nature climate change

LETTERS

PUBLISHED ONLINE: 1 DECEMBER 2013 | DOI: 10.1038/NCLIMATE2058

High Arctic wetting reduces permafrost carbon feedbacks to climate warming

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The carbon (C) balance of permafrost regions is predicted to be extremely sensitive to climatic changes[1–3]. Major uncertainties exist in the rate of permafrost thaw and associated C emissions (33–508 Pg C or 0.04–1.69 °C by 2100; refs 2,3) and plant C uptake. In the High Arctic, semi-deserts retain unique soil–plant–permafrost interactions[4,5] and heterogeneous soil C pools[6] (>12 Pg C; ref. 7). Owing to its coastal proximity, marked changes are expected for High Arctic tundra[8]. With declining summer sea-ice cover[9], these systems are simultaneously exposed to rising temperatures[9], increases in precipitation[10] and permafrost degradation[11]. Here we show, using measurements of tundra–atmosphere C fluxes and soil C sources (^{14}C) at a long-term climate change experiment in northwest Greenland, that warming decreased the summer CO_2 sink strength of semi-deserts by up to 55%. In contrast, warming combined with wetting increased the CO_2 sink strength by an order of magnitude. Further, wetting while relocating recently assimilated plant C into the deep soil decreased old C loss compared with the warming-only treatment. Consequently, the High Arctic has the potential to remain a strong C sink even as the rest of the permafrost region transitions to a net C source as a result of future global warming.

The Arctic is greening[8,12] and sequestering increasing amounts of atmospheric CO_2 (ref. 12). At the same time, permafrost thawing is releasing ancient soil C (ref. 13) to the atmosphere. The timing and balance of these two processes determine the sign and strength of the Arctic's C cycle feedbacks to climate change[14].

In the High Arctic (>70° N), precipitation regimes and soil–plant water relations may be as important in regulating C cycling as thermal conditions[4,15]. However, we lack data sets addressing how water–temperature interactions control C cycling, including magnitudes of tundra–atmosphere C exchange and stability of old permafrost C pools that have accumulated over millennia[16–18].

High Arctic tundra is typically water limited and dominated by a few dwarf shrub and graminoid species. As in other dry, cold landscapes, precipitation comes from limited, often ephemeral, growing season rainfall and winter snow. The amount and frequency of rainfall and the extent to which rain infiltrates soils has been identified as an important control on the C balance of semi-arid ecosystems, with small events stimulating C loss by microbial decomposition, and larger events stimulating plant C uptake[15,19]. In cold and dry permafrost landscapes, precipitation alters both soil water availability and temperature distribution, as percolating water delivers heat to depth and can pool on the permafrost table influencing microbial processes at the active layer–permafrost interface. We hypothesize that along with temperature precipitation is a critical factor regulating the C dynamics in the High Arctic today and will become even more important over the next decades. We explored the magnitudes of tundra–atmosphere C exchange and loss of old permafrost C pools under today's and predicted future climate conditions with experimental wetting and warming[20] in northwest Greenland.

Few studies have investigated multi-factorial climate manipulations in the High Arctic. Two summer-long studies investigated the effects of long-term (>10 years) temperature and/or water manipulations on C cycling in High Arctic tundra[21,22]. Year-round passive 1–2 °C warming increased plant cover without changing ecosystem respiration (R_{eco}; ref. 22), whereas irrigation with or without warming increased R_{eco} (refs 21,22). Neither study detected changes in soil C storage—probably owing to the extreme variability in C pools in patterned ground[6,7].

Here, we quantified net ecosystem exchange of CO_2 (NEE), gross primary productivity (GPP) and R_{eco}, from a High Arctic semi-desert over two or three consecutive summers in a set of long-term (about 10 years) summer warming and/or wetting treatments in northwest Greenland (Supplementary Information). We also measured sources of R_{eco} and below-ground CO_2 using their radiocarbon (^{14}C) contents. Our unique approach allowed us to detect changes in land–atmosphere C exchange and within-soil C dynamics. The experiment consists of a control and three treatments: +4 °C warming, wetting and +4 °C warming× wetting, set up to mimic conditions of about 2050 (refs 20,23). Weather strongly differed among years, with 2012 being the wettest and 2011 the warmest (Supplementary Table 1).

