Seasonal hysteresis of net ecosystem exchange in response to temperature change: patterns and causes

SHULI NIU*†, YIQI LUO*, SHENFENG FEI*, LEONARDO MONTAGNANI‡§, GIL BOHRER¶, IVAN A. JANSSENS‖, BERT GIELEN‖, SERGE RAMBAL**, EDDY MOORS†† and GIORGIO MATTEUCCI‡‡

*Department of Botany and Microbiology, University of Oklahoma, Norman, Oklahoma 73019, USA, †State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China, ‡Servizi Forestali, Agenzia per l' Ambiente, Provincia Autonoma di Bolzano, 39100 Bolzano, Italy, §Faculty of Sciences and Technologies, Free University of Bozen-Bolzano, Piazza Università 1, 39100 Bolzano, Italy, ¶Dept. of Civil & Environ. Engineering & Geodetic Sci. Ohio State University, Columbus, Ohio 43210, USA, ‖Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk, Belgium, **DREAM, CEFE, CNRS, UMR5175, 1919 route de Mende, F-34293 Montpellier, Cedex 5, France, ††ESS-CC, Alterra, Wageningen UR, PO Box 47, 6700 AA Wageningen, Netherlands, ‡‡National Research Council, Institute of Agroenvironmental and Forest Biology, 00015 Monterotondo Scalo (RM), Italy

Abstract

Understanding how net ecosystem exchange (NEE) changes with temperature is central to the debate on climate change-carbon cycle feedbacks, but still remains unclear. Here, we used eddy covariance measurements of NEE from 20 FLUXNET sites (203 site-years of data) in mid- and high-latitude forests to investigate the temperature response of NEE. Years were divided into two half thermal years (increasing temperature in spring and decreasing temperature in autumn) using the maximum daily mean temperature. We observed a parabolic-like pattern of NEE in response to temperature change in both the spring and autumn half thermal years. However, at similar temperatures, NEE was considerably depressed during the decreasing temperature season as compared with the increasing temperature season, inducing a counter-clockwise hysteresis pattern in the NEE–temperature relation at most sites. The magnitude of this hysteresis was attributable mostly (68%) to gross primary production (GPP) differences but little (8%) to ecosystem respiration (ER) differences between the two half thermal years. The main environmental factors contributing to the hysteresis responses of NEE and GPP were daily accumulated radiation. Soil water content (SWC) also contributed to the hysteresis response of GPP but only at some sites. Shorter day length, lower light intensity, lower SWC and reduced photosynthetic capacity may all have contributed to the depressed GPP and net carbon uptake during the decreasing temperature seasons. The resultant hysteresis loop is an important indicator of the existence of limiting factors. As such, the role of radiation, LAI and SWC should be considered when modeling the dynamics of carbon cycling in response to temperature change.

Keywords: carbon cycle, climate change, day length, ecosystem respiration, gross ecosystem productivity, leaf area index, seasonal variation, temperature sensitivity

Received 25 February 2011 and accepted 10 April 2011

Introduction

Our ability to predict future CO_2 concentration in the atmosphere and its effect on climate depends to a large extent on our understanding of terrestrial ecosystem carbon cycling and its dependency on climate (Peters *et al.*, 2007). The temperature response of ecosystem-CO_2 exchange is attracting special attention because terrestrial biotic feedbacks, such as increased respiration can play a determining role in accelerating global warming (Cox *et al.*, 2000). Although studies on temperature response of ecosystem carbon cycling have made great progress in the past decades, there is still large uncertainty, which reduces the accuracy of model predictions for future climate (Jones & Donnelly, 2004; Field *et al.*, 2007; Luo, 2007; Heimann & Reichstein, 2008; Mahecha *et al.*, 2010).

One paradox for complicating temperature response of carbon cycling is that other impacting factors such as radiation, soil water content (SWC), and vegetation index may influence temperature response. These impacting factors vary with season and space, determining different seasonal and latitudinal temperature-response patterns of carbon fluxes. For example, Richardson *et al.*

Correspondence: Shuli Niu, Department of Botany and Microbiology, University of Oklahoma, Norman, Oklahoma 73019, USA, tel. +1 405 325 8578, fax +1 405 325 7619, e-mail: sniu@ou.edu

(2010) recently found that anomalies in ecosystem productivity respond more weakly to temperature anomalies in autumn than in spring because of light or drought limitations. Similar results were also reported with weekly net ecosystem productivity positively related to temperature in spring but showed no relationship with temperature in autumn (Hu *et al.*, 2010). By comparison, in spring, higher air temperature may advance onset of photosynthesis, and at this time, solar radiation is usually not limiting and photosynthetic capacity is higher (Suni *et al.*, 2003b; Richardson *et al.*, 2009), which may lead to higher gross primary productivity (GPP). However, during autumn, light availability is much lower and higher autumn temperature therefore increases GPP much less than it stimulates respiration (Piao *et al.*, 2008). It is also expected that ER responds more strongly to temperature in autumn than in spring because of the accumulation of respiring biomass and higher availability of labile substrates for decomposition (Piao *et al.*, 2008; Vesala *et al.*, 2010). Net ecosystem exchange of CO_2 (NEE) in response to temperature change is the result from a combination of processes that affect respiration and photosynthesis, and therefore may also display a differential response to temperature change between seasons. Nevertheless, there is still a lack of empirical information to address the issues of different temperature responses of NEE in different seasons.

The different temperature response of ecosystem carbon cycling in different seasons may cause a hysteresis phenomenon. Hysteresis occurs when an increase in a given independent variable, x, does not cause the same magnitude of response in a dependent variable, y, compared with when variable x decreases by the same amount (Zeppel *et al.*, 2004). For example, if NEE responds differently to temperature change in the spring (when temperature is increasing) compared with autumn (when temperature is decreasing), then hysteresis with respect to temperature will occur. Such a hysteretic temperature response has often been reported for soil respiration (SR), which typically exhibits both a daily and seasonal hysteresis in its relationship with temperature (Tang *et al.*, 2005; Gaumont-Guay *et al.*, 2006; Vargas & Allen, 2008). To our knowledge, however, there are only very few studies on the occurrence of hysteresis in the response of NEE to environmental factors (but see Nakai *et al.*, 2003; Vourlitis *et al.*, 2005; Mahecha *et al.*, 2007; Pingintha *et al.*, 2010). The underlying mechanisms and processes therefore remain to be explained. Hysteresis is a significant factor in the seasonal patterns of NEE and therefore should be investigated if a more complete understanding of seasonal or annual NEE is desired.

The Eddy-covariance method monitors continuously NEE and the associated environmental factors, which enables the analysis of the temperature response pattern of NEE and its components (Baldocchi *et al.*, 2001). This research strives to answer the following scientific questions: (1) is the hysteresis of NEE in its response to temperature change common across forest ecosystems? and (2) how do biotic and abiotic drivers affect the hysteretic nature of the response of NEE to temperature? Addressing and quantifying seasonal hysteresis dynamics will greatly improve our mechanistic understandings of ecosystem carbon cycling and responses to temperature and improve our capacity to predict annual NEE and its spatial distribution.

To answer these questions, the temperature responses of NEE were analyzed for 20 mid- and high-latitude forests that had more than 8 years of data available. We focused on this geographic region because the mid and high latitudes in the Northern Hemisphere have large enough seasonal temperature variation to determine the temperature response. Moreover, these forests are known to significantly contribute to the current terrestrial carbon sink (Fang *et al.*, 2006) and will be exposed to stronger warming in the next 50–100 years (IPCC, 2007). We specifically hypothesize that: (1) the hysteretic response of NEE consistently occurs at mid- and high-latitude forests, but the hysteresis loops may be of different magnitudes among sites; (2) biotic drivers, GPP and LAI, and abiotic drivers, radiation and SWC, all affect the hysteretic relationship between NEE and temperature; (3) the roles of drivers in regulating hysteresis loops are drastically different among sites.

