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Moisture effects on temperature sensitivity of CO_2 exchange in a subarctic heath ecosystem

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Abstract. Carbon fluxes between natural ecosystems and the atmosphere have received increased attention in recent years due to the impact they have on climate. In order to investigate independently how soil moisture and temperature control carbon fluxes into and out of a dry subarctic dwarf shrub dominated heath, monoliths containing soil and plants were incubated at three different moisture levels and subjected to four different temperature levels between 7 and 20 °C. Ecosystem CO_2 exchange was monitored continuously day and night during the 16 to 18 days that each of three experiments lasted. Additionally, the carbon allocation pattern of the plants was investigated by labelling monoliths with $^{14}CO_2$ followed by harvest of above and below ground plant parts. The results revealed that the three different soil moisture levels caused distinctly differing levels of CO_2 fluxes. Also, both carbon fixation calculated as gross ecosystem production (GEP) and carbon release measured as ecosystem respiration (ER) increased with increasing temperatures, with ER increasing faster than GEP. Hence, short term carbon loss from the ecosystem accelerated with raised temperatures. Temperature sensitivity of the ecosystem was dependent on the soil moisture level, shown by differing Q_{10} values of both GEP and ER at different soil moisture levels. It is therefore highly important to take soil moisture levels into consideration when evaluating responses of ecosystem carbon balance to changes in temperature. The greatest C fixation took place via the two most dominant species of the ecosystem, *Vaccinium uliginosum* and *Empetrum hermaphroditum*, with the former being responsible for the different size of C fixation at the three moisture levels.

Introduction

Arctic land areas cover 5% of the global land surface, but contain 14% of the total terrestrial soil carbon (C) stores (Post et al. 1982), or an amount equivalent to 28% of the total C in the atmosphere (Melillo et al. 1990). Hence, changes of the C balance in the Arctic following climatic changes may be important as they can affect the CO_2 concentration of the atmosphere and thereby provide feedback mechanisms on climate change.

Ecosystem C balance is a function of C fixation through photosynthesis of atmospheric CO_2 by plants, and plant respiration plus heterotrophic decomposition of soil organic matter (SOM), which ultimately results in release of CO_2 to the atmosphere. Temperature followed by soil moisture are considered the primary predictors of CO_2 fluxes in and out of ecosystems (Flanagan and Veum 1974; Heal

et al. 1981; Bowden et al. 1998), but also factors such as SOM quality (Nadelhoffer et al. 1991; Christensen et al. 1999) and nutrient availability (Robinson et al. 1995, 1997; Christensen et al. 1997; Shaver et al. 1998; Johnson et al. 2000; Jonasson et al. 2001) affect the fluxes.

Carbon exchange has been studied extensively in wet ecosystems of the Arctic (Billings et al. 1982; Oberbauer et al. 1991; Oechel et al. 1993, 1995, 1998, 2000; Johnson et al. 1996, 2000; Hobbie and Chapin 1998; Shaver et al. 1998; Soegaard and Nordstroem 1999; Christensen et al. 2000; Soegaard et al. 2000) and, for instance, increased C release has been observed following lowering of the water table in microcosm experiments (Billings et al. 1982; Johnson et al. 1996). However, temperature becomes increasingly important for C release as soils of wet ecosystems dry out (Billings et al. 1982, Oechel et al. 1993, 1995, 2000).

Fewer studies have been performed in the mesic and dry arctic ecosystems (Oberbauer et al. 1996; Christensen et al. 1997; Jones et al. 1998; Illeris and Jonasson 1999; Welker et al. 1999, 2000), which cover 44 and 58% of the low and high arctic ice free land areas, respectively (data from Bliss and Matveyeva 1992). Due to the area extent of these ecosystem types, it is, however, of importance also to study C cycling processes there. In contrast to the wet ecosystems, carbon release is potentially limited by low soil water content, and may decrease under drier conditions as well as increase under wetter conditions than at present (Oberbauer et al. 1996; Illeris and Jonasson 1999).

