

Small-scale hydrological variation determines landscape CO₂ fluxes in the high Arctic

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Abstract We explored the influence of small-scale spatial variation in soil moisture on CO₂ fluxes in the high Arctic. Of five sites forming a hydrological gradient, CO₂ was emitted from the three driest sites and only the wettest site was a net sink of CO₂. Soil moisture was a good predictor of net ecosystem exchange (NEE). Higher gross ecosystem photosynthesis (GEP) was linked to higher bryophyte biomass and activity in response to the moisture conditions. Ecosystem respiration (R_e) rates increased with soil moisture until the soil became anaerobic and then R_e decreased. At well-drained sites R_e was driven by GEP, suggesting substrate and moisture limitation of soil respiration. We propose that spatial variability in soil moisture is a primary driver of NEE.

Keywords High Arctic · Carbon dioxide fluxes · Spatial variability · Soil moisture · Vegetation

Introduction

Tundra ecosystems store 192 Tg C or 19% of the global soil carbon pool (Post et al. 1982), and there is concern that a proportion of this carbon might be metabolized under predicted climate change scenarios at high latitudes (McGuire et al. 1995; Kirschbaum 1995; Oechel et al. 1997; Prentice et al. 2001; Jones et al. 2005). The net effect of climate change on the carbon balance will depend on the balance of net primary production and decomposition (Hobbie and Chapin 1998; Welker et al. 2004), which is likely to vary along hydrological gradients. In this context it is important to understand relationships between landscape hydrology and those ecosystem characteristics that contribute to CO₂ fluxes, as tundra ecosystem responses to climate warming will be mediated by spatial variation in hydrology. For example, increased surface desiccation and lower soil moisture content may reduce decomposition in dry soils (Rosswall et al. 1975; Latter et al. 1998; Sjögersten and Wookey 2002; Illeris et al. 2003; Sjögersten and Wookey 2004). Vegetation is likely to respond to change in moisture availability and, interestingly, responses may differ between the bryophyte and vascular plant communities. Bryophytes tend to respond positively to increased water

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availability (Potter et al. 1995; Longton 1997), whilst vascular plants appear to be more resilient to changes in soil moisture (Gold and Bliss 1995; Robinson et al. 1998). To date arctic CO₂ flux research has been focused on the effects of warming on vegetation (Parsons et al. 1994; Shaver et al. 1998; Hobbie and Chapin 1998; Rustad et al. 2001; Oechel and Billings 1992; Welker et al. 2004) whilst fewer studies have investigated effects of moisture availability as a control on net primary production (NPP) and CO₂ fluxes (Potter et al. 1995; Ostendorf 1996; Robinson et al. 1998; Illeris et al. 2004). In this paper we investigate spatial variation in CO₂ fluxes in relation to hydrology in the high Arctic.

The high Arctic is characterized by extreme climate, a shallow active layer, complex hydrological patterns, and strong abiotic controls of biological activity both in winter and during the short growing season. Hydrology is strongly driven by the melting of snow, the active layer in the permafrost and glaciers during the summer period, as well as by slope and soil type. Tundra landscapes are heterogeneous and can encompass a mosaic of wetland areas, riparian systems, well-drained heath lands, ridge-top vegetation and polar deserts. The vegetation community at any site is determined largely by its hydrology, and both NPP and decomposition rates differ greatly between areas of contrasting moisture status (Muc et al. 1989; Giblin et al. 1991; Cheng et al. 1998). Wetter areas exhibit slow decomposition and tend to be more productive than drier areas, whilst soil organic matter at sites with intermediate soil moisture content will be more decomposed and with NPP potentially constrained by soil moisture (Giblin et al. 1991; Cheng et al. 1998). Ecosystems with contrasting hydrology often differ dramatically in their function as carbon stores; wet systems generally act as CO₂ sinks, whilst well-drained areas might be much weaker sinks or even CO₂ sources (Fan et al. 1992; Jones et al. 1998; Soegaard et al. 2000; Heikkinen et al. 2002; McFadden et al. 2003; Welker et al. 2004). Superimposed on landscape hydrology, inter-annual variation in light, precipitation and temperature will control the balance between ecosystem respiration and photosynthesis rate determining the net sink/sources strength of CO₂ (Lloyd 2001). Substantial efforts have been put into estimating the carbon sink strength of tundra wetland areas (Billing et al. 1982; Vourlitis and Oechel 1997;

Shaver et al. 1998; Sommerkorn et al. 1999; Svensson et al. 1999), whilst the dry sparsely vegetated tundra that dominates the high Arctic (Bliss and Matveyeva 1992) has been less studied e.g. Lloyd (2001). It is essential to quantify the role of soil moisture as a control of landscape CO₂ fluxes in order to accurately predict the effects of climate change on the C balance in this region.

