

Thermal optimality of net ecosystem exchange of carbon dioxide and underlying mechanisms

Shuli Niu¹, Yiqi Luo^{1,2}, Shenfeng Fei¹, Wenping Yuan³, David Schimel⁴, Beverly E. Law⁵, Christof Ammann⁶, M. Altaf Arain⁷, Almut Arneth^{8,9}, Marc Aubinet¹⁰, Alan Barr¹¹, Jason Beringer¹², Christian Bernhofer¹³, T. Andrew Black¹⁴, Nina Buchmann¹⁵, Alessandro Cescatti¹⁶, Jiquan Chen¹⁷, Kenneth J. Davis¹⁸, Ebba Dellwik¹⁹, Ankur R. Desai²⁰, Sophia Etzold¹⁵, Louis Francois²¹, Damiano Gianelle²², Bert Gielen²³, Allen Goldstein²⁴, Margriet Groenendijk²⁵, Lianhong Gu²⁶, Niall Hanan²⁷, Carole Helfter²⁸, Takashi Hirano²⁹, David Y. Hollinger³⁰, Mike B. Jones³¹, Gerard Kiely³², Thomas E. Kolb³³, Werner L. Kutsch³⁴, Peter Lafleur³⁵, David M. Lawrence³⁶, Linghao Li³⁷, Anders Lindroth⁸, Marcy Litvak³⁸, Denis Loustau³⁹, Magnus Lund⁸, Michal Marek⁴⁰, Timothy A. Martin⁴¹, Giorgio Matteucci⁴², Mirco Migliavacca¹⁶, Leonardo Montagnani^{43,44}, Eddy Moors⁴⁵, J. William Munger⁴⁶, Asko Noormets⁴⁷, Walter Oechel⁴⁸, Janusz Olejnik⁴⁹, Kyaw Tha Paw U⁵⁰, Kim Pilegaard⁵¹, Serge Rambal⁵², Antonio Raschi⁵³, Russell L. Scott⁵⁴, Günther Seufert¹⁶, Donatella Spano⁵⁵, Paul Stoy⁵⁶, Mark A. Sutton³⁰, Andrej Varlagin⁵⁷, Timo Vesala⁵⁸, Ensheng Weng¹, Georg Wohlfahrt⁵⁹, Bai Yang²⁶, Zhongda Zhang¹ and Xuhui Zhou²

¹Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019, USA; ²Institute of Global Environmental Change Research, Fudan University, Shanghai, China; ³College of Global Change and Earth System Science, Beijing Normal University, Beijing 100875, China; ⁴NEON, Inc., 5340 Airport Blvd, Boulder, CO 80301, USA; ⁵College of Forestry, Oregon State University, Corvallis, OR 97331-2209, USA; ⁶Federal Research Station Agroscope Reckenholz-Tänikon, Reckenholzstr. 191, 8046 Zürich, Switzerland; ⁷School of Geography and Earth Sciences, McMaster University, Hamilton, ON, Canada L8S 4K1; ⁸Department of Physical Geography and Ecosystems Analysis, Lund University, 223 62 Lund, Sweden; ⁹Atmospheric Environmental Research, Institute of Meteorology and Climate Research, Karlsruhe Institute of Technology, Germany; ¹⁰Faculté Universitaire des Sciences Agronomiques de Gembloux, Unité de Physique des Biosystèmes, B-5030 Gembloux, Belgium; ¹¹Climate Research Division, Environment Canada, Saskatoon, SK S7N 3H5, Canada; ¹²School of Geography and Environmental Science, Monash University, Clayton, Vic 3800, Australia; ¹³Institute of Hydrology and Meteorology, Chair of Meteorology, Technische Universität Dresden, 01062 Dresden, Germany; ¹⁴Land and Food Systems, University of British Columbia, Vancouver, BC, Canada V6T 1Z4; ¹⁵ETH, Zurich, Institute of Plant Science, Universitätsstrasse 2, Zürich 8092, Switzerland; ¹⁶European Commission, Joint Research Center, Institute for Environment and Sustainability, Ispra, Italy; ¹⁷Department of Environmental Sciences (DES), University of Toledo, Toledo, OH 43606, USA; ¹⁸Earth System Science Center, Pennsylvania State University, State College, PA 16802, USA; ¹⁹Wind Energy Division, Risø National Laboratory for Sustainable Energy, Technical University of Denmark, P.O. 49, DK-4000 Roskilde, Denmark; ²⁰Department of Atmospheric and Oceanic Sciences, University of Wisconsin, Madison, WI, 53706, USA; ²¹Unité de Modélisation du Climat et des Cycles Biogéochimiques (UMCCB) Université de Liège, B-4000 Liège, Belgium; ²²Sustainable Agro-ecosystems and Bioresources Department, IASMA Research and Innovation Centre, Fondazione Edmund Mach, Via E. Mach 1, 38010 San Michele all'Adige, (TN), Italy; ²³Department of Biology, University of Antwerpen, Universiteitsplein 1, Wilrijk, B-2610, Belgium; ²⁴Department of Environmental Science, Policy and Management, University of California, Berkeley, California 94720, USA; ²⁵Department of Earth Science, Faculty of Earth and Life Sciences, VU University Amsterdam, Boelelaan 1085, 1081 HV Amsterdam, the Netherlands; ²⁶Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831 USA; ²⁷Geographic Information Science Center of Excellence (GIScCE), South Dakota State University, 1021 Medary Ave., Wecota Hall 506B, Brookings, SD 57007-3510, USA; ²⁸Centre for Ecology and Hydrology (CEH), Bush Estate, Penicuik, Midlothian, Scotland EH26 0QB, UK; ²⁹Hokkaido University N9, W9, Kita-ku, Sapporo, Hokkaido, 060-8589, Japan; ³⁰USDA Forest Service, Northern Research Station, Durham, NH 03824, USA; ³¹Botany Department, Trinity College of Dublin, Dublin, Ireland; ³²Civil and Environmental Engineering Department, University College Cork, Cork, Ireland; ³³School of Forestry, Northern Arizona University, Flagstaff, AZ 86001, USA; ³⁴Johann Heinrich von Thünen-Institute (vTI), Institute for Climate Research, Braunschweig, Germany; ³⁵Department of Geography, Trent University, Peterborough, ON K9J 7B8, Canada; ³⁶National Center for Atmospheric Research, Boulder, CO 80305, USA; ³⁷State Key laboratory of Vegetation and Environmental Changes, Institute of Botany, Chinese Academy of Sciences; ³⁸Biology Department, University of New Mexico, Albuquerque, NM 87131-001, USA; ³⁹INRA, UR1263 EPHYSE, F-33140, Villenave d'Ornon, France; ⁴⁰Institute of Systems Biology and Ecology, Academy of Sciences of the Czech Republic, Poříčí 3b, CZ-60300 Brno, Czech Republic; ⁴¹University of Florida, Gainesville, FL 32611, USA; ⁴²National Research Council, Institute of Agroenvironmental and Forest Biology, 00015 Monterotondo Scalo (RM), Italy; ⁴³Servizi Forestali, Agenzia per l'Ambiente, Provincia Autonoma di Bolzano, 39100, Bolzano, Italy; ⁴⁴Faculty of Science and Technology, Free University of Bolzano, Piazza Università 1, 39100 Bolzano, Italy; ⁴⁵ESS-CC, Alterra, Wageningen UR, PO Box 47, 6700 AA Wageningen, The Netherlands NL; ⁴⁶Department of Earth and Planetary Sciences, Harvard University, Cambridge, MA, 02138, USA; ⁴⁷North Carolina State University/USDA Forest Service, Southern Global Change Program, Raleigh, NC, 27606, USA; ⁴⁸Department of Biology, San Diego State University, San Diego, CA 92182-4614, USA; ⁴⁹Meteorology Department, Poznan University of Life Sciences (PULS), 60-667 Poznan, Poland; ⁵⁰Atmospheric Science Group, LAWR, UC Davis, Davis, CA 95616, USA; ⁵¹Biosystems Division, Risø National Laboratory for Sustainable Energy, Technical University of Denmark, P.O. 49, DK-4000 Roskilde, Denmark; ⁵²DREAM, CEFE, CNRS, UMR5175, 1919 route de Mende, F-34293 Montpellier, Cedex 5, France; ⁵³CNR – Istituto di Biometeorologia (IBIMET), Via Giovanni Caproni 8, 50145 Firenze, Italy; ⁵⁴USDA-ARS Southwest Watershed Research Center, Tucson, AZ 85719, USA; ⁵⁵Department of Economics and Woody Plant Ecosystems, University of Sassari, Sassari, Italy; ⁵⁶Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT 59717, USA; ⁵⁷A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky pr., 33 Moscow, 119071, Russia; ⁵⁸Department of Physics, FI-00014, University of Helsinki, Finland; ⁵⁹University of Innsbruck, Institute of Ecology Sternwartestr 15, Innsbruck 6020, Austria