Materials and Methods

Site selection and data processing

NEE and meteorological data used in this analysis were taken from standardized files from the AmeriFLUX and CARBOEUROPE networks. Data from 20 sites that have more than 8 years data length (total of 203 site years) were used in this study to investigate the temperature response of NEE (Table 1). The data have been quality controlled and gap-filled by consistent methods (Papale *et al.*, 2006; Moffat *et al.*, 2007). Half-hourly averaged global radiation (R_g), air temperature (T_a), precipitation (PPT) and SWC data were used together with eddy covariance fluxes of CO_2 (NEE), and the calculated ecosystem respiration (ER) and GPP. We used the gap-filled database because we needed to calculate daily NEE and temperature, as well as annual temperature in a specific year. Negative NEE is defined as net CO_2 uptake by the ecosystem. So, increasing carbon sequestration means more negative NEE.

Daily meteorological and flux variables were synthesized based on half-hourly values. The daily values were not estimated in this analysis when missing hourly values exceeded

Table 1 Site characteristics, climatic index, and studied period of flux sites in this analysis

Site name	Full name	Veg*	Lat†	Lon‡	PPT§(mm)	T_a (°C)	Period	References
BE-Bra	Brasschaat	MF	51.31	4.52	742.7	10.01	1997–2009	Gielen et al. (2010)
BE-Vie	Vielsam	MF	50.31	6.00	1065.12	7.37	1997–2006	Aubinet et al. (2001)
CZ-Bk1	Bily Kriz	ENF	49.5	18.54	1025.75	4.72	2000–2008	Reichstein et al. (2005)
DE-Hai	Hainich	DBF	51.08	10.45	780.29	7.15	2000–2007	Knohl et al. (2003)
DE-Tha	Tharandt	ENF	50.96	13.57	643.09	8.12	1997–2006	Arain & Restrepo-Coupe, (2005)
DK-Sor	Soroe	DBF	55.49	11.65	952	8.7	1997–2005	Pilegaard et al. (2003)
FI-Hyy	Hyytiala	ENF	61.85	24.29	620.2	2.18	1997–2005	Suni et al. (2003c)
FR-Pue	Puechabon	EBF	43.74	3.59	734.55	12.96	2000–2008	Rambal et al. (2004)
FR-Hes	Hesse	DBF	48.67	7.06	793.3	9.24	1997–2008	Granier et al. (2000)
IT-Ren	Renon	ENF	46.59	11.43	964.67	6.21	1999–2009	Montagnani et al. (2009)
IT-Col	Collelongo	DBF	41.85	13.59	970.88	7.32	1996–2007	Valentini et al. (1996)
US-Blo	Blodgett	ENF	38.9	−120.63	1630	12.5	1997–2006	Goldstein et al. (2000)
US-MMS	Morgan_Monroe	DBF	39.32	−86.41	1031.57	10.85	1999–2006	Schmid et al. (2000)
IT-Ro1	Roccarespampani1	DBF	42.41	11.93	763.66	15.35	2000–2008	Rey et al. (2002)
NL-Loo	Loobos	ENF	52.17	5.74	786.16	9.36	1997–2003/2005–2009	Dolman et al. (2002)
UK-Gri	Griffin	ENF	56.61	−3.80	1622.95	6.6	1998–2006	Rebmann et al. (2005)
US-Ha1	Harvard forest	DBF	43.54	−72.17	1071	6.62	1992–2006	Urbanski et al. (2007)
US-Ho1	Howland forest	ENF	45.2	−68.74	1070.29	5.27	1996–2004	Hollinger et al. (2004)
US-UMB	Univ. of Mich. Biological station	DBF	45.56	−84.71	803.44	5.83	1998–2006	Gough et al. (2008)
US-NR1	Niwot_Ridge	ENF	40.03	−105.54	595.24	0.43	1998–2007	Monson et al. (2002)

*Vegetation.
†Positive value indicates north latitude.
‡Negative value indicates west longitude.
§Precipitation.
DBF, deciduous broadleaf forest; EBF, evergreen broadleaf forest; ENF, evergreen needleaf forest; MIX, mixed deciduous and evergreen needleaf forest.

25% of the day. We used daily accumulated NEE rather than half-hourly values to obtain the temperature response curve with the intention of minimizing undesired noise in the data caused by asynchrony between diel changes in photosynthesis and respiration. Daily values are more robust than hourly values to reflect ecosystem responses to temperature over the season. To avoid confounding influences of clouds on the temperature responses (Urban et al., 2007), only NEE in days when the clearness index [i.e., the ratio of the global solar radiation received on the surface to the extraterrestrial solar radiation (Falayi et al., 2008)] was larger than 0.5 was used for this analysis.

We used the MODIS MOD15A2 product to generate the daily leaf area index (LAI) data. For each flux tower site, 8-Day composite data at the same location were analyzed. The satellite LAI data were first filtered based on its quality control information to discard the data under unfavorable conditions,

such as cloudiness. Then, unrealistically low LAI values in the middle of the growing season were also screened (i.e., one measurement was <30% of the highest LAI, but the adjacent two measurements were all higher than 70% percent of the highest LAI). The gaps in those processed data were filled to daily resolution by linearly connecting two closest available data points.

Temperature response curves

We split the years into two parts according to the maximum temperature in summer (Fig. 1). The increasing-temperature season (spring) was defined as the first part of the year, from the beginning of the Julian year to the time when the maximum daily mean air temperature was reached (during the summer). The decreasing-temperature season (autumn)
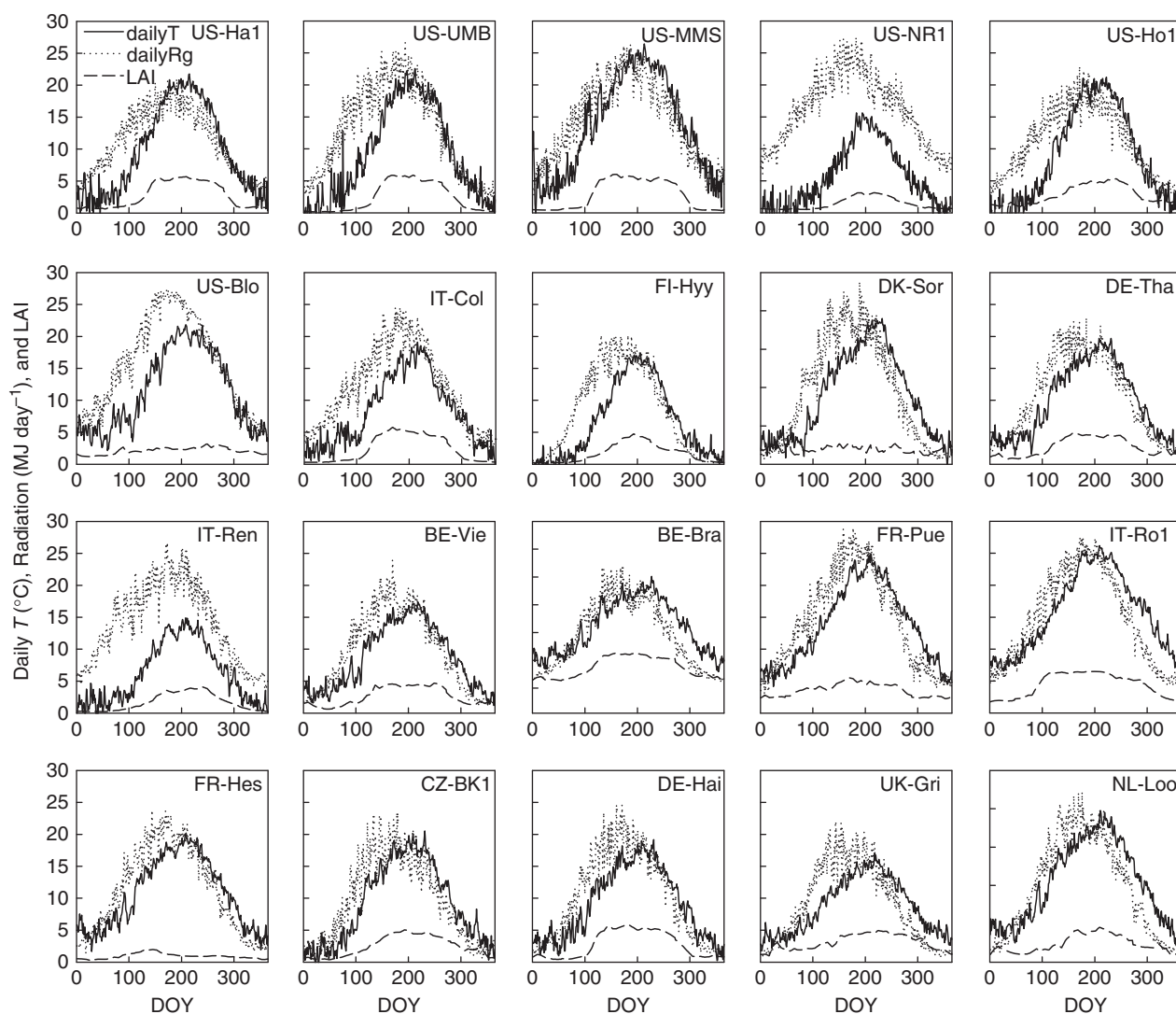
Fig. 1 Seasonal dynamics in daily temperature (*T*), daily accumulated global radiation (Rg) and leaf area index (LAI) at the 20 sites. DOY means days of year.

