Global Convergence in the Temperature Sensitivity of Respiration at Ecosystem Level

Miguel D. Mahecha,1,2* Markus Reichstein,1 Nuno Carvalhal,3,4 Gitta Lasslop,5 Holger Lange,6 Sonia I. Seneviratne,7 Rodrigo Vargas,8 Christof Ammann,9 M. Altaf Arain,7 Alessandro Cescatti,8 Ivan A. Janssens,9 Mirco Migliavacca,10 Leonardo Montagnani,11,12 Andrew D. Richardson13

The respiratory release of carbon dioxide (CO₂) from the land surface is a major flux in the global carbon cycle, antipodal to photosynthetic CO₂ uptake. Understanding the sensitivity of respiratory processes to temperature is central for quantifying the climate–carbon cycle feedback. We approximated the sensitivity of terrestrial ecosystem respiration to air temperature (Q₁₀) across 60 FLUXNET sites with the use of a methodology that accounts for confounding effects. Contrary to previous findings, our results suggest that Q₁₀ is independent of mean annual temperature, does not differ among biomes, and is confined to values around 1.4 ± 0.1. The strong relation between photosynthesis and respiration, by contrast, is highly variable among sites. The results may partly explain a less pronounced climate–carbon cycle feedback than suggested by current carbon cycle climate models.

Quantifying the intensity of feedback mechanisms between terrestrial ecosystems and climate is a central challenge for understanding the global carbon cycle and a prerequisite for reliable future climate scenarios (1, 2). One crucial determinant of the climate–carbon cycle feedback is the temperature sensitivity of respiratory processes in terrestrial ecosystems (3, 4), which has been subject to much debate (5–10). On the one hand, empirical studies have found high sensitivities of soil respiration to temperature, with values of Q₁₀ (here an indicator of the sensitivity of terrestrial ecosystem respiration to air temperature) well above 2 (11, 12). Dependences of Q₁₀ values on mean temperatures (J, 13) have been attributed to the acclimatization of soil respiration (5), among other factors (13). On the other hand, global-scale models often make use of globally constant Q₁₀ values of 2 or below to generate carbon dynamics consistent with global atmospheric CO₂ growth rates (3, 14, 15). Nonetheless, several models have directly included empirical dependencies of the parameterization of respiratory processes to environmental dynamics (16–18). This inclusion is questionable, given that single-site studies have indicated that factors seasonally covarying with temperature can confound the experimental retrieval

References and Notes
15. This work used eddy covariance data acquired by the FLUXNET community and in particular by the following networks: Ameriflux (U.S. Department of Energy, Biological and Environmental Research, Terrestrial Carbon Program (DE-FG02-04ER63913), 31. B. Fekete, C. Vorosmarty, J. Roads, C. Willmott, and University of East Anglia, and the GEWEX project GPCP. We thank Mahendra K. Karki at NASA for extracting the MOD17 required surface meteorological variables from the GMAO reanalysis dataset and Maosheng Zhao at NTSG of University of Montana for calculating the respective daytime VPD. We further acknowledge support by the European Commission FP7 projects COMBINE and CARBO-Extreme and a grant from the Max-Planck Society establishing the MPRG Biogeochemical Model-Data Integration. C.B., D.P., M.R., P.C., D.B., and S.L. conceived the study. C.B., R.R., C.B., M.J., F.I.W., and N.V. contributed process modeling. C.B., A.B., G.B.B., M.L., F.I.W., and N.V. contributed model development. C.B., C.R., D.P., E.T., M.J., M.R., and N.C. contributed diagnostic modeling results. C.B., A.B., G.B.B., M.L., F.W., and N.V. contributed process model results. C.B. performed the analyses. C.B. and M.R. wrote the manuscript. All other authors contributed with data or substantial input to the manuscript.

Supporting Online Material
www.sciencemag.org/cgi/content/full/science.1184984/DC1
Materials and Methods
SDM Text
Tables S1 to S34
References
20 November 2009; accepted 8 June 2010
Published online 5 July 2010.
10.1126/science.1184984
Include this information when citing this paper.

