



The amount and timing of precipitation control the magnitude, seasonality and sources (^{14}C) of ecosystem respiration in a polar semi-desert, northwestern Greenland

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Abstract. This study investigates how warming and changes in precipitation may affect the cycling of carbon (C) in tundra soils, and between high Arctic tundra and the atmosphere. We quantified ecosystem respiration (R_{eco}) and soil pore space CO_2 in a polar semi-desert in northwestern Greenland under current and future climate conditions simulated by long-term experimental warming ($+2^\circ\text{C}$, $+4^\circ\text{C}$), water addition ($+50\%$ summer precipitation), and a combination of both ($+4^\circ\text{C} \times +50\%$ summer precipitation). We also measured the ^{14}C content of R_{eco} and soil CO_2 to distinguish young C cycling rapidly between the atmosphere and the ecosystem from older C stored in the soil for centuries to millennia.

We identified changes in the amount and timing of precipitation as a key control of the magnitude, seasonality and sources of R_{eco} in a polar semi-desert. Throughout each summer, small ($< 4\text{ mm}$) precipitation events during drier periods triggered the release of very old C pulses from the deep soil, while larger precipitation events ($> 4\text{ mm}$), more winter snow and experimental irrigation were associated with higher R_{eco} fluxes and the release of recently fixed (young) C. Warmer summers and experimental warming also resulted in higher R_{eco} fluxes ($+2^\circ\text{C} > +4^\circ\text{C}$), but coincided with losses of older C.

We conclude that in high Arctic, dry tundra systems, future magnitudes and patterns of old C emissions will be controlled as much by the summer precipitation regime and win-

ter snowpack as by warming. The release of older soil C is of concern, as it may lead to net C losses from the ecosystem. Therefore, reliable predictions of precipitation amounts, frequency, and timing are required to predict the changing C cycle in the high Arctic.

1 Introduction

Climatic changes and their effects on terrestrial ecosystems are amplified in the Arctic (Serreze and Barry, 2011). Globally, the Arctic is undergoing the largest temperature increase, with a predicted rise in surface air temperature of $2\text{--}11^\circ\text{C}$ by 2100 (Collins et al., 2013), and permafrost degradation (Romanovsky et al., 2010). A deeper active layer associated with permafrost thaw is affecting the Arctic's surface hydrology: lakes are disappearing (Smith et al., 2005) and river run-off is increasing (Fichot et al., 2013). Other abiotic changes accompanying warming include increasing cold season precipitation, declining duration of snow cover and regionally distinct changes in snow depth (Callaghan et al., 2011), and wetting due to atmospheric transport of moisture into the Arctic (Zhang et al., 2013) and to enhanced sea evaporation resulting from retreating of winter sea ice (Bintanja and Selten, 2014). The implications of these changes for regional biogeochemistry are largely unknown, especially

in the high Arctic ($> 70^\circ \text{N}$), where most non-Alpine tundra ecosystems currently exist within 100 km of the coastline (Bhatt et al., 2010; Post et al., 2013). Its coastal proximity makes this ecosystem particularly vulnerable to changes in summer sea ice extent and the associated warming and changes in precipitation.

Long-term multifactorial climate change experiments are a crucial tool for mimicking the future and for unraveling how coupled abiotic and biotic changes are manifested in the biogeochemistry of terrestrial ecosystems, including high Arctic tundra (Welker et al., 1997; Heimann and Reichstein, 2008). In particular, the cycling of carbon (C) within soils and between the tundra and the atmosphere is only partially understood. Most of our current understanding of soil C dynamics is based on studies of organic soils in the low Arctic (Post et al., 1982; Gorham, 1991; Tarnocai, 2000; Welker et al., 2000; Ping et al., 2008; Tarnocai et al., 2009). Fewer studies have been conducted in the high Arctic (Lloyd, 2001; Welker et al., 2004; Illeris et al., 2003; Huemmerick et al., 2010; Lamb et al., 2011; Christiansen et al., 2012; Henry et al., 2012; Schaeffer et al., 2013).

An estimated 12 Pg of organic C have accumulated in polar (semi-)deserts (Horwarth and Sletten, 2010), which cover approximately one-third of the ice-free Arctic (Wookey and Robinson, 1997; Jones et al., 2000). Changes in the C dynamics of the high Arctic and potential feedbacks to the climate system depend on the balance between enhanced plant fixation and microbial degradation of organic matter and C release (Welker et al., 2004). While no projections are available for the high Arctic only, models estimate emissions between 33 and 508 Pg C from circumpolar permafrost (equivalent to 0.04–1.69 $^\circ\text{C}$ warming) by 2100 (Koven et al., 2011; McDougall et al., 2012; Schneider von Deimling et al., 2012; Schuur et al., 2013). While there is evidence that the high Arctic is going to experience higher temperatures and precipitation levels (Vavrus et al., 2012), to date, only a few long-term field experiments have explored the interactions between a warmer and wetter high Arctic as it affects organism and ecosystem function (Welker et al., 1993; Wookey et al., 1993, 1995; Robinson et al., 1995; Sharp et al., 2013; Lupascu et al., 2014a). Others have typically focused on the consequences of summer warming only, with few studies capable of estimating how the level of warming in the near or longer term might influence tundra function and structure (Welker et al., 1997, 2004; Arft et al., 1999; Lamb et al., 2010; Elmendorf et al., 2012). However, results from these 2 $^\circ\text{C}$ passive warming experiments do not provide a means of forecasting beyond the next decades (Welker et al., 1997), while the Arctic could be warmer by 11 $^\circ\text{C}$ by 2100 (Collins et al., 2013). Furthermore, some studies may suffer from short experimental monitoring periods (Lloyd, 2001; Illeris et al., 2003; Huemmerick et al., 2010). At high latitudes, terrestrial–atmospheric C exchange displays extreme inter-annual variability, which can exceed experimental treatment effects (Lupascu et al., 2014b). Thus, short-term monitoring

can bias the general understanding of the ecosystem response to environmental variations (Grøndhal et al., 2008).

In addition, (semi-)arid ecosystems, such as polar semi-deserts, are very sensitive to changes in precipitation regimes (Cable et al., 2011). Continuous precipitation, or individual but large events, may increase soil water availability due to deeper infiltration of precipitation into soils, which in turn may stimulate net primary productivity, but hinder microbial respiration and nitrogen mineralization if soils become saturated (Knapp et al., 2008; Pouliot et al., 2009). On the other hand, isolated and small precipitation events can trigger large pulses of ecosystem respiration (R_{eco}) (Tang and Baldocchi, 2005; Sponseller, 2007; Vargas and Allen, 2008; Carbone et al., 2011). These pulses have been related to multiple factors, including the amount, seasonality, and intensity of precipitation, the timing between such events, and antecedent soil water content (SWC) (Huxman et al., 2004; Schwinning and Sala, 2004; Jarvis et al., 2007; Carbone et al., 2011). Currently, we do not know how C dynamics and the stability of permafrost C are affected by precipitation frequency.

Measurements of R_{eco} can be used to infer changes in soil C dynamics without compromising soil structure and biota (Heimann and Reichstein, 2008). Measurements of R_{eco} can be used to infer changes in soil C dynamics without compromising soil structure and biota (Heimann and Reichstein, 2008). Understanding R_{eco} seasonal dynamics is key for a deeper comprehension of the interannual variability in ecosystem C budgets (Goulden et al., 1996). In addition, radiocarbon (^{14}C) analysis of R_{eco} is a valuable tool for understanding the decomposition of recent vs. older C. The rapid cycling of recently assimilated C between plants and soil microbes has almost no effect on atmospheric CO_2 levels, but decomposition of older C pools, formerly disconnected from the active C cycle, represents a net addition of C to the atmosphere. Assessing soil C feedbacks to rising atmospheric CO_2 levels thus requires distinguishing of R_{eco} sources, i.e., plants and microorganisms living in the rhizosphere from free-living microbes decomposing soil organic matter (Trumbore 2006, 2009).

