REPORT

CARBON CYCLE

The whole-soil carbon flux in response to warming

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Soil organic carbon harbors three times as much carbon as Earth's atmosphere, and its decomposition is a potentially large climate change feedback and major source of uncertainty in climate projections. The response of whole-soil profiles to warming has not been tested in situ. In a deep warming experiment in mineral soil, we found that CO_2 production from all soil depths increased with 4°C warming; annual soil respiration increased by 34 to 37%. All depths responded to warming with similar temperature sensitivities, driven by decomposition of decadal-aged carbon. Whole-soil warming reveals a larger soil respiration response than many in situ experiments (most of which only warm the surface soil) and models.

Globally, almost 3000 Pg C is stored as soil organic carbon (SOC) (*1*). Warming is expected to increase microbial decomposition of SOC, thereby releasing more CO_2 into the atmosphere. However, the amount and rate of this response are highly uncertain because the mechanisms controlling the microbial accessibility of SOC are not fully understood (*2*). Empirical determination of the temperature response from whole-soil profiles (0 to >100 cm) has been difficult. The majority of in situ warming experiments focus on warming the top 5 to 20 cm of surface soil (table S1); thus, they may miss the response of subsoils (below 20 cm), which contain >50% of global SOC stocks (*3*). Alternatives to field manipulations are not ideal; incubations have large experimental artifacts, whereas seasonal temperature gradients confound warming with factors such as phenology and soil moisture (*4*). As a result, we currently lack data on the whole-soil response to warming (*5*).

Uncertainty surrounding the SOC warming response increases with soil depth because the mechanisms that control subsoil OC's long turnover times [often thousands of years (*6*, *7*)] are unknown, as is the temperature sensitivity of these mechanisms (*8*). Such long turnover times do not preclude subsoil OC from playing an active role in global carbon cycling (*6*, *9*). If the slow turnover times of subsoil OC are due to inherent chemical recalcitrance, then subsoil OC may be more responsive to warming than surface SOC according to kinetic theory (*10*). However, if reduced microbial access to SOC (*11*) slows turnover times as a result of physical protection (in aggregates), mineral associations (formation of organo-mineral complexes), or spatial heterogeneity of microbially active "hotspots" (i.e., roots or preferential flow paths), then subsoil OC may be less responsive to warming than surface SOC (*11*, *12*), although we lack a theoretical or empirical basis for such a prediction. The subsoil response to temperature has been tested in laboratory incubations with inconsistent results (*11*, *13*, *14*) but has yet to be tested in situ.

Here, we present results from a controlled, replicated in situ deep mineral soil warming experiment to determine the response of an undisturbed whole-soil profile to warming (+4°C). We tested the sensitivity of soil CO_2 production to warming from 0 to 100 cm and whether there was acclimation over 2 years. We used radiocarbon to determine whether warming resulted in the decomposition of older SOC. This study was located in a coniferous temperate forest in soils classified as alfisols containing 16.6 ± 1 kg C m^{-2} in the top meter. Alfisols cover 13.5% of Earth's ice-free land area and store 8% of global soil C (*15*).

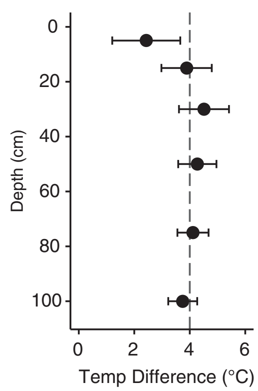

Fig. 1. Mean temperature difference between the control and heated plots by depth over the study period (March 2014 through February 2016). Error bars denote SD of the temporal variability.

Over the next century, subsoils are projected to warm at roughly the same rate as surface soils. Intergovernmental Panel on Climate Change simulations of global average soil temperature under Representative Concentration Pathway 8.5 predict that the whole-soil profile will warm 4°C by 2100 in our study region (*16*). We warmed soils 4° ± 0.75°C from 10 cm down to 100 cm in the soil profile in three pairs of control and heated plots from November 2013 through February 2016 (Fig. 1 and figs. S1 and S2). We used 22 heating rods, each 2.4 m deep, arranged around plots 3 m in diameter (*17*) with two additional circular heating cables buried 5 cm below the soil surface at radii of 0.5 and 1 m from the plot center. This method imposed 4°C warming while preserving the natural depth gradient and temporal variations in soil temperature. At 5 cm, because of the lack of aboveground heating, the heated plots were on average only 2.4° ± 1.2°C warmer than the control. Soil moisture was slightly decreased in the warmed plots by an average of 1.5 to 3.5% volumetric water content (fig. S3). The soil respiration response, which included microbial and root respiration (but see supplementary text), was determined monthly from seven replicate surface flux measurements per plot and by measuring gas well CO_2 concentrations at five depths (15, 30, 50, 70, and 90 cm), from which depth-resolved CO_2 production estimates were modeled using Fick's law.

