

UC Berkeley

UC Berkeley Previously Published Works

Title

The whole-soil carbon flux in response to warming

Permalink

<https://escholarship.org/uc/item/1b60g2n2>

Journal

Science, 355(6332)

ISSN

0036-8075

Authors

Hicks Pries, Caitlin E
Castanha, C
Porras, RC
[et al.](#)

Publication Date

2017-03-31

DOI

10.1126/science.aal1319

Peer reviewed

Cite as: C. E. Hicks Pries *et al.*, *Science*
10.1126/science.aal1319 (2017).

The whole-soil carbon flux in response to warming

Caitlin E. Hicks Pries,* C. Castanha, R. Porras, M. S. Torn*

Climate Sciences Department, Climate and Ecosystem Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, CA 94720, USA.

*Corresponding author. Email: cehpries@lbl.gov (C.E.H.P.); mstorn@lbl.gov (M.S.T.)

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 this deep warming experiment in mineral soil, CO₂ production from all soil depths increased significantly with 4°C warming—annual soil respiration increased by 34–37%. 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, releasing more CO₂ 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 five to 20 cm of surface soil (table S1) and may thus 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 while seasonal temperature gradients confound warming with other factors like phenology and soil moisture (4). As a result, we currently lack data on the whole-soil warming response (5).

Uncertainty surrounding the SOC warming response increases with soil depth because the mechanisms controlling subsoil OC's long turnover times (often 1000's of years; (6, 7) and their temperature sensitivity are unknown (8). These 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 due to 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), subsoil OC may be less responsive to warming than surface SOC (11, 12), but we lack a theoretical or empirical basis with which to predict this. 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 CO₂ production to warming from 0 to 100 cm and whether there was acclimation over 2 years. We used radiocarbon to determine if 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).

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 (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, 2.4 m deep heating rods arranged around 3 m diameter plots (17) with two additional circular heating cables buried 5 cm below the soil surface at 0.5 and 1 m radii from plot center. This method imposed 4°C warming while preserving the natural depth gradient and temporal variations in soil temperature. At 5 cm, due to 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 1.5–3.5% 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 CO₂ concentrations at five depths (15, 30, 50, 70, and 90 cm), from which depth-

resolved CO₂ production estimates were modeled using Fick's Law.

Warming 4°C increased whole profile soil respiration by 34-37%, depending on the measurement method. The response measured from the surface was a 34% increase from 1100 ± 31 to 1450 ± 43 g C m⁻² y⁻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 y⁻¹. The mean Q₁₀, the factor by which respiration increases due to a 10°C rise in temperature, for the whole-soil profile (measured from the surface) was 2.4 ± 0.3 ; this Q₁₀ is “apparent” because it describes the emergent response of many processes and is constrained by field conditions. For each sampling date, Q₁₀ was calculated comparing the respiration and soil temperature (10 cm) in each control and heated plot pair. By directly comparing plot pairs to calculate Q₁₀ 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 Q₁₀ of 2.4 is equivalent to the estimated global median for soil respiration (18) and similar to the mean Q₁₀ of 2.6 for sites spanning the 10-20°C temperature range in the global soil respiration database (19).

There was no decline in temperature sensitivity (Q₁₀) of whole profile soil respiration over 27 months of warming (linear regression, $p = 0.5$; fig. S5), indicating soil respiration did not acclimate to warming or become substrate limited in line with a recent meta-analysis (20). Generally, the greatest production rates and Q₁₀'s occurred in the wet winter months (fig. S5). However, there were no clear seasonal trends due to the compensatory effects of low soil temperature and high soil moisture in this Mediterranean climate ($r = -0.8$, fig. S4).

The observed 34-37% 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). While 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 since 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 only warmed 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, and about 20% of soil respiration and 10% of the warming response occurred below 30 cm, where 32% of the SOC stock resides (Table 1). CO₂ production within all soil depth increments increased significantly due to warming (Treatment effect, $p = 0.0001$; Fig. 2A and table S2). All depth increments were sensitive to warming with a mean apparent Q₁₀ of 2.7 ± 0.3 (Fig. 2B). There was an increase in Q₁₀ for depth increments above 30 cm, but depth was not a significant effect in a regression model ($p > 0.17$; table S2). As a result of the slightly lower Q₁₀ at depth, subsoils below 30 cm contributed more to total CO₂ 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 Q₁₀ was greater than the Q₁₀ used by most Earth system models (26).