Soil temperature and moisture usually covary, however, and hence it is difficult to study their influences on CO_2 fluxes independently in the field. For instance, increased temperature is often followed by decreased soil moisture levels due to increased evaporation (Oechel et al. 1993, 1995; Robinson et al. 1995; Illeris et al. submitted), and therefore it is not possible to interpret whether changes in fluxes of CO_2 are due to temperature changes, soil moisture changes, or a combination of the two. Future climate change scenarios uniformly predict temperature increases for most of the Arctic (IPCC 2001), whereas predictions on precipitation patterns and soil moisture regimes vary and are more uncertain (Maxwell 1997; Rowntree 1997). Hence, it is of importance to separate temperature and moisture effects when assessing possible future changes of carbon fluxes.

This study is aimed towards investigating independently how changes in temperature and soil moisture in the short term affects carbon fluxes in a specific dry subarctic ecosystem. We incubated monoliths containing soil and plants from a heath dominated by dwarf shrubs at three different moisture levels for a period of 16 days and exposed them to four temperature levels. CO_2 fluxes were measured continuously both day and night and photosynthesis was calculated as gross ecosystem production (GEP) based on measured daytime net ecosystem production (NEP) and night-time ecosystem respiration (ER). This experimental design allowed us to study processes in a specific ecosystem, which are relevant to the debate on carbon balances connected to global change scenarios. We expected to find enhanced fluxes as temperature increased, and differing temperature responses of GEP and ER with differing moisture levels. Moreover, we investigated whether fixation of C by the different plant species differed among the three moisture levels.

This was done by labelling with ^{14}C by the end of one of the experiments followed by a harvest of above and below-ground plant parts. If we found differing GEP at the different moisture levels, we expected to see a corresponding different C fixation pattern. The advantage of this type of closed environment experimental approach is that a very detailed picture of the specific short-term ecosystem responses may be obtained.

Methods

Monolith sampling

In late August 1999, monoliths of 25 cm × 25 cm and 15 cm deep were taken from a dry *Empetrum hermaphroditum* Hagerup dominated dwarf shrub heath 380 m a.s.l. near Abisko (68°19′N, 18°51′E) in N. Sweden. *Vaccinium uliginosum* L. was subdominant in the vegetation, and mosses were abundant beneath the canopy of the vascular species. The soil consisted of a well developed humus-layer (5–20 cm deep) with an organic matter content of about 90% on top of mineral soil and rocks. It is classified as a gelic gleysol underlain by bedrock consisting mainly of mica schist. The general climate in Abisko (situated 30 m lower in altitude than the sampling site) is subarctic with a mean annual temperature of −0.8 °C, mean July temperature of 11 °C, and a annual total precipitation of 304 mm. The monoliths were collected by inserting aluminum frames into the soil, and cutting around them with a knife, where after the frames containing the monoliths were lifted up. Within a week, the monoliths were transported to Lund University, where they were stored for 11 weeks at 10 °C and 12 h of light. During this period the deciduous species went through senescence and leaf loss. The monoliths were then stored at winter conditions (5 °C and darkness) for an additional period of 3.5 months. Prior to initiation of the manipulations, they were exposed to 10 h of daylight for a period of 3–8 weeks (depending on which experiment the specific monolith were used for) in order to promote budburst. During the entire pre-manipulation period, the monoliths were regularly watered with deionised water.

Experimental setup

Figure 1 shows the experimental set-up. A related type of set-up was also reported on by Christensen et al. (2003). The same experiment was repeated three times (A–C), each time with three new monoliths. In each experiment, the three monoliths were placed in a temperature-controlled room and the plants were exposed to 300 μmol m^{-2} s^{-1} of photosynthetic active radiation 10 h per day. A water bath placed below the lights helped to minimise diurnal temperature variations. Transparent Plexiglas covers were sealed around the monoliths using silicone sealing. Hence, the light level just below the lights was high, but diminished to the mentioned level just above the plants. The volume of the chambers were 12.5 l and they

