mechanical invasiveness; and the nanoFETs have high spatial and temporal resolution for recording.

References and Notes
19. Materials and methods are available as supporting material on Science Online.
29. We thank G. Yellen, W. C. Claycomb, B. P. Bean, P. T. Ellinor, G. H. Yu, D. Casanova, B. P. Timko, and T. Divir for help with experiments and data analysis. C.M.L. acknowledges support from a NIH Director’s Pioneer Award (5DP1OD003900), a National Security Science and Engineering Faculty Fellow (NSSF) award (N00024-09-1-0078), and the McKnight Foundation Neuroscience award.

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www.sciencemag.org/cgi/content/full/329/5993/830/DC1
Materials and Methods
Figs. S1 to S5

References
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Terrestrial Gross Carbon Dioxide Uptake: Global Distribution and Covariation with Climate

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Terrestrial gross primary production (GPP) is the largest global CO2 flux driving several ecosystem functions. We provide an observation-based estimate of this flux at 123 ± 8 petagrams of carbon per year (Pg C year−1) using eddy covariance flux data and various diagnostic models. Tropical forests and savannas account for 60%. GPP over 40% of the vegetated land is associated with precipitation. State-of-the-art process-oriented biosphere models used for climate predictions exhibit a large between-model variation of GPP’s latitudinal patterns and show higher spatial correlations between GPP and precipitation, suggesting the existence of missing processes or feedback mechanisms which attenuate the vegetation response to climate. Our estimates of spatially distributed GPP and its covariation with climate can help improve coupled climate–carbon cycle process models.

Terrestrial plants fix carbon dioxide (CO2) as organic compounds through photosynthesis, a carbon (C) flux also known at the ecosystem level as gross primary production (GPP). Terrestrial GPP is the largest global carbon flux, and it drives several ecosystem functions, such as respiration and growth. GPP thus contributes to human welfare because it is the basis for food, fiber, and wood production. In addition, GPP, along with respiration, is one of the major processes controlling land-atmosphere CO2 exchange, providing the capacity of terrestrial ecosystems to partly offset anthropogenic CO2 emissions.

Although photosynthesis at the leaf and canopy level are quite well understood, only tentative observation-based estimates of global terrestrial GPP have been possible so far. Plant- and stand-level GPP has previously been calculated as two times biomass production (J, 2), with substantial
variation between biomes and sites (3–5). In the absence of direct observations, a combined GPP of all terrestrial ecosystems of 120 Pg C year\(^{-1}\) was obtained (6) by doubling global biomass production estimates (7) without an empirical basis of spatially resolved biomass production and its relationship to GPP. A global terrestrial GPP of 100 to 150 Pg C year\(^{-1}\) is consistent with the observed variation of \(^{13}\)CO in the atmosphere (8, 9). However, the ability of \(^{13}\)CO to constrain GPP dep-

\[\text{Flux Tower Sites.} \]

\[\text{Amplitude based on atmospheric CO2 data and an inversion of atmospheric CO2 transport with model.} \]

\[\text{In this approach, we combined gridded information about the seasonal NEE am}\]

\[\text{bly lines show the results for northern extratropical regions from an independent diagnostic model. In this approach, we combined gridded information about the seasonal NEE amplitude based on atmospheric CO2 data and an inversion of atmospheric CO2 transport with empirical relationships between annual GPP and the seasonal amplitude of NEE derived at flux tower sites.} \]

\[\text{Fig. 1. (A) Distributions of global GPP (Pg C year}\]
which combines recently derived global WUE fields with the long-term averaged evapotranspiration at the watershed scale. This is an important constraint at the global scale, but the spatial resolution is too coarse to use the WUE approach for estimating the spatial distribution of GPP. The light-use efficiency approach (LUE) (21, 22) was applied by combining in situ Bayesian calibration with an uncertainty propagation per vegetation and climate class. The Miami model (23) simply exploits the empirically obtained dependence of photosynthesis on temperature and precipitation. The second step, the mapping of flux tower GPP to the land surface, was performed by applying these diagnostic models to fields of remote sensing (24–26) and climatic data (27–29), which are now available with improved accuracy and high spatial resolution. In so doing, we take into account several sources of uncertainty, including uncertainty from model parametrization and from explanatory variables (16).