At all depths, respiration was dominated by carbon fixed within the past 50 years based on ¹⁴CO₂ values ($40.9 \pm 1.7\%$; Fig. 3A), as previously seen in other soils (27, 28). There was no significant difference in soil profile ¹⁴CO₂ 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 sensitivities 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 ¹⁴C of heterotrophic respiration ($42.5 \pm 3.7\%$; from short-term, root-free soil incubations) was similar to the soil ¹⁴CO₂ and also did not differ among 10-20, 45-55, and 85-95 cm depths (Depth effect, $p = 0.28$). The heterotrophic and soil ¹⁴CO₂ values are consistent with the modern Δ^{14} C of the free light fraction SOC ($35.9 \pm 16\%$), which is not physically or mineral-protected, making the light fraction a likely source of respired CO₂. Light fraction SOC remained modern throughout the soil profile, unlike bulk and dense-fraction, mineral-associated SOC, which became significantly more depleted with depth (Depth x Fraction interaction, $p = 0.02$; Fig. 3B). A similar proportion of SOC was in the light fraction at 5-15, 40-50, and 90-100 cm depths (Depth effect, $p = 0.62$; Table 1). Thus, while the amount of SOC decreased significantly with depth, 25-36% 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 20–25% 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 ¹⁴C₂ 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 y⁻¹, corresponding to 2.8 g C per kg 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 y⁻¹ due to 4°C warming. This estimate assumes 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 Q₁₀, the strength of the soil organic carbon-climate change feedback may be currently underestimated.