Author for correspondence:

Shuli Niu

Tel: +1 405 325 8578

Email: sniu@ou.edu

Received: 15 December 2011

Accepted: 26 January 2012

New Phytologist (2012) **194**: 775–783

doi: 10.1111/j.1469-8137.2012.04095.x

Key words: climate change, optimum temperature, temperature acclimation, temperature adaptation, thermal optimality.

Summary

- It is well established that individual organisms can acclimate and adapt to temperature to optimize their functioning. However, thermal optimization of ecosystems, as an assemblage of organisms, has not been examined at broad spatial and temporal scales.
- Here, we compiled data from 169 globally distributed sites of eddy covariance and quantified the temperature response functions of net ecosystem exchange (NEE), an ecosystem-level property, to determine whether NEE shows thermal optimality and to explore the underlying mechanisms.
- We found that the temperature response of NEE followed a peak curve, with the optimum temperature (corresponding to the maximum magnitude of NEE) being positively correlated with annual mean temperature over years and across sites. Shifts of the optimum temperature of NEE were mostly a result of temperature acclimation of gross primary productivity (upward shift of optimum temperature) rather than changes in the temperature sensitivity of ecosystem respiration.
- Ecosystem-level thermal optimality is a newly revealed ecosystem property, presumably reflecting associated evolutionary adaptation of organisms within ecosystems, and has the potential to significantly regulate ecosystem–climate change feedbacks. The thermal optimality of NEE has implications for understanding fundamental properties of ecosystems in changing environments and benchmarking global models.

Introduction

Ecosystems are represented in most Earth system models in order to simulate the responses and feedbacks of land processes to climate change (Chapin *et al.*, 2002; Friedlingstein *et al.*, 2006). Virtually all ecosystem carbon cycle models use temperature response functions that have been developed from our understanding of biochemical processes of enzymes and/or physiological processes of leaf photosynthesis and organic matter decomposition (Enquist *et al.*, 2003; Friedlingstein *et al.*, 2006) because we lack essential knowledge about ecosystem-level responses to temperature change.

The integrated response of ecosystem processes to temperature change is influenced by the responses of its constituents, including plants, animals, microbes, and their interactions. It is well documented that plants (Mooney *et al.*, 1978; Berry & Bjorkman, 1980; Atkin & Tjoelker, 2003), animals (Parmesan, 2006), and microbes (Bradford *et al.*, 2008) acclimate and/or adapt to prevailing environmental conditions in a way that can optimize their functioning under varying temperatures, which is collectively termed optimality (Parker & Maynard Smith, 1990). Thus, we hypothesize that the integrated response of an ecosystem, as an assemblage of interacting organisms, might also demonstrate thermal optimality under temperature change (Loreau, 2010). Nevertheless, thermal optimality at the ecosystem level has not yet been carefully examined.

Net ecosystem exchange (NEE) of carbon dioxides is an ecosystem process that reflects the balance of gross primary productivity (GPP) and ecosystem respiration (R_c), and is often used to approximate net ecosystem productivity (NEP = $-NEE$) (Chapin *et al.*, 2006). Previous studies have shown that plant photosynthesis and GPP can acclimate to temperature change via an increase in optimum temperature in a warmer environment

(Mooney *et al.*, 1978; Baldocchi *et al.*, 2001; Niu *et al.*, 2008). It has also been documented that R_c responds exponentially to temperature as long as there is no soil water limitation (Law *et al.*, 1999), and its temperature sensitivity (Q_{10}) decreases in a warmer environment, a process also described as temperature acclimation (Lloyd & Taylor, 1994; Luo *et al.*, 2001; Tjoelker *et al.*, 2008; Piao *et al.*, 2010). The temperature acclimation of either GPP or R_c can lead to changes in the temperature response of NEP. As illustrated in the conceptual Fig. 1, if GPP acclimates to temperature by increasing its optimum temperature in a warmer environment while R_c stays unchanged (Fig. 1a), the optimum temperature of NEP at the maximum differences between GPP and R_c may also shift upward. Alternatively, if R_c acclimates to temperature with decreasing Q_{10} at higher temperature, while GPP stays unchanged (Fig. 1b), the optimum temperature of NEE will also increase. If both GPP and R_c acclimate, the optimum temperature of NEE will likely increase more than that in the previously described two conditions (Fig. 1c). A recent study suggests thermal adaptation of NEE based on a positive relationship between the optimum temperature of NEE and the average summer temperature across space (Yuan *et al.*, 2011). Still, we do not know yet which of these possible processes contributes to the shift of optimum temperature of NEE, and whether or not the optimum temperature of NEE shifts over time.

