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Mineralization and distribution of nutrients in plants and microbes in four arctic ecosystems: responses to warming

I.K. Schmidt[1,2,3], S. Jonasson[1], G. R. Shaver[2], A. Michelsen[1] & A. Nordin[2]
[1]*Botanical Institute, University of Copenhagen, Øster Farimagsgade 2 D, DK-1353 Copenhagen K, Denmark (address for correspondence: Danish Forest and Landscape Research Institute, Hørsholm Kongevej 11, DK-2970 Hørsholm, Denmark);* [2]*The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543, USA;* [3]*Corresponding author**

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Abstract

Mineralization and nutrient distribution in plants and microbes were studied in four arctic ecosystems at Abisko, Northern Sweden and Toolik Lake, Alaska, which have been subjected to long-term warming with plastic greenhouses. Net mineralization and microbial immobilization were studied by the buried bag method and ecosystem pool sizes of C, N and P were determined by harvest methods. The highest amounts of organic N and P were bound in the soil organic matter. Microbial N and P constituted the largest labile pools often equal to (N) or exceeding (P) the amounts stored in the vegetation. Despite large pools of N and P in the soil, net mineralization of N and P was generally low during the growing season, except in the wet sedge tundra, and in most cases lower than the plant uptake requirement. In contrast, the microorganisms immobilized high amounts of nutrients in the buried bags during incubation. The same high immobilization was not observed in the surrounding soil, where the microbial nutrient content in most cases remained constant or decreased over the growing season. This suggests that the low mineralization measured in many arctic ecosystems over the growing season is due to increased immobilization by soil microbes when competition from plant roots is prevented. Furthermore, it suggests that plants compete well with microbes for nutrients in these four ecosystems. Warming increased net mineralization in several cases, which led to increased assimilation of nutrients by plants but not by the microbes.

Introduction

Plant growth and productivity in arctic and subarctic ecosystems generally are limited by low availability of N (nitrogen) and/or P (phosphorus) (Jonasson et al., 1996, 1999b; Shaver and Chapin 1980, 1986, 1995). Plant growth is also affected by short-term (year to decade) temperature enhancement, partly because of direct effects of warming, but mostly because of indirect effects of increasing nutrient mineralization in the warmed soils (Callaghan and Jonasson, 1995; Graglia et al., 1997; Havström et al., 1993; Shaver et al., 1998; Wookey et al., 1993). Increased mineralization rates are likely, therefore, to be a key driver for ecosystem changes in response to predicted, future warming of the Arctic (Shaver et al., 1992).

Net mineralization measured by the buried bag method (Eno, 1960) is a good predictor of productivity in temperate forest ecosystems (Nadelhoffer et al., 1984, 1985). The few existing data from arctic ecosystems do not show the same picture. Net mineralization measured in the bags is often low or even negative during the growing season (Giblin et al., 1991; Hart and Gynther, 1989; Jonasson et al., 1993; Schmidt et al., 1999) and in most cases far lower than the plant uptake requirement (Jonasson et al., 1999a; Schimel et al., 1996; Shaver and Chapin, 1991). Net mineralization measured in buried bags is an estimate of the balance between mineralization and microbial immobilization

* FAX No: +45-4576-3233; Tel.: +45-4576-3200; E-mail: iks@fsl.dk

of nutrients in the absence of plant roots. Hence, the lack of plant nutrient uptake may lead to higher nutrient immobilization inside the bags than outside, which reduces the estimate of mineralization. Furthermore, plants may also assess organic nutrient compounds, which also may explain part of the imbalance between measured mineralization and plant nutrient uptake.

Microbial N and P pools are large in arctic soils, often comparable to, or exceeding, the pools in the sparse vegetation (Jonasson et al., 1999a). This suggests that small changes in the balance between microbial nutrient uptake and microbial nutrient release may lead to large fluctuations in pools of N and P available to plants (Chapin et al., 1978; Jonasson et al., 1996, Schmidt et al., 1997). It has also been suggested that microbes immobilize large amounts of nutrients during the growing season that subsequently are released during the winter due to microbial die back (Giblin et al., 1991; Hobbie and Chapin 1996; Jonasson et al., 1993; Nadelhoffer et al., 1992; Schmidt et al., 1999).

Measured mineralization of organic matter takes only inorganic plant nutrients into account. However, recently, several experiments have demonstrated that arctic plants are able to take up amino acids (Chapin et al., 1993; Kielland 1994; Schimel and Chapin, 1996) and ericaceous dwarf shrubs are even potentially able to utilize more complex N-containing compounds like proteins, due to their mycorrhizal association (Read, 1991), although the importance of organic N uptake has yet to be quantified in the field.

We measured net mineralization and immobilization of N and P during one growing season in four tundra ecosystems in N. Sweden and Alaska by the buried bag method. All four ecosystems had been subjected to long-term warming by plastic greenhouses. Immobilization was measured as the changes in microbial biomass N and P content before and after incubation in the buried bags. Furthermore, we measured the changes in microbial nutrient content in the soil during the same period to compare immobilization of N and P in microbes within and outside the bags. The overall aims were; first, to evaluate whether the low net mineralization measured in buried bags in arctic ecosystems during the growing season was due to immobilization of nutrients by the microorganisms. Second, we determined whether immobilization of N and P occurred to the same extent in the soils inside and outside the buried bags. Plant biomass and nutrient mass have been measured previously in all four ecosystems (Chapin et al., 1995; Jonasson et al., 1999b; Shaver et al., 1998). From the microbial and plant data, we can determine the distribution of nutrients in plants and microbes and infer changes in the strength of competition between plants and microbes in response to warming.

Materials and methods

Study sites

The study took place in four tundra ecosystems, a low altitude heath and a high altitude fellfield near Abisko Scientific Research Station in North Sweden (68°20′N, 20°51′E), and in a tussock tundra and a wet sedge community at the Arctic Long Term Ecological Research (LTER) site at Toolik Lake, Alaska (68°38′N, 149°34′W).