©Max Planck Institute for Biogeochemistry, 07745 Jena, Germany.
1Institute for Atmospheric and Climate Science, ETH Zurich, Universitätstrasse 16, 8092 Zürich, Switzerland. 2Faculdade de Ciências e Tecnologia, FCT, Universidade Nova de Lisboa, 2829-516 Caparica, Portugal. 3Norsk Institutt for Skog og Landskap, N-1431 Ås, Norway. 4Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720, USA. 5Agroscope ART, DISAT, University of Milan-Bicocca, 20126 Milano, Italy. 6EuroForsk, Agenzia per l’Ambiente, Provincia Autonoma di Bolzano, 39100 Bolzano, Italy. 7Faculty of Sciences and Technologies, Free University of Bozen-Bolzano, Piazza Università 1, 39100 Bolzano, Italy. 8Harvard University Department of Organismic and Evolutionary Biology, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, MA 02138, USA. 9To whom correspondence should be addressed. E-mail: mmahecha@bgc-jena.mpg.de
of the intrinsic temperature dependence of respiration (8, 9, 19). Davidson and Janssens (20) therefore proposed to distinguish intrinsic temperature sensitivities by quantifying the inherent kinetic properties of substrate decomposition from apparent temperature responses. Moreover, it has been recognized that the direct inference of process sensitivities from emergent ecosystem behavior is not possible (19, 21).

Our aim here was to retrieve the unconfounded (intrinsic) temperature sensitivities of ecosystem respiration across different climates and ecosystems, to resolve the question of whether we have to account for a globally varying and environmentally controlled $Q_{10}$ in global carbon cycle modeling. The study is based on a global collection of eddy covariance CO$_2$ flux observations—the FLUXNET (22, 23) LaThuile Database—which allows us to investigate greenhouse gas fluxes in response to meteorological variables across ecosystems. To minimize the influence of confounding effects, we apply a model-data fusion approach, scale-dependent parameter estimation (SCAPE) (24), that investigates processes on different time scales. The SCAPE concept exploits the idea that measured time series $Y_f(i), i = 1, ..., N$, result from superimposed modes of characteristic variability $X_f$, where the index $f$ indicates the attributable frequency class per subsignal (fig. S1). In SCAPE we can distinguish rapid and slow system responses (here, direct responses to temperature versus long-term organic matter dynamics described by the base respiration $R_b$). SCAPE differentiates the parameter estimation process according to identified time scales. We can therefore report temperature sensitivities ($Q_{10,sc}$) derived from specific (high-frequency) subsignals $X_f$ such that confounding factors that operate on other (generally low-frequency) scales are excluded. Moreover, a nonparametric estimate of the low-frequency $R_b$ time series is directly provided (24). In an experiment with artifical data (24) (fig. S2), we show that with this methodology the unconfounded $Q_{10,sc}$ of respiration is retrieved within ±0.1 units, even under unfavorable conditions of noise (fig. S3) (25).

The examination of the ecosystem respiration data shows that the unconfounded $Q_{10,sc}$ values are generally lower than temperature sensitivities reported by conventional estimates (Fig. 1) with very few exceptions (table S1). Conventional estimates would suggest an average sensitivity to air temperature of $Q_{10} ≈ 2.3$ across sites. The corresponding 95% confidence range is $2.0 ≤ Q_{10} ≤ 2.6$, estimated via a block bootstrapping across sites (24). This large range of possible $Q_{10}$ values is very likely caused by confounding factors. However, once we derive the sensitivities using SCAPE, the weighted arithmetic mean is $Q_{10,sc} = 1.4$; the 95% confidence range collapses to the narrow interval of $1.3 ≤ Q_{10,sc} ≤ 1.5$. The observed systematic difference between apparent and short-term temperature sensitivities corresponds exactly to what was expected by theoretical considerations reported previously (9).