Warming by 4°C increased whole-profile soil respiration by 34 to 37%, depending on the measurement method. The response measured from the surface was a 34% increase from 1100 ± 31 g C m^{-2} $year^{-1}$ to 1450 ± 43 g C m^{-2} $year^{-1}$ (treatment effect, $P < 0.0001$; table S2). The response estimated from gas well data was a similar 37% increase from 1300 to 1750 g C m^{-2} $year^{-1}$. The mean Q_{10}, the factor by which respiration increases as a result of a 10°C rise in temperature, for the whole-soil profile (measured from the surface) was 2.4 ± 0.3; this Q_{10} is "apparent" because it describes the emergent response of many processes and is constrained by field conditions. For each sampling date, Q_{10} was calculated by comparing the respiration and soil temperature (10 cm) in each control and heated plot pair. By directly comparing plot pairs to calculate Q_{10} instead of fitting a curve to all respiration and temperature data, we avoided confounding the temperature response with seasonal changes in soil moisture (fig. S4) or plant inputs (*4*). A Q_{10} of 2.4 is equivalent to the estimated global median for soil respiration (*18*) and similar to the mean Q_{10} of 2.6 for sites spanning the 10° to 20°C temperature range in a global soil respiration database (*19*).

There was no decline in temperature sensitivity (Q_{10}) of whole-profile soil respiration over 27 months of warming (linear regression, $P = 0.5$; fig. S5), which indicates that soil respiration did not acclimate to warming or become substrate-limited, in line with a recent

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Table 1. Mean soil carbon properties ± SE (n = 3) in 10-cm increments from 0 to 100 cm.

Mid depth (cm)	%C	C:N	$\delta^{13}C$ (‰)	C stock ($g\ C\ m^{-2}$)	Proportion total C	Proportion C in free light fraction	Proportion C in occluded light fraction	Proportion C in dense fraction
5	8.3 ± 0.8	28.1 ± 2.7	−25.3 ± 0.3	6052 ± 478	0.365 ± 0.015			
15	3.0 ± 0.3	24.8 ± 1.5	−25.1 ± 0.0	3048 ± 399	0.183 ± 0.018	0.23 ± 0.03	0.15 ± 0.01	0.48 ± 0.05
25	1.9 ± 0.1	23.7 ± 1.3	−24.9 ± 0.1	2223 ± 139	0.134 ± 0.002			
35	1.1 ± 0.1	23.9 ± 0.5	−24.4 ± 0.2	1331 ± 94	0.080 ± 0.002			
45	0.7 ± 0.1	24.1 ± 0.1	−23.8 ± 0.1	903 ± 68	0.055 ± 0.004	0.25 ± 0.02	0.10 ± 0.03	0.47 ± 0.04
55	0.5 ± 0.1	25.9 ± 1.9	−23.7 ± 0.1	751 ± 108	0.045 ± 0.005			
65	0.3 ± 0.0	23.6 ± 1.2	−23.2 ± 0.1	429 ± 5	0.026 ± 0.001			
75	0.4 ± 0.1	26.0 ± 1.7	−23.1 ± 0.4	553 ± 98	0.034 ± 0.008			
85	0.4 ± 0.1	30.3 ± 2.6	−23.5 ± 0.2	563 ± 124	0.034 ± 0.006			
95	0.5 ± 0.2	34.4 ± 3.6	−23.8 ± 0.4	718 ± 192	0.044 ± 0.014	0.36 ± 0.03	0.10 ± 0.03	0.46 ± 0.09