The vegetation at the Abisko sites was dominated by the circumpolar evergreen dwarf shrub *Cassiope tetragona*. The tussock tundra consisted of mixed vegetation of deciduous and evergreen shrubs, whereas mosses and rhizomatous sedges dominated the wet sedge tundra. The tussock tundra around Toolik Lake has been intensively studied since 1976, and there are several tussock tundra areas around Toolik Lake that have been subjected to experimental warming. The present study area is situated on the south side of the lake, similar but not identical to the tussock tundra where most of the previous research has taken place (Chapin et al., 1995) referred to in the text as the old tussock tundra. The mean annual precipitation is 299 mm at the Abisko Scientific Research Station, which reflect conditions at the heath site, whereas the high altitude fellfield site probably receives more than 500 mm precipitation annually (Björn E. Holmgren, personal communication). More than one-third of the long-term mean annual precipitation falls during the summer at the Abisko sites and about half of the mean annual precipitation of 347 mm is summer precipitation at the Toolik site. The four ecosystems range from dry to wet tundra and the soil reaction ranges from low to high pH. See Table 1 for details.

Experimental design

The four tundra communities were subjected to air and soil temperature enhancement during the growing season of 4–5 and 1–2 °C, respectively, by plastic greenhouses replicated six times at the Abisko sites and four and two times at the Toolik sites and maintained since 1989. The greenhouses at Abisko were dome-shaped 1.2 × 1.2 m constructions (Havström et

Table 1. Vegetation and soil characteristics of the organic layer, except at the wet sedge tundra, where only the upper 30 cm of the organic layer was sampled. Data are based on Jonasson et al. (1999a,b), Schmidt et al. (1999, unpublished), Chapin et al. (1995), Shaver and Chapin (1991), Shaver et al. (1998, unpublished). Mean annual and growing season temperature are from nearby weather stations in Abisko (long-term) and Toolik (1991–1998) with *in situ* measurement from the sampling period in parentheses. Soil temperatures are measured in 5–10 cm depth at Abisko and at 10 cm depth in Toolik

	Low altitude heath Abisko	High altitude heath Abisko	Tussock tundra Toolik	Wet sedge Toolik
Altitude m a.s.l.	450	1150	780	730
Vegetation	Dominated by ericoid dwarf shrubs and mosses	Dominated by ericoid dwarf shrubs and mosses	Mixture of mosses, graminoids, deciduous and evergreen dwarf shrubs	Rhizomatous sedges (Carex, Eriophorum ssp)
Plant biomass measured (g m^{-2} $year^{-1}$)	1250 (excl. coarse roots)	400 (excl. coarse roots)	1070 (excl. fine roots)	150 (excl. fine roots)
Total plant biomass estimate	1500	425	1470[a]	370[b]
NPP (g m^{-2} $year^{-1}$)	300	85	330[a]	100
pH_{H_2O}	7.1	5.2	4.6	6.0
Depth of organic matter (cm)	10–15	2–3	15	>51
% organic matter	74	52	62	76
Soil C (gC m^{-2})	6819	1010	5655	12859
Soil N (gN m^{-2})	257	40	182	657
Soil P (gP m^{-2})	15.5	5.1	19.5	21.9
Annual air temperature (°C)	−0.7	−4.8	−8.5	−8.5
Summer air temperature (°C)	9.9 (9.6)	5.8 (n.d.)	9.0 (9.9)	9.0 (9.9)
Summer soil temperature (°C)	(6.7)	(6.0)	(6)	(8)
Water content June (% of DW)	401	271	860	630
Water content August (% of DW)	378	195	650	700

[a]Root biomass and root production from Shaver and Chapin (1991).
[b]Root biomass data from Nadelhoffer et al. (unpublished).

al., 1993; Jonasson et al., 1999b), whereas the greenhouses at the Toolik sites were 2.5 × 5 m rectangular constructions fixed onto a permanent wooden frame (Shaver et al., 1998). The greenhouses at Abisko were of thin plastic and reduced the photosynthetically active radiation by approximately 10%, while the plastic used at Toolik was thicker and reduced the light by about 20%. The greenhouses were raised each year in June after snowmelt and maintained to late August. Havström et al. (1993), Jonasson et al. (1999b) and Michelsen et al. (1996a) give additional details of treatment effects on a variety of other parameters at the Abisko sites, and Gough et al. (1999), Johnson et al. (1999) and Shaver et al. (1995, 1998) give details from the Toolik sites.

Net mineralization and microbial immobilization of N and P

Net mineralization of N and P and microbial uptake of mineralized nutrients were measured in the field by the buried bag technique (Adams et al., 1989; Eno, 1960), which enables measurements that account for the differences and fluctuations in soil temperature, while the water content is kept constant. The technique prevents plant uptake of mineralized nutrients, but allows uptake by the microorganisms.

The seasonal net mineralization was expressed as the difference in inorganic N (NH_4-N and NO_3-N) and inorganic P in the soil before and after incubation in the bags. NO_3-N was below detection limits in the samples at all of the sites. The microbial N and P nutrient immobilization was defined as the changes in the microbial N and P content before and after incubation. This is the amount of nutrients the microbes immobilize inside the bags when competition from plant roots is prevented. Net mineralization and microbial nutrient immobilization form only parts of gross mineralization. We are ignoring re-assimilation of nutrients among microbes during the incubation period and incorporation of microbial products in the soil. Furthermore, changes in dissolved organic nitrogen (DON) during incubation were quantified because nitrogen may be released as DON during microbial

Table 2. An overview over when the experimental warming was initiated and plant and soil sampling took place in five arctic ecosystems

	Heath	Fellfield	Tussock tundra	Wet sedge	Old tussock tundra
Experiment initiated	1989	1989	1989	1989	1981
Plant harvest	1993	1993	1999	1994	1989
Soil sampling					
-soil profiles	1996		1997	1997	
-mineralization	1994	1994	1999	1999	

dieback, or microbes may assimilate DON during re-growth. A more thorough presentation of the mineralization at the Abisko sites in response to various treatments are given in Schmidt et al. (1999).

