Redefinition and global estimation of basal ecosystem respiration rate

Wenping Yuan,[1] Yiqi Luo,[2] Xianglan Li,[1] Shuguang Liu,[3,4] Guirui Yu,[5] Tao Zhou,[6] Michael Bahn,[7] Andy Black,[8] Ankur R. Desai,[9] Alessandro Cescatti,[10] Barbara Marcolla,[11] Cor Jacobs,[12] Jiquan Chen,[13] Mika Aurela,[14] Christian Bernhofer,[15] Bert Gielen,[16] Gil Bohrer,[17] David R. Cook,[18] Danilo Dragoni,[19] Allison L. Dunn,[20] Damiano Gianelle,[11] Thomas Grünwald,[15] Andreas Ibrom,[21] Monique Y. Leclerc,[22] Anders Lindroth,[23] Heping Liu,[24] Luca Belelli Marchesini,[25] Leonardo Montagnani,[26,27,28] Gabriel Pita,[29] Mirco Rodeghiero,[11] Abel Rodrigues,[30] Gregory Starr,[31] and Paul C. Stoy[32]

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[1] Basal ecosystem respiration rate (BR), the ecosystem respiration rate at a given temperature, is a common and important parameter in empirical models for quantifying ecosystem respiration (ER) globally. Numerous studies have indicated that BR varies in space. However, many empirical ER models still use a global constant BR largely due to the lack of a functional description for BR. In this study, we redefined BR to be ecosystem respiration rate at the mean annual temperature. To test the validity of this concept, we conducted a synthesis analysis using 276 site-years of eddy covariance data, from 79 research sites located at latitudes ranging from ~3°S to ~70°N. Results showed that mean annual ER rate closely matches ER rate at mean annual temperature. Incorporation of site-specific BR into global ER model substantially improved simulated ER compared to an invariant BR at all sites. These results confirm that ER at the mean annual

[1]College of Global Change and Earth System Science, Beijing Normal University, Beijing, China.
[2]Department of Botany and Microbiology, University of Oklahoma, Norman, Oklahoma, USA.
[3]U.S. Geological Survey, Earth Resources Observation and Science Center, Sioux Falls, South Dakota, USA.
[4]Geographic Information Science Center of Excellence, South Dakota State University, Brookings, South Dakota, USA.
[5]Key Laboratory of Ecosystem Network Observation and Modeling, Synthesis Research Center of Chinese Ecosystem Research Network, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China.
[6]State Key Laboratory of Earth Surface Processes and Resource Ecology, Beijing Normal University, Beijing, China.
[7]Institute of Ecology, University of Innsbruck, Innsbruck, Austria.
[8]Faculty of Land and Food Systems, University of British Columbia, Vancouver, B. C., Canada.
[9]Atmospheric and Oceanic Sciences Department, Center for Climatic Research, Nelson Institute for Environmental Studies, University of Wisconsin-Madison, Madison, Wisconsin, USA.
[10]Institute for Environment and Sustainability, Joint Research Centre, European Commission, Ispra, Italy.
[11]Sustainable Agro-ecosystems and Bioresources Department, Fondazione Edmund Mach-IASMA Research and Innovation Centre, San Michele all'Adige, Italy.
[12]Alterra, Earth System Science-Climate Change, Wageningen University, Wageningen, Netherlands.
[13]Department of Earth, Ecological, and Environmental Sciences, University of Toledo, Toledo, Ohio, USA.
[14]Climate and Global Change Research, Finnish Meteorological Institute, Helsinki, Finland.
[15]Chair of Meteorology, Institute of Hydrology and Meteorology, Technische Universität Dresden, Dresden, Germany.
[16]Department of Biology, University of Antwerp, Wilrijk, Belgium.
[17]Department of Civil, Environmental, and Geodetic Engineering, Ohio State University, Columbus, Ohio, USA.
[18]Climate Research Section, Environmental Science Division, Argonne National Laboratory, Argonne, Illinois, USA.
[19]Department of Geography, Indiana University, Bloomington, Indiana, USA.
[20]Department of Physical and Earth Sciences, Worcester State College, Worcester, Massachusetts, USA.
[21]Risø DTU National Laboratory for Sustainable Energy, Biosystems Division, Technical University of Denmark, Roskilde, Denmark.
[22]Department of Crop and Soil Sciences, College of Agricultural and Environmental Sciences, University of Georgia, Griffin, Georgia, USA.
[23]Geobiosphere Science Centre, Physical Geography and Ecosystems Analysis, Lund University, Lund, Sweden.
[24]Laboratory for Atmospheric Research, Department of Civil and Environmental Engineering, Washington State University, Pullman, Washington, USA.
[25]Department for Innovation in Biological, Agro-Food and Forest Systems, University of Tuscia, Viterbo, Italy.
[26]Forest Services of Autonomous Province of Bolzano, Bolzano, Italy.
[27]Laboratory of Chemical Physics, Agency for the Environment of Autonomous Province of Bolzano, Bolzano, Italy.
[28]Faculty of Science and Technology, Free University of Bolzano, Bolzano, Italy.
[29]Department of Mechanical Engineering, Instituto Superior Técnico, Lisbon, Portugal.
[30]Unidade de Silvicultura e Produtos Florestais, Instituto Nacional dos Recursos Biológicos, Oeiras, Portugal.
[31]Department of Biological Sciences, University of Alabama, Tuscaloosa, Alabama, USA.
[32]Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, Montana, USA.

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temperature can be considered as BR in empirical models. A strong correlation was found between the mean annual ER and mean annual gross primary production (GPP). Consequently, GPP, which is typically more accurately modeled, can be used to estimate BR. A light use efficiency GPP model (i.e., EC-LUE) was applied to estimate global GPP, BR and ER with input data from MERRA (Modern Era Retrospective-Analysis for Research and Applications) and MODIS (Moderate resolution Imaging Spectroradiometer). The global ER was 103 Pg C yr $^{-1}$, with the highest respiration rate over tropical forests and the lowest value in dry and high-latitude areas.

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1. Introduction

[2] Increasing atmospheric CO_2 concentration from fossil fuel combustion has emphasized our need to better understand global sources and sinks of carbon [*Le Quéré et al.*, 2009], and their responses to environmental changes. Net ecosystem exchange (NEE) of CO_2 between terrestrial ecosystems and the atmosphere is driven by ecosystem respiration (ER), the sum of soil heterotrophic respiration and plant autotrophic respiration, and gross primary production (GPP). Previous studies have found soil respiration, a major component of ER, accounts for a global annual carbon emission of 75~80 Pg C annually [*Schlesinger*, 1977; *Raich and Potter*, 1995], which is more than 10 times the current rate of fossil fuel combustion [*Marland et al.*, 2008]. Thus, small changes in ER can have a significant impact on the global carbon budget and therefore on the atmospheric CO_2 concentration [*Friedlingstein et al.*, 2006]. Despite the considerable scientific efforts to study ER, there is still limited knowledge on temporal and spatial variations of ER and limited understanding of the environmental controlling mechanisms and of the controlling factors involved, including climate, plant biophysics and soil properties [*Reichstein et al.*, 2003; *Rodeghiero and Cescatti*, 2005; *Davidson and Janssens*, 2006; *Palmroth et al.*, 2005, 2006; *Mahecha et al.*, 2010].

[3] In the past decades, quite different approaches have been taken to obtain global estimations of ER. These include mechanistic models [*Schimel et al.*, 1997; *Parton et al.*, 1998; *Schimel et al.*, 2000; *Cramer et al.*, 2001] that are based on process-level understanding and analysis of ecosystem carbon fluxes and their responses to environmental change. The accuracy of the mechanistic models relies on how well these processes are represented in the models. For example, carbon allocation has been found difficult to represent well in models [*Litton et al.*, 2007], although some rules have emerged [see *Palmroth et al.*, 2006]. Moreover, comprehensive models attempting to incorporate many processes can suffer a drawback of having to specify a large number of parameters thus yielding a substantial uncertainty. For example, a parameter inversion study showed that only four of seven parameters in a process-based respiration model could be reasonably estimated from direct flux tower observations of NEE [*Xu et al.*, 2006].