By making use of the new data streams and the ensemble of five diagnostic models, we present an observation-based estimate of an average global terrestrial GPP of 123 Pg C year\(^{-1}\) during the period 1998 to 2005 (Fig. 1A). Uncertainties and preprocessing of tower CO\(_2\) flux measurements, tower representativeness, flux partitioning into GPP, uncertainties of climate and remote sensing data sets, and structural uncertainties of the diagnostic models propagate to a global uncertainty with a 95% confidence range from 102 to 135 Pg C year\(^{-1}\) or a robust estimate of standard deviation (30) of 8 Pg C year\(^{-1}\). Results from the LUE approach were higher when using National Centers for Environmental Prediction (NCEP) radiation. However, we do not show NCEP-driven results because NCEP radiation and precipitation is known to be biased (31, 32). The Miami model overestimates GPP compared to other approaches, particularly in sparsely vegetated areas with strong seasonality, such as savannas, shrublands, and tundra (16) (table S5), because it does not account for the effect of climate-independent changes in vegetation structure (e.g., degradation) and vegetation type on GPP. Indeed, residuals of this model correlate significantly with mean annual fraction of absorbed photosynthetically active radiation (FAPAR) from remote sensing (fig. S14). Hence, being a classic model, it is shown only for comparison, but results from the Miami model were not taken into account in the following analyses.

Table 1. GPP for biomes of the world as defined by Prentice et al. (6). Combining the biome extent (fig. S17) with the spatially explicit GPP distributions by the approaches MTE1, MTE2, ANN, LUE, WUE, and KGB led to the respective median GPP per unit area separately for each biome (fig. S4). These medians were then multiplied by the biome area (6, 7) (fig. S4) to estimate GPP in column 2. The estimated GPP total of 122 Pg C year\(^{-1}\) does not equal our overall median of 123 Pg C year\(^{-1}\) because the biome area defined by fig. S17 and by (6) differ slightly. The third column shows GPP as estimated by using NPP numbers from Saugier et al. (7) under the assumption that NPP/GPP = 0.5 (6).

<table>
<thead>
<tr>
<th>Biome</th>
<th>GPP (Pg C year(^{-1}))</th>
<th>GPP = 2 × NPP* (Pg C year(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical forests</td>
<td>40.8</td>
<td>43.8</td>
</tr>
<tr>
<td>Temperate forests</td>
<td>9.9</td>
<td>16.2</td>
</tr>
<tr>
<td>Boreal forests</td>
<td>8.3</td>
<td>5.2</td>
</tr>
<tr>
<td>Tropical savannas and grasslands</td>
<td>31.3</td>
<td>29.8</td>
</tr>
<tr>
<td>Temperate grasslands and shrublands</td>
<td>8.5</td>
<td>14</td>
</tr>
<tr>
<td>Deserts</td>
<td>6.4</td>
<td>7</td>
</tr>
<tr>
<td>Tundra</td>
<td>1.6</td>
<td>1</td>
</tr>
<tr>
<td>Croplands</td>
<td>14.8</td>
<td>8.2</td>
</tr>
<tr>
<td>Total</td>
<td>121.7</td>
<td>125.2</td>
</tr>
</tbody>
</table>

*Based on integrated numbers for biomes (6, 7)

Fig. 2. Partial correlation in the spatial domain between GPP from Fig. 1B and either (A) CRU precipitation, (B) CRU air temperature, or (C) ECMWF ERA-Interim short-wave radiation after applying a moving 4.5° by 4.5° spatial window and subsequent median filtering. Shown are significant correlations (P < 0.01) of which the correlation coefficient is higher/lower than ± 0.2.
photosynthesis is subject to an increasingly continental climate (Fig. 1B).