REFERENCES AND NOTES

- M. Köchy, R. Hiederer, A. Freibauer, Global distribution of soil organic carbon—Part I: Masses and frequency distributions of SOC stocks for the tropics, permafrost regions, wetlands, and the world. *Soil* **1**, 351–365 (2015). doi:10.5194/soil-1-351-2015
- M. W. Schmidt, M. S. Torn, S. Abiven, T. Dittmar, G. Guggenberger, I. A. Janssens, M. Kleber, I. Kögel-Knabner, J. Lehmann, D. A. C. Manning, P. Nannipieri, D. P. Rasse, S. Weiner, S. E. Trumbore, Persistence of soil organic matter as an ecosystem property. *Nature* **478**, 49–56 (2011). doi:10.1038/nature10386 Medline
- E. G. Jobbágy, R. B. Jackson, The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.* **10**, 423–436 (2000). doi:10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2
- M. Reichstein, C. Beer, Soil respiration across scales: The importance of a model-data integration framework for data interpretation. *J. Plant Nutr. Soil Sci.* **171**, 344–354 (2008). doi:10.1002/jpln.200700075
- T. W. Crowther, K. E. O. Todd-Brown, C. W. Rowe, W. R. Wieder, J. C. Carey, M. B. Machmuller, B. L. Snoek, S. Fang, G. Zhou, S. D. Allison, J. M. Blair, S. D. Bridgman, A. J. Burton, Y. Carrillo, P. B. Reich, J. S. Clark, A. T. Classen, F. A. Dijkstra, B. Elberling, B. A. Emmett, M. Estiarte, S. D. Frey, J. Guo, J. Harte, L. Jiang, B. R. Johnson, G. Krøe-Dulay, K. S. Larsen, H. Laudon, J. M. Lavallee, Y. Luo, M. Lupascu, L. N. Ma, S. Marhan, A. Michelsen, J. Mohan, S. Niu, E. Pendall, J. Peñuelas, L. Pfeifer-Meister, C. Poll, S. Reinsch, L. L. Reynolds, I. K. Schmidt, S. Sistla, N. W. Sokol, P. H. Templer, K. K. Treseder, J. M. Welker, M. A. Bradford, Quantifying global soil carbon losses in response to warming. *Nature* **540**, 104–108 (2016). doi:10.1038/nature20150 Medline
- A. A. Berhe, J. W. Harden, M. S. Torn, J. Harte, Linking soil organic matter dynamics and erosion-induced terrestrial carbon sequestration at different landform positions. *J. Geophys. Res.* **113**, G04039 (2008). doi:10.1029/2008.JG000751
- K. Eusterhues, C. Rumpel, M. Kleber, I. Kögel-Knabner, Stabilisation of soil organic matter by interactions with minerals as revealed by mineral dissolution and oxidative degradation. *Org. Geochem.* **34**, 1591–1600 (2003). doi:10.1016/j.orggeochem.2003.08.007
- C. Rumpel, I. Kögel-Knabner, Deep soil organic matter—a key but poorly understood component of terrestrial C cycle. *Plant Soil* **338**, 143–158 (2011). doi:10.1007/s11104-010-0391-5
- J. Koarashi, W. C. Hockaday, C. A. Masiello, S. E. Trumbore, Dynamics of decadal cycling carbon in subsurface soils. *J. Geophys. Res.* **117**, G03033 (2012). doi:10.1029/2012.JG002034
- E. A. Davidson, I. A. Janssens, Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **440**, 165–173 (2006). doi:10.1038/nature04514 Medline
- J. Gillabel, B. Cebrian-Lopez, J. Six, R. Merckx, Experimental evidence for the attenuating effect of SOM protection on temperature sensitivity of SOM decomposition. *Glob. Change Biol.* **16**, 2789–2798 (2010). doi:10.1111/j.1365-2486.2009.02132.x
- C. Salomé, N. Nunan, V. Pouteau, T. Z. Lerch, C. Chenu, Carbon dynamics in topsoil and in subsoil may be controlled by different regulatory mechanisms. *Glob. Change Biol.* **16**, 416–426 (2010). doi:10.1111/j.1365-2486.2009.01884.x
- N. Fierer, A. S. Allen, J. P. Schimel, P. A. Holden, Controls on microbial CO₂ production: A comparison of surface and subsurface soil horizons. *Glob. Change Biol.* **9**, 1322–1332 (2003). doi:10.1046/j.1365-2486.2003.00663.x
- C.-E. Gabriel, L. Kellman, Investigating the role of moisture as an environmental constraint in the decomposition of shallow and deep mineral soil organic matter of a temperate coniferous soil. *Soil Biol. Biochem.* **68**, 373–384 (2014). doi:10.1016/j.soilbio.2013.10.009
- H. Eswaran, E. Van Den Berg, P. Reich, Organic carbon in soils of the world. *Soil Sci. Soc. Am. J.* **57**, 192–194 (1993). doi:10.2136/sssaj1993.036159950057000100034x
- IPCC, *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge Univ. Press, 2013); www.ipcc.ch/report/ar5/wg1/.
- P. J. Hanson, K. W. Childs, S. D. Wullschlegel, J. S. Riggs, W. K. Thomas, D. Todd, J. M. Warren, A method for experimental heating of intact soil profiles for application to climate change experiments. *Glob. Change Biol.* **17**, 1083–1096 (2011). doi:10.1111/j.1365-2486.2010.02221.x
- J. W. Raich, W. H. Schlesinger, The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B* **44**, 81–99 (1992). doi:10.3402/tellusb.v44i2.15428
- B. Bond-Lamberty, A. Thomson, A global database of soil respiration data. *Biogeosciences* **7**, 1915–1926 (2010). doi:10.5194/bg-7-1915-2010
- J. C. Carey, J. Tang, P. H. Templer, K. D. Kroeger, T. W. Crowther, A. J. Burton, J. S. Dukes, B. Emmett, S. D. Frey, M. A. Heskell, L. Jiang, M. B. Machmuller, J. Mohan, A. M. Panetta, P. B. Reich, S. Reinsch, X. Wang, S. D. Allison, C. Bamminger, S. Bridgman, S. L. Collins, G. de Dato, W. C. Eddy, B. J. Enquist, M. Estiarte, J. Harte, A. Henderson, B. R. Johnson, K. S. Larsen, Y. Luo, S. Marhan, J. M. Melillo, J. Peñuelas, L. Pfeifer-Meister, C. Poll, E. Rastetter, A. B. Reinmann, L. L. Reynolds, I. K. Schmidt, G. R. Shaver, A. L. Strong, V. Suseela, A. Tietema, Temperature response of soil respiration largely unaltered with experimental warming. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 13797–13802 (2016). doi:10.1073/pnas.1605365113 Medline
- M. Lu, X. Zhou, Q. Yang, H. Li, Y. Luo, C. Fang, J. Chen, X. Yang, B. Li, Responses of ecosystem carbon cycle to experimental warming: A meta-analysis. *Ecology* **94**, 726–738 (2013). doi:10.1890/12-0279.1 Medline
- Z. Wu, P. Dijkstra, G. W. Koch, J. Peñuelas, B. A. Hungate, Responses of terrestrial ecosystems to temperature and precipitation change: A meta-analysis of experimental manipulation. *Glob. Change Biol.* **17**, 927–942 (2011). doi:10.1111/j.1365-2486.2010.02302.x
- X. Pang, B. Zhu, X. Lü, W. Cheng, Labile substrate availability controls temperature sensitivity of organic carbon decomposition at different soil depths. *Biogeochemistry* **126**, 85–98 (2015). doi:10.1007/s10533-015-0141-0
- C. D. Koven, W. J. Riley, Z. M. Subin, J. Y. Tang, M. S. Torn, W. D. Collins, G. B. Bonan, D. M. Lawrence, S. C. Swenson, The effect of vertically resolved soil biogeochemistry and alternate soil C and N models on C dynamics of CLM4.