included the remainder of the year, from the time of the maximum air temperature in the summer to the end of the Julian year.

For each season, NEE observations were divided into $1\,°C$-temperature bins. The mean NEE per bin (over all years, and days per season per site) was calculated and $3\,°C$-running means were used to analyze the NEE trends with temperature. We quantified the hysteresis strength as the mean seasonal difference between the daily NEE in the increasing- vs. the decreasing-temperature seasons (ΔNEE). A similar analysis was done with GPP. We then calculated the mean differences of seasonally averaged daily T_a, PPT, R_g, SWC, LAI, and ER between the increasing- and decreasing-temperature seasons. This was done to test the drivers accounting for the hysteresis of NEE response to temperature at the seasonal scale.

As an additional test of the effects of radiation on the eventual hysteresis, we compared the hysteresis calculated with the full dataset with the one calculated only with midday values of air temperature and GPP. We assumed that R_g at midday is ample for photosynthesis. Similarly, to test the contribution of SWC to the hysteresis response of GPP, we compared the hysteresis of GPP between the full dataset and a subset of the data using only the 30% wettest days.

Statistical analyses

We used paired t-test to analyze the significance of the hysteresis between the increasing and decreasing temperature curves with the same temperature range. The difference was considered to be significant if $P < 0.05$. In order to reveal any spatial patterns of NEE hysteresis across the sites, we analyzed the relationship of NEE differences between the seasons (ΔNEE) and site temperature, precipitation, and global radiation by simple regression. We used simple regression also to examine the relationship of ΔNEE and ΔGPP with the differences of abiotic and biotic factors between the increasing and decreasing temperature seasons across the sites. Multiple regression were used to examine the main processes or factors controlling the hysteresis of NEE and GPP and to quantify the degree to which the hysteresis of NEE and GPP was explained by these factors. The relationship was considered to be significant if $P < 0.05$. All statistical analyses were performed using SPSS 13.0 for Windows (SPSS Inc., Chicago, IL USA).

Results

The seasonal dynamics of daily mean temperature showed a symmetric pattern between the increasing and decreasing temperature seasons (Fig. 1). In contrast, at all sites daily R_g was higher during the increasing than during decreasing temperature seasons (Fig. 1). LAI was also asymmetric between the two seasons, but this difference was not consistent across sites, with some sites exhibiting higher-, and others lower LAI values in the increasing than in the decreasing temperature season.

There were parabolic-like patterns of NEE in response to temperature in both spring and autumn (Fig. 2). As temperature increased in the spring, NEE increased (became more negative) and peaked at the optimum temperature (at which ecosystem net CO_2 uptake reaches a maximum value). Afterwards NEE decreased (became less negative) with decreasing temperature in autumn (Fig. 2). At the same temperature, NEE in the decreasing temperature season was less (lower carbon uptake) than in the increasing temperature season, forming a significant hysteresis loop in 18 out of 20 sites ($P < 0.05$ for all except US-Ha1 and US-UMB). Although the counter-clockwise hysteresis pattern was quite consistent across sites (90% of the studied forests exhibited this pattern), the magnitude of the hysteresis loop differed strongly among the sites. The loop was large at FR-Pue, IT-Ro1, US-Hol, UK-Gri, and DK-Sor, but much smaller at US-MMS, IT-Ren and DE-Hai. Across the sites, the magnitudes of the NEE hysteresis loops (manifested by the mean difference of NEE (ΔNEE) between the increasing and decreasing temperature seasons) significantly correlated with the differences in GPP (ΔGPP, Fig. 3a), but only marginally correlated with the differences in ER (ΔER, Fig. 3b). Stepwise multiple regression analyses demonstrated that ΔGPP and ΔER in combination could explain 76% of changes in ΔNEE, while ΔGPP alone could explain 68% of changes in ΔNEE.

GPP also showed a seasonal hysteresis in response to temperature change (Fig. 4). GPP increased with increasing temperature in spring and peaked then. Afterwards, it sharply decreased with decreasing temperature until the end of the growing season (Fig. 4). At the same temperature, GPP was typically lower during the decreasing than during the increasing temperature season. The magnitude of hysteresis was different among the sites, with large loops at US-Blo, IT-Co1, DK-Sor, FR-Pue, and IT-Ro1, but minor loops at FI-Hyy, IT-Ren, and DE-Hai. Across the sites, the magnitudes of the hysteresis loops of both GPP and NEE were positively correlated with site mean annual T_a but showed no relationship with annual PPT, mean annual R_g or latitude (Fig. 5).