Although vegetated and bare areas each cover approximately 50% of the local surface[6], vegetated areas contributed 83–91% to R_{eco} and 61–95% to NEE at the landscape scale. Year-to-year variations in weather (Supplementary Table 1), particularly precipitation, were reflected in marked changes in R_{eco}, NEE and GPP (Fig. 1a and Table 1), and soil water content (SWC; 11.7 ± 3.9, 14.9 ± 3.2 and 18.3 ± 3.0% in the vegetated control plot in 2010, 2011 and 2012, respectively). During the warmer year 2011, we observed higher R_{eco} and GPP compared with 2010. During the wettest year 2012, R_{eco} was the highest. This is consistent with experimental treatment results, whereby wetting caused the strongest R_{eco} increase (Fig. 1a), and warming × wetting increased GPP threefold and NEE by a factor of 6.5–8.7 in vegetated areas (Table 1). In contrast, experimental warming-only stimulated R_{eco} by merely 15–25%, and decreased NEE by 14–22%. We expect that

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NATURE CLIMATE CHANGE DOI: 10.1038/NCLIMATE2058

Table 1 | NEE (± s.d.) of a High Arctic semi-desert for bare and vegetated areas and the landscape, extrapolated to the entire High Arctic semi-deserts area (~10^6 km²), and separated into R_{eco} (± s.d.) and GPP (± s.d.) for vegetated areas (negative NEE values indicate fluxes of C from the atmosphere to the ecosystem).

Year	Plot	NEE (Tg C)			R_{eco} (Tg C)			GPP (Tg C)
		Landscape	Bare	Veg.	Landscape	Bare	Veg.	Veg.
2010	Control	−8.5 ± 0.5	8.1 ± 0.9	−25.2 ± 0.4	41.0 ± 10.4	4.9 ± 2.5	36.1 ± 10.1	61.3 ± 10.1
	+4 °C × W	−76.8 ± 1.3	9.1 ± 2.3	−162.6 ± 1.0	62.3 ± 3.4	10.3 ± 2.4	52.0 ± 0.4	214.6 ± 1.1
2011	Control	−6.3 ± 0.8	15.1 ± 1.6	−27.6 ± 0.4	94.6 ± 9.7	12.7 ± 7.5	81.9 ± 6.2	109.5 ± 6.2
	+4 °C × W	−110.6 ± 2.7	20.3 ± 5.2	−241.5 ± 1.4	137.6 ± 6.7	17.7 ± 6.2	119.9 ± 2.5	361.4 ± 2.9
	+4 °C	−3.9 ± 1.8	13.9* ± 3.6	−21.7 ± 0.3	110.4 ± 17.4	12.2 ± 6.4	98.2 ± 16.2	119.9 ± 16.2

*Estimated from regression (see Supplementary Information).

