the same period that the greenhouses and shading screens were in place and weighed before and after exposure. The average temperature was calculated according to a calibration formula provided by the manufacturer (Th Cells, Woden, Australia).

Soil collection

On 19 (heath) and 26 June (fellfield) 1991, soon after thawing of the soil, we collected a soil plug from the humus layer of a *Cassiope* stand of each unfertilized treatment plot and from the area just outside the fertilized plots, i.e. 48 plugs altogether. Each soil plug was divided into two equal parts of about 4×4 cm area and 5 cm depth at the heath site, and $5 \times 5 \times 3$ cm at the fellfield site. The depths of the soil plugs corresponded approximately to the humus depths at the collection points. One set of the cut plugs was immediately brought to the laboratory for extraction of inorganic nitrogen (N_i) and phosphorus (P_i), and the other was put in sealed polyethylene bags, to prevent uptake of mineralised nutrients by plant roots, and placed inside the experimental plots close to the location of sampling near a *Cassiope* stand, or for those collected outside the fertilized plots, close to a *Cassiope* stand within the plots. The upper part of the soil plugs was adjusted to the upper level of the humus layer and covered with a moss layer collected from the adjacent vegetation mat. The polyethylene is impermeable to water, but allows gas exchange (Eno 1960). Note that no soil plugs were collected from the fertilized plots. These plots were used only for incubation, in order to increase the total number of incubation plots.

Another set of 60 plugs was collected at a vegetationally similar and homogeneous small area of about 1×1 m outside the blocks at both sites. Twelve of these plugs were brought to the laboratory for immediate analysis, and the remaining 48 were stored overnight at 4° C and reciprocally transplanted and incubated, as above, on the day after collection between the 8×6 plots of the heath and fellfield sites, close to the other non-transplanted, incubated plugs.

On 2 (fellfield) and 6 (heath) September 1991, we collected all of the incubated plugs, plus new plugs of undisturbed soil from the previous collection sites (non-temperature manipulated plots only).

The sampling scheme thus allows us to examine:

1. The seasonal changes of plant available N and P in soils subjected to plant nutrient uptake and mineralization over the growing season; from the content of N_i and P_i of unincubated and undisturbed soil in spring and autumn
2. The seasonal net N and P mineralization; from differences in the content of N_i and P_i of unincubated soils in spring and that of incubated soil samples in autumn
3. Temperature effects on mineralization; from the experimental perturbation, the reciprocal transplant of soil plugs and from the natural temperature gradient of soils between the two altitudes

Soil analyses

In the laboratory, the soil was weighed after removal of living roots and stones > 2 mm diameter. A subsample of 15 g of fresh soil from

each plug was extracted immediately in 100 ml 1*M* KCl for 1 h, filtered and the extracts were frozen. The remaining soil was dried at 70° C to constant weight after which the water content was calculated. A subsample of the dried soil was ashed to determine loss on ignition and was used to estimate soil organic matter (SOM). Another twelve subsamples of the soils used for transplantation, and of those used for incubation at the site of collection, were analysed for total N and P after digestion in a mixture of sulphuric and selenous acids (Kedrowski 1983).

Total N and extractable NH_4^+ were determined by the salicylate method, NO_3^- by the cadmium reduction method and total and extractable P were analysed by the molybdate method. The concentration values of extractable ions were recalculated to content per unit SOM after taking the differences of water content and loss on ignition of the extracted samples into account. The samples were analysed blockwise in appropriate time sequences (e.g. June samples, followed by incubated and unincubated samples collected in September) to minimize any risk of systematic analytical errors. The analytical instruments, a spectrophotometer for the analysis of NH_4^+ and the Aquatec system (Tecator, Höganäs, Sweden) for all other analyses, were recalibrated after measurements of the samples within each block had been completed. Due to the mosaic pattern of the vegetation, the blocks were not considered to be statistical blocks, but merely a means of dispersing the treatments evenly over the areas of investigation.