In this study, we present measurements of R_{eco} and below-ground CO_2 and their sources conducted over three consecutive summers in a ~ 10 year climate manipulation experiment in northwestern Greenland to address the following questions:

1. How does the natural, short-term variability in summer precipitation (amount and frequency) and previous winter snow affect the magnitude and sources of R_{eco} ?
2. How does a simulated long-term increase in summer rainfall and temperature alter the seasonal patterns of soil CO_2 and R_{eco} fluxes?
3. How do precipitation, irrigation and warming alter the sources of R_{eco} ?

Table 1. Temperature \pm SD and total precipitation (rain + snow, in mm decade⁻¹ of water; \pm SD) trends at Thule airport (THU), Greenland from 1952–2012. Only statistically significant trends are reported. Errors correspond to $+/-1\sigma$, or a 68 % confidence level.

Period Year	Annual	Mean temperature		Annual	Total precipitation	
		Summer (JJA) °C decade ⁻¹	Winter (DJF)		Summer (JJA) mm decade ⁻¹	Winter (DJF)
1952–2012	0.28 \pm 0.06	0.26 \pm 0.09	0.22 \pm 0.17	–	4.20 \pm 1.75	–
1962–2012	0.44 \pm 0.08	0.63 \pm 0.11	–	–	5.76 \pm 2.28	–
1972–2012	0.79 \pm 0.10	0.79 \pm 0.15	0.87 \pm 0.33	18.00 \pm 5.80	10.95 \pm 3.15	6.09 \pm 2.03
1982–2012	0.95 \pm 0.15	0.55 \pm 0.23	1.47 \pm 0.48	23.36 \pm 9.90	10.08 \pm 5.39	8.74 \pm 3.42
1992–2012	1.80 \pm 0.26	1.69 \pm 0.37	2.90 \pm 0.71	48.30 \pm 20.74	20.05 \pm 10.90	15.40 \pm 7.20

Addressing these temporally detailed questions complements our earlier report that focused on the annual C budgets of these systems (Lupascu et al., 2014a).

2 Material and methods

2.1 Site description

This study was carried out in a polar semi-desert in the high Arctic of northwest Greenland near Thule US Air Force Base (76°32' N, 68°50' W; 200–350 m a.s.l.). Here, prostrate dwarf-shrub tundra occupies approximately 8 % of the ice-free Arctic land surface (Walker et al., 2005). At our site, vascular plant cover is approximately 50 %, and the patterned ground is a mixture of nonsorted nets, weakly formed stripes and frost boils with a patchy cryptogamic crust. The vascular plant community is dominated by the deciduous dwarf shrub *Salix arctica* Pall., the graminoid *Carex rupestris* All., and the wintergreen dwarf shrub *Dryas integrifolia* Vahl. The live biomass and litter of these three species account for approximately 70 % of vascular plant cover.

The soil is a Typic Haploturberl (USDA, 1999) with a maximum thaw depth of about 1 m. Within the top 40 cm, soil bulk density is approximately 1.1 g cm⁻³, and the soil organic C content varies between 0.2 and 1.6 % in mass for vegetated areas and between 0.1 and 0.2 % in mass for bare areas.

2.2 Climate change experiment

Measurements were conducted from the middle of May to the end of August during the period 2010–2012 in a long-term climate change experiment established in 2003 to mimic climate scenarios of 2030 and 2050 (Sullivan et al., 2008; ACIA, 2005). The experiment consists of four treatments in a randomized complete block design: +2 °C soil warming by infrared radiation (+2 °C), +4 °C soil warming (+4 °C), and irrigation (*W*) and +4 °C soil warming \times irrigation (+4 °C \times *W*) alongside an ambient climate control. Each treatment regime and each control plot were about 5 m apart from each other, with a sample size of $n = 1 - 3$ per

treatment. Each year we initiated warming during the first week of June, when the plots are about 50 % snow free, and we maintained it to the end of August. We used irrigation (+2 mm of deionized water every week in June and August, and +4 mm in July) to increase the magnitude of growing season precipitation by approximately 50 % (relative to 1971–2000), while maintaining seasonal patterns (Sullivan et al., 2008). The plots (2.0 \times 0.8 m²) were oriented to span the transition between vascular plants and bare soil/cryptogamic crust, so that each comprised approximately 50 % of the plot area, to facilitate scaling from the plot to ecosystem level.

2.3 Climate trends 1952–2012

We used temperature and precipitation data from the Thule airport (THU) weather station for the period 1952–2012. Daily mean temperatures were calculated as the mean of the daily minimum and maximum temperatures. We calculated annual, summer (June, July, August), and winter (December, January, February) temperature and total precipitation (rain-fall plus snow) trends for the most recent climate normal period (1983–2012). In addition, to evaluate how temperature and precipitation changed during the entire 61-year period, we calculate the same trends for the last 20, 30, 40, 50 and 60 years, corresponding to 1992–2012, 1982–2012, 1972–2012, 1962–2012, and 1952–2012, respectively, and we estimated how the trends over the shorter recent periods compare with the longer ones (Table 1). We used linear least square fit and regression line trend analysis to evaluate change for the various overlapping periods and on the latest climatological normal period. All reported trends are acknowledged to be significant if they exceed one standard deviation (1σ) of the respective data set.

2.4 Ecosystem respiration fluxes and soil pore space CO₂ concentrations

We measured R_{eco} and soil CO₂ concentrations approximately 2–3 times a week between 10:00 and 13:00 local time. Ecosystem respiration was measured using opaque, dynamic chambers (30 cm i.d., 8 L volume). This method has been used for decades and its limitations have been widely

discussed in the literature (e.g., Davidson et al., 2002). Chamber bases were inserted at the beginning of each measurement season to about 2 cm in depth, sealed with soil material on the outside, and left in place for the entire sampling season. Vegetation was not clipped. We quantified CO₂ emissions by circulating the air in the chamber's headspace between the chamber and an infrared gas analyzer connected to a data logger (LI-840, LI-1400, LI-COR Biosciences, Lincoln, NE, USA) at a rate of 0.5 L min⁻¹. Emission rates were calculated from the slope of time vs. CO₂ concentration curves using a linear regression.

We used the daily R_{eco} measurement (10:00–13:00 LT) as a proxy for mean daily R_{eco} (based on measurements taken every six hours once per month), because of the high correlation between the two ($r^2 = 0.90$). When daily measurements were missing, we estimated daily R_{eco} values using the relationship between respiration and temperature (Lloyd and Taylor, 1994), described by the Arrhenius-type Eq. (1), where the effective activation energy for respiration varies inversely with temperature:

$$R_{\text{eco}} = Ae^{\frac{-E_0}{(T-T_0)}}, \quad (1)$$

with $E_0 = 308.56$ K and $T_0 = 227.13$ K, and where A is a data-set-dependent variable. Variable A was first obtained from the R_{eco} data collected in situ. We hence calculated the daily R_{eco} for the missing days using the average daily temperature (T). We estimated cumulative summertime R_{eco} as the sum of the daily values.

We monitored soil CO₂ concentrations using vertical, stainless steel gas wells (0.35 cm i.d., 0.6 cm o.d.) inserted into the soil to 20, 30, 60 or 90 cm in depth and closed off with rubber septa (Blue Septa, Grace, Deerfield, IL, USA). Wells were installed ($n = 1 - 2$ per treatment) from the soil surface in 2010 as soon as the thaw of the active layer allowed for it, and these remained in the same location throughout the entire study period, including the winters. Soil gas was obtained with 60 mL syringes (BD, Franklin Lakes, NJ, USA). We collected soil gas using 6 mL syringes (BD, Franklin Lakes, NJ, USA). We discarded the first 60 mL sample and injected the second into an infrared gas analyzer connected to a data logger (LI-800, LI-1400, LI-COR). We then manually recorded the peak concentration.