Soil and plant sampling and analysis

Two 10-cm (3 cm at the high altitude site) deep soil samples from the organic layer of each plot were collected in mid June at the Abisko sites in the sixth experimental year and in early June at the Alaskan sites in the 11th year. The aboveground live biomass, but not the litter layer, was removed. One undisturbed soil core was placed in a polyethylene bag, sealed and replaced in one of the holes for incubation during the summer and covered with mosses. The second soil sample was brought to the laboratory, where roots were removed by sieving (Abisko samples) or by hand (Alaska samples). The soil was thereafter used for determination of extractable inorganic N and P, DOC (dissolved organic carbon) and DON, microbial N, P and C, total soil C, N and P, pH, water content and loss on ignition as an estimate of SOM (soil organic matter). The incubated samples were collected in late August, along with a second unincubated sample from each plot. Soil sampling took place in inter-tussock areas in the tussock tundra. Peak season plant biomass has previously been estimated, and the tissue nutrient content measured, after destructive sampling in the 5th year at the Abisko sites and the 6th and 11th year at the wet sedge and tussock tundra, respectively. Original data on plant nutrients are published in Jonasson et al. (1999b) and in Shaver et al. (1998) and supplemented with unpublished data by Shaver et al. Furthermore, soil samples were collected from a profile down to the mineral soil (30 cm depth at the wet sedge site) for ecosystem pool sizes. Table 2 gives an overview of the year of sampling in the different ecosystems.

In the laboratory, 10 g sorted soil from each sample were extracted in 50 ml 0.5 M K_2SO_4 or 0.5 M $NaHCO_3$ (fellfield soil) for 1 h. Starting at the same time as the extraction, another subsample was fumigated with chloroform for 24 h to release microbial biomass C, N and P (Jenkinson and Powlson, 1976; Tate et al., 1988), followed by extraction with K_2SO_4 as above. The extracts were filtered through Whatman GF-D filters and frozen until analysis. DOC was analyzed in the extracts using a Shimadzu Total Organic Carbon Analyzer, TOC 5000A, N was analyzed with the indophenol blue method after acid digestion and P with the molybdenum blue method. $NaHCO_3$ was used as an extractant for the fellfield soil because earlier experiences had shown that extraction of this particular soil type with K_2SO_4 gave a very low extractability of P (Jonasson et al., 1993, 1996). Inorganic C from carbonates in the extractant was removed from the extracts of the high altitude fellfield soil by addition of HCl prior to analysis. The microbial C, N and P content was estimated as the difference in C, N and P content of the extracts of the unfumigated and the fumigated soil samples. To convert the amounts of microbial C, N and P released by chloroform fumigation and extraction (CFE) to total microbial biomass C, N and P we assume an extractability for C of 0.45 (Wu et al., 1990; Joergensen, 1996) and of 0.40 for N and P (Jonasson et al., 1996).

Calculations

Soil, plant and microbial C, N and P pools were calculated per m^2 of the entire organic layer except at the wet sedge tundra, where data represent the upper 30 cm of the organic horizon. Between-ecosystem differences were tested by one-way ANOVA followed by Tukey's posteriori test using appropriate transformation. The wet sedge site was omitted from the statistical analyses due to insufficient number of replicates.

The wet sedge site consisted of only two replicate blocks. Replicate samples from each of the two blocks were lumped before extraction and analyses. Within ecosystems, Student *t*-tests were used to compare the effect of the greenhouse and to compare the measured parameters within the buried bags with the levels outside the bags sampled on the same day in August.

The absolute values for most variables vary highly among ecosystems. In order to facilitate inter-site comparison most figures are based on the relative pool size distribution, the relative greenhouse response or the relative response in buried bags compared to the field.

Plant biomass was measured in all four ecosystems by destructive harvesting at peak season in late July, with original data in Shaver et al. (1998, unpublished) and Jonasson et al. (1999b). Fine root biomass was not sampled at the tussock tundra, whereas coarse roots are missing from the Abisko biomass. Estimates of these fractions are included in Table 1 and Figs. 2 and 3. Plant N and P mass data are available for three sites, whereas the N and P content were estimated in the tussock tundra assuming that 1% and 0.1% of total biomass were N and P, respectively, in accordance with N and P concentrations at two nearby tussock tundra sites (Chapin et al., 1995; Hobbie and Chapin, 1998). NPP was measured at the Toolik sites and we added fine root production using the data in Shaver and Chapin (1991) for the tussock site, whereas NPP was estimated as 20% of the peak season biomass at the Abisko sites (see production:biomass ratios in Shaver and Chapin (1991)). Plant uptake requirement of N and P in the net primary production (NPP) were estimated to 25% of NPP-N and NNP-P, respectively, taking the presumably high resorption of nutrients into account (Berendse and Jonasson 1992; Jonasson 1983, 1989; Jonasson and Chapin 1985; Malmer and Nihlgård 1980; Shaver and Chapin, 1991).

