

Responses of Plant Litter Decomposition and Nitrogen Mineralisation to Simulated Environmental Change in a High Arctic Polar Semi-Desert and a Subarctic Dwarf Shrub Heath

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## Responses of plant litter decomposition and nitrogen mineralisation to simulated environmental change in a high arctic polar semi-desert and a subarctic dwarf shrub heath

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Impacts of climate change were simulated in two contrasting European arctic ecosystems, a high arctic polar semi-desert and a subarctic dwarf shrub heath, by increasing temperature (using polythene tents), precipitation and soil nutrient (NPK) availability. The effects of these treatments and their interactions on plant litter decomposition and soil nutrient fluxes were assessed. Polythene tents increased air, litter and soil temperatures but reduced litter and soil moisture contents. At both sites, litter decomposition was significantly retarded in the tent treatments due probably to reduced litter moisture contents. The tent treatment had no effect on extractable soil N pools or net total N mineralisation at either site, although the treatment significantly reduced net seasonal nitrification values at the subarctic site. The additional precipitation treatment significantly increased litter decomposition at the dwarf shrub heath site and the net amount of N mineralised at the polar semi-desert site. Litter decomposition was increased, as was net N mineralisation, by the application of nutrients. The results suggest that soil temperature increases of up to 1°C, which may occur by the end of the next century as an effect of a predicted 4°C rise in air temperature, have only small effects on total N mineralisation in the short term in arctic soils.

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Tundra ecosystems contain 11% of the world's soil carbon pool (Melillo et al. 1990), and soils hold 95% of the organically bound plant nutrients within the ecosystem (Jonasson 1983). Decomposition and nutrient mineralisation are strongly reduced in the Arctic by low soil temperatures, high (Flanagan and Veum 1974) or low soil moisture contents and the recalcitrant nature of organic matter (Van Cleve and Yarie 1986). In arctic ecosystems, because of slow decomposition rates in cold, or excessively wet or dry soil environments, plant growth is of-

ten limited by nutrient availability (e.g. Shaver and Chapin 1980, Wookey et al. 1993, 1994).

General Circulation Models (GCMs) predict an increase in global mean surface temperature of between 1.5 and 4.5°C (Mitchell et al. 1990) as the result of a doubling in CO<sub>2</sub> concentrations from the pre-industrial level (ca 275 ppm). Warming may be most pronounced in polar regions, where temperatures could increase by 4.5 to 6°C in summer and 8 to 12°C in winter (Mitchell et al. 1990, Maxwell 1992). Most GCMs predict en-

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hanced precipitation at high latitudes, and high resolution models indicate an average increase of 20–25% in precipitation over northern North America in all seasons (Mitchell et al. 1990, Maxwell 1992). Changes in summer soil moisture are not clear; one model predicts increased soil moisture in coastal areas on the Eurasian side of the Arctic Basin and decreased soil moisture further inland (Boer et al. 1991, cited in Maxwell 1992). However, other models predict drying of soils throughout the whole area above 60°N (Maxwell 1992).

These predicted changes could have marked effects on ecological processes. Increased rates of litter decomposition and large releases of carbon and nutrients from soil organic matter could occur in the Arctic in response to the predicted temperature increase, and a number of studies have focused on this aspect (e.g. Billings et al. 1982, 1983, Nadelhoffer et al. 1991, 1992). Enhanced precipitation and changes in soil moisture regime could also affect element mineralisation and decomposition in arctic ecosystems (Heal and French 1974). Litter quality may be ameliorated (Van Cleve et al. 1983) or become even more recalcitrant (Callaghan and Jonasson 1995) as a result of warming. These complex changes in soil processes could eventually lead to increased net primary production, which may act as a negative feedback to climate change if phytomass increases (thereby increasing C storage in plants), or if the amount of carbon fixed in net primary production exceeds the amount of C lost in decomposition (leading to greater C storage in soils, Shaver et al. 1992). For example, maximum soil organic matter accumulation occurred in arctic Alaska during the Holocene climate optimum when temperatures were 2°C warmer than present (Marion and Oechel 1993). Alternatively, an increase in net carbon flux to the atmosphere from arctic tundra soils may occur due to warming (Lashof 1989) and a lower water-table (Billings et al. 1982, 1983), particularly in the short term, creating a positive feedback to climate change.

Indeed, under current ambient CO<sub>2</sub> conditions, whole ecosystem respiration is already occurring at a greater rate than is whole ecosystem photosynthesis in an area of tussock tundra in Alaska (Oechel et al. 1993, 1994). These authors believe the most likely cause to be decreases in site waterlogging following recently reported temperature rises for northern latitude ecosystems, since increases of up to 1.5°C per decade have already occurred in some arctic regions over the past 30 years (Jones and Briffa 1992). A concomitant increase in nutrient mineralisation should be realised from enhanced decomposition (Oechel et al. 1994), although other work from the European sub-arctic suggests that N and P mineralisation will be small due to the buffering of relatively large increases in air temperature by soils, and to microbial immobilisation of nutrients (Jonasson et al. 1993). Our study aims to provide further information on the effect of simulated climate change on nutrient cycling by using two contrasting European Arctic ecosystems (a high arctic polar semi-desert community and a subarctic

dwarf shrub heath). It is part of a larger project examining the effects of temperature, precipitation and nutrient perturbations, both singly and in factorial combinations, on plant and soil processes (Wookey et al. 1993, 1994, Parsons et al. 1994). Here, we focus on the effects of these perturbations on (1) plant litter decomposition and (2) soil nutrient mineralisation in both ecosystems.

## Materials and methods

### Research sites and experimental design

The polar semi-desert site is situated within the *Dryas octopetala* L. zone of Svalbard (Brattbakk 1986), 3 km to the west of Ny-Ålesund in northwestern Spitsbergen (78° 56' N, 11° 50' E) at an elevation of 22 m a.s.l. Approximately 70% of the ground surface is unvegetated; the soil is a lithosol developed over limestone and organic matter is present mostly under mats of *Dryas octopetala*. The area is a well-drained interfluvium with little sign of frost-heave or sorting. The subarctic dwarf shrub heath is 2 km south-southeast of the Abisko Scientific Research Station (68° 21' N, 18° 49' E) at an elevation of 400 m a.s.l. in Swedish Lapland. There is virtually complete vegetation cover (quantified on 10–15 June 1991) at this site where the soil is an iron podsol, with a moderately well-developed raw humus horizon, and the leached A<sub>2</sub> horizon resting directly on bedrock (Soneson and Lundberg 1974). Full details of the research sites, including vegetation and microclimate, are provided in Wookey et al. (1993).