In this study we aimed to assess the relative contribution of hydrologically different ecosystems to the landscape C balance, and to determine the mechanisms by which moisture availability influences CO₂ fluxes. We used both a natural moisture gradient and experimental water addition in a high-Arctic valley as a model system to answer the following specific questions: (i) Can net ecosystem exchange of CO₂ (NEE) be predicted by soil moisture content? (ii) Can NEE at well-drained sites be altered by increased water availability? (iii) How are the individual components of NEE (gross ecosystem photosynthesis (GEP) and ecosystem respiration (R_c)) influenced by soil moisture and temperature?

Materials and methods

Site description

The study sites are located in a high-Arctic valley, Adventdalen, on the western side of Svalbard, Norway 78°10.186' N 16°06.498' E. The whole area is underlain by permafrost and this, in combination with glacial melt, strongly influences the hydrology since the active layer is only 0.5–1 m deep. The sites are located between the foothill of the mountains to the south of Adventdalen and the river Adventelva. Climate in the area is cold; precipitation is low and most falls as snow during the winter. The mean annual temperature is -6.7°C , the January mean temperature is -15.3°C and the July mean temperature is 5.8°C (1961–2000 average). The mean annual precipitation is 190 mm (1988–2000 average). During the short growing season between June and August, air temperature is generally above zero (Table 1).

Site selection was based on plant species composition, soil moisture content and position in the landscape. The five sites we used encompassed the full range of moisture conditions found in this valley, ranging from very dry, sparsely vegetated heath to a

Table 1 Mean air temperature and total precipitation at Svalbard Lufthavn (ca. 10 km from the field site) during the growing season (June–August) of 2003, 2004 and the long term average (www.met.no)

	2003	2004	1961–1990
Air temperature (°C)	5.4	5.1	4.2
Precipitation (mm)	12.6	24.4	11.3

lush riverbed system. They are subsequently denoted xeric, dry, mesic, moist and wet. The elevation difference between the sites is negligible: four of the sites are located on the old inactive flood plane whilst the dry site is just at the foot of the hills to the south. The xeric site is vegetated by *Dryas octopetala*, *Poa arctica* and *Hypnum* spp., and ca. 25–50% of the surface is bare or partly covered by a cyanobacterial crust. No organic horizon is present above the silty mineral soil that has drought/frost cracks running through it. The dry site is more species rich with *Salix polaris*, *D. octopetala*, *Carex rupestris*, *Luzula confusa*, *Polygonum viviparum*, and *Oxyria digyna*. Mosses provide substantial ground cover, with *Tomentypnum nitens*, *Hylocomium splendens*, and *Sanionia uncinata* most prevalent; total ground cover is ca. 80–90%. There is a shallow organic horizon on top of the mineral soil that consists of well-drained medium to coarse-grained talus deposits. The mesic site is a *Alopecurus borealis* heath with a high percentage cover of *S. polaris*. *Luzula confusa* and *P. viviparum* are also abundant, and a thick moss mat composed of *T. nitens*, *H. splendens* and *S. uncinata* provides 100% ground cover. Although generally well drained, this site tends to get water saturated late in the growing season. The mineral soil is similar to that at the xeric site, i.e. silty, but without cracks. The moist site is dominated by mosses, mainly *Aulacomnium turgoides* and *T. nitens*, with a sparse cover of vascular plants, most notably *Dupontia* spp. and *Ranunculus spetsbergensis*. The water table is close to the surface (10–30 cm) and the deep organic horizon (ca. 20 cm) is composed of a thick layer of poorly decomposed moss. At the wet site the dominating moss is *Calliergon richardsonii*, and the graminoid cover is denser than at the moist site, the two main species being *Dupontia* spp. and *Calamagrostis stricta*. Other species include *Equisetum arvense* and some forbs, e.g. *Cardamine nymanii*. This site is a riverbed and the soil is water saturated throughout the

growing season; the organic horizon has a variable depth with a large proportion of poorly decomposed moss and tends to be mixed with silt. In some areas the organic horizon is shallow due to erosion by the stream. Below the organic horizon there is a mineral layer composed of a mixture of gravel and silt. The soils at the two wettest sites showed gleying and smell indicative of anoxic conditions.

Experimental design

In order to investigate both CO₂ flux at sites with contrasting hydrology and effects of alleviating water limitation at dry sites, we used the natural moisture gradient composed of the five sites described above in combination with a water addition treatment to the three driest sites (xeric, dry and mesic).