With the advent of eddy-covariance measurements of NEE, together with detailed meteorological variables (Baldocchi *et al.*, 2001), it has become possible to characterize the ecosystem-level temperature response. In this study, we quantified temperature responses of NEE to determine whether NEE exhibits thermal optimality over time and space, and we further explored the underlying mechanisms. Here, we define acclimation as short-term reversible adjustments of NEE over time and

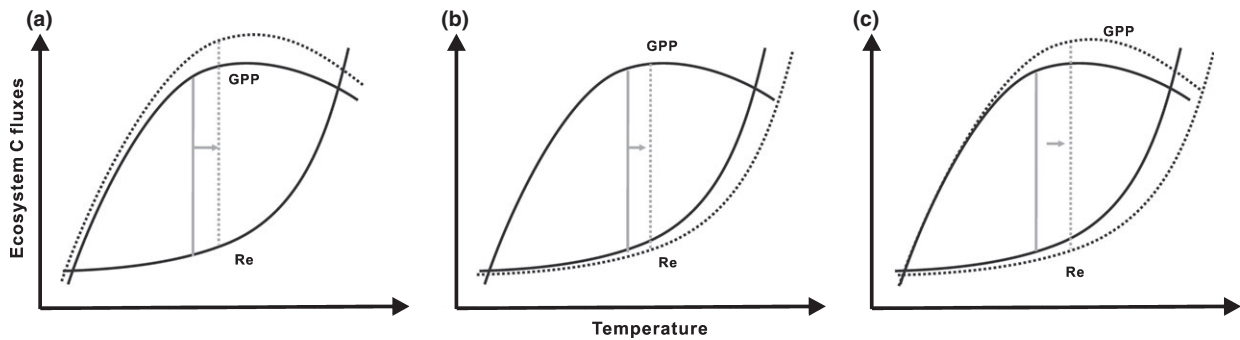


Fig. 1 Conceptual figure for the shifts of optimum temperature of net ecosystem productivity (NEP; $NEP = -NEE$ (net ecosystem exchange)) as a result of the changes in optimum temperature of gross primary productivity (GPP) or the temperature sensitivity of respiration. (a) Here it is assumed that in a warmer year or at a warmer site, the optimum temperature of NEP shifts higher owing to a shift of optimum temperature of GPP. In (b) it is assumed that the shifts in the optimum temperature of NEP are the result of the temperature acclimation of R_e (decrease of Q_{10}). In (c) it is assumed that the optimum temperature of NEP shifts higher owing to acclimation of both GPP and R_e . The dashed curves represent the temperature response curve in a warmer year or at a warmer site. The vertical lines refer to the maximum NEP.

adaptation as geographical changes which are the result of long-term genetic and species compositional changes in ecosystems and the physiological adjustment of those organisms to the prevailing environment. The thermal optimum of NEE and its acclimation and adaptation together are described as thermal optimality. Thermal optimality of whole ecosystem carbon exchange is here assumed to represent ensemble responses of multiple temperature optima of productivity, metabolic, and decomposition processes among organisms within the ecosystem.

Materials and Methods

Site information and data analysis

Ecosystem carbon fluxes and meteorological data used in this analysis were taken from standardized files from the North America Carbon Program (NACP), AmeriFlux, CARBOEUROPE, and the FLUXNET-LaThuile datasets. These data have been quality-controlled and gap-filled using consistent methods (Papale *et al.*, 2006; Moffat *et al.*, 2007). We analyzed only those sites that have at least 1 yr of complete meteorological data because we needed to calculate mean annual temperature, precipitation and solar radiation. In total, 169 sites with 818 site-years were used to investigate the optimum temperature of NEE (T_{opt}^{NEE}). The sites included eight major terrestrial biomes: deciduous broadleaf forests (DBF), mixed forests (MF), evergreen needleleaf forests (ENF), grasslands (GRA), evergreen broadleaf forests (EBF), wetlands (WET), savanna (SAV) and shrubs (SHR) (Supporting Information, Table S1, Fig. S1). The climatic zones of the sites included the polar tundra arctic, continental temperate, subtropical Mediterranean, and tropical areas. The quality-controlled and gap-filled database, including eddy-covariance fluxes of CO_2 (NEE), GPP and R_e , were used together with solar radiation, air temperature, and precipitation in this study.

We used daily accumulated NEE rather than half-hourly values to obtain the temperature response curve with the intention of avoiding diurnal variations caused by asynchrony between cyclic

changes in photosynthesis and respiration. Daily values, which integrate diurnal cycles of photosynthesis and respiration, are more robust than hourly values in reflecting ecosystem responses to temperature over the season. Hourly data during a few h near midday were used to test the robustness of the temperature response functions of NEE as discussed in the supplementary materials.

For each site or year, temperatures were binned in 1°C daily temperature. The daily air temperature and NEE were averaged in each temperature bin to quantify the temperature response of NEE. In practice, the running mean of every three temperature bins was calculated, and the value T_{opt}^{NEE} , at which the maximum carbon uptake was attained, was determined from the curve relating NEE with temperature. The robustness of the parabolic pattern of NEE response to temperature was analyzed as shown in the supplementary materials (Figs S2–S7). We used the same method of calculating T_{opt}^{NEE} to estimate the optimum temperature of GPP (T_{opt}^{GPP}).

To determine the temperature dependence of R_e , we fitted the daily mean temperature and R_e data to a modified Van't Hoff equation: $R_e = R_b e^{bT}$ (Lloyd & Taylor, 1994). The parameter b determines temperature sensitivity of respiration (Q_{10}) and can be expressed in terms of the Q_{10} coefficient as $b = \ln(Q_{10})/10$. Although there are other types of R_e acclimation, for example, changes in absolute R_e rates with a constant Q_{10} (type II), and functional switches in both absolute R_e and Q_{10} (type III) (Atkin & Tjoelker, 2003; Bradford *et al.*, 2008), we only assessed type I acclimation (changes in Q_{10}) in this study as a result of the limitation of eddy flux data to address the other two types.

Uncertainty assessment

The bootstrapping method, which is a statistical technique based on building a sampling distribution by resampling from the dataset, was used to estimate the uncertainty of each optimum temperature (Banks *et al.*, 2010). We constructed a number of resamplings of the observed dataset (of equal size to the observed

dataset), each of which was obtained by random sampling with replacement from the original datasets. We estimated one optimal temperature from each resampled dataset. This was done 5000 times to obtain 5000 optimum temperatures, from which we computed a mean and standard deviation of $T_{\text{opt}}^{\text{NEE}}$, as well as the distribution of statistics for each site or year (Fig. S8). The same methods were used to obtain the mean and standard deviation of $T_{\text{opt}}^{\text{GPP}}$ and Q_{10} .

Statistical analysis

To examine the potential thermal acclimation of $T_{\text{opt}}^{\text{NEE}}$ and the underlying mechanisms, we analyzed the relationship of $T_{\text{opt}}^{\text{NEE}}$ with environmental factors and with $T_{\text{opt}}^{\text{GPP}}$ and Q_{10} across the years within each site and across all site-years at 12 sites with >10 yr of data. Because each site has relatively few yr of data, we used standardized residual analysis to remove outliers by using a magnitude of ± 2.0 to omit points from the regression. One outlier was removed from each of IT-Ren (Renon, Italy, 2007) and Ru-Fyo (Fyodorovskoye, Russia, 2006). To examine the potential thermal adaptation of $T_{\text{opt}}^{\text{NEE}}$, we used linear regression to analyze the relationship of $T_{\text{opt}}^{\text{NEE}}$ with environmental factors and with $T_{\text{opt}}^{\text{GPP}}$ and Q_{10} across all the 169 sites. All the regression analyses were performed using SPSS 11.0 for Windows (SPSS Inc., Chicago, IL, USA).