Six replicate plots, each measuring 1.5 m × 1.5 m, of eight treatments (a factorial combination of three perturbations: tent 'T', water 'W' and nutrients (fertilisers 'F')) were allocated randomly in 1991. Increased temperatures were produced using open-topped polythene tents (Havström et al. 1993), which were erected and removed at the start and end of each growing season from 1991 to 1993. Polythene tents were chosen to simulate climate warming because they provide a vertical temperature profile more similar to the natural environment than can be obtained with heating cables on, or below, the soil surface. Polythene tents of similar design already have a proven record in the Arctic (Havström et al. 1993), are simple to use in remote areas, and are robust. Using these tents, mean air and soil (at 50 mm depth) temperatures were increased throughout the day by 3.5 and 0.7°C respectively at the semi-desert site (Wookey et al., 1993). Mean air temperature was increased at the dwarf shrub heath site by 2.8°C and mean soil temperature was decreased by 0.3°C (Wookey et al., 1993). Tents were removed where possible during 'ambient' precipitation events. Photon flux density was reduced by the presence of open-topped tents by only 6% (polar semi-desert) and by 21.3% (dwarf shrub heath), and relative humidity was consistently lower beneath the polythene tents both at the dwarf shrub heath and at the polar semi-desert

(Wookey et al. 1993). The magnitude of the reduction was, however, generally less than 15% and was probably driven by the warming of air within the tents and exclusion of some precipitation (Wookey et al. 1993). Water additions to watered plots were made six or seven times during each season at a rate equivalent to a nominal 50 % increase in natural summer precipitation (a total addition of 45 mm at Ny-Ålesund and 58 mm at Abisko). The solutes nitrogen, phosphorus and potassium were supplied in solution at total rates of 5, 5 and 6.3 g m<sup>-2</sup> yr<sup>-1</sup> respectively (as NH<sub>4</sub>NO<sub>3</sub>, KH<sub>2</sub>PO<sub>4</sub> and KCl) at Ny-Ålesund and double these amounts at Abisko. The amount of fertiliser applied at the subarctic site was twice that at Ny-Ålesund since rates analogous to those used in Abisko have been shown to cause damage to *Dryas octopetala* at another high Arctic site (Henry et al. 1986). Solutes were added 4 and 5 times each year from 1991 during the growing season at Ny-Ålesund and Abisko, respectively, to provide the total added annual nutrient flux. Since the solutes were added in small water volumes, equivalent amounts of water minus solutes were added to all the non-fertilised (-F) plots.

### Treatment effects on soil microclimate

The following measurements were carried out in 1994. Air temperature and soil temperature at 5 mm depth (=litter) and 50 mm depth under *Dryas octopetala* (Ny-Ålesund) or *Empetrum hermaphroditum* (Abisko) were recorded both within and outside the tents at both sites. Readings were taken every 10 min and integrated over each hour during a six-week period in midsummer using a data logger (Delta-T Devices Ltd, Burwell, UK). Since automatic data-recording was only possible from a limited number of plots, on two occasions at the polar semi-desert site air temperature and soil temperature (5 mm depth) under vegetation (= litter temperature) were measured using a hand-held thermocouple in three replicates of all treatments. This was performed to check that there were no effects on litter temperature due to differing vegetation responses, and hence thermal conduction through the vegetation, between treatments.

At the polar semi-desert site, in order to quantify changes in litter layer moisture content with treatment, fifty-four 40 × 40 mm 1 mm-mesh litter bags were made each containing approximately 200 mg fresh weight of *Festuca vivipara* (L.) Smith litter cut into 1–2 cm lengths. These were oven-dried at 40°C, a temperature chosen to preclude structural changes in the litter which could affect its moisture-holding capacity. Three litter bags were placed on each replicate of treatments -T-W-F, -T+W-F, +T-W-F and +T+W-F at the polar semi-desert site on 11 July, collected on 16 July (after a rain event), weighed, dried at 40°C for 72 h and reweighed to get the litter bag moisture content. These bags were then replaced in the field as before. Identical litter bags containing no litter (i.e. comprising mesh

only) were placed on 5 replicates of treatments +T-W-F and -T+W-F (chosen as having the probably most widely different moisture contents) and treated as above in order to quantify the moisture content of the mesh alone. This procedure was repeated on 1 August (6 h after a water addition) and 16 August (after a rain shower).

A core (51 mm diam.) was taken from the organic soil in each plot (after Jonasson et al. 1993) at both sites for determination of gravimetric water content three times during the field season [at Ny-Ålesund these were on 30 June (6 d after the tents were put on the plots, but with no enhanced precipitation applications), 19 July (24 h after enhanced precipitation application (watering) with 21 l per plot) and 8 August (24 h after watering with 6 l per plot). At Abisko the dates were 15 July, 28 July and 12 August (all 6 d after water applications with 10 l per plot). The cores were sieved to remove roots and stones > 2 mm diameter and dried at 105°C for 72 h.

### Litter bag preparation and sampling

Decomposition of *Salix polaris* Wahlenb. litter was measured in the high Arctic because it was the only deciduous dwarf shrub present in this polar semi-desert community (Wookey et al. 1993). Samples (approx. 100 mg) of air-dried *Salix polaris* litter, collected in June 1992 in the vicinity of the Ny-Ålesund site, were placed within 1 mm-mesh nylon bags, measuring 60 × 60 mm. Three hundred and twenty-four bags were prepared and six placed on each plot at the ground surface under *Dryas octopetala* ssp. *octopetala* on 3 July 1992. On each of two sampling occasions (24 August 1992, after 7 weeks, and 17 August 1993, after 13.5 months), 3 bags were removed randomly from each plot and returned to the laboratory.

Three hundred and twenty-four (60 × 60 mm) and 162 (70 × 70 mm) similar bags of *Vaccinium uliginosum* L. and *Betula pubescens* Ehrh. ssp. *tortuosa* litter (approx. 50 and 250 mg litter samples respectively, collected from close to the dwarf shrub heath site in June 1992) were prepared, and six bags of each species were placed on each plot under *Empetrum hermaphroditum* Hagerup on 10 June 1992 at the Abisko site. Three bags of *V. uliginosum* litter were removed from each plot on 5 September 1992 (after 12 weeks), and 3 bags of litter of each species were removed on 1 September 1993 (after 15 months). Decomposition of two litter types was studied at the Abisko site because the predominant deciduous dwarf shrub was *Vaccinium uliginosum* (Wookey et al. 1993), but the plant community occurred under a stand of *Betula pubescens* ssp. *tortuosa* (Sonesson and Lundberg 1974). Litter bags were placed under mats of *D. octopetala* (Ny-Ålesund) or *E. hermaphroditum* (Abisko) because this is where litter was found to accumulate in each ecosystem, probably since it was blown away from under the deciduous shrubs in winter. Despite the effects of the plant species above the mesh bag on litter decom-

position (e.g. Blair et al. 1990), the main comparison within sites was between the treatments, which all had litter bags placed under the same plant species in order to reduce the effects of changes in edaphic and microtopographical factors. Each litter bag was cleaned of debris by dipping it into 100 ml deionised water, and dried at 80°C for 48 h. Air-dry to oven-dry conversion factors were obtained for the original litter.