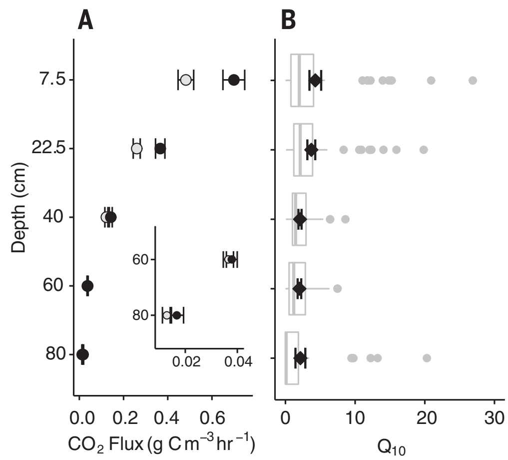

Fig. 2. Warming response of different soil depths. (**A**) Mean CO_2 production (±SE) by depth increment in the control (gray circles) and heated (black circles) plots averaged over 20 months (n = 3). The depth increments are 0 to 15 cm, 15 to 30 cm, 30 to 50 cm, 50 to 70 cm, and 70 to 90 cm. The inset expands the two deepest increments. (**B**) Mean apparent Q_{10} (±SE, black diamonds) averaged over 20 months is similar across depths, with a slight increase at depths above 30 cm. The box plots in gray show the median (thick gray line), the 25th and 75th percentiles (thin vertical lines), and outliers (gray circles).

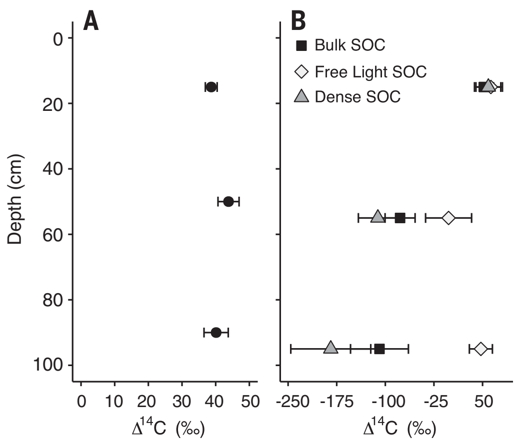

Fig. 3. Potential sources of respired CO_2. (**A**) Mean radiocarbon values (±SE) of soil profile CO_2 are modern (>0‰) and do not differ among depths (n = 6, P = 0.77) or between treatments (not shown; n = 9, P = 0.21). (**B**) Mean radiocarbon values (±SE) of bulk SOC, free light-fraction SOC, and mineral-associated dense-fraction SOC. A potential source of the modern soil profile CO_2 is the free light fraction, which is also modern and does not differ significantly among depths, unlike the bulk and dense-fraction SOC (n = 3, P = 0.02).

meta-analysis (*20*). Generally, the greatest production rates and Q_{10}s occurred in the wet winter months (fig. S5). However, there were no clear seasonal trends, a result of the compensatory effects of the opposing seasonal cycles of soil temperature and moisture in this Mediterranean climate (r = −0.8; fig. S4).

The observed 34 to 37% increase in soil respiration due to warming is larger than the 9% (*21*) and 12% (*22*) average increases in soil respiration calculated in meta-analyses of warming experiments and is larger than most responses from individual warming experiments (table S1). Although our large warming response may be a function of our soil type or forest ecosystem (*21*), it is also due in part to warming the whole-soil profile. Most warming studies likely miss a substantial proportion of the warming response by only warming the surface soil. The magnitude of the missing response is unclear because most studies do not report warming below 20 cm (table S1). Furthermore, in the few warming studies that measured warming at multiple depths, the magnitude of warming attenuated with depth (table S1). If anything, our measured increase in soil respiration underestimates the actual response to 4°C warming, because the top 5 cm of the soil profile was warmed by only 2.4°C.

About 50% of soil respiration and 40% of the warming response occurred below 15 cm in the soil profile, where 63% of the SOC stock (to 1 m) resides; about 20% of soil respiration and 10% of the warming response occurred below 30 cm, where 32% of the SOC stock resides (Table 1). CO_2 production from soil depth increments increased significantly as a result of warming (treatment effect, P = 0.03; Fig. 2A and table S2). All depth increments were sensitive to warming, with a mean apparent Q_{10} of 2.7 ± 0.3 (Fig. 2B). There was an increase in Q_{10} for depth increments above 30 cm, but depth was not a significant effect in a regression model (P > 0.10; table S2). As a result of the slightly lower Q_{10} at depth, subsoils below 30 cm contributed more to total CO_2 production in the control plots than in the warmed plots (23.4% versus 19.8%). This relatively consistent response across depth increments contrasts with those of many lab incubations (*11*, *13*, *23*). Our results support the assumption of depth-resolved terrestrial biosphere models (*24*, *25*) that SOC has similar temperature sensitivities across depths, but do not support the magnitude of modeled temperature sensitivity. Our soil's Q_{10} was greater than the Q_{10} used by most Earth system models (*26*).