- Biogeosciences* **10**, 7109–7131 (2013). doi:10.5194/bg-10-7109-2013
25. D. S. Jenkinson, K. Coleman, The turnover of organic carbon in subsoils. Part 2. Modelling carbon turnover. *Eur. J. Soil Sci.* **59**, 400–413 (2008). doi:10.1111/j.1365-2389.2008.01026.x
 26. K. E. O. Todd-Brown, J. T. Randerson, W. M. Post, F. M. Hoffman, C. Tarnocai, E. A. G. Schuur, S. D. Allison, Causes of variation in soil carbon simulations from CMIP5 Earth system models and comparison with observations. *Biogeosciences* **10**, 1717–1736 (2013). doi:10.5194/bg-10-1717-2013
 27. C. L. Phillips, K. J. McFarlane, D. Risk, A. R. Desai, Biological and physical influences on soil ¹⁴C₂ seasonal dynamics in a temperate hardwood forest. *Biogeosciences* (2013). doi:10.5194/bg-10-7999-2013
 28. E. A. Davidson, S. E. Trumbore, Gas diffusivity and production of CO₂ in deep soils of the eastern Amazon. *Tellus B* **47**, 550–565 (1995). doi:10.3402/tellusb.v47i5.16071
 29. A. H. Goldstein, N. E. Hultman, J. M. Fracheboud, M. R. Bauer, J. A. Panek, M. Xu, Y. Qi, A. B. Guenther, W. Baugh, Effects of climate variability on the carbon dioxide, water, and sensible heat fluxes above a ponderosa pine plantation in the Sierra Nevada (CA). *Agric. For. Meteorol.* **101**, 113–129 (2000). doi:10.1016/S0168-1923(99)00168-9
 30. N. Fierer, O. A. Chadwick, S. E. Trumbore, Production of CO₂ in soil profiles of a California annual grassland. *Ecosystems* **8**, 412–429 (2005). doi:10.1007/s10021-003-0151-y
 31. J. M. Melillo, P. A. Steudler, J. D. Aber, K. Newkirk, H. Lux, F. P. Bowles, C. Catricala, A. Magill, T. Ahrens, S. Morrisseau, Soil warming and carbon-cycle feedbacks to the climate system. *Science* **298**, 2173–2176 (2002). doi:10.1126/science.1074153 Medline
 32. B. Bond-Lamberty, A. Thomson, Temperature-associated increases in the global soil respiration record. *Nature* **464**, 579–582 (2010). doi:10.1038/nature08930 Medline
 33. C. Le Quéré, R. M. Andrew, J. G. Canadell, S. Sitch, J. I. Korsbakken, G. P. Peters, A. C. Manning, T. A. Boden, P. P. Tans, R. A. Houghton, R. F. Keeling, S. Alin, O. D. Andrews, P. Anthoni, L. Barbero, L. Bopp, F. Chevallier, L. P. Chini, P. Ciais, K. Currie, C. Delire, S. C. Doney, P. Friedlingstein, T. Gkritzalis, I. Harris, J. Hauck, V. Haverd, M. Hoppema, K. Klein Goldewijk, A. K. Jain, E. Kato, A. Körtzinger, P. Landschützer, N. Lefèvre, A. Lenton, S. Liener, D. Lombardozi, J. R. Melton, N. Metz, F. Millero, P. M. S. Monteiro, D. R. Munro, J. E. M. S. Nabel, S. Nakaoka, K. O’brien, A. Olsen, A. M. Omar, T. Ono, D. Pierrot, B. Poulter, C. Rödenbeck, J. Salisbury, U. Schuster, J. Schwinger, R. Séférian, I. Skjelvan, B. D. Stocker, A. J. Sutton, T. Takahashi, H. Tian, B. Tilbrook, I. T. van der Laan-Luijckx, G. R. van der Werf, N. Viovy, A. P. Walker, A. J. Wiltshire, S. Zaehle, Global carbon budget 2016. *Earth Syst. Sci. Data* **8**, 605–649 (2016). doi:10.5194/essd-8-605-2016
 34. J. A. Bird, M. S. Torn, Fine roots vs. needles: A comparison of ¹³C and ¹⁵N dynamics in a ponderosa pine forest soil. *Biogeochemistry* **79**, 361–382 (2006). doi:10.1007/s10533-005-5632-y
 35. C. Rasmussen, M. S. Torn, R. J. Southard, Mineral assemblage and aggregates control carbon dynamics in a California conifer forest. *Soil Sci. Soc. Am. J.* **69**, 1711–1721 (2005). doi:10.2136/sssaj2005.0040
 36. A. B. Moyes, D. R. Bowling, Interannual variation in seasonal drivers of soil respiration in a semi-arid Rocky Mountain meadow. *Biogeochemistry* **113**, 683–697 (2013). doi:10.1007/s10533-012-9797-x
 37. R. J. Millington, Gas diffusion in porous media. *Science* **130**, 100–102 (1959). doi:10.1126/science.130.3367.100-a Medline
 38. P. Moldrup, T. Olesen, T. Komatsu, P. Schjønning, D. E. Rolston, Tortuosity, diffusivity, and permeability in the soil liquid and gaseous phases. *Soil Sci. Soc. Am. J.* **65**, 613 (2001). doi:10.2136/sssaj2001.653613x
 39. R. Jassal, A. Black, M. Novak, K. Morgenstern, Z. Nescic, D. Gaumont-Guay, Relationship between soil CO₂ concentrations and forest-floor CO₂ effluxes. *Agric. For. Meteorol.* **130**, 176–192 (2005). doi:10.1016/j.agrformet.2005.03.005
 40. J. S. Vogel, D. E. Nelson, J. R. Southon, ¹⁴C background levels in an accelerator mass spectrometry system. *Radiocarbon* **29**, 323–333 (1987). doi:10.1017/S0033822200043733
