Soil plus root respiration and microbial biomass following water, nitrogen, and phosphorus application at a high arctic semi desert

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Abstract. In order to investigate the effects of anticipated increased precipitation and changing soil nutrient levels on soil CO_2 efflux from high arctic semi desert, a field experiment was carried out in Northeast Greenland. Water, phosphorus, and nitrogen were added to plots in a fully factorial design. Soil microbial biomass carbon was analysed after one year, and respiration from soil plus roots was measured *in situ* throughout the third growing season after initiation of the experiment. Soil plus root respiration was enhanced by up to 47%, and the microbial biomass by 24%, by the weekly water additions, but not by nutrient additions. The direct effect of increased soil moisture on CO_2 efflux suggests that future changes of precipitation levels and patterns may strongly affect below-ground respiration in arctic semi deserts, with direction of responses depending upon amounts and frequencies of precipitation events. Morover, low CO_2 emission at low light intensities regardless of treatment suggests that the major part of the below-ground respiration originated from turnover of recently fixed C. Hence, the more recalcitrant soil organic matter C pool may not change in proportion to changes in below-ground respiration rate.

Introduction

As a result of anthropogenic global warming, General Circulation Models (GCMs) predict increasing amounts of precipitation at high latitudes (Maxwell 1997; Rowntree 1997; Houghton et al. 2001), which may result in increased summer soil moisture, but temperature induced higher evaporation may, on the other hand, result in summer drought (Maxwell 1992). Together with temperature controlled increased mineralization, and hence, increased soil nutrient levels (Nadelhoffer et al. 1991; Jonasson et al. 1993, 1996a; Chapin et al. 1995), changes in soil moisture level may influence carbon (C) balances of arctic ecosystems and cause feedbacks to global C budgets. This is of importance because the arctic and alpine areas of the world contain 14% of the global soil C pool (Post et al. 1982). Enhanced decomposition in the Arctic induced by higher temperature or changed soil moisture and nutrient regimes may potentially cause the region to act as a source of CO_2 to the

atmosphere and thereby enhance global warming further. Alternatively, climatic change may increase primary production and lead to the Arctic acting as a future sink of C. To clarify the characteristics and limiting factors of these two opposite processes, the controls on C cycling in the Arctic must be understood. Much effort already has been expended in the Subarctic and in wet and moist arctic ecosystems to unravel these controls (Oberbauer et al. 1991, 1996; Oechel et al. 1993, 1995; Christensen et al. 1997, 2000; Hobbie and Chapin 1998; Jones et al. 1998; Shaver et al. 1998; Illeris and Jonasson 1999; Soegaard and Nordstroem 1999; Johnson et al. 2000; Soegaard et al. 2000), while few studies yet have quantified CO_2 fluxes in the drier high arctic areas (Christensen et al. 1998; Jones et al. 2000; Wütrich et al. 1999). Hence, controls governing C budgets in the dry Arctic are still unclear. Approximately one-third of the ice-free Arctic is covered by polar desert and semi desert (Wookey and Robinson 1997; Jones et al. 2000), and in the high Arctic these ecosystems hold 42% of the total terrestrial C stores (data from Bliss and Matveyeva (1992)). These areas are poorly vegetated, and a warmer and wetter climate could cause them to act as C sinks in the future as a consequence of enhanced primary production.

Soil moisture also may influence arctic ecosystems in an indirect way through its effect on nutrient availability (Oberbauer and Dawson 1992; Gold and Bliss 1995). For example, Gold and Bliss (1995) found that some high arctic plant communities benefited from continued surface runoff from melting snow because the melting water facilitated cyanobacterial nitrogen fixation and thereby enhanced nutrient availability. Direct evidence of increased litter decomposition after an increase in nutrient availability was found in a high arctic polar semi desert at Svalbard whereas water addition did not affect the decomposition rate (Robinson et al. 1995, 1997). In contrast, Christensen et al. (1998) did not see any changes in soil respiration after fertilization of a drained fen in high arctic Greenland. Hence, it is still unclear how soil respiration in the high Arctic is affected by changes in water and nutrient availability, and data on soil and root respiration responses to environmental manipulations in high arctic semi deserts are missing.