Extractable N and net seasonal N mineralisation

Extractable N is the N displaced from soil exchange sites by an excess of a replacement ion (usually greater than N in soil solution). Using an in situ soil incubation technique, we calculated net seasonal N mineralisation as the end-of-season extractable N value minus the spring figure (Eno 1960). Two organic soil cores (51 mm diameter, 6 cm depth) were taken from each plot (after Jonasson et al. 1993; *n*=6 Ny-Ålesund, 30 June 1993; *n*=4 Abisko, 17 June 1993) as close together as possible and surface vegetation was removed; one was placed in a polyethylene bag which was sealed, replaced in the soil and covered with a mat of native vegetation. (This method prevented the current year's application of fertiliser and water, and soil drying, from having an effect on the N mineralisation rate because the bags were sealed). The other core was taken back to the laboratory and frozen (−18°C) since immediate extraction and analysis was impossible, and air-drying may cause loss of ammonium (Allen 1989). However, freezing can increase the release of some extractable constituents (Allen 1989). The incubated soil cores were retrieved on 25 August 1993 and 7 September 1993 at Ny-Ålesund and Abisko, respectively, and frozen immediately. The soils were thawed at 2°C immediately before extraction and weighed after removal of roots and stones > 2 mm diameter. A sub-sample of soil (5 g) from each core was extracted with 50 ml 6% (8mM) KCl on a rotary shaker for 1 h and filtered (Whatman no. 4; after Allen 1989). A further sub-sample from each core was dried at 105°C for 72 h from which the moisture content was calculated. Extractable NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N were determined by the salicylate method (Rowland 1983) and the cadmium reduction method (Skalar 1990), respectively. The results were expressed as g N m<sup>-2</sup> of vegetated soil using mg N extracted from 5 g soil, multiplied by the total weight of the 2 mm fraction of each core, then converted to g N per m<sup>-2</sup> using the core's area.

Six cores were taken at the end of the season at each site in organic soil outside the plot areas for determination of pH and soil moisture content (after Allen 1989) and depth of organic horizon.

Statistical analysis

Main effects of the factorial design of tent/temperature,

water and nutrient treatments were evaluated by multifactorial GLMs (General Linear Models). Factor interactions were investigated by analysis of Least Squares Means (lsmeans). All measured parameters were subjected to a test for homogeneity of variance before performing statistical analyses, and appropriate data transformations were made where necessary. F values and degrees of freedom for the 'Type III' sums of squares were used as the basis for statistical comparisons between treatments, their interactions and main effects.

Results

Treatment effects on soil microclimate

General characteristics of the soils at the two sites are documented in Table 1. The effect of the tents on relative air humidity and photon flux density are detailed in Wookey et al. (1993), and outlined in the Materials and methods section. Typical seasonal mean temperature results from the tents are shown in Figs 1, 2 and Table 1. Polythene tents increased mean hourly air temperatures by maxima of 1.6°C at the polar semi-desert (Fig. 1a), and 3.6°C at the sub-arctic site (Fig. 2 a), and mean hourly soil temperatures under vegetation at 50 mm depth were raised by maxima of 1.3 and 1.1°C by the tent treatment, respectively (Figs 1c, 2 c). The datalogger results show that mean hourly litter temperatures at both sites were slightly decreased by the tents (Fig. 1b, 2b; mean decrease over the whole monitoring period was −0.1 and −0.5°C at Ny-Ålesund and Abisko, respectively), although the spot measurements using the handheld thermocouple at the polar semi-desert site suggest that at mid-day the litter temperature in the tented treatments was 3.5°C higher (*P* < 0.001, tented vs open) than in the open plots for a corresponding 2.6°C increase in air temperature (*P* < 0.001, tented vs open) on 28 June. Similar results were obtained on 19 July, with air temperature increased by 0.6°C and litter temperature by 0.8°C, (*P* < 0.01, tented vs open plots), with no significant main effects of the other treatments on either date.

Litter moisture, measured gravimetrically, was reduced significantly in the tent treatment at one sampling out of three, and the enhanced precipitation treatment

Table 1. Mean summer soil temperature, soil characteristics (*n* = 6) and extractable-N (−T−W−F treatments, 30/6/93, *n* = 5, Ny-Ålesund; 17/6/93, *n* = 5, Abisko) at the two sites (mean ± S. E.).

	Ny-Ålesund	Abisko
Soil temperature at 50 mm depth (°C)	6.1	5.5
pH	6.9–8.0	4.0–4.5
Soil moisture (% dwt)	47.0 ± 12.3	153.8 ± 29.8
Depth of organic horizon (mm)	0–50	0–> 90
Extractable NH <sub>4</sub> <sup>+</sup> -N (g m <sup>-2</sup> )	0.11 ± 0.03	0.04 ± 0.03
Extractable NO <sub>3</sub> <sup>-</sup> -N (g m <sup>-2</sup> )	0.04 ± 0.02	0.004 ± 0.001

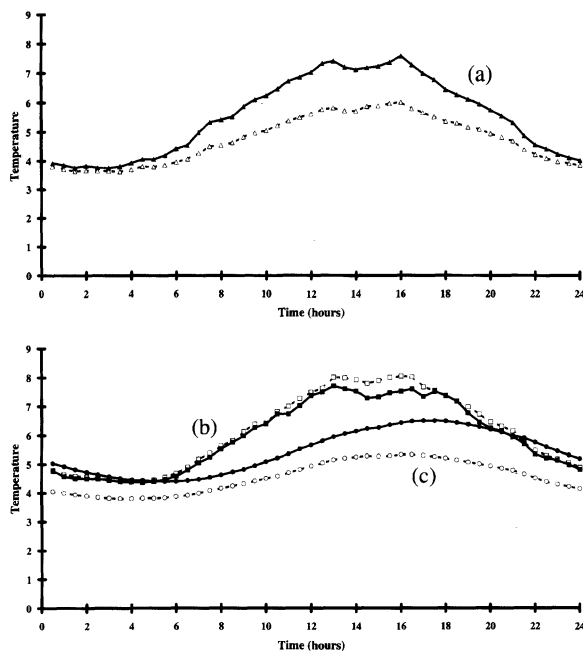


Fig. 1. Temperature data (seasonal mean hourly values in °C) expressed on a diel basis at the polar-semi desert site, (a) air temperature (360 mm above ground level), (b) litter temperature (~5 mm) and (c) soil temperature (~50 mm). Continuous lines represent tented plots, broken lines represent open (ambient) plots.