Plots (50 × 60 cm²) were selected to be representative of the vegetation and soil at each site. Five plots were established at each of the two wettest sites, to be used in the water gradient study only. At the three drier sites that were to receive water addition, five pairs of two plots were selected at each site, and plots within each pair were randomly allocated to a treatment. The control plots were also used in the water gradient study. The water treatment was applied twice a week during the growing season (4 July to 20 August 2003, and 12 June to 30 August 2004). The water additions were designed to explore water limitations rather than to represent natural variation or precipitation changes predicted with climate change, and hence a substantial amount of water was applied compared to the mean annual precipitation. Water was applied 14 times in 2003 and 20 times in 2004 with 33 mm added on each occasion; in total 1122 mm of water was added to each experimental plot. The water was collected from nearby streams and had very low levels of nutrients: 0.7 μmol NH₄⁺ dm⁻³, whilst NO₃⁻ and PO₄³⁻ concentrations were below the detection limit. Overall, water addition significantly influenced soil moisture content ($F_{1,14} = 6.23$, $P < 0.05$). At the xeric site the volumetric soil water content increased by 72% in response to the water addition, from 0.18 ± 0.01 to 0.31 ± 0.01 m³ m⁻³; at the dry site the water content increased by 8% from 0.33 ± 0.02 to 0.35 ± 0.05 m³ m⁻³; finally at the mesic site the water addition had no effect on soil moisture: water content in the control plots was 0.43 ± 0.03 compared to 0.43 ± 0.04 m³ m⁻³ in watered plots.

Flux measurements

Ecosystem CO₂ fluxes were estimated on two occasions (July and August) in 2003 and on three occasions (June, July and August) in 2004, with all measurements made between 10:00 and 16:00. The measurement days included a wide range of phenological stages, productivity, light, and temperature conditions.

Ecosystem CO₂ fluxes were measured with custom-built cuvettes attached to EGM-4 Infra Red Gas Analyzers (IRGAs) (PP Systems, Hitchin, UK). This is an open system with an air flow of 10 l min⁻¹ through a 12 l clear plastic bell chamber of 30 cm base diameter which is mounted on a steel ring (5 cm deep) inserted into the soil. CO₂ concentration was analyzed every 8 s, with the analyzer switching between reference air and samples from the cuvette every 30 s. CO₂ flux was calculated from the difference in CO₂ concentration between the reference and the sample air, the flow rate and the ground surface area, and two-minute averages were recorded. Both net ecosystem exchange (NEE) and ecosystem respiration (R_e) were measured at each plot in the following sequence: the system was allowed to settle for 5–10 min, NEE data were collected over the next 20 min, a hood was placed over the cuvette to exclude light and stop photosynthesis, the system was allowed 5–10 min to settle, and then R_e was measured for 15 min. To obtain an indication of gross ecosystem photosynthesis (GEP), R_e fluxes were subtracted from NEE fluxes. Our data illustrate maximum sink strength, since they come from daytime measurements.

Photosynthetically active radiation (PAR), air temperature and humidity were recorded simultaneously with the CO₂ fluxes. At the same time, measurements were made of soil temperature at 7 cm depth with temperature probes (RS components, UK), and soil moisture was integrated over the top 6 cm using a hand held Theta probe and meter (ΔT devices, Burwell, UK). Three measurements were taken in each plot to incorporate some of the spatial variation. On average, cuvette air temperatures were ca. 3°C higher during NEE than R_e measurements.

Plant biomass and soil data collection

To determine the relationship between CO₂ flux measurements and the vegetation at each site, two

cores of 4.5 cm diameter were collected from each plot at the end of the growing season in 2004. Photosynthetically active vascular plant and moss biomass fractions were separated, dried and weighed. Additionally, the depth of the organic horizon and soil pH (in a 1:2 fresh soil: distilled water mixture) were measured at each site. Total soil C and N content in the top 2-cm below the moss soil interface were analyzed on pooled samples from each site (two subsamples were collected from each plot) on a Carlo Erba NA1500 elemental analyzer.

Laboratory incubation experiment

To test the sensitivity of ecosystem respiration to variation in temperature and moisture, cores were collected from the three sites on the moisture gradient with intermediate moisture levels (i.e. dry, mesic and moist). Twenty intact cores with the vegetation remaining on the top were collected from each site at the end of the growing season. The cores were 6-cm in diameter and taken to 6-cm depth into the soil, and were stored at 2°C until the experiment began. They were kept at the original field moisture content and placed in 10-cm diameter, 10-cm high plastic containers, with lids to reduce moisture loss. Four incubator temperatures (2, 6, 10 and 14°C) were used to study the temperature response of R_e . The cores were incubated at the lowest temperature first and then at successively higher temperatures, with three hours equilibration at each temperature before measurement.

During CO₂ flux measurement cores were taken out of the incubators and their containers to allow air mixing, and four cores from one site were placed together in a cuvette connected to a EGM-4 IRGA. Five separate cuvette – IRGA systems were used so that all 20 cores from one site could be measured simultaneously. The cuvettes were covered with black polythene to exclude light, and respiration rates were measured for 30 min at ca. 15 degrees, the temperature in the soil cores did not change significantly during the measurement period. After the temperature series was completed, cores were placed at 2°C and all soil cores were wetted with 85-ml distilled water that had been incubated at the same temperature as the cores. This is the same amount of water that was applied in one water addition in the field experiment. Soils were allowed to equilibrate for

24 h after the water addition and then CO₂ fluxes were measured with cores being put through the temperature series as described above in order to derive an average response to the increased water content across a range of temperatures.