[4] Since mechanistic models are limited by our understanding of the complex processes and appropriate parameterization, ER at regional to global scales is often modeled as a simple exponential or Arhennius-type function of temperature. For example, a common form of ER is the exponential function [*Luo and Zhou*, 2006]:

$$ER = BR \times Q_{10}^{\frac{T-T_0}{10}} \quad (1)$$

where BR is basal respiration rate at a given reference temperature (T_0; e.g., 0 or 10°C), Q_{10} is the relative change in ER per 10°C increase, and T is air temperature. When simulating ER or its components (i.e., soil respiration) at the global scale, BR is often considered globally invariant. One example is the study by *Raich et al.* [2002], in which globally distributed soil respiration is simulated using a fixed BR value of 1.25 g C m^{-2} d^{-1}. However, an increasing body of evidence suggests that the error introduced by the assumption of constant BR is not negligible [*Tjoelker et al.*, 2001; *Janssens and Pilegaard*, 2003; *Wang et al.*, 2010]. *Sampson et al.* [2007] suggested that BR varies systematically with photosynthesis. *Larsen et al.* [2007] found that ecosystem respiration depends strongly on photosynthesis in a temperate heath and incorporated GPP as a parameter in their respiration model. Spatial differences in global BR have also been linked to variations in leaf area index (LAI), which suggests that photosynthetic activity correlates with ER [*Curiel Yuste et al.*, 2004; *Mahecha et al.*, 2010; *Migliavacca et al.*, 2011]. The large spatial variation in BR is not surprising given its underlying mechanisms which include changes in carbon substrate supply from photosynthesis and quantity of respiring biomass [*Davidson and Janssens*, 2006]. What is lacking is an adequate algorithm to predict variation across the globe.

[5] Spatial patterns of BR are rarely investigated [*Reichstein et al.*, 2003]. Recently, *Bahn et al.* [2010] found a relationship between mean annual soil respiration and soil respiration rate at mean annual temperature, which has important implications for quantifying BR. Previous studies have also shown strong correlation between mean annual ecosystem respiration and GPP [*Janssens et al.*, 2001]. Given these findings, we argue that BR can be more reliably used in models if it is redefined in equation (1) to be ecosystem respiration at the mean annual temperature, and that this latter quantity can be easily estimated by exploiting correlations between annual GPP and ER. In this study, we evaluate the finding of *Bahn et al.* [2010] using eddy covariance (EC) flux tower estimates of ER, and couple it

Table 1. Name, Location, Vegetation Type, and Available Years of the Study Sites[a]

Site	Ecosystem Type	Latitude, Longitude	AP	AMT	Available Years	Reference
US-Bar	DBF	44.06°N, 71.28°W	1245	5.61	2004–2005	*Richardson et al.* [2007]
US-AK87	DBF	63.92°N, 145.38°W	289	−2.10	2002–2003	*Liu et al.* [2005]
US-ChR	DBF	35.93 °N, 84.33°W	986	6.85	2006	-
IT-Col	DBF	41.83°N, 13.58°E	970	7.32	1997–1998; 2000–2001	*Valentini et al.* [2000]
US-DK2	DBF	35.97 °N, 79.10°W	1169	14.36	2001–2005	*Pataki and Oren* [2003]
US-Goo	DBF	34.25°N, 89.97°W	1425	15.89	2003–2006	*Bolstad et al.* [2004]
DE-Hai	DBF	51.06°N, 10.45°E	780	7.15	2000–2003	*Reichstein et al.* [2005]
FR-Hes	DBF	48.66°N, 7.05°E	793	9.24	1997–2003	*Reichstein et al.* [2005]
US-MMS	DBF	39.32°N, 86.41°W	1030	12.42	2002–2003	*Schmid et al.* [2000]
IT-LMa	DBF	45.56°N, 7.15°E	1720	−1.99	2003	-
IT-PT1	DBF	45.20°N, 9.05°E	973	13.27	2002–2003	*Migliavacca et al.* [2009]
IT-Ro1	DBF	42.40°N, 11.91°E	763	15.36	2000–2003	*Tedeschi et al.* [2006]
IT-Ro2	DBF	42.38°N, 11.91°E	760	15.40	2002–2003	*Tedeschi et al.* [2006]
US-Oho	DBF	41.55°N, 83.84°W	843	8.53	2004–2005	*Noormets et al.* [2008]
US-WBW	DBF	35.95°N, 84.28°W	1372	13.71	2000–2001; 2004	*Wilson and Baldocchi* [2000]
US-WCr	DBF	45.90°N, 90.07°W	787	4.02	2000; 2002 2005–2006	*Cook et al.* [2004]
IS-Gun	DBF	60.83°N, 20.21°E	1214	4.40	1997–1998	*Albert et al.* [2004]
CA-Oas	DBF	53.62°N,106.19°W	430	0.34	2002–2005	*Griffis et al.* [2003]
US-SP1	EBF	29.73°N, 82.21°W	1330	21.70	2001;2003;2005–2006	*Kim et al.* [2006]
IT-Cpz	EBF	41.70°N, 12.36°E	777	15.99	1997; 2000–2003	*Garbulsky et al.* [2008]
CN-DingHuShan	EBF	23.17°N, 112.57°E	1956	20.90	2003–2005	*Yu et al.* [2006]
PT-Esp	EBF	38.63°N, 8.60°E	634	16.80	2002–2003	*Rodrigues et al.* [2011]
PT-Mi1	EBF	38.53°N, 8.00°E	628	16.17	2003	*David et al.* [2004]
FR-Pue	EBF	43.73°N, 3.58°E	734	12.96	2001–2003	*Rambal et al.* [2004]
BR-Sa3	EBF	3.01°S, 54.97°W	1965	24.65	2001–2003	*Miller et al.* [2004]
BR-Sa1	EBF	2.85°S, 54.95°W	2111	25.90	2002–2003	*Saleska et al.* [2003]
US-BLh	ENF	44.15°N, 103.56°E	560	6.60	2005–2006	-
CA-Obs	ENF	53.98°N,105.12°W	405	0.79	2000–2005	*Griffis et al.* [2003]
US-Blo	ENF	38.89°N,120.63°W	1290	10.40	2001–2004	*Goldstein et al.* [2000]
CA-Man	ENF	55.87°N, 98.48°W	420	−3.55	1994–2004	*Dunn et al.* [2007]
US-AKCon	ENF	63.88°N, 145.73°W	289	−2.10	2002–2003	*Liu et al.* [2005]
US-SP3	ENF	29.75°N, 82.16°W	1330	21.70	1999; 2001–2003	*Kim et al.* [2006]
US-DK3	ENF	35.97°N, 79.09°W	1169	14.36	1998–2005	*Stoy et al.* [2006]
ES-ES1	ENF	39.33°N, 0.31°E	551	17.85	1999–2003	-
RU-Fyo	ENF	56.45°N, 32.91°E	711	3.90	1999–2003	-
UJ-Gri	ENF	56.60°N, 3.78°E	1622	6.60	1997–1998;2000–2001	-
US-Ho1	ENF	45.20°N, 68.74°W	1070	5.27	1996–2004	*Hollinger et al.* [2004]
US-Ho2	ENF	45.20°N, 68.74°W	1064	5.13	1999–2001	*Hollinger et al.* [2004]
CA-Ojp	ENF	53.91°N,104.69°W	405	0.12	2000–2003	*Griffis et al.* [2003]
FR-LBr	ENF	44.71°N, 0.76°E	924	12.49	1997–1998;2000;2003	*Berbigier et al.* [2001]
NL-Loo	ENF	52.16°N, 5.73°E	786	9.36	1996–2002	*Dolman et al.* [2002]
US-Me2	ENF	44.45°N, 121.55°W	704	7.88	2002–2005	*Sun et al.* [2004]
US-Me1	ENF	44.43°N, 121.56°W	522	6.28	2000–2002	*Sun et al.* [2004]
US-NR1	ENF	40.03°N, 105.54°W	595	0.43	1999–2004	*Monson et al.* [2005]
SE-Nor	ENF	60.08°N, 17.46°E	561	5.45	1996–1997;1999;2003	*Lindroth et al.* [1998]
IT-Ren	ENF	46.58°N, 11.43°E	1010	4.20	1999	*Montagnani et al.* [2009]
IT-SRo	ENF	43.71°N, 10.28°E	897	14.77	1999–2003	*Chiesi et al.* [2005]
IT-Sod	ENF	67.36°N, 26.64°E	499	−1.0	2000–2003	-
DE-Tha	ENF	50.95°N, 13.56°E	820	7.7	1997–2003	*Grünwald and Bernhofer* [2007]
CA-NS2	ENF	55.90°N. 98.52°W	499	−2.88	2002–2004	*Goulden et al.* [2006]
CA-NS4	ENF	55.91°N, 98.38°W	502	−2.87	2002–2005	*Goulden et al.* [2006]
DE-Wet	ENF	50.45°N, 11.45°E	870	5.74	2002–2003	-
US-Wrc	ENF	45.82°N,121.95°W	2451	9.45	2004–2006	*Cook et al.* [2004]
IL-Yat	ENF	31.33°N, 35.05°E	276	17.56	2002–2003	-
CN-QianYanZhou	ENF	26.73°N, 115.05°E	1542	17.90	2003;2005;2007	*Yu et al.* [2006]
IT-Amp	GRS	41.94°N, 13.65°E	945	10.60	2003	*Gilmanov et al.* [2007]
HU-Bug	GRS	46.68°N, 19.60°E	562	10.40	2003	-
US-AK99	GRS	63.92°N, 145.73°W	289	−2.10	2002–2003	*Liu et al.* [2005]
US-Dk1	GRS	35.97°N, 79.09°W	1169	14.36	2001–2005	*Novick et al.* [2004]
CN-HaiBei	GRS	37.48°N, 101.33°E	580	−1.70	2004–2007	*Yu et al.* [2006]
CA-Let	GRS	49.70°N, 112.94°W	398	5.36	1999–2004	*Flanagan and Johnson* [2005]
IT-Mal	GRS	46.11°N, 11.70°E	1200	6.30	2003	-
IT-MBo	GRS	46.01°N, 11.05°E	1184	5.39	2003	*Marcolla et al.* [2011]
AT-Neu	GRS	47.10°N, 11.31°E	1040	6.25	2002–2003	*Wohlfahrt et al.* [2008]
CH-Oe1	GRS	47.28°N, 7.71°E	944	9.13	2002–2003	*Ammann et al.* [2007]
IT-Pia	GRS	42.58°N, 10.06°E	460	16.00	2002–2003	*Reichstein et al.* [2005]
US-Walnut	GRS	37.52°N, 96.85°W	406	15.46	2002–2004	*Song et al.* [2005]
CN-XiLin	GRS	43.88°N, 117.45°E	450	−0.40	2004;2006–2007	*Yu et al.* [2006]
BE-Bra	MIX	51.30°N, 4.51°E	742	10.01	1999–2002	*Gielen et al.* [2010]
CN-ChangBaiShan	MIX	42.40°N, 128.08°E	663	2.16	2003–2006; 2007	*Yu et al.* [2006]
IT-Lav	MIX	45.95°N, 11.26°E	757	8.74	2001–2002	*Marcolla et al.* [2003]