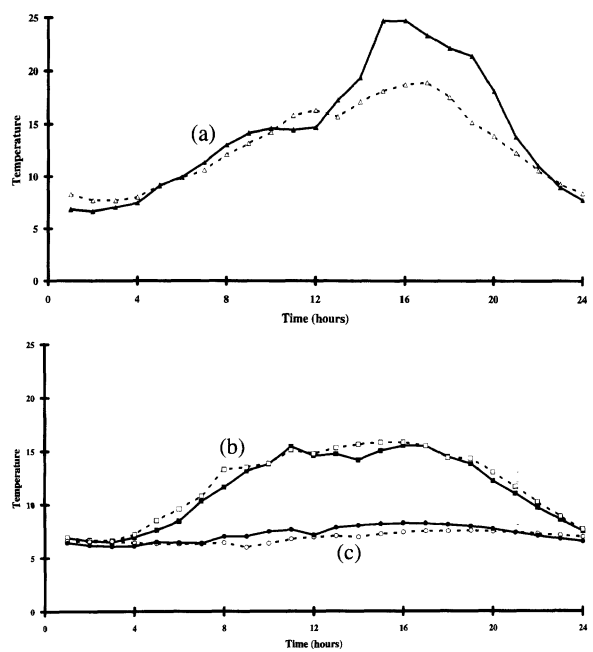


Fig. 2. Temperature data (seasonal mean hourly values in °C) expressed on a diel basis at the dwarf shrub heath site, (a) air temperature (360 mm above ground level), (b) litter temperature (~5 mm) and (c) soil temperature (~50 mm). Key to symbols as Fig. 1.

had no effect on litter moisture (Table 2), even after only 6 h since water application at the polar semi-desert site. There were no significant differences in soil moisture content between treatments on any occasion at the polar semi-desert site, but the tent treatment significantly reduced soil moisture at the subarctic site (Table 3).

### Mass loss from litter bags

The tent treatments significantly retarded litter decomposition compared with the open 'ambient' plots at both sites (Table 4). The enhanced precipitation treatments significantly increased weight loss of *V. uliginosum* and *B. pubescens* ssp. *tortuosa* litter at Abisko, as did the fertiliser treatments with *S. polaris* and *V. uliginosum* litter

at Ny-Ålesund and Abisko, respectively. There was a  $T \times F$  interaction with *S. polaris* litter, in which significantly more weight was lost in the untented fertilised treatments than in the untented unfertilised treatments ( $P < 0.01$ ).

### Extractable N and net seasonal N mineralisation

There were no significant differences between treatments in extractable  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^+\text{-N}$  or total inorganic N pools at the June sampling at the polar semi-desert site. At the August sampling, mineral N was predominantly present as nitrate (Figs 3a, b), and nitrate and total N pools were significantly larger than in June ( $P < 0.001$ , GLM, results not shown). The pool of extractable total N

Table 2. Mean ( $\pm$  S.E.,  $n = 6$ ) moisture content of mesh litter bags containing *Festuca vivipara* tillers, and mesh alone, at the polar semi-desert site on three sampling occasions. Means within a column with different letters are significantly different ( $P < 0.01$ , Tukey's HSD). Sampling was carried out on 16 July (after a rain event), 1 August (6 h after a water addition) and 16 August (after a rain shower).

Treatment	Moisture content (as % litter bag dwt)		
	16 July	1 August	16 August
-T-W-F	142.2 $\pm$ 5.2 <sup>a</sup>	103.4 $\pm$ 7.6 <sup>a</sup>	125.3 $\pm$ 10.1 <sup>a</sup>
-T+W-F	139.0 $\pm$ 2.4 <sup>a</sup>	113.9 $\pm$ 7.1 <sup>a</sup>	114.8 $\pm$ 8.7 <sup>a</sup>
+T-W-F	100.2 $\pm$ 16.9 <sup>a</sup>	91.2 $\pm$ 9.9 <sup>a</sup>	46.4 $\pm$ 21.1 <sup>b</sup>
+T+W-F	125.0 $\pm$ 12.9 <sup>a</sup>	86.3 $\pm$ 11.4 <sup>a</sup>	40.4 $\pm$ 10.4 <sup>b</sup>
Mesh only -T+W-F	33.9 $\pm$ 2.3 <sup>b</sup>	28.3 $\pm$ 1.3 <sup>b</sup>	43.2 $\pm$ 3.4 <sup>b</sup>
Mesh only +T-W-F	25.6 $\pm$ 7.5 <sup>b</sup>	13.6 $\pm$ 4.9 <sup>b</sup>	1.0 $\pm$ 0.2 <sup>b</sup>

Table 3 a. Mean ( $\pm$  S.E.,  $n = 6$ ) soil moisture content at the polar semi-desert site on three sampling occasions, 30 June (6 d after the tents were erected, but before enhanced precipitation applications), 19 July (24 h after watering with 21 l per +W plot) and 8 August (24 h after watering with 6 l per +W plot).

Treatment	Moisture content (as % soil dwt)		
	30 June	19 July	8 August
-T-W-F	45.8 $\pm$ 7.0	46.7 $\pm$ 7.0	39.8 $\pm$ 7.0
-T-W+F	63.3 $\pm$ 6.7	51.5 $\pm$ 7.5	46.7 $\pm$ 8.2
-T+W-F	53.5 $\pm$ 8.8	71.4 $\pm$ 18.3	47.8 $\pm$ 11.6
-T+W+F	61.1 $\pm$ 5.0	73.0 $\pm$ 21.9	77.3 $\pm$ 19.1
+T-W-F	50.4 $\pm$ 3.9	68.7 $\pm$ 16.2	44.7 $\pm$ 9.2
+T-W+F	43.9 $\pm$ 7.1	45.4 $\pm$ 13.5	59.1 $\pm$ 15.4
+T+W-F	79.8 $\pm$ 12.0	60.8 $\pm$ 13.4	69.2 $\pm$ 11.4
+T+W+F	71.3 $\pm$ 20.7	53.3 $\pm$ 8.4	56.5 $\pm$ 11.1

b. Mean ( $\pm$  S.E.,  $n = 6$ ) soil moisture content at the dwarf shrub heath site on three sampling occasions. On 28 July and 12 August there were significant ( $P < 0.001$ ,  $P < 0.01$ ) tent main effects (GLM,  $n = 24$ ). All samplings were six d after watering +W plots.