Data analysis

At the three well-drained field sites there were some occasions on which NEE exceeded R_e . When this was the case, NEE could be predicted by total green biomass ($F_{1,8} = 6.54$, $P < 0.05$). It is likely that the high NEE values are caused by stress respiration that is related to water deficit in combination with the warming associated with the cuvettes. In the data analysis we included all NEE data points, whilst for photosynthesis data points for which $NEE > R_e$ were set to zero.

Prior to the main statistical analysis described below we analyzed treatment effects on NEE, GEP and R_e for the two years and revealed that differences among sites were consistent among sites with contrasting soil moisture content. Therefore, the final analyses were conducted on plot averages of the five sampling dates throughout. Data were analyzed in SAS for Windows V. 8.2 employing a variety of statistical models. Differences in NEE, GEP and R_e among the five sites were tested for using general linear models (GLM) with site as a fixed effect followed by Tukey post hoc comparisons. To avoid pseudo-replication, we used generalized linear mixed models (GLMM) with 'site' as the random effect for all other analyses on the field data. Here, models were fitted by the method of residual maximum likelihood (REML). Denominator degrees of freedom were estimated using Satterthwaite's approximation (Littell et al. 1996), and the residual variances were modeled as constant to the mean using PROC MIXED. The effect of water addition was analyzed for each of the three sites separately using mixed models with 'block' (i.e. pair of control and watered plots) as random effect and treatment as a fixed effect. The relationships between GEP and bryophyte/vascular plant biomass were conducted on log-transformed data to improve homogeneity of the variance, using 'site' and 'block' as random effects. A similar model structure, but no log-transformation, was used to test for the effect of water addition on live moss biomass. We used GLM to explore the

relationship between R_e and GEP after combining the three well-drained sites since the response variables from these sites were best described by a common equation, contrasting the data from the moist and wet site which were kept separately.

Data from the incubation experiment were analyzed using GLMM, whereby autocorrelation between measuring periods within cores was modeled on the basis of an unstructured co-variance matrix.

Results

Environmental conditions

The summers of 2003 and 2004 were warm compared to the long-term average, and the summer of 2004 had double the average precipitation (Table 1). Light levels were low: two-third of the measurements taken were at photon flux densities below 400 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$. Soil temperature tended to be lower at sites with higher soil moisture content, except for the wet riverbed site that was as warm as the xeric site in mid-season (Table 2). Soil moisture was lowest at the xeric site and increased successively at the dry, mesic, moist and wet site, respectively.

The amount of photosynthetically active plant tissue (bryophytes and vascular plants combined) differed among the five sites ($F_{4,20} = 11.28$, $P < 0.0001$), with the lowest biomass at the xeric site and the highest at the wet site. Those differences were also apparent for green moss biomass ($F_{4,20} = 11.54$, $P < 0.0001$) and green vascular plant biomass ($F_{4,20} = 3.75$, $P < 0.05$) alone (Table 3). The wetter sites had deeper and less decomposed organic horizons, and this tended to be associated with higher soil C/N ratio. There was little difference in soil pH between sites (Table 3).

CO₂ fluxes across the moisture gradient

The net ecosystem exchange of CO₂ (NEE) varied significantly among sites, with the three relatively well-drained sites tending to be sources of CO₂ to the atmosphere whilst the two wetter sites acted as CO₂ sinks (Fig. 1a). NEE is determined by the balance of gross ecosystem photosynthesis (GEP) and ecosystem respiration (R_e). GEP differed significantly among sites and was lower at the three well-drained sites compared to the moist and the wet site (Fig. 1b). R_e

Table 2 Soil temperature ($^{\circ}\text{C}$) and volumetric moisture content ($\text{m}^3 \text{m}^{-3}$) measured at the time of CO_2 flux measurements during summer 2003 and 2004

Site	Soil temperature ($^{\circ}\text{C}$)	Soil moisture ($\text{m}^3 \text{m}^{-3}$)
Xeric	7.6 (3.4–9.3)	0.18 (0.07–0.31)
Dry	6.1 (2.8–8.0)	0.32 (0.29–0.36)
Mesic	5.3 (3.7–6.8)	0.43 (0.34–0.59)
Moist	5.3 (3.3–6.8)	0.53 (0.38–0.61)
Wet	7.6 (4.4–9.8)	0.61 (0.60–0.61)

Mean values and the range (in parenthesis) are shown

also differed among sites, gradually increasing from the xeric to the moist site and decreasing again at the wet site (Fig. 1c).

Soil moisture proved to be a powerful predictor of NEE with greatest efflux of CO_2 at intermediate soil moisture (Fig. 2). Net carbon sequestration only occurred where soil moisture content exceeded $0.55 \text{ m}^3 \text{ m}^{-3}$.

GEP rates increased with soil moisture content (i.e. more negative C flux at higher soil moisture) (Fig. 3a). The strong positive relationship between the amount of photosynthetically active moss tissue

and soil moisture (Fig. 3b) suggests that moss biomass may directly influence GEP.

