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Litter, warming and plants affect respiration and allocation of soil microbial and plant C, N and P in arctic mesocosms

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Abstract

In a mesocosm experiment, we studied decomposition rates as CO_2 efflux and changes in plant mass, nutrient accumulation and soil pools of nitrogen (N) and phosphorus (P), in soils from a sub-arctic heath. The soil was incubated at 10 °C and 12 °C, with or without leaf litter and with or without plants present. The purpose of the experiment was to analyse decomposition and nutrient transformations under simulated, realistic conditions in a future warmer Arctic.

Both temperature enhancement and litter addition increased respiration rates. Temperature enhancement and surprisingly also litter addition decreased microbial biomass carbon (C) content, resulting in a pronounced increase of specific respiration. Microbial P content increased progressively with temperature enhancement and litter addition, concomitant with increasing P mineralisation, whereas microbial N increased only in the litter treatment, at the same time as net N mineralisation decreased. In contrast, microbial biomass N decreased as temperature increased, resulting in a high mobilisation of inorganic N.

Plant responses were closely coupled to the balance of microbial mineralisation and immobilisation. Plant growth and N accumulation was low after litter addition because of high N immobilisation in microbes and low net mineralisation, resulting in plant N limitation. Growth increased in the temperature-enhanced treatments, but was eventually limited by low supply of P, reflected in a low plant P concentration and high N-to-P ratio. Hence, the different microbial responses caused plant N limitation after litter addition and P limitation after temperature enhancement. Although microbial processes determined the main responses in plants, the plants themselves influenced nutrient turnover. With plants present, P mobilisation to the plant plus soil inorganic pools increased significantly, and N mobilisation non-significantly, when litter was added. This was presumably due to increased mineralisation in the rhizosphere, or because the nutrients in addition to being immobilised by microbes also could be absorbed by plants. This suggests that the common method of measuring nutrient mineralisation in soils incubated without plants may underestimate the rates of nutrient mobilisation, which probably contributes to a commonly observed discrepancy of measured lower rates of net nutrient mineralisation than uptake rates in arctic soils.
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Keywords: Microbial biomass; Microbial nutrient immobilisation; Microbial population fluctuations; Nutrient pools; Nutrient transformations; Plant-microbe interactions; Temperature enhancement

1. Introduction

Climate scenarios have projected a summer warming over the arctic land surfaces before the end of the current century between 4.0 and 7.5 °C and even greater change in winter (McCarthy et al., 2001). The warming is likely to increase decomposition and mineralisation rates (Nadelhoffer et al., 1992; Robinson et al., 1997; Jonasson et al., 1999a), which in turn will increase the supply rates of nutrients to the plant available nutrient pool. Increased nutrient availability will change plant community composition with increase of species with high nutrient uptake rates, such as graminoids and deciduous shrubs, which will replace plant life forms with lower uptake and growth rates, such as mosses and evergreen shrubs (Potter et al., 1995; Chapin et al., 1996; Press et al., 1998). The combination of changes in microbial process rates in a warmer Arctic and the changes in species composition, and thereby, the substrate for decomposition, is likely to increase respiratory loss of carbon (C) from the soils to the atmosphere (Hobbie, 1996), at the same time as C sequestration by plants is likely

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to increase. The balance between these gains and losses will determine to what extent the entire C balance of the Arctic will change (Shaver et al., 2000), and if these changes will affect the global C balance, considering that the Arctic contains about 15% of the total amount of terrestrial soil-bound C (Post et al., 1982).

Although we have a general knowledge of the controls of nutrient and C cycling, many details of the controls still remain to be explored in order to increase our understanding of ecosystem processes and thereby also our ability to predict effects of climate change in the Arctic. For instance, most mineralisation studies in the region have shown a discrepancy between estimated low net nutrient mineralisation (i.e. the release to the soil of inorganic nutrients) of e.g. nitrogen (N) and a much higher annual plant nutrient uptake (Shaver and Chapin, 1991; Schimel and Chapin, 1996; Schimel et al., 1996; Jonasson et al., 1999b). These results are generally based on measured mineralisation rates in soils without the presence of plants by the buried bag method (Eno, 1960) and also often without litter. The methodology, hence, does not account for effects on decomposition and mineralisation by soil, litter and plants in concert. For instance, the flow of root exudates is prevented, with consequences for the supply of labile C to the microbes (Johnson et al., 2000). Indeed, the supply of labile C from root exudates is considered to strongly regulate microbial activity (Anderson and Domsch, 1985; Smith and Paul, 1990), and may also be crucial for the balance between microbial net nutrient mineralisation and immobilisation, particularly in nutrient-deficient soils (Verhoeven et al., 1990; Updegraff et al., 1995; Hobbie, 1996; Jonasson and Shaver, 1999). Hence, without presence of plants, microbes may absorb and immobilise part of the gross mineralised nutrients that would have been taken up by plants if they had been present, causing underestimation of net nutrient mineralisation. Furthermore, possible effects of the litter overlayering the soil organic matter (SOM) are not accounted for by the traditional methodology.

The objective with the present study was to analyse decomposition and nutrient transformations under more closely simulated natural conditions than commonly done in similar studies and also to account for effects of a future climate warming. To achieve this, we constructed mesocosms and used the traditional method of measurements of mineralisation by soil incubation (Eno, 1960). However, we modified the method by including plants and litter and did the measurements at two temperatures of 10 and 12 °C. In the mesocosms, we measured treatment effects on plant plus soil respiration and on major pools and fluxes of N and phosphorus (P), i.e. the most commonly production-limiting nutrients in arctic ecosystems (Shaver and Chapin, 1980, 1986, 1995; Jonasson et al., 1996, 1999a).

The soil was from a subarctic heath, the plant was a local fast-growing grass, and the litter was from a local deciduous species. Hence, the plant and litter in the mesocosms were selected from life forms predicted to increase in abundance in a future warmer climate (Chapin et al., 1996). The low temperature of 10 °C is close to the present July average at the site of soil collection, and the temperature difference by 2 °C from 10 to 12 °C is well within the range of likely predicted warming in the Arctic within the next decades (McCarthy et al., 2001).

We expected a general increase of respiration rates, N and P mineralisation with temperature enhancement, with plants included and with litter added due to enhanced microbial activity at higher temperature, stimulation of microbial activity by the presence of root exudates and due to the addition of easily decomposable litter. Second, we expected increase of soil inorganic (i.e. net mineralised) nutrients and microbial N, P and C with litter addition as a consequence of the extra source of nutrients and C added with the litter. Third, we expected a decrease of soil inorganic and microbial nutrients with plants present due to efficient plant sequestration of inorganic nutrients and a trade-off of nutrient uptake between plants and microbes. Fourth, in mesocosms with plants, we expected higher increase of the pools of soil inorganic plus plant nutrients (henceforward called 'nutrient mobilisation') than of the soil inorganic nutrient pool in mesocosms without plants (i.e. net mineralisation) due to stimulation of nutrient mineralisation in the rhizosphere.

2. Materials and methods

2.1. Soil sampling

Soil used in the experiment was collected from the organic horizon of a tundra heath located just above the forest line at 450 m a.s.l. at Mt Paddusstieva, near Abisko Scientific Research Station, northern Sweden (68°21′N, 18°49′E). The site is dominated by the circumpolar dwarf shrub *Cassiope tetragona* (L.) D. Don, together with other evergreen and deciduous dwarf shrubs and mosses. The climate is sub-arctic montane, with a growing season of about 3 months, lasting from mid-late June to early-mid September (Havström et al., 1993; Michelsen et al., 1996).