Results

Environmental perturbations

The average air temperature over the measuring period was 10.9° C at the heath site and 6.8° C at the fell-field (Table 1). The lower temperature enhancement treatment raised the mean air temperature of the heath plots significantly by an average of 2.8° C and the fellfield plots by 2.4° C whereas the higher temperature enhancement treatment increased the air temperatures by 3.9 and 4.9° C, respectively. The temperatures of the shaded plots differed from the controls by 0.1° C: hence, the shading screen had a negligible effect on the air temperature.

The day-time (0700–1900 hours) canopy temperature (not shown) was raised by 2.6 and 4.6° C in the low- and high-temperature enhancement treatments at the heath site, and by 2.4 and 5.9° C in the corresponding treatments at the fellfield site. The shading screen had a slight effect, decreasing the canopy temperature at the heath site from 11.5 to 10.9° C and at the fell-field site from 10.4 to 9.6° C. All differences were significant at $P<0.05$ (Scheffe's *S*-test). Night temperatures (1900–0700 hours) differed by a maximum of 0.5° C between controls and treatments.

Day-time soil temperature at the heath varied considerably less than the air temperature there (Table 1). Both the low and the high temperature enhancement treatments increased soil temperature significantly by 0.9° C. The shading screen, however, had a cooling effect lowering the soil temperature significantly by 2.0° C. On the fellfield, soil temperature was increased significantly by 1.1 and 1.9° C in the two temperature-enhancement treatments and was decreased slightly, by 0.4° C, in the shading treatment. As with the air and canopy temperature, there were no changes in soil temperature at night time.

Since the soil temperatures (but not the integrated air temperature) had to be measured on different occasions at the two sites for practical reasons, the soil temperatures in Table 1 can only be compared between treatments, and not between sites. The soil temperature at the fellfield was measured during periods when the air temperature at the meteorological station at Abisko was

Table 1. Temperatures, water content (% wet weight) and % soil organic matter in control and treatment plots at the heath and fellfield

Treatment	Integrated air temp.	Soil temp.	Water content		Soil organic matter
			June	September	
Heath					
Control	10.9 ± 0.03^a	9.1 ± 0.17^a	78.3 ± 0.9^a	80.5 ± 0.7^a	79.9 ± 3.2^a
Shade	11.0 ± 0.05^a	7.1 ± 0.14^b	78.7 ± 1.2^a	81.2 ± 1.4^a	78.0 ± 4.3^a
Low temp.	13.7 ± 0.12^b	10.0 ± 0.06^c	79.6 ± 0.8^a	81.1 ± 0.8^a	83.1 ± 2.5^a
High temp.	14.8 ± 0.46^b	10.0 ± 0.14^c	80.9 ± 0.6^a	82.9 ± 0.4^a	84.9 ± 1.8^a
n	3	3	12	12	12
$F_{df\ groups,\ error}$	$66.6_{3,8}$	$109.9_{3,8}$	$1.51_{3,44}$	$1.36_{3,44}$	$0.99_{3,44}$
P	0.0001	0.0001	0.224	0.269	0.405
Fellfield					
Control	6.8 ± 0.09^a	7.8 ± 0.11^a	67.3 ± 2.7^a	71.9 ± 1.4^a	53.6 ± 5.3^a
Shade	6.9 ± 0.10^a	7.4 ± 0.07^b	69.5 ± 1.9^a	71.7 ± 2.1^a	54.7 ± 4.6^a
Low temp.	9.2 ± 0.19^b	8.9 ± 0.22^c	67.8 ± 2.4^a	70.4 ± 2.0^a	52.9 ± 4.7^a
High temp.	11.7 ± 0.07^c	9.7 ± 0.18^d	67.3 ± 2.4^a	70.5 ± 2.0^a	53.2 ± 5.7^a
n	3	3	12	12	12
$F_{df\ groups,\ error}$	$361.5_{3,8}$	$45.4_{3,8}$	$0.20_{3,44}$	$0.16_{3,44}$	$0.03_{3,44}$
P	0.0001	0.0001	0.894	0.923	0.995