The reported range of $Q_{10,sc}$ values is low, given that soil organic matter incubation experiments, which should not be hampered by seasonally confounding effects, typically find sensitivities of $Q_{10} > 2$ (7, 26, 27). We argue that this discrepancy is due to the controlled laboratory conditions, which partially exclude a number of factors relevant to ecosystem respiration. Measurements at ecosystem level always include multiple processes, such as the mobilization, transport, and transfer (e.g., via depolymerization) of carbon compounds, such that they are metabolizable in the mitochondria. At the end, the rate-limiting step will determine the overall temperature response of a chemical reaction chain, and the overall $Q_{10}$ is lower than for the individual processes (28). For instance, it has been shown that the mycorrhizal respiration is largely limited by the carbon supply from the roots but is virtually insensitive to temperature variations (29, 30). Moreover, growth respiration of plants is largely independent of temperature (31). Because ecosystem respiration is a mixed response of temperature-sensitive and -insensitive subprocesses, we assume that the comparable low $Q_{10,sc}$ values reported here are plausible estimates.

Despite a narrow range of identified $Q_{10,sc}$ values, the site-to-site variability in the $Q_{10,sc}$ estimates does not fully disappear. These differences may be partially caused by a propagation of noise in the nighttime eddy covariance data into parameter estimates. Also, slightly delayed system responses (32) can affect our estimates at ecosystem level. Minor confounding factors operating at comparable time scales, as the effective system responses may also play a role. The latter are not easily distinguishable, given that we are confronted with a signal comprising both soil and plant respiration at ecosystem level. Hence, it is very likely that the intrinsic temperature sensitivities of the involved subprocesses are confined to an even narrower range compared to our approximation at ecosystem level. This is remarkable because it implies a convergence of relative proportions of temperature-sensitive and -insensitive respiration fluxes among ecosystems.

To clarify whether a general environmental control might explain the site-to-site variability in the temperature sensitivities of ecosystem respiration, we investigated the relationship of mean annual temperature to the approximated intrinsic $Q_{10,sc}$ and apparent $Q_{10}$ (Fig. 2). The $Q_{10,sc}$ estimates do not confirm the previously found or hypothesized patterns (Fig. 2B). Our results show a global convergence in the temperature sensitivity of terrestrial ecosystem respiration: An almost universal $Q_{10,sc}$ value across climate zones and ecosystem types (see also Fig. 1) is identified. Using the conventional estimates of $Q_{10}$ instead,
we reproduce the effects of an apparent temperature control on the sensitivity (Fig. 2A). This underscores the problem that some unconsidered process, such as substrate supply, can be erratically interpreted as an oversensitivity of ecosystem metabolic processes to temperature.

Our analysis further emphasizes that despite having comparable short-term temperature sensitivities, ecosystems strongly differ in their carbon metabolism on longer time scales (Fig. 3): Low-frequency ecosystem responses are reflected in the temporal dynamics of the base respiration $R_b$ (Fig. S5). These time series show a tight relationship with corresponding low-frequency modes in independently estimated time series of gross primary productivity $GPP_b$ (Fig. S6). If we allow $R_b$ to respond to $GPP_b$ with a time delay of a few days, which is a plausible assumption (32), all relationships are close to linear (Fig. S7), confirming recent findings (34). The ratio $1 - (R_b/GPP_b)$ hints at how the low-frequency dynamics of carbon uptake is propagated to the metabolism potential of labile soil organic carbon by autotrophic and heterotrophic respiration (19). Contrary to the global convergence in the temperature sensitivity, Fig. 3 shows that the low-frequency dynamics within the ecosystem spreads over a wide range. Consequently, future analyses of the climate–carbon cycle feedback have to emphasize the role of long-term dynamics in the terrestrial carbon cycle, rather than focusing on the short-term sensitivities. In particular, the role of intricate nonbiological stabilization processes versus carbon supply rates needs to be further investigated when trying to predict climate change effects on soil carbon dynamics.