2.5 Soil temperature and water content

With each R_{eco} measurement, we manually recorded soil temperature with a digital thermometer (15-077, Thermo Fisher Scientific, Waltham, MA, USA) at 5 and 10 cm depth and SWC at 10 cm (Hydrosense, Campbell Scientific, Logan, UT, USA). In the vegetated plots, we also continuously monitored SWC at 5 cm in depth with Hydra II soil moisture and salinity sensors (SDI-12/RS485, Stevens, Portland, OR, USA) connected to a CR1000 data logger (Campbell Scientific). Data were acquired every 15 min.

2.6 Sampling for isotope analyses

We collected gas samples for isotope analysis monthly. To sample R_{eco} , we left the chambers closed until the CO₂ concentration inside the chamber was $\geq 2\times$ that of ambient air (up to 24–48 h). After each concentration measurement, the CO₂ was collected by circulating the air inside the chamber through drierite (W.A. Hammond Drierite Co. Ltd., Xenia, OH, USA), followed by a pre-conditioned, activated molecular sieve (13X powder-free 133 8/12 beads, Grace) trap at a rate of 0.5 L min⁻¹ for 15 min (Gaudinski et al., 2000). Compared to other methods used to trap CO₂ in the field (e.g., Dörr and Münnich, 1986; Charman et al., 1999), small, light-weight molecular sieve traps are ideal for use in remote field locations, as they do not require cryo- or caustic liquids. Small ¹⁴C memory effects can be overcome by pre-conditioning traps (630 °C for 45 min under vacuum) and sampling enough CO₂ in the field (0.3–2 mg C). For each set of R_{eco} samples, we collected two samples of CO₂ from ambient air on a molecular sieve (15 min at 0.5 L min⁻¹) in a well-ventilated area nearby the experimental site. Soil gas from the different depths was collected in pre-evacuated, stainless steel canisters via flow-restricting stainless steel capillaries (0.010 × 0.063 × 30 cm, Fisher).

2.7 Isotope analyses of CO₂

Radiocarbon analysis is a valuable tool for understanding the sources of R_{eco} (respiration of plants vs. microbes). Plants respire CO₂ with a ¹⁴C content that is similar or slightly enriched compared to atmospheric CO₂. Soil microbes respire a range of C sources that vary in age from days to millennia. Due to radioactive decay, older soil organic matter is depleted in ¹⁴C ($t_{1/2} = 5730$ years). By contrast, CO₂ derived from the decomposition of soil C made from photosynthetic products this year to ~60 years ago is enriched in ¹⁴C. This is because during the late 1950s and early 1960s, testing of nuclear bombs above ground almost doubled the naturally produced ¹⁴C activity in atmospheric CO₂. Since test cessation, the amount of bomb ¹⁴C (a.k.a. “modern” C) in the atmosphere has been declining as a consequence of mixing with terrestrial and ocean C pools and dilution of fossil fuel CO₂ emissions (i.e., ¹⁴C free). The mixing of this bomb ¹⁴C tracer into terrestrial C pools over the last five decades can be used to infer C dynamics (Trumbore, 2006).

In order to analyze the ¹⁴C content, CO₂ is released from molecular sieve traps by baking at 630 °C for 45 min, or extracted from canisters using a vacuum line, purified cryogenically, and converted to graphite using sealed tube Zn reduction (Xu et al., 2007). A split of the CO₂ is analyzed for its $\delta^{13}\text{C}$ value (GasBench II, DeltaPlus, Thermo). The ¹⁴C content of the graphite is measured with the use of accelerator mass spectrometry (NEC 0.5MV 1.5SDH-2 AMS) at the KC-CAMS laboratory at UC Irvine (Southon and Santos, 2007). Data are reported relative to NIST OX-I (SRM 4990a) and

Table 2. Cumulative precipitation and mean air temperature (\pm SD) at Thule airport (THU) for the measurement period.

		Precipitation (mm)			Average T ($^{\circ}$ C)		
		2010	2011	2012	2010	2011	2012
Snow	Sep–May ^a	1104.9	1505.8	1306.8	n.d.	n.d.	n.d.
Rain	May	5.8	9.9	53.1	−1.9 (3.7)	−4.7 (4.4)	−3.8 (3.7)
	Jun	5.1	0.3	34.5	2.9 (2.8)	3.6 (3.0)	3.6 (3.3)
	Jul	48.0	19.6	50.0	6.6 (1.8)	8.7 (2.0)	7.6 (1.6)
	Aug	25.9	6.9	23.6	6.9 (1.5)	6.0 (2.2)	4.6 (3.3)
	Jun–Aug ^b	84.8	36.7	161.3	5.3 (2.8)	6.1 (3.1)	5.3 (3.3)

^a Preceding winter; defined as snow pack height, not water equivalent. ^b Cumulative values for the snow-free period. n.d. means “not determined”.

OX-II (SRM 4990c) following Stuiver and Polach (1977). The measurement uncertainty for $\Delta^{14}\text{C}$ is 2–3 per mill.

The ^{14}C content of R_{eco} is corrected for the amount of CO_2 from ambient air present in each chamber:

$$\Delta^{14}\text{C}_{\text{cor.}} = \frac{\Delta^{14}\text{C}_{\text{obs.}} - (f_{\text{air}} \times \Delta^{14}\text{C}_{\text{air}})}{(1 - f_{\text{air}})}, \quad (2)$$

with ($\Delta^{14}\text{C}_{\text{cor.}}$) being the actual ^{14}C content of R_{eco} , ($\Delta^{14}\text{C}_{\text{obs.}}$) the measured ^{14}C content of R_{eco} , ($\Delta^{14}\text{C}_{\text{air}}$) the measured ^{14}C content of ambient CO_2 , and (f_{air}) the fraction of CO_2 derived from ambient air, calculated as the ratio of CO_2 concentrations inside the chamber immediately before trapping to the CO_2 concentration in the atmosphere.

2.8 Statistical analyses

Control and treatment plots had a sampling size of $n = 1 - 3$. Our sample for vegetated areas consisted of a total of 960 observations for R_{eco} , with the control plot as an experimental unit. We conducted a two-way analysis of variance (ANOVA) to examine the fixed effects of measurement year (2010, 2011, and 2012), treatment type (control +2 $^{\circ}$, +4 $^{\circ}$ C, W and +4 $^{\circ}$ C \times W), plot type (vegetated vs. bare areas), and the interaction of the four on R_{eco} . The same analysis was applied for SWC, soil temperature at 5 cm, pore space CO_2 and ^{14}C analyses.

3 Results

3.1 Climate and weather

Data from the Thule operations site showed a mean annual air temperature of $-11.4 \pm 1.3^{\circ}\text{C}$ and mean annual total precipitation of 122.6 ± 45.4 mm during the period 1952–2012. About half of the precipitation occurred from October to April as snow.

Table 1 shows annual, summer and winter temperature and total precipitation linear trends for the past 20, 30, 40, 50, and 60 years; all trends were significant at the 1- σ level. Annual temperature and total precipitation trends for shorter recent

periods were larger, indicating both accelerated warming and precipitation during the entire 60-year period (Supplement Figs. 1, 2). Overall temperature increased more during the winter months. We observed a significant and consistent increase in total summer precipitation trends, while in winter, precipitation trends were very variable.

During the last climate normal period (1983–2012), the air temperature trend was $1.0 \pm 0.2^{\circ}\text{C decade}^{-1}$, with the strongest warming of $1.5 \pm 0.5^{\circ}\text{C decade}^{-1}$ during the winter months. During the same normal period, we found a large positive trend in total annual precipitation, with the strongest increase of 10.1 ± 5.3 mm decade $^{-1}$ observed during summer.

The three years of this study showed very variable weather conditions (Table 2). Cumulative summer precipitation varied by a factor of 4 from 2010 to 2012, with the largest values in 2012 and the lowest in 2010. The maximum values of cumulative snowfall were observed in the winter of 2010/2011. Average summer air temperature was highest in 2011, with the maximum difference observed in July (+1–2 $^{\circ}$ C); similar temperatures were observed in 2010 and 2011.