Data are means ± SE. For each column, means with the same superscript letter are not significantly different from one another. (Scheffe's *S*-test where significance was obtained by one-way ANOVA). Soil temperatures are presented as integrated hourly means and were measured on 3–10 July, 6–16 August and on 4–6 September on the heath and on 29 June–2 July, 25 July–5 August and on 22 August–1 September on the fellfield. Integrated air temperatures were measured from 29 June to 6 September (heath) and 2 September (fellfield), and water content in heath soil was measured on 19 June and 6 September and in fellfield soil on June 26 and September 2

on an average 2–3° C higher than during the period of soil temperature measurement at the heath site. We assume therefore, that the average seasonal soil temperature was at least 4° C higher at the heath site than at the fellfield. This assumption is supported by the integrated air temperature measurements (Table 1) and the differences expected from an altitudinal lapse rate of 0.6° C per 100 m (Callaghan et al. 1989).

Soil organic content, soil moisture and total N and P content

The loss on ignition, approximating soil organic content, was about 80% in the heath soil and about 55% in the fellfield soil. Soil water content in June varied around 79% of the wet weight of the heath soil, and around 68% of the fellfield soil (Table 1). The water content of the incubated plugs in September did not differ significantly between the treatments (Table 1), nor were there any treatment effects on the water content of undisturbed soils within the plots (Havström et al. 1993), which was comparable to the June level.

Total soil N, calculated as percentage of soil dry weight (Table 2) was higher in the heath soil than in the fellfield soil, whereas the P content was higher in the fellfield soil. However, because the fellfield soil contained less organic matter than the heath soil, calculations based on soil organic matter (SOM) gave higher N, and particularly P, values in the fellfield soil than in the heath soil (Table 2).

Soil inorganic N and P content in untransplanted samples

There was no significant difference ($P > 0.05$, one-way ANOVA) in soil NH_4^+ or inorganic P content across the blocks, the treatment plots ($P > 0.05$, one-way ANOVA; Fig. 1) or between samples collected inside and outside temperature- and light-manipulated plots in June ($P > 0.05$, two-way ANOVA) when the experiment started. The content of NO_3^- in both the heath and the fellfield soils was negligible and the P_i content in the fellfield soil was < 1 μg g^{-1} SOM and not possible to measure with confidence. The non-significant differences across treatment plots allow us to assume that the 2 years of treatment before the start of the experiment had little or no effect on the extractable nutrient pools. Nor was there any significant difference in September between the chemical content of soil plugs incubated in fertilized and unfertilized plots ($P > 0.05$, two-way ANOVA). Any possible indirect effect of fertilization on mineralization, as e.g. changed radiation regime to the soil by enhanced plant growth was, consequently, too weak to affect the rate of mineralization. This allows us to consider the experiments as consisting of four treatments: (a) control, (b) low temperature enhancement, (c) high temperature enhancement and (d) shading, each with 12 replicate samples.

Comparisons of undisturbed soils between June and September showed that (a) mean September levels of N_i in undisturbed soil from the heath tended to be lower ($P = 0.07$; t- test) than the June levels, whereas (b) the P_i content of the heath soil and the content of N_i in the fellfield soil tended to increase over the summer ($P = 0.11$ and 0.09, respectively; Fig. 1).