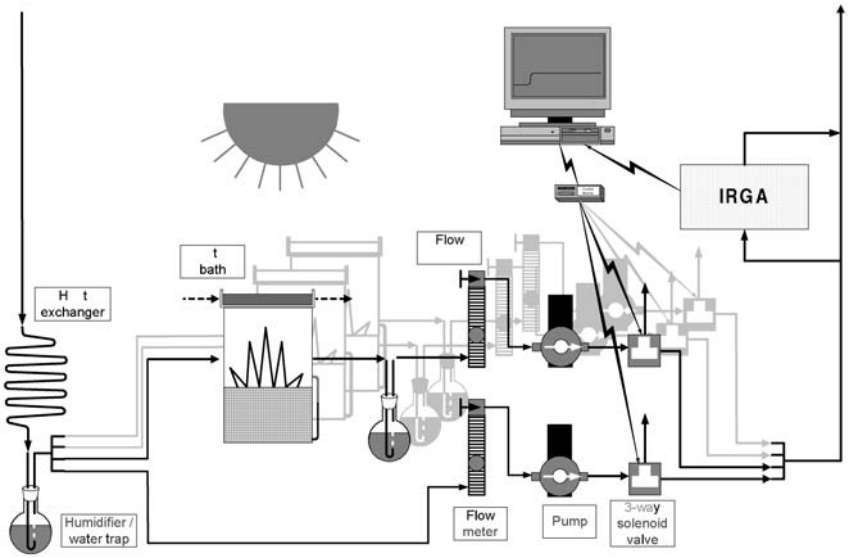

Figure 1. Schematic illustration of the experimental system, the details of which are described in the text. The shaded part indicates the multiple channels operated simultaneously.

were flushed continuously with ambient air at an average flow rate of 800 ml min^{-1}. Thus, the turnover time of air in the chamber was on average 15.6 min. The air humidity was maintained at a constant level (Figure 1). Flowstat, rotameters and solenoid valves controlled the airflow. An infrared gas analyser (PP Systems EGM-2) with a measurement accuracy of $<2\%$ operated continuously and recorded the concentration of CO_2 in the input and output air of all channels with 8 min intervals. The sensitivity of the gas analyser was less than 2 ppm, and the measured concentration differences between incoming and outgoing air was well above 10 ppm. A PC was used for data logging and for controlling the solenoid valves.

Temperature of the laboratory was regulated stepwise every fourth (sometimes fifth) day. During day 1–3, room temperature was 7 °C. The temperature was increased to 10 °C day 4–7, to 15 °C day 8–11, and to 20 °C day 12–15. Air temperatures of the laboratory, chamber air in one of the three chambers, and in the soil at 5 cm depth in each chamber were logged every 8 min by Tinytalk® II Temperature Data loggers.

Soil moisture was manipulated in each of the three chambers in the following way: two of the monoliths were watered regularly with deionised water through a rubber tube, which was placed in a hole in the Plexiglas chamber close to the bottom of the monoliths. The rubber tube was kept air sealed so that no air from outside entered the chambers neither when adding water nor in the time between water additions. One monolith, in the following called the wet monolith, was watered to a level of approximately 2 cm above its base (that is water was standing

13 cm below soil surface). The other monolith, called the mesic monolith, was kept moist only at its base. Two weeks prior to each experiment, watering of the third monolith, called the dry monolith, ceased, and it was not watered at any time during the experimental period. Due to technical problems, soil moisture was only monitored during experiment C. This was done by ThetaProbes (ML2X, Delta-T devices Ltd, Cambridge, UK) inserted into the soil in each of the monoliths, and hourly logging of volumetric soil moisture content (0–6 cm depth) through the experimental period.

^{14}C-labelling

After finishing the temperature cycle in experiment A, 18.5 MBq of $^{14}CO_2$ was added as sodium [^{14}C]bicarbonate (*Amersham Pharmacia Biotech*) solution to each monolith, and phosphoric acid was added to acidify the bicarbonate and release the ^{14}C as $^{14}CO_2$. Labelling was carried out over a 2 h period, after which the chambers where flushed completely. Two days later, above and below-ground plant material was harvested. Above ground plant parts were sorted to species level and divided into green and stem material, and roots were sorted in a fine ($<$1 mm) and coarse ($>$1 mm) fraction. All material was dried and weighed. For the analyses of ^{14}C in the plants, sub samples of all fractions were oxidised in a Packard sample oxidiser, and the CO_2 was trapped in Carbo-Sorb^{R} scintillation cocktail. Scintillation counting was on a Packard Tri-Carb 2100TR liquid scintillation analyser.

Data handling

The repeated replicated experiments A–C, showed comparable logged values of both temperatures and CO_2 concentrations. The statistical handling of the data is, hence, based on all three experiments.