Results

We used results from the five sites (Fig. 2) to illustrate the general pattern of peak-curve temperature responses of NEE with the optimum temperature shifting over different temperature zones (from cold to warm). NEE increased (i.e. became more negative) with temperature in the lower temperature range to reach a maximum, and then declined (became less negative) as temperature increased further (Fig. 2). The temperature responses of NEE were caused by the relative changes in GPP and R_c . At low temperatures, GPP increased more than R_c for a unit of temperature change. Nevertheless, at higher temperatures, R_c increased further with temperature (without water limitation), while GPP leveled off or even decreased (Fig. S9). As a consequence, there was always a well-defined $T_{\text{opt}}^{\text{NEE}}$, at which NEE attained the maximum value (Fig. 2).

Twelve sites with measurements longer than 10 yr in our database were examined to illustrate interannual shifts of $T_{\text{opt}}^{\text{NEE}}$. In comparison with the values obtained in the average year, $T_{\text{opt}}^{\text{NEE}}$ shifted to a higher temperature in warmer years at each site (Fig. 3). Across all years, $T_{\text{opt}}^{\text{NEE}}$ tended to increase with annual mean air temperature at all sites, although this was statistically significant only at some sites (Fig. 4a). Across all years of the 12 sites, annual air temperature explained 35% of the changes in $T_{\text{opt}}^{\text{NEE}}$. Solar radiation had no significant relationship with $T_{\text{opt}}^{\text{NEE}}$ across years within any site or across all site-years ($P > 0.05$, Fig. 4b). Although there was no significant relationship of $T_{\text{opt}}^{\text{NEE}}$ with precipitation across the years within any site ($P = 0.11\text{--}0.97$), we found that across all site-years, precipitation explained 23% of the

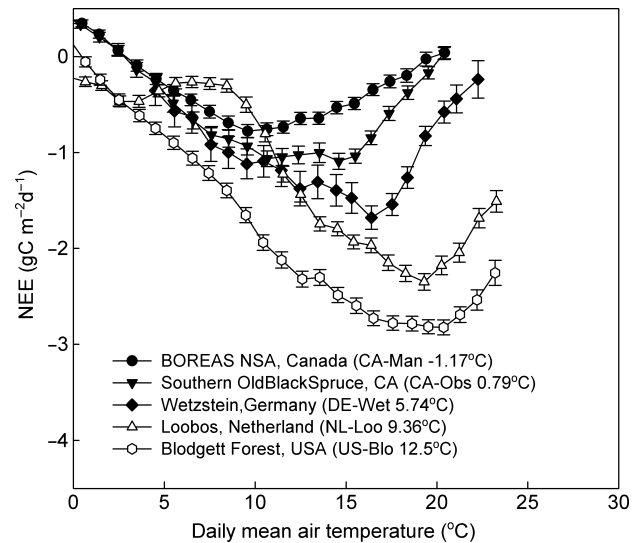


Fig. 2 The general pattern of peak-curve temperature response of net ecosystem exchange (NEE) at five representative sites over different temperature zones (mean annual temperature ranges from -1.17 to 12.5°C). At all five sites, net ecosystem CO_2 uptake (negative NEE) increased with temperature in the low range, reached a maximum, and then declined in the high range.

changes in $T_{\text{opt}}^{\text{NEE}}$ ($P < 0.01$, Fig. 4c). Multiple (stepwise) regression analysis showed that air temperature and precipitation together explained 39% of changes in $T_{\text{opt}}^{\text{NEE}}$, while temperature and precipitation alone explained 31 and 8%, respectively, of the changes in $T_{\text{opt}}^{\text{NEE}}$, suggesting that temperature was the main factor regulating the shifts of $T_{\text{opt}}^{\text{NEE}}$ across site-years.

Across all site-years, $T_{\text{opt}}^{\text{NEE}}$ was correlated positively with $T_{\text{opt}}^{\text{GPP}}$, but negatively with Q_{10} (Fig. 5). Multiple regression analysis showed that $T_{\text{opt}}^{\text{GPP}}$ and Q_{10} together explained 36% of the changes in $T_{\text{opt}}^{\text{NEE}}$, but the contribution of $T_{\text{opt}}^{\text{GPP}}$ was greater (29%) than Q_{10} (7%). The optimum temperature of GPP ($T_{\text{opt}}^{\text{GPP}}$) was positively related to mean annual air temperature across the site-years at the Canadian sites and at the other 10 sites (Fig. S10a). Solar radiation and precipitation contributed little to the shifts of $T_{\text{opt}}^{\text{GPP}}$. Changes in Q_{10} correlated negatively with temperature and precipitation, but were not related to the changes in solar radiation (Fig. S10).

Globally, $T_{\text{opt}}^{\text{NEE}}$ was higher at warmer than at cold sites, leading to a positive relationship between $T_{\text{opt}}^{\text{NEE}}$ and annual mean air temperature regardless of climate zone (Fig. 6a). Mean annual precipitation and solar radiation together only explained 5% of the changes in $T_{\text{opt}}^{\text{NEE}}$ based on multiple regression analysis. Across all sites, $T_{\text{opt}}^{\text{NEE}}$ had a positive linear relationship with $T_{\text{opt}}^{\text{GPP}}$, but no significant relationship with Q_{10} (Fig. 6b,c).

Discussion

We found an universal peak-curve pattern of NEE in response to temperature, a phenomenon which was first reported in a high-elevation subalpine forest (Huxman *et al.*, 2003). The peak pattern of the temperature response curve could be explained by relative