At all depths, respiration was dominated by carbon fixed within the past 50 years according to $^{14}CO_2$ values (40.9 ± 1.7‰; Fig. 3A), as previously seen in other soils (*27*, *28*). There was no significant difference in soil profile $^{14}CO_2$ between control and warmed plots (treatment effect, P = 0.21), so warming did not preferentially increase decomposition of old relative to new SOC. Thus, the "carbon-quality-temperature" hypothesis—that older, and potentially more recalcitrant, SOC has greater temperature sensitivity than younger SOC—was not supported. The radiocarbon sampling occurred in February, when the respiration response was greatest and plants were less active (*29*), so the carbon source was mainly heterotrophic. Furthermore, the ^{14}C of heterotrophic respiration (42.5 ± 3.7‰; from short-term, root-free soil incubations) was similar to the soil $^{14}CO_2$ and also did not differ among depths of 10 to 20 cm, 45 to 55 cm, and 85 to 95 cm (depth effect, P = 0.28). The heterotrophic and soil $^{14}CO_2$ values are consistent with the modern $\Delta^{14}C$ of the free light-fraction SOC (35.9 ± 16‰), which is not physically protected or mineral-protected, making the light fraction a likely source of respired CO_2. Light-fraction SOC was modern throughout the soil profile, unlike bulk and dense-fraction, mineral-associated SOC, which became significantly more depleted with depth (depth × fraction interaction, P = 0.02; Fig. 3B). A similar proportion of SOC was in the light fraction at depths of 5 to 15 cm, 40 to 50 cm, and 90 to 100 cm (depth effect, P = 0.62; Table 1). Thus, although the amount of SOC decreased significantly with depth, 25 to 36% of SOC below 30 cm was decadal-aged light fraction. Subsoil likely had similar temperature sensitivities to surface soil because this modern SOC pool, not protected in aggregates or by minerals, drove the warming response.

Despite having bulk residence times on the order of 1000 years, the decomposition of subsoil carbon responds to warming. Subsoils (>30 cm) contributed to 20 to 25% of whole-profile soil respiration and to 10% of the warming response in a temperate alfisol. These values had not been observed before and are substantial when projecting potential soil carbon feedbacks to climate change. Given the presence of decadal-cycling SOC (*9*) and the predominance of modern $^{14}CO_2$ throughout diverse soil profiles (*27*, *28*, *30*), other subsoils are likely also responsive to warming. In our study, warming caused subsoils to respire an additional 47 g C m^{-2} $year^{-1}$, corresponding to 2.8 g C per kg of whole-profile soil C. As a preliminary test of global significance, extrapolating the subsoil response to all mineral soil orders (leaving out cryosols, histosols, and moisture-limited aridisols) on a C stock basis [1091 Pg (*15*)], subsoils could lose 3.1 Pg C $year^{-1}$ as a result of 4°C warming. This estimate assumes that all mineral soils have similar microbial accessibility and depth distributions of SOC and is based on our soil's initial response, which may be transient (*31*). However, this potentially large subsoil response to warming should not be ignored. The response would be roughly 3% of current global ecosystem respiration (*32*) and roughly 30% of current anthropogenic emissions (*33*). Because previous warming experiments have missed the response of deeper soils to warming, and because terrestrial models often have a low Q_{10}, the strength of the SOC-climate feedback may be currently underestimated.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/355/6332/1420/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S6
Tables S1 to S5
References (*34*–*78*)

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Digging deeper into soils

Soils contain about twice as much carbon as Earth's atmosphere, so their response to warming is crucial to understanding carbon fluxes in a changing climate. Past studies have heated soil to a depth of 5 to 20 cm to examine such fluxes. Hicks Pries *et al.* heated the ground to a depth of 100 cm. Extending measurements to that depth revealed that 4°C of warming increased annual soil respiration by 34 to 37%––a considerable amount more than previously observed.

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