Here we report on soil microbial biomass and soil plus root respiration through the growing season in experimental plots in a high arctic semi desert situated on a dry gravel terrace in NE Greenland. The aim was to identify the factors that control below ground respiration in such high arctic ecosystems by adding water, nitrogen, and phosphorus in a fully factorial experiment. We expected to find increased respiration in the watered plots due to expected water limitation of microbial activity in semi deserts. If enhanced respiration in watered plots was an indirect effect of increased nutrient availability, then we also expected fertilization to lead to higher respiration levels. As soil microbial biomass primarily is related to soil organic matter and labile C availability, we did not expect a short-term response in microbial biomass to water or fertilizer addition.

Methods

Site description and experimental design

The experiments took place a few hundred meters south of Zackenberg Research Station in NE Greenland (74°30′ N, 21°00′ W). The research station has a short meteorological record starting in 1996. The mean annual temperature is ≈ -10 °C with an annual precipitation of about 200 mm of which the main part falls as snow during winter months. In 1999, when we measured CO_2 fluxes, mean temperatures for June, July and August were respectively 1.5 °C, 6.2 °C and 2.9 °C. The short growing season lasts approximately from the end of June to the end of August.

The study site was established in 1996 in a semi desert on a dry gravel terrace adjacent to the river delta banks of the Zackenberg River. Soil organic matter content (0–12 cm depth) is 5.4 ± 0.3%, pH is 6.86 ± 0.03, and the soil is poor in nutrients. The semi desert has been classified floristically as belonging to the plant communities found on abrasion plateaus (Bay 1998), and comprises almost 50% bare soil. The sparse vegetation is dominated by *Kobresia myosuroides* Vill., *Dryas octopetala* L. x *integrifolia* M. Vahl., and *Salix arctica* Pall., and with *Carex rupestris* All. as a subdominant.

The experiment contains 48 plots of 0.5 × 0.5 m distributed over six blocks. On 10 August 1996 and 30 June 1997, two plots within each block, each of which had eight plots, were fertilized either with nitrogen (N) as NO_3NH_4 at a rate of 3.75 g N m^{-2}, with phosphorus (P) as Na_2HPO_4 at a rate of 0.81 g P m^{-2}, with both N and P (NP), or left unperturbed. Nutrients were not added in 1998 and 1999 because the fertilizer already added was considered sufficient to lead to longer-term changes in soil nutrient availability. From 1997 and onward one of the paired plots with nutrient added, plus one of the controls in each block, were watered weekly with 2 l of water, corresponding to 8 mm of precipitation per plot. The water applications were initiated 25 June, 3 July, and 2 July in 1997, 1998, and 1999, respectively, and ended in late August all years. The water used was snowmelt water from a nearby pool, and the addition corresponded to at least a doubling of the growing season precipitation. That is, the experiment was fully factorial with six blocks each with eight treatments: control plots (C), plots to which N, P or NP was added, all in a watered (W) and an unwatered version.

Respiration measurements

Measurements of CO_2 emission took place during the growing season of 1999. Black 23 cm long PVC tubes with an inner diameter of 10.2 cm were inserted into the soil in each plot to a depth of 10 cm. The tubes were placed in areas without vegetation above ground. We therefore measured below-ground respiration only originating from root activity plus soil microbial and soil faunal activity.

The CO_2 flux measurements were carried out with a PP Systems EGM-2 infrared gas analyser attached to a PVC lid fitting airtight over the chambers. The CO_2 concentration and chamber air temperature were measured at intervals of 8 sec.

during 120 sec. and the CO_2 emission rate was calculated by integration over the measured values as g CO_2 m^{-2} h^{-1}.

In order to determine how long watering affected the CO_2 flux, and what the appropriate time for measuring the flux after watering would be, we measured the flux immediately before the first water addition to the plots in July 1999 and four times within 48 hours after addition. Based on these data, we decided to measure respiration weekly at midday four hours after watering of the plots for the rest of the season.

Immediately after the weekly flux measurements at each plot, soil temperatures at 2, 4 and 8 cm depth were measured adjacent to each chamber with a handheld digital thermometer. During the first five measurements, soil temperatures were recorded in three plots only. Additionally the volumetric soil moisture content was recorded at five positions close to the margin of each plot with a Theta Probe ML2x (Delta-T Devices Ltd, Cambridge). The mean plot value of the moisture measurements was used for further calculations. Hourly means of incoming radiation were registered at the meteorological station of Zackenberg. We averaged these data from the periods where we registered CO_2-fluxes (usually a period of two to three hours) in order to obtain a value of photosynthetic active radiation (PAR) during measurements.