Table 1. (continued)

Site	Ecosystem Type	Latitude, Longitude	AP	AMT	Available Years	Reference
IT-Non	MIX	44.68°N, 11.08°E	741	13.56	2001–2002	*Reichstein et al.* [2005]
DK-Sor	MIX	55.48°N, 11.63°E	573	8.03	1999–2003	*Pilegaard et al.* [2011]
US-Syl	MIX	46.24°N, 89.34°W	826	3.81	2002–2006	*Desai et al.* [2005]
US-UMB	MIX	45.55°N, 84.71°W	803	5.83	1999–2002	*Curtis et al.* [2005]
BE-Vie	MIX	50.30°N, 6.00°E	1065	7.37	1997–2003	*Aubinet et al.* [2001]
US-Brw[b]	TUN	71.32°N, 156.62°W	85	−12.77	2004–2005	*Oechel et al.* [2000]

[a]DBF: deciduous broadleaf forest; EBF: evergreen broadleaf forest; ENF: evergreen needleleaf forest; GRS: grassland; MIX: mixed forest; TUN: tundra.
[b]Data filtering did not follow the criterion of other sites. The days were indicated as missing when missing data was >50%, and the years were indicated as missing when missing days were >50%. AP: annual precipitation (mm); AMT: annual mean temperature (°C).

with observed correlations between GPP and ER to develop a novel method for estimating global BR.

2. Materials and Methods

2.1. Eddy Covariance Data

[6] Eddy covariance (EC) data were used in this study to derive ER rate at mean annual temperature and investigate the correlation of annual mean ER with GPP. The data were obtained from the AmeriFLUX (http://public.ornl.gov/ameriflux), EuroFLUX (http://www.fluxnet.ornl.gov/fluxnet/index.cfm) [*Valentini*, 2003], and ChinaFLUX networks (http://www.chinaflux.org). Seventy-nine sites encompassing 276 site-years were included in this study, covering 6 major terrestrial biomes: evergreen broadleaf forest (EBF), deciduous broadleaf forest (DBF), mixed forest (MIX), evergreen needleleaf forest (ENF), grassland (GRS) and tundra (TUN) (Table 1). Supplementary information on the vegetation, climate, and soil from the sites noted above is available online. Half-hourly or hourly averaged photosynthetically active radiation (PAR), air temperature (T_a), and friction velocity (u*) were used together with NEE of CO_2. When available, data sets that were gap-filled by site principal investigators were used. For other sites, data filtering and gap-filling were conducted with the following procedures.

[7] An outlier ("spike") detection technique was applied, and the spikes were removed, following *Papale et al.* [2006]. Because nighttime CO_2 flux can be underestimated by EC measurements under stable conditions [*Falge et al.*, 2001], nighttime data with low-turbulence conditions were removed based on a u*-threshold criterion (site-specific 99% threshold criterion following [*Reichstein et al.*, 2005] and [*Papale et al.*, 2006]).

[8] Nonlinear regression methods were used to fill NEE data gaps [*Falge et al.*, 2001]. Nonlinear regression relationships between measured fluxes and meteorological conditions were fitted using a 7-day moving window. Equation (1) was used to fill the missing nighttime fluxes (NEE_{night}), and BR and Q_{10} are the fitted model parameters. A Michaelis–Menten type light response function was used to fill the missing daytime fluxes (NEE_{day}) [*Falge et al.*, 2001]:

$$NEE_{day} = \frac{\alpha \times PAR \times F_{GPP,sat}}{F_{GPP,sat} + \alpha \times PAR} - A_{day} e^{\left(B_{day} T_a\right)} \qquad (2)$$

where $F_{GPP,sat}$ (gross primary productivity at saturating light), α (initial slope of the light response function), A_{day} and B_{day} are fitted parameters. The nonlinear regression procedure (PROC NLIN) in the STATISTICAL ANALYSIS SYSTEM (SAS Institute Inc., Cary, NC, USA) was used to fit the relationships between measured fluxes and environmental factors.

[9] To avoid uncertainties introduced by the extrapolation to daily ER (ER_{day}), we used only observed nighttime ER to examine the equivalence relationship between mean annual ER and its rate at the mean annual temperature. Nocturnal ER and nocturnal temperature were calculated based on half-hourly or hourly values. Daily average nocturnal ER values were excluded from analysis when missing hourly data exceeded 20% of the time on a given day. Based on the daily nighttime data set, yearly mean nocturnal ER and nocturnal mean temperature were calculated. If missing daily data exceeded 20% of entire year, the value of that year was excluded. On average, 30% of the years were rejected due to insufficient nocturnal observations. The rejected years varied among sites from 60% (Blodgett) to 10% (Howland).

[10] In order to characterize the ER rate when nighttime air temperature equals annual mean nighttime temperature, data aggregation was conducted according to the following procedures. From temperatures of −30°C to maximum air temperature, daily temperature bins were defined through 1°C increments of air temperature. The daily nocturnal air temperature and ER were averaged through every temperature range over all years within individual sites. These binned data were used to generate temperature curves of ER at each site. An example of this curve is shown in Figure 1, and the intersection of this curve with mean annual temperature was used to determine the ER rate.