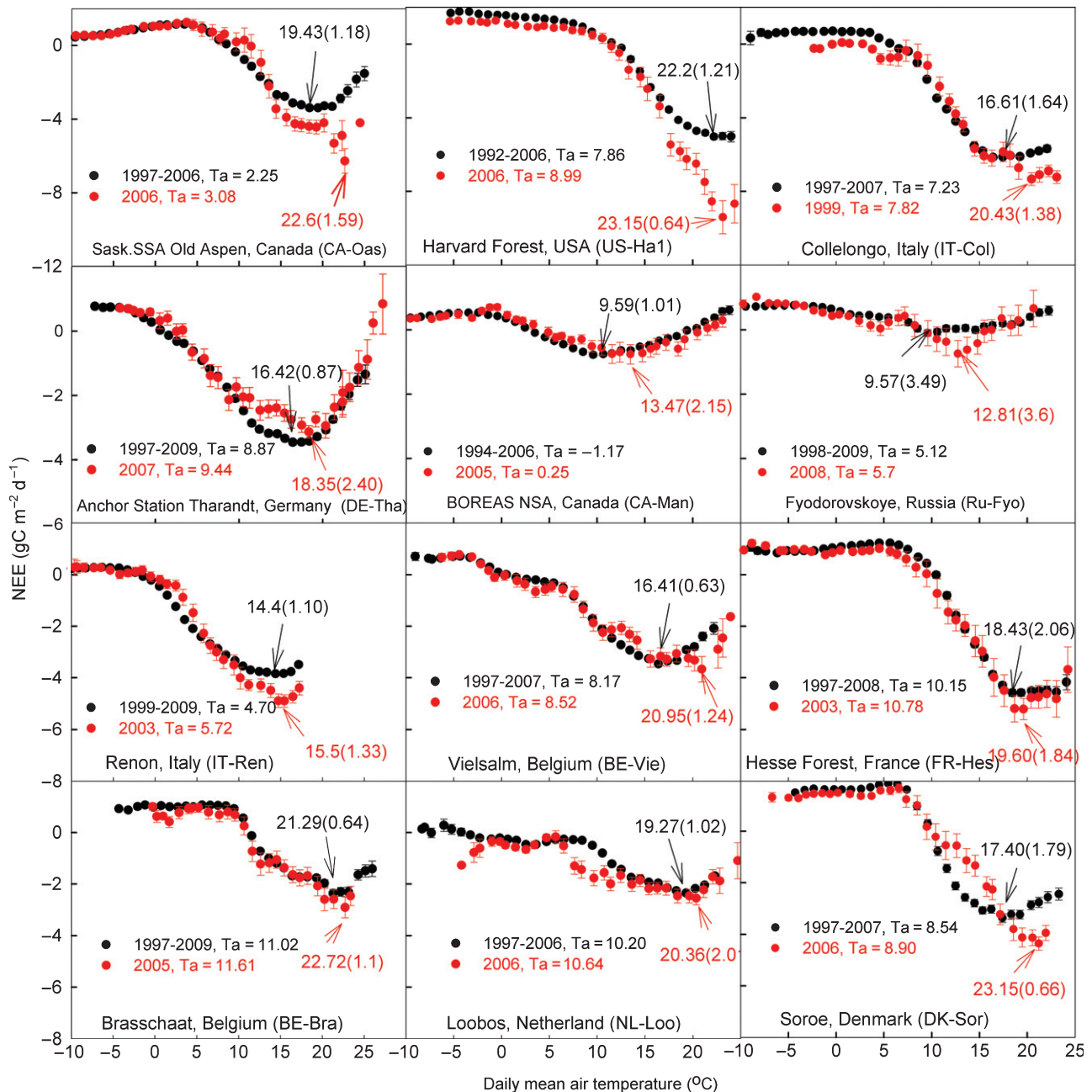


Fig. 3 Shift of the optimum temperature of net ecosystem exchange (NEE) to a higher value in a warmer year compared with the average of all studied years at the 12 sites with > 10 yr of data length. Black closed circles, average over all years; red closed circles, represent a warmer year (mean ± 1 SD). T_a is annual mean temperature. The numbers labeled in the figures are the optimum temperatures of NEE and their standard deviation.

changes in GPP and R_c . The increase in carbon uptake at low temperature resulted from a relatively larger increase in GPP than R_c for a given change in temperature. The decrease of carbon uptake at higher temperatures resulted from the continuous increase in R_c against the leveling-off or decline of GPP (Figs 1, S9).

Shifts of T_{opt}^{NEE} across years were primarily caused by temperature (Fig. 4), suggesting thermal acclimation at interannual scales. The upward trend of T_{opt}^{NEE} with increasing temperature was largely the result of the shifts of optimum temperature in photosynthesis (Fig. 5), which has been well documented at plant level (Mooney *et al.*, 1978; Berry & Bjorkman, 1980; Niu

et al., 2008; Gunderson *et al.*, 2010) and primarily results from increased electron transport capacity and/or greater heat stability of Rubisco (Sage & Kubien, 2007). In addition, extended growing seasons, increased nitrogen mineralization, and enhanced root growth (Penuelas & Filella, 2001; Churkina *et al.*, 2005; Luo *et al.*, 2009) may also have contributed to the increased CO_2 uptake under higher temperatures, leading to the upward shift in the optimum temperature of GPP in warmer years (Fig. S10a). For example, fine roots in boreal ecosystems are more active in warmer years, allowing greater access to water and nutrients (Jarvis & Linder, 2000; Pregitzer *et al.*, 2000). Although respiration

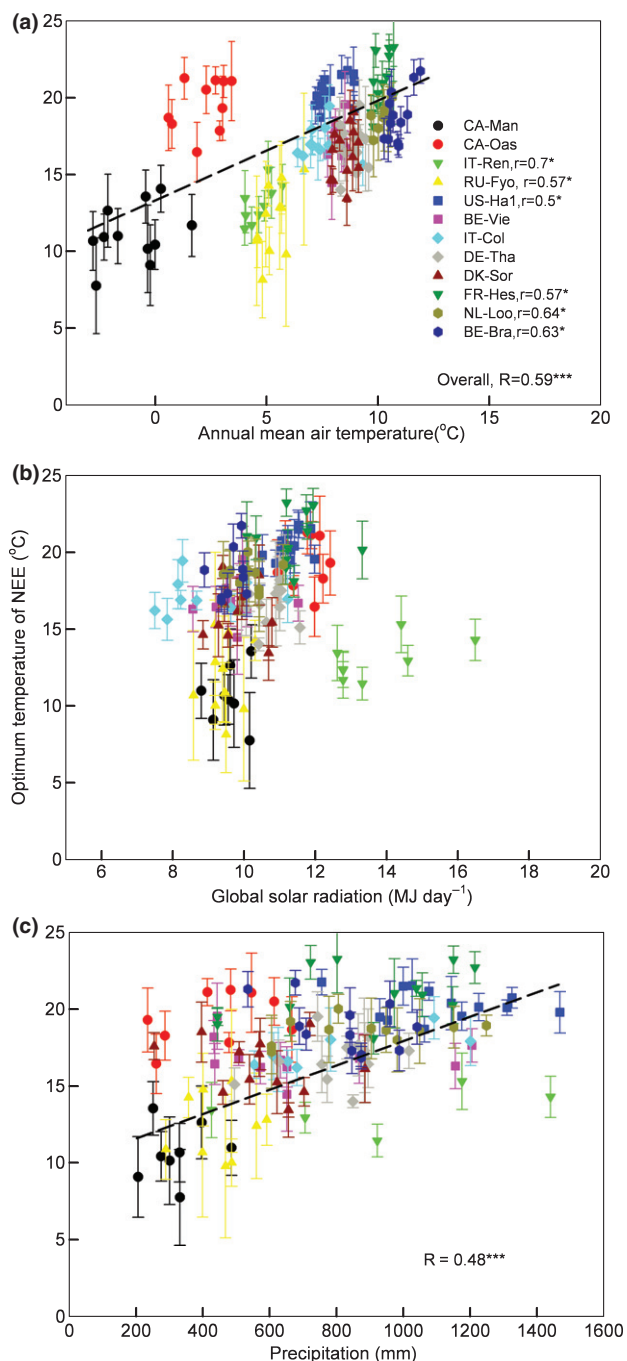


Fig. 4 The relationship between optimum temperature of net ecosystem exchange (NEE; mean \pm SD) and annual mean air temperature (a), global solar radiation (b) and precipitation (c) at the 12 sites with > 10 yr of data. * and *** indicate that the relationship was significant at the $P < 0.1$ and 0.001 levels, respectively. Site abbreviations and names are as follows: CA-Man, BOREAS NSA, Canada; CA-Oas, Sask.SSA Old Aspen, Canada; IT-Ren, Renon, Italy; Ru-Fyo, Fyodorovskoye, Russia; US-Ha1, Harvard Forest, USA; BE-Vie, Vielsalm, Belgium; IT-Col, Collelongo, Italy; DE-Tha, Anchor Station Tharandt, Germany; DK-Sor, Soroe, Denmark; FR-Hes, Hesse Forest, France; NL-Loo, Loobos, Netherlands; and BE-Bra, Brasschaat, Belgium.