Microbial biomass

In order to measure soil microbial biomass C, two soil samples were taken to a depth of 5 cm in each plot with a 4 cm diameter soil corer on 7 August 1997. Immediately after sampling, the two subsamples were lumped, handsorted to remove plant roots, and passed through a 2 mm sieve to remove stones. A subsample was dried at 80 °C to constant mass and weighed to calculate the soil water content. The dry soil was later analysed for loss on ignition by igniting the samples for 6 hours at 550 °C. The chloroform fumigation-extraction method (Jenkinson and Powlson 1976; Brookes et al. 1985) was used to determine microbial biomass C. Fumigated and unfumigated subsamples of 10 g fresh soil were extracted in 50 ml 0.5 M K_2SO_4 for 1 hour, and sieved through Whatman glass microfibre GF/D filters. Determination of microbial C was performed by analysing the extracts for dissolved organic C with an organic carbon analyser (Shimadzu TOC 5000A, Shimadzu Corporation, Kyoto, Japan) and calculating the difference in carbon content between fumigated and unfumigated samples. An extractability factor of 0.35 was used to account for incomplete extrability of microbial C by the fumigation-extraction method, as in other studies of tundra soils (Cheng and Virginia 1993; Jonasson et al. 1996b).

Data treatment

All data were tested for homogeneous variances by Levene's test and appropriate transformations were made where necessary. Treatment effects on respiration, microbial biomass, soil temperature, and soil moisture were tested separately for each
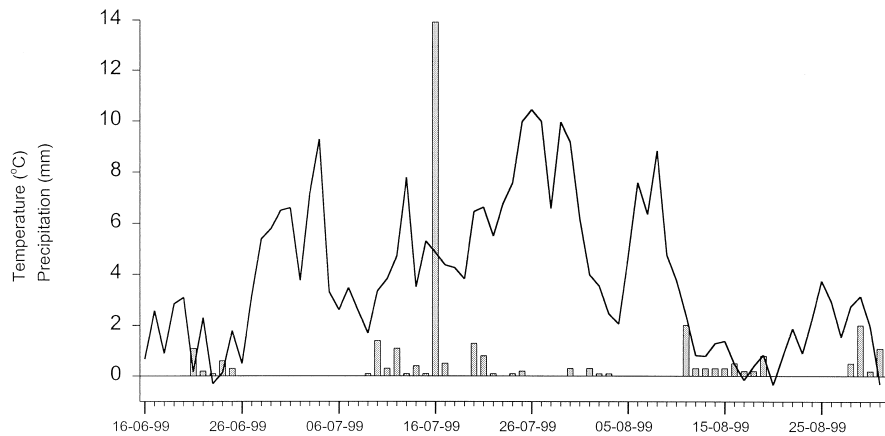
Figure 1. Mean diurnal air temperature line and precipitation bars at Zackenberg during the 1999 growing season

date of measurement by four-way ANOVAs with nitrogen (N), phosphorus (P), water addition (W), and block as main effects, and with all interactions between N, P, and W. Block was included as a main effect in the analyses to separate differences among the blocks from treatment effects. Because of the small number of soil temperature measurements made on the first four days, ANOVAs on this parameter were only performed with the weekly measurements thereafter. One-way ANOVA with day as factor followed by Tukey's test was used to test for differences in soil moisture between sampling dates. Spearman rank correlation was used to test for relationship between respiration and soil temperature plus soil moisture. Because there was a significant correlation between respiration and soil temperature (for temperature at 2 cm depth: $r_s = 0.63$, $P < 0.0001$, $n = 56$), soil temperature at 2 cm depth was included as a covariate in the ANOVAs on respiration at the weekly measurements starting on 9 July. Furthermore, the treatment effects on respiration across all measurements during the season were tested by a repeated measurement ANOVA. All statistical analyses were carried out with SAS (Statistical Analysis Systems Institute 1997).