Treatment	Mean moisture content (as % soil dwt)		
	15 July	28 July	12 August
-T-W-F	117.3 $\pm$ 17.5	178.9 $\pm$ 23.8	94.1 $\pm$ 10.1
-T-W+F	116.8 $\pm$ 25.3	210.3 $\pm$ 12.3	119.5 $\pm$ 10.8
-T+W-F	136.6 $\pm$ 20.1	216.1 $\pm$ 16.6	121.5 $\pm$ 19.4
-T+W+F	153.3 $\pm$ 23.3	183.7 $\pm$ 30.1	105.7 $\pm$ 11.2
+T-W-F	105.1 $\pm$ 11.8	109.3 $\pm$ 8.3	68.9 $\pm$ 13.1
+T-W+F	85.3 $\pm$ 21.1	115.1 $\pm$ 13.2	78.1 $\pm$ 8.0
+T+W-F	64.0 $\pm$ 19.4	113.0 $\pm$ 9.6	94.0 $\pm$ 14.9
+T+W+F	139.4 $\pm$ 41.5	189.0 $\pm$ 12.8	91.9 $\pm$ 14.2

was significantly higher in the fertilised and watered treatments at this time ( $P < 0.01$ , GLM). Greater net seasonal nitrification and total N mineralisation were found in the fertilised treatments (Fig. 3b, c), and the latter was also found in the watered treatments (Fig. 3c).

At Abisko, by contrast, mineral N was predominantly present as ammonium (Fig. 4a, b), and  $\text{NH}_4^+$ -N and total N pools were larger in September than in June ( $P < 0.001$ , GLM). Extractable N was significantly higher in the fertilised treatment at both samplings ( $P < 0.001$ , GLM, results not presented), although extractable  $\text{NO}_3^-$ -N pools were not significantly lower at the September sampling compared to June. There was no significant difference between the treatments in the net amount of total N mineralised over the season (Fig. 4c), although net nitrification was significantly reduced in the tented or fertilised treatments (Fig. 4b).

There was no difference between treatments or sampling date in soil moisture content, except at Ny-Ålesund where the soil in the tented plots contained significantly ( $P < 0.05$ ) more water than the 'ambient' controls (actual values not presented here).

Table 4 a. Decomposition of *Salix polaris* litter in mesh bags at the polar semi-desert site. After 7 weeks there was a significant tent  $\times$  fertiliser interaction ( $P < 0.01$ ) and a significant main effect ( $P < 0.01$ , GLM,  $n = 24$ ) of the tent factor. There were significant tent ( $P < 0.05$ ) and fertiliser ( $P < 0.001$ ) main effects at the second sampling date.

Treatment	Percentage initial weight remaining (mean $\pm$ S.E., $n = 6$ )	
	After 7 weeks	After 13.5 months
-T-W-F	88.04 $\pm$ 1.84	87.27 $\pm$ 1.09
-T-W+F	85.81 $\pm$ 1.06	85.17 $\pm$ 1.83
-T+W-F	87.23 $\pm$ 1.06	88.10 $\pm$ 1.08
-T+W+F	85.08 $\pm$ 0.94	83.17 $\pm$ 2.89
+T-W-F	91.79 $\pm$ 0.72	87.73 $\pm$ 1.19
+T-W+F	93.67 $\pm$ 0.64	84.81 $\pm$ 2.53
+T+W-F	91.85 $\pm$ 0.87	89.78 $\pm$ 0.97
+T+W+F	92.01 $\pm$ 0.97	87.90 $\pm$ 1.21

b. Decomposition of *Vaccinium uliginosum* litter in mesh bags at the dwarf shrub heath site. There were significant main effects (GLM,  $n = 24$ ) of the tent ( $P < 0.01$ ) and watering ( $P < 0.05$ ) factors after 3 months. At the second sampling date, there were significant main effects of the tent ( $P < 0.001$ ), watering ( $P < 0.05$ ) and fertiliser ( $P < 0.05$ ) factors.

Treatment	Percentage initial weight remaining (mean $\pm$ S.E., $n = 6$ )	
	After 3 months	After 15 months
-T-W-F	80.42 $\pm$ 0.58	60.78 $\pm$ 1.54
-T-W+F	78.46 $\pm$ 0.77	59.99 $\pm$ 1.19
-T+W-F	79.75 $\pm$ 0.97	57.71 $\pm$ 1.28
-T+W+F	78.34 $\pm$ 1.41	54.83 $\pm$ 1.87
+T-W-F	83.47 $\pm$ 1.06	66.18 $\pm$ 1.96
+T-W+F	82.62 $\pm$ 0.38	63.23 $\pm$ 1.18
+T+W-F	80.23 $\pm$ 1.82	65.11 $\pm$ 1.28
+T+W+F	79.58 $\pm$ 1.87	61.05 $\pm$ 2.70

c. Decomposition of *Betula pubescens* ssp. *tortuosa* litter in mesh bags at the dwarf shrub heath site. There were significant tent ( $P < 0.01$ ) and watering ( $P < 0.05$ ) main effects (GLM,  $n = 24$ ).

Treatment	Percentage initial weight remaining (mean $\pm$ S.E., $n = 6$ )	
	After 15 months	
-T-W-F	76.37 $\pm$ 0.67	
-T-W+F	75.00 $\pm$ 0.72	
-T+W-F	74.87 $\pm$ 1.66	
-T+W+F	73.47 $\pm$ 0.64	
+T-W-F	79.91 $\pm$ 0.98	
+T-W+F	77.82 $\pm$ 1.36	
+T+W-F	76.67 $\pm$ 0.79	
+T+W+F	75.75 $\pm$ 1.47	

## Discussion

### Treatment effects on soil microclimate

The increases in air temperature caused by the open-topped tents both here and in the study of Wookey et al. (1993) are within the range of the more conservative predictions for the Arctic by GCMs by the end of the next century (Mitchell et al. 1990). However, polythene tents not only increase air, litter (periodically) and soil temperature, but also reduce relative humidity, photon