normally increases with temperature, water stress and respiratory acclimation during high temperatures can offset or reverse the direct temperature effect (Luo *et al.*, 2001; Irvine *et al.*, 2008;

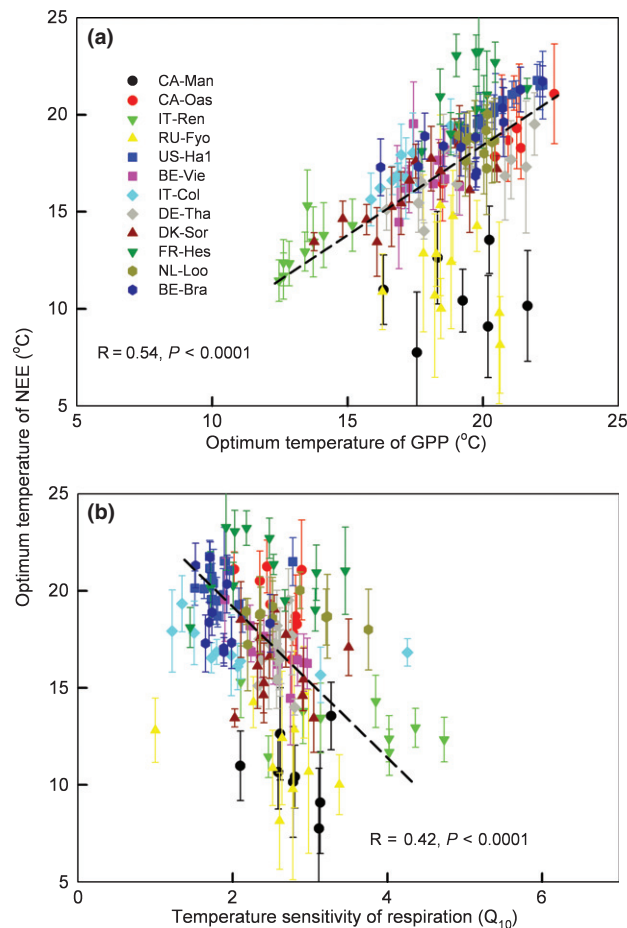


Fig. 5 The relationship of optimum temperature of net ecosystem exchange (NEE) to optimum temperature of gross primary productivity (GPP) (a) and temperature sensitivity of respiration (Q_{10}) (b) across the site-years at the 12 sites with > 10 yr of data.

Scott *et al.*, 2009). Increases in GPP overcompensated for any respiration increases at higher temperature, leading to the upward shift of $T_{\text{opt}}^{\text{NEE}}$ in warmer years. The relative roles of these processes may vary at different sites, leading to site-specific responses of $T_{\text{opt}}^{\text{NEE}}$ to temperature (Fig. 4). Thus, the mechanisms underlying thermal optimization of NEE across temporal scales most likely vary among sites and require further investigation.

Shifts of $T_{\text{opt}}^{\text{NEE}}$ with annual mean air temperature across space are consistent with previous studies on geographical shifts of optimum temperature of GPP and NEE with summer or growing season temperatures (Baldocchi *et al.*, 2001; Yuan *et al.*, 2011), also suggesting thermal adaptation of NEE. Such spatial shifts in $T_{\text{opt}}^{\text{NEE}}$ likely result from processes at several hierarchical scales and may involve adaptive changes of various organisms. At the ecosystem level, thermal adaptation of NEE likely reflects associated changes in the structure and function of plant, animal, and microbial communities, which are likely the result of both long-term genetic changes and physiological adjustment to the prevailing environment (Diaz *et al.*, 2001; Janssens *et al.*, 2001; Knohl *et al.*, 2005; Larsen *et al.*, 2007). At the community level, species competition may also be a very important determinant of the changes in $T_{\text{opt}}^{\text{NEE}}$. The universal existence of $T_{\text{opt}}^{\text{NEE}}$ and its

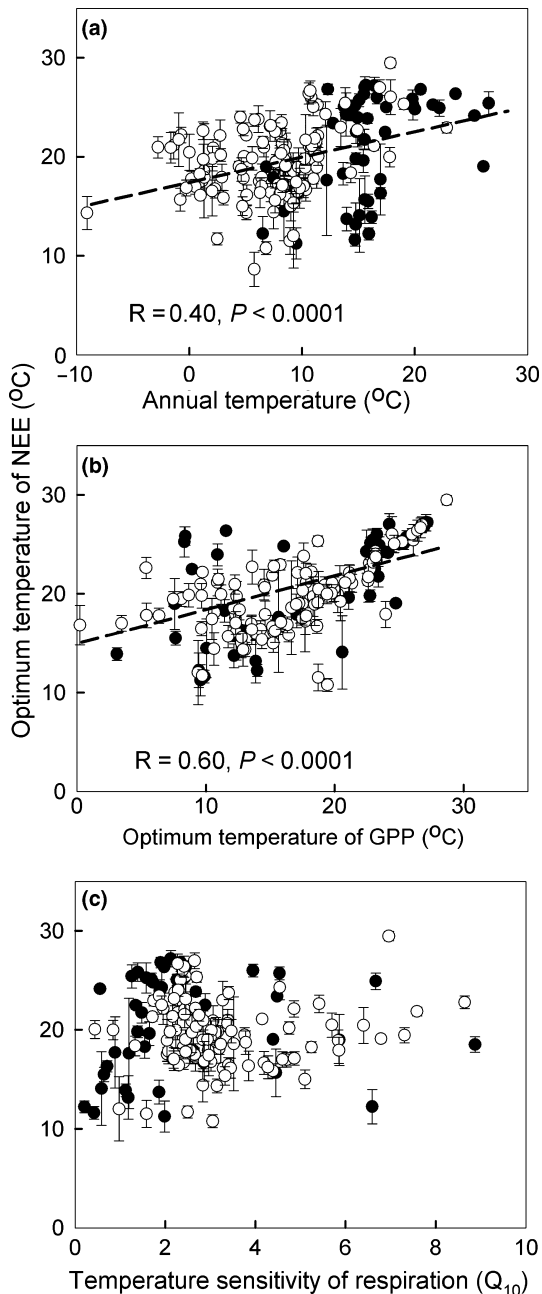


Fig. 6 The relationship of optimum temperature of net ecosystem exchange (NEE; means \pm SD) to annual mean air temperature (a), optimum temperature of gross primary productivity (GPP) (b), and temperature sensitivity of respiration (Q_{10}) (c) in tropical and subtropical areas (closed circles) and temperate and boreal areas (open circles) across all 169 sites.