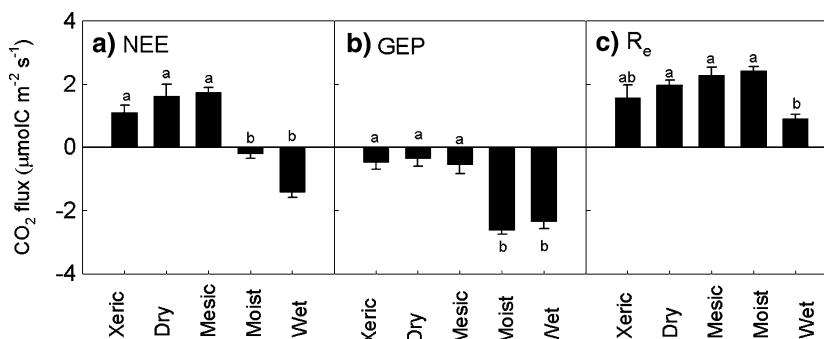
In the watering experiment at the three drier sites, water addition significantly enhanced GEP (i.e. C flux became more negative) at the mesic site only, with a 120% increase in photosynthesis ($F_{1,4} = 7.71$, $P = 0.05$, Fig. 3c). Water addition did not influence R_e at these sites ($P > 0.3$), so the pattern for NEE resembled that for GEP, with watering causing a reduction in carbon efflux from the mesic site ($F_{1,4} = 4.79$, $P = 0.09$). Overall, water addition increased the amount of photosynthetically active moss tissue at the three sites ($F_{1,14} = 4.44$, $P = 0.05$) and, indeed, moss biomass in the control and watered plots was a good predictor of GEP across these sites (Fig. 3c). There was no effect of watering on vascular plant biomass, and vascular plant biomass did not explain any of the variation in GEP.

Ecosystem respiration increased linearly with soil moisture between the xeric and the moist sites and then steeply declined at the anaerobic wet site (Fig. 4). Wetter sites tended to be colder, apart from the wettest riverbed site where soil temperature was

Table 3 Vegetation and soil description of five sites forming a moisture gradient. “Moss” and “vascular” represent the amount of green, photosynthetically active tissue (i.e. only the green growing tips of moss and green leaves on the vascular plants) Mean \pm 1 S.E

Site	Moss (g m^{-2})	Vascular (g m^{-2})	Organic horizon (cm)	pH	C/N
Xeric	1.3 ± 0.3	7.4 ± 1.1	0.0 ± 0.0	5.95 ± 0.07	19.4
Dry	9.3 ± 0.9	9.6 ± 0.6	2.0 ± 0.3	5.82 ± 0.09	17.9
Mesic	16.9 ± 0.6	5.7 ± 0.2	3.0 ± 0.3	5.63 ± 0.07	26.5
Moist	14.8 ± 0.6	2.8 ± 0.6	$20.2^a \pm 1.9$	5.95 ± 0.07	46.3
Wet	27.2 ± 3.1	9.1 ± 0.4	$5.0^a \pm 1.5$	6.01 ± 0.04	31.8

^aMostly poorly decomposed moss tissue

**Fig. 1** CO_2 fluxes across the moisture gradient with positive values representing CO_2 emissions and negative values CO_2 uptake. (a) Net ecosystem exchange of CO_2 (NEE), $F_{4,20} = 35.46$, $P < 0.0001$. (b) Gross ecosystem photosynthesis (GEP), $F_{4,20} = 21.47$, $P < 0.0001$. (c) Ecosystem respiration

(R_e), $F_{4,20} = 6.48$, $P < 0.01$. Values presented are means and standard errors for each site after averaging over all sampling dates spanning two growing seasons. Bars with different letters indicate significant difference at $P < 0.05$

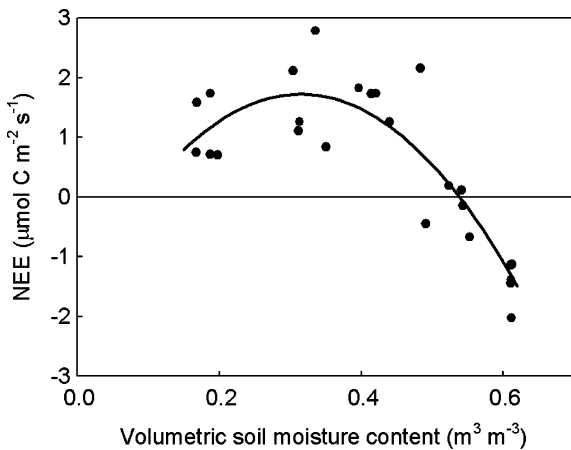
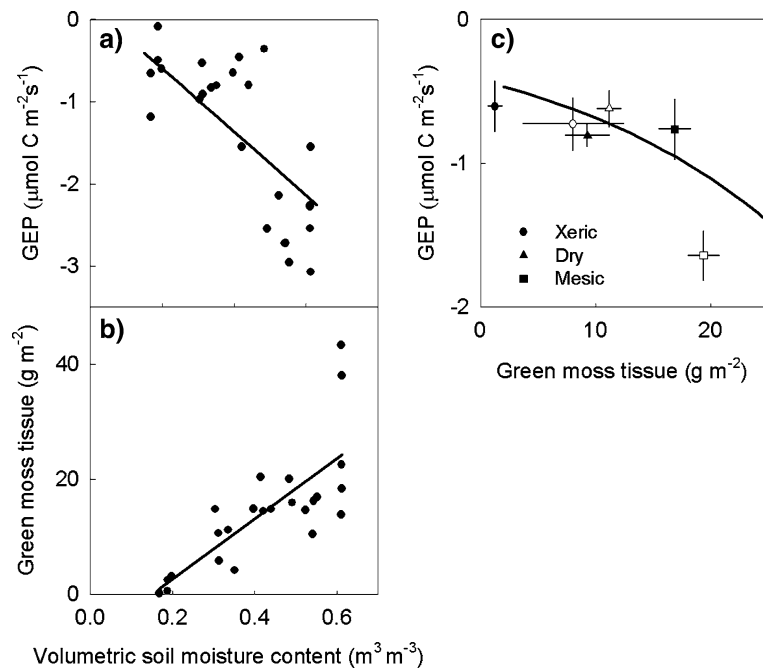