In the last week of August 2000, 128 soil cores of 10 by 10 cm sides and 6.5 cm depth were collected in the heath. The upper 2–3 cm that contained green parts of mosses and vascular plants were discarded. The cores were brought to a laboratory in Copenhagen and re-cut to 7 by 7 cm sides and 6.5 cm depth that fitted into the pots used for the experiment. The rest of the cores were used for initial soil analyses. In the $7 \times 7 \times 6.5\ cm^3$ cores, we cut a central incision to about 2/3 of the core depth, into which we could 'sandwich' the roots of seedlings. The soils were kept refrigerated at 10 °C during all manipulations prior to the start of the experiment.

2.2. Experimental design

On 20 September 2000, we placed 64 pots with soils in each of two temperature- and light-controlled growth chambers at 10 and 12 °C, respectively. The diurnal light intensity was set to 8 h of darkness and 16 h of light adjusted to 250 μmol m^{-2} s^{-1}. To half of the soil cores at each temperature, we 'sandwiched' grass seedlings with an initial mass of 18.8 ± 1.25 mg in the prepared incisions, and on 10 November when the seedlings were established, we placed 3 g of litter on the top of the soil. Hence, the design was fully factorial with three factors viz. temperature, litter and plants, each with two levels, making up eight treatments, each with 16 replicates per treatment level. The eight treatments were: basal treatment at 10 °C, enhanced temperature to 12 °C, litter added and the combination of enhanced temperature and litter added, all with or without plants present.

The litter was dry leaves of Mountain Birch, *Betula tortuosa* Led., collected near the site at leaf fall the previous autumn, cut to small pieces of about 5×5 mm^2 before addition. The plants were viviparous spikelets of *Festuca vivipara* (L.) Sm. from plants collected at Abisko. The spikelets were pre-grown during two months before the start of the experiment. In some cases, the spikelets showed signs of withering. We, therefore, discarded two pots per treatment with seedlings of the poorest performance.

Pots were distributed randomly among treatments. Their water holding capacity was individually estimated at the start of the experiment by watering until saturation and weighing and later we watered with 10-day intervals to the weight at field capacity. In addition, about 1.5 ml of water was sprayed on the top of the soil cores between the watering occasions to avoid drying of the surface.

2.3. Soil respiration

Soil respiration was measured once weekly from week 12 to week 22 of the experiment. The plants were covered by aluminium foil to exclude light and to prevent photosynthetic CO_2 uptake, and a 165 ml headspace was sealed to the upper part of the pots. Eight millilitre of air was collected from the headspace with a syringe after 0, 10 and 20 min, while keeping the pots in the growth chambers at the set temperature. The CO_2 concentration was analysed with an infrared gas analyser (E6M-1, PP systems, Hertfordshire, UK.) and the respiration rates were estimated using regression of the CO_2 concentration against time.

2.4. Plant and litter harvest, analyses of total N and P

Harvest was done on 5 March 2001, i.e. after about 22 weeks of incubation. We weighed the whole soil core, estimated the water content of soil and litter gravimetrically in sub-samples, and calculated the dry weight of the litter and soils of the cores. The litter and plants, including roots, were extracted from the soil plugs, dried at 70 °C to constant weight and finely ground for analysis. The pieces of litter were still structurally easily discernible. We, therefore, trust that the remaining litter was recovered almost completely, although we cannot guarantee that some small fragments were left in the soil. The roots were more difficult to extract and some of the finest roots had to be left in the soil. On the other hand, because all roots were recently formed, there were no dead roots to collect, which facilitated the extraction. After extraction, the roots were gently washed to remove attached soil particles.

About 25 mg of material was digested in 5 ml of concentrated H_2SO_4 with 20 mg H_2SeO_3 and 1 ml of 30% H_2O_2 added. The digest was analysed for P by the molybdenum blue method and for N by the indophenol method, in both cases using a Hitachi U-2000 spectrophotometer. The analyses also included ten litter samples and seedlings that were harvested and dried at the date of transplantation on 20 September 2000 for determination of pre-incubation nutrient content.

2.5. Soil and litter analyses

After drying and weighing the soil for determination of water content, a sub-sample was finely ground and ashed at 550 °C for determination of loss on ignition and a second sub-sample was used for determination of total C using an ELTRA CS 500 C analyser.

Fifteen gram fresh soil and 1.5 g of litter were extracted for 1 h in 75 ml and 15 ml 0.5 M K_2SO_4, respectively, and filtered through Whatman GF-D filter to recover inorganic N and P, dissolved organic C (DOC) and N (DON). Another subsample was fumigated with $CHCl_3$ for 24 h to release the nutrients in the microbial biomass (Jenkinson and Powlson, 1976), after which the soil or litter was extracted and filtered as above. The extracts were frozen at −25 °C until analysis.

All fumigated and unfumigated samples were analysed on a Shimadzu TOC-5000A total organic C analyser, and microbial C was estimated as the difference between dissolved organic C in fumigated and unfumigated (DOC) samples. Inorganic and microbial P was determined by the molybdenum method, the NH_4^+–N content by the indophenol method and NO_3^-–N by the cadmium reduction method (Allen, 1989). Sub samples of all extracts were digested in concentrated H_2SO_4 and selenous acid mixture with H_2O_2 added to reduce all organic N to NH_4^+–N. The digests were diluted with distilled water and analysed using the indophenol method. Microbial P was determined by subtracting the P content in unfumigated soils from the content in fumigated soils, DON by subtracting the NH_4–N content in the unfumigated and undigested extract from the content in the unfumigated and digested extract and microbial N was determined by subtracting the concentration in the unfumigated, digested sample from the concentration in the fumigated, digested sample (Brookes et al., 1982, 1985; Vance et al., 1987; Jonasson et al., 1996).

The average soil mass per pot was 38.6 g (SEM = 0.8 g), with no significant difference ($P > 0.05$) among treatment means. Unless otherwise stated, the data, therefore, are expressed as changes (Δ) in pools per pot during the incubation. The microbial contents are expressed as extractable fractions, i.e. without accounting for less than complete extractability.

2.6. Statistical analyses

Treatment effects on nutrient pools were tested by one way or factorial analyses of variance with temperature, litter and plant as main factors, and with all interactions between main factors. The analyses were initially run with full models. However, when interactions proved non-significant ($P > 0.05$), they were pooled with the error df to improve the model (Zar, 1996). For soil respiration we used repeated-measures ANOVA with date as the within subject factor. Analyses of plant mass and nutrient concentration were performed with log or arc-sin transformed data, respectively. Statistics on mineralisation and immobilisation pools, however, were performed on untransformed data due to the occurrence of negative values. Statistical analyses were performed with JMP 5.0 software (SAS Institute) using type III sum of squares. Throughout the paper, values are mean ± 1SEM.

3. Results

3.1. Soil and litter nutrients

SOM content was 88.4 ± 0.2% of soil dry mass containing 417 ± 1 mg C g^{-1} dry soil. Total soil N and P measured previously at the site of collection are about 17 mg N and 0.9 mg P per g dry soil (Jonasson et al., 1993, 1999a; Schmidt et al., 1999). Among the inorganic fractions, ammonium strongly dominated over nitrate.

The extractable microbial nutrient fractions constituted a much higher proportion than the soluble organic and inorganic fractions. Microbial C concentration (3.47 ± 0.17 mg g^{-1} SOM), for instance, was about three times higher than the concentration of the DOC fraction (1.09 ± 0.07 mg g^{-1} SOM), and the microbial N fraction (0.53 ± 0.02 mg g^{-1} SOM) was almost five times higher than the DON fraction (0.11 ± 0.02 mg g^{-1} SOM) and more than 10 times higher than the soil inorganic fraction (0.049 ± 0.004 mg g^{-1} SOM).