acclimation and adaptation to temporal and spatial temperature changes strongly suggest thermal optimality of NEE. Compared with previous studies (Baldocchi *et al.*, 2001; Yuan *et al.*, 2011), this study holistically reveals the thermal optimality of NEE via acclimation and adaptation and withstands more rigorous uncertainty analysis. A particularly novel point found here is the identification of the relative roles of photosynthesis and respiration. The shifts of $T_{\text{opt}}^{\text{NEE}}$ are mostly attributable to changes in GPP rather than in R_c . Although respiration has been documented to

be the main determinant of intraregional forest carbon balance variation (Valentini *et al.*, 2000), our study clearly showed that the temperature response of GPP overrides R_c in determining thermal optimality of NEE. According to Atkin & Tjoelker (2003) and Bradford *et al.* (2008), changes in Q_{10} as used in this study only reflect type I acclimation. However, if the type II and type III acclimation occur, the upward shift of $T_{\text{opt}}^{\text{NEE}}$ in a warmer environment can also happen. Owing to the limitations of eddy flux data, we can only address type I acclimation in this study. This might cause partial assessment on R_c acclimation.

Thermal acclimation/adaptation of NEE, in conjunction with the adaptation of GPP (Baldocchi *et al.*, 2001) and plant and soil respiration (Atkin & Tjoelker, 2003; Bradford *et al.*, 2008), will influence the long-term responses and feedback of ecosystem carbon storage to global temperature changes. Shifts of $T_{\text{opt}}^{\text{NEE}}$ with interannual variations in temperature may dampen short-term temperature effects on ecosystem carbon balances and could contribute to a lower apparent sensitivity of global ecosystem carbon uptake to temperature than to rainfall (Tian *et al.*, 1998; Angert *et al.*, 2005). These shifting thermal optima with temperature over time and space may lower the sensitivity of the carbon cycle feedback to future climate warming (Frank *et al.*, 2010; Mahecha *et al.*, 2010).

The observed patterns of thermal optimality over time and space represent a useful benchmark for evaluating the capability of Earth system models (Randerson *et al.*, 2009; Frank *et al.*, 2010). Benchmarking against these observed sensitivities is not sufficient to validate models but represents an important first step in assessing model capabilities on centennial time scales (Randerson *et al.*, 2009; Frank *et al.*, 2010). Models that replicate short-term patterns of ecosystem optimization are not guaranteed to succeed on longer timescales. However, models that do not replicate these observed temperature sensitivities will almost certainly fail to simulate biosphere and carbon cycle responses to climate change accurately. Further research is needed to explore whether land process models can reproduce this thermally optimal pattern across space and time.

Acknowledgements

This work was financially supported by the Terrestrial Carbon Program at the Office of Science, US Department of Energy, grants DE-FG02-006ER64317 and the US National Science Foundation (NSF), grant DEB 0444518, DEB 0743778, DEB 0840964, DBI 0850290, and EPS 0919466 to Y.L. We used the eddy covariance data acquired by the FLUXNET community and, in particular, by the following networks: AmeriFlux (US Department of Energy, Biological and Environmental Research, Terrestrial Carbon Program (DE-FG02-04ER63917 and DE-FG02-04ER63911)), GHG-Europe, Fluxnet-Canada Research Network and Canadian Carbon Program (supported by CFCAS, NSERC, BIOCAP, Environment Canada, and NRCAN), GreenGrass, KoFlux, LBA, NECC, OzFlux, TCOS-Siberia, and USCCC. We acknowledge the financial support to the eddy covariance data harmonization provided by the Office of Science US Department of Energy for AmeriFlux,

CarboEuropeIP, FAP-GTOS-TCO, iLEAPS, NitroEurope, Max Planck Institute for Biogeochemistry, National Science Foundation, University of Tuscia, Université Laval and Environment Canada, and database development and technical support from the Berkeley Water Center, Lawrence Berkeley National Laboratory, and Microsoft Research eScience.