Fig. 2 Relationship between net ecosystem exchange of CO_2 and soil moisture content across the moisture gradient. moisture: $F_{1,2}=21.74$, $P=0.06$; moisture²: $F_{1,2}=13.76$, $P=0.08$

influenced strongly by moving water. Since moisture content and soil temperature were confounded we could not combine the two in a multiple regression. However, when analyzed separately over the gradient they can be compared (i.e. excluding the wettest location) moisture was a much stronger predictor of R_e than soil temperature ($F_{1,2}=123.36$, $P<0.01$ and $F_{1,2}=35.99$, $P<0.05$, respectively). From this we conclude that soil moisture, rather than soil temperature, accounted for trends in R_e . The higher respiration rates at the mesic and moist sites are thus

Fig. 3 (a) Regression between gross ecosystem photosynthesis (GEP) and soil moisture, $F_{1,4}=5.31$, $P=0.09$. (b) Regression between moss biomass (green tissue) and soil moisture, $F_{1,3}=23.89$, $P<0.05$. (c) Relationship between moss biomass (green tissue) and GEP at the three drier sites, including control (filled symbols) and watered (unfilled symbols) plots ($F_{1,3}=144.34$, $P<0.01$)



probably due to a combination of the larger carbon stock and intermediate soil moisture content at these sites. At the three well-drained sites, R_e was strongly linked to GEP, whereas at the wetter sites an increase in GEP (i.e. more negative C flux) resulted in only a modest increase in R_e (Fig. 5).

Laboratory incubation; temperature and moisture response of R_e

R_e increased with temperature, and the temperature response of the cores was similar in magnitude for all three sites. Dry and mesic cores had lower respiration rates than moist cores at all incubation temperatures prior to the wetting (Fig. 6a). Effects of wetting were greatest in the well drained soils with the greatest response and highest absolute respiration rates in the dry soil, followed by the mesic, and then only a minor response in the moist soil (Fig. 6b).

Discussion

Overall patterns in CO_2 fluxes across the moisture gradient

Hydrology was the key control of CO_2 fluxes, explaining the net ecosystem exchange (NEE) of CO_2

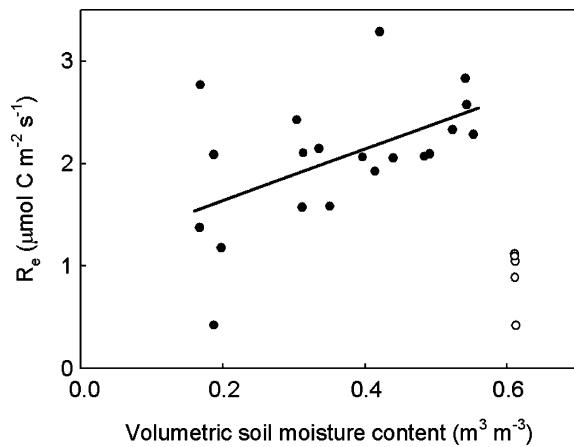


Fig. 4 Linear model of soil moisture as a predictor of ecosystem respiration, $F_{1,2}=123.36$, $P<0.01$). The model excludes the wettest site (unfilled symbols)

by the ecosystems present across the moisture spectra in this high arctic valley. Only the wettest site was a CO_2 sink whilst the well-drained sites were CO_2 sources to the atmosphere. Both photosynthesis and ecosystem respiration varied in response to soil moisture, determining the relationship between NEE and hydrology. Both GEP and R_e were found to be moisture limited; at the mesic site GEP rates increased in response to water addition in the field and R_e increased in both dry and mesic soils after water additions in the laboratory. Previous comparison of NEE between wet and dry sites in the high Arctic, based on eddy correlation measurements showed wet sites being stronger sinks of CO_2 than drier sites