3.2 Soil water content

We found that interannual differences ($F = 147$; $P < 0.0001$) in snowfall and summer precipitation patterns have a strong influence on the seasonal SWC pattern (Fig. 1b, d, f). At the beginning of the growing season, SWC was strongly coupled to snowfall, with higher values in 2011 and 2012 than in 2010. In July and August, SWC was driven by rainfall regimes, with the highest average summer SWC observed in 2012 ($31.8 \pm 3.7\%$ vol.), compared to 2010 and 2011 (15.1 ± 4.4 and $17.2 \pm 4.4\%$ vol.). Weekly irrigation (W and +4 $^{\circ}$ C \times W) increased average summer SWC ($F = 2.5$; $P < 0.001$) by $+3.8 \pm 1.4\%$ vol. relative to the control, but did not change the seasonal pattern. Induced lamp warming (+2 $^{\circ}$ C) did not affect SWC. In the +4 $^{\circ}$ C treatment, SWC tended to be lower compared to control conditions, but it was not statistically significant.

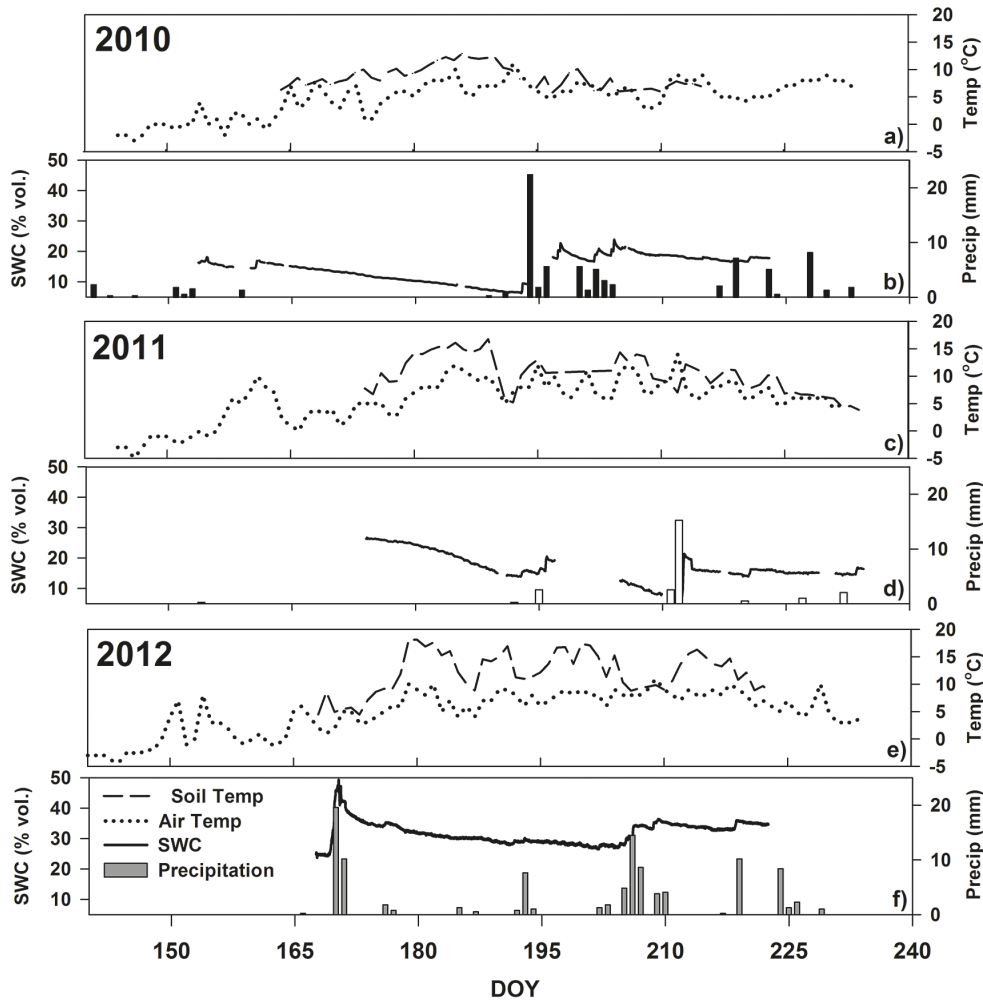


Figure 1. Seasonal patterns of soil temperature and SWC along with precipitation and air temperature in 2010 (a, b), 2011 (c, d) and 2012 (e, f).

3.3 Soil Temperature

Soil temperatures at 5 cm showed a significant difference between years (Fig. 1a, c, e; $F = 38.8$, $p < 0.001$), with 2011 being the warmest (10.0 ± 0.4 °C; control plot) and 2010 the coldest (7.7 ± 0.4 °C; control plot).

Induced lamp-warming $+2$ °C, $+4$ °C, and $+4$ °C \times W had a strong effect ($F = 13.0$, $p < 0.001$) on our experimental plots, altering soil temperature compared to control conditions. The $+2$ °C (9.7 ± 0.3 °C), $+4$ °C (10.6 ± 0.3 °C) and $+4$ °C \times W (10.7 ± 0.3 °C) treatments showed overall warmer soil temperatures ($P < 0.001$) than the control (8.9 ± 0.3 °C). Irrigation (8.5 ± 0.2 °C), on the other hand, while marginally decreasing soil temperature, was not statistically different from the control plot.

3.4 Rates of ecosystem respiration

Ecosystem respiration was consistently affected by changes in seasonal, interannual and experimental changes in precipitation and air temperature. In 2010, we started measurements on DOY 151, a couple of weeks after snowmelt commenced, and we divided the season into two distinct periods, dry and wet. From the beginning of June (DOY 151) to the middle of July (DOY 195), R_{eco} fluxes were low and stable (control: 0.28 ± 0.11 $\mu\text{mol C m}^{-2} \text{s}^{-1}$), and became larger during the second half of the season (control: 0.60 ± 0.29 $\mu\text{mol C m}^{-2} \text{s}^{-1}$; Fig. 2a). In the following years (2011, 2012), R_{eco} fluxes followed a different seasonal pattern, with a similar-sized maximum in July (control: 2.36 ± 0.18 $\mu\text{mol C m}^{-2} \text{s}^{-1}$; Fig. 2a). During all years, bare areas displayed similar seasonal patterns as vegetated areas, but with reduced R_{eco} fluxes (< 1 $\mu\text{mol C m}^{-2} \text{s}^{-1}$; Supplement Fig. 3a, b, c).

Point measurements of soil conditions indicated that in the control (Fig. 2b) and all treatments (Supplement Fig. 4),

Table 3. Cumulative summertime R_{eco} fluxes from high Arctic tundra in 2010–2012 under four treatments (+2 °C, +4 °C, +4 °C × W and W) and control (average ± SE (standard error), $n = 1–3$).

	2010 g C m ⁻² summer ⁻¹	2011 g C m ⁻² summer ⁻¹	2012 g C m ⁻² summer ⁻¹
Vegetated			
Control	36.1 (10.1)	81.9 (6.2)	126.4 (n.a.)
+2 °C	50.8 (19.6)	106.2 (20.5)	189.1 (n.a.)
+4 °C	41.4 (13.9)	98.2 (16.2)	158.0 (n.a.)
+4 °C × W	52.0 (0.4)	119.9 (2.5)	188.1 (n.a.)
W	55.2 (7.9)	134.2 (10.9)	172.9 (15.2)
Bare			
Control	4.9 (2.5)	12.7 (7.5)	20.4 (n.a.)
+2 °C	8.3 (1.4)	14.3 (1.5)	23.8 (n.a.)
+4 °C	7.9 (2.1)	12.2 (6.4)	24.4 (n.a.)
+4 °C × W	10.3 (3.4)	17.7 (6.2)	15.9 (n.a.)
W	8.9 (1.3)	12.7 (4.8)	13.0 (0.9)

n.a. means “not available”.

R_{eco} fluxes were positively correlated with soil temperature ($R^2 = 0.57 \pm 0.13$). Episodic cold snaps, commonly associated with summer rainfall events, dramatically reduced R_{eco} fluxes within a few hours (Fig. 2a; Supplement Fig. 3) because of a negative correlation of daily R_{eco} with SWC ($R^2 = 0.37 \pm 0.11$) (Fig. 2c). Ecosystem respiration fluxes were highest at 10–15 % SWC (Fig. 2c).