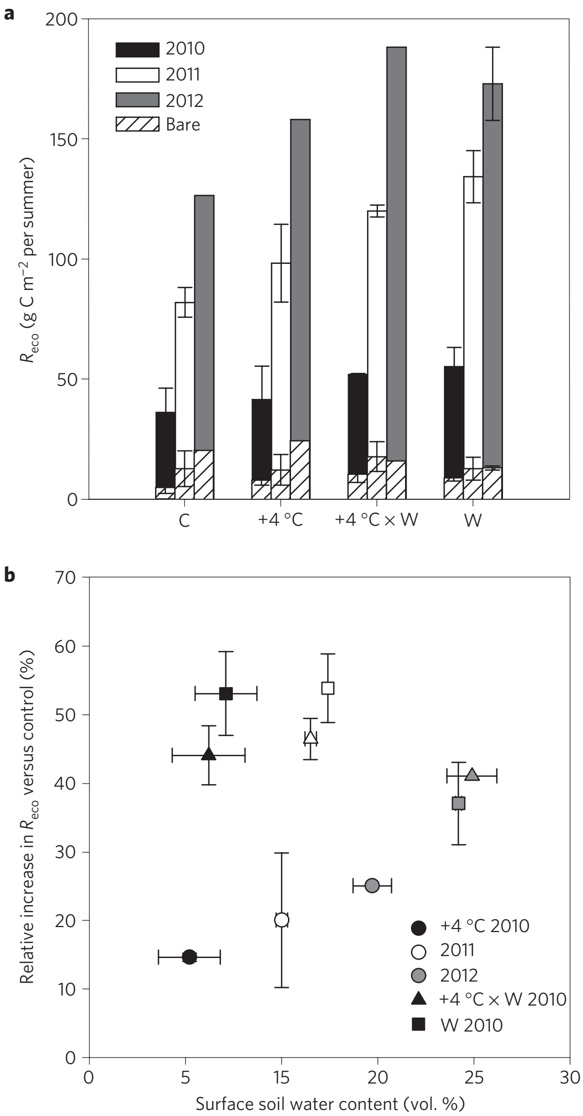

Figure 1 | Summertime R_{eco} for the different experimental treatments. **a**, Cumulative summertime R_{eco} from 2010 to 2012 under three treatments (+4 °C, +4 °C × wetting (W) and W) and a control (C) (average ± s.e.m., $n = 1$–3). (Three-way analysis of variance (ANOVA). Year difference: $F(2, 1583) = 673.0$, $p < 0.001$; treatment condition: $F(3, 1583) = 22.3$, $p < 0.001$; year by treatment interaction: $F(6, 1583) = 4.3$, $p < 0.001$.) **b**, Percentage increase of R_{eco} in treatments compared with the control as a function of SWC (0–10 cm, vegetated plots alone).

the proportional stimulation of R_{eco} due to wetting will be greater in drier years/regions, and decrease with increasing SWC, whereas the opposite is expected for warming (Fig. 1b). Our data demonstrate the important role of increased precipitation in enhancing CO_2 uptake in High Arctic semi-deserts.

Organic C in permafrost soils of this region can be >30,000 yrs old[4,6]. At our site, the mean age of organic C in a vegetated control area ranged from ~1,500 to more than 13,000 years BP; being youngest at the surface and oldest at depth (Supplementary Table 2). Owing to cryoturbation, however, the age of soil C is not necessarily correlated with depth, and pockets of old C may be found near the surface[6]. To quantify the loss of old permafrost C under warming and/or wetting, we measured the ^{14}C content of R_{eco} and of pore space CO_2 as an age proxy. Ecosystem respiration and pore space CO_2 can originate from two different sources distinguishable with ^{14}C: microorganisms decomposing old C, which respire CO_2 with a ^{14}C content lower than that of present atmospheric CO_2; and plants and microorganisms, decomposing root exudates or plant litter, which both respire young CO_2 with a ^{14}C content similar to or higher than that of present atmospheric CO_2 (ref. 25).

During colder and wetter summers (2010, 2012), R_{eco} was dominated by young C recently fixed from the atmosphere (Fig. 2a), indicating that emissions were driven by the respiration of plants and topsoil microorganisms with smaller contributions from older C in the deep soil. In contrast, the large decrease in the ^{14}C content of R_{eco} during the warmest summer (2011) reflected a loss of old, deep C.

A similar image of ecosystem function under climate manipulations emerged from ^{14}C measurements of CO_2 produced belowground. A decade of experimental wetting resulted in on average younger CO_2 produced (Fig. 2b and Supplementary Fig. 1). As the age of soil C increased with depth (Supplementary Table 2), our results indicated that wetting translocated younger C from the surface to depth, where it was decomposed by microorganisms in addition to older C pools. The much younger pore space ^{14}C–CO_2 signature is consistent with translocated younger C contributing the greatest to CO_2 production at these depths. On the basis of the ^{14}C data alone, however, this does not mean that there is no change in the overall rate of decomposition of old C. In contrast, experimental warming-only resulted in older CO_2 being respired at all depths, except the rooting zone (Fig. 2b), indicating that long-term warming increased the loss of mainly slow-accumulating, old C pools. This was most visible during the drier and warmer year 2011, when older CO_2 was observed at 90 cm in all treatments in bare areas—probably owing to higher rates of decomposition of old, *in situ* C and reduced inputs of younger surface C (Fig. 2b).