The estimated average value for $Q_{10,GPP}$ at ecosystem level likely also underlies recent observations of moderate global temperature responses of respiration in the long term (35). Also, modeling studies reporting that the global carbon cycle can be well modeled only if it is based on ecosystem-level $Q_{10,GPP}$ values below 2 (36) are empirically confirmed by our findings. Consequently, carbon process model results will need to be investigated for their capacity to predict similar short-term $Q_{10,GPP}$ and the variation of $R_b$ at ecosystem level. However, given the nontrivial ecophysiological interpretation of a multitude of processes summing up to the observed ecosystem respiration, our results do not justify the prescription of $Q_{10,GPP} = 1.4$ for all rate constants in soil carbon models. Rather, a deeper understanding of the different factors and processes limiting soil carbon mobilization is needed for overcoming the “dead-soil box modeling paradigm” (37). Moreover, continuous time series of soil respiration, measured with automatic chambers, should be analyzed with the presented methodology, using soil temperature as a driving variable. Such studies could allow exclusive insights to the soil system, whereas our analysis at ecosystem level included aboveground respiration. Furthermore, we suggest exploring the SCAPE methodology in other fields of research, where confounding factors at different scales obscure the intrinsic relation between two variables of interest.

Our findings offer substantial evidence for the existence of universal intrinsic temperature sensitivities of terrestrial ecosystem respiration. The empirically inferred results suggest a $Q_{10,R_b} = 1.4$ at ecosystem level. These results reconcile the empirical evidence with findings that the global carbon cycle can be well modeled only with an ecosystem level sensitivity of $Q_{10} < 2$. Moreover, our results may partly explain recent findings indicating a less pronounced climate–carbon cycle sensitivity (38) than assumed by current climate–carbon cycle model parameterizations. Contrary to the global convergence in temperature sensitivities, we find complex patterns in the low-frequency influence of photosynthetic carbon uptake and available assimilates on ecosystem respiration dynamics. Future research should strive for an in-depth understanding of carbon pathways through slow pools in terrestrial ecosystems.

References and Notes

24. See supporting material on Science Online.
25. The whole methodology and results are also reproducible with the Arrhenius model, because this is linearizable in an analog way. However, for the sake of a more intuitive parameter interpretation we chose the $Q_{10,GPP}$ model here.
39. This work is the outcome of the La Thuile FLUXNET workshop 2007, which would not have been possible without the support provided by CarboEurope, FAO-GTOS-TCO, the Integrated Land Ecosystem-Atmosphere Processes Study (ILEAPS, a core project of IGBP), Max Planck Institute for Biogeochemistry, NSF, University of Tuscia, and U.S. Department of Energy. Moreover, we acknowledge database and technical support from the Berkeley Water Center, Lawrence Berkeley National Laboratory, Microsoft Research eScience, Oak Ridge National Laboratory, University of California–Berkeley, and University of Virginia. The following networks provided flux data: AmeriFlux, AsiaFlux, CarboEurope, ChinaFlux, Fluxnet-Canada, Canadian Carbon Program, LBA, NECC, OzFlux, TCOS–Siberia, and USCC. AmeriFlux is supported by U.S. Department of Energy, Biological and Environmental Research, Terrestrial Carbon Program grant DE-FG02-04ER63917. This work was also supported by the European Research Council via the ERC-Staring Grant QUASOM, the European Commission project CARBO-Extreme (FP7-ENV-2008-1-226701), and a grant by the Max Planck Society establishing the MNPG Biogeochemical Model-Data Integration. We appreciate the collaboration of the FLUXNET synthesis team as documented at (22), and we thank M. Bahn, D. Baldocchi, H.-R. Kühnich, D. Papale, P. Rayner, M. Rodıgiero, and S. Zaehle for very valuable comments. M.D.M., M.R., N.C., and G.L. conceived the study and developed the methodology with substantial input from H.L.M.D.M. performed the analysis and co-wrote the paper with M.R. All other authors gave substantial scientific input during the analysis and/or writing phase.

Supporting Online Material

www.sciencemag.org/cgi/content/full/1189587/DC1 Materials and Methods

SOM Text

Figs. S1 to S7
Table S1
References