The 3.0 g of litter added at the start of the experiment contained 29.5 mg N and 3.67 mg P. During incubation, there was a significant increase in the loss of mass, N and P with temperature enhancement ($F_{1,56} = 29.9$, $P < 0.0001$; $F_{1,56} = 8.9$, $P = 0.004$; $F_{1,56} = 15.0$, $P = 0.0003$, respectively), and the loss of N also increased significantly ($F_{1,56} = 5.5$, $P = 0.023$) with presence of plants (Fig. 1).

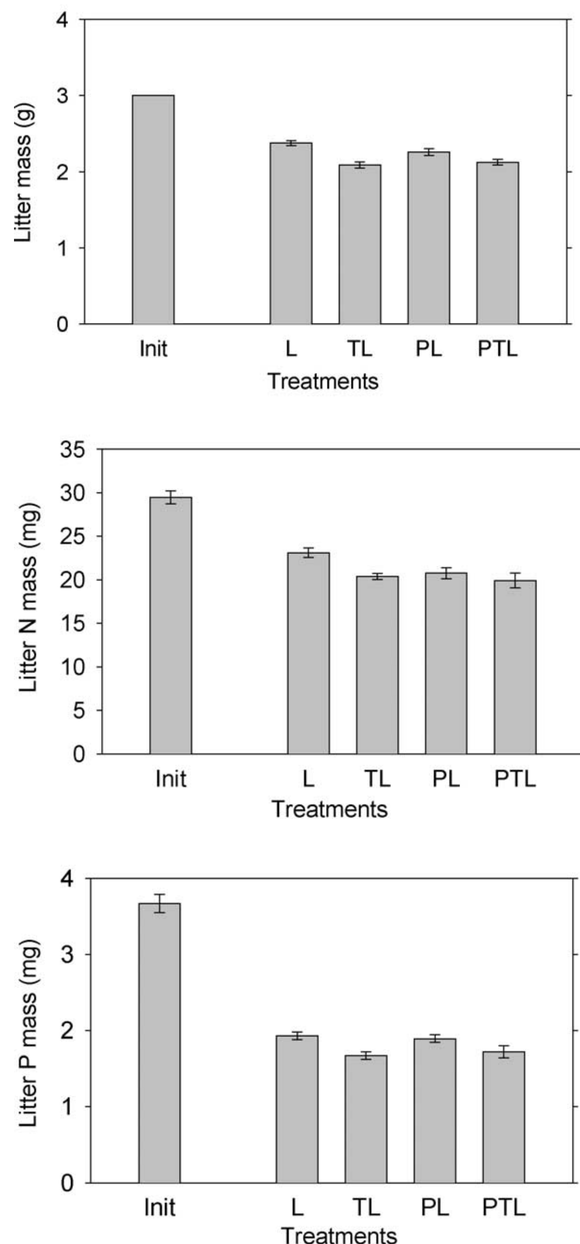

Fig. 1. Mass, N and P content in litter after 22 weeks of incubation in a factorial experiment without plants included at 10 °C (L) and 12 °C (TL), and with plants included at 10 °C (PL) and at 12 °C (PTL). Init is initial amounts before incubation. Data are means ± SEM.

The litter nutrient concentrations, however, did not change significantly in response to any treatment.

3.2. Responses in plant mass, nutrient content and tissue nutrient concentration

The seedling mass was on an average 18.8 mg at the start of the experiment, of which N constituted 0.22 mg and P 0.07 mg. The seedlings accumulated mass during the incubation with the lowest gains in the two treatments held at 10 °C (Table 1). The mass doubled in the temperature-enhanced treatment and reached a maximum

Table 1
Plant biomass increment and tissue N and P concentrations after growth of plant seedlings during 22 weeks in a factorial experiment at 10 °C (P), 12 °C (PT), litter addition at 10 °C (PL) and at 12 °C (PTL)

Treatment	Plant mass increment (mg pot^{-1})	Plant N (mg g^{-1})	Plant P (mg g^{-1})
P	60.4 ± 15.6	10.0 ± 0.9	0.73 ± 0.09
PT	121.0 ± 23.1	9.4 ± 0.8	0.46 ± 0.07
PL	77.4 ± 12.3	9.2 ± 0.5	1.07 ± 0.08
PTL	271.4 ± 44.3	8.0 ± 0.4	0.70 ± 0.06

Data are means ± SEM.

in the combined litter addition and temperature enhanced treatment. This resulted in a highly significant ($F_{1,56} = 22.4$, $P < 0.0001$) temperature effect, and a significant ($F_{1,56} = 9.7$, $P = 0.003$) effect of litter addition, mainly due to a synergistic litter × temperature interaction ($F_{1,56} = 6.2$, $P = 0.016$) rather than due to a response to litter addition alone.

The plant N accumulation followed an almost identical pattern (Table 2), but the response to litter addition and the litter × temperature interaction only tended to be significant ($F_{1,56} = 2.9$, $P = 0.093$ and $F_{1,56} = 2.9$, $P = 0.097$, respectively). In contrast, N concentrations were not significantly affected by the treatments (Table 1), although the mean concentration in the combined litter + temperature enhancement treatment was 20% lower than in the 10 °C treatment.

The plant P accumulation (Table 2) increased significantly with litter addition ($F_{1,56} = 31.6$, $P < 0.0001$), particularly in combination with increased temperature. Plant P also increased ($F_{1,56} = 8.9$, $P = 0.004$) with temperature enhancement solely as an effect of a significant ($F_{1,56} = 8.7$, $P = 0.005$) synergistic litter × temperature interaction. In fact, it appears that the plants even lost P during incubation both after the temperature increase from 10 to 12 °C and in the samples kept at 10 °C, which may be because we failed in extracting all plant roots at the harvest.

P concentration (Table 1) did not follow the changes in P accumulation, as there was a significant, positive, litter addition effect ($F_{1,56} = 14.1$, $P < 0.0004$) and a significant negative temperature effect ($F_{1,56} = 17.4$, $P = 0.0001$), but no litter × temperature interaction ($F_{1,56} = 0.4$, $P = 0.52$).

3.3. Treatment effects on respiration

Soil respiration, i.e. respiration measured in pots without plants, differed slightly and significantly over the sampling dates. However, there was no trend associated with the time the samples had been incubated that could indicate a continuous depletion of labile C fractions. When pooled over all treatments, respiration was highest, reaching 6.5 ± 0.2 μg CO_2 g SOM^{-1} h^{-1} at the third of the nine sampling dates and lowest with 5.7 ± 0.2 μg CO_2 g SOM^{-1} h^{-1} at the sixth measurement occasion (data not shown).

Temperature enhancement increased respiration averaged over the days of measurement significantly ($F_{1,1310} = 305$, $P < 0.0001$) by 33% (Fig. 2). This increase is of the same magnitude as in other, but not all, studies of decomposition in the Arctic within temperature intervals around 10 °C (Davis et al., 1991; Nadelhoffer et al., 1992; Hobbie, 1996; Jonasson et al., 1996; Schmidt et al., 1999). Litter addition also increased respiration significantly ($F_{1,1310} = 175$, $P < 0.0001$) by 23%, which is larger than the 8% increase of substrate mass by the litter addition, reflecting the higher decomposability of litter than of SOM. The combination of temperature enhancement and litter addition caused the greatest increase by 64% in comparison with respiration in pots kept at 10 °C without litter addition.