The CO_2 flux of each monolith was calculated from the difference in CO_2 concentrations between incoming and outgoing chamber air and expressed as mg CO_2 m^{-2} h^{-1}. ER was measured as the mean value of the last six CO_2 flux measurements registered during the dark period, that is over a period of 48 min. The CO_2 flux measured when light was switched on represents NEP, and to estimate the photosynthetic component of the flux, that is, GEP, we took the difference between the measured ER and the mean value of the first six measurements of NEP after the system had stabilised at daytime. That is we used values of NEP for calculating GEP after the light had been switched on for ca. 60 min allowing enough time for stabilisation of the photosynthesises rates.

Treatment effects on GEP and ER were tested by repeated measurements ANOVA. Since the same monoliths (experimental units) were exposed to different temperatures, we considered the temperature to be a repeated factor and moisture to be a treatment factor. We considered each experiment (A–C) as a block, which we included if significant to separate possible differences among the experiments from

the treatment effects. Prior to the ANOVA, data were tested for homogeneous variances by Levene's test. All data sets were homogeneous. Data used in the ANOVA were always from the last day that the monoliths were exposed to a certain temperature.

The temperature coefficients (Q_{10}) of GEP and ER were calculated using the standard Arrhenius exponential growth equation (Panikov 1995). This was done for two temperature ranges (5–15 and 10–20 °C). Differences between temperature coefficients in different temperature ranges and of the different moisture treatments were tested with a repeated measurements ANOVA with temperature range as the repeated factor and moisture and block as treatment factors.

All statistical analyses were carried out with SAS (Statistical Analyses System Institute 1997).

Results

Manipulations and CO_2 fluxes

Soil moisture in experiment C was 0.09 $m^3\,m^{-3}$ in the dry chamber, 0.25 $m^3\,m^{-3}$ in the mesic chamber, and 0.30 $m^3\,m^{-3}$ in the wet chamber. The dry chamber became slightly drier (from 0.094 to 0.090 $m^3\,m^{-3}$) during the experimental period as a consequence of evapotranspiration combined with no water addition during the experiment (Figure 2(a)).

Temperatures, both of air and soil, went through diurnal oscillations caused by heating from the light sources when they were switched on during daytime (Figure 2(b)), and hence, day temperatures were always higher than night temperatures. Still, a main temperature level difference was seen in air- and soil temperatures during the experiments, as room temperature was regulated stepwise from 7 to 20 °C (Figure 2(b)). Soil temperatures in the dry monoliths were always higher than in the mesic monoliths, while the wet monoliths had the lowest soil temperatures (Figure 2(b)).

Chamber net CO_2 fluxes followed the same pattern throughout all the experiments (Figure 2(c)). When light was switched on in the morning, the chamber CO_2 concentration decreased rapidly as photosynthesis started. Correspondingly, when light was switched off, the CO_2 concentration increased as only respiration drove the CO_2 exchange in the system. As a consequence of falling temperatures during the night after the lamps were switched off (Figure 2(b)) respiration, and hence the flux rate decreased continuously (Figure 2(c)). Likewise, the respiration increased in the chambers each day as a consequence of rising temperatures after the lamps were switched on.

Treatment effects

As temperature was increased during the experiments, both night and day time fluxes increased (Figure 2(c)), and the calculated ER and GEP increased