[11] For estimating the correlation of GPP to ER, care must be taken when relying on the empirically derived values. *Vickers et al.* [2009] argued that there is a spurious correlation between GPP and ER when these component fluxes are jointly estimated from the observed NEE. *Lasslop et al.* [2010] attempted to minimize spurious correlations between GPP and ER by maximizing the amount and quality of data that go into their estimation. We follow the philosophy of this approach by calculating daily ER as the sum of NEE_{night} and daytime ER (ER_{day1}), extrapolated using equation (1) with daytime air temperatures and with BR and Q_{10} fitted by half hourly nighttime measurements. Daily GPP was synthesized based on daily NEE and daytime ER (ER_{day2}), which was estimated by equation (2) and $F_{GPP,sat}$, α, A_{day} and B_{day} were fitted only based on daytime flux measurements using a 7-day moving window. In this fashion, daily ER was estimated only based on parameters derived from nighttime measurements and GPP was esti-

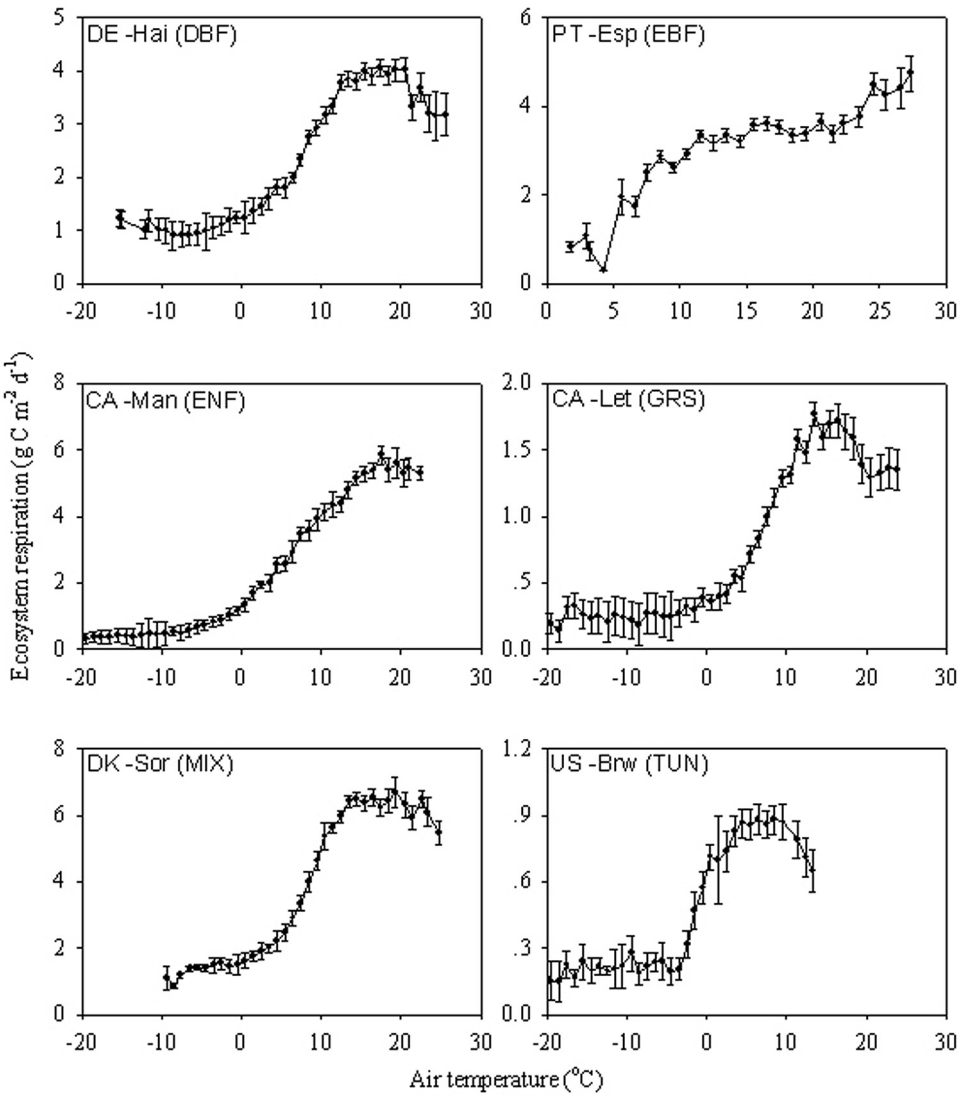

Figure 1. Examples of temperature response curves of ecosystem respiration with standard errors. DBF: deciduous broadleaf forest; EBF: evergreen broadleaf forest; ENF: evergreen needleleaf forest; GRS: grassland; MIX: mixed forest; TUN: tundra. Annual mean temperature at US-Brw and CA-Man are below 0°C.

mated based on parameters using daytime measurements, which is intended to avoid issues with spurious correlation. The same data filtering criterion as given above (i.e., 20%) was used to estimate missing data.

2.2. BR Model Evaluation

[12] Observed ER at EC sites was used to compare simulations of ER using invariant and variable BR, where equation (1) was used to model ER using two different parameterization schemes. To estimate Q_{10}, globally heterogeneous Q_{10} values of soil respiration were estimated from assimilation of observed soil carbon content into a process-based terrestrial carbon model (Carnegie-Ames-Stanford Approach model) [*Zhou et al.*, 2009]. We assumed the temperature sensitivity (Q_{10} value) of ER is the same as that for soil respiration with the risk of inducing model errors. Relative Predicted Errors (RPE) and coefficient of determination (R^2) were used to quantify the improvement in model predictions using the variable BR instead of the invariant. The RPE was computed as:

$$RPE(\%) = \frac{\overline{S} - \overline{O}}{\overline{O}} \times 100\% \quad (3)$$

where $\overline{S}$ and $\overline{O}$ are mean simulated and observed values, respectively.

2.3. EC-LUE Model

[13] The spatial pattern of GPP is used as a driver for global BR. We used a simple, validated light use efficiency GPP model, the EC-LUE model, to estimate global GPP values [*Yuan et al.*, 2007]. The EC-LUE model may have the most potential to adequately address the spatial and temporal dynamics of GPP because its parameters (i.e., the potential light use efficiency and optimal growth temperature) have been shown to be relatively invariant across the

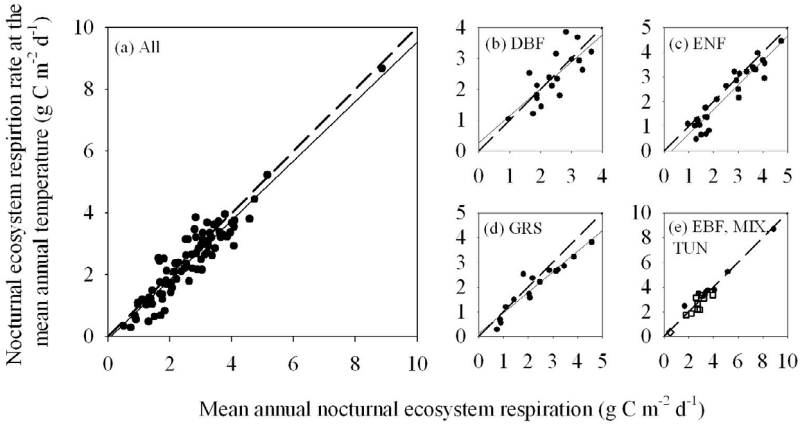

Figure 2. The relationship between mean annual nocturnal ecosystem respiration and nocturnal ecosystem respiration at mean annual nocturnal temperature across (a) all study sites: $y = 0.96\times - 0.07$, $R^2 = 0.87$; (b) deciduous broadleaf forests: $y = 0.87\times + 0.26$, $R^2 = 0.58$; (c) evergreen needleleaf forests: $y = 0.98\times - 0.28$, $R^2 = 0.88$; (d) grasslands: $y = 0.83\times + 0.12$, $R^2 = 0.89$; and (e) evergreen broadleaf forests (solid dots; $y = 0.88\times + 0.66$, $R^2 = 0.97$), mixed forests (open squares; $y = 0.82\times + 0.32$, $R^2 = 0.60$) and tundra (open diamond). Short dashes represent the 1:1 line. Mean annual nocturnal ecosystem respiration is the mean value for all available years for which missing data are less than 20% of the entire year's data at each site, and ecosystem respiration rate at the mean annual temperature is determined from temperature response curves of ecosystem respiration shown in Figure 1.

various plant functional types, and is driven by only four variables: normalized difference vegetation index (NDVI), photosynthetically active radiation (PAR), air temperature, and the ratio of sensible to latent heat flux (Bowen ratio). EC-LUE has recently been modified to include the ratio of evapotranspiration (ET) to net radiation instead of the Bowen ratio. The revised RS-PM (Remote Sensing-Penman Monteith) model was used to quantify ET [*Yuan et al.*, 2010]. Fifty-four eddy covariance towers, including various ecosystem types, were selected to calibrate and evaluate the revised EC-LUE model. Using estimated ET by revised RS-PM model as input, the EC-LUE model showed good performance in both calibration and validation sites, explaining 75% and 58% of the observed 8-day variation of GPP, respectively.

