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

M. Lupascu¹, J. M. Welker², U. Seibt^{3,4}, X. Xu¹, I. Velicogna^{1,5}, D. S. Lindsey¹,
and C. I. Czimczik¹

¹Department of Earth System Science, University of California, Irvine, Irvine, California
92697-3100, USA

²Department of Biological Sciences, University of Alaska, Anchorage, Anchorage, Alaska
99508, USA

³Department of Atmospheric and Oceanic Science, University of California, Los Angeles, Los
Angeles, California, 90095, USA

⁴Bioemco, University Pierre Marie Curie Paris 6, Thiverval-Grignon, 78850, France

⁵Jet Propulsion Laboratory, California Institute of Technology, Pasadena, 91109, CA, USA

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Correspondence to: M. Lupascu (mlupascu@uci.edu)

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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 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) plant 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 winter 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.

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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 3–8°C by 2100 (Meehl et al., 2007), 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 (Peterson et al., 2002). Other abiotic changes accompanying the warming include increasing cold season precipitation, declining duration of snow cover and regionally distinct changes in snow depth (Callaghan et al., 2011), wetting due to increased atmospheric transport of moisture into the Arctic (Zhang et al., 2013), and a decline in summer sea ice extent (Johannessen et al., 2004). The implications of these changes for the regional biogeochemistry are largely unknown, especially in the High Arctic (> 70° 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 extend and associated warming and, or changes in precipitation.

Long-term multifactorial climate change experiments are a crucial tool to mimic the future and unravel 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 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 and only more recent 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).

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In the High Arctic, 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 PgC from circumpolar permafrost (equivalent to 0.04–1.69 °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., 2013). 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 °C passive warming experiments do not provide a means to forecast beyond the next decades (Welker et al., 1997), even as the Arctic could be warming 6 °C by 2050 (IPCC, 2007; Koenig et al., 2012). 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 interannual variability, which can exceed experimental treatment effects. 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 penetration of precipitation into soils, which in turn may stimulate net primary productivity, but hin-

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der 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 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 ecosystem respiration (R_{eco}) can be used to infer changes in soil C dynamics without compromising soil structure and biota (Heimann and Reichstein, 2008). And, understanding seasonal dynamics of R_{eco} is key to understanding the interannual variability in ecosystem C budgets (Goulden et al., 1996). In addition, radio-carbon (^{14}C) analysis of R_{eco} is a valuable tool to understand 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. Thus, assessing soil C feedbacks to rising atmospheric CO_2 levels requires distinguishing R_{eco} sources, i.e. plants and microorganism 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 belowground CO_2 and their sources conducted over three consecutive summers at 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, or temperature alter the seasonal patterns of soil CO_2 and R_{eco} fluxes?

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by infrared radiation (+2 °C), +4 °C soil warming (+4 °C), irrigation (W) and +4 °C soil warming \times irrigation (+4 °C $\times W$) alongside an ambient climate control. Each year we initiate warming during the first week of June, when the plots are about 50 % snow-free and we maintain it through the end of August. We use 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) are 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 are calculated as the mean of the daily minimum and maximum temperatures. We calculate annual, summer (June, July, August), winter (December, January, February) temperature and total precipitation (rainfall plus snow) trends for the most recent climate normal period (1983–2012). In addition, to evaluate how temperature and precipitation change during the entire 61 yr period, we calculate the same trends for the last 20, 30, 40, 50 and 60 yr corresponding to 1992–2012, 1982–2012, 1972–2012, 1962–2012, 1952–2012 respectively, and we estimate 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 ($1 - \sigma$) of the respective dataset.

2.4 Ecosystem respiration fluxes and soil pore space CO₂ concentrations

We measure R_{eco} and soil CO₂ concentrations approximately 2–3 times a week between 10:00 and 13:00 LT. The first one is measured using opaque, dynamic chambers (30 cm i.d., 8 L $V = 8$), a method that has been used for decades and its limitations have been widely discussed in the literature (e.g. Davidson et al., 2002). Chamber bases are inserted at the beginning of each measurement season to about 2 cm depth, sealed with soil material on the outside, and left in place for the entire sampling season. Vegetation is not clipped. We quantify 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 are calculated from the slope of time vs. CO₂ concentration curves using a linear regression.