Our ^{14}C data interpretation is supported by CO_2 exchange results from vegetated areas. We estimated GPP as the difference between NEE and R_{eco} (Table 1). In the warming and warming × wetting

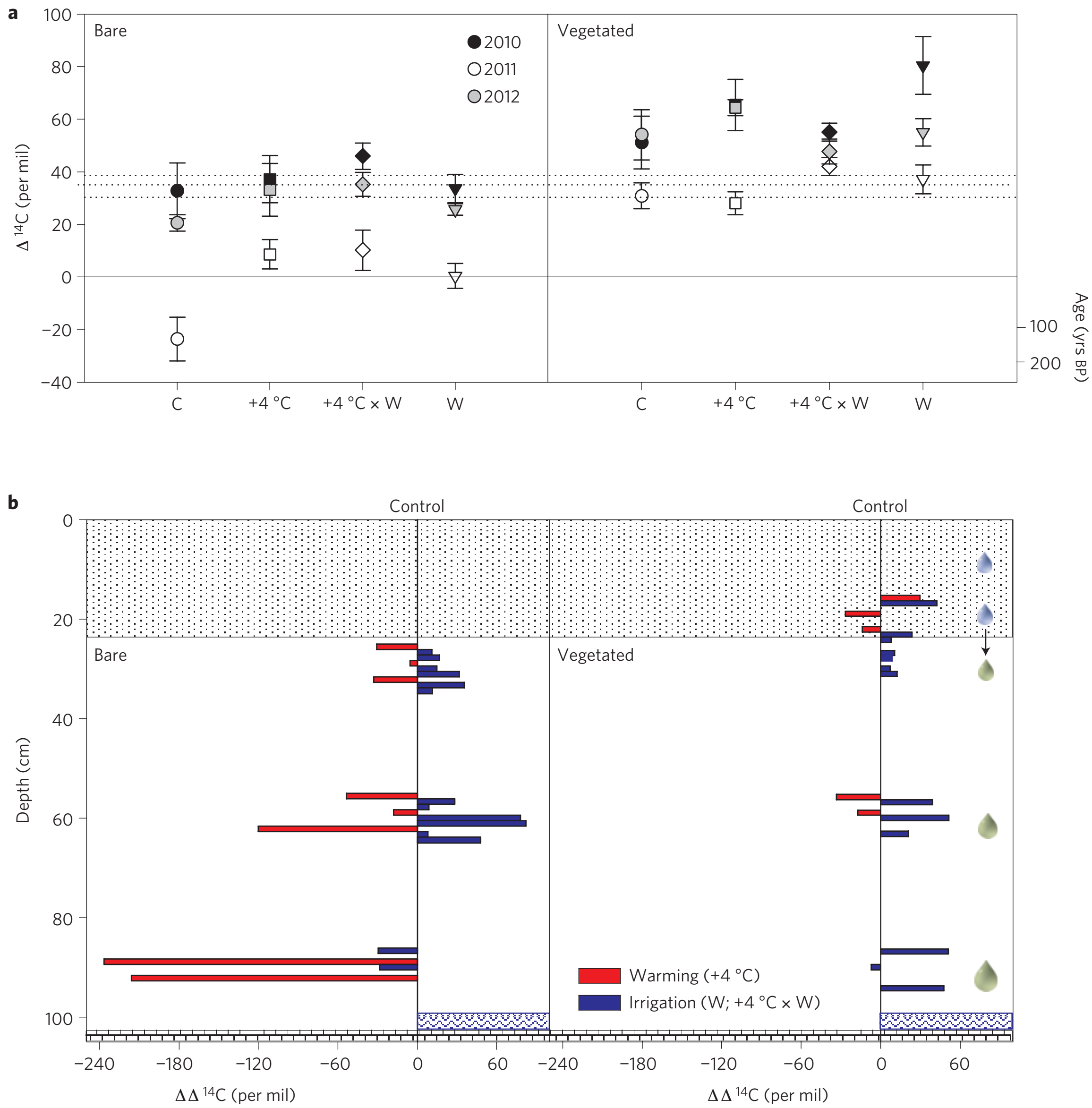

Figure 2 | Radiocarbon content of R_{eco} and pore space CO_2 a, Radiocarbon content of R_{eco} (average ± s.e.m., $n = 6$–12) from bare and vegetated areas from 2010 to 2012. The dotted lines indicate the range of $^{14}CO_2$ in ambient air. (Three-way ANOVA. Year difference: $F(2,146) = 55.2$, $p < 0.001$; treatment condition: $F(3,146) = 0.8$, $p < 0.475$; bare versus vegetated: $F(1,146) = 51.8$, $p < 0.001$.) Root-respired $^{14}CO_2$was 31 ± 2 to 54 ± 11 per mill ($n = 2$–3). **b**, Pore space $^{14}CO_2$ of treatments relative to the control in bare (left) and vegetated (right) areas from 2010 to 2012 ($\Delta\Delta^{14}C = \Delta^{14}C_{Control} - \Delta^{14}C_{Treatment}$). (Three-way ANOVA. Year difference: $F(2,116) = 1.3$, $p < 0.274$; treatment condition: $F(2,116) = 15.7$, $p < 0.001$; bare versus vegetated: $F(1,116) = 41.8$, $p < 0.001$. Each bar represents the difference between a sample collected in a treatment versus in a control plot ($n = 1$ per sampling event per treatment, samples were collected 2–3 times per summer). Negative values indicated that CO_2 generally originated from an older C pool in the warming treatment than the control. In the wetting treatments (W, +4 °C × W), positive numbers indicated that CO_2 originated from a younger C pool. Water percolating through the topsoil (blue drop) gets enriched in young