Results

Environmental parameters

Until 26 June and after 12 August air temperatures were slightly above freezing, whereas during most of the measuring period, temperatures varied around 5 °C with a diurnal maximum of 10.4 °C on 26 July (Figure 1). During the entire growing season (here defined as 15 June–30 August), there was only 32.2 mm precipitation, which came mostly in small amounts except for 16 July when a storm event was followed by almost 14 mm rainfall within 24 hours.
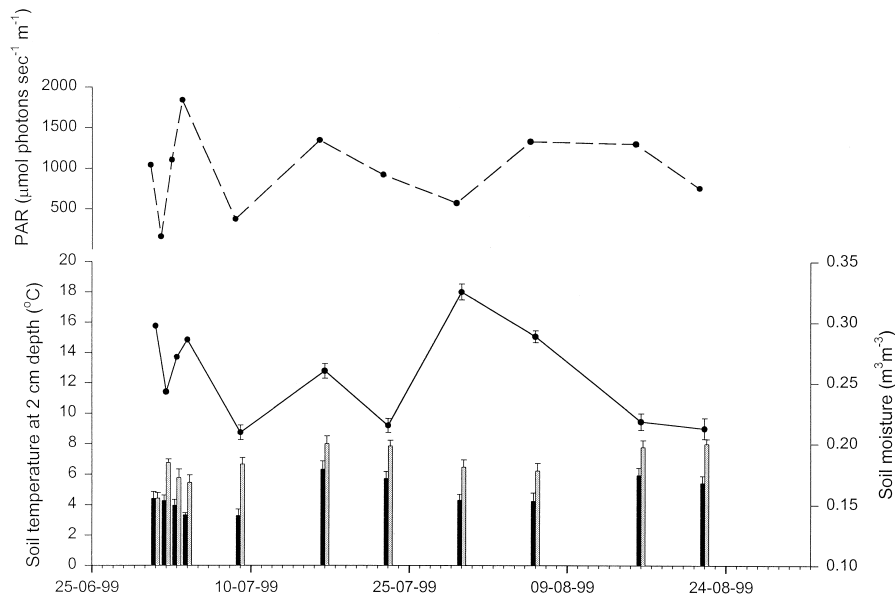
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Figure 2. Soil moisture in control plots (n = 6, black bars) and watered plots (n = 6, grey bars), mean soil temperature at 2 cm depth in control plots (line), and mean photosynthetic active radiation (PAR) during the periods of CO_2 flux measurements (broken line). The first measurements on 1 July were done before watering started, and the values for 2 July are from the measurements done in the evening, 10 hours after watering

Soil temperatures at 2 cm depth in all plots varied between 6.1 °C and 21.2 °C, at 4 cm depth between 5.8 °C and 18.3 °C, and at 8 cm depth between 4.5 °C and 16.5 °C. In general, the soil temperatures were at a seasonal maximum in late July coinciding with the highest air temperatures, and fell to the lowest levels in late August (Figure 2). Also, the soil temperatures were significantly lower in watered than non-watered plots by on average 1.1 °C and 0.9 °C at 2 and 4 cm depth, respectively (separate ANOVAs for each date). Incoming PAR during CO_2 flux measurements in general varied with the same pattern as soil temperature (Figure 2). The lowest value was registered on the evening of 2 July with a mean value during CO_2-flux measurements of only 160 μmol photons sec^{-1} m^{-2}, and the highest value was registered on 4 July with 1841 μmol photons sec^{-1} m^{-2} during flux measurements. Soil moisture was always higher in watered plots than non-watered plots (separate ANOVAs for each date, $P < 0.05$, Figure 2), except for the first measurement, which was performed before watering started. Following the single high precipitation event on 16 July, the soil moisture level increased significantly on 17 and 23 July compared to the previous and later measuring dates. Also, following nine days with moderate amounts of precipitation each day by mid-August (Figure 1) the soil moisture level increased significantly (Figure 2).
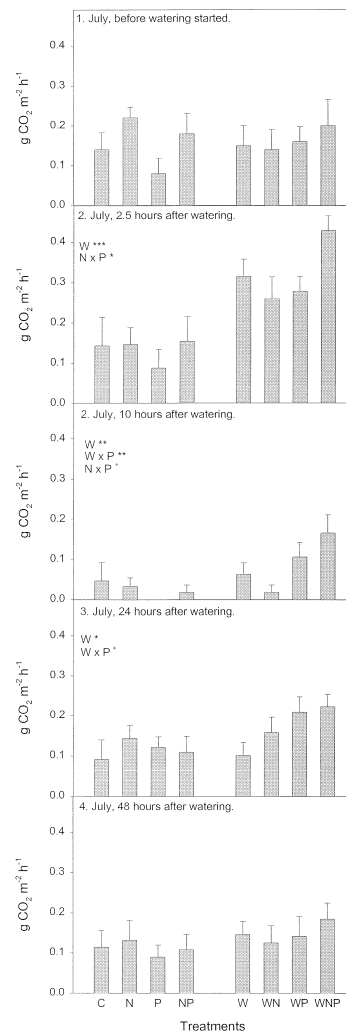
Figure 3. Soil plus root respiration at the semi desert following water application. Treatments are: C-control, N-nitrogen amendment, P-phosphorus amendment, W-water addition, and combinations thereof. Results of ANOVAs with significant main factor effects of treatments and interactions are shown in the top of the figures as +, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Respiration