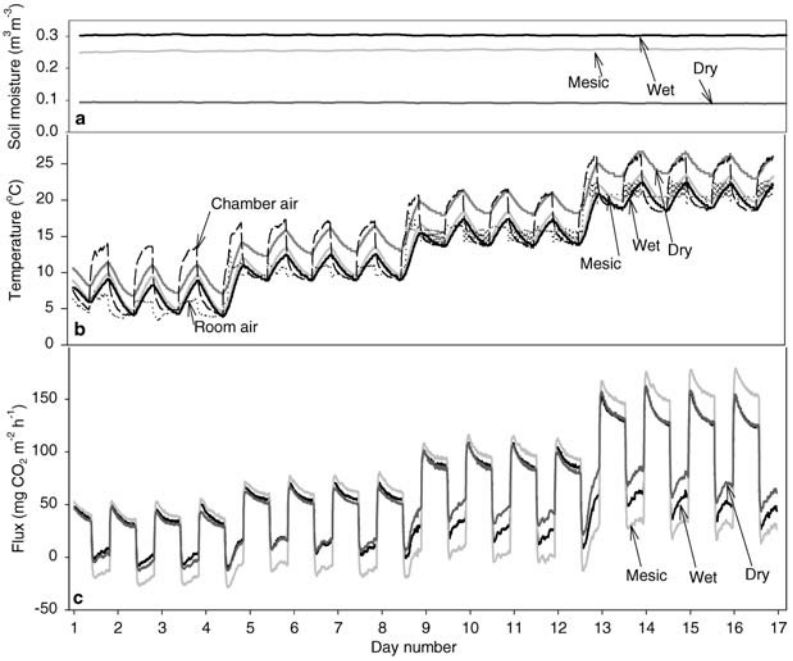

Figure 2. Soil moisture (a), air and soil temperatures (b) and chamber fluxes of CO_2 (c) registered in the three chambers (wet, mesic and dry) during experiment B. Room temperature was set to 7 °C day 1–4, 10 °C day 5–8, 15 °C day 9–12 and 20 °C day 13–17. The very fluctuating room air temperature from day 9 and through the rest of the experiment was due to the thermostat regulating temperature in the laboratory. By convention, negative fluxes means transport of CO_2 into the ecosystem, and positive fluxes transport out of the system.

significantly (Figure 3, Table 1). In all experiments, the night-time flux was always highest and daytime flux was lowest from the mesic monoliths (Figure 2(c)). Hence, the mesic monoliths had both higher respiration and photosynthesis than the dry and wet monoliths (Figures 2(c) and 3), and, seemingly, maximum ER and GEP of the monoliths were found in the mesic chamber. In accordance with this, moisture exerted a significant effect on ER and GEP (Table 1).

Carbon fixation

The major part of fixed C was still found in the green part of the plants in the monoliths after 2 days. Between 16 and 31% of the recovered ^{14}C was in roots (Figure 4(b)), while the recovered ^{14}C in leaves of *V. uliginosum* and *E. hermaphroditum* ranged between 53 and 70% of the totals. The concentration was 20 times higher per gram leaf of *V. uliginosum* than of *E. hermaphroditum* (not shown),

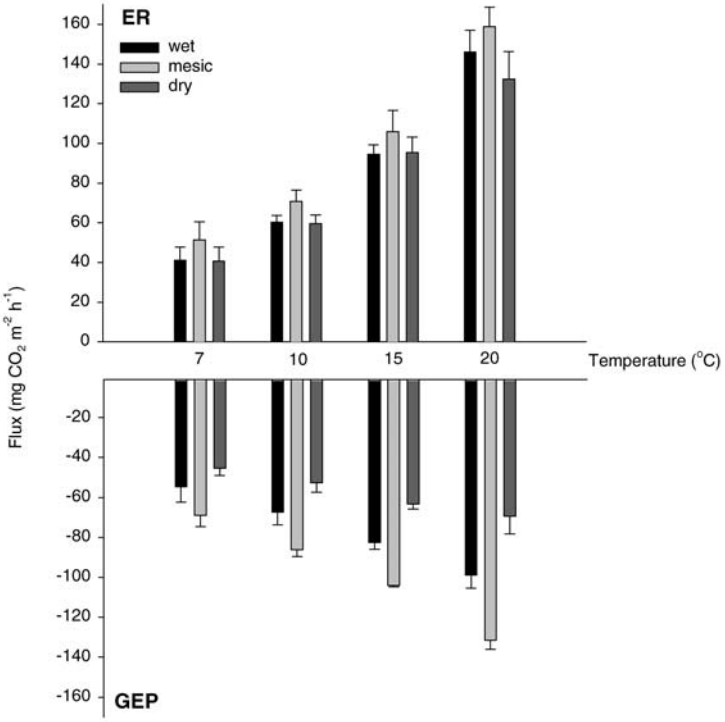

Figure 3. GEP and ER in the three chambers (wet, mesic and dry). Data are means ± S.E. of the three replicate experiments and the calculated values from the last day that each monolith were exposed to a certain temperature. For ER the mean value of the last six measurements at night were used (see Figure 2(b)), and GEP was calculated as the difference of the mean of the last six measurements at night and the mean of the first six measurements after light was switched on each day. Room temperature was set to 7 °C day 1–4, 10 °C day 5–8, 15 °C day 9–12 and 20 °C day 13–16.