 41. A. Golchin, J. Oades, J. Skjemstad, P. Clarke, Soil structure and carbon cycling. *Soil Res.* **32**, 1043–1068 (1994). doi:10.1071/SR9941043
 42. C. W. Swanston, M. S. Torn, P. J. Hanson, J. R. Southon, C. T. Garten, E. M. Hanlon, L. Ganio, Initial characterization of processes of soil carbon stabilization using forest stand-level radiocarbon enrichment. *Geoderma* **128**, 52–62 (2005). doi:10.1016/j.geoderma.2004.12.015
 43. J. A. Bird, M. Kleber, M. S. Torn, ¹³C and ¹⁵N stabilization dynamics in soil organic matter fractions during needle and fine root decomposition. *Org. Geochem.* **39**, 465–477 (2008). doi:10.1016/j.orggeochem.2007.12.003
 44. N. Fierer, J. M. Craine, K. McLaughlan, J. P. Schimel, Litter quality and the temperature sensitivity of decomposition. *Ecology* **86**, 320–326 (2005). doi:10.1890/04-1254
 45. C. A. Sierra, Temperature sensitivity of organic matter decomposition in the Arrhenius equation: Some theoretical considerations. *Biogeochemistry* **108**, 1–15 (2012). doi:10.1007/s10533-011-9596-9
 46. D. Bates, M. Mächler, B. Bolker, S. Walker, Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015). doi:10.18637/jss.v067.i01
 47. R Development Core Team, *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, 2014; www.R-project.org).
 48. A. Zuur et al., *Mixed Effects Models and Extensions in Ecology with R* (Springer, 2009).
 49. J. A. Andrews, K. G. Harrison, R. Matamala, W. H. Schlesinger, Separation of root respiration from total soil respiration using carbon-13 labeling during free-air carbon dioxide enrichment (FACE). *Soil Sci. Soc. Am. J.* **63**, 1429 (1999). doi:10.2136/sssaj1999.6351429x
 50. Q. Hua, M. Barbetti, A. Z. Rakowski, Atmospheric radiocarbon for the period 1950–2010. *Radiocarbon* **55**, 2059–2072 (2013). doi:10.2458/azu_js_rc.v55i2.16177
 51. S. R. Saleska, J. Harte, M. S. Torn, The effect of experimental ecosystem warming on CO₂ fluxes in a montane meadow. *Glob. Change Biol.* **5**, 125–141 (1999). doi:10.1046/j.1365-2486.1999.00216.x
 52. J. Harte, M. S. Torn, F.-R. Chang, B. Feifarek, A. P. Kinzig, R. Shaw, K. Shen, Global warming and soil microclimate: Results from a meadow-warming experiment. *Ecol. Appl.* **5**, 132–150 (1995). doi:10.2307/1942058
 53. X. Lin, Z. Zhang, S. Wang, Y. Hu, G. Xu, C. Luo, X. Chang, J. Duan, Q. Lin, B. Xu, Y. Wang, X. Zhao, Z. Xie, Response of ecosystem respiration to warming and grazing during the growing seasons in the alpine meadow on the Tibetan plateau. *Agric. For. Meteorol.* **151**, 792–802 (2011). doi:10.1016/j.agrformet.2011.01.009
 54. C. Luo, G. Xu, Z. Chao, S. Wang, X. Lin, Y. Hu, Z. Zhang, J. Duan, X. Chang, A. Su, Y. Li, X. Zhao, M. Du, Y. Tang, B. Kimball, Effect of warming and grazing on litter mass loss and temperature sensitivity of litter and dung mass loss on the Tibetan plateau. *Glob. Change Biol.* **16**, 1606–1617 (2010). doi:10.1111/j.1365-2486.2009.02026.x
 55. Y. Luo, S. Wan, D. Hui, L. L. Wallace, Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* **413**, 622–625 (2001). doi:10.1038/35098065 Medline
 56. X. Zhou, S. Wan, Y. Luo, Source components and interannual variability of soil CO₂ efflux under experimental warming and clipping in a grassland ecosystem. *Glob. Change Biol.* **13**, 661–775 (2007).
 57. Y. Luo, R. Sherry, X. Zhou, S. Wan, Terrestrial carbon-cycle feedback to climate warming: Experimental evidence on plant regulation and impacts of biofuel feedstock harvest. *Glob. Change Biol. Bioenergy* **1**, 62–74 (2009). doi:10.1111/j.1757-1707.2008.01005.x
 58. J. Zhou, K. Xue, J. Xie, Y. Deng, L. Wu, X. Cheng, S. Fei, S. Deng, Z. He, J. D. Van Nostrand, Y. Luo, Microbial mediation of carbon-cycle feedbacks to climate warming. *Nat. Clim. Chang.* **2**, 106–110 (2012). doi:10.1038/nclimate1331
 59. V. Suseela, R. T. Conant, M. D. Wallenstein, J. S. Dukes, Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. *Glob. Change Biol.* **18**, 336–348 (2012). doi:10.1111/j.1365-2486.2011.02516.x
 60. W. Liu, Z. Zhang, S. Wan, Predominant role of water in regulating soil and microbial respiration and their responses to climate change in a semiarid grassland. *Glob. Change Biol.* **15**, 184–195 (2009). doi:10.1111/j.1365-2486.2008.01728.x
 61. S. D. Allison, K. K. Treseder, Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. *Glob. Change Biol.* **14**, 2898–2909 (2008). doi:10.1111/j.1365-2486.2008.01716.x