Average respiration across treatments varied more than threefold, from less than 0.07 g CO_2 m^{-2} h^{-1} on 2 July (evening) and 22 August (midday) to more than 0.23 g CO_2 m^{-2} h^{-1} on 2 July (midday) (Figures 3 and 4).

There was no difference in soil respiration among treatments prior to initiation of watering. After water applications, respiration rates increased from 2.5 hours to

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24 hours after watering, and levelled off to non-significant effects after 48 hours (Figure 3).

The seven weekly measurements carried out between 9 July and 22 August showed daytime respiration levels in controls of around 0.15 g CO_2 m^{-2} h^{-1} until mid-August, after which the respiration levelled off (Figure 4). Water application affected respiration significantly on three dates, and also interacted significantly, or close to significantly, with P addition on 9 July, 17 July, 16 August and 22 August, with higher respiration than expected from the effect when only water or P was added. There was no main effect of fertilizer addition, but significant N × P interactions were recorded on 23 July and 6 August and tendencies towards significant effects were recorded on 30 July and 22 August. When testing all data over the season, the repeated measurements ANOVA showed a significant effect of water addition on respiration, a significant interaction between phosphorus and watering, and a tendency ($P < 0.10$) towards an N × P interaction (Table 1).

Microbial biomass and dissolved organic carbon

Microbial biomass C varied between 7700 μg g^{-1} SOM and 12000 μg g^{-1} SOM (Figure 5), and was significantly higher in watered than non-watered plots (F = 6.83, P = 0.01). Mean dissolved organic carbon concentration in the soil was 1086 ± 88 μg DOC g^{-1} SOM with no effects of treatments, and there were no treatment effects on SOM content.

Discussion

Treatment effects

The measured flux levels from control plots are comparable to the few other records of respiration from the high Arctic (Wütrich et al. 1999; Jones et al. 2000), suggesting that the measured fluxes are representative of the large areas of polar semi desert.

Water addition enhanced the CO_2 flux between 2.5 and 24 hours after the first water application (Figure 3), and there was an overall water effect across the season (Figure 4, Table 1). Furthermore, water addition increased respiration after all additions, showing up either as a main effect in the ANOVAs or as an interaction effect when combined with the added nutrients. The strongest responses occurred on 30 July and 6 August, coinciding with the lowest mid-season soil moisture content. In contrast, on the other dates, the lower effect coincided with high soil moisture content after precipitation. For instance, the lower effect on 17 and 23 July probably is because of the high precipitation event on 16 July (Figure 1) corresponding to about twice the amount added by watering. This also led to twice as high soil moisture content both on 17 and 23 July than on the previous measuring date (9 July) and a 50% increase compared to the following measuring date on 30
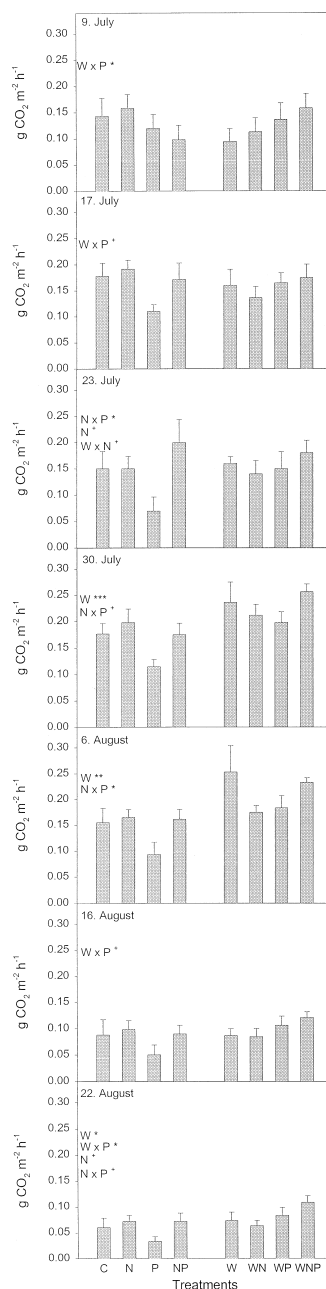
Figure 4. Weekly ecosystem respiration of the semi desert during the 1999 growing season. Treatments are: C-control, N-nitrogen amendment, P-phosphorus amendment, W-water addition, and combinations thereof. Results of ANOVAs with significant main factor effects of treatments and interactions are shown in the top of the figures as: +, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Table 1. Repeated measurements ANOVA of the effect of application of nitrogen, phosphorus, water, and combinations thereof on below-ground respiration in a high arctic semi desert