The increased CO_2 efflux with both litter addition and warming coincided with a reduction of soil microbial biomass C (Fig. 3A and D). Hence, the concomitant changes in respiration rate and microbial biomass C led to pronounced increase of specific respiration, i.e. the respiration to microbial biomass C ratio (Table 3).

In contrast to the increase of respiration after litter addition and warming, the presence of plants reduced respiration ($F_{1,1310} = 36.0$, $P < 0.0001$) in all treatments by 10–15%. This is surprising because photosynthesis was prevented, and the total respiration in pots with plants was expected to increase to above the level of soil respiration in pots without plants due to additional efflux of plant-respired CO_2. However, the decline coincided with reduced release of inorganic N when plants were present (Fig. 3E and F) and a trend of reduced DON accumulation (Fig. 4), suggesting N limitation of decomposition caused by the N sink in plants.

Table 2
Plant nitrogen and phosphorus uptake, net N and P mineralisation, and N and P mobilisation to plant plus soil inorganic pools (the sum of plant uptake and net mineralisation) after 22 weeks of incubation in a factorial experiment at 10 °C (P), 12 °C (PT), litter addition at 10 °C (PL) and at 12 °C (PTL)

Treatment	Nitrogen			Phosphorus		
	Plant uptake (mg pot^{-1})	Mineralisation (mg pot^{-1})	Mobilisation (mg pot^{-1})	Plant uptake (mg pot^{-1})	Mineralisation (mg pot^{-1})	Mobilisation (mg pot^{-1})
P	0.68 ± 0.25	0.14 ± 0.49	0.82 ± 0.53	−0.020 ± 0.007	−0.013 ± 0.010	−0.033 ± 0.011
PT	1.15 ± 0.26	0.71 ± 0.51	1.86 ± 0.62	−0.020 ± 0.007	0.058 ± 0.016	0.039 ± 0.015
PL	0.69 ± 0.15	−0.08 ± 0.26	0.61 ± 0.25	0.025 ± 0.013	0.132 ± 0.029	0.158 ± 0.031
PTL	2.12 ± 0.41	−1.20 ± 0.22	0.92 ± 0.48	0.125 ± 0.030	0.099 ± 0.011	0.224 ± 0.032

Data are means ± SEM.

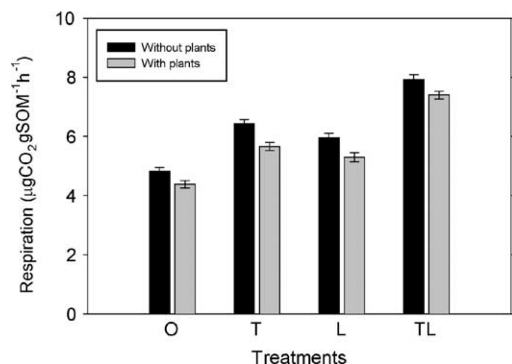

Fig. 2. Respiration pooled over nine sampling dates during 22 weeks of factorial soil incubation without or with plants. The treatments are: incubation without litter added at 10 °C (0) and at 12 °C (T) and incubation with litter added at 10 °C (L) and at 12 °C (TL). Data are means ± SEM.

3.4. Responses in microbial nutrient fractions

Average soil microbial C content increased during incubation and C was, hence, net immobilised in the biomass (Fig. 3A and D). Across treatments, there was a progressive decline of C incorporation with increasing temperature, with presence of plants and with litter addition. However, although this trend was evident, the variations within treatments were high and the statistical test showed a significant effect of litter addition only ($F_{1,114} = 7.2$, $P = 0.009$). This decline of microbial C with litter addition is surprising as it contrasts to increase of microbial C in other studies of responses to litter additions we are aware of (e.g. Wardle, 1992; Aggangan et al., 1999; Fisk and Fahey, 2001). We cannot exclude the possibility, however, that compounds in *B. tortuosa* litter are toxic to some soil microbes, as litter extract of this species previously has

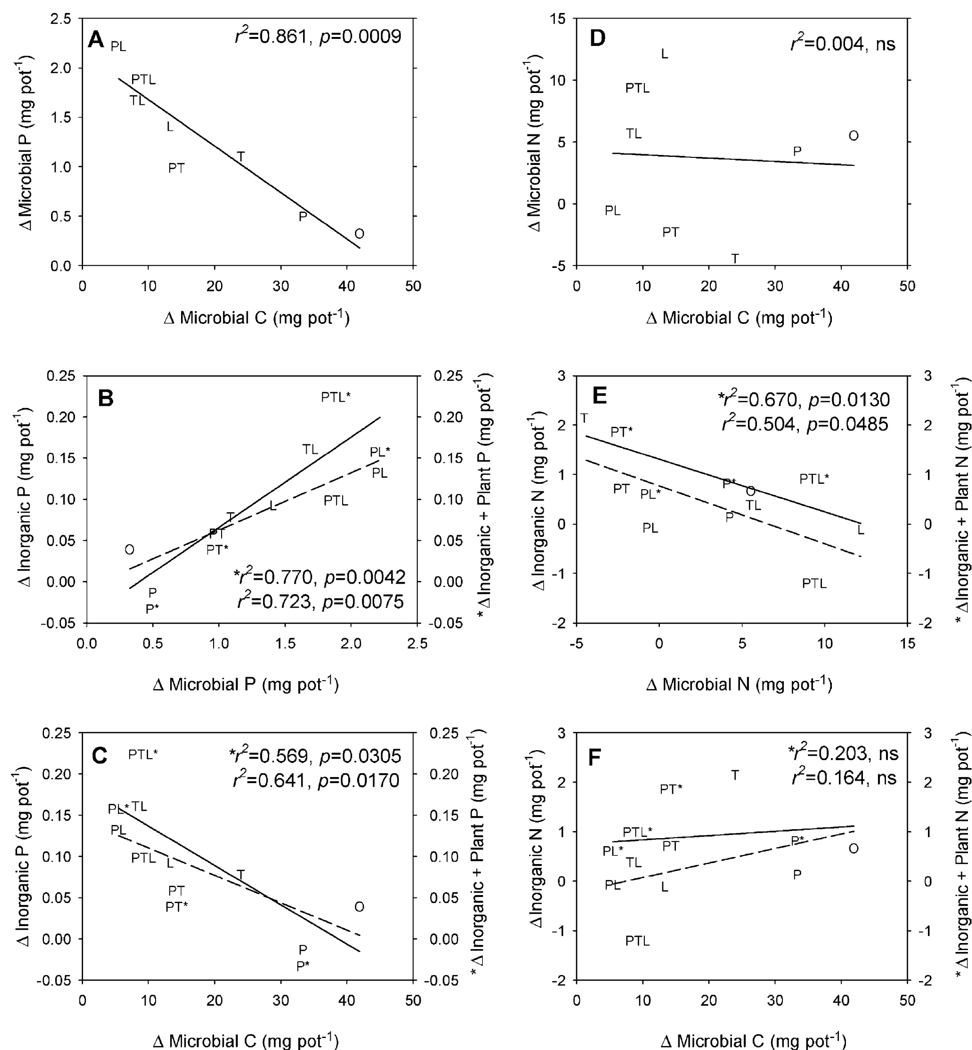

Fig. 3. Regression data of changes (*Δ*) in microbial C, microbial N and P, soil pools of inorganic N and P (net mineralisation) and in inorganic + plant N and P after 22 weeks of incubation in a factorial experiment. The treatments are: incubation without plants and litter at 10 °C (O) and at 12 °C (T), incubation with plants included at 10 °C (P) and at 12 °C (PT), with litter added at 10 °C (L) and 12 °C (TL) and with combinations of plants included and litter added at 10 °C (PL) and at 12 °C (PTL). Symbols without asterisks and hatched regression lines in Figs. B, C, E and F show data-points and regressions with changes in soil inorganic pools only, while symbols with asterisk (* and *r^2) and fully drawn regression lines are data-points and regressions with the summed changes in inorganic and plant pools.