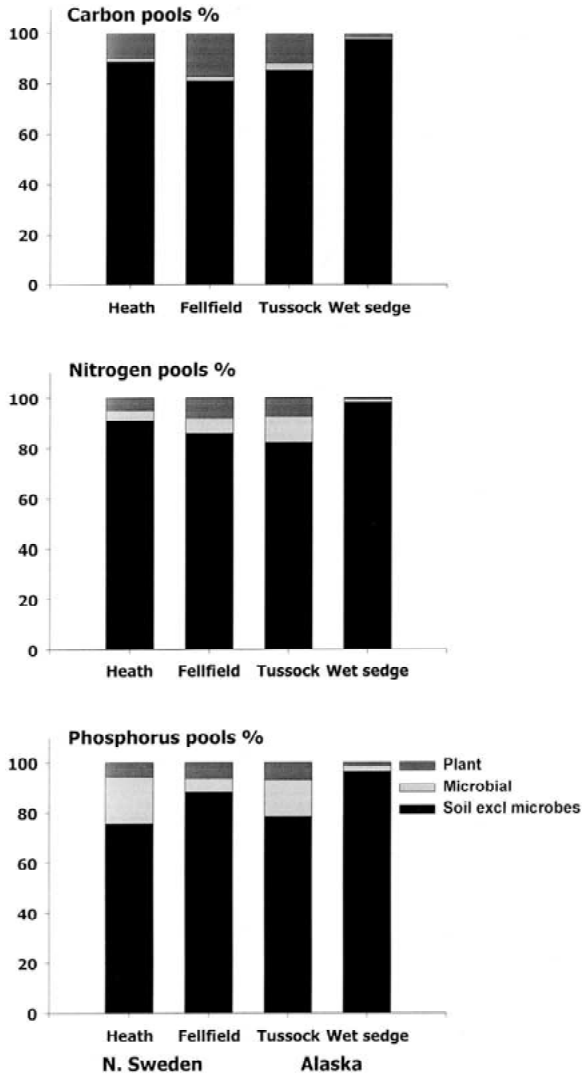

Figure 1. Fractions (%) of ecosystem pools of C, N and P in soil, microbial biomass and plants above and below ground in four tundra ecosystems. The soil and microbial fractions are the amounts in the entire organic layer except at the wet sedge tundra, where they include the content in the upper 30 cm of a deeper organic horizon. The soil fractions are means of the content in June and August.

Results

Ecosystem C, N and P distribution

The ecosystem C pool was distributed similarly in three of the four ecosystems (Fig. 1), with 12–19% of the ecosystem carbon stored in live biomass C (i.e., plant plus microbial biomass C). The C was partitioned into 1.5–3% in the microbial biomass, 10–17% in the plants and the remaining 81–88% in the dead part of the soil organic matter. The highest fraction of live biomass C was found in the fellfield. The wet sedge tundra, in contrast, had very low contribution from live biomass with only 0.5 and 1.5% of the ecosystem C stored in microbial and plant biomass, respectively. Because we measured to 30-cm depth only, and the organic horizon in the wet sedge site is at least 50 cm (Table 1), the proportion of ecosystem C in live biomass is less than 1% of the total accumulated C pool. The microbial biomass C concentration in the upper 10 cm of the SOM was highest in the tussock

Table 3. The microbial (Mic) biomass C concentration (mg C g^{-1} DW SOM) and microbial biomass C/N, C/P and N/P ratios in control and greenhouse plots in June and August. The biomass and ratios were measured in soil after incubation in buried bags. Different letters after microbial biomass C denote significant differences among sites for each time at $P < 0.05$ (Tukey's test)

	Control				Greenhouse			
	Mic C	C/N	C/P	N/P	Mic C	C/N	C/P	N/P
Low altitude heath								
June in field	7.0b	7.0	25.7	3.8	7.1b	6.6	28.3	4.3
August in field	9.0b	9.5	30.8	3.9	9.1ab	8.1	29.7	3.9
August in bags	6.7b	6.1	21.1	3.6	7.0ab	5.5	18.2	3.3
High altitude heath								
June in field	9.3b	8.6	73.4	8.5	9.6b	6.7	60.9	9.1
August in field	9.2b	7.6	64.9	8.7	8.2b	6.0	57.2	9.4
August in bags	8.4b	6.4	56.9	9.2	9.2ab	5.1	54.6	10.4
Mesic tussock tundra								
June in field	17.7a	8.4	47.3	5.6	18.7a	12.2	99.7	8.5
August in field	18.5a	10.4	96.9	9.8	15.4a	11.2	89.4	8.3
August in bags	14.6a	6.9	40.7	5.7	12.2a	7.0	41.5	5.6
Wet sedge								
June in field	4.7	13.3	208	15.9	4.7	17.3	203	12.1
August in field	4.4	13.9	166	11.6	3.7	13.5	167	12.4
August in bags	4.2	10.9	176	16.9	4.8	14.3	196	13.9

tundra with 18 mg C g^{-1} SOM, significantly higher than the 7–9 mg C g^{-1} SOM at the heath and fellfield (Table 3). The wet sedge tundra had the lowest concentration of microbial biomass C with 4.5 mg C g^{-1} SOM.

The relative content of N and P varied among the four ecosystems. The live biomass N accounted for 17% of total ecosystem N at the tussock tundra, 14% at the fellfield, 10% at the heath, but only 2% in the wet sedge tundra (Fig. 1). In all four ecosystems the fraction of N was roughly the same in plant and microbial biomass. The heath and tussock tundra had approximately 25% of P bound in live biomass, whereas the proportion was 12 and 3% in the fellfield and wet sedge tundra, respectively. About two-thirds of live biomass P was in the microbes in the tussock tundra and heath. The fellfield and wet sedge tundra had about equal amounts of P in plants and microbes.

Inorganic N constituted a small proportion, ca 1%, of the total labile N pool in the soil inorganic, microbial and DON pools (Fig. 2) except in the wet sedge tundra, where the proportion was 4%. Although the major part of labile soil N was found in the microbial

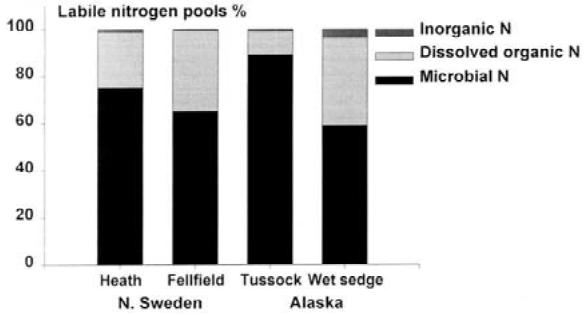

Figure 2. Partitioning of labile soil N into inorganic N, dissolved organic N and microbial N in the upper 10 cm or the entire soil organic layer (fellfield) in four tundra ecosystems. Data represent means of the pool sizes in June and August.

biomass, the DON pool contributed with as much as 35% in the wet sedge tundra and the fellfield, 25% in the heath and 10% in the tussock tundra.