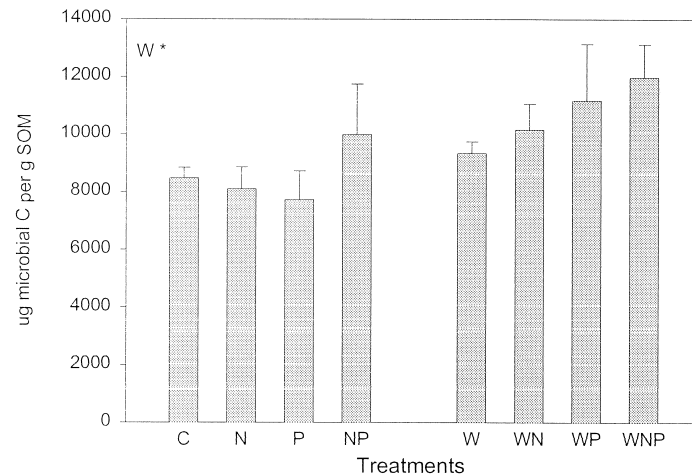|	df	F	P
Block	5	3.16	**0.0190**
Nitrogen	1	2.84	0.1013
Phosphorus	1	0.06	0.8096
Water	1	11.62	**0.0017**
Nitrogen * Phosphorus	1	2.87	0.0992
Nitrogen * Water	1	0.84	0.3662
Phosphorus * Water	1	6.30	**0.0170**
Nitrogen * Phosphorus * Water	1	0.28	0.6026

Figure 5. Microbial biomass C in 1997 after two growing seasons of fertilization and one season of water addition. Treatments are: C-control, N-nitrogen amendment, P-phosphorus amendment, W-water addition, and combinations thereof. Results of ANOVAs with significant main factor effects of treatments and interactions are shown in the top of the figures as: +, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

July (Figure 2). Similarly, the soil moisture level on 16 August was also high (Figure 2), and this probably explains the lack of a main effect of water application on the CO_2 flux on that day (Figure 4). Yet, water additions to plots with added P or N stimulated respiration at these dates.

Increased microbial biomass in the watered plots (Figure 5) may have contributed to the increased respiration. Microbial biomass may increase rapidly in dry soil after watering (Gallardo and Schlesinger 1995) and when exposed to repeated cycles of drying and rewetting because surviving microbes can utilise carbon and nutrients released from microbes killed during the dry period (Wardle and Parkinson 1990). However, the increased microbial biomass does not explain the fluctuations between small and large effects of watering among the dates. Hence, it ap-

pears that the response to increased water rather than being related to changes in microbial biomass is a response in microbial activity.

A decline in microbial activity could be due to reduced mobility of microorganisms as the soil dries out and the water film "shrinks" around soil particles and disappears from the coarser pores. Also, it could be because microbial cells are highly permeable, and hence, will have similar water potential inside the cell as the water potential in the soil solution, causing loss of cell water and eventually death if the environment dries out. Some microbes are capable of selective transport of soil solution ions into the cell, and hence can maintain high cell water content by osmotic regulation. However, even this strategy may end up being detrimental to the cells because the high intracellular salt concentration eventually may limit the cellular enzyme machinery (Killham (1994) p 161).