All experimental treatments ($F = 28.0$, $p < 0.001$) increased R_{eco} fluxes relative to the control (Table 3), without changes in seasonal patterns (Supplement Fig. 3). Irrigation (+51 ± 14 %) and +4 °C × W (+46 ± 2 %) had a positive effect on R_{eco} ($p < 0.001$). Remarkably, warming by +2 °C (+40 ± 10 %; $p < 0.001$) increased R_{eco} more than warming by +4 °C (+20 ± 5 %; $p < 1$). In all treatments, cumulative summer R_{eco} was highest in 2012 (e.g., control 126 g C summer⁻¹) compared to 2011 (81.9 ± 6.2 g C summer⁻¹) and 2010 (36.1 ± 10.1 g C summer⁻¹) ($F = 714.0$, $p < 0.001$).

3.5 Soil pore space CO₂ concentrations

Pore space CO₂ concentrations were strongly affected by changes in SWC due to snowmelt, natural precipitation and experimental water addition, and by air temperature changes, but not by experimental warming (Fig. 3). With depth, CO₂ concentrations increased to 60 cm, followed by a decrease toward the permafrost table (Fig. 3, middle panel). Throughout the season, CO₂ concentrations displayed a first peak during the snowmelt (with the exception of 2010, when we missed the snowmelt) and other various peaks associated with maximum air temperatures and active layer depth and small precipitation events (Fig. 3, top panel). The magnitude of the

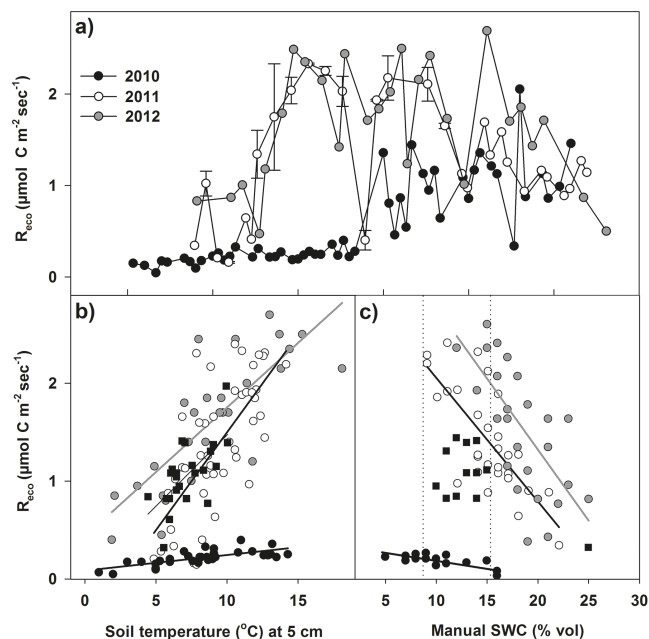


Figure 2. Seasonal patterns and correlations of ecosystem respiration (R_{eco}), soil water content (SWC) and soil temperature under control conditions (average ± SE, $n = 1–3$ plots) during the summers of 2010–2012: (a) daily R_{eco} flux, (b) correlation between daily R_{eco} flux and soil temperature at 5 cm in depth measured manually during the flux measurement, and (c) correlation between daily R_{eco} flux and SWC at 5 cm in depth measured manually during the flux measurement. (In (b) and (c), black circles indicate the early, dry period. Black squares indicate the late, wet period of the summer of 2010.)

snowmelt peak between years implies a positive correlation with snowpack.

Irrigation (W, +4 °C × W) had the strongest effect on pore space CO₂ concentrations ($p < 0.001$). For instance, we observed higher concentrations at all depths (e.g., 2011, +4 °C × W: 2900 ± 522, 8845 ± 419, and 5577 ± 350 ppm for 30, 60, and 90 cm, respectively) compared to the control (e.g., 2011 control: 4488 ± 323, 3681 ± 266, 3248 ± 217 ppm), except at 90 cm in 2010 (Fig. 3, middle panel). On the other hand, experimental warming (+2, +4 °C) marginally increased CO₂ only in the upper mineral soil, while at greater depth concentrations, it was similar to or lower than in the control.

Carbon dioxide concentrations at depths showed little variation between years compared to the three-fold differences in R_{eco} observed between 2010, 2011 and 2012. However, 2010 exhibited the lowest CO₂ concentrations compared to 2011 and 2012 (Fig. 3, middle and bottom panels).

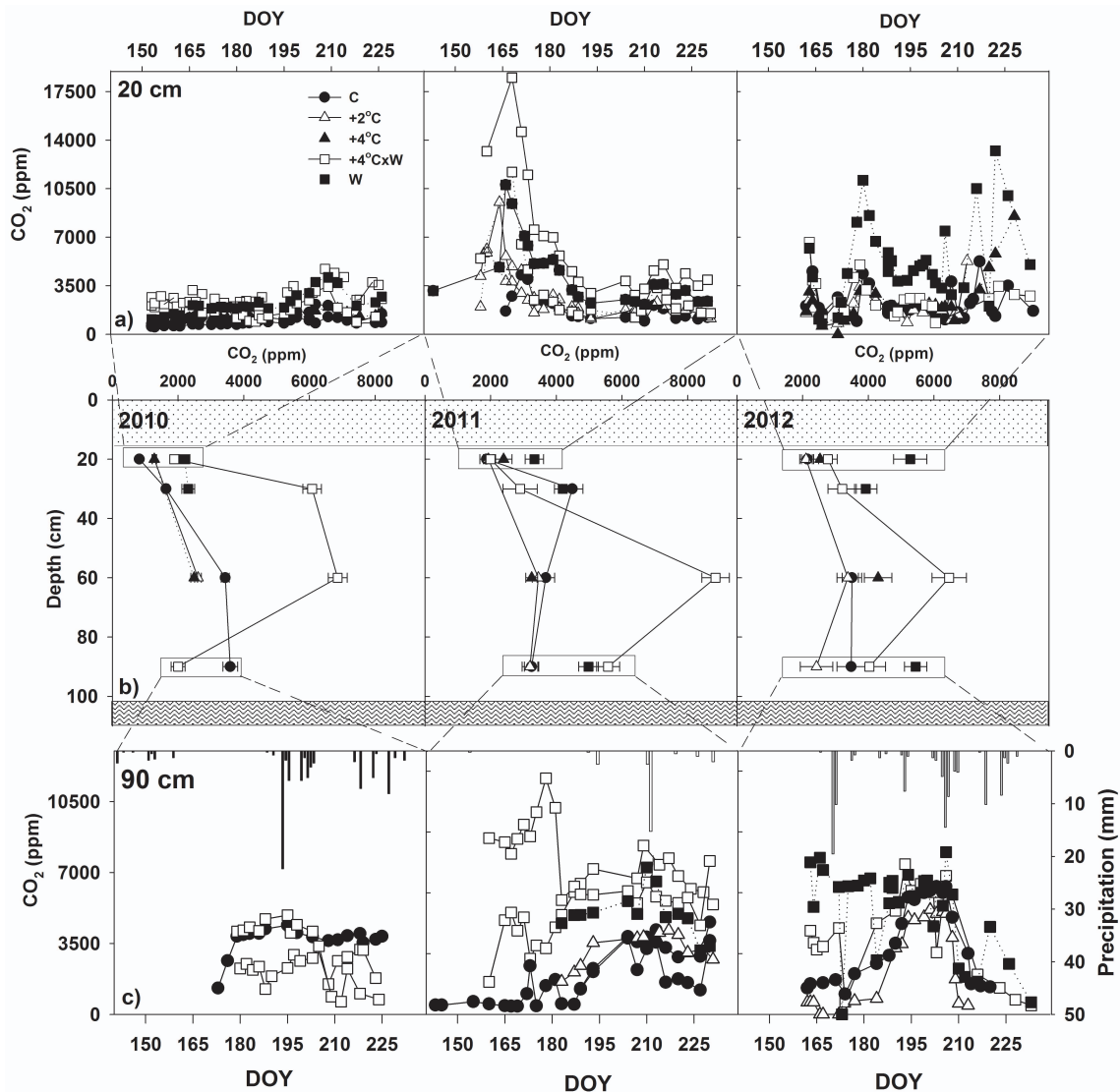


Figure 3. Middle panel: seasonal mean of pore space CO_2 concentration along the soil profile for the four treatments ($+2^\circ\text{C}$, $+4^\circ\text{C}$, $+4^\circ\text{C} \times W$ and W) and control over the sampling years 2010–2012 (hatched areas represent the estimated rooting zone, zig-zag areas represent the permafrost table). Top panel: pore space CO_2 concentration at 20 cm depth. Bottom panel: pore space CO_2 concentration at 90 cm depth and seasonal precipitation pattern.