Table 3
C content (means ± SEM) in soil organic matter (SOM) and litter, integrated respiration at nine occasions over the 22 weeks, and specific respiration (the ratio of respiration to total microbial C content) after 22 weeks of incubation in a factorial experiment

Treatment	Microbial C (mg pot^{-1})			Respiration (μg C pot^{-1}h^{-1})	Specific respiration (μg C mg C_{mic}^{-1} h^{-1})
	SOM	Litter	Total		
0	161 ± 14	0	161	50 ± 1.1	0.31
T	129 ± 11	0	129	66 ± 1.5	0.51
P	161 ± 8	0	161	46 ± 1.5	0.28
PT	163 ± 8	0	163	65 ± 1.7	0.40
L	144 ± 8	6 ± 0.9	150	60 ± 1.5	0.40
TL	157 ± 6	12 ± 0.9	169	74 ± 1.4	0.44
PL	124 ± 9	7 ± 1.1	131	49 ± 1.4	0.37
PTL	177 ± 7	8 ± 0.7	185	83 ± 1.6	0.45

The treatments are: incubation without plants and litter at 10 °C (0) and at 12 °C (T), incubation with plants included at 10 °C (P) and at 12 °C (PT), with litter added at 10 °C (L) and 12 °C (LT) and with combinations of plants included and litter added at 10 °C (PL) and at 12 °C (PLT).

shown growth-inhibiting effect on plants (Schmidt et al., 1997a).

The microbial C mass of between 6 and 12 mg per pot (Table 4) in the litter after incubation made up between 4 and 7% of the total microbial pool in soil cores with added litter (Table 3). It increased significantly ($F_{1,114} = 15.4$, $P = 0.0002$) with temperature enhancement, contrasting with the decreasing trend in SOM, and tended to decrease ($F_{1,114} = 3.5$, $P = 0.07$) when plants were present. However, this was an interaction effect ($F_{1,114} = 7.1$, $P = 0.01$) of particularly high microbial mass in the cores after addition of litter when kept at 12 °C.

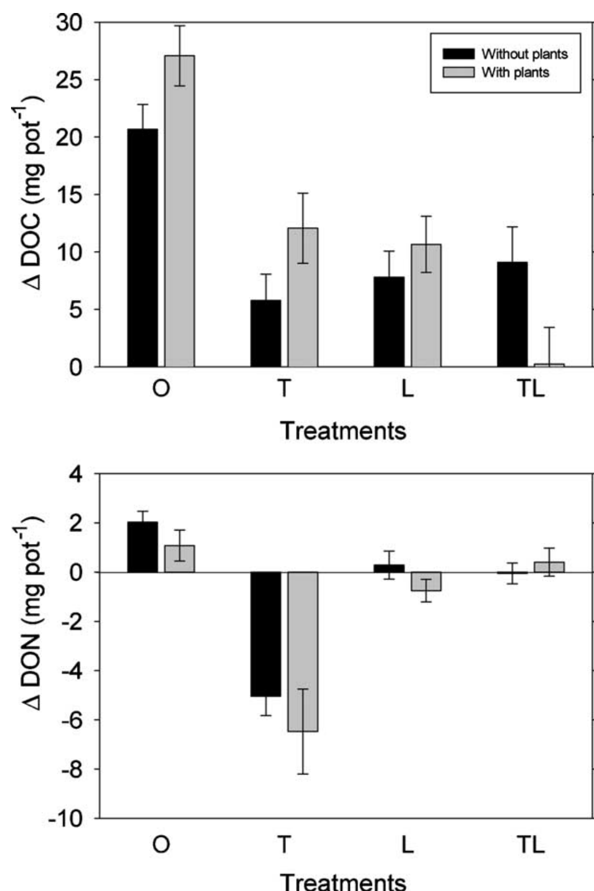

Fig. 4. Changes (Δ) in dissolved organic C (DOC) and N (DON) in soils after 22 weeks of factorial incubation without and with plants. The treatments are: incubation without litter added at 10 °C (0) and at 12 °C (T) and incubation with litter added at 10 °C (L) and at 12 °C (TL). Data are means ± SEM.

The treatment effects in incorporation of soil microbial P correlated negatively and strongly ($P = 0.0009$; $R^2 = 0.86$) with the effects in microbial C (Fig. 3A), resulting in decreased C-to-P ratios in all treatments. The incorporation of microbial P increased significantly ($F_{1,114} = 3.9$, $P = 0.051$) with temperature and litter addition ($F_{1,114} = 42.3$, $P < 0.0001$), but there was also a significant temperature × litter interaction ($F_{1,114} = 4.0$, $P = 0.048$) due to a lower response than expected in the combined temperature enhancement, litter addition treatment, particularly in pots with plants. The presence of plants generally resulted in increasing immobilisation. However, the effect of plants only approached significance ($F_{1,114} = 2.6$, $P = 0.107$) due to a lower response than expected to temperature enhancement from 10 to 12 °C in pots with added litter when plants were present. This interaction, in fact, corresponded with a similar effect in microbial C, which increased in the same treatment relative to the response at 10 °C but without causing any significant interaction.

Microbial P in the litter varied between 0.29 and 0.36 mg per pot, making up 3.5–4.5% of the total soil plus

Table 4
Microbial C, N and P content in litter after 22 weeks of incubation in a factorial experiment without presence of plants at 10 °C (L), at 12 °C (TL), and with plants present at 10 °C (PL) and at 12 °C (PTL)

Treatment	Microbial C (mg pot^{-1})	Microbial N (mg pot^{-1})	Microbial P (mg pot^{-1})
L	6.0 ± 0.9	0.78 ± 0.05	0.34 ± 0.03
TL	11.9 ± 0.9	0.98 ± 0.06	0.36 ± 0.03
PL	6.7 ± 1.1	0.72 ± 0.06	0.34 ± 0.04
PTL	7.8 ± 0.7	0.81 ± 0.05	0.29 ± 0.04

Data are means ± SEM.

litter microbial P and did not change with any treatment (Table 4).

Soil microbial N (Fig. 3D) showed a response pattern that was different from both microbial C and P, as the microbial immobilisation in some cases decreased during incubation. Furthermore, there was no consistent increase or decrease with temperature enhancement and litter addition. Instead, while litter addition increased the incorporation of microbial N ($F_{1,114} = 18.5$, $P < 0.0001$), temperature enhancement caused a significant ($F_{1,114} = 5.6$, $P = 0.019$) decrease. The presence of plants gave no significant effect ($F_{1,114} = 2.2$, $P = 0.14$). However, all three factors interacted significantly, or close to significantly, in all possible combinations, creating a complicated response pattern. This was mainly because microbial N in pots with litter added increased strongly in the absence of plants during the incubation but it changed little, and even decreased, in the presence of plants. Hence, instead of being absorbed by the microbes at a similar rate as C to maintain an even C-to-N ratio, the microbial N absorption rate varied with the treatments, seemingly independent of C sequestration rates, with high absorption rate after litter addition but with low rate as temperature was increased. This resulted in a far from significant correlation between microbial N and C (Fig. 3D).

Microbial N in the litter varied between 0.7 and 1.0 mg per pot and made up between 2.5 and 4.5% of total microbial N (Table 4). Contrary to N in SOM, temperature enhancement increased the amounts ($F_{1,114} = 6.3$, $P = 0.015$) but N was reduced slightly ($F_{1,114} = 4.0$, $P = 0.05$) when plants were present.