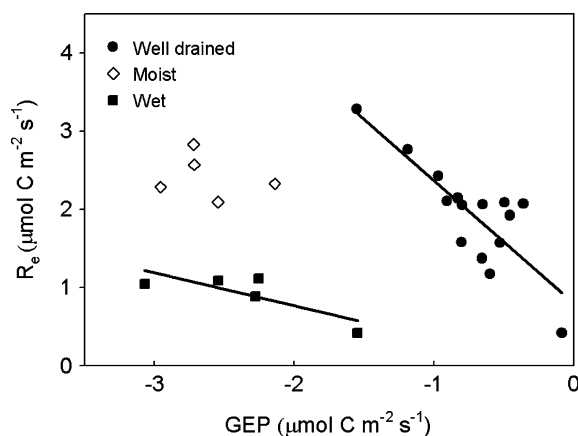


Fig. 5 Regressions describing the relationship between ecosystem respiration and gross ecosystem photosynthesis (GEP) at the wet, moist and well-drained sites. For this analysis the three well-drained sites were combined and three drainage classes were used. $\text{GEP} \times \text{drainage}$: $F_{2,1}=4.59$, $P<0.05$

(Soegaard et al. 2000). In this study we have been able to establish a relationship between NEE and spatial variation in soil moisture in the landscape. Additionally, our data illustrate that in some parts of the high Arctic, the sink strength of wet areas might be balanced by CO_2 emissions from mesic and dry sites.

The importance of water as a control of NEE

Moisture proved to be the strongest driver of NEE across the moisture gradient, and sites switched from being carbon sources to C sinks at around $0.55 \text{ m}^3 \text{ H}_2\text{O m}^{-3}$, providing only a relatively narrow moisture window for ecosystems to act as C sinks. NEE rates at peak biomass for the wettest site in our study are similar to other relatively productive wet areas in the high Arctic (Christensen et al. 2000; Welker et al. 2004). Temperature and light are obviously important as drivers of the vegetation development over the growing season (Fan et al. 1992; Lloyd 2001; Welker et al. 2004), but differences among landscape units with contrasting ecosystems tend to control NEE to a greater extent than seasonal factors (Fan et al. 1992; Oechel et al. 1997; Christensen et al. 2000). Although C cycling in the Arctic may be influenced by a wide range of factors, including nutrient availability, snow accumulation, and biological interactions, our data suggest that small-scale hydrological variation in soil moisture is of overriding importance to the carbon balance. To gain a mechanistic understanding of this control of NEE fluxes within the landscape, the two separate components of NEE, i.e. gross ecosystem photosynthesis (GEP) and ecosystem respiration (R_e), must be considered.

Moisture limitation of GEP

GEP rates showed a substantial shift between the mesic and moist sites with higher assimilation rates at wetter sites. Our data suggest that this strong impact of soil moisture on GEP rates reflects moisture limitations in the moss layer. Indeed, reduction of moisture limitation (by watering) had a particularly strong effect on GEP rates at the mesic site that had a dense moss layer with a drought sensitive surface.

Two interlinked mechanisms are likely to explain the positive response of the bryophytes to increased moisture availability: (i) direct physiological response

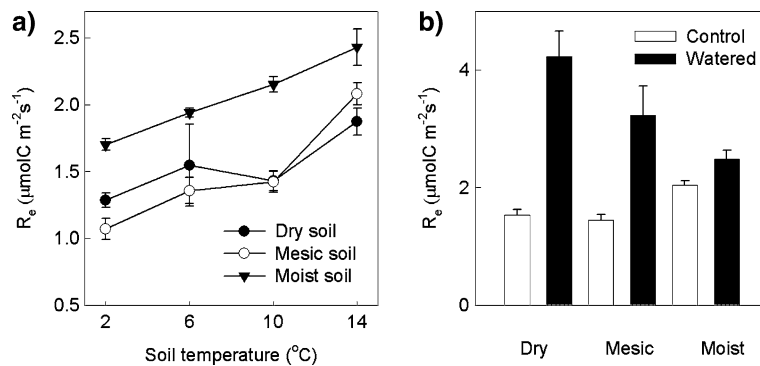


Fig. 6 Ecosystem respiration (R_e) in laboratory-incubated soils from the moist, mesic and dry sites. **(a)** Temperature response in soils at field moisture conditions (site: $F_{2,12}=28.69$, $P<0.001$, **(b)** R_e measured after water addition (site \times water

addition: $F_{2,12}=20.0$, $P<0.001$). The data points are mean values across the temperature range used for the incubation per soil type and corresponding SE

to reduced water stress in the bryophytes increasing their photosynthetic rate (Oechel and Collin 1976; Uchida et al. 2002), and (ii) longer term effects of increased activity leading to increased growth and biomass (Potter et al. 1995). Both of these will result in increased C assimilation. In our study, improved moisture availability over just two summers resulted in increased green biomass of bryophytes, illustrating that bryophytes are an important and responsive component of these systems. In fact, at the driest site the increase in moss biomass was not accompanied by an increase in GEP. This was because biomass had not increased sufficiently to overcome problems of desiccation, and so at the time of CO_2 flux measurement the physiological activity of the moss is constrained. Conversely, at the mesic site the increase in moss biomass was only small, but there was a large increase in GEP due to watering enabling greater physiological activity.