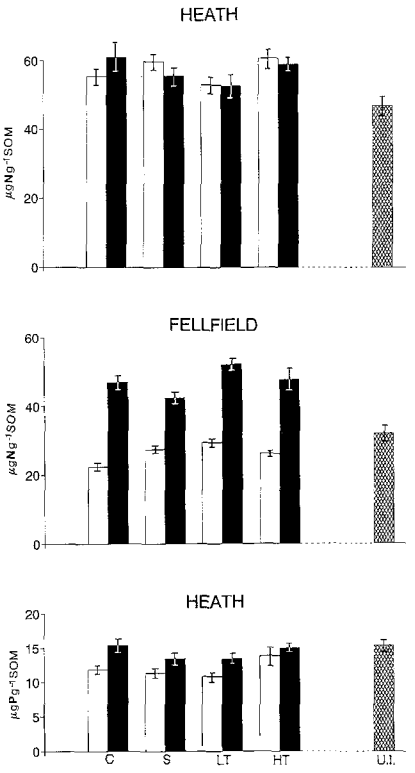

Fig. 1. Spring (June) and autumn (September) concentrations of inorganic nitrogen and phosphorus per gram soil organic matter (*SOM*) in control (*C*), shaded (*S*), low-(*LT*) and high-temperature (*HT*) greenhouses at the low-altitude heath and the high-altitude fellfield. (P_i levels at the fellfield were too low to be measured accurately). June concentrations: *open bars;* incubated September samples: *filled bars;* unincubated September controls (U.I.): *hatched bars*. The differences between spring and autumn samples were significant at $P < 0.001$ for N_i on the fellfield and at $P < 0.08$ for P_i on the heath, but the seasonal differences of N_i on the heath and all treatment effects were not significant (paired comparisons two-factor ANOVA)

Table 2. Content of total N and P (means ± SE) in untransplanted and transplanted soils of the heath and the fellfield ($n = 12$)

	Untransplanted soils		Transplanted soils	
	% Dry wt	% SOM	% Dry wt	% SOM
Nitrogen				
Heath	1.72 ± 0.09	2.31 ± 0.17	1.33 ± 0.05	1.52 ± 0.06
Fellfield	1.14 ± 0.09	2.53 ± 0.11	0.98 ± 0.11	2.48 ± 0.11
Phosphorus				
Heath	0.09 ± 0.003	0.12 ± 0.014	0.07 ± 0.002	0.08 ± 0.002
Fellfield	0.12 ± 0.007	0.26 ± 0.019	0.11 ± 0.007	0.29 ± 0.016

SOM: soil organic matter

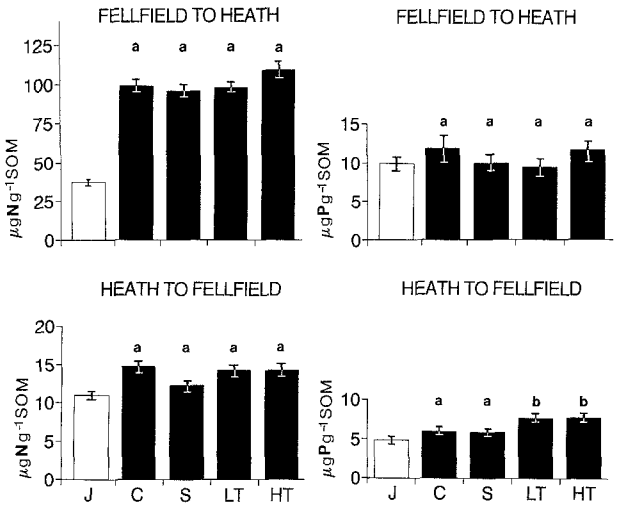

Fig. 2. Spring *(open bars)* and autumn *(filled bars)* concentrations of inorganic N and P in samples reciprocally transplanted between the heath and fellfield sites. *J* is data on June samples and the treatments are denoted as in Fig. 1. Identical *letters* above the bars denote non-significant treatment effects during summer incubation. Seasonal differences were significant for N_i in both reciprocally transplanted soils (both $P<0.001$, *t*-test) and for P_i in heath soil transplanted to the fellfield ($P=0.08$ for transplant to the non-temperature increased control plus shaded plots and $P<0.001$ for transplants to the temperature-increased plots)