3.5. Responses in soil inorganic nutrients

Inorganic P, like microbial P, correlated negatively with microbial C ($P = 0.017$; $R^2 = 0.64$) (Fig. 3C). It showed a response pattern that was very similar to microbial P, with which it correlated positively at $P = 0.008$ ($R^2 = 0.72$; Fig. 3B). Inorganic P increased significantly with temperature enhancement ($F_{1,114} = 6.8$, $P = 0.010$) and litter addition ($F_{1,114} = 31.0$, $P < 0.0001$) and tended to decrease with plants present ($F_{1,114} = 2.7$, $P = 0.10$). However, in the combination with litter addition at 10 °C, inorganic P increased in pots with plants, resulting in a significant temperature × litter addition × plant interaction ($F_{1,114} = 5.2$, $P = 0.025$).

As for microbial N, inorganic N (Fig. 3F) did not correlate significantly with microbial C, but it correlated negatively ($P = 0.049$; $R^2 = 0.50$) with microbial N (Fig. 3E). Litter addition and presence of plants significantly reduced inorganic N ($F_{1,114} = 21.0$, $P < 0.0001$ and $F_{1,114} = 11.8$, $P = 0.0008$, respectively). However, there were also significant litter addition × temperature ($F_{1,114} = 6.6$, $P = 0.011$) and plant × temperature ($F_{1,114} = 6.0$, $P = 0.016$) interactions due to a much lower response to combined litter addition and temperature enhancement than expected from the single factor responses, particularly with plants present. The response was particularly strong in the combination of litter addition, temperature enhancement and presence of plants and led to a loss of inorganic N during the incubation, reflecting the combined high N uptake in both microbes and plants (Fig. 3E and F, Table 2).

3.6. Responses in nutrient mobilisation

Despite the increasing microbial immobilisation of P with temperature enhancement and litter addition (Fig. 3A), there was yet a net supply of P to the soil inorganic plus plant P pool (i.e. of mobilised P). The slope of the regression of changes in inorganic plus plant P on microbial P in Fig. 3B suggests a linear release rate of 0.11 mg P per mg increase of the microbial fraction along the range of estimated microbial P content. Hence, the absolute amount of mobilised P increased with increasing microbial P content but decreased with increasing microbial C content. Indeed, at the high microbial C content in the 10 °C treatment, net P release approached zero and no P was absorbed by the plants (Table 2).

For N, the significant negative correlation between the microbial and mobilised fractions resulted in a decrease of about 0.11 mg released N per mg increase of the microbial fraction (Fig. 3E). This was because temperature enhancement led to high N mineralisation, coincident with a loss of microbial N during incubation. In contrast, litter addition decreased the mobilisation rate of inorganic N, and even depleted the N pool during incubation, coincident with the high rate of microbial N immobilisation. At high microbial immobilisation, the mobilisation rate of N, hence, approached zero, which took place at an immobilisation rate of about 10–15 mg N per pot, shown by the intercept of the regression line with the x-axis in Fig. 3E. This occurred despite a loss of N from litter of 6.4 to 9.6 mg N pot^{-1}.

Contrary to what we expected, there were no significant main effects of presence of plants on P ($F_{1,112} = 0.07$, $P = 0.80$) and N ($F_{1,112} = 1.3$, $P = 0.27$) mobilisation (Fig. 5). However, there was a synergistic plant × litter interaction for P ($F_{1,112} = 13.9$, $P = 0.0003$), showing a mobilisation of extra P when litter was added. A similar trend, although non-significant, also occurred for N ($F_{1,112} = 1.8$, $P = 0.18$). Unfortunately, the tests were relatively insensitive due to large variance in the data sets.

3.7. Treatment effects on DOC and DON

The change in content of DOC during incubation (Fig. 4) correlated significantly with the changes in microbial C ($P = 0.040$; $R^2 = 0.53$), as it decreased significantly with litter addition ($F_{1,114} = 24.7$, $P < 0.0001$) and temperature enhancement ($F_{1,114} = 25.4$, $P < 0.0001$). The presence of

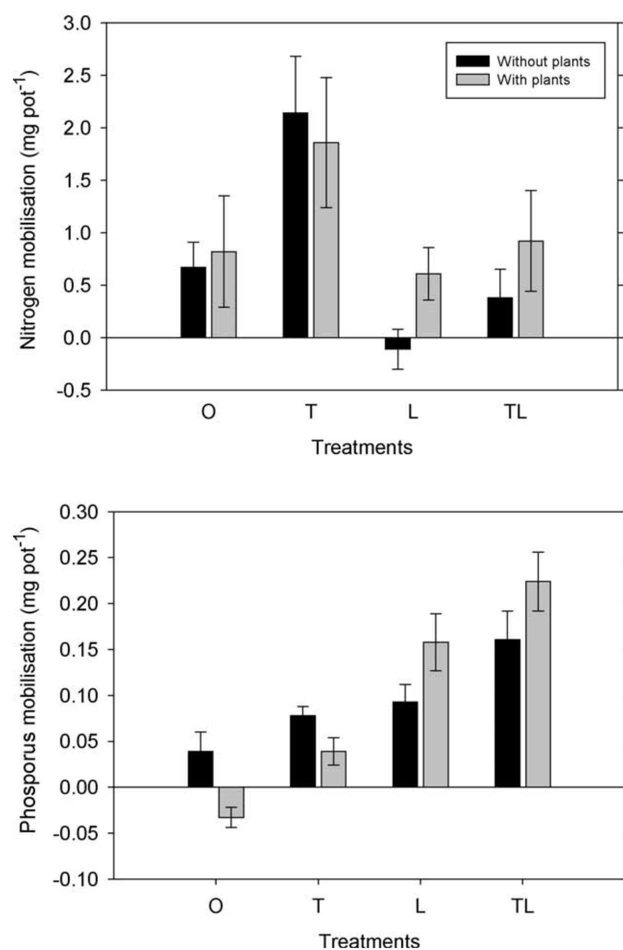

Fig. 5. Nitrogen and phosphorus mobilisation to the soil inorganic pools in mesocosms without plants and to the soil inorganic plus plant pools in mesocosms with plants after 22 weeks of factorial incubation. The treatments are: incubation without litter added at 10 °C (0) and at 12 °C (T) and incubation with litter added at 10 °C (L) and at 12 °C (TL). Data are means ± SEM.

plants increased DOC in all treatments except when litter addition and temperature enhancement were combined, causing significant litter × plant ($F_{1,114} = 6.1$, $P = 0.015$) and litter × temperature ($F_{1,114} = 8.1$, $P = 0.005$) interactions.

The changes in DON (Fig. 4) also showed a pattern of variation similar to that in microbial N with which it correlated at $P = 0.031(R^2 = 0.57)$ although with a much more pronounced decline in the 12 °C treatment and lesser response in both litter addition treatments. The overall response was a highly significant decline of DON with temperature enhancement ($F_{1,114} = 39.8$, $P < 0.0001$) and a lesser decline with litter addition ($F_{1,114} = 13.8$, $P = 0.0003$). However, the combination of litter addition and temperature enhancement caused a lower response than expected from the individual treatments and showed up as a significant litter addition × temperature enhancement interaction ($F_{1,114} = 48.4$, $P < 0.0001$)

4. Discussion

With this experiment, we have shown that decomposition and nutrient transformations are strongly affected by a complicated network of interactions between the substrate, the presence of plants and the climatic conditions. Many of the responses we found were surprising. For instance, litter addition caused a decrease of microbial biomass C (Fig. 3A and D), which is contrary to the usually reported increase of microbial C (e.g. Wardle, 1992; Aggangan et al., 1999; Fisk and Fahey, 2001), but respiration increased, however, leading to increased specific respiration. Such increase is commonly observed in association with disturbance of the system, as, e.g. litter addition, and has been interpreted as decline of the efficiency of microbial utilisation of carbon for microbial growth (Wardle and Ghani, 1995). Also, when microbial biomass is measured as total (active plus inactive) biomass as we did, specific respiration is likely to increase when the proportion of active microbial biomass increases (Fisk and Fahey, 2001). In our case, we believe that the increase of specific respiration was because the dieback of microbes led to release of labile C from the dying microbes that ‘fuelled’ the reduced but highly active surviving populations.