2.4. Model Driver Data

[14] For global estimates of GPP, we used input data sets for net radiation (R_n), air temperature (T), relative humidity (R_h) and photosynthetically active radiation (PAR) from the MERRA (Modern Era Retrospective-Analysis for Research and Applications) [*Bosilovich et al.*, 2008] archive for 2000~2003 [*Global Modeling and Assimilation Office*, 2004]. MERRA is a NASA reanalysis for the satellite era using a new version of the Goddard Earth Observing System Version 5 (GEOS-5). MERRA uses data from all available surface weather observations globally every 3 h, and GEOS-5 was used to assimilate these point data on a short time sequence, and produces an estimate of climatic conditions over the globe, at 10 m above the land surface (approximating canopy height conditions) and at a resolution of 0.5° latitude by 0.6° longitude.

[15] The global 8-day MODIS (MODerate resolution Imaging Spectroradiometer) leaf area index (LAI) (MOD15A2) and 16-day MODIS NDVI (MOD13A2) were also used in this study. Quality control (QC) flags were examined to screen and reject NDVI and LAI data of insufficient quality. We temporally filled the missing or unreliable LAI and NDVI at each 1-km MODIS pixel based on their corresponding quality assessment data fields as proposed by *Zhao et al.* [2005]. If the first (or last) 8-day LAI (16-day NDVI) was unreliable or missing, it was replaced by the closest reliable 8-day (16-day) value. All of those satellite data sets were resampled to the geographic projection and spatial resolution of the global MERRA data set.

3. Results and Discussion

3.1. Equivalence Relation Between Mean Annual Ecosystem Respiration and Ecosystem Respiration Rate at Mean Annual Temperature

[16] Analysis of data from 79 EC sites with 276 site-years worldwide verified the equivalence relation between mean annual nocturnal ER and ER rate at mean annual nocturnal air temperature (Figure 2a). The slope of this correlation is not significantly different from 1, and the intercept does not significantly differ from 0 ($p < 0.05$). This equivalence relation is observed to be consistent in various natural ecosystem types: evergreen broadleaf forest (EBF), deciduous broadleaf forest (DBF), evergreen needleleaf forest (ENF), mixed forest (MIX), grassland (GRS) and tundra (TUN) (Figures 2b, 2c, 2d, and 2e).

[17] One surprising finding is that our model predicts a positive BR at several eddy flux sites where the mean annual temperatures are below 0° (e.g., US-Brw, CA-Man). Even at these sites, ER rate at mean annual nocturnal temperature can still represent mean annual nocturnal ER very well, contradictory with the assumption that biological activity is minimal when temperatures are below freezing. Slow growth of roots has been reported throughout the winter in northern ecosystems [*Hansen et al.*, 1996]. Moreover, the ability of cold-adapted microbes to survive and grow below

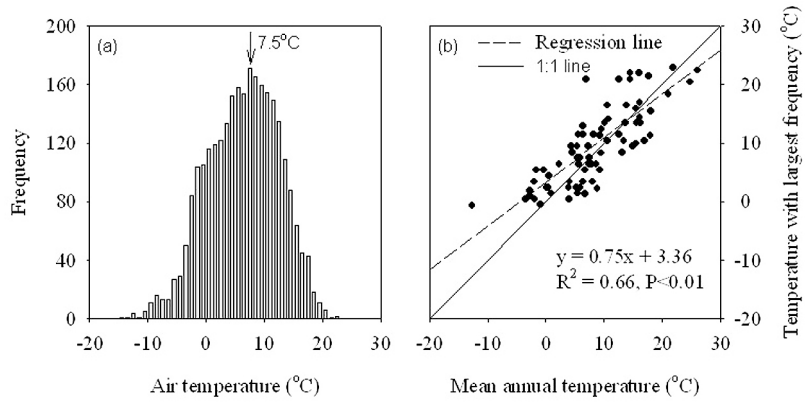

Figure 3. (a) Frequency distribution of air temperature at Vielsalm, Belgium where mean annual temperature equals 7.37°C, and (b) the relation between mean annual temperature and the temperature at the maximum of the frequency distribution function.

0° has been documented [*Gilichinsky*, 1995], and respiration in frozen soils has been demonstrated repeatedly in the laboratory [*Clein and Schimel*, 1995; *Panikov*, 1999]. Microbial activity is possible in soils below 0° exploits the small amounts of unfrozen water, allowing for diffusion of microbial substrates and waste products [*Ostroumov and Siegert*, 1996]. Recent work has confirmed that, although rates are low, the cumulative winter CO_2 flux from tundra soils may account for a significant amount of their annual carbon budget [*Fahnestock et al.*, 1999; *Grogan and Chapin*, 1999; *Welker et al.*, 2000].

[18] The mechanism for the equivalence across all sites is still unclear, but the studies on thermal responses of respiration may provide some insights for understanding this finding. Temperature is the most fundamental climatic factor influencing the kinetics of biochemical reactions, and impacts almost all ecosystem carbon cycle processes. At undisturbed ecosystems, thermal conditions directly determine respiring substrate supply in soil, which strongly regulates the spatial heterogeneity of ER. For example, it is widely acknowledged that soil organic content decreases along gradients of increasing temperature [*Jenny*, 1980; *Post et al.*, 1982, 1985]. Plant autotrophic respiration also has been shown to adapt to the prevailing ambient temperature by adjustment of enzyme activity and substrate availability [*Atkin and Tjoelker*, 2003].

[19] Moreover, annual mean temperature works as a specific indictor for local thermal conditions because the temperature throughout the year in most regions fluctuates closely around the mean annual temperature. Correlation analyses showed that the temperature at the maximum of the frequency distribution function occurs typically around the mean annual temperature (Figure 3). Therefore respiration rate at the mean annual temperature has the highest potential to represent the most frequent value of ecosystem respiration in a given area. For this reason, a linear relation can persist with mean annual temperature and ER across sites from different regions although a nonlinear relationship exists between temperature and ER at a particular site.

3.2. Correlation Between GPP and Ecosystem Respiration

[20] Our derived annual mean ER strongly correlated with annual mean GPP across the flux tower sites (Figure 4). This result is consistent with previous studies such as *Janssens*

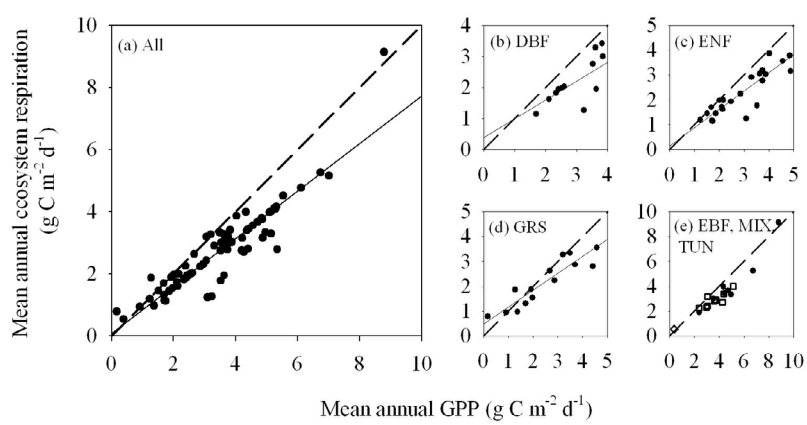

Figure 4. Correlation between mean annual GPP and ecosystem respiration across (a) all study sites: y = 0.76× + 0.07, R^2 = 0.85; (b) deciduous broadleaf forests: y = 0.60× + 0.38, R^2 = 0.64; (c) evergreen needleleaf forests: y = 0.74× + 0.13, R^2 = 0.89; (d) grasslands: y = 0.67× + 0.49, R^2 = 0.90; and (e) evergreen broadleaf forests (solid dots; y = 1.07× − 1.13, R^2 = 0.91), mixed forests (open squares; y = 0.55× + 0.89, R^2 = 0.68) and tundra (open diamond). Short dashes are 1:1 line.