We use the daily R_{eco} measurement as a proxy for mean daily R_{eco} . When daily measurements are missing we estimate daily R_{eco} values using the relationship between respiration and temperature (Lloyd and Taylor, 1994), described by an 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 calculate the daily R_{eco} for the missing days using the average daily temperature (T). We estimate cumulative summertime R_{eco} as the sum of the daily values.

We monitor 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 depth and closed off with rubber septa (Blue septa, Grace, Deerfield, IL, USA). Wells were installed from the soil surface in 2010 as soon as the thaw of the active layer allowed and remained in the same location throughout the entire study period including the winters. Soil gases

were obtained with 60 mL syringes (BD, Franklin Lakes, NJ, USA). We collect soil gas using 60 mL syringes (BD, Franklin Lakes, NJ, USA). We discard the first 60 mL sample and inject the second into an infrared gas analyzer connected to a data logger (LI-800, LI-1400, LI-COR), we then manually record the peak concentration.

5 2.5 Soil temperature and water content

With each R_{eco} measurement we manually record 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 monitor SWC at 5 cm depth with Hydra II soil moisture and salinity sensors (SDI-12/RS485, Stevens, Portland, OR, USA) connected to a CR1000 datalogger (Campbell Scientific). Data are acquired every 15 min.

2.6 Sampling for isotope analyses

We collect gas samples for isotope analysis monthly. To sample R_{eco} , we leave the chambers closed until the CO_2 concentration inside the chamber is $\geq 2\times$ that in ambient air (up to 24–48 h). After each concentration measurement, the CO_2 is 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 CO_2 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 radiocarbon memory effects can be overcome by pre-conditioning traps (630°C for 45 min under vacuum) and sampling enough CO_2 in the field (0.3–2 mg C). For each set of R_{eco} samples, we collect two samples of CO_2 from ambient air on molecular sieve (15 min at 0.5 L min^{-1}) in a well-ventilated area nearby the experimental site. Soil gas

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from the different depths was collected in pre-evacuated, stainless steel canisters via flow-restricting stainless steel capillaries (0.010cm × 0.063cm × 30 cm, Fisher).

2.7 Isotope analyses of CO₂

Radiocarbon (¹⁴C) analysis is a valuable tool for understanding the sources of R_{eco} (respiration of plants that fix CO₂ from the atmosphere vs. respiration of microbes that decompose soil C of various ages to CO₂). 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 ($t_{1/2} = 5730$ yr). In contrast, CO₂ derived from the decomposition of soil C made from photosynthetic products years to decades ago is enriched in ¹⁴C. This is because during the late 1950s and early 1960s, testing of nuclear bombs aboveground almost doubled the naturally produced ¹⁴C activity in atmospheric CO₂. After test cessation, the amount of bomb-¹⁴C (aka “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 accelerator mass spectrometry (NEC 0.5MV 1.5SDH-2 AMS) at the KCCAMS laboratory at UC Irvine (Southon and Santos, 2007). Data are reported relative to NIST OX-I (SRM 4990a) and OX-II (SRM 4990c) following Stuiver and Polach (1977). The measurement uncertainty for $\Delta^{14}\text{C}$ is 2–3‰.

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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 in R_{eco} derived from ambient air, calculated from measurements of CO_2 concentrations in ambient air as well as in the chamber immediately before trapping.

3 Results

3.1 Climate and weather

Data from the Thule operations site show 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 occurs during October–April as snow.

Table 1 shows annual, summer and winter temperature and total precipitations linear trends for the past 20, 30, 40, 50, 60 yr, all trends are significant at the 1 s level. Annual temperature and total precipitations trends for shorter recent periods are larger, indicating both accelerated warming and precipitation during the entire 60 yr period. Overall temperature increases more during the winter months. We observe a significant and consistent increase in total summer precipitation trends while in winter precipitation trends are very variable.

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

sonal patterns as vegetated areas, but with reduced R_{eco} fluxes ($< 1 \text{ mmolCm}^{-2} \text{ s}^{-1}$; data not shown).

Point measurements of soil conditions indicate that in the control (Fig. 1c) and all treatments (data not shown), R_{eco} fluxes are positively correlated to 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. 1b). Surprisingly, R_{eco} fluxes are negatively correlated to SWC ($R^2 = 0.37 \pm 0.11$) (Fig. 1d). Ecosystem respiration fluxes are highest at 10–15 % SWC (Fig. 2c and d).