The relationships of ΔNEE or ΔGPP with ΔR_g, ΔPPT, ΔSWC, or ΔLAI between the increasing and decreasing temperature seasons showed that only ΔR_g and ΔLAI were significantly correlated with ΔNEE and ΔGPP across the sites (Fig. 6a–d). Neither ΔNEE nor ΔGPP had a significant relationship with either ΔPPT across the 20 sites or ΔSWC across the 14 sites that had SWC data (Fig. 6e–h). ΔLAI correlated positively with ΔR_g ($R^2 = 0.25$, $P = 0.02$). Stepwise multiple regression analyses revealed that ΔR_g was the main environmental factor and could explain 55% and 60% of the changes in ΔNEE and ΔGPP, respectively.
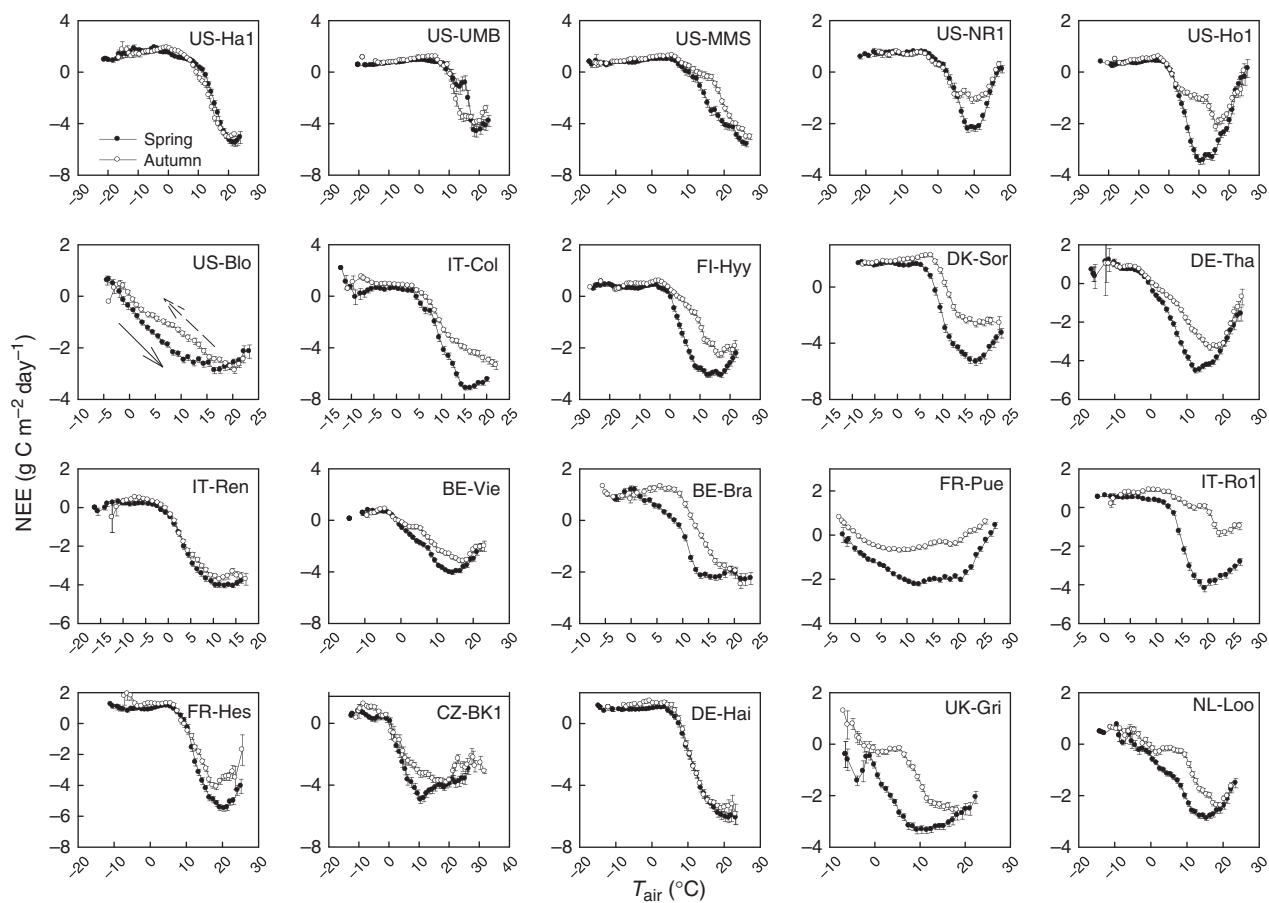
Fig. 2 Temperature response curves of net ecosystem exchange (NEE, mean ± 1SE) during the increasing (solid) and decreasing (open) temperature. The area between the increasing and decreasing temperature response curves is the hysteresis loop. The direction of a hysteresis response around this loop can be either clockwise or counter-clockwise as illustrated in the US-BIo panel. The solid arrow indicates the direction of the response during the spring, and the dashed arrow indicates the direction of the response during the autumn.
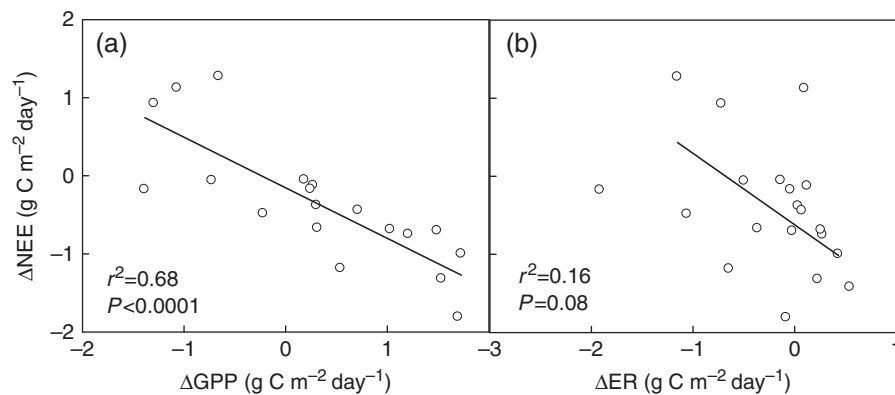
Fig. 3 Relationship of NEE differences (ΔNEE) with GPP differences (ΔGPP, A) between the increasing and decreasing temperature across the 20 sites, or the relationship of ΔNEE with ER differences (ΔER, B) across the 20 sites. The relationship was significant if $P < 0.05$.

To provide evidence that R_g contributes to the seasonal hysteresis of GPP in response to temperature, we used the midday values of temperature and GPP on clear days to construct temperature response curves of GPP. Clearly, under enough R_g condition, the hysteresis loop disappeared at most sites (i.e. US-NR1, US-Blo, BE-Vie,
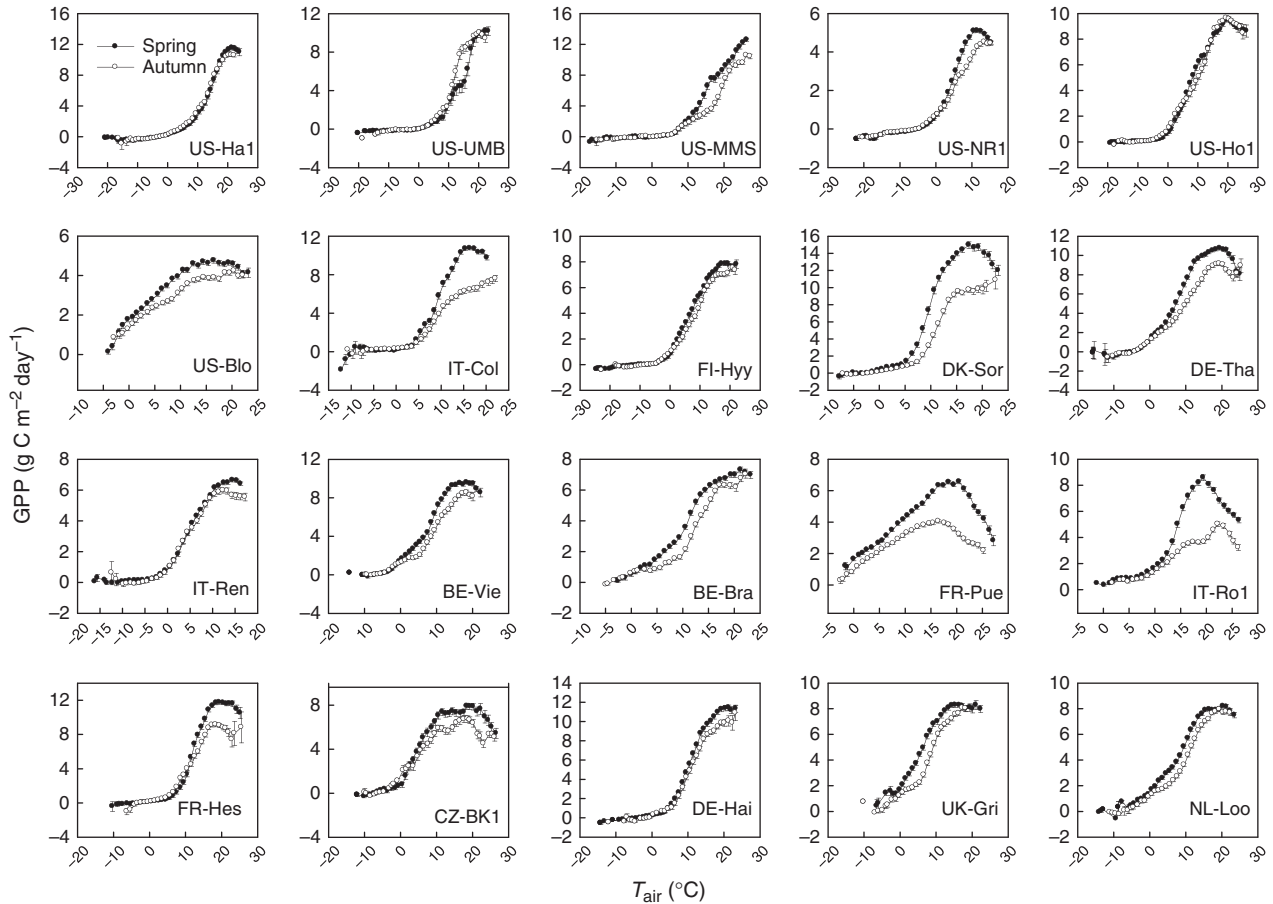
Fig. 4 The temperature response curves of GPP (mean ± 1SE) during the increasing (solid) and decreasing (open) temperature.