Net mineralization and immobilization of N and P

Within-ecosystem variation was very high for both net N and P mineralization and N and P immobilization in

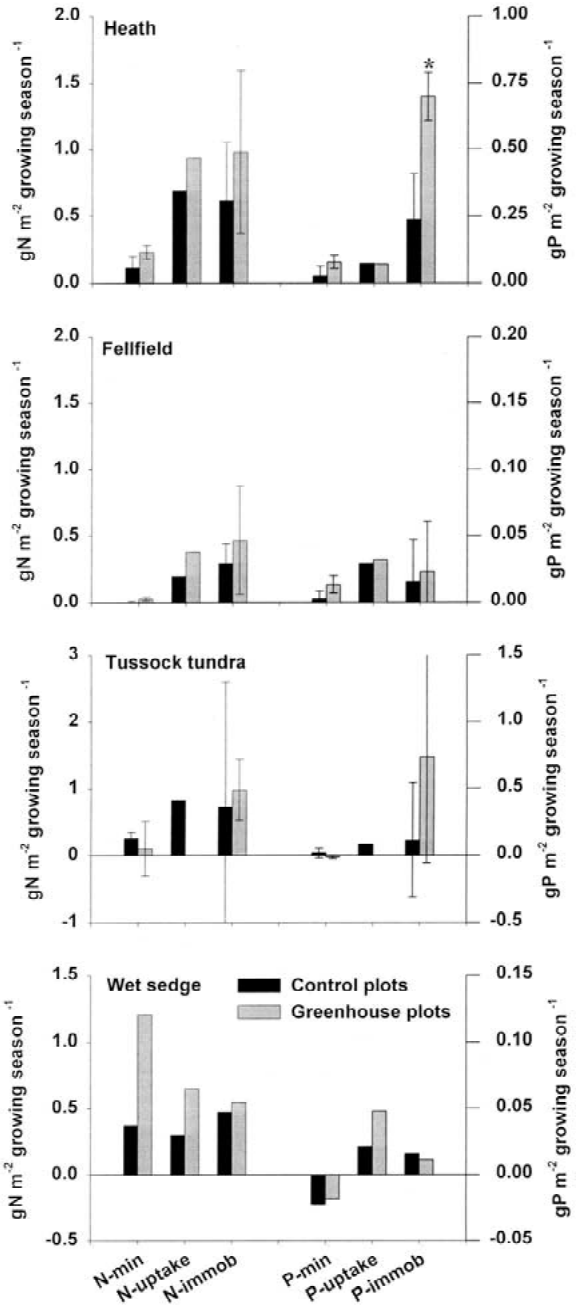

Figure 3. Net N and P mineralization and microbial immobilization (g m^{-2}) in buried bags and estimated plant uptake during one growing season in control and greenhouse plots in four tundra ecosystems (means ± SE). SE is not shown for the wet sedge tundra due to low number of replicates. Plants for estimation of nutrient uptake were not available from the greenhouses at the tussock tundra. Greenhouse effects were tested by Student's *t*-test. Level of significance: $^{*}P<0.05$.

the buried bags at all sites and showed only one case of significant effect of warming, viz. P immobilization at the heath (Fig. 3). However, net mineralization of N was positive during the growing season in all four ecosystems (Fig. 3) with higher mean mineralization in the warmed plots than in the controls except at the tussock tundra. The growing season net N mineralization was negligible at the fellfield and approximately 0.1, 0.25 and 0.35 g N m^{-2} at the heath, tussock tundra and wet sedge tundra, respectively. Net P mineralization (Fig. 3) was low or negative with a non-significant increase in mineralization in the greenhouses at the Abisko sites, but net mineralization was approximately the same in control and greenhouse plots at the Alaskan sites. The amount of dissolved organic nitrogen (DON) also changed during the incubation (Fig. 4). At the Abisko sites, the amount of DON decreased in the buried bags whereas DON increased in the buried bags at the Alaskan sites.

In all four ecosystems, the microbial biomass N and P increased in the buried bags during the growing season (Fig. 4). Roughly 0.7 g N m^{-2} was immobilized over the growing season at the tussock tundra and heath, whereas 0.3 and 0.5 g were immobilized at the fellfield and wet sedge tundra, respectively (Fig. 3). The estimated plant uptake of N was approximately the same as (heath and tussock tundra) or one-third lower (fellfield and wet sedge tundra) than the immobilization in the bags. More N was immobilized in the warmed plots in all four ecosystems although the differences were non-significant. The immobilization of P increased significantly in the warmed plots at the heath site (Fig. 3). While the data showed similar levels and patterns in plant uptake and immobilization of N, there were no obvious similarities between P immobilization and plant uptake requirement.

The effect of buried bags

Figure 4 shows the relative changes over the summer in microbial biomass C, N and P content in the buried bags and in the soil outside the bags. The significant effects denoted in the figure represent differences between the microbial content in the soils of the buried bags and in the surrounding soil the same day in August.