62. S. M. Niinistö, J. Silvola, S. Kellomäki, Soil CO₂ efflux in a boreal pine forest under atmospheric CO₂ enrichment and air warming. *Glob. Change Biol.* **10**, 1363–1376 (2004). doi:10.1111/j.1365-2486.2004.00799.x
63. D. Comstedt, B. Boström, J. D. Marshall, A. Holm, M. Slaney, S. Linder, A. Ekblad, Effects of elevated atmospheric carbon dioxide and temperature on soil respiration in a boreal forest using $\delta^{13}\text{C}$ as a labeling tool. *Ecosystems* **9**, 1266–1277 (2006). doi:10.1007/s10021-006-0110-5
64. S. Wan, R. J. Norby, J. Ledford, J. F. Weltzin, Responses of soil respiration to elevated CO₂, air warming, and changing soil water availability in a model old-field grassland. *Glob. Change Biol.* **13**, 2411–2424 (2007). doi:10.1111/j.1365-2486.2007.01433.x
65. C. T. Garten Jr., A. T. Classen, R. J. Norby, Soil moisture surpasses elevated CO₂ and temperature as a control on soil carbon dynamics in a multi-factor climate change experiment. *Plant Soil* **319**, 85–94 (2009). doi:10.1007/s11104-008-9851-6
66. E. Lellei-Kovács, E. Kovács-Láng, T. Kalapos, Z. Botta-Dukát, S. Barabás, C. Beier, Experimental warming does not enhance soil respiration in a semiarid temperate forest-steppe ecosystem. *Community Ecol.* **9**, 29–37 (2008). doi:10.1556/ComEc.9.2008.1.4
67. B. A. Emmett, C. Beier, M. Estiarte, A. Tietema, H. L. Kristensen, D. Williams, J. Peñuelas, I. Schmidt, A. Sowerby, The response of soil processes to climate change: Results from manipulation studies of shrublands across an environmental gradient. *Ecosystems* **7**, 625–637 (2004). doi:10.1007/s10021-004-0220-x
68. C. Beier, B. Emmett, P. Gundersen, A. Tietema, J. Peñuelas, M. Estiarte, C. Gordon, A. Gorissen, L. Llorens, F. Roda, D. Williams, Novel approaches to study climate change effects on terrestrial ecosystems in the field: Drought and passive nighttime warming. *Ecosystems* **7**, 583–597 (2004). doi:10.1007/s10021-004-0178-8
69. A. Schindlbacher, S. Zechmeister-Boltenstern, R. Jandl, Carbon losses due to soil warming: Do autotrophic and heterotrophic soil respiration respond equally? *Glob. Change Biol.* **15**, 901–913 (2009). doi:10.1111/j.1365-2486.2008.01757.x
70. L. E. Rustad, I. J. Fernandez, Experimental soil warming effects on CO₂ and CH₄ flux from a low elevation spruce-fir forest soil in Maine, USA. *Glob. Change Biol.* **4**, 597–605 (1998). doi:10.1046/j.1365-2486.1998.00169.x
71. D. R. Bronson, S. T. Gower, M. Tanner, S. Linder, I. Van Herk, Response of soil surface CO₂ flux in a boreal forest to ecosystem warming. *Glob. Change Biol.* **14**, 856–867 (2007). doi:10.1111/j.1365-2486.2007.01508.x
72. P. J. McHale, M. J. Mitchell, F. P. Bowles, Soil warming in a northern hardwood forest: Trace gas fluxes and leaf litter decomposition. *Can. J. For. Res.* **28**, 1365–1372 (1998). doi:10.1139/x98-118
73. A. R. Contosta, S. D. Frey, A. B. Cooper, Seasonal dynamics of soil respiration and N mineralization in chronically warmed and fertilized soils. *Ecosphere* **2**, art36 (2011). doi:10.1890/ES10-00133.1
74. W. T. Peterjohn, J. M. Melillo, P. A. Steudler, K. M. Newkirk, F. P. Bowles, J. D. Aber, Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Ecol. Appl.* **4**, 617–625 (1994). doi:10.2307/1941962
75. J. M. Melillo, S. Butler, J. Johnson, J. Mohan, P. Steudler, H. Lux, E. Burrows, F. Bowles, R. Smith, L. Scott, C. Vario, T. Hill, A. Burton, Y.-M. Zhou, J. Tang, Soil warming, carbon-nitrogen interactions, and forest carbon budgets. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 9508–9512 (2011). doi:10.1073/pnas.1018189108 Medline
76. W. T. Peterjohn, J. M. Melillo, F. P. Bowles, P. A. Steudler, Soil warming and trace gas fluxes: Experimental design and preliminary flux results. *Oecologia* **93**, 18–24 (1993). doi:10.1007/BF00321185
77. I. P. Hartley, A. Heinemeyer, P. Ineson, Effects of three years of soil warming and shading on the rate of soil respiration: Substrate availability and not thermal acclimation mediates observed response. *Glob. Change Biol.* **13**, 1761–1770 (2007). doi:10.1111/j.1365-2486.2007.01373.x
78. P. Ineson, D. G. Benham, J. Poskitt, A. F. Harrison, K. Taylor, C. Woods, Effects of climate change on nitrogen dynamics in upland soils. 2. A soil warming study. *Glob. Change Biol.* **4**, 153–161 (1998). doi:10.1046/j.1365-2486.1998.00119.x