CZ-BK1, DE-Hai, NL-Loo) or became smaller in some sites (DK-Sor, DE-Tha, BE-Bra, FR-Pue, FR-Hes, UK-Gri, Fig. 7). Although sites IT-Col, DK-Sor, FR-Pue, and IT-Ro1 still had obvious hysteresis loop when excluding the potential R_g limitation, the reduction of hysteresis loops at the majority of the sites suggests that R_g very likely contributes to the hysteresis of GPP between the increasing and decreasing temperature seasons. From the sites that still had large hysteresis loops under ample radiation, we selected four (DE-Tha, DK-Sor, IT-Co1, and IT-Ro1) that had SWC data to test the potential effect of SWC on the hysteresis loop in GPP. Only the 30% highest SWC-days were used in each site. Results showed that the hysteresis loop disappeared at DE-Tha, DK-Sor, and IT-Co1, and became much smaller at IT-Ro1 (Fig. 8), suggesting that SWC also contributes to the hysteresis loop in GPP.

Discussion

The robust parabolic-like temperature response of NEE was well documented in previous studies (Huxman

et al., 2003; Niu *et al.*, 2011). What is less widely reported is the hysteresis in the pattern of NEE as a function of temperature. This hysteresis phenomenon was previously found for SR in response to soil temperature (Moren & Lindroth, 2000; Drewitt *et al.*, 2002; Gaumont-Guay *et al.*, 2006). Similar hysteretic temperature-response patterns of the observed ecosystem-atmosphere exchange were previously reported for a diurnal hysteresis of NEE in a broadleaf deciduous forest (Nakai *et al.*, 2003), but this study now shows that NEE also has this hysteresis pattern at the annual scale and, more importantly, across the vast majority of mid- and high-latitude forests (Fig. 2). The common hysteresis at seasonal-annual scales supports our previous hypothesis one, which was not previously reported in the literature. These observations of hysteresis are helpful to understand seasonal or inter-annual variation of NEE and the asymmetric response of ecosystem to any type of reoccurring phenomena on a variety of time scales (Mahecha *et al.*, 2007). The large differences in hysteresis-loop magnitudes among sites indicate that the limitations imposed by other environmental factors
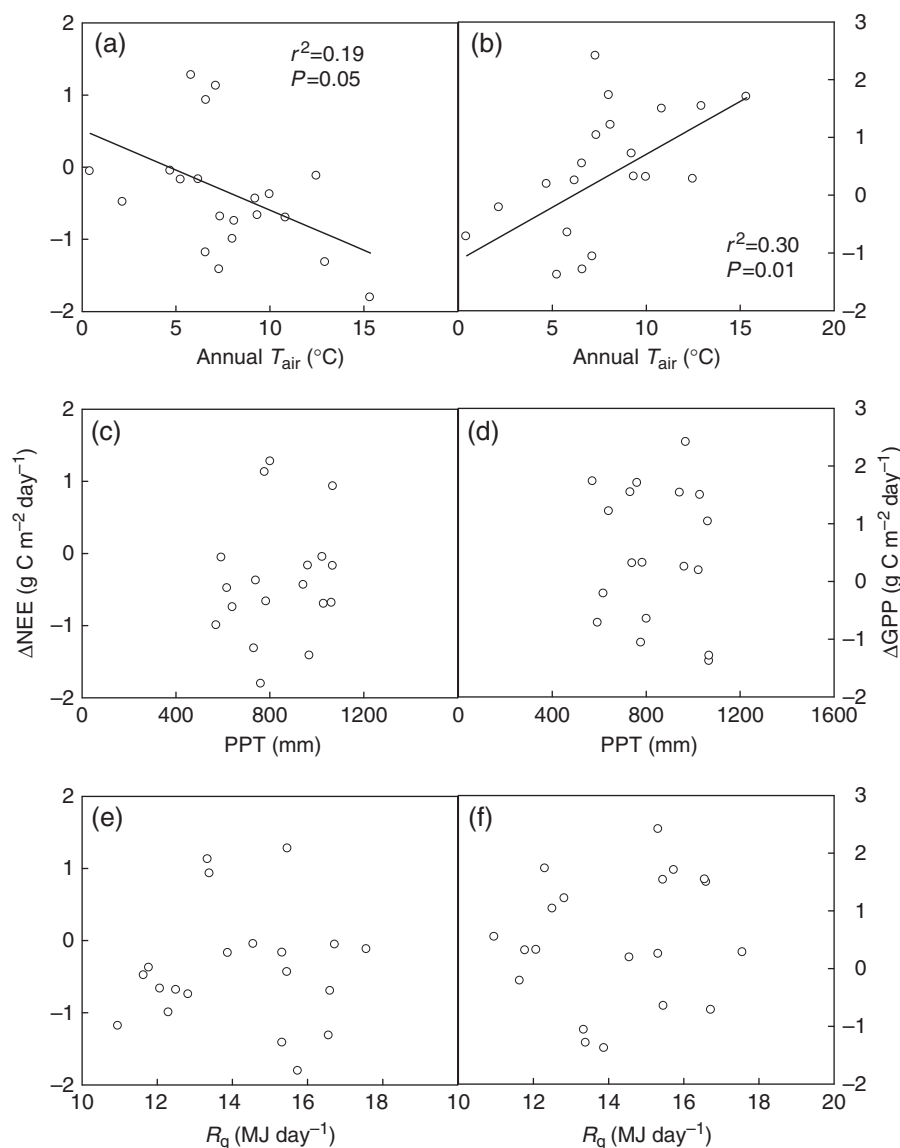
Fig. 5 The magnitude of NEE hysteresis in response to mean annual air temperature (T_{air}), precipitation (PPT), and global radiation (R_g) across the sites. The relationship was significant if $P < 0.05$.

vary with sites. The general pattern is that the magnitude of hysteresis was larger in the warmer than cold sites, but had no relationship with either PPT or R_g (Fig. 5).

NEE is the balance of GPP and ER. A lot of studies have shown the coordinated changes in GPP and ER among ecosystems and over time (Janssens et al., 2001; Knohl et al., 2005; Larsen et al., 2007; Baldocchi, 2008), and the dependence of SR on plant photosynthesis (Sampson et al., 2007). So, the temperature response of NEE should be explained by the relative changes in GPP and ER with temperature. Our results showed that the counter-clockwise hysteresis loop of NEE in re-