There were no significant seasonal differences in microbial biomass C, N and P between June and August in the surrounding soil (Fig. 4, black bars, Student's *t*-test), except for microbial biomass C at the heath, which was significantly higher in August

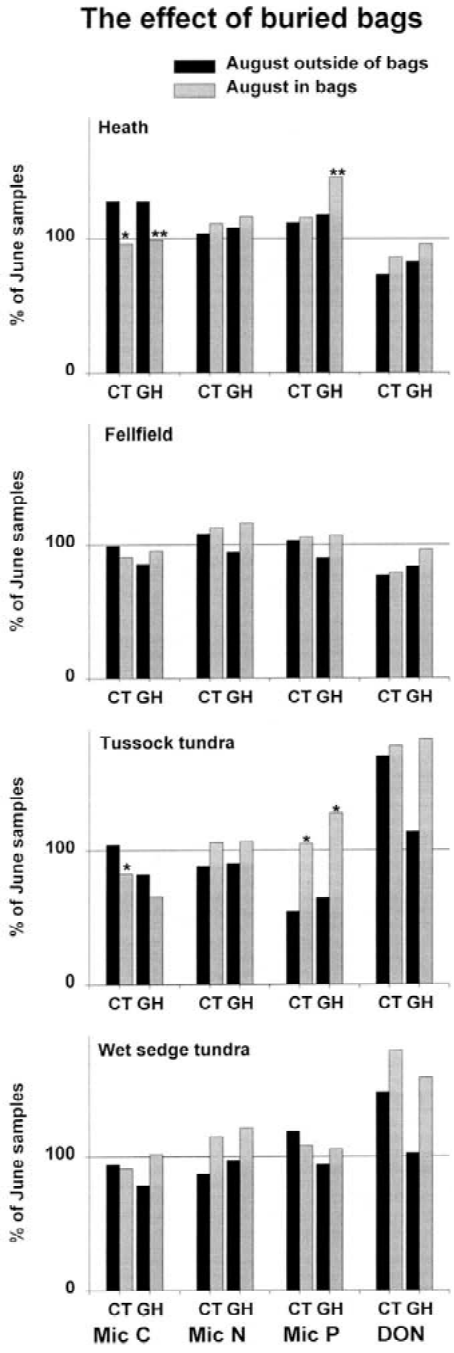

Figure 4. Microbial biomass C, N and P pool sizes in August in buried bags and in the surrounding soil compared to the levels in June. Values higher than 100% represent gains, whereas values below 100% represent losses of microbial biomass C, N or P. Differences in microbial C, N and P in the surrounding soil in August compared to the amounts in the buried bags in control (CT) and greenhouse (GH) plots were tested by Student's *t*-test. Levels of significance: $^{*}P<0.05$, $^{**}P<0.01$.

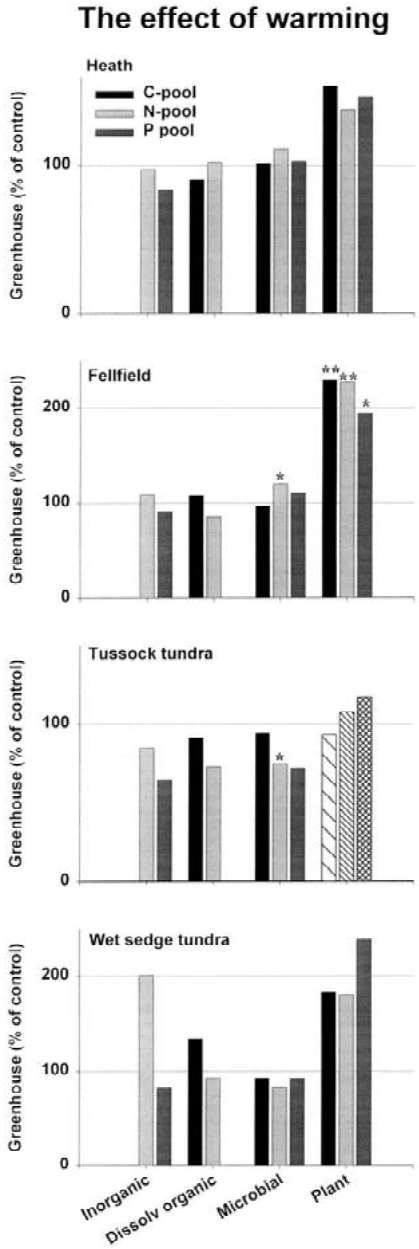

Figure 5. The relative pool size of inorganic N and P, dissolved organic N and C, microbial biomass C, N and P and plant C, N and P in greenhouse plots compared to control plots. The plant biomass in the heath and the fellfield were harvested after 5 years of experimental heating, whereas the wet sedge tundra was harvested the sixth year. Plant biomass has not yet been harvested in the greenhouses at the tussock tundra, but for comparison we have added data from a nearby old tussock site. Inorganic, dissolved organic and microbial pool sizes represent means of the amounts in June and August measured in the sixth year at the heath and fellfield and the 11th year at the tussock and wet sedge tundra. Original plant data are from Shaver et al. (1998, unpublished) and Jonasson et al. (1999b). Differences in greenhouse plots compared to control plots were tested by Student's *t*-test. Levels of significance: $\dagger P<0.1$, $^{*}P<0.05$, $^{**}P<0.01$.

($P<0.05$). Due to high variation in microbial P, the mean reduction of P by about 40% in the tussock tundra was not significant.

Within the buried bags (Fig. 4, grey bars), microbial biomass C remained at the same level (heath) or decreased non-significantly during incubation. In contrast, the content of microbial N and P increased over the growing season in all four ecosystems with similar or a relatively higher increase in the greenhouses than in the controls, but significantly so only for P in the warmed plots at the heath ($P<0.001$, Student's *t*-test). It is striking that the gain in microbial N and P over the growing season was higher in the buried bags than in the surrounding soil, except in the control plots at the wet sedge tundra. The higher immobilization in the buried bags was significant for P in both the control and warmed plots at the tussock tundra and in the control plots at the heath. In most cases, the increase in microbial N and P content in the buried bags resulted in decreasing C/N and C/P biomass ratios (Table 3). The N/P biomass ratio did not generally change during the same time period.

The amount of DON decreased both in the buried bags and in the surrounding 'unbagged' soil at the Abisko sites, whereas the Alaskan sites showed a net release of DON in the buried bags and in the control plots of the surrounding soil. In contrast to the high release of DON in the buried bags in the greenhouses at the Alaskan sites, there were no seasonal changes in the amount of DON in the surrounding soil in the greenhouses.