Table 1. Repeated measurements ANOVA of the effect of temperature (repeated factor) and moisture on GEP and ER in the monoliths of the 3 experiments.

	df	*P*
GEP		
Temperature	3	*0.0027*
Moisture	2	*0.0003*
Temperature × Moisture	6	0.0664
ER		
Block	2	*0.0061*
Temperature	3	*0.0056*
Moisture	2	*0.0289*
Temperature × Moisture	6	0.9481

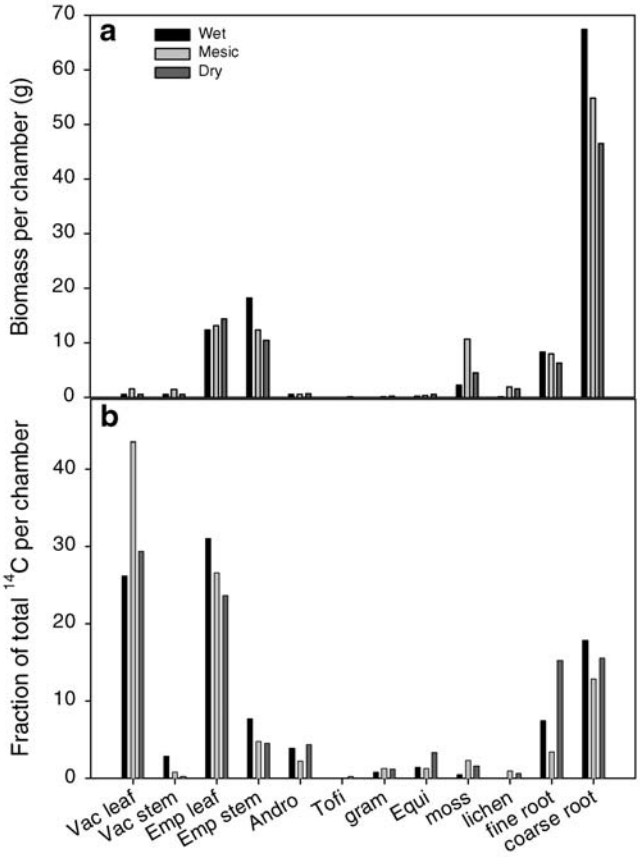

Figure 4. Plant biomass in the three chambers in experiment A (a), and fixed ^{14}C in the above (distributed on species) and below ground plant parts in the wet, mesic and dry monolith (b). Species and plant parts are as follows: Vac leaf, leaves of *V. uliginosum*; Vac stem, stems of *V. uliginosum*; Emp leaf, leaves of *E. hermaphroditum*; Emp stem, stems of *E. hermaphroditum*; Andro, *A. polifolia*; Tofi, *Tofieldia pusilla*; gram, graminoids; Equi, *Equisetum scirpoides*. Fine roots are roots with diameter < 1 mm, coarse roots are roots with diameter > 1 mm.

but the biomass of *E. hermaphroditum* was much higher than that of *V. uliginosum* (Figure 4(a)). In the mesic monolith, which showed highest GEP (Figure 3), *V. uliginosum* accounted for the greatest part of the fixed C, whereas the wet monolith showed greatest C uptake by *E. hermaphroditum*.

Temperature sensitivity of ecosystem CO_2 exchange

Q_{10} values of GEP ranged between 1.16 and 1.63 (Table 2). There was a non-significant difference between the three moisture levels with highest values in the

Table 2. Mean Q_{10} values (±S.E.) of GEP and ER calculated from experiment A–C at two temperature intervals (5–15 °C and 10–20 °C) in wet (*W*), mesic (*M*) and dry (D) monoliths.

	W	*M*	*D*
GEP (5–15)	1.63 ± 0.18	1.63 ± 0.23	1.34 ± 1.16
GEP (10–20)	1.63 ± 0.18	1.41 ± 0.25	1.16 ± 0.07
ER (5–15)	2.64 ± 0.22	2.12 ± 0.52	2.14 ± 0.52
ER (10–20)	2.64 ± 0.22	1.57 ± 0.44	1.57 ± 0.26

wet monoliths and lowest Q_{10} in dry monoliths. In the mesic and dry monoliths, Q_{10} was non-significantly higher in the 5–15 °C temperature interval than in the 10–20 °C temperature interval. The Q_{10} values of ER were higher than those of GEP, ranging between 1.57 and 2.64. There was a significant effect of moisture ($P = 0.01$) on ER with the highest values in the wet monoliths plus higher values at the lower than the higher investigated temperature interval in mesic and dry monoliths (Table 2).