sponse to temperature at most sites is regulated mostly by photosynthesis of woody plants rather than ER (Fig. 3). Although ΔER explained only 8% of ΔNEE across the 20 sites, its contribution was significant according to the stepwise multiple regression analysis. Moreover, from Fig. 3b, we can see that ER in spring was lower than that in autumn at most sites, which may partly contribute the higher net carbon uptake in spring than in autumn. There has been a wide range of studies showing that ER at similar T_a was enhanced in late autumn because of fresh litter deposition and thus higher labile carbon availability, as well as the higher standing biomass that accumulated during the growing
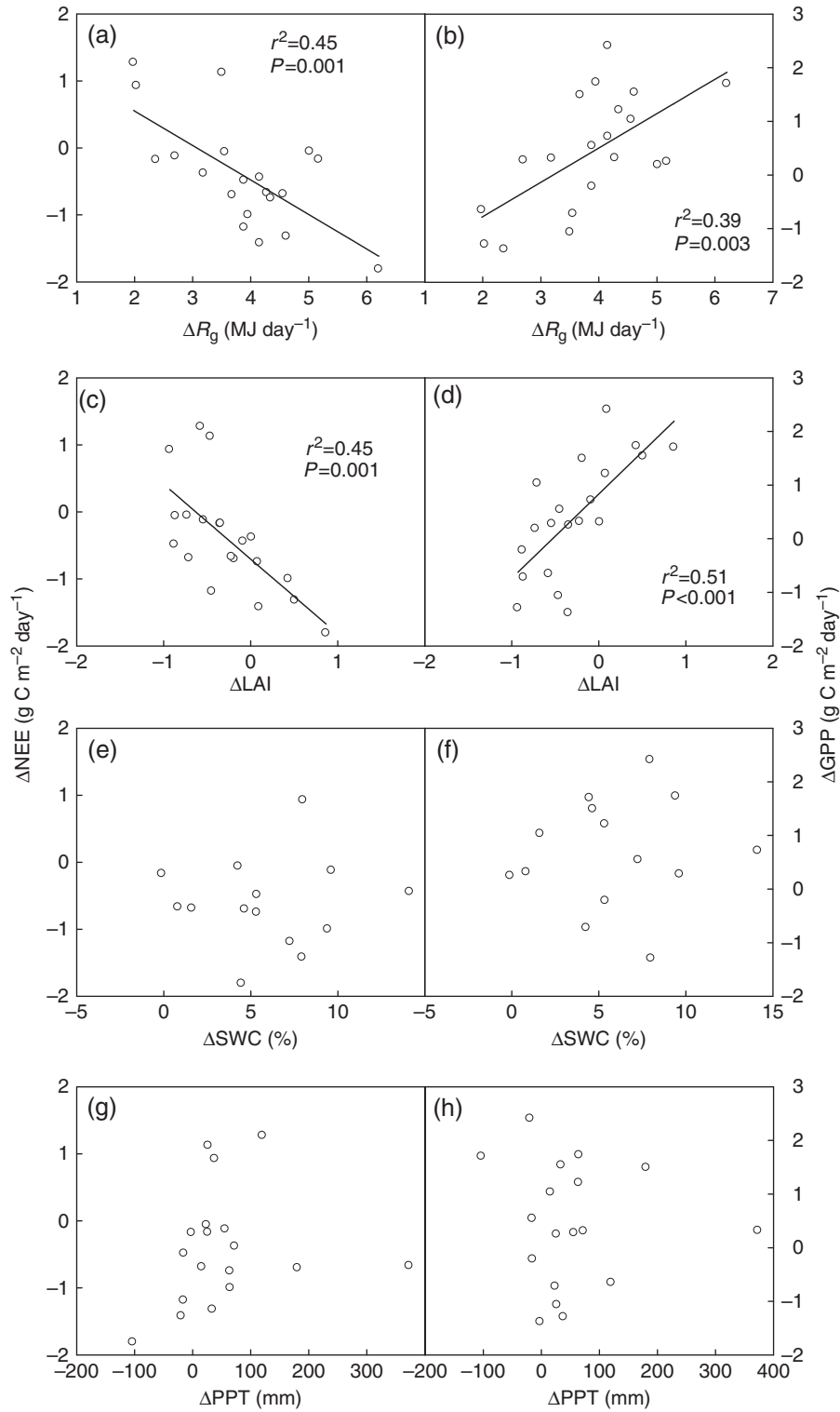
Fig. 6 Abiotic and biotic factors contributing to the hysteresis of NEE and GPP. The Δ values were calculated as the average during increasing temperature minus the average during the decreasing temperature. R_g: global radiation, LAI: leaf area index, PPT: precipitation, SWC: soil water content. The relationship was significant if $P < 0.05$.
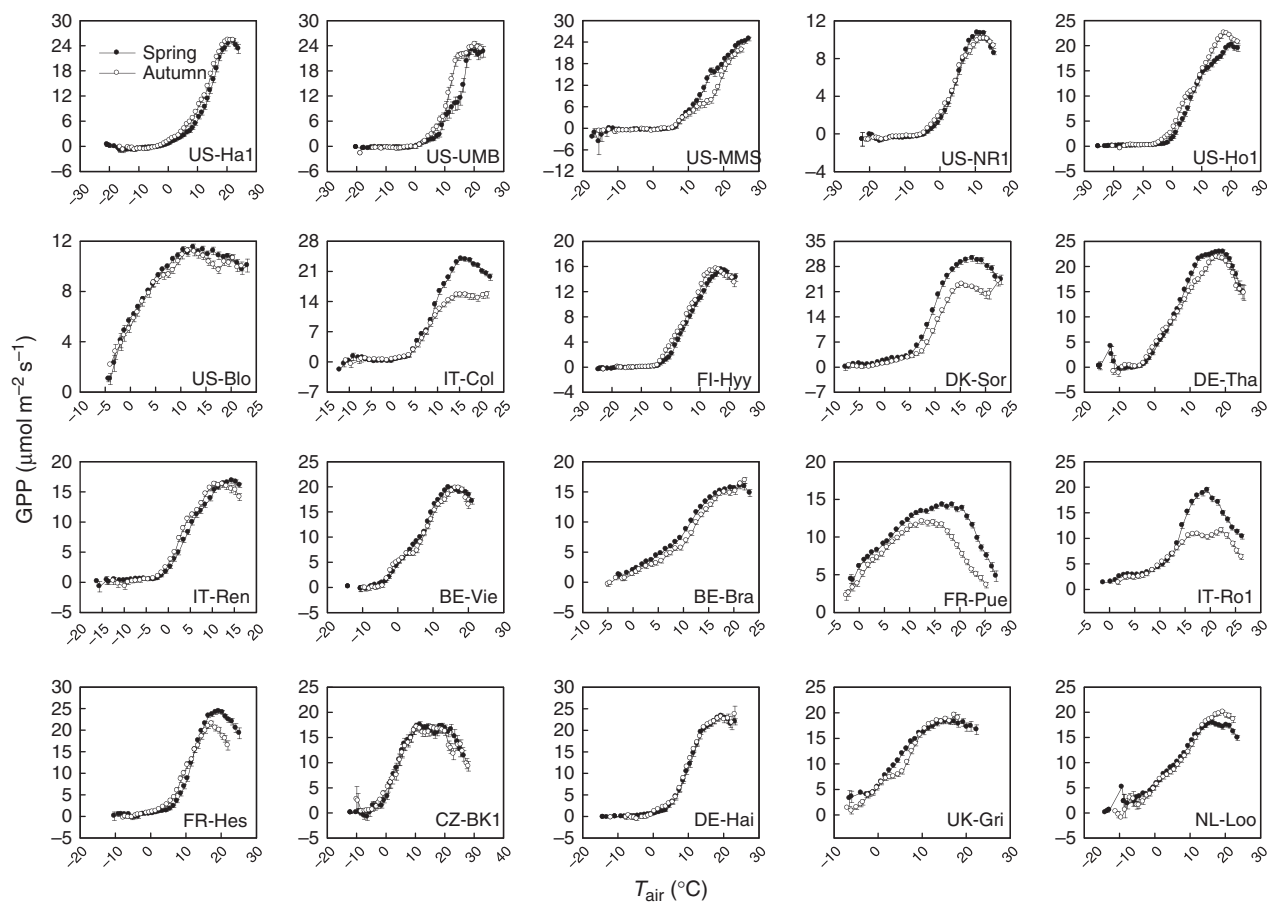
Fig. 7 The response curves of midday GPP (mean ± 1 SE) to midday temperature during the increasing (solid) and decreasing (open) temperature.

season (Piao *et al.*, 2008; Vesala *et al.*, 2010). Since R_g reaches a maximum value much earlier than temperature does (Fig. 1), and GPP mainly responds to radiation and temperature, whereas ER responds primarily to temperature and standing biomass. There is a time lag between the maximum of GPP and the maximum of ER (Skinner & Adler, 2010). This time lag may contribute to the seasonal hysteresis of NEE in response to temperature. In fact, a wide range of studies have shown the lagged ER response to temperature at diel or seasonal scales (Tang *et al.*, 2005; Gaumont-Guay *et al.*, 2006; Bahn *et al.*, 2008; Graf *et al.*, 2008). Thus, we conclude that the counter-clockwise hysteresis of NEE in the mid- and high-latitude forests are mostly due to the higher GPP in the increasing temperature season and partly due to the higher ER in the decreasing temperature season.