All experimental treatments ($F = 22.3$, $p < 0.001$) increase R_{eco} fluxes relative to control (Table 3), without changes in seasonal patterns (data not shown). Irrigation ($+51 \pm 1 \%$) and $+4^\circ\text{C}$ warming \times irrigation ($+46 \pm 0 \%$) have the strongest positive effect on R_{eco} . Remarkably, warming by $+2^\circ\text{C}$ ($+40 \pm 1 \%$) increases R_{eco} more than warming by $+4^\circ\text{C}$ ($+20 \pm 1 \%$). In all treatments, cumulative summer R_{eco} is highest in 2012 (e.g. control $126 \text{ gCsummer}^{-1}$) compared to 2011 ($81.9 \pm 6.2 \text{ gCsummer}^{-1}$) and 2010 ($36.1 \pm 10.1 \text{ gCsummer}^{-1}$) ($F = 673.0$, $p < 0.001$).

3.4 Soil pore space CO_2 concentrations

Pore space CO_2 concentrations are 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. 2). With depth, CO_2 concentrations increase to 60 cm followed by a decrease toward the permafrost table (Fig. 2 middle panel). Throughout the season, CO_2 concentrations display a bi-modal pattern, with a first peak during the snowmelt and a second peak associated with maximum air temperatures and active layer depth (Fig. 2 top panel). The magnitude of the snowmelt peak between years is positively correlated with snowpack.

Irrigation (W , $+4^\circ\text{C} \times W$) has the strongest effect on pore space CO_2 concentrations. For instance, we observe higher concentrations at all depths (e.g. 2011, $+4^\circ\text{C} \times W$: 2900 ± 522 , 8845 ± 419 , $5577 \pm 350 \text{ ppm}$ for 30, 60 and 90 cm, respectively) compared

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to the control (e.g. 2011, control: 4488 ± 323 , 3681 ± 266 , 3248 ± 217 ppm), except at 90 cm in 2010 (Fig. 2 middle panel). On the other hand, experimental warming (+2, +4 °C) slightly increases CO₂ only in the upper mineral soil, while at greater depth concentrations are similar or lower than in the control.

Carbon dioxide concentrations at depths show little variation between years compared to the three-fold differences in R_{eco} observed between 2010, 2011 and 2012. However, 2010 exhibits the lowest CO₂ concentrations compared to 2011 and 2012 (Fig. 2 middle and bottom panel).

3.5 Sources of ecosystem respiration

The ¹⁴C content (as $\Delta^{14}\text{C}$) of R_{eco} shows large differences between bare and vegetated areas and between years, but only minor variations from month to month and between treatments (Fig. 3). We find significant difference ($F = 51.8$, $p < 0.001$) between bare (e.g. control: 32.8 ± 10.5 , -23.6 ± 8.3 , 20.6 ± 3.1 ‰ in 2010, 2011, 2012, respectively) and vegetated plots (e.g. control: 51.8 ± 10.0 , 30.8 ± 4.9 , 54.1 ± 9.5 ‰ in 2010, 2011, 2012, respectively), with the vegetated areas emitting younger C at all times.

In all years, a complex mixture of C sources contribute to R_{eco} during snowmelt, including 1) older C, fixed before 1950 (up to -339 ‰), 2) modern C, fixed decades ago (up to $+162$ ‰) and 3) recently fixed C ($+35$, $+32$, $+29$ ‰ in 2010, 2011, and 2012, respectively). In July and August, recently fixed C dominates R_{eco} , the period that corresponds to maximum above- and belowground plant growth. We find that episodically, very old C can, however, dominate R_{eco} (Fig. 3). These pulses of ancient C efflux appear to be associated either with freeze-thaw cycles during spring or with rain pulses during summer. After about 7 days of no rain, small rainfall pulses (< 4 mm) results in emissions of old C from depth to the surface (Fig. 4a), with ¹⁴C contents of up to -208 ‰. This old R_{eco} coincides with an increase in both concentration and age of soil CO₂ near the permafrost table (up to -279 ‰; Fig. 4b and c). This phenomenon occurs rapidly: following experimental irrigation (~ 3.2 mm; Fig. 4c insert) CO₂ concentrations within the soil profile increase up to 16 % within 6 h and then decreases within 24 h.

Higher summer precipitation in 2010 and 2012 (Table 2) also significantly affect 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. 3). Irrigation and/or warming do not statistically affect sources of R_{eco} .