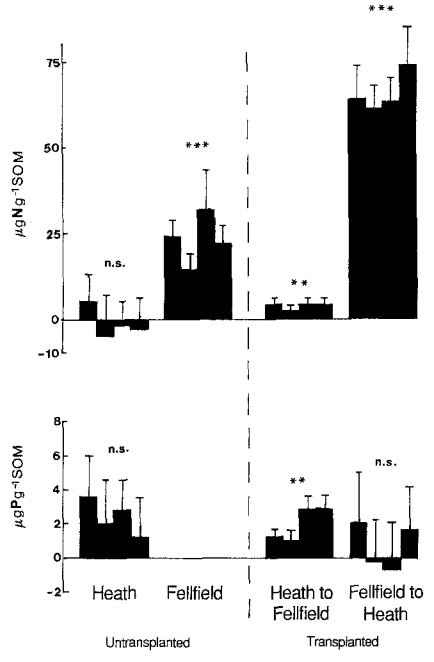

Fig. 3. Net seasonal N and P mineralization in untransplanted and transplanted soils of the heath and fellfield measured as differences in levels of inorganic N and P after one summer's soil incubation. *Bars* from *left to right* of each group are: controls, shaded, low and high temperature enhancement treatments. Significance levels for net mineralization are: ** $P<0.01$ and *** $P<0.001$. The statistical tests are as in Figs. 1 and 2

Comparisons of undisturbed soils in September with incubated soils in September showed that (a) the incubation raised the N_i level of the fellfield soil above that of the undisturbed soil ($P=0.02$), whereas (b) there were no significant differences in N_i and P_i levels between the incubated and undisturbed soil of the heath ($P=0.13$ and 0.62, respectively; Fig. 1). The P_i levels at the fellfield, and the NO_3^- level at both sites, were still too low to be measured with confidence.

Comparisons of undisturbed soils in June with incubated soils in September showed that (a) the content of N_i in the fellfield soil increased significantly, and almost doubled (Fig. 1), in comparison to the levels in June, thus indicating significant net mineralization. (b) P_i increased by 19% in the heath soil, which was close to significant ($P=0.08$), whereas (c) the level of N_i in the heath soil did not change significantly from June to September ($P=0.97$) and (d) P_i remained at a low and immeasurable level in the fellfield soil over the summer. The changes in temperature and radiation regimes caused by the greenhouses and the shading screens did not, however, stimulate any significant treatment effects ($P>0.05$) on inorganic N or P pool sizes in the incubated samples (all analyses performed with a paired comparisons factorial ANOVA with time of the year and the temperature manipulations as factors; Sokal and Rohlf 1981).

Soil inorganic N and P in transplanted samples

The initial, June, levels of inorganic N and P in soil for transplantation collected outside the experimental blocks at the heath were significantly lower than those of the soil collected inside the experimental blocks (cf. Figs. 1 and 2). In contrast, the initial N_i level of the fellfield soil used for transplantation was about one third higher, and the soil contained considerably more P_i than the soil of the experimental blocks of the same site (9.9 μg P_i g^{-1} SOM as compared with the unmeasurable amounts inside the blocks). These differences occurred even though the soil samples at both the heath and fellfield sites were collected close to each other and in the same vegetation type.

As with the untransplanted samples, the temperature and shading manipulations had no effect on the levels of inorganic N but average N_i levels across all treatments were significantly higher in September than in June in both soils (Figs. 2, 3). The increase, which demonstrates net N mineralization, was particularly pronounced in the fellfield soil moved to the heath, in which N_i increased by a factor of 3, whereas it increased by about 30% in soils transplanted from the heath to the fellfield. N_i, in all cases, refers to NH_4^+–N, as the level of NO_3^-–N was low and could not be measured accurately.

Inorganic phosphorus in soils transplanted from the fellfield to the heath showed, in contrast to N_i, no significant net mineralization (Fig. 3), but the samples transplanted in the opposite direction increased their P_i content by 20% ($P=0.08$, *t*-test) after incubation in control plots, and by 60% ($P<0.001$) when incubated in the temperature enhancement plots.