Discussion

Manipulation of moisture and temperature

Despite the larger difference in moisture between the dry and mesic chambers than between the mesic and wet chambers (Figure 2(a)), we obtained three different levels of CO_2 fluxes throughout all temperature levels in the experiment (Figures 2(c) and 3). Likewise, the stepwise room air temperature regulation resulted in stepwise changes in chamber air and soil temperatures (Figure 2(b)), and parallel increases of CO_2 fluxes at each step (Figures 2(c) and 3). We are aware that the higher soil temperature in the dry monolith than in the mesic and wet monoliths (Figure 2(b)) confounds the partitioning of moisture and temperature effects on the fluxes. This effect will add to the effects caused by the pre-set levels of moisture and temperature and could not be eliminated in this particular experimental design. The temperature differences were probably due to a combination of the larger heat capacity and, hence, greater 'thermal inertia' of wet relative to dry soils and more energy being used for evapotranspiration in the wet and mesic monoliths than in the dry monolith. However, we do not see any major problems in this because it mimics the temperature conditions in soils with different moisture contents under natural conditions.

The advantage of this type of controlled environment study is that one may obtain a very detailed picture in the short term of the individual components of ecosystem responses. A disadvantage is that it is difficult to maintain realistic conditions for the monoliths in the long term and, hence, results from this type of study is generally temporally limited.

CO_2 fluxes

The light levels of approximately $300\,\mu mol\,m^{-2}\,s^{-1}$ was lower than the 24 h average summer radiation, but GEP was comparable to values measured *in situ* at midsummer in a comparable dwarf shrub heath nearby (Illeris et al. submitted). Furthermore, ER was within the range of values measured at other dry dwarf shrub heaths in the Abisko area (Christensen et al. 1997, 1998; Illeris and Jonasson 1999), and in Alaska (Oberbauer et al. 1996). We are therefore confident that the CO_2 exchange closely resembled those under natural conditions.

At all temperatures both GEP and ER showed highest values in the mesic chamber with a soil moisture content of $0.25\,m^3\,m^{-3}$, and declined both in the wet chamber with a soil moisture content of $0.30\,m^3\,m^{-3}$, and particularly in the dry chamber held at $0.09\,m^3\,m^{-3}$ (Figure 3). Presumably optimum soil moisture for GEP and ER was approximately $0.25\,m^3\,m^{-3}$. Optimum soil moisture content for decomposition ranges usually between 200 and 500% of the soil dry mass (Heal et al. 1981). The soil volumetric moisture content of $0.25\,m^3\,m^{-3}$ corresponds to 240% of the soil dry mass, which is within this range.

In contrast, the optimum temperatures for GEP and ER were not reached within the temperature range of the experiment, as can be inferred from the continuous rise in both GEP and ER (Figure 3). Photosynthesis of arctic plants has maximum levels at temperatures 7–10 °C higher than the actual summer temperatures (Semikhatova et al. 1992), and maximum levels for ER are considered to be in the temperature range of 20–30 °C (Flanagan and Veum 1974). As the long term mean July temperature at Abisko is 11 °C, maximum photosynthesis of the plants is likely to be around the upper temperature levels of 20 °C used in the experiment, whereas maximum for ER probably is well above the upper temperature used.

Sensitivity to moisture and temperature

Although both ER and GEP were significantly influenced by the soil moisture level (Table 1), it was apparent from for example, the *P*-values in Table 1, that GEP was more sensitive to different moisture levels than ER. Furthermore, the response of GEP to increased temperature was less pronounced in the dry monoliths than in the mesic and wet monoliths (Figures 2 and 3). If photosynthesising plants are subjected to dry conditions, stomata conductance of the leaves is reduced in order to decrease water loss through transpiration, resulting in decreased diffusion of CO_2 to the interior of the leaves, and decreased photosynthetic rates (Ögren and Öquist 1985; Enquist and Ebersole 1994). This probably explains the reduction of GEP in the dry monoliths when temperature increased.