4 Discussion

4.1 Climatic trends

Our study site, including the experimental treatments and control, is undergoing (winter-) warming and (summer-) wetting. Analysis of annual temperature and annual total precipitations trends show accelerated warming and precipitation during 1952–2012. Overall we find a larger increase in winter than in summer temperatures and larger increase in summer than in winter precipitation. During the past climate normal period we calculate a warming trend of $1.0 \pm 0.2^\circ\text{C decade}^{-1}$ which is consistent with the strong recent warming detected on the west coast of Greenland since 1991 (Hanna et al., 2012). In the more recent period (1992–2012) the annual warming and precipitation trends are two times larger than in the last normal period (1983–2012), with significant contribution from winter temperature and summer precipitation increase. The observed climate trends show that our experiment is based on relevant scenarios of warming and wetting.

4.2 Magnitude and seasonality of ecosystem respiration

We show that the magnitude of R_{eco} is strongly modulated by SWC and hence precipitation over the course of this three-year study. Early in the growing season R_{eco} fluxes are positively correlated to the amount of snow accumulated over the previous winter, which is 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

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modulations in magnitude driven by changes in SWC. This is evident in the summer of 2010 with two clearly distinct periods, a dry and a wet one. Although R_{eco} in both periods are correlated with temperature, the highest R_{eco} fluxes occur during the wet period, due to the more favorable SWC conditions (10–15 %-vol, Fig. 1c and d).

5 While on short time scales R_{eco} fluxes are negatively correlated to increasing SWC (Fig. 1d), over longer time periods R_{eco} fluxes increase under wetter conditions. In previous work, Lupascu et al. (2013) showed that inter-annual differences in summer R_{eco} budgets can be explained by difference in SWC. Ecosystem respiration is highest in 2012, the year with the maximum SWC, due to higher summer precipitation and
10 higher snowfall levels in the previous winter. Further, irrigation with or without warming (W , $+4^\circ\text{C} \times W$) strongly enhances R_{eco} above control levels. The apparent incongruity between the short- and long-term response of R_{eco} to water addition is 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 a short-term decrease in soil temperature during precipitation events (data not shown).

Here, we present further evidence that polar semi-deserts are very sensitive to changes in SWC over multiple time scales. Warming by $+4^\circ\text{C}$ stimulated R_{eco} less than $+2^\circ\text{C}$ warming – probably a result of reduced SWC and thus drought stress,
20 which may decrease plant photosynthetic activity and respiration (Welker et al., 1993; Llorens et al., 2004; Sullivan and Welker, 2007; Pinhero and Chaves, 2011) and, or microbial activity (Schimel et al., 2006). Our results agree with previous studies showing that higher SWC stimulate R_{eco} fluxes using experimental manipulations in the High Arctic (Illeris et al., 2003; Christiansen et al., 2012; Lupascu et al., 2013) 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).

25 The seasonal trend of R_{eco} fluxes is primarily controlled by temperature. Fluxes of R_{eco} peaked in midsummer along with a maximum in air temperatures and active layer depth, and decrease dramatically during cold episodes, which typically coincide with

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rainfall events. Both experimental warming treatments (+2 and +4 °C) stimulate R_{eco} fluxes above control levels (Fig. 1; Table 3). These findings corroborate earlier experimental warming studies in the High Arctic showing that higher soil temperatures stimulate R_{eco} (Welker et al., 2004; Oberbauer et al., 2007; Strebel et al., 2010; Sharp et al., 2013) including those conducted previously under control condition-only at a similar polar semi-desert, 10 km from our experimental site (Czimczik and Welker, 2010).

Warming may be affecting soil respiration by directly stimulating microbial processes, or indirectly by stimulating plant growth above- and belowground; 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, 2005; Sullivan et al., 2007). Collectively, these processes promote increased respiration in these nutrient-limited communities (Arens et al., 2008; Schaeffer et al., 2013).

4.3 Carbon dioxide concentrations within the soil profile

Measurements of CO_2 concentrations at different depths offer insights on CO_2 production along the soil profile (Davidson and Trumbore, 1995). Concentrations generally peaked at 60 cm depth, below the rooting zone (0–30 cm), with a minimum near the permafrost table at about 1 m depth, where temperatures are close to 0 °C. Similar to R_{eco} , magnitudes of soil CO_2 concentrations are strongly affected by changes in SWC. In the topsoil, CO_2 concentrations are highest during the beginning of the growing season, following snowmelt (2011, 2012; Fig. 2 top panel). This probably reflects 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 CO_2 that was previously trapped in the frozen active layer with limited diffusivity during the winter (Albert and Perron, 2000; Schimel et al., 2006).