Discussion

Environmental effects of the perturbations

The increases of air temperature by 2–3° C above ambient in the low temperature enhancement treatment, and by 4–5° C in the high temperature treatment correspond closely to the predicted range of increase for the next century as a consequence of a doubling of atmospheric CO_2 concentration (Mitchell et al. 1990). The soil temperature increase of only about 1° C at the heath and of 1.2–1.9° C on the fellfield is, however, somewhat lower than that of 2–3° C predicted to occur after a 50-year period during which air temperature was predicted to increase by 4° C (Kane et al. 1992). Other studies (Wookey et al. in press) show similar relationships between air warming and soil temperature change to ours, and indicate that soils even may cool slightly with air warming.

In contrast to the temperature, the soil moisture levels were not significantly affected by the treatments. The lack of differences even between open controls and plastic-covered greenhouses could be due to the gently sloping ground at both sites, permitting lateral soil water transport into the covered plots.

Net nutrient mineralization and responses to the manipulations

At the heath site, net N mineralization (Fig. 3) was low in both the untransplanted and transplanted soil, as indicated by the small differences between the initial N_i concentration in June and that of the incubated soil in September (Fig. 1), whereas P was mineralized in close to significant ($P < 0.08$) amounts (Fig. 3). In contrast, at the fellfield site, N mineralization was proportionally high ($P < 0.001$) both in the untransplanted and transplanted soil types, and P mineralization extremely low (transplanted soil) or even unmeasurable (untransplanted soil). This shows that the total content of N and P in the soils (Table 2) was a poor predictor of net mineralization and nutrient availability: the content of total P was highest in soils of the fellfield (Table 2) where net P mineralization and the inorganic P pool was lowest, and the level of total N per unit SOM was comparable at the two sites, at least in untransplanted soils, but the net mineralization differed greatly.

As with soil N and P content, the vegetation type was apparently also a poor predictor of plant nutrient availability: the amounts of N_i and P_i varied greatly between the set of samples collected within the blocks (Fig. 1) and those used for transplantation but collected just outside the blocks (Fig. 2). For instance, the P_i level, which was too low to be measured within the blocks at the fellfield, was much higher in the soil collected outside the blocks (Fig. 2). This was unexpected because both sites had seemingly homogeneous vegetation.

Contrary to what we had expected, there were no effects on net mineralization of the temperature manipulations (Fig. 1), showing that an increase of the air temperature by up to 5° C does not necessarily have a seasonal or a short-term effect on net nutrient mineralization. This is probably because the air temperature rise was followed by a smaller increase (only 1–2° C) of soil temperature than might be expected from the warming of the air.

Nutrient immobilization

Strong microbial N immobilization has been shown in forest (Vitousek and Matson 1985) and tundra soils (Marion et al. 1982), and low plant uptake of P in a permafrost soil was most likely caused by biological or non-biological P fixation in the soil (Jonasson and Chapin 1991). Furthermore, microbial immobilization is the most probable reason for low recovery of nutrients in nutrient-limited tundra vegetation after application of fertilizer (Shaver et al. 1986), although some arctic plants with conservative strategies may be selectively unresponsive to extra nutrients. Also, weak responses in tundra plant growth to fertilizer applied in relatively small amounts (an order of magnitude greater than the annual incorporation into the vegetation), as compared to application of amounts 5 times higher (Shaver and Chapin 1980) could indicate microbial immobilization of nutrients. In fact, it has been suggested that plants of nutrient-deficient communities have a limited response to enhancement of the soil nutrient pool because of strong competition for nutrients by decomposers (Chapin et al. 1986).

Our results support these indications of nutrient immobilization in tundra soils. The proportionally high net N and low (unmeasurable) P mineralization in the fellfield soil (Fig. 3) indicates that P was strongly immobilized in comparison to N during the decomposition process. This pattern was similar in the fellfield soil transplanted to the heath (Fig. 2), in which the P_i content did not change during the summer incubation at a soil temperature 4–5° C above that at their site of origin, i.e. there was no net mineralization of P (Fig. 3) whereas the N content tripled. In contrast, N_i in heath soil did not increase during the incubation and was, hence, more strongly immobilized than P which increased by 20% at this site. The same pattern was apparent also in the heath soil transplanted to the fellfield in which both N_i and P_i increased (Fig. 3) but the proportional increase in P_i, and hence net mineralization, was greater than that of N_i (Fig. 2). Consequently, one or a few nutrients can be strongly immobilized while others are not. Furthermore, this immobilization can remain high even after a large temperature increase such as that of 4–5° C experienced by fellfield soil transplanted to the heath.