Soil nutrients in general are transported with bulk soil water or move by diffusion to sites where plants or microbes use them. Hence, nutrient mobility is constrained by low soil water content. However, contrary to our expectations, no increase in respiration was seen in fertilized plots two years after application of nutrients (Figures 3 and 4), despite increased plant cover and flowering in fertilized plots (pers. obs.). The ecosystem respiration response to watering, therefore, probably was not caused by indirect nutrient effects.

The positive interaction between water and phosphorus is because the measured CO_2-efflux decreased in P fertilized plots (Figure 4) but increased to a level close to that of the control plots when combined with water addition. Similar low ecosystem respiration in P amended plots was observed by Christensen et al. (1998) in a subarctic heath. This decline is obviously counteracted by increased moisture and may be associated with slightly increased pH in the soil when adding P as Na_2HPO_4. At pH levels higher than 6.8, the balance between carbon dioxide and bicarbonate in the water phase of the soil may change in favour of bicarbonate, and hence reduce CO_2 efflux from the soil (Prescott et al. (1993), pp 824–825).

In conclusion, the treatment responses on the combined soil and plant respiration, seemingly, all owed directly to soil water limitation in this semi desert. On average, the respiration increased by 25% in the watered plots compared to control plots. Our results suggest that responses to future changes in precipitation will depend on the rainfall pattern. Precipitation could fall either regularly throughout the season, or, as some GCMs predict, with increasing frequency of extreme precipitation events (Rowntree 1997; Houghton et al. 2001), like the one on 16 July (Figure 1). Assuming the latter scenario, the periods of soil dryness may last for longer periods than at present, and respiration may decline. In contrast, if the increased precipitation falls regularly throughout the season, and the soil never dries out, soil respiration may increase because soil moisture will not limit respiratory activity at any time during the season. Assuming that the soil moisture content does not affect photosynthesis or the size of the future plant biomass, a 25% increase in carbon release will, therefore, represent a considerable difference to carbon budgets of the one-third of the ice-free Arctic which is covered by polar desert and semi desert.

Soil versus root respiration

The measured flux originated from below ground sources because there were no aboveground plant parts in the chambers. However, the very low rate of respiration in all plots, e.g. of 0.05 g CO_2 m^{-2} h^{-1} in control plots on the evening of 2 July, 10 hours after watering (Figure 3), as compared to two to three times higher mid-day values just before (2 July) or just after (3 July) suggests that the main part of the respiration came from roots and from turnover of root exudates. This is because the evening measurements were performed under very low light intensities compared to all other measurements (Figure 2), causing low photosynthetic activity presumably leading to decreased root exudation. Because soil microbes prefer labile carbohydrates to more recalcitrant SOM (Verburg et al. 1998), respiration probably declines at low light intensities due to substrate limitation. This is in accordance with Christensen et al. (1997) and Craine et al. (1999) who recorded 40% reductions in soil CO_2 flux in subarctic heath and temperate grassland after shading plants. Furthermore, respiration of recently fixed plant C dominates ecosystem respiration in wet sedge tundra and sub-arctic heath (Johnson et al. 2000; Grogan et al. 2001). As soil temperature in the evening of 2 July was about 3.5 °C higher than on 9 July (Figure 2) but the CO_2 flux in control plots only about one third of that on 9 July, low soil temperatures could not explain the low flux on the evening of 2 July. Furthermore, as the three dominant plant species in this ecosystem form ectomycorrhiza (Michelsen et al. 1998), it is reasonable to assume that a large part of the soil microbial biomass in the ecosystem consists of ectomycorrhizal fungi. Hence, soil microbial activity may be reduced by low light levels leading to low photosynthetic activity because ectomycorrhizal fungi utilize C fixed recently by the plants.

If a large part of the respired C originates from labile components in root exudates, any change in respiration rates could be associated with changes in the plant component of the ecosystem. This means that the stock of soil C with long to medium-long turnover may not necessarily change in spite of changes in respiration rate. The major part of soil respiration may therefore be a product of turnover of the most labile C fraction in the soil, as suggested for antarctic desert soil by Burkins et al. (2001). In order to obtain firm evidence of the seemingly high importance of recently fixed C respiration of tundra soils, research efforts must be directed towards the use of isotopic labelling of C in photosynthates.

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