C (green drop) that is decomposed by microbes in addition to the old *in situ* C at depth. From top to bottom: the dot pattern represents the topsoil, which includes the litter layer and rooting zone containing young C; the blue zigzag pattern represents pooling of water on the permafrost table; the brick pattern represents the permafrost table).

treatments, GPP and R_{eco} increased relative to control conditions. For warming × wetting, the more than threefold increase in GPP far exceeded the 40% increase in R_{eco}, indicating that the additional (recently fixed) C was stored in the standing plant biomass, litter or mineral soil. In contrast, the increase in GPP (9%) was slightly lower than that in R_{eco} (20%) for warming-only, and release of (older) soil C must have contributed to R_{eco}. Increases in leaf area (data not shown) may underlie the increase in GPP. At the landscape scale, increases in deciduous shrub cover and biomass have also been proposed to result in increasing GPP (ref. 24).

As we observed the largest changes in the ^{14}C content of R_{eco} interannually, we calculated the loss of old C during each year under ambient conditions using a two-pool model as a first approximation of C source proportions. Emissions of old C were 7.1 ± 2.4, 40.5 ± 7.8 and 23.8 ± 6.4 $g\,C\,m^{-2}$ for the summer of 2010, 2011 and 2012, respectively (Fig. 3a). This indicates that warmer and wetter conditions during the growing season (for example 2012) will result in smaller losses of old C from High Arctic semi-deserts than warmer and drier conditions (for example, 2011).