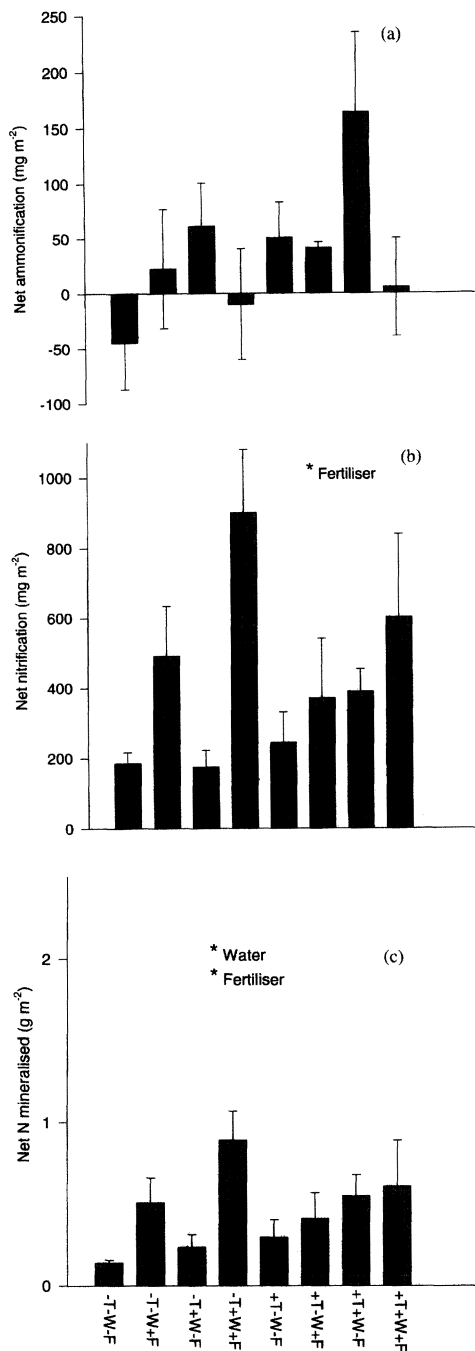


Fig. 3. Mean ( $\pm$  S. E.) net (a)  $\text{NH}_4^+\text{-N}$ , (b)  $\text{NO}_3^-\text{-N}$  and (c) total inorganic N mineralised at Ny-Ålesund,  $n = 6$  (for main effects statistics  $n = 24$ ). \*,  $P < 0.05$ , treated vs untreated, GLM.

flux density (Wookey et al. 1993), air velocity (the reduction of the latter is probably a main cause of temperature increase within the vegetation inside the tents) and litter (Ny-Ålesund) and soil moisture (Abisko) contents. The measurements of soil and litter moisture contents are, by nature, simply 'snapshots', although the effect of

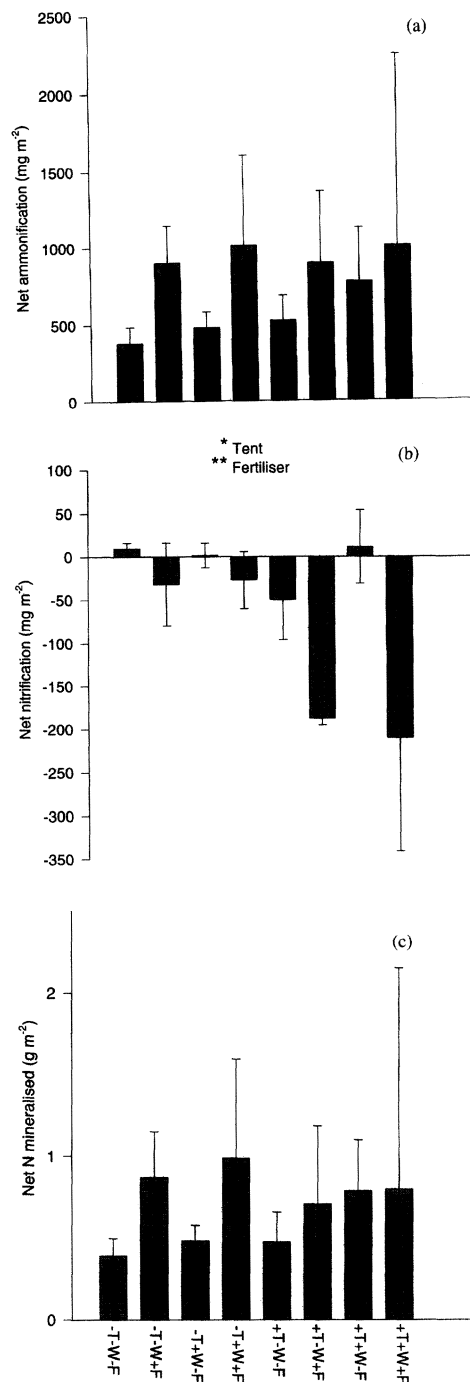


Fig. 4. Mean ( $\pm$  S. E.) net (a)  $\text{NH}_4^+\text{-N}$ , (b)  $\text{NO}_3^-\text{-N}$  and (c) total inorganic N mineralised at Abisko,  $n = 4$  (for main effects statistics,  $n = 16$ ). \*, \*\*,  $P < 0.05$ , 0.01, treated vs untreated, GLM.

the tents on soil moisture at Ny-Ålesund is smaller than the natural variation of soil water content from one area within the plot to another. Despite the possibility of tent artifacts (e.g. exclusion of some precipitation and a reduction in the number of wetting and drying events) re-



ducing litter and soil moisture, as some GCMs predict drying of soils above 60°N (Maxwell 1992), lower litter and soil moisture contents may be an effect of environmental change. However, it is unclear from our study how much of a decrease in soil moisture content the temperature increase alone produces.

### Litter mass loss

We studied the decomposition of litter which had not been formed under the experimental perturbations (i.e. collected from the field-sites but not from the experimental plots), since it was impractical to study the decomposition of litter produced within the experiments. This is because it is likely to take several years for the feedback of the perturbations on litter quality to operate in the Arctic. For example, in senescent leaves of *Salix polaris* actually collected from the experimental plots at the high Arctic site on 17 to 25 August 1993, the mean ( $\pm$  S. E.) C:N ratio was highest in the -T-W-F ( $66.7 \pm 0.1$ ) treatment, followed by +T-W-F ( $62.3 \pm 4.6$ ), -T+W-F ( $58.1 \pm 3.4$ ), -T-W+F ( $37.4 \pm 5.6$ ) and +T+W+F ( $33.5 \pm 1.5$ ). Thus, only the +F treatments changed litter quality as indicated by the C:N ratio after the treatments had been applied for 3 seasons. Additionally, our results above show that soils will not warm sufficiently for the availability of nitrogen, a nutrient strongly limiting to plant growth, to be increased. Thus, this feedback to litter quality may not even occur.

The rate of litter decomposition is controlled by temperature and moisture regime, resource quality and the activity of decomposer organisms (Swift et al. 1979). Soil temperature has been shown to be the most important control on litter decomposition in boreal forest ecosystems (Van Cleve and Yarie 1986, Sparrow et al. 1992), and increases in soil temperature usually increase decomposition (Anderson 1973, Berg et al. 1984, Van Cleve and Yarie 1986, Dyer et al. 1990). The periodic increase in temperature inside the tents under the vegetation and some exclusion of precipitation and reduced litter moisture may have reduced decomposition since temperature and moisture frequently act together to determine decomposition rates (Heal and French 1974, Bunnell et al. 1977, Meentemeyer 1978). The increased litter decomposition in the watered compared to the unwatered treatment at Abisko (Table 4) may have been due to enhanced leaching of soluble materials, or to increased microbial activity. Similarly, supplementary N, P and K added to natural materials often stimulates their decomposition (Swift et al. 1979), as occurred here (Table 4). However, N added to decomposing organic matter can also have no or a negative effect on microbial activity in the long term, especially in recalcitrant resources such as straw or wood (Fog 1988).