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In some cases CO₂ concentrations at depth also rise in response to snowmelt, but with a time delay of a few weeks that increases with depth.

We find that CO₂ concentrations near the permafrost table are very sensitive to the occurrence and magnitude of precipitation events. Small precipitation events (< 4 mm) stimulate CO₂ concentrations in a matter of hours by either increasing CO₂ production or reducing the available gas-filled pore space. Larger precipitation events result in a sharp decline of CO₂ concentrations, as water pooling on the permafrost table likely restrict microbial activity by reducing oxygen availability or trapping existing CO₂ by disrupting the gas-phase connectivity (Stonestrom and Rubin, 1989).

Irrigation treatments further substantiate the importance of water on microbial activity. In general, long-term irrigation results in higher CO₂ concentrations, while long-term warming by 4 °C does not significantly alter CO₂ concentrations compared to control conditions. In a separate study focusing on inter-annual C budgets, Lupascu et al. (2013) show that long-term climate manipulations in these same experimental plots, dramatically change the ¹⁴C content of CO₂ at depths. Furthermore, irrigation results in the presence of younger C respired compared to the control. In contrast, experimental warming (+4 °C) shows more depleted ¹⁴C and hence a larger fraction of older C being released at all depths. In conclusion, these two studies show 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 find that R_{eco} and soil CO₂ in vegetated areas are always younger compared to bare areas in this patchy landscape driven in large part by differential frost heave. Plant respiration is typically a large component of R_{eco} with a ¹⁴C content similar to, or occasionally slightly higher than, atmospheric CO₂ (Schuur and Trumbore, 2006; Czimczik et al., 2006), and that flux can mask the relatively smaller emissions of older CO₂ at depth. Microorganisms in the top-soil that decompose plant exudates or litter further contribute to the ¹⁴C enrichment of

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R_{eco} in vegetated areas. In addition, the bulk C pool in the vegetated areas is younger than in the bare areas due to the continuous input of fresh litter (data not shown). Thus, future assessments of high arctic R_{eco} budgets need to carefully account 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 to 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) show that the contribution of old C to R_{eco} in a snowfence manipulation experiment in the Low Arctic of Alaska declines at the end of the growing season; they attribute this to water pooling on the permafrost table.

Here, we observe 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. 3), we identify a complex mixture of C sources with old C likely coming from residual CO_2 trapped over the winter (Schimel et al., 2006). This supports findings from our initial study in these NW 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 is not covered in our study.

We also observe episodic emissions of old CO_2 following smaller precipitation events ($< 4 \text{ mm day}^{-1}$) after about 7 days of no rain (Fig. 4). These small precipitation events enhance CO_2 concentrations at depth and triggered 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 CO_2 upwards into overlying soil horizons by displacing air space within

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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 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; Boroken and Matzner, 2009; Unger et al., 2010) and, or C availability (Kieft et al., 1987; Fierer and Schimel, 2002; Jarvis et al., 2007). Different mechanism 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 do not have enough data to identify which mechanism is responsible for this episodic old C release. Additional experiments, particularly at 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. Larger rain events stimulate plant C uptake

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and ecosystem C sequestration, but with a delay compared to microbial activity (Jarvis et al., 2007; Carbone et al., 2011). In our experiment we detect the CO₂ pulses but we are unable to detect the magnitude of these pulses. This might 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 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 demonstrate 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 find that contributions of older C to R_{eco} are undetectable during wet periods with intense precipitation (> 4 mm day⁻¹) during the summer. This is likely a consequence of water pooling on the permafrost table leading to a decrease of microbial decomposition of older C at depth. This data further supports 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., 2013).

While we find that precipitation events affect the short-term variability in the age of R_{eco} , the irrigation treatments appear to not effect the age or seasonality of R_{eco} fluxes. This does not necessarily indicate that episodic release of old C is minor component of the summertime R_{eco} flux. It is 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 are generally hard to detect in R_{eco} as fluxes integrate C dynamics over the entire soil profile and are dominated by the ¹⁴C-enriched respiration of plants and microorganisms in the topsoil.

5 Conclusions

This study illustrates 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 shows 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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Table 1. Temperature and total precipitation (rain + snow, in mm decade^{-1} of water) trends at Thule airport (THU), Greenland from 1952 to 2012. Only statistically significant trend are reported.