The effect of greenhouse on C, N and P pools

Inorganic N and P, DOC and DON and microbial biomass C and P were relatively unaffected by warming except in the wet sedge tundra, where greenhouses doubled the extractable inorganic N (Fig. 5). Microbial biomass N increased significantly in the greenhouse plots at the fellfield and decreased at the tussock tundra. In contrast to the relatively small changes in the soil fractions, plant biomass C, N and P increased by about 50% at the heath and by about 100% at the fellfield and the wet sedge tundra. The available data for tussock tundra are from a different site at Toolik Lake and thus not directly comparable. The relative increase in biomass in response to warming was highest at the fellfield and lowest at the heath. As plant samples were lumped before analyses of N and P mass at the wet sedge tundra, data have not been analyzed statistically.

Discussion

Within ecosystem C, N and P partitioning

Even though total plant biomass, soil water content, pH, depth of OM and litter quality were highly different among the four ecosystems, they all had a remarkably high fraction of microbial N and P compared to the amounts stored in the plant biomass.

Competition for limited nutrients between plants and microbes has long been recognized in arctic ecosystems (Chapin et al., 1978; Giblin et al., 1991; Jonasson et al., 1993; Michelsen et al., 1999; Nadelhoffer et al., 1991, 1992; Schmidt et al., 1997). The disproportionately higher fraction of N and especially P measured in the microbial biomass compared to the plants in the four ecosystems suggests that even small fluctuation in the microbial N and P content will increase or decrease plant available nutrients to an extent of potentially affecting plant growth. It has earlier been demonstrated that fluctuations in microbial biomass N and P directly influenced plant biomass in growth chamber (Schmidt et al., 1997) and field experiments (Michelsen et al., 1999). In the present study, a 5–10% decrease in the microbial biomass N and P will release enough nutrients to cover the annual plant uptake requirement in all of the four ecosystems. It is almost impossible to detect short-term changes in microbial nutrient content at that level due to the high spatial heterogeneity in the soils even on a small scale. The small and non-significant changes in seasonal microbial N and P content that we measured may, therefore, fully account for the comparably high fluctuations in plant available N and P.

Coupling of net mineralization, microbial immobilization and plant nutrient requirement

Net mineralization during the growing season accounted for only 0.1–4‰ of total soil N and P in the upper 10 cm with the lowest proportion in the fellfield and highest proportion in the tussock tundra and the heath. The net release of N and P in the buried bags could cover less than 10% of estimated plant uptake at the fellfield increasing to 15% of the N and 35% of the P at the heath and 30% of the plant N uptake and 20% of the plant P uptake at the tussock tundra. Nitrogen was mineralized in excess of plant uptake requirement at the wet sedge, as it was also the case in an earlier study (Shaver et al., 1998). In contrast, P mineralization in wet sedge tundra was negative. The results are in accordance with the lack of response in plant production

to N fertilizer but a highly significant increase with addition of P-fertilizer at the wet sedge site (Shaver et al., 1998). The high N mineralization measured at the wet sedge tundra suggests that N is likely leached from the system. The high N production may reflect large transport of N compounds from topographically higher surrounding areas.

Low or negative growing season net mineralization has been observed in many arctic ecosystems (Giblin et al., 1991; Jonasson et al., 1993; Schmidt et al., 1999). This has been followed by higher release of nutrients during the non-growing season (Giblin et al., 1991; Hobbie and Chapin 1996; Schmidt et al., 1999), presumably originated from dying microbes during freeze–thaw cycles (Clein and Schimel, 1995). Plant nutrient acquisition should then mainly take place during early spring and late autumn (Chapin et al., 1978; Kielland and Chapin, 1992). An isolated look at the large immobilization of nutrients in the microbes during the growing season in the buried bags could support this. However, the lower immobilization in the soil outside compared to inside the buried bags ($P<0.012$ for N and $P<0.006$ for P across all sites; Student's *t*-test) indicated that plant nutrient uptake was not restricted to periods with low demand by microbes.

Indeed, if we assume that the difference between immobilization in the buried bags and in the soil outside the bags reflects a pool of nutrients that is available to the plants, this pool, together with the mineralized N and P can support the plant uptake of N in the Alaskan ecosystems and P at the heath and tussock tundra. At the Abisko sites, we observed a decrease in DON over the growing season, significant at the fellfield site. The decrease was highest outside the bags, which indicated that N also in these ecosystems was available over the growing season in sufficient amounts to cover the estimated plant uptake.

In alpine and arctic tundra, recent research found immobilization of N in microbes very early in the spring prior to plant growth followed by a decrease at the onset of plant growth (Brooks et al., 1998: Lipson et al., 1999; Schmidt, Nordin and Shaver, unpublished) or in late season after plant senescence (Fisk and Schmidt, 1996: Jaeger et al., 1999). This suggests that microbes function as an important short-term sink for the most labile fractions of nitrogen preventing leaching losses in periods when the plant uptake is low. Furthermore, it suggests that plants during the growing season have access to nutrients in amounts corresponding to the annual uptake. The different interpretation of results (i.e., that plant nutrients are released during the non-growing or the growing season) may be a consequence of differences in time of sampling and the definition of growing season if very large pools move between the microbes and the plants within few weeks during early spring and late autumn.

Methodological considerations

The assessment of N availability is complicated as every method imposes some artificial conditions. The buried bag method prevents uptake of nutrients by plant roots but also the supply of labile carbon to soil microbes in form of root exudates. Furthermore, soil water content changes little in the buried bags. In contrast, all the sites, except for the wet sedge tundra, were dryer in July than in June when the incubation was initiated. The water content in the control soils increased to June levels towards the end of the growing season, but remained low until late August in the greenhouses. This drying of the upper soil may create a different vertical distribution of microbes in soil surrounding the buried bags than inside the bags and may explain the large seasonal difference in microbial P in the surrounding soil in the tussock tundra but not in the buried bags.