The differences of NEE or GPP between the increasing and decreasing temperature seasons significantly correlated with the differences of daily R_g and LAI (Fig. 6). This result supports the widely used light use efficiency model (Landsberg & Waring, 1997), in which GPP is calculated by intercepted radiation, a function of LAI and incident radiation. Because LAI and R_g are auto-correlated ($P = 0.02$), we only showed the evidence for the role of R_g in regulating hysteresis of GPP (Fig. 7). Daily accumulated R_g was always lower in autumn than in spring for all the sites (Fig. 1), leading to lower GPP in autumn. Our results are consistent with previous studies showing that carbon assimilation of many boreal coniferous forest ecosystems is light-limited in autumn (Suni *et al.*, 2003a; Mäkelä *et al.*, 2006; Vesala *et al.*, 2010). Using only the ample radiation at midday, the hysteresis loop disappeared or became considerably smaller at most sites (Fig. 7), providing evidence that radiation contributes to the regulation of the hysteresis of GPP.

The role of SWC in this study was less consistent. Across all forest sites with SWC data, differences in mean SWC did not correlate with the differences in NEE or GPP between the increasing and decreasing temperature seasons (Fig. 6e,f). Thus, SWC likely did not contribute to the differences in hysteresis of NEE or GPP across sites. However, for the four sites (DK-Sor,

DE-Tha, IT-Co1, and IT-Ro1), excluding SWC limitation (by considering only the 30% wettest days) decreased or even entirely removed the hysteresis loop (Fig. 8). This suggests that SWC does contribute to the hysteresis of GPP- and thus NEE- at least at these four sites (out of 14 with SWC data). Similarly, some previous studies
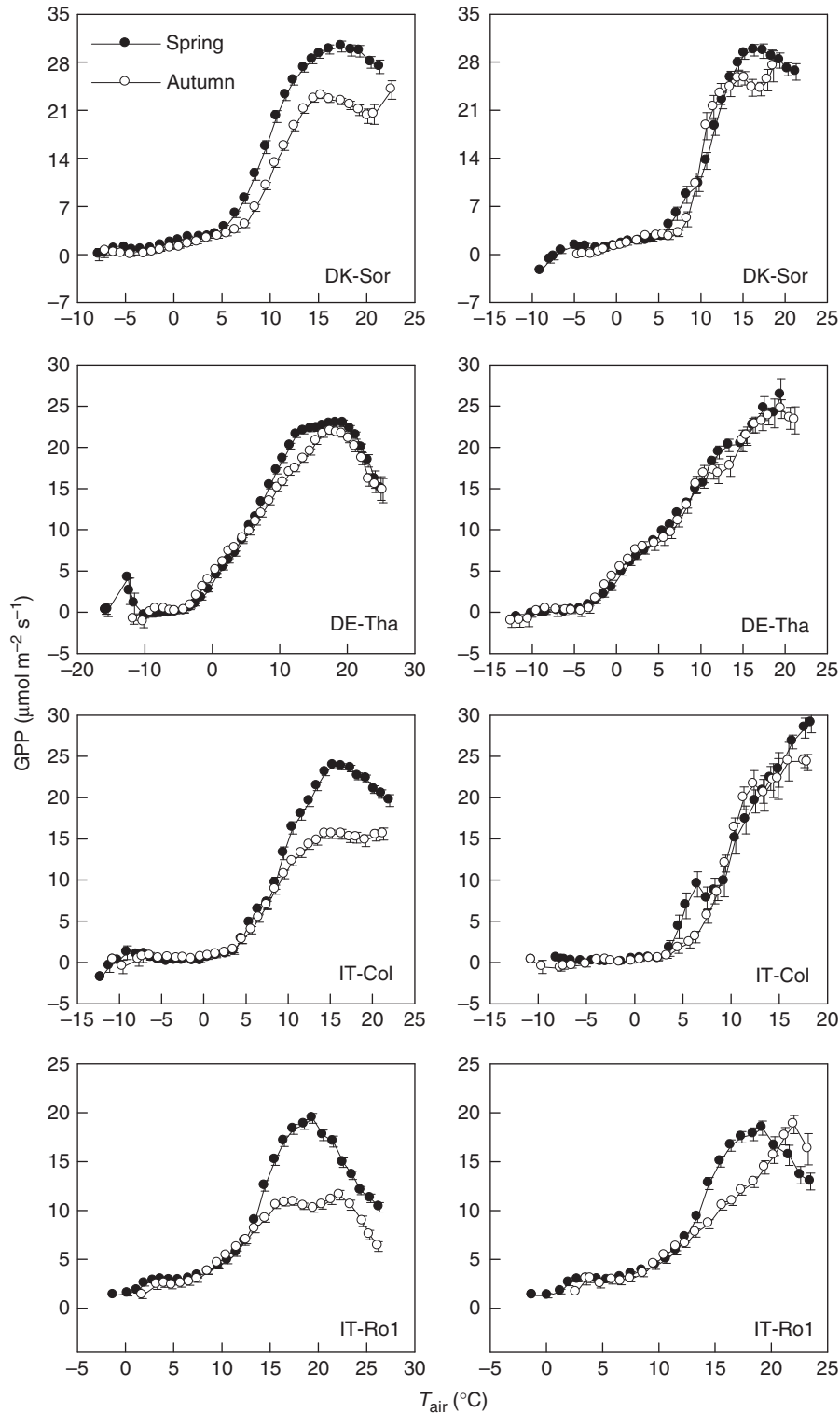
Fig. 8 Contribution of soil water content (SWC) to hysteresis of GPP (mean ± 1SE). The left panels used all SWC data while the right panels used only the 30% highest SWC-days at each site.

illustrated the influence of drought on the hysteresis of NEE in response to radiation, with much larger hysteresis loops during water stressed periods (Vourlitis et al., 2005; Pingintha et al., 2010). There are still sites, i.e. IT-Rol, have lower GPP in the decreasing temperature season even with enough radiation and SWC (Fig. 8), suggesting other drivers may contribute to the seasonal hysteretic temperature response of NEE and GPP. The key drivers in regulating hysteresis loops vary among sites, supporting our previous hypothesis two and three.

Although some previous studies have described the effect of temperature or R_g impact on NEE, the characterization of these variables impact being linked through hysteresis is largely unexplored. The magnitude of hysteresis in the NEE-temperature relationship is an important indicator of the existence of seasonal asymmetries of GPP and ER. The role of R_g, SWC and LAI in controlling the relationship between carbon fluxes and temperature should be considered when modeling the dynamics of carbon cycling in ecosystems with strong seasonality in these factors.

Conclusions

Data from long-term eddy-covariance measurements at multiple sites shows that NEE asymmetrically responds to temperature change in spring and autumn, forming a seasonal counter-clockwise hysteresis loop in NEE-temperature response in most mid- and high-latitude forests. The hysteresis of NEE could be explained mostly (68%) by the temperature response of GPP rather than that of ER. Daily accumulated R_g and LAI were the primary drivers controlling the differences of NEE and GPP between spring and autumn. SWC also contributed to the hysteresis of NEE and GPP at some sites. The results suggest that different temperature responses of carbon fluxes during spring and autumn in a year are attributable to limitation of R_g, LAI, and SWC. The consistent presences of hysteresis in the response of NEE and GPP to temperature suggests that asymmetric seasonal temperature response should be considered when simulating carbon cycling and its responses to climatic changes.

References

Arain AA, Restrepo-Coupe N (2005) Net ecosystem production in a temperate pine plantation in southeastern Canada. *Agricultural and Forest Meteorology*, **128**, 223–241.

Aubinet M, Chermanne B, Vandenhaute M, Longdoz B, Yernaux M, Laitat E (2001) Long term carbon dioxide exchange above a mixed forest in the Belgian Ardennes. *Agricultural and Forest Meteorology*, **108**, 293–315.