Also contrary to what we expected, presence of plants reduced mesocosm respiration in all treatments (Fig. 2), presumably due to N limited decomposition caused by high uptake of labile N by the plants.

In addition to the unexpected responses in respiration, the experiment revealed an intricate network of nutrient interactions between plants, microbes and the inorganic nutrient pools under the different temperature regimes that were difficult to predict beforehand. The general treatment response in plants was a closely matched accumulation of biomass and N content and an even tissue N concentration across treatments, but different responses in P mass and tissue P concentrations (Tables 1 and 2). For N, the responses in the plants seem to be a consequence of responses in the microbial and soil inorganic N pools. As a consequence of an unexpected lack of treatment effect of litter addition on N mineralisation, plant N content did not respond to the treatment, while the content increased strongly in the temperature-enhanced treatment, coincident with the decline of microbial biomass and enhanced net N mineralisation. When the two treatments were combined, the mobilisation of N to the plant plus soil inorganic N pools was intermediate to the changes in pool sizes in the litter addition and temperature-enhanced treatment (Table 2, Fig. 5), as expected, but the proportion increased strongly in plants and decreased in the soil inorganic pool (Table 2).

In contrast to the low changes in inorganic and plant N pools after litter addition at 10 °C, P in these pools increased strongly (Table 2), although plant uptake was modest and not significantly different from the uptake at 10 °C without litter addition. Plant P concentration increased, however, strongly. Hence, it appears that plant P availability was high,

but plant growth and the sink strength for P was low due to N limitation by the high immobilisation in the microbes. The imbalance in N and P supply to plants is mirrored in a low plant tissue N-to-P ratio of 8.4.

On the other hand, when temperature was increased by 2 °C, mobilisation to the plant plus soil inorganic P pools was low (Table 2, Fig. 5), despite high biomass accumulation (Table 1), resulting in a decrease of tissue P concentration as an effect of dilution. Apparently, the modest increase of P mobilisation following the 2 °C increase of the temperature was too low to allow the plants to absorb P at the same rate as C accumulated. However, N was amply supplied and absorbed by the plants, which increased the plant N-to-P ratio to 18.8. This ratio is indicative of plant P limitation (Koerselman and Meuleman, 1996; Schmidt et al., 1997b), which probably explains why plants did not absorb still more N from the soil inorganic pool, which was at a maximum in this treatment despite the high plant uptake.

Hence, the treatments apparently led to N limitation of plant growth when litter was added and to P limitation when temperature was increased, and the pattern of distribution of nutrients between the plant and soil inorganic pools can be explained by the response in the microbial community. This is further illustrated by the strong plant growth response in the combined litter addition, temperature-enhancement treatment (Table 1). In this case, the conditions for high mobilisation of N was satisfied by the net release of N from microbes due to the increased temperature, although counteracted by the immobilisation due to the litter addition, and reflected in a pool sizes of plant + soil inorganic N and of microbial N intermediate to those in the single treatments (Fig. 5, Table 4). The demand for P was satisfied by an added effect of net release after both temperature enhancement and litter addition. This led to high N uptake in plants coincident with strong depletion of the soil inorganic pool, while the plant uptake of P still left appreciable amount of soil inorganic P.

The microbial nutrient mobilisation/immobilisation apparently was a main determinant of the nutrient availability to plants (Harte and Kinzig, 1993; Kaye and Hart, 1997), while we found no evidence that plant competed with microbes for nutrients. Instead, the microbes in most cases increased their nutrient pools concomitant with increases also in the plants. It is likely, however, that the plants themselves played an active role in nutrient mobilisation. As we hypothesised, N mobilisation to the plant plus soil inorganic pools tended to increase when plants were present as compared with the mobilisation to the inorganic pool in the absence of plants and particularly when litter was added. However, the plant effect was not significant because there was no extra mobilisation to the plant plus soil inorganic pool in the 12 °C treatment where N supply was high also without plants present (Fig. 5) and plants probably were P limited. In contrast, the mobilisation of P to the plant plus soil inorganic pools increased strongly in combination with litter addition (Fig. 5).

Unfortunately, the tests were relatively insensitive due to large variations within treatments and the plant uptake most likely was underestimated because of less than complete extraction of fine roots from the soil. Nevertheless, the results indicate that measurements of mineralisation without plants present in these soils may underestimate mineralisation (Jonasson et al., 2001), at least under some circumstances, as shown by the synergistic plant × litter response and the extra mobilisation of N in all cases when this element was limiting growth. It is likely therefore that estimation of net mineralisation in the absence of plants explains part of the discrepancy between net mineralisation and plant uptake rates commonly reported from arctic soils (Shaver and Chapin, 1991; Schimel and Chapin, 1996; Schimel et al., 1996; Jonasson et al., 1999b).

Overall, we conclude that our experiment has revealed a network of responses that are closely coupled to processes within and interactions between major ecosystem components and temperature levels. These responses make predictions of ecosysstem functioning in a changing environment extremely difficult and cannot be foreseen without taking the complexity of the ecosystem structure into account.

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References

Aggangan, R.T., O'Connell, A.M., McGrath, J.F., Dell, B., 1999. The effects of *Eucalyptus globules* Labill. leaf litter on C and N mineralization in soils from pasture and native forest. Soil Biol. Biochem. 31, 1481–1487.

Allen, S.E., 1989. Chemical Analysis of Ecological Material, second ed., Blackwell Scientific Publications, Oxford, UK.

Anderson, J.P.E., Domsch, K.H., 1985. Determination of ecophysiological maintenance requirements of soil microorganisms in a dormant state. Biol. Fertil. Soils 1, 81–89.

Brookes, P.C., Powlson, D.S., Jenkinson, D.S., 1982. Measurements of microbial biomass phosphorus in soil. Soil Biol. Biochem. 14, 319–329.

Brookes, P.C., Landman, A., Pruden, G., Jenkinson, D.S., 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in the soil. Soil Biol. Biochem. 17, 837–842.

Chapin, F.S. III, Bret-Harte, M.S., Hobbie, S.E., Zong, H., 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. J. Veg. Sci. 7, 347–358.

Davis, J., Schober, A., Bahn, M., Sveinbjörnssen, B., 1991. Soil carbon and nitrogen turnover at and below the elevated treeline in Northern Fennoscandia. Arct. Alp. Res. 23, 279–282.

Eno, C.F., 1960. Nitrate production in the field by incubating the soil in polyethylene bags. Soil Sci. Soc. Am. Proc. 24, 277–279.

Fisk, M.C., Fahey, T.J., 2001. Microbial biomass and nitrogen cycling responses to fertilization and litter removal in young northern hardwood forests. Biogeochem 53, 201–223.

Harte, J., Kinzig, A.P., 1993. Mutualism and competition between plants and decomposers: implications for nutrient allocation in ecosystems. Am. Nat. 141, 829–846.