The latitudinal pattern derived by the different diagnostic models falls into a quite narrow range (Fig. 1C). In contrast, there is a larger range among an ensemble of five process-oriented biosphere models (Fig. 1C); in comparison to our data-oriented range, some consistently overestimate GPP, and others underestimate tropical GPP while matching or slightly overestimating GPP in the temperate zone (fig. S26). A standard global parametrization of the process-oriented models has been applied in this study; it was not optimized against flux tower GPP because we aimed at evaluating the process-based GPP fields and their correlations to climatic variables. For comparison, we show results by an additional, completely different approach of scaling GPP from flux tower sites to the regional scale (fig. S16), where a relationship between the seasonal NEE amplitude and annual GPP is derived at flux tower sites and applied to the seasonal NEE amplitude derived through atmospheric inversion [update of (33)]. This approach leads to values at the upper end of the range of the diagnostic bottom-up approaches in northern extratropical regions but is still at the lower end of the range estimated by the process-oriented models. The differences between process-oriented and data-oriented estimates could lie in human-induced degradation of GPP by land use (34). However, other reasons are possible, including insufficient model parametrization or structural model errors that lead to an overestimation of GPP.

Partial correlation analyses between GPP and climatic variables for 4.5° by 4.5° moving windows show that spatial variation of GPP is associated with precipitation in 50 to 70% of the area of non-tundra herbaceous ecosystems (Fig. 2A and Table 2). Also, 50% of the crop production occurs in regions where photosynthesis is colimited by precipitation, stressing the importance of water availability for food security. Interestingly, GPP in the same proportion of temperate forest areas correlates positively with precipitation (Table 2). In contrast, the spatial GPP variability in only 30% of tropical and boreal forests seems to be associated positively with precipitation, but GPP of more than half of the boreal forests correlates positively with air temperature (Table 2). Therefore, the GPP of these biomes seems to be robust against a moderate climate variation in the order of magnitude of the current spatial variability of climate, given the very low probability of a decrease in air temperature in the boreal zone.

We find negative correlations of productivity with incoming short-wave radiation, in particular in savannahs, the Mediterranean, and Central Asian grasslands (Fig. 2C and tables S6 to S8).

Table 2. Percentage of biome area for which GPP is climatically controlled, indicated by a median partial correlation coefficient higher than 0.2 (or 0.5 in brackets). Several climate grids (CRU, ECMWF ERA-Interim, and GPCP precipitation) were used to perform a partial correlation between the median GPP map (Fig. 1B) and climate variables for 4.5° by 4.5° moving windows (16). Then, the fractional area with significant (P < 0.01) partial correlation higher than 0.2 (0.5) was calculated.

<table>
<thead>
<tr>
<th>Biome</th>
<th>P* controlled</th>
<th>T† controlled</th>
<th>R‡ controlled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical forests</td>
<td>29 (12)</td>
<td>39 (26)</td>
<td>4 (1)</td>
</tr>
<tr>
<td>Temperate forests</td>
<td>50 (26)</td>
<td>42 (23)</td>
<td>6 (2)</td>
</tr>
<tr>
<td>Boreal forests</td>
<td>20 (5)</td>
<td>55 (31)</td>
<td>21 (7)</td>
</tr>
<tr>
<td>Tropical savannas and grasslands</td>
<td>55 (31)</td>
<td>16 (5)</td>
<td>3 (0)</td>
</tr>
<tr>
<td>Temperate grasslands and shrublands</td>
<td>69 (41)</td>
<td>37 (18)</td>
<td>6 (1)</td>
</tr>
<tr>
<td>Deserts</td>
<td>61 (37)</td>
<td>18 (6)</td>
<td>8 (2)</td>
</tr>
<tr>
<td>Tundra</td>
<td>24 (13)</td>
<td>37 (27)</td>
<td>32 (12)</td>
</tr>
<tr>
<td>Croplands</td>
<td>51 (25)</td>
<td>28 (13)</td>
<td>5 (1)</td>
</tr>
</tbody>
</table>

*Precipitation †Air temperature ‡Short-wave radiation

These negative partial correlations may indicate an additional indirect effect of radiation or temperature on GPP by the water balance. Both climatic variables are usually associated with higher evapotranspiration rates, which will yield more negative water balances with higher temperature or radiation levels with consequent negative effects on primary productivity in these water-limited regions. This interpretation is possible notwithstanding a direct effect of temperature on vegetation by heat stress as well as increased levels of diffuse radiation associated with overall lower levels of radiation (35).