3.6 Sources of ecosystem respiration

The ^{14}C content of R_{eco} showed large differences between bare and vegetated areas and between years, but only minor variations from month to month and between treatments (Fig. 4). We found significant differences ($F = 51.8$, $p < 0.001$) between bare (e.g., control 32.8 ± 10.5 , -23.6 ± 8.3 , and 20.6 ± 3.1 per mill in 2010, 2011, and 2012, respectively) and vegetated plots (e.g., control 51.8 ± 10.0 , 30.8 ± 4.9 , and 54.1 ± 9.5 per mill in 2010, 2011, and 2012, respectively), with the vegetated areas emitting younger C at all times.

During snowmelt, a complex mixture of C sources contributed to R_{eco} , including (1) older C, fixed before 1950 (up to -339 per mill), (2) modern C, fixed decades ago (up to $+162$ per mill), and (3) current year photosynthates ($+35$, $+32$, $+29$ per mill in 2010, 2011, and 2012, respectively). In July and August, the period that corresponds to maximum above- and below-ground plant growth is dominated by modern C.

However, we found that episodically very old C can dominate R_{eco} (Fig. 4). These pulses of ancient C efflux appeared to be associated either with freeze–thaw cycles during spring or with rain pulses during summer. After about seven days of no rain, small rainfall pulses (< 4 mm) resulted in emissions

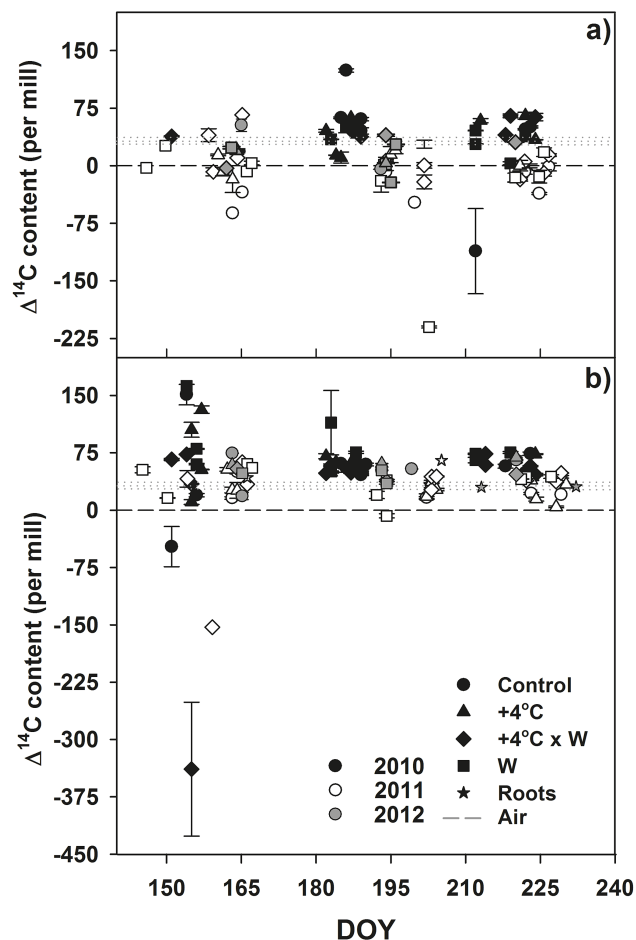


Figure 4. Radiocarbon content (per mill) of R_{eco} from bare (a) and vegetated (b) areas for three treatments ($+4^{\circ}\text{C}$, $+4^{\circ}\text{C} \times \text{W}$ and W) and control over the sampling years 2010–2012. (Dotted lines indicate the range of $^{14}\text{CO}_2$ in ambient air, star symbols represent root respiration in control areas.)

of old C from depth to the surface (Fig. 5a), with ^{14}C contents of up to -208 per mill. This old R_{eco} coincided with an increase in both the concentration and age of soil CO_2 near the permafrost table (up to -279 per mill; Fig. 5b, c). This phenomenon occurs rapidly: following experimental irrigation (~ 3.2 mm; Fig. 5c insert and Supplement Fig. 5), CO_2 concentrations within the soil profile increased by up to 16% within 6 h, and then decreased within 24 h.

Higher summer precipitation in 2010 and 2012 (Table 2) also significantly affected the mean age of R_{eco} ($F = 55.2$, $p < 0.001$), but shows consistently younger R_{eco} (summer average) than observed in 2011 (Fig. 4). Irrigation and warming did not statistically affect sources of R_{eco} .

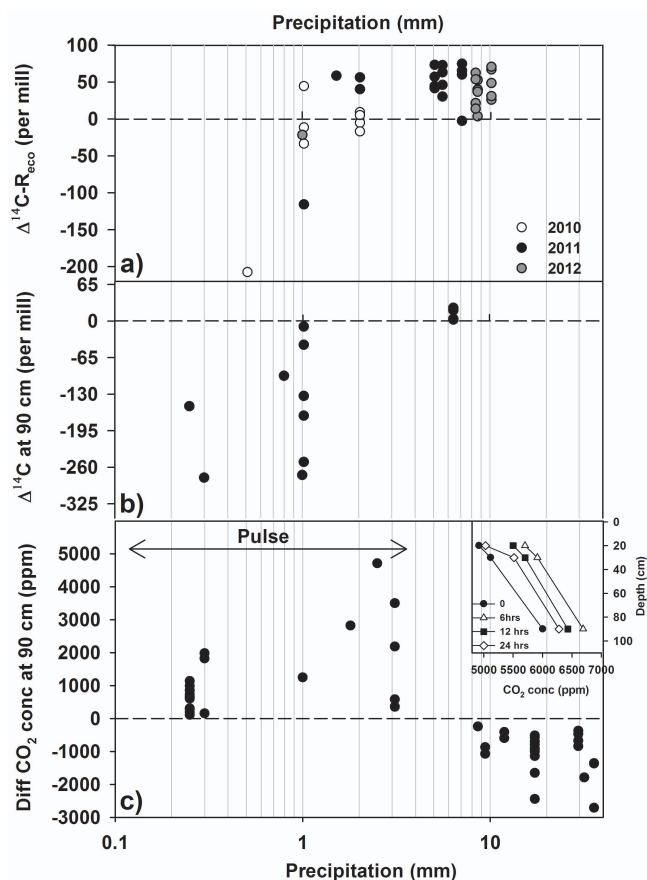


Figure 5. Radiocarbon content ($\Delta^{14}\text{C}$, per mill) of (a) R_{eco} and (b) pore space CO_2 at 90 cm depth within 24 h of a precipitation event vs. precipitation amount (mm). (c) Difference in pore space CO_2 concentration at 90 cm depth before and after a precipitation event vs. precipitation amount (small insert shows CO_2 concentration along the soil profile before and 6, 12 and 24 h after a precipitation event).