ACKNOWLEDGMENTS

Data presented in this paper are available in the supplementary online material, tables S3 to S5. This work was supported as part of the Terrestrial Ecosystem Science Program by the Director, Office of Science, Office of Biological and Environmental Research, of the U.S. Department of Energy under Contract No. DE-AC02-05CH11231. Thanks to Biao Zhu, Bryan Curtis, Paul Cook, Alex Morales, Justin Erspamer, Ariel Thomson, Jen York, Caitlin O'Neill, Corinna West, Erik Poppleton, Rose Abramoff, and Katerina Georgiou.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/cgi/content/full/science.aal1319/DC1
 Materials and Methods
 Supplementary Text
 Figs. S1 to S6
 Tables S1 to S5
 References (34–78)

30 September 2016; accepted 24 February 2017
 Published online 9 March 2017
 10.1126/science.aal1319

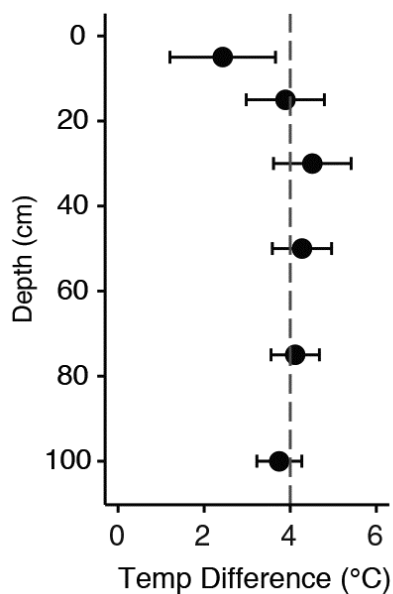


Fig. 1. The mean temperature difference between the control and heated plots by depth over the study period (March 2014 through February 2016). The error bars are the standard deviation of the temporal variability.