After four decades of research on the global magnitude of primary production of terrestrial vegetation (23, 36), we present an observation-based estimate of global terrestrial GPP. Although we arrive at a global GPP of similar magnitude as these earlier estimates, our results add confidence and spatial details. The large range of GPP results by process-oriented biosphere models indicates the need for further constraining CO2 uptake processes in these models. Furthermore, our spatially explicit GPP results contribute to a quantification of the climatic control of GPP. Complementing theoretical or process-oriented results (37, 38) about climatic limitations of GPP, our observation-based results now constitute empirical evidence for a large effect of water availability on primary production over 40% of the vegetated land (Fig. 3A) and up to 70% in savannahs, shrublands, grasslands, and agricultural areas (Table 2). Our findings imply a high susceptibility of these ecosystems’ productivity to projected changes of precipitation over the 21st century (39), but a robustness of tropical and boreal forests. Results of current process models show a large range and a tendency to overestimate precipitation-associated GPP (Fig. 3B). Most likely, the association of GPP and climate in process-oriented models can be improved by including negative feedback mechanisms (e.g., adaptation) that might stabilize the systems. Our high spatial resolution GPP estimates, their uncertainty, and their relationship to climate drivers should be useful for evaluating and thus improving coupled climate–carbon cycle process models.
Global Convergence in the Temperature Sensitivity of Respiration at Ecosystem Level

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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 terrestrial ecosystem respiration to air temperature (Q10) across 60 FLUXNET sites with the use of a methodology that circumvents 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.

O
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). Dependencies of Q10 values on mean temperatures (12, 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
16. Materials and methods are available as supporting material on Science Online.
30. Median absolute deviation times 1.48.
40. 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-FG02-04ER639131), Afirflux, Asiaflux, CarbonAfrica, CarboEuropeP, Carbitaly, CarboMont, ChinaFlux, Florida-Canada (supported by CFCAS, NSERC, BSCAP, Environment Canada, and NRCan), GreenGrass, KoFlux, LBA, NECC, OzFlux, TCOS-Siberia, and USCC. We acknowledge the support to the eddy covariance data harmonization provided by CarboEuropeP, FAO-GTOS-TCO, Integrated Land Ecosystem-Atmosphere Processes Study, Max Planck Institute for Biogeochemistry, National Science Foundation, University of Texas, Université Laval and Environment Canada and U.S. Department of Energy and the database development and technical support from Berkeley Water Center, Lawrence Berkeley National Laboratory, Microsoft Research eScience, Oak Ridge National Laboratory, University of California–Berkeley, and University of Virginia. Remotely sensed land cover data (APAR and LAI) were available through the Joint Research Centre of the European Commission, the National Aeronautics and Space Administration, and the projects GLC2000 and CYCLOPES. Climate data came from the European Centre for Medium-Range Weather Forecasts, the Climate Research Unit of the University of East Anglia, and the GMES project GPCP. We thank Mahendra K. Karki at GMAO/NASA for extracting the MOD17 required surface meteorological variables from the GMAO reanalysis dataset and Maosheng Zhao at NSRG of University of Montana for calculating the respective daytime VPD. We further acknowledge support by the European Commission FP7 project COMBINE and CARBO-Extreme and a grant from the Max-Planck Society establishing the MPRG Biogeochemical Model-Data Integration. C.B., D.P., R.C., P.C., D.B., and S.L. conceived the study. 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 modeling results. C.B. and M.R. performed the analysis. C.B. and M.R. wrote the manuscript. Other authors contributed with data or substantial input to the manuscript.

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