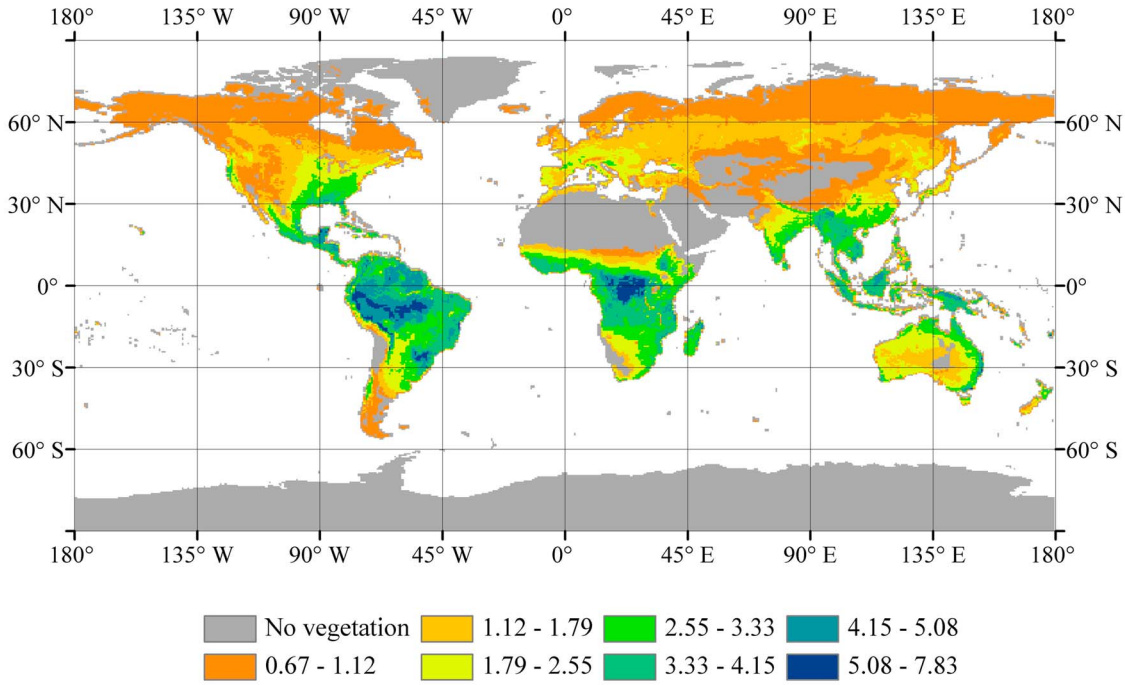

Figure 5. The global pattern of basal ecosystem respiration rate (g C m^{-2} day^{-1}) in this study, which equals ecosystem respiration rate at mean annual temperature.

et al. [2001], *Reichstein et al.* [2007] and *Baldocchi* [2008]. As previously discussed in the methods, our estimates of GPP and ER are based on the method proposed by *Lasslop et al.* [2010] which reduces error from any possible spurious correlation arising from derivation of these two quantities from the same observation of NEE [*Vickers et al.*, 2009].

[21] Other lines of evidence also explain this significant correlation. Soil respiration, an important component of ER, has been found to have a strong correlation with Net Primary Production (NPP) across a variety of biomes [*Raich and Schlesinger*, 1992] with assimilate supply [*Bahn et al.*, 2008], with aboveground net primary productivity in northern peatlands [*Moore*, 1986] and with aboveground litter production in forest ecosystems [*Schlesinger*, 1977; *Raich and Nadelhoffer*, 1989; *DeForest et al.*, 2009]. These studies indicate a tight link between plant productivity and ecosystem respiration because primary production provides the organic substrate that drives soil metabolic activity. Plant autotrophic respiration is clearly and closely coupled with photosynthetic activity [*Heilmeier et al.*, 1997]. However, it is also the case that the largest fraction of heterotrophic respiration originates from decomposition of young organic matter (dead leaves and fine roots). Thus, both root respiration and heterotrophic respiration will appear to be dependent on primary productivity [*Janssens et al.*, 2001]. Consequently, the relationship between annual ER and GPP should not be surprising.

3.3. Global Estimate of Basal Ecosystem Respiration Rate

[22] Using our new definition of BR and by coupling the two correlations shown in Figures 2 and 4, we can easily obtain BR from estimated GPP, which has been successfully simulated by the previously described EC-LUE model [*Yuan et al.*, 2007]. By then applying the correlation of BR to mean annual temperature through all ecosystem types, we estimated BR based on simulated GPP by EC-LUE model.

[23] The derived spatial pattern of the BR at global scale shows a large spatial heterogeneity (Figure 5). Since we redefined BR as ER rate at the mean annual temperature, so the spatial pattern of BR depends strongly on thermal conditions. In general, BR is high over the tropical rain forests and subtropical forest regions like the southeastern United States and the Pantanal region of South American. Basal rate decreases with latitude in the northern and southern hemispheres, which is partically caused by the decreasing mean temperature.

3.4. Global Estimation of Ecosystem Respiration

[24] The Q_{10} equation with the site-specific BR accounts for 71% of the variation of monthly ER across all study sites (Figure 6a). Individually, the coefficient of determination (R^2) varies from 0.30 at Audubon site to 0.91 at the DE-Tha site (data not shown). These results were compared with those obtained with a globally invariant BR, which was set to the mean value of global BR over the vegetation regions (2.16 g C m^{-2} day^{-1}). In that case, the Q_{10} equation only explained about 50% of variation of monthly ER across the all study sites ranging from 25% to 84% (Figure 6b), and the relative predictive error was 35% averaged over all sites, compared to 23% using the site-specific BR.

[25] We assessed the global spatial and seasonal patterns of ER from 2000 to 2003 by the model using our globally heterogeneous BR (Figure 7). ER of the southern hemispheric tropics remains consistently high throughout the year while that of the major deserts of northern Africa and Australia remain consistently low. The major seasonal change occurs in the high northern latitudes, where ER shows a

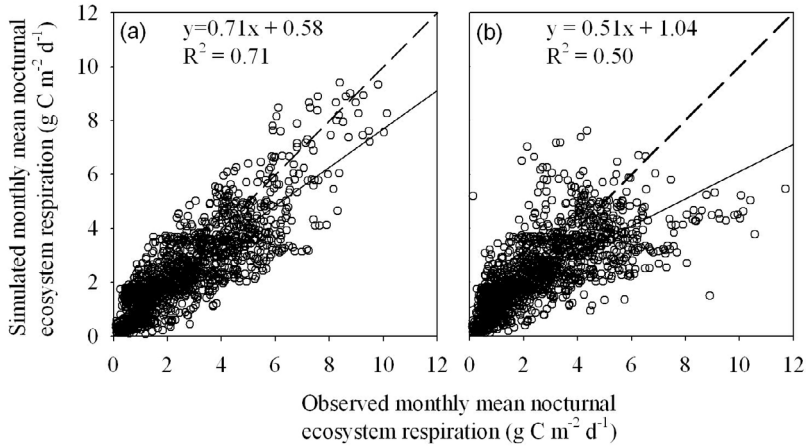

Figure 6. Model validation of Q_{10} equation across the all study sites using (a) heterogeneous basal ecosystem respiration rate and (b) invariant value. The short dashed lines are the 1:1 line, and the solid lines are the linear regression line.

higher variation between northern summer and winter. The variant BR model estimates that ER releases 103 Pg C yr^{-1} from the land ecosystems to the atmosphere (Figure 8a). Rates of ER are highest in the tropical moist forest regions and lowest in cold tundra and dry desert regions.