As the High Arctic spans only ∼10% of the Northern Hemisphere permafrost area, it contains a relatively small fraction

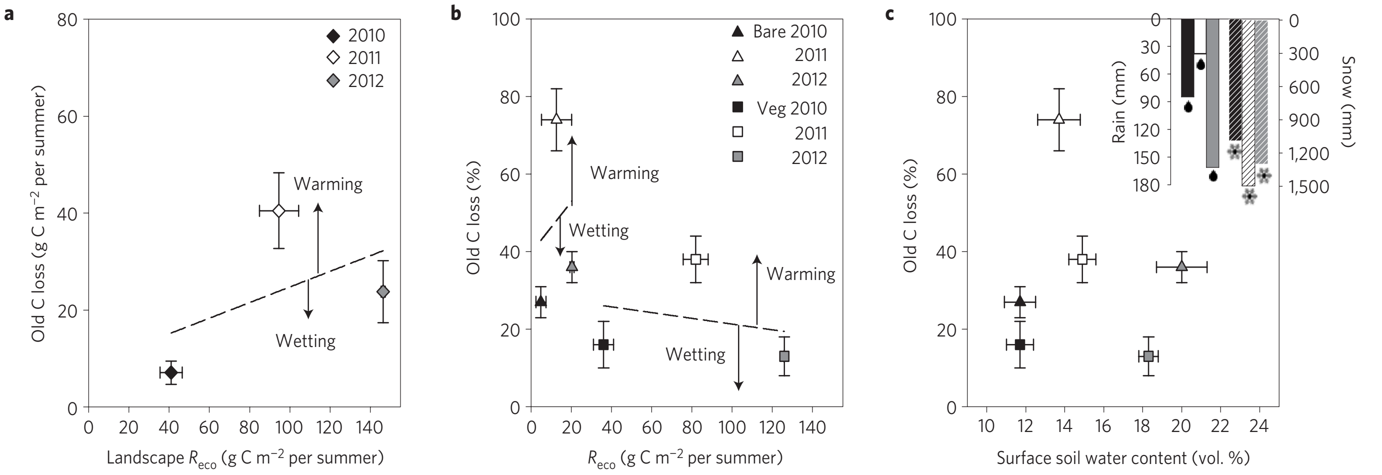

Figure 3 | Loss of old C as a function of warming and wetting. a, Loss of old C (R_{eco}) versus landscape (bare + vegetated) R_{eco} (average ± propagated error). **b**, Percentage loss of old C versus R_{eco}. **c**, Surface SWC in bare and vegetated areas from 2010 to 2012 (average ± s.e.m.). The legend in **b** also applies to **c**. The inset in **c** shows cumulative rain (June–August) and previous winter snow (September–May) amounts. The dashed lines represent a linear regressions.

of the total permafrost C. However, any increases in old permafrost C decomposition would have long-lasting implications for atmospheric CO_2. Decomposition of old C that was not part of the active C cycle for millennia results in a net flux of C to the atmosphere whereas rapid C cycling between plants and microbes has a near zero effect on atmospheric CO_2 (ref. 25).

Earlier work from moist acidic tundra in the Low Arctic showed that loss of old C can be described as a direct function of R_{eco} (ref. 13). At our High Arctic semi-desert site, however, old C loss was strongly modulated by SWC and thus precipitation. Older C contributions accounted for 13 ± 5 to 38 ± 6% of R_{eco} in vegetated, and 27 ± 4 to 74 ± 8% in bare areas (Fig. 3b). We observed the highest relative old C losses at intermediate R_{eco} and SWC (Fig. 3b,c).

Although both warming and wetting stimulated R_{eco} and losses of old permafrost C, proportionally less old C was lost in a wetting scenario. We attribute this to: higher precipitation leaching recently assimilated plant C from the surface to depth (Fig. 2b), forming an important C source for microorganisms; and water pooling on the permafrost table during heavy precipitation events, limiting the decomposition of older C at depth.

The local trajectories of arctic surface hydrology are highly uncertain. Depending on ice content, relief and temperature, permafrost thaw may locally result in either increasing or decreasing SWC (ref. 26). On a regional scale, however, an overall wetting of the Arctic is expected as a consequence of increased moisture in the atmosphere due to reduced sea ice[27] and added transport into the Arctic[10].