The small and nonsignificant difference of inorganic N, and the lack of difference of inorganic P, between incubated soils and the September pool of nutrients in undisturbed heath soil (Fig. 1) provide an additional indication of strong nutrient immobilization. Since plant nutrient uptake could not take place in the incubated samples, their nutrient levels should have been higher unless immobilization was also high.

Plant nutrient supply in a changing climate

Previous studies, e.g. by Billings and coworkers (Billings et al. 1982, 1983), have shown significant responses of soil respiration to increased temperatures, and it has been assumed that increases in temperature due to climate change would lead to a significant positive feedback to climate change and would also stimulate the release of soil nutrients (e.g. Melillo et al. 1990). However, our results do not indicate that an air temperature rise of 4–5° C will exert any strong effect on net nutrient mineralization and therefore, plant nutrient availability, for three main reasons. Firstly, since the soil temperature increase will probably be lower than the change in air temperature, at least during the first decades of air warming (Kane et al. 1992; Wookey et al. in press; this study), and because the net nutrient mineralization is relatively insensitive to temperature changes within the range of normal between-year variations (Nadelhoffer et al. 1991), any notable effect of increasing mineralization would require a rise of the summer air temperature by more than 4–5° C. Such an increase has indeed been predicted for the Arctic (Maxwell 1992), but it is suggested to result mainly from increases in winter temperatures, rather than those in summer which affect soil processes.

Secondly, the instantaneous pool of plant available nutrients and the net mineralization (Giblin et al. 1991; Nadelhoffer et al. 1991; this study) fluctuate widely from site to site, even within the same plant community. The changes of nutrient availability to the plants which could occur after a few degrees of warming will, therefore, probably be small in comparison with the spatial heterogeneity of nutrient availability. Consequently, only limited changes in plant community composition would be expected.

Thirdly, if the same nutrient element is limiting both plant and microbial growth, any increase in that particular nutrient due to enhanced microbial activity in a warmer soil could cause increased microbial immobilization, such as that indicated in our study, rather than enhanced plant uptake. However, in the longer term, enhanced microbial respiration combined with strong nutrient immobilization will result in a continuous decline of the carbon-to-nutrient ratio of the soil organic matter, an improvement of its quality for the decomposers, a release of the decomposers from nutrient limitation, followed by a subsequent increase of nutrients available to the plants.

In addition to our evidence that a moderate rise in temperature will not have any strong effect on net nutrient mineralization and plant nutrient availability, there is evidence that other aspects of climate change may actually reduce plant nutrient availability (Callaghan et al. 1992). Thus, increased C:N ratios in plant material grown in high CO_2 environments reduce initial decomposition rates (Couteaux et al. 1991) while increases in UV–B radiation change plant litter quality (Tevini and Teramura 1989) and may further reduce decomposition. On the other hand, plant nutrient availability may increase for other reasons and affect plant productivity or community composition; e.g. by changed moisture regime (Billings et al. 1983; Oechel and Billings 1992), extension of the growing season, or by increased exploitation of soil volume for plant roots if the active layer increases in depth in permafrost areas.

Acknowledgements. We are much indebted to Professor Mats Sonesson and the staff at the Abisko Scientific Research Station for logistic support, to Dr. Frank Berendse, Professor Terry Chapin and Dr. Anders Michelsen for critical comments of earlier versions of the manuscript, to Eva Nilsson, Kirsten Bach Jensen and Vivian Alden for laboratory assistance, and to Karin Larsen for preparing the figures. The work was financed by the Swedish Natural Science Research Council grant No. B–BU 4903–307.

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