[26] Although validation of global ER is not feasible, we are able to compare our result with other global estimates of ER derived from upscaling of other ecological observations. *Raich et al.* [2002] estimated global soil respiration to be 80.4 (range 79.3 ~ 81.8) Pg C yr^{-1} averaged from 1980 to 1994 using a climate-driven regression model, which is about 77% of our global annual ER. This ratio of soil respiration and ER is similar to those reported at various geographical areas and ecosystem types ranging from 43 to

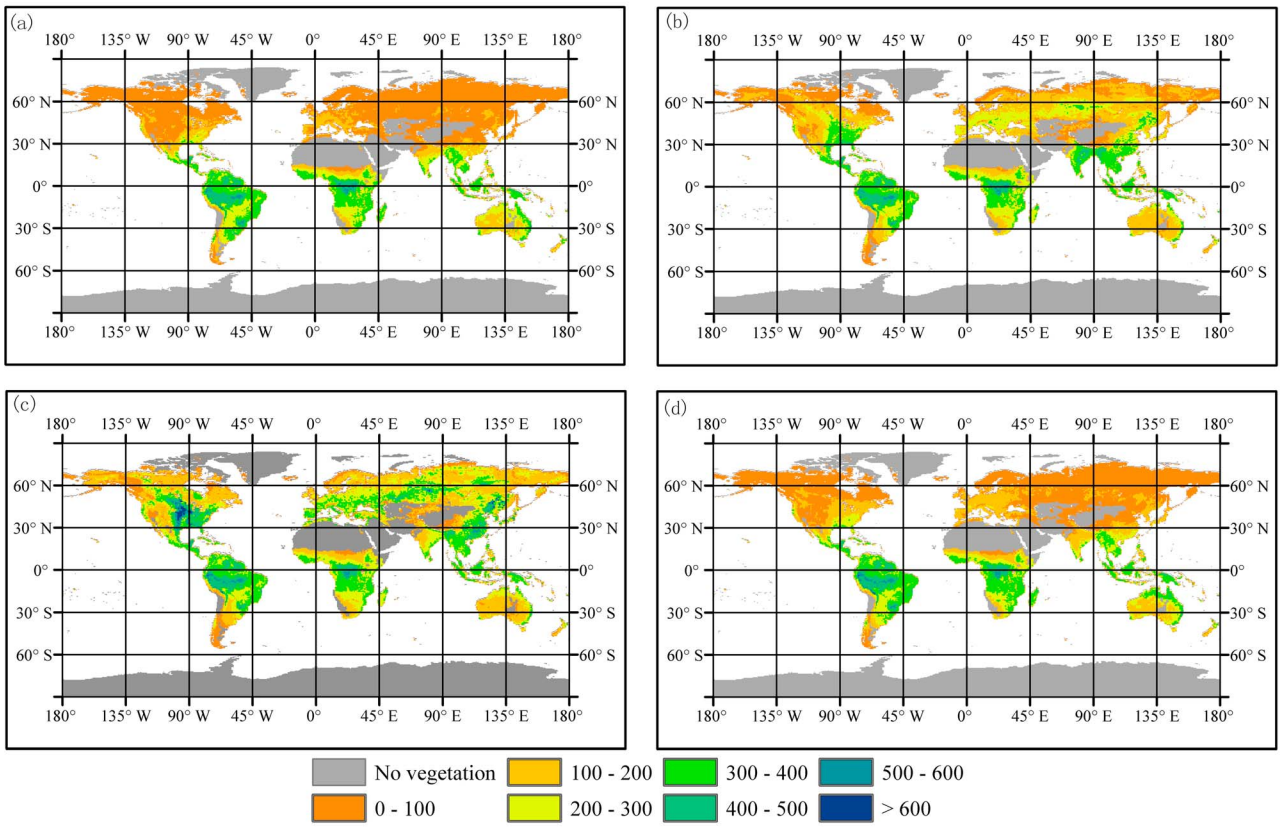

Figure 7. Seasonal variations of global ecosystem respiration (g C m^{-2}) as predicted by the Q_{10} equation with the spatially heterogeneous basal ecosystem respiration rate: (a) aggregated ER of January, February, and March; (b) April, May, and June; (c) July; August, and September; and (d) October, November, and December.

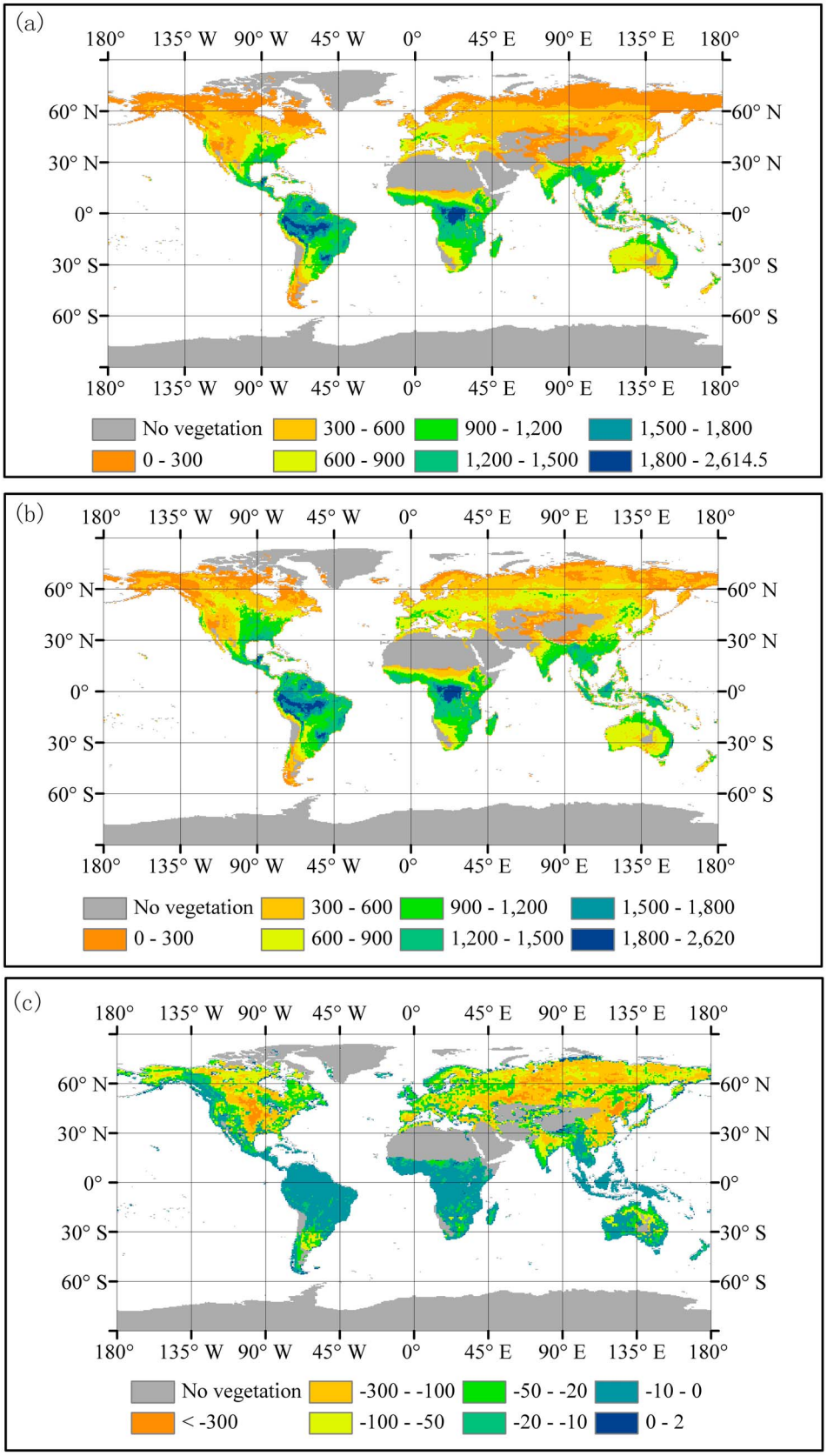

Figure 8. Global annual ecosystem respiration (ER) (g C m^{-2} yr^{-1}) (a) using only gross primary production (GPP) derived by EC-LUE and the relation of GPP and ER, (b) using the Q_{10} equation with a spatially heterogeneous basal ecosystem respiration rate, and (c) the difference between these two methods.