One of the criticisms of the buried bag method has been that a large carbon pool with high C/N ratio is released from severely damaged roots, which may promote immobilization of nutrients in the microbes (Adams et al., 1989). However, there are several indications that the carbon limitation is higher inside the bags than outside the bags. Firstly, DOC inside the bags was significantly lower than outside in the field ($P<0.05$; data not shown), indicating that the microbial access to labile C was lower in the bags. Secondly, the microbial biomass C in several cases decreased in the bags during the incubation, while the content outside the bags increased during the same period and was significantly higher than inside the bags in several cases by late August (Fig. 4; Table 3). This may reflect C limitation in the bags. An alternative explanation for the lower microbial C content in the bags could be that the fungal component of the microbial community, which has higher C to nutrient ratio than bacterial biomass, decreased in the buried bags. Obviously, the mycorrhizal component of the soil will decrease when the roots are dying, but we observed the same decrease in the wet sedge tundra where mycorrhizal associations presumably are less frequent. Furthermore, we know that only 20% of

the microbial biomass at the Abisko sites is fungal (Schmidt et al., 2000) and decreased mycorrhizal biomass cannot fully account for the changes we observed in microbial C:N ratio. We know, however, that microbes can assimilate high amounts of nutrients after fertilization without biomass changes (Jonasson et al., 1996; Michelsen et al., 1999; Schmidt et al., 1997) leading to decreased C:N ratio. Hence, the ratio can change without changes in the fungal to bacterial ratio (Schmidt et al., 2000). Therefore, the high immobilization of N in microbes will probably always take place regardless of the amount of available C when N availability increases.

The organic N pool also underwent large changes. At the Abisko sites the decrease in DON-N outside the bags was higher than the net N mineralization. It has been suggested that arctic plants may shortcut the nitrogen cycle by uptake of organic N in N deficient ecosystems (Chapin et al., 1993; Kielland 1994; Schimel and Chapin, 1996; Michelsen et al., 1996b, 1998). A high plant uptake of organic N might therefore together with the microbial immobilization explain why plant N uptake often is higher than the estimation of N mineralization by the buried bag method.

Distribution of C, N and P in soil, microbes and plants: the effect of warming

The plant and microbial pool sizes of C, N and P in the warmed plots, relative to the pool sizes in control plots, indicate that plants compete well for nutrients (Fig. 5). After 5 years of experimental warming at the heath and fellfield and 6 years at the wet sedge site, plant C, N and P pools were higher in the heated plots, whereas nutrients in the microbial biomass were approximately at the same level as in the control. The lack of responses in the microbial biomass C, N and P, despite an increased activity indicated by the increased mineralization, is probably due to the concomitant increased grazing by, e.g., nematodes, which doubled their population density in response to warming at the heath (Ruess et al., 1999). Nine years of warming, at the 'old' tussock site, did not result in changes in total plant biomass but did slightly increase the N and P mass (Chapin et al., 1995). This is similar to results from a 3-year experimental warming in the same tussock tundra area as the present study (Hobbie and Chapin, 1998). In contrast, large changes in C, N and P distribution on both community and species level were observed.

It can be argued that we compared nutrient pools in plant biomass harvested in one year with microbial and inorganic pools measured another year. In each of the ecosystems, we have sampled the soil in at least two different years. The microbial biomass C, N and P have varied between years, whereas the treatment effects have been similar (data not shown). Net mineralization has also been measured in two different years except in the tussock tundra, and although with somewhat different responses, showing the same low mineralization at the Abisko sites (Jonasson et al., 1993; Schmidt et al., 1999) and considerable net N mineralization at the wet sedge tundra (Shaver et al., 1998).

Nutrient limitation has been identified as a major constraint to increased carbon accumulation by the vegetation in response to warming (Chapin et al., 1995). Interestingly, the increase in total biomass in the greenhouses was exactly the same as after addition of fertilizer to the heath and only 10% lower at the fellfield and at the 'old' tussock tundra (Chapin et al., 1995; Jonasson et al., 1999b). Only the wet sedge tundra displayed a higher biomass response after fertilization than after warming (Shaver et al., 1998). In contrast, plant N and P mass increased more dramatically after fertilizer addition than in the greenhouses at all sites. The fact that plant biomass increased by about the same magnitude in the greenhouses at the heath and fellfield as after fertilizer application in excess of uptake indicated that further plant biomass accumulation is not entirely dependent on increased mineralization in the greenhouses. It may be that community changes must take place before more carbon can be accumulated in plant biomass. The responses observed to long-term fertilization at the 'old' tussock tundra also point to that explanation. The relatively small response of plant biomass concomitant with large changes in the community structure observed after 9 years of fertilizer application (Chapin et al., 1995) was followed by larger biomass accumulation in the next six years (Shaver et al., unpublished data).

Conclusions

The apparently low net mineralization measured during the growing season in these arctic ecosystems was due to high immobilization of nutrients in the microbes in the buried bags, i.e., where plants were denied access to the mineralized nutrients. The same high immobilization was not observed in the sur-

rounding soil, which indicates that the plants were able to sequester considerable amounts of nutrients and compete efficiently with microbes under, non-experimental, 'natural' conditions.

Greenhouses increased both net mineralization and immobilization in some but not all cases. The opposing effects of the two processes make net mineralization in buried bags a poor indicator of changes in plant available nutrients as a high net mineralization may reflect high gross mineralization or low immobilization.

The vegetation was sensitive to long-term warming with similar responses in the three ecosystems. Plant C, N and P increased by 50–100% in the warmed plots. In contrast, the microbial C and P and in two ecosystems also microbial N remained unchanged or decreased. This suggests that plants were able to sequester extra nutrients made available by microorganisms in response to warming. Whether this response is transient or sustained over a longer period of time is not known at present, as the longest lasting experiments have been in operation for less than two decades. Results from several warming experiments suggest that changes in nutrient availability is much more responsive in the short term (1–10 years) (Hartley et al., 1999; Shaver et al., 2000) but will likely have longer term effects as such changes may alter the competition among species with effects on species composition, litter quality and nutrient availability.

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