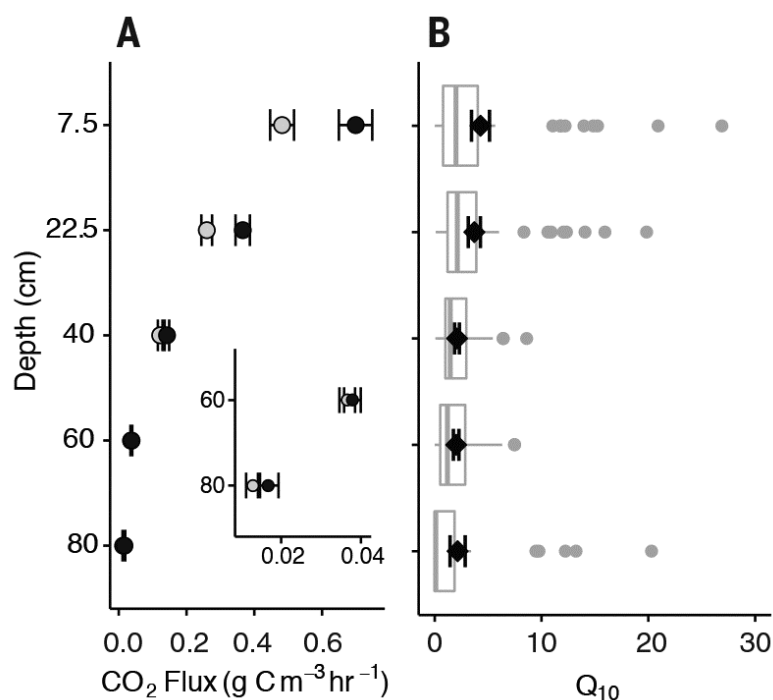


Fig. 2. (A) Mean CO₂ production (\pm SE) by depth increment in the control (grey circles) and heated (black circles) plots averaged over 20 months ($n = 3$). The depth increments are as follows: 0-15, 15-30, 30-50, 50-70, and 70-90 cm. The inset expands the 50-70 and 70-90 cm depths. (B) Mean apparent Q_{10} (\pm SE, black diamonds) averaged over 20 months is similar across depths with a slight, insignificant increase at depths above 30 cm. The boxplots in grey show the median (thick grey line), the 25th and 75th percentiles (thin vertical lines), and outliers (grey circles).

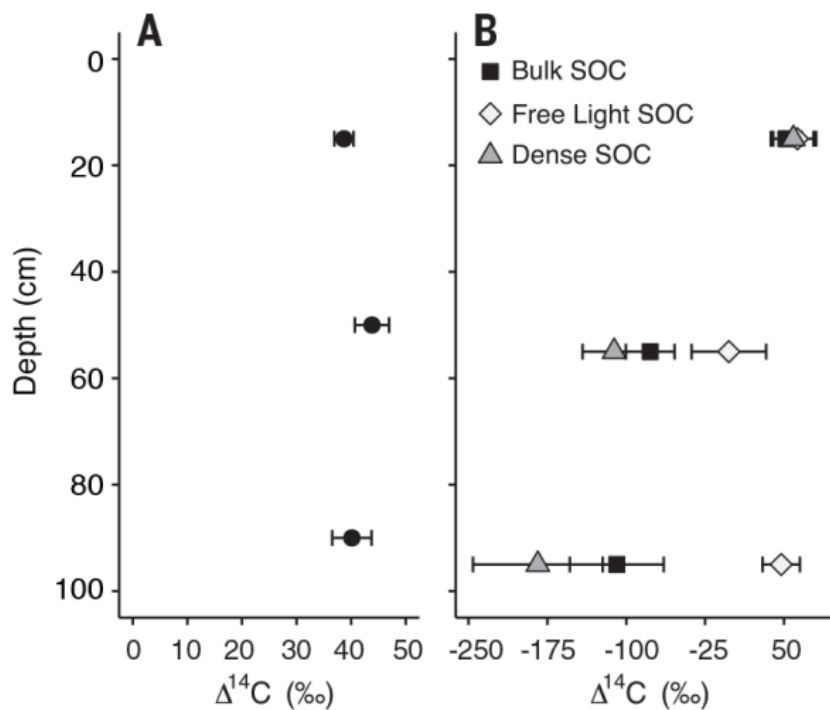


Fig. 3. (A) Mean radiocarbon values (\pm SE) of soil profile CO_2 are modern ($>0\text{‰}$) and do not differ among depths ($n = 6$, $p = 0.77$) or between treatments (not shown, $n = 9$, $p = 0.21$). (B) Mean radiocarbon values (\pm SE) of bulk, free light, and dense mineral-associated SOC. A potential source of the modern soil profile CO_2 is the free light fraction, which is also modern and does not differ significantly among depths ($n = 3$, $p = 0.02$).

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

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



The whole-soil carbon flux in response to warming

Caitlin E. Hicks Pries, C. Castanha, R. Porras and M. S. Torn (March 9, 2017)
published online March 9, 2017

Editor's Summary

This copy is for your personal, non-commercial use only.

- Article Tools** Visit the online version of this article to access the personalization and article tools:
<http://science.sciencemag.org/content/early/2017/03/08/science.aal1319>
- Permissions** Obtain information about reproducing this article:
<http://www.sciencemag.org/about/permissions.dtl>

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published weekly, except the last week in December, by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. Copyright 2016 by the American Association for the Advancement of Science; all rights reserved. The title *Science* is a registered trademark of AAAS.