The observed low impact of vascular plants on GEP was most likely due to their small photosynthetically active biomass compared to that of mosses. In more productive tundra-like areas at lower latitudes, vascular plants tend to outcompete bryophytes (van der Wal et al. 2005) and exert greater control on GEP rates (Soegaard et al. 2000; MacFadden et al. 2003). However, at high latitudes bryophytes benefits from having lower light compensation points than vascular plants, especially at low temperatures (Longton 1997). Indeed, a substantial proportion of the CO_2 flux measurements in this study were at light conditions below or just above the light compensation point for arctic

vegetation, and these low light levels are likely to have reduced vascular plant photosynthesis but allowed photosynthesis by mosses to continue (Christensen et al. 1997; Heikkinen et al. 2002; Sommerkorn et al. 1999; Johnson et al. 2000; Muraoka et al. 2002).

On the basis of this study we cannot separate the contribution of the vascular plants and the mosses on GEP, but in a Siberian wetland mosses accounted for 26–31% of the assimilated carbon (Sommerkorn et al. 1999). At our high-Arctic system, mosses may even play a greater role in C assimilation, as is exemplified by the relationship between GEP and mosses, but not vascular plants. Our data thus demonstrate the crucial role of bryophytes in ecosystem carbon assimilation across a wide range of moisture conditions in the high Arctic.

Links between R_e , moisture and carbon availability

Respiration rates were related to soil moisture content in a complex way. Respiration rates were lowest at the driest and wettest sites on the moisture gradient, similar to R_e on a toposequence in Alaska (Giblin et al. 1991), and rates were highest at the moist site where carbon stocks were greatest. Anaerobic conditions, and thus low decomposition rates, are likely to explain the low R_e at the wet site (Christensen et al. 1999; Fang and Moncrieff 1999). At the three driest sites, a large proportion of R_e was linked to plant activity, as also observed by Illeris et al. (2003), suggesting that recently assimilated

carbon is the main component of the CO₂ efflux from well-drained sites.

In contrast to our findings, Mc Fadden et al. (2003) note that in low arctic ecosystems, R_e (measured by eddy correlation) tends to be rather constant among sites with different moisture status over the growing season, and that variation in NEE is primarily caused by different assimilation rates at sites with different moisture status. This is not the case in the high Arctic valley system studied here, where contrasting moisture conditions are reflected in both different respiration and photosynthesis rates.

The lack of response of R_e to the water addition in the field is probably due to the well-drained nature of the field sites that did not allow the soil moisture to increase to a level at which the heterotrophic microbial community could benefit from relieved water stress. The laboratory incubation did indeed show that when the soils were allowed to fully absorb the water applied, respiration rates increased more in the well-drained soils than in the moist soil. Interestingly, soil temperature did not explain variation in R_e between sites, and moisture conditions proved to be of greater influence. The most likely explanation for the overriding effect of soil moisture is the control it exerts on carbon stocks and well as the redox potential in the soil at each site. In general, our data support the conceptual model described by Ostendorf (1996), in which respiration is limited by substrate availability on dry ridges and anaerobic conditions in the wet valley bottoms.

Temporal versus spatial variability

Inter-annual variation is likely to moderate the CO₂ assimilation/efflux of an ecosystem. For example, Lloyd (2001) describes a shift from a net sink to a net source of CO₂ at a polar semi-desert site in response to different levels of cloudiness in two subsequent years. Similarly, the source strength of the three well-drained sites in our study could also be sensitive to changes in weather among years. Indeed, the 2003 and 2004 growing seasons were warm compared to the long-term mean growing season temperature, and 2004 had double the normal precipitation. However, the fact that we obtained a strong relationship between moisture and NEE even in an extremely wet year suggest that the moisture limitation at the drier sites is likely to persist among years. It is likely that the relative dif-

ferences in CO₂ sink/source strength between sites will remain, even if absolute CO₂ fluxes are altered due to inter-annual variation in weather conditions.

Conclusions

In a high Arctic valley, spatial variation in soil moisture strongly influenced ecosystem CO₂ fluxes, with drier sites acting as sources and the wettest site as a sink of CO₂. Moisture controlled GEP through a moisture deficit limiting photosynthesis in the moss layer. The combination of low carbon input to the soil and the moisture deficit appeared to restrict R_e at the dry end of the moisture gradient. Where water saturation occurs, decomposition, and thus R_e , are restricted and organic matter accumulates. Our results illustrate the complex interactions among the components of the CO₂ cycle and moisture conditions, and underline the importance of incorporating small-scale spatial heterogeneity of the hydrology, and resultant vegetation, when modeling the CO₂ fluxes of high latitude regions.

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