Havström, M., Callaghan, T.V., Jonasson, S., 1993. Differential growth responses of *Cassiope tetragona*, an arctic dwarf-shrub, to environmental perturbations among three contrasting high- and subarctic sites. Oikos 66, 389–402.

Hobbie, S.E., 1996. Temperature and plant species control over litter decomposition in Alaskan Tundra. Ecol. Monogr. 66, 503–522.

Jenkinson, D.S., Powlson, D.S., 1976. The effect of biocidal treatments on metabolism in soil. V. A. method for measuring soil biomass. Soil Biol. Biochem. 8, 209–213.

Johnson, L.C., Shaver, G.R., Cades, D.H., Rastetter, E., Nadelhoffer, K., Giblin, A., Laundre, J., Stanley, A., 2000. Plant carbon-nutrient interactions control CO_2 exchange in Alaskan wet sedge tundra ecosystems. Ecology 81, 453–469.

Jonasson, S., Shaver, G.R., 1999. Within-stand nutrient cycling in arctic and boreal herbaceous and forested wetlands. Ecology 80, 2139–2150.

Jonasson, S., Havström, M., Jensen, M., Callaghan, T.V., 1993. In situ mineralization of nitrogen and phosphorus of arctic soils after perturbations simulating climate change. Oecologia 95, 179–186.

Jonasson, S., Michelsen, A., Schmidt, I.K., Nielsen, E.V., Callaghan, T.V., 1996. Microbial biomass C, N and P in two arctic soils and the responses to addition of NPK fertilizer and carbon: implications for plant nutrient uptake. Oecologia 106, 507–515.

Jonasson, S., Michelsen, A., Schmidt, I.K., Nielsen, E.V., 1999a. Responses in microbes and plants to changed temperature, nutrient and light regimes in the Arctic. Ecology 80, 1828–1843.

Jonasson, S., Michelsen, A., Schmidt, I.K., 1999b. Coupling of nutrient cycling and carbon dynamics in the Arctic, integration of soil microbial and plant processes. Appl. Soil Ecol. 11, 135–146.

Jonasson, S., Shaver, G.R., Chapin, F.S. III, 2001. Biogeochemistry in the Arctic: patterns, processes and controls. In: Schulze, E.D., Harrison, S.P., Heimann, M., Holland, E.A., Lloyd, J.J., Prentice, I.C., Schimel, D. (Eds.), Global Biogeochemical Cycles in the Climate System, Academic Press, New York, pp. 139–150.

Kaye, J.P., Hart, S.C., 1997. Competition for nitrogen between plants and soil microorganisms. Trends Ecol. Evol. 12, 139–143.

Koerselman, W., Meuleman, A.F.M., 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. J. Appl. Ecol. 33, 1441–1450.

McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J., White, K.S., 2001. Climate change 2001: impacts, adaptation, and vulnerability, Contributions of Working Group II to the Third Assessment Report of the International Panel of Global Change, Cambridge University Press, Cambridge, UK.

Michelsen, A., Jonasson, S., Sleep, D., Havström, M., Callaghan, T.V., 1996. Shoot biomass, $\delta^{13}C$, nitrogen and chlorophyll responses of two arctic dwarf shrubs to *in situ* shading, nutrient application and warming simulating climatic change. Oecologia 105, 1–12.

Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R., Linkins, A.E., 1992. Microbial processes and plant nutrient availability in arctic soils. In: Chapin, F.S. III, Jefferies, R.L., Reynold, J.F., Shaver, G.R., Svoboda, J. (Eds.), Arctic ecosystems in a changing climate, an ecophysiological perspective, Academic Press, San Diego, pp. 281–300.

Post, W.M., Emanuel, W.R., Zinke, P.J., Stangenberger, A.G., 1982. Soil carbon pools and world life zones. Nature 298, 156–159.

Potter, J.A., Press, M.C., Callaghan, T.V., Lee, J.A., 1995. Growth responses of *Polytrichum commune* Hedw. and *Hylocomium splendens* (Hedw.) Br. Eur. to simulated environmental change in the Subarctic. New Phytol. 131, 533–541.

Press, M.C., Potter, J.A., Burke, M.J.W., Callaghan, T.V., Lee, J.A., 1998. Response of a subarctic dwarf shrub heath community to simulated environmental change. J. Ecol. 86, 315–327.

Robinson, C.H., Michelsen, A., Lee, J.A., Whitehead, S.J., Callaghan, T.V., Press, M.C., Jonasson, S., 1997. Elevated atmospheric CO_2 affects decomposition of *Festuca vivipara* (L.) Sm. litter and roots in experiments simulating environmental change in two arctic ecosystems. Global Change Biol. 3, 37–49.

Schimel, J.P., Chapin, F.S. III, 1996. Tundra plant uptake of amino acid and NH_4^+ nitrogen in situ: plants compete well for amino acid N. Ecology 77, 2142–2147.

Schimel, J.P., Kielland, K., Chapin, F.S. III, 1996. Nutrient availability and uptake by tundra plants. In: Reynolds, J.F., Tenhunen, J.D. (Eds.), Landscape Function and Disturbance in Arctic Tundra, Ecological Studies Series, Springer, Berlin, Heidelberg, pp. 203–221.

Schmidt, I.K., Michelsen, A., Jonasson, S., 1997a. Effects on plant production after addition of labile carbon to arctic/alpine soils. Oecologia 112, 305–313.

Schmidt, I.K., Michelsen, A., Jonasson, S., 1997b. Effects of labile soil carbon on nutrient partitioning between an arctic graminoid and microbes. Oecologia 112, 557–565.

Schmidt, I.K., Jonasson, S., Michelsen, A., 1999. Mineralization and microbial immobilization of N and P in arctic soils in relation to season, temperature and nutrient amendment. Appl. Soil Ecol. 11, 147–160.

Shaver, G.R., Chapin, F.S. III, 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. Ecology 61, 662–675.

Shaver, G.R., Chapin, F.S. III, 1986. Effect of fertilizer on production and biomass of tussock tundra, Alaska, U.S.A. Arct. Alp. Res. 18, 261–268.

Shaver, G.R., Chapin, F.S. III, 1991. Production/biomass relationships and element cycling in contrasting arctic vegetation types. Ecol. Monogr. 61, 1–31.

Shaver, G.R., Chapin, F.S. III, 1995. Long-term responses to factorial NP fertilizer treatment by Alaskan wet and moist tundra sedge species. Ecography 18, 259–275.

Shaver, G.R., Canadell, J., Chapin, F.S., Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L., Rustad, L., 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. Bioscience 50, 871–882.

Smith, J.L., Paul, E.A., 1990. The significance of soil microbial biomass estimations. In: Bollag, J.M., Stotsky, G. (Eds.), Soil Biochemistry, Marcel Dekker, Basel, pp. 357–396.

Updegraff, K., Pastor, J., Bridgham, S.D., Johnston, C.A., 1995. Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. Ecol. Appl. 5, 151–163.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19, 703–707.

Verhoeven, J.T.A., Maltby, E., Schmitz, M.B., 1990. Nitrogen and phosphorus mineralization in fens and bogs. J. Ecol. 78, 713–726.

Wardle, D.A., 1992. A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. Biol. Rev. 67, 321–358.

Wardle, D.A., Ghani, A., 1995. A critique of the microbial metabolic quotient (qCO_2) as a bioindicator of disturbance and ecosystem development. Soil Biol. Biochem. 27, 1601–1610.

Zar, J.H., 1996. Biostatistical Analysis, third ed., Prentice-Hall, Englewood Cliffs, NJ.