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

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Table 2. Precipitation and 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)

^aPreceding winter; defined as snow pack height, not water equivalent.

^bCumulative values for the snow-free period.

n.d. not determined.

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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, $n = 1$ –3).

	2010 gCm ⁻² summer ⁻¹	2011 gCm ⁻² summer ⁻¹	2012 gCm ⁻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)

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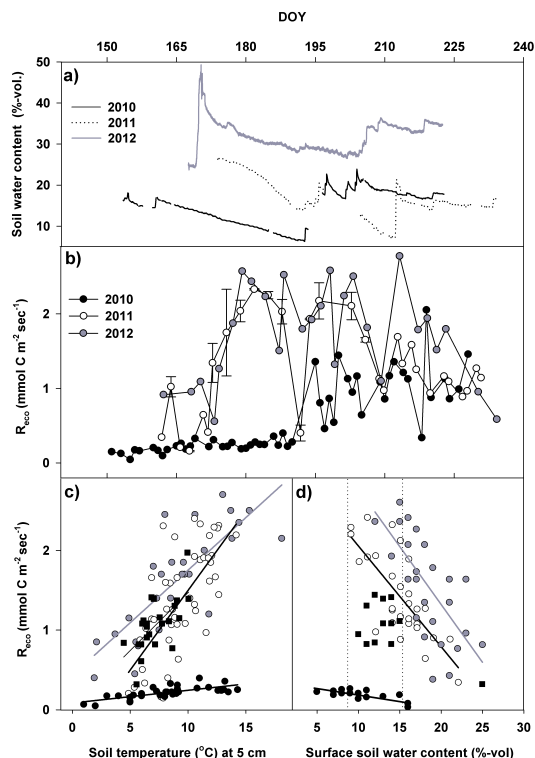


Fig. 1. Seasonal patterns and correlations of ecosystem respiration (R_{eco}), soil water content (SWC) and soil temperature under control conditions (average \pm SE, $n = 1$ –3 plots) during the summers of 2010–2012: **(a)** continuous SWC at 5 cm depth, **(b)** daily R_{eco} flux **(c)** correlation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

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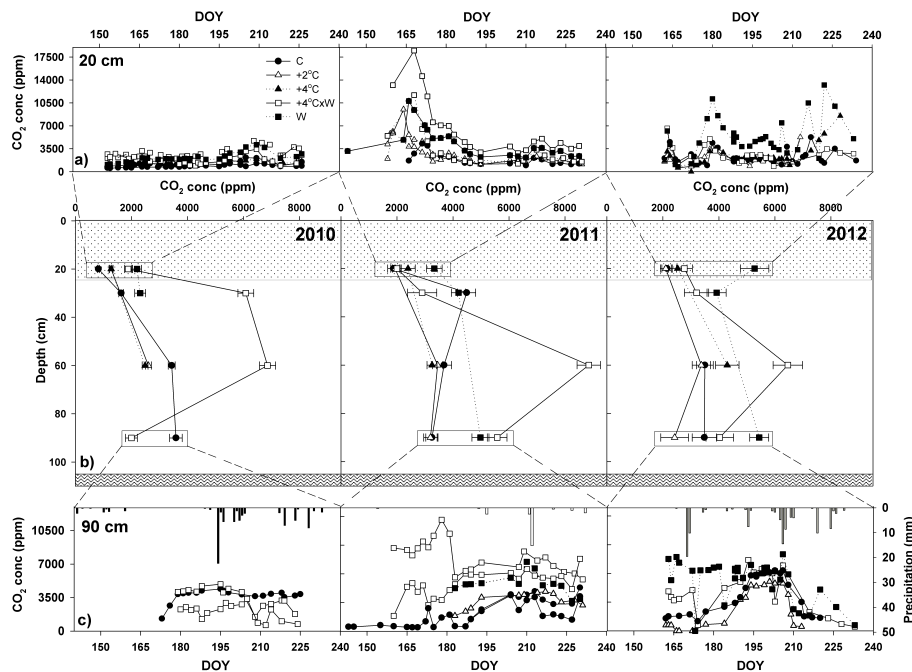


Fig. 2. Middle panel: seasonal mean of pore space CO_2 concentration along the soil profile for the four treatments ($+2^\circ\text{C}$, $+4^\circ\text{C}$, $+4^\circ\text{C} \times W$ and W) and control over the sampling years 2010–2012 [hatched areas represent the estimated rooting zone]. Top panel: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