We studied two extreme scenarios: warming-only versus warming combined with a 50% increase in summer precipitation—providing upper and lower estimates to the High Arctic C feedback. Extrapolating to the area of High Arctic semi-deserts (~10^6 km^2, ~50% of the ice-free High Arctic), these ecosystems would take up 6.3–8.5 Tg C per summer at present (Table 1). Wetting and warming would boost uptake by an order of magnitude to 76.8–110.6 Tg C owing to strongly enhanced GPP, whereas warming-only would reduce the summer C sink to 3.9 ± 1.8 Tg C. Further, wetting dampens the loss of old permafrost C pools, which would be lost more rapidly under warming-only. Our data indicate that the net C balance and loss of old C in High Arctic semi-deserts are strongly related to changes in precipitation and SWC. A better understanding of arctic wetting will thus be a key challenge for better predictions of changes in the biogeochemistry of High Arctic ecosystems. Our study integrates information on NEE, GPP, R_{eco} and the contribution of old C from permafrost, for present conditions as well as a range of climate change treatments. With this unique combination, we provide a critical benchmark data set to evaluate process-based models of High Arctic ecosystems, and simulations of their changing C cycle in response to climate change.

Methods

The multifactorial experiment, established in 2003, consists of a control and three treatments: +4 °C warming; wetting; and +4 °C warming × wetting. The warming treatment was based on temperature models to mimic ~2050 (ref. 23). Irrigation treatments increase growing season precipitation by approximately 50% relative to 1971–2000 (ref. 20). Measurements were conducted from the end of May to the end of August.

NEE was measured with automated clear chambers coupled to a Picarro G1301 analyser. GPP was calculated by the difference between NEE and R_{eco}.

Ecosystem respiration and soil pore space CO_2 concentrations were measured at least three times a week with infrared gas analysers. Ecosystem respiration was measured using opaque chambers, and soil CO_2 concentrations were measured using stainless-steel gas wells inserted throughout the active layer.

Gas samples for ^{14}C analysis were collected monthly. Ecosystem respiration, CO_2 in ambient air and root-respired CO_2 were captured on molecular sieve traps. Roots were manually extracted, rinsed and incubated in CO_2-free air for 24 h. Soil gas was collected in pre-evacuated canisters using flow-restricting capillaries. Concentrations of organic C along the soil profile were measured by elemental analysis.

For ^{14}C analysis, CO_2 was released from molecular sieve traps by heating at 650 °C for 45 min or extracted from canisters on a vacuum line, purified cryogenically and reduced to graphite through zinc reduction and analysed at UC Irvine's W. M. Keck Carbon Cycle Accelerator Mass Spectrometer facility[28]. Soil samples were first combusted to CO_2 in pre-combusted, evacuated quartz tubes with cupric oxide for 2 h at 900 °C.

We used a two-pool mixing model[29] to estimate the contributions from older, below-ground permafrost soil C versus young, surface soil C to R_{eco}.

Received 24 April 2013; accepted 29 October 2013; published online 1 December 2013

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Acknowledgements

This work was made possible by assistance from US Air Force Base Thule, Greenland, CH2M Hill Polar Services, and the KCCAMS laboratory. We thank all research assistants: A. Stills, D. S. Lindsey, J. Thomas, J. Yi and M. Ruacho, and research engineer C. Lett. This work was financially supported by the US National Science Foundation (ARC-0909514 to C.I.C. and ARC-0909538 to J.M.W.) and the European Research Council (FP/2007-2013, ERC Grant Agreement no. 202835) to U.S.

Author contributions

J.M.W. and C.I.C. conceived and designed the experiment. M.L., X.X. and C.I.C. processed and analysed radiocarbon samples. M.L. performed research and analysed radiocarbon and R_{eco} data. U.S. and K.M. analysed NEE data. All authors commented on the analysis and presentation of the data and were involved in the writing.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to M.L.

Competing financial interests

The authors declare no competing financial interests.

ERRATUM

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Nature Clim. Change http://dx.doi.org/10.1038/nclimate2058 (2013); published online 1 December 2013; corrected online 9 December 2013.

In the version of this Letter originally published, in the legend for Fig. 2b, the label for Irrigation should have been 'W; 4 °C × W'. This error has now been corrected in all versions of the Letter.