### Soil nitrogen

The contrast in the predominant form of mineral N (Figs 3 and 4; and indeed, in the soils in general; Table 1) be-

tween the two sites re-emphasises the importance of the two-site comparison in this study. Pool sizes of the extractable N are not necessarily good indicators of availability, since small nutrient pools do not necessarily mean that the processes controlling the pool sizes are not occurring rapidly. Hence, net mineralisation values are very useful in this context, although the values for nitrate-N availability may be underestimates if denitrification has taken place to an appreciable extent within the incubated cores. The tent treatment had very little effect on short-term seasonal net total N mineralisation at either site, in agreement with the findings of Jonasson et al. (1993) who used a similar experimental design in a fell-field and treeline ecosystem at Abisko, where soil temperatures were increased by +1 to +2°C, and by up to +4.8°C in soils transplanted between ecosystems. In other work, increases in soil temperature [Van Cleve et al. (1983; +9°C); Nadelhoffer et al. (1991; 3 to 15°C); Melillo et al. (unpublished; +5°C)] have been shown to stimulate N mineralisation strongly. The lack of effect of the tent treatments on total net N mineralisation may be explained by microbial immobilisation of gross mineralised N, or because the soil temperature increases were not as high as in the other studies. Nadelhoffer et al. (1992) have shown that there was no difference in the amount of N mineralised between 3 and 9°C in moist tundra or wet sedge tundra soils, but mineralisation was increased by up to 10 times in the range of 9 to 15°C. Even so, in the Arctic, increased air temperatures have been shown to result in lower soil temperatures probably due to the insulation of soil by plant cover and low conductivity of heat (Coulson et al. 1993, Wookey et al. 1993, this study), and soil temperatures in tundra ecosystems are known to be substantially buffered compared with air temperature (Van Cleve and Alexander 1981). The cause of the tent effect on net nitrification at Abisko is unclear.

The mechanism by which the enhanced precipitation treatment increased N mineralisation at the polar semi-desert site (Fig. 3c) is also unclear, since there was no significant increase in bulk moisture content in the mineralisation cores collected from this treatment. If it is assumed that the difference between the amount of N extracted from the cores collected at the start and end of the season is the net N mineralisation for that year, 0.1 and 0.4 g N m<sup>-2</sup> yr<sup>-1</sup> were mineralised at the high and sub-arctic sites, respectively. This agrees well with other estimates (0.1 to 0.6 g m<sup>-2</sup> yr<sup>-1</sup>; Giblin et al. 1991, Nadelhoffer et al. 1992) for tundra ecosystems, although our value, small as it is, for the high arctic, may even be an overestimate as it is for organic soil only.

### Conclusions

This study shows that: (1) In the short term there will be relatively little stimulation of total N mineralisation in two very different arctic soils due to small rises in soil tempera-

ture induced by relatively large increases in air temperature. (2) Although the polythene tents produced air temperature increases in line with GCM predictions, the induced rises in soil temperature are much lower, probably due to high soil heat capacity and insulation by vegetation in tundra ecosystems. (3) The tent treatment also produced a net decrease in litter and soil moisture, which may be realistic in the context of predicted climate change, but which complicates the interpretation of decomposition data. (4) Other aspects of climate change (for example, enhanced precipitation) may increase N mineralisation and decomposition. (5) Fertiliser (NPK) increased litter decomposition and soil nutrient pools and fluxes.