4 Discussion

4.1 Climatic trends

Analysis of annual temperature and precipitation trends showed accelerated warming and precipitation from 1952 to 2012. Overall, we found a larger increase in winter than in summer temperatures, and a larger increase in summer than in winter precipitation. During the past climate normal period, we calculated a warming trend of $1.0 \pm 0.2^{\circ}\text{C decade}^{-1}$, which was consistent with the strong recent warming detected on the western coast of Greenland since 1991 (Hanna et al., 2012). In the more recent period (1992–2012), the annual warming and precipitation trends were two times larger than in the last normal period (1983–2012), with significant contributions from winter temperature and summer precipitation increase. The observed

climate trends showed that our experiment was based on relevant scenarios of warming and wetting.

4.2 Magnitude and seasonality of ecosystem respiration

The seasonal trend of R_{eco} fluxes was primarily controlled by temperature. Fluxes of R_{eco} peaked in midsummer along with a maximum in air temperatures and active layer depth, and decreased dramatically during cold episodes, which typically coincided with rainfall events. Both experimental warming treatments (+2 and +4 °C) stimulated R_{eco} fluxes above control levels (Table 3), but warming by +4 °C stimulated R_{eco} less than by +2 °C. Soil water content tended to be lowest in the +4 °C treatment, but the drying was not statistically significant. These findings corroborated earlier experimental warming studies in the high Arctic showing that higher soil temperatures stimulated R_{eco} (Welker et al., 2004; Oberbauer et al., 2007; Strebel et al., 2010; Sharp et al., 2013), including those conducted previously under control conditions only at a similar polar semi-desert, 10 km from our experimental site (Czimeczik and Welker, 2010).

Warming may be affecting soil respiration by directly stimulating microbial processes, or indirectly by stimulating plant growth above and below the ground; greater root exudation could in turn accelerate microbial litter and soil C decomposition and nutrient mineralization in all of these studies (Rustad et al., 2001; Robinson, 2002). Some of the observed warming effects in early summer may however be related to co-occurring changes in plant phenology (Yuste et al., 2004), with root growth and exudation stimulating R_{eco} (Sullivan and Welker, 2007; Sullivan et al., 2007). Collectively, these processes promote increased respiration in these nutrient-limited communities (Arens et al., 2008; Schaeffer et al., 2013).

We showed that the magnitude of R_{eco} was strongly modulated by SWC and hence precipitation over the course of this three-year study. Early in the growing season, R_{eco} fluxes implied a positive correlation with the amount of snow accumulated over the previous winter, which was similar to the findings from more southern systems in a grassland and subalpine forest (Chimner and Welker, 2005; Monson et al., 2006). After snowmelt, the general seasonal pattern of R_{eco} follows the rises in air and soil temperatures, with modulations in magnitude driven by changes in SWC. This was evident in the summer of 2010, with two clearly distinct periods, a dry and a wet one. Although R_{eco} in both periods was correlated with temperature, the highest R_{eco} fluxes occurred during the wet period, due to the more favorable SWC conditions (10–15 % vol.; Fig. 2b, c).

On short timescales, R_{eco} fluxes were negatively correlated with increasing SWC (Fig. 2c). Over longer timescales, R_{eco} fluxes increased under wetter conditions. In previous work, Lupascu et al. (2014a) showed that interannual differences in summer R_{eco} budgets can be explained by differences in SWC. Ecosystem respiration was highest in 2012,

the year with the maximum SWC, due to higher summer precipitation and higher snowfall levels in the previous winter. Furthermore, irrigation with or without warming (W , +4 °C \times W) strongly enhanced R_{eco} above control levels. The apparent incongruity between the short- and long-term responses of R_{eco} to water addition was likely due to a time lag in the response of plant growth and respiration to water behind that of microbial respiration, which is commonly on the order of days (Carbone et al., 2011; Ogle and Reynolds, 2004), as well as to a short-term decrease in soil temperature and air-filled pore space during precipitation events.

Here, we present further evidence that polar semi-deserts are very sensitive to changes in SWC over multiple timescales. Our results agree with previous studies showing that higher SWC stimulates R_{eco} fluxes using experimental manipulations in the high Arctic (Illeris et al., 2003; Christiansen et al., 2012; Lupascu et al., 2014a) by promoting leaf area, inferred by increases in the normalized difference vegetation index (NDVI; Sharp et al., 2013) and microbial biomass (Christiansen et al., 2012).

4.3 Carbon dioxide concentrations within the soil profile

Measurements of CO₂ concentrations at different depths offer insights into CO₂ production along the soil profile (Davidson and Trumbore, 1995). Concentrations generally peaked at 60 cm in depth, below the rooting zone (0–30 cm), with a minimum near the permafrost table at about 1 m in depth, where temperatures were close to 0 °C. Similar to R_{eco} , magnitudes of soil CO₂ concentrations were strongly affected by changes in SWC. In the topsoil, CO₂ concentrations were highest at the beginning of the growing season, following snowmelt (2011, 2012; Fig. 3, top panel). This probably reflected new microbial activity within the topsoil stimulated by water, C and nutrient inputs from melting snow leaching through the litter layer (Hirano et al., 2005; Scott-Denton et al., 2006), as well as the release of older CO₂ that was previously trapped in the frozen active layer, with limited diffusivity during the winter (Albert and Perron, 2000; Schimel et al., 2006). In some cases, CO₂ concentrations at depth also rose in response to snowmelt, but with a time delay of a few weeks that increased with depth.

We found that CO₂ concentrations near the permafrost table were very sensitive to the occurrence and magnitude of precipitation events. Small precipitation events (< 4 mm) stimulated CO₂ concentrations in a matter of hours by either increasing CO₂ production or reducing the available gas-filled pore space. Larger precipitation events resulted in a sharp decline in CO₂ concentrations, as water pooling on the permafrost table either (a) restricted microbial activity by reducing oxygen availability, (b) trapped existing CO₂ by disrupting the gas-phase connectivity (Stonestrom and Rubin, 1989) or (c) flushed out the existing CO₂.

Irrigation treatments further substantiated the importance of water in microbial activity. In general, long-term irrigation resulted in higher CO₂ concentrations, while long-term warming by 4 °C did not significantly alter CO₂ concentrations compared to control conditions. In a separate study focusing on inter-annual C budgets, Lupascu et al. (2014a) showed that long-term climate manipulations in these same experimental plots dramatically changed the ¹⁴C content of CO₂ at depths. Furthermore, irrigation resulted in the presence of younger C respired compared to the control. By contrast, experimental warming (+4 °C) showed more depleted ¹⁴C, and hence a larger fraction of older C being released at all depths. In conclusion, these two studies showed that water along with temperature is a crucial driver of microbial activity in these high Arctic soils.

4.4 Sources of ecosystem respiration

Changes in plant density and community composition are additional manifestations of long-term changes in climate and permafrost regime. We found that R_{eco} and soil CO₂ in vegetated areas were always younger compared to bare areas in this patchy landscape, driven in large part by differential frost heave. Plant respiration was typically a large component of R_{eco} , with a ¹⁴C content similar to, or occasionally slightly higher than, atmospheric CO₂ (Schoor and Trumbore, 2006; Czimczik et al., 2006), and that flux could mask the relatively smaller emissions of older CO₂ at depth. Microorganisms in the topsoil that decomposed plant exudates or litter further contributed to the ¹⁴C enrichment of R_{eco} in vegetated areas. In addition, the bulk C pool in the vegetated areas was younger than in the bare areas, due to the continuous input of fresh litter (Supplement Table 1). Thus, future assessments of high Arctic R_{eco} budgets need to account carefully for changes in vegetation cover and structure (Forbes et al., 2010; Bonfils et al., 2012), as greater plant biomass coupled with fresh C inputs to depth as well as associated changes in albedo are likely to affect the magnitude of old C emissions into the atmosphere.

Seasonally, the contribution of old C to R_{eco} should peak in mid- to late summer, when active layer depth is deepest, but its relative contribution should be highest after peak plant biomass. Plant respiration commonly masks contributions of older C in R_{eco} , resulting in young emissions during the summer time, as observed here and previously (Schoor et al., 2009; Czimczik and Welker, 2010; Nowinski et al., 2010). However, Natali et al. (2011) showed that the contribution of old C to R_{eco} in a moist acidic tundra snowfence manipulation experiment in Alaska declines at the end of the growing season; they attributed this to water pooling on the permafrost table.