99% [*Goulden et al.*, 1996; *Lavinge et al.*, 1997; *Law et al.*, 1999; *Janssens et al.*, 2001; *Griffis et al.*, 2004; *Davidson et al.*, 2006; *Zhang et al.*, 2009]. However, other studies reported higher annual global soil respiration [*Potter and Klooster*, 1998; *Bond-Lamberty et al.*, 2004]. For example, a recent study showed global soil respiration is 98 Pg C yr^{-1}, which is 20–30% higher than the previous estimates [*Bond-Lamberty and Thomson*, 2010]. Both model structure and parameters play an important role in differences of global soil respiration estimates, thus model intercomparison at the global scale is much needed.

[27] Due to lack of estimate of Q_{10} for ER globally, we assumed that the temperature sensitivity of plant autotrophic respiration is the same as soil respiration, and used soil respiration Q_{10} values reported by *Zhou et al.* [2009] to estimate global ER patterns. Although some studies have reported differences in the Q_{10} values between soil respiration and plant autotrophic respiration, a recent study showed that the root autotrophic and soil heterotrophic respiration responded equally to the temperature increase [*Schindlbacher et al.*, 2009]. *Piao et al.* [2010] reported that Q_{10} for plant autotrophic respiration varied from 1.9 to 2.5 across the global scales, which are close to the range of 1.2–2.6 with the mean value of 1.92 for soil respiration over the vegetation regions in the *Zhou et al.* [2009]. The results reported by *Zhou et al.* [2009] are close to the constant Q_{10} value of 1.4 at various ecosystem types [*Mahecha et al.*, 2010], Q_{10} value of 1.5 based on global soil respiration data set [*Bond-Lamberty and Thomson*, 2010] and a recent tracer-transport inverse model derived Q_{10} values that range from 1.96 to 2.16 [*Jones and Cox*, 2001]. Moreover, we compared mean Q_{10} values using equation (1) with those from *Zhou et al.* [2009] over all sites, and found a significant correlation (Q_{10}_Inversion = 0.69 × Q_{10}_Zhou + 0.48, $R^2 = 0.36$, $P < 0.01$).

[28] We can also compare global annual ER using two different methods: (1) ER estimation using only global GPP and the relation between annual GPP and ER (ER_{GPP}); (2) ER estimation using the Q_{10} model and the spatially heterogeneous basal respiration in this study and Q_{10} values derived by *Zhou et al.* [2009] (ER_{Q10}). The results showed global mean annual ER_{GPP} was 92 Pg C (Figure 8a), which was 89% of ER_{Q10} (103 Pg C; Figure 8b). The higher estimations of ER_{Q10} occur relatively uniformally in all parts of the globe.

[29] Many studies have shown that Q_{10} decreases with increasing temperature [*Andrews et al.*, 2000; *Janssens and Pilegaard*, 2003; *Chen et al.*, 2010], and Figure 1 also showed decreased ER at high temperature. Although Q_{10}-type equations have been widely used to estimate ecosystem respiration at the various temporal and spatial scales, our and other previous studies showed the estimation uncertainties resulting from temporal constant of Q_{10}. Our globally variant BR model should be beneficial in helping further constrain Q_{10}, by reducing the number of unconstrained parameters in empirical carbon cycle models.

4. Summary

[30] BR and its spatial variability are crucial for projecting climate change impacts on terrestrial carbon cycling and future atmospheric CO_2 concentration. This study has demonstrated the equivalence of the mean annual ER and the ER rate at mean annual temperature at the global scale, which offers good opportunity to retrieve the global pattern of BR by combining this finding with observed correlation of mean annual ER with GPP. Flux tower evaluation supports our redefinition of BR as the ER rate at mean annual temperature, and develops the correlation between the new BR and GPP for estimating global patterns of BR. The results showed the spatially heterogeneous BR results in a better estimation of ER at different sites. Our study provides an innovative method for generating global BR, and will be useful to estimate spatial patterns of ER.

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M. Aurela, Climate and Global Change Research, Finnish Meteorological Institute, Helsinki FIN-00101, Finland.

M. Bahn, Institute of Ecology, University of Innsbruck, Sternwartestr. 15, A-6020 Innsbruck, Austria.

C. Bernhofer and T. Grünwald, Chair of Meteorology, Institute of Hydrology and Meteorology, Technische Universität Dresden, D-01062 Dresden, Germany.

A. Black, Faculty of Land and Food Systems, University of British Columbia, 2357 Main Mall, Vancouver, BC, V6T 1Z4, Canada.

G. Bohrer, Department of Civil, Environmental, and Geodetic Engineering, Ohio State University, 417E Hitchcock Hall, 2070 Neil Ave., Columbus, OH 43210, USA.

A. Cescatti, Institute for Environment and Sustainability, Joint Research Centre, European Commission, Via E. Fermi 2749, I-21027 Ispra, Italy.

J. Chen, Department of Earth, Ecological, and Environmental Sciences, University of Toledo, MS 604, Toledo, OH 43606, USA.

D. R. Cook, Climate Research Section, Environmental Science Division, Argonne National Laboratory, Argonne, IL 60439, USA.

A. R. Desai, Atmospheric and Oceanic Sciences Department, Center for Climatic Research, Nelson Institute for Environmental Studies, University of Wisconsin-Madison, 1225 W. Dayton St., AOSS 1549, Madison, WI 53706, USA.

D. Dragoni, Department of Geography, Indiana University, Bloomington, IN 47405, USA.

A. L. Dunn, Department of Physical and Earth Sciences, Worcester State College, Worcester, MA 01602, USA.

D. Gianelle, B. Marcolla, and M. Rodeghiero, Sustainable Agro-ecosystems and Bioresources Department, Fondazione Edmund Mach-IASMA Research and Innovation Centre, Via E. Mach 1, I-38010 San Michele all'Adige (TN), Italy.

B. Gielen, Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610, Wilrijk, Belgium.

A. Ibrom, Risø DTU National Laboratory for Sustainable Energy, Biosystems Division, Technical University of Denmark, DK-4000 Roskilde, Denmark.

C. Jacobs, Alterra, Earth System Science–Climate Change, Wageningen University, Wageningen NL-6700 AA, Netherlands.

M. Y. Leclerc, Department of Crop and Soil Sciences, College of Agricultural and Environmental Sciences, University of Georgia, Griffin, GA 30223, USA.

X. Li and W. Yuan, College of Global Change and Earth System Science, Beijing Normal University, Beijing 100875, China. (wenpingyuancn@yahoo.com)

A. Lindroth, Geobiosphere Science Centre, Physical Geography and Ecosystems Analysis, Lund University, Lund S-22100, Sweden.

H. Liu, Laboratory for Atmospheric Research, Department of Civil and Environmental Engineering, Washington State University, Pullman, WA 99164-2910, USA.

S. Liu, USGS EROS Center, 47914 252nd St., Sioux Falls, SD 57198, USA.

Y. Luo, Department of Botany and Microbiology, University of Oklahoma, 770 Van Vleet Oval, Norman, OK 73019, USA.

L. B. Marchesini, DIBAF, University of Tuscia, Viterbo I-01100, Italy.

L. Montagnani, Faculty of Science and Technology, Free University of Bolzano, Piazza Università 1, I-39100, Bolzano, Italy.

G. Pita, Department of Mechanical Engineering, Instituto Superior Técnico, Lisboa P-1049-001, Portugal.

A. Rodrigues, Unidade de Silvicultura e Produtos Florestais, INRB, Quinta do Marquês, Oeiras P-2780-159, Portugal.

G. Starr, Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487, USA.

P. C. Stoy, Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT 59717, USA.

G. Yu, Key Laboratory of Ecosystem Network Observation and Modeling, Synthesis Research Center, CERN, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China.

T. Zhou, State Key Laboratory of Earth Surface Processes and Resource Ecology, Beijing Normal University, Beijing 100875, China.