References

- Angert A, Biraud S, Bonfils C, Henning CC, Buermann W, Pinzon J, Tucker CJ, Fung I. 2005. Drier summers cancel out the CO₂ uptake enhancement induced by warmer springs. *Proceedings of the National Academy of Sciences, USA* 102: 10823–10827.
- Atkin OK, Tjoelker MG. 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science* 8: 343–351.
- Baldocchi D, Falge E, Gu LH, Olson R, Hollinger D, Running S, Anthoni P, Bernhofer C, Davis K, Evans R *et al.* 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bulletin of the American Meteorological Society* 82: 2415–2434.
- Banks HT, Holm K, Robbins D. 2010. Standard error computations for uncertainty quantification in inverse problems: asymptotic theory vs. bootstrapping. *Mathematical and Computer Modelling* 52: 1610–1625.
- Berry J, Bjorkman O. 1980. Photosynthetic Response and Adaptation to Temperature in Higher-Plants. *Annual Review of Plant Physiology and Plant Molecular Biology* 31: 491–543.
- Bradford MA, Davies CA, Frey SD, Maddox TR, Melillo JM, Mohan JE, Reynolds JF, Treseder KK, Wallenstein MD. 2008. Thermal adaptation of soil microbial respiration to elevated temperature. *Ecology Letters* 11: 1316–1327.
- Chapin FS, Matson PA, Mooney HA. 2002. *Principles of Terrestrial Ecosystem Ecology*. New York, NY, USA: Springer.
- Chapin FS, Woodwell GM, Randerson JT, Rastetter EB, Lovett GM, Baldocchi DD, Clark DA, Harmon ME, Schimel DS, Valentini R *et al.* 2006. Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems* 9: 1041–1050.
- Churkina G, Schimel D, Braswell BH, Xiao XM. 2005. Spatial analysis of growing season length control over net ecosystem exchange. *Global Change Biology* 11: 1777–1787.
- Diaz S, Cabido M, Casanoves F. 2001. Functional implications of trait-environment linkages in plant communities. In: Weiher E, Keddy P, eds. *Ecological Assembly Rules: perspectives, Advances, Retreat*. Cambridge, UK: Cambridge University Press, 338–362.
- Enquist BJ, Economo EP, Huxman TE, Allen AP, Ignace DD, Gillooly JF. 2003. Scaling metabolism from organisms to ecosystems. *Nature* 423: 639–642.
- Frank DC, Esper J, Raible CC, Buntgen U, Trouet V, Stocker B, Joos F. 2010. Ensemble reconstruction constraints on the global carbon cycle sensitivity to climate. *Nature* 463: 527–532.
- Friedlingstein P, Cox P, Betts R, Bopp L, Von Bloh W, Brovkin V, Cadule P, Doney S, Eby M, Fung I *et al.* 2006. Climate-carbon cycle feedback analysis: results from the (CMIP)-M-4 model intercomparison. *Journal of Climate* 19: 3337–3353.
- Gunderson CA, O'Hara KH, Campion CM, Walker AV, Edwards NT. 2010. Thermal plasticity of photosynthesis: the role of acclimation in forest responses to a warming climate. *Global Change Biology* 16: 2272–2286.
- Huxman TE, Turnipseed AA, Sparks JP, Harley PC, Monson RK. 2003. Temperature as a control over ecosystem CO₂ fluxes in a high-elevation, subalpine forest. *Oecologia* 134: 537–546.
- Irvine J, Law BE, Martin JG, Vickers D. 2008. Interannual variation in soil CO₂ efflux and the response of root respiration to climate and canopy gas exchange in mature ponderosa pine. *Global Change Biology* 14: 2848–2859.
- Janssens IA, Lankreijer H, Matteucci G, Kowalski AS, Buchmann N, Epron D, Pilegaard K, Kutsch W, Longdoz B, Grunwald T *et al.* 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology* 7: 269–278.
- Jarvis P, Linder S. 2000. Botany - Constraints to growth of boreal forests. *Nature* 405: 904–905.
- Knohl A, Werner RA, Brand WA, Buchmann N. 2005. Short-term variations in delta C-13 of ecosystem respiration reveals link between assimilation and respiration in a deciduous forest. *Oecologia* 142: 70–82.
- Larsen KS, Ibrom A, Beier C, Jonasson S, Michelsen A. 2007. Ecosystem respiration depends strongly on photosynthesis in a temperate heath. *Biogeochemistry* 85: 201–213.
- Law BE, Baldocchi DD, Anthoni PM. 1999. Below-canopy and soil CO₂ fluxes in a ponderosa pine forest. *Agricultural and Forest Meteorology* 94: 171–188.
- Lloyd J, Taylor JA. 1994. On the Temperature-Dependence of Soil Respiration. *Functional Ecology* 8: 315–323.
- Loreau M. 2010. Evolution of ecosystems and ecosystem properties. In: Loreau M, ed. *From populations to ecosystems, theoretical foundations for a new ecological synthesis*. Princeton, NJ, USA: Princeton University Press, 225–259.
- Luo Y, Sherry R, Zhou X, Wan S. 2009. Terrestrial carbon-cycle feedback to climate warming: experimental evidence on plant regulation and impacts of biofuel feedstock harvest. *Global Change Biology Bioenergy* 1: 62–74.
- Luo Y, Wan S, Hui D, Wallace LL. 2001. Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* 413: 622–625.
- Mahecha MD, Reichstein M, Carvalhais N, Lange H, Seneviratne SI, Vargas R, Ammann C, Arain MA, Cescatti A, Janssens IA *et al.* 2010. Global convergence in the temperature sensitivity of respiration at ecosystem level. *Science* 329: 838–840.
- Moffat AM, Papale D, Reichstein M, Hollinger DY, Richardson AD, Barr AG, Beckstein C, Braswell BH, Churkina G, Desai AR *et al.* 2007. Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes. *Agricultural and Forest Meteorology* 147: 209–232.
- Mooney HA, Bjorkman O, Collatz GJ. 1978. Photosynthetic acclimation to temperature in desert shrub, *larea-divaricata*. 1. Carbon-dioxide exchange characteristics of intact leaves. *Plant Physiology* 61: 406–410.
- Niu S, Li Z, Xia J, Han Y, Wu M, Wan S. 2008. Climatic warming changes plant photosynthesis and its temperature dependence in a temperate steppe of northern China. *Environmental and Experimental Botany* 63: 91–101.
- Papale D, Reichstein M, Aubinet M, Canfora E, Bernhofer C, Kutsch W, Longdoz B, Rambal S, Valentini R, Vesala T *et al.* 2006. Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation. *Biogeosciences* 3: 571–583.
- Parker GA, Maynard Smith J. 1990. Optimality theory in evolutionary biology. *Nature* 348: 27–33.
- Parnesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37: 637–669.
- Penuelas J, Filella I. 2001. Phenology - Responses to a warming world. *Science* 294: 793–795.
- Piao SL, Luysaert S, Ciais P, Janssens IA, Chen AP, Cao C, Fang JY, Friedlingstein P, Luo YQ, Wang SP. 2010. Forest annual carbon cost: a global-scale analysis of autotrophic respiration. *Ecology* 91: 652–661.
- Pregitzer KS, King JA, Burton AJ, Brown SE. 2000. Responses of tree fine roots to temperature. *New Phytologist* 147: 105–115.
- Randerson JT, Hoffman FM, Thornton PE, Mahowald NM, Lindsay K, Lee YH, Nevison CD, Doney SC, Bonan G, Stockli R *et al.* 2009. Systematic assessment of terrestrial biogeochemistry in coupled climate-carbon models. *Global Change Biology* 15: 2462–2484.
- Sage RF, Kubien DS. 2007. The temperature response of C₃ and C₄ photosynthesis. *Plant, Cell & Environment* 30: 1086–1106.
- Scott RL, Jenerette GD, Potts DL, Huxman TE. 2009. Effects of seasonal drought on net carbon dioxide exchange from a woody-plant-encroached semiarid grassland. *Journal of Geophysical Research-Biogeosciences* 114: doi: 10.1029/2008JG000900.
- Tian HQ, Melillo JM, Kicklighter DW, McGuire AD, Helfrich JVK, Moore B, Vorosmarty CJ. 1998. Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature* 396: 664–667.
- Tjoelker MG, Oleksyn J, Reich PB, Zytewski R. 2008. Coupling of respiration, nitrogen, and sugars underlies convergent temperature acclimation

in *Pinus banksiana* across wide-ranging sites and populations. *Global Change Biology* 14: 782–797.

Valentini R, Matteucci G, Dolman AJ, Schulze ED, Rebmann C, Moors EJ, Granier A, Gross P, Jensen NO, Pilegaard K *et al.* 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* 404: 861–865.

Yuan W, Luo Y, Liang S, Yu G, Niu S, Stoy P, Chen J, Desai AR, Lindroth A, Gough CM *et al.* 2011. Thermal adaptation of net ecosystem exchange. *Biogeosciences* 8: 1453–1463.

Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Global map of site distribution.

Figs S2–S7 Robustness test of the parabolic temperature response curves of NEE.

Fig. S8 Uncertainty test for $T_{\text{opt}}^{\text{NEE}}$ using bootstrapping methods.

Fig. S9 Examples of temperature response curves of NEE, GPP and R_c in the average vs warmer years.

Fig. S10 Relationship of $T_{\text{opt}}^{\text{GPP}}$ and Q_{10} with environmental factors.

Table S1 Site information

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.



About *New Phytologist*

- *New Phytologist* is an electronic (online-only) journal owned by the New Phytologist Trust, a **not-for-profit organization** dedicated to the promotion of plant science, facilitating projects from symposia to free access for our Tansley reviews.
- Regular papers, Letters, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as ready' via *Early View* – our average time to decision is <25 days. There are **no page or colour charges** and a PDF version will be provided for each article.
- The journal is available online at Wiley Online Library. Visit **www.newphytologist.com** to search the articles and register for table of contents email alerts.
- If you have any questions, do get in touch with Central Office (np-centraloffice@lancaster.ac.uk) or, if it is more convenient, our USA Office (np-usaoffice@ornl.gov)
- For submission instructions, subscription and all the latest information visit **www.newphytologist.com**