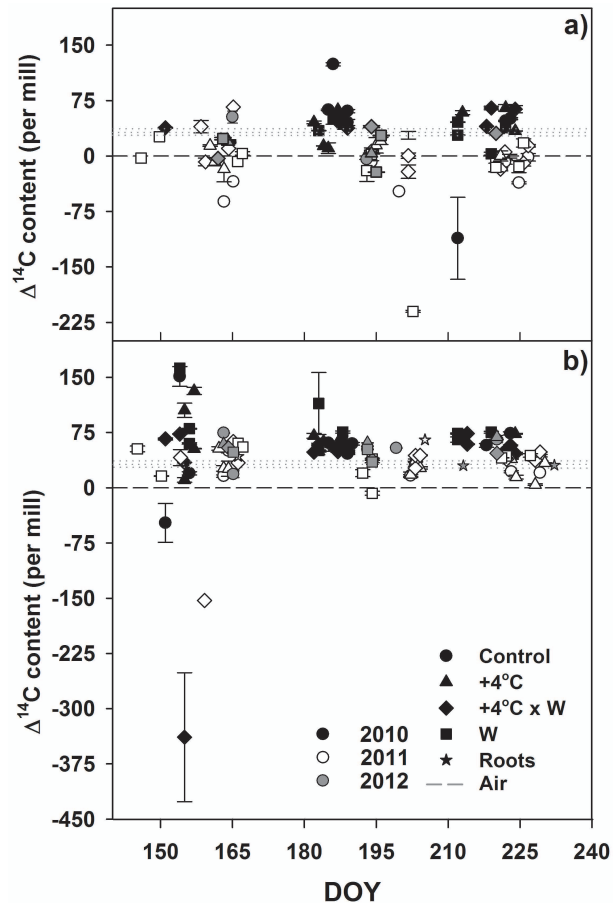


Fig. 3. Radiocarbon content (per mill) of R_{eco} from bare (a) and vegetated areas (b) for three treatments (+4°C, +4°C × W and W) and control over the sampling years 2010–2012 (dotted lines indicate range of $^{14}\text{CO}_2$ in ambient air).

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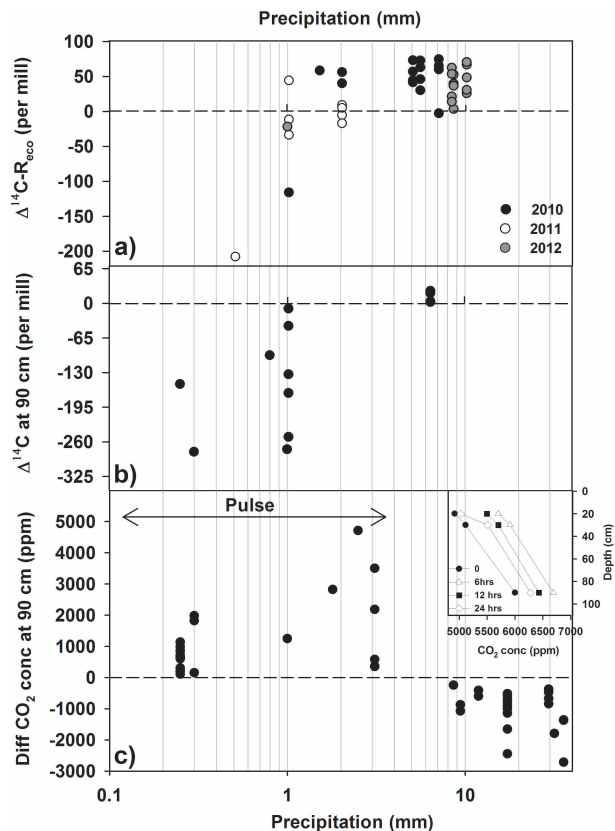


Fig. 4. Radiocarbon content ($\Delta^{14}\text{C}$, ‰) of (a) R_{eco} and of (b) pore space CO₂ at 90 cm depth within 24 h of a precipitation event vs. precipitation amount (mm). (c) Difference in pore space CO₂ concentration at 90 cm depth before and after a precipitation event vs. precipitation amount (small insert shows CO₂ concentration along the soil profile before and 6, 12 and 24 h after a precipitation event).