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## References

- Allen, S. E. (ed.) 1989. Chemical analysis of ecological materials. – Blackwell, Oxford.
- Anderson, J. M. 1973. Carbon dioxide evolution from two deciduous woodland soils. – *J. Appl. Ecol.* 10: 361–378.
- Berg, B., Ekbohm, G. and McClaugherty, C. 1984. Lignin and holocellulose relations during long-term decomposition of some forest litters. Long-term decomposition in a Scots pine forest. IV. – *Can. J. Bot.* 62: 2540–2550.
- Billings, W. D., Luken, J. O., Mortensen, D. A. and Petersen, K. M. 1982. Arctic tundra: a sink or source for atmospheric carbon dioxide in a changing environment? – *Oecologia* 53: 7–11.
- , Luken, J. O., Mortensen, D. A. and Petersen, K. M. 1983. Increasing atmospheric carbon dioxide: possible effects on arctic tundra. – *Oecologia* 58: 286–289.
- Blair, J. M., Parmalee, R. W. and Beare, M. H. 1990. Decay rates, nitrogen fluxes and decomposer communities of single- and mixed-species foliar litter. – *Ecology* 71: 1976–1985.
- Brattbakk, I. 1986. Vegetasjonsregioner – Svalbard og Jan Mayen. – Nasjonalatlas for Norge, Kartblad 4.1.3.
- Bunnell, F. L., Tait, D. E. N., Flanagan, P. W. and Van Cleve, K. 1977. Microbial respiration and substrate weight loss-I. A general model of the influences of abiotic variables. – *Soil. Biol. Biochem.* 9: 33–40.
- Callaghan, T. V. and Jonasson, S. 1995. Implications from environmental manipulation experiments for arctic plant biodiversity changes. – In Chapin, F. S. III. and Körner, C. (eds), *Arctic and alpine biodiversity: Patterns, causes and ecosystem consequences*. Springer, New York, pp. 151–166.
- Coulson S., Hodkinson, I. D., Strathdee, A., Bale, J. S., Block W., Worland, M. R. and Webb, N. R. 1993. Simulated climate change: the interaction between vegetation type and microhabitat temperatures at Ny Ålesund, Svalbard. – *Polar Biol.* 13: 67–70.
- Dyer, M. L., Meentemeyer, V. and Berg, B. 1990. Apparent controls of mass loss rate of leaf litter on a regional scale. – *Scand. J. For. Res.* 5: 1–13.
- Eno, C. F. 1960. Nitrate production in the field by incubating the soil in polyethylene bags. – *Soil Sci. Soc. Am. Proc.* 24: 277–279.
- Flanagan, P. W. and Veum, A. K. 1974. Relationships between respiration, weight loss, temperature and moisture in organic residues in tundra. – In: Holding, A. J., Heal, O. W., MacLean, S. F., Jnr and Flanagan, P. W. (eds), *Soil organisms and decomposition in tundra*. Tundra Biome Steering Committee, Stockholm, pp. 249–278.
- Fog, K. 1988. The effect of added nitrogen on the rate of decomposition of organic matter. – *Biol. Rev.* 63: 433–462.
- Giblin, A. E., Nadelhoffer, K. J., Shaver, G. R., Laundre, J. A. and McKerrow, A. J. 1991. Biogeochemical diversity along a riverside toposequence in Arctic Alaska. – *Ecol. Monogr.* 61: 415–435.
- Havström, M., Callaghan, T. V. and 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.
- Heal, O. W. and French, D. D. 1974. Decomposition of organic matter in tundra. – In: Holding, A. J., Heal, O. W., Maclean, S. F. and Flanagan, P. W. (eds), *Soil organisms and decomposition in tundra*. IBP Tundra Biome Steering Committee, Stockholm, pp. 279–309.
- Henry, G. H. R., Freedman, B. and Svoboda, J. 1986. Effects of fertilisation on three tundra plant communities of a polar desert oasis. – *Can. J. Bot.* 64: 2502–2507.
- Jonasson, S. 1983. Nutrient content and dynamics in north Swedish shrub tundra areas. – *Holarct. Ecol.* 6: 295–304.
- , Havström, M., Jensen, M. and Callaghan T. 1993. In situ mineralisation of nitrogen and phosphorus of arctic soils after perturbations simulating climate change. – *Oecologia* 95: 179–186.
- Jones, P. D. and Briffa, K. R. 1992. Global surface air temperature variations during the twentieth century; Part 1. spatial, temporal and seasonal detail. – *Holocene* 2: 165–179.
- Lashof, D. A. 1989. The dynamic greenhouse: feedback processes that may influence future concentrations of atmospheric trace gases and climatic change. – *Clim. Change* 14: 213–242.
- Marion, G. M. and Oechel, W. C. 1993. Mid- to late-Holocene carbon balance in Arctic Alaska and its implications for future global warming. – *Holocene* 3: 193–200.
- Maxwell, B. 1992. Arctic climate: potential for change under global warming. – In: Chapin, F. S. III., Jeffries, R. L., Reynolds, J. F., Shaver, G. R. and Svoboda, J. (eds), *Arctic ecosystems in a changing climate. An ecophysiological perspective*. Academic Press, San Diego, CA, pp. 11–34.
- Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. – *Ecology* 59: 465–472.
- Melillo, J. M., Callaghan, T. V., Woodward, F. I., Salati, E. and Sinha, S. K. 1990. Effects on ecosystems. – In: Houghton, J. T., Jenkins, G. T. and Ephraums, J. J. (eds), *Climate change, the IPCC scientific assessment*. Cambridge Univ. Press, Cambridge, pp. 282–310.
- Mitchell, J. F. B., Manabe, S., Tokioka, T. and Meleshoko, V. 1990. Equilibrium climate change. – In: Houghton, J. T., Jenkins, G. J. and Ephraums, J. J. (eds), *Climate change, the IPCC scientific assessment*. Cambridge University Press, Cambridge, pp. 131–172.
- Nadelhoffer, K. J., Giblin, A. E., Shaver, G. R. and Laundre, J. L. 1991. Effects of temperature and substrate quality on element mineralisation in six arctic soils. – *Ecology* 72: 242–253.
- , Giblin, A. E., Shaver, G. R. and Linkens, A. E. 1992. Microbial processes and plant nutrient availability in arctic soils. – In: Chapin, F. S. III., Jeffries, R. L., Reynolds, J. F., Shaver, G. R. and Svoboda, J. (eds), *Arctic ecosystems in a changing climate. An ecophysiological perspective*. Academic Press, San Diego, CA, pp. 281–300.
- Oechel, W. C., Hastings, S. J., Vourlitis, G., Jenkins, M., Reichers, G. and Grulke, N. 1993. Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. – *Nature* 361: 520–523.
- , Cowles, S., Grulke, N., Hastings, S. J., Lawrence, B., Prudhomme, T., Reichers, G., Strain, B., Tissue, D. and Vourlitis,

- G. 1994. Transient nature of CO<sub>2</sub> fertilisation in Arctic tundra. – *Nature* 371: 500–503.
- Parsons, A. N., Welker, J. M., Wookey, P. A., Press, M. C., Callaghan, T. V. and Lee, J. A. 1994. Growth responses of four sub-arctic dwarf shrubs to simulated climate change. – *J. Ecol.* 82: 307–318.
- Rowland, A. P. 1983. An automated method for the determination of ammonium-N in ecological materials. – *Comm. Soil. Sci. Plant Anal.* 14: 49–63.
- Shaver, G. R. and Chapin, F. S. III. 1980. Response to fertilisation by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. – *Ecology* 61: 662–675.
- , Billings, W. D., Chapin, F. S. III, Giblin, A. E., Nadelhoffer, K. J., Oechel, W. C. and Rastetter, E. B. 1992. Global change and the carbon balance of Arctic ecosystems. – *BioScience* 42: 433–441.
- Skalar 1990. Skalar methods. – Skalar Analytical BV, Breda, Netherlands.
- Sonesson, M. and Lundberg, B. 1974. Late Quaternary forest development of the Torneträsk area, North Sweden. 1. Structure of modern forest ecosystems. – *Oikos* 25: 121–133.
- Sparrow, S. D., Sparrow, E. B. and Cochran, V. L. 1992. Decomposition in forest and fallow subarctic soils. – *Biol. Fertil. Soils* 14: 253–259.
- Swift, M. J., Heal, O. W. and Anderson, J. M. 1979. Decomposition in terrestrial ecosystems. – Blackwell, Oxford.
- Van Cleve, K. and Alexander 1981. Nitrogen cycling in tundra and boreal ecosystems. – In: Clark, F. E. and Rosswall, T. (eds), *Terrestrial nitrogen cycles*. Ecological Bulletins, Stockholm 33: 375–404.
- and Yarie, J. 1986. Interaction of temperature, moisture and soil chemistry in controlling nutrient cycling and ecosystem development in the taiga of Alaska. – In: Van Cleve, K., Chapin, F. S. III., Flanagan, P. W., Viereck, L. A. and Dyrness, C. T. (eds), *Forest ecosystems in the Alaskan taiga. A synthesis of structure and function*. Springer, New York, pp. 160–189.
- , Oliver, L. K., Sceltnner, R., Viereck, L. A. and Dyrness, C. T. 1983. Productivity and nutrient cycling in taiga forest ecosystems. – *Can. J. For. Res.* 13: 747–766.
- Wookey, P. A., Parsons, A. N., Welker, J. M., Potter, J. A., Callaghan, T. V., Lee, J. A. and Press, M. C. 1993. Comparative responses of phenology and reproductive development to simulated environmental change in sub-arctic and high arctic plants. – *Oikos* 67: 490–502.
- , Welker, J. M., Parsons, A. N., Press, M. C., Callaghan, T. V. and Lee, J. A. 1994. Differential growth, allocation and photosynthetic responses of *Polygonum viviparum* L. to simulated environmental change at a high arctic polar semi-desert. – *Oikos* 70: 131–139.