Contrary to the moisture effects, the results suggest that ER is more sensitive to increasing temperatures than GEP. Hence, in the short term, ecosystem carbon balances may change towards increased C release under higher temperatures than at present. This is shown in two ways. Firstly, the increasing net flux each day during the light period (Figure 2(c)) suggests that the light-induced daily increase in

temperature (Figure 2(b)) influenced ER more strongly than it influenced GEP. Secondly, Q_{10} values were higher for ER than for GEP (Table 2), indicating a stronger response of ER than GEP to increasing temperatures. Indeed, it has been suggested that ER increases exponentially with temperature, while GEP has a long flat optimum (Lindroth et al. 1998) and in accordance with our findings, Kirschbaum (1995) found much higher Q_{10} values of soil respiration than of net primary productivity at low temperatures. Additionally, Zamolodchikov et al. (2000) reported a change in the carbon balance from net sink to net source at 14 °C in Russian tundra, due to dominance of respiratory outflux above this temperature.

The sensitivity to temperature changes was also dependent on soil moisture conditions (Table 2), as Q_{10} values for both GEP and ER consistently were highest in the wet monoliths and lowest in the dry monoliths. Moisture dependent Q_{10} values of ER were also found in a forest site by Xu and Qi (2001). In the present study Q_{10} of GEP showed the highest change from the dry to the mesic monolith, whereas the major change in Q_{10} of ER was from the mesic to the wet monolith. Hence, the resulting relative temperature sensitivity of whole ecosystem CO_2 fluxes (Q_{10} of GEP/Q_{10} of ER) was highest in the mesic monolith and lower in both the wetter and the drier monoliths. Hence, the temperature sensitivity of this specific ecosystem differs depending on moisture level. Differing temperature sensitivity of ER and plant respiration have been found in cold and warm soils (Lloyd and Taylor 1994; Kirschbaum 1995; Tjoelker et al. 2001), and may be explained by differing and limiting soil moisture levels in the studied ecosystems. We may conclude that it is of importance to take moisture into consideration when evaluating short-term ecosystem carbon balance responses to changes in temperature and also to other factors affecting CO_2 fluxes such as substrate quality.

Carbon fixation and allocation

As expected, the ^{14}C labelling showed that the greatest part of C-uptake in the ecosystem took place via *E. hermaphroditum* and *V. uliginosum*, the two most dominant species (Figure 4). Also, as expected, the evergreen *E. hermaphroditum* had a lower photosynthetic rate than the deciduous *V. uliginosum* due to its different leaf morphology and leaf longevity than *V. uliginosum*. However, since the biomass of *E. hermaphroditum* in the chambers was much higher than the biomass of *V. uliginosum* (Figure 4(a)), the total C fixation of the two species was almost equal (Figure 4(b)).

In order to minimise water loss from leaves of *E. hermaphroditum*, stomata are placed on the inner surface of the inrolled leaves, and their movements in response to drought are reduced compared with species without inrolled leaves. This probably explains that we did not find any difference in ^{14}C concentration in *E. hermaphroditum* leaves in monoliths kept at different moisture levels. The biggest fraction of C in the mesic monolith was found in *V. uliginosum*, whereas almost no difference between the two species was found in the other monoliths (Figure 4(b)). This indicates that the high photosynthesis found in the mesic monoliths (Figure 3)

was due to C assimilation of *V. uliginosum* only. Contrary to our study, restrained growth of *E. hermaphroditum* has been seen in waterlogged soils (Oberbauer and Miller 1982) and soils with added water (Shevtsova et al. 1997). Also Karlsson (1985) did not find any difference in photosynthesis of *V. uliginosum* after addition of water to a dwarf shrub heath. However, decreased photosynthesis of other deciduous species (*Betula nana and Salix pulchra*) has been found in dry periods (Matthes-Sears et al. 1988). In conclusion these results suggest that CO_2 exchange of some arctic plant species do not react to changed soil moisture regimes over broad intervals. Other species such as *V. uliginosum* in our experiment, and *B. nana* and *S. pulchra* in other experiments (Matthes-Sears et al. 1988), are sensitive to changes in soil moisture and may cause C fixation of whole ecosystems to change under different soil moisture regimes than at present.

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