Here, we observed old R_{eco} during two distinct time periods: (a) at the beginning of the growing season and (b) episodically after smaller precipitation events following a dry period. At the beginning of the growing season (Fig. 4), we

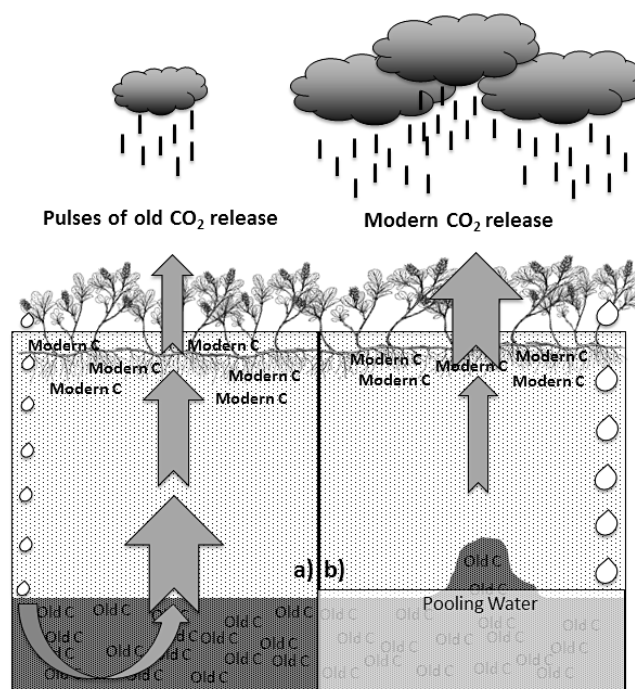


Figure 6. Conceptual representation of old C release from semi-deserts in the high Arctic in response to different precipitation regimes. (a) Small episodic rain events (< 4 mm) stimulate microbial decomposition of older C at depth more than rhizosphere respiration, and mostly old C is released into the atmosphere as a pulse within 24 h. In addition, any rain event flushes old CO₂ upward by reducing the air-filled pore space. (b) Large amounts of rain (> 4 mm) become enriched in modern C when percolating through the topsoil. This C is preferentially used by microbes at depth and respired as CO₂. Furthermore, the water pools on the permafrost table and reduces microbial decomposition of old C at depth, while rhizosphere respiration is increased. Consequently, mostly modern C is released into the atmosphere.

identified a complex mixture of C of different ages, with old C likely coming from residual CO₂ trapped over the winter (Schimel et al., 2006). This supported findings from our initial study in these northwestern Greenland polar semi-deserts (Czimczik and Welker, 2010). Ancient C can be a measurable part of R_{eco} , especially before leaf emergence and senescence, when fresh C inputs are minimal. Further work is needed to investigate potential emissions of old C during freeze-up as well as winter, since these time periods were not covered in our study.

We also observed episodic emissions of old CO₂ following smaller precipitation events (< 4 mm per day) after about seven days of no rain (Figs. 5, 6a). These small precipitation events enhanced CO₂ concentrations at depth and triggered a release of older C within 24 h of the rain event. Two processes may explain our observations: (1) water rapidly percolating through the active layer down to the permafrost table, which can facilitate the diffusion of old CO₂ upwards

into overlying soil horizons by displacing air space within the soil pores (Huxman et al., 2004); (2) decomposition of old C deeper in the active layer may be stimulated by cycles of drying and rewetting, the so-called “Birch effect” (Birch, 1964). Enhanced microbial activity and mineralization of soil C and nitrogen in response to drying and rewetting has been extensively described in surface soils of temperate and semi-arid ecosystems in both field and laboratory studies (Fierer and Schimel, 2002; Jarvis et al., 2007). It is possible that the Birch effect also extends to permafrost soils, including the bottom of the active layer.

The Birch effect has been attributed to rapidly increasing mineralization rates in response to changing moisture conditions (Inglisma et al., 2009; Borken and Matzner, 2009; Unger et al., 2010) and/or C availability (Kieft et al., 1987; Fierer and Schimel, 2002; Jarvis et al., 2007). Different mechanisms have been proposed to explain the change in C availability, including (1) drying and rewetting of soils shatters soil aggregates, exposing previously unavailable organic substrates to decomposition (e.g., Deneff et al., 2001); (2) “priming” – increased decomposition of old and potentially more recalcitrant C at depth via inputs of fresh labile C leached from the litter layer and/or rooting zone (Fontaine et al., 2007); (3) relocation of labile C produced by photo-degradation in the litter layer to depth (Ma et al., 2012); and (4) drying causing an increase in dead microbial biomass, which is rapidly recycled by new microorganisms and fungi after rewetting (e.g., Bottner, 1985). Recycling of microbial biomass at depth would result in the production of old CO₂, as microbes carry the same ¹⁴C signature as their C source (Petsch et al., 2001). Here, we did not have enough data to identify which mechanism was responsible for this episodic old C release. Additional experiments, particularly at a higher frequency, are needed to quantify the significance of water pulses on C cycling in permafrost soils and the mechanisms involved.

In (semi-)arid ecosystems, including polar semi-deserts, discrete precipitation events play a complex role in regulating the magnitude and sources of R_{eco} and net ecosystem exchange (Huxman et al., 2004; Thomey et al., 2011). Small precipitation events cause immediate and strong increases in microbial respiration and net C loss from the ecosystem to the atmosphere (Fig. 6a). Larger rain events stimulate plant C uptake and ecosystem C sequestration, but with a delay compared to microbial activity (Jarvis et al., 2007; Carbone et al., 2011). In our experiment, we detected the CO₂ pulses, but we were unable to detect the magnitude of these pulses. This might be partially due to the fact that in order to collect sufficient CO₂ for ¹⁴C analysis, we left our chambers closed for at least 24 h, which could have modified the natural concentration gradient in the active layer. In Mediterranean ecosystems, pulses can account for up to 10 % of the C lost over a year (Xu et al., 2004; Tang and Baldocchi, 2005; Jarvis et al., 2007; Carbone et al., 2011).

Our data demonstrated for the first time that losses of older C from high Arctic permafrost soils can be episodic in nature and controlled by precipitation events – making them very difficult to quantify with discrete measurements. We found that contributions of older C to R_{eco} were undetectable during wet periods with intense precipitation (> 4 mm per day) during the summer (Fig. 6b). This was a consequence of water pooling on the permafrost table, checked through the wells during our daily CO₂ measurements, leading to a decrease in the microbial decomposition of older C at depth. These data further supported earlier findings showing that interannually, wetter summers coincided with younger R_{eco} being released due to inputs of recently assimilated C from the litter layer and/or rooting zone (Lupascu et al., 2014a).

While we found that precipitation events affect the short-term variability in the age of R_{eco} , the irrigation treatments appear not to effect the age or seasonality of R_{eco} fluxes. This did not necessarily indicate that episodic release of old C was a minor component of the summertime R_{eco} flux. It was likely a consequence of two factors: (1) our sampling frequency was low (monthly), due to the high cost and effort required for ¹⁴C analysis both in situ and in the laboratory; (2) changes in contributions of older, ¹⁴C-depleted C from depth were generally hard to detect in R_{eco} , as fluxes integrate C dynamics over the entire soil profile and were dominated by the ¹⁴C-enriched respiration of plants and microorganisms in the topsoil.

5 Conclusions

This study illustrated the complexity of temperature and water controls on the stability of old C in permafrost soils in semi-arid soils of the high Arctic. Accurately describing C cycling and feedbacks to the atmosphere requires not only an understanding of future temperature changes, but also of precipitation amounts, frequencies and form (rain or snow). Our analysis showed that soils of polar semi-deserts episodically release old C with light rain events. However, understanding the magnitude of these episodic contributions to the summertime and annual R_{eco} budget and the overall loss of old C from high Arctic tundra requires further investigation.

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