Bahn M, Rodeghiero M, Anderson-Dunn M et al. (2008) Soil respiration in European grasslands in relation to climate and assimilate supply. *Ecosystems*, **11**, 1352–1367.

Baldocchi D (2008) Breathing of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Australian Journal of Botany*, **56**, 1–26.

Baldocchi D, Falge E, Gu LH 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.

Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model (vol 408, pg 184, 2000). *Nature*, **408**, 750–750.

Dolman AJ, Moors EJ, Elbers JA (2002) The carbon uptake of a mid latitude pine forest growing on sandy soil. *Agricultural and Forest Meteorology*, **111**, 157–170.

Drewitt GB, Black TA, Nesic Z et al. (2002) Measuring forest floor CO_2 fluxes in a Douglas-fir forest. *Agricultural and Forest Meteorology*, **110**, 299–317.

Falayi EO, Adepitan JO, Rabiu AB (2008) Empirical models for the correlation of global solar radiation with meteorological data for Iseyin, Nigeria. *International Journal of Physical Sciences*, **3**, 210–216.

Fang JY, Brown S, Tang YH, Nabuurs GJ, Wang XP, Shen HH (2006) Overestimated biomass carbon pools of the northern mid- and high latitude forests. *Climatic Change*, **74**, 355–368.

Field CB, Lobell DB, Peters HA, Chiariello NR (2007) Feedbacks of terrestrial ecosystems to climate change. *Annual Review of Environment and Resources*, **32**, 1–29.

Gaumont-Guay D, Black TA, Griffis TJ, Barr AG, Jassal RS, Nesic Z (2006) Interpreting the dependence of soil respiration on soil temperature and water content in a boreal aspen stand. *Agricultural and Forest Meteorology*, **140**, 220–235.

Gielen B, Verbeeck H, Neirynck J, Sampson DA, Vermeiren F, Janssens IA (2010) Decadal water balance of a temperate Scots pine forest (*Pinus sylvestris* L.) based on measurements and modelling. *Biogeosciences*, **7**, 1247–1261.

Goldstein AH, Hultman NE, Fracheboud JM et al. (2000) Effects of climate variability on the carbon dioxide, water, and sensible heat fluxes above a ponderosa pine plantation in the Sierra Nevada (CA). *Agricultural and Forest Meteorology*, **101**, 113–129.

Gough CM, Vogel CS, Schmid HP, Su HB, Curtis PS (2008) Multi-year convergence of biometric and meteorological estimates of forest carbon storage. *Agricultural and Forest Meteorology*, **148**, 158–170.

Graf A, Weihermuller L, Huisman JA, Herbst M, Bauer J, Vereecken H (2008) Measurement depth effects on the apparent temperature sensitivity of soil respiration in field studies. *Biogeosciences*, **5**, 1175–1188.

Granier A, Ceschia E, Damesin C et al. (2000) The carbon balance of a young Beech forest. *Functional Ecology*, **14**, 312–325.

Heimann M, Reichstein M (2008) Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature*, **451**, 289–292.

Hollinger DY, Aber J, Dail B et al. (2004) Spatial and temporal variability in forest-atmosphere CO_2 exchange. *Global Change Biology*, **10**, 1689–1706.

Hu J, Moore DJP, Burns SP, Monson RK (2010) Longer growing seasons lead to less carbon sequestration by a subalpine forest. *Global Change Biology*, **16**, 771–783.

Huxman TE, Turnipseed AA, Sparks JP, Harley PC, Monson RK (2003) Temperature as a control over ecosystem CO_2 fluxes in a high-elevation, subalpine forest. *Oecologia*, **134**, 537–546.

IPCC (2007) Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In: *Climate Change 2007: The Physical Science Basis* (eds Solomon S, Qin D, Manning M et al.) Cambridge University Press, Cambridge, UK.

Janssens IA, Lankreijer H, Matteucci G et al. (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology*, **7**, 269–278.

Jones MB, Donnelly A (2004) Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO_2. *New Phytologist*, **164**, 423–439.

Knohl A, Schulze ED, Kolle O, Buchmann N (2003) Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany. *Agricultural and Forest Meteorology*, **118**, 151–167.

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.

Landsberg JJ, Waring RH (1997) A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management*, **95**, 209–228.

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.

Luo Y (2007) Terrestrial carbon-cycle feedback to climate warming. *Annual Review of Ecology Evolution and Systematics*, **38**, 683–712.

Mahecha MD, Reichstein M, Carvalhais N *et al.* (2010) Global convergence in the temperature sensitivity of respiration at ecosystem level. *Science*, **329**, 838–840.

Mahecha MD, Reichstein M, Lange H *et al.* (2007) Characterizing ecosystem-atmosphere interactions from short to interannual time scales. *Biogeosciences*, **4**, 743–758.

Mäkelä A, Kolari P, Karimaki J, Nikinmaa E, Peramaki M, Hari P (2006) Modelling five years of weather-driven variation of GPP in a boreal forest. *Agricultural and Forest Meteorology*, **139**, 382–398.

Moffat AM, Papale D, Reichstein M *et al.* (2007) Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes. *Agricultural and Forest Meteorology*, **147**, 209–232.

Monson RK, Turnipseed AA, Sparks JP, Harley PC, Scott-Denton LE, Sparks K, Huxman TE (2002) Carbon sequestration in a high-elevation, subalpine forest. *Global Change Biology*, **8**, 459–478.

Montagnani L, Manca G, Canepa E *et al.* (2009) A new mass conservation approach to the study of CO_2 advection in an alpine forest. *Journal of Geophysical Research-Atmospheres*, **114**, D07306, doi: 10.1029/2008JD010650.

Moren AS, Lindroth A (2000) CO_2 exchange at the floor of a boreal forest. *Agricultural and Forest Meteorology*, **101**, 1–14.

Nakai Y, Kitamura K, Suzuki S, Abe S (2003) Year-long carbon dioxide exchange above a broadleaf deciduous forest in Sapporo, Northern Japan. *Tellus Series B-Chemical and Physical Meteorology*, **55**, 305–312.

Niu S, Yuan W, Luo Y *et al.* (2011) Thermal optimality of net ecosystem exchange of carbon dioxide. *The 2010 Fall Meeting of American Geophysical Union (AGU)*, 13–17 December 2010, San Francisco, CA, USA.

Papale D, Reichstein M, Aubinet M *et al.* (2006) Towards a standardized processing of net ecosystem exchange measured with eddy covariance technique: algorithms and uncertainty estimation. *Biogeosciences*, **3**, 571–583.

Peters W, Jacobson AR, Sweeney C *et al.* (2007) An atmospheric perspective on North American carbon dioxide exchange: carbontracker. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18925–18930.

Piao SL, Ciais P, Friedlingstein P *et al.* (2008) Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature*, **451**, 49–40.

Pilegaard K, Mikkelsen TN, Beier C, Jensen NO, Ambus P, Ro-Poulsen H (2003) Field measurements of atmosphere-biosphere interactions in a Danish beech forest. *Boreal Environment Research*, **8**, 315–333.

Pingintha N, Leclerc MY, Beasley JP, Durden D, Zhang G, Senthong C, Rowland D (2010) Hysteresis response of daytime net ecosystem exchange during drought. *Biogeosciences*, **7**, 1159–1170.

Rambal S, Joffre R, Ourcival JM, Cavender-Bares J, Rocheteau A (2004) The growth respiration component in eddy CO_2 flux from a *Quercus ilex* mediterranean forest. *Global Change Biology*, **10**, 1460–1469.

Rebmann C, Gockede M, Foken T *et al.* (2005) Quality analysis applied on eddy covariance measurements at complex forest sites using footprint modelling. *Theoretical and Applied Climatology*, **80**, 121–141.

Reichstein M, Falge E, Baldocchi D *et al.* (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology*, **11**, 1424–1439.

Rey A, Pegoraro E, Tedeschi V, De Parri I, Jarvis PG, Valentini R (2002) Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. *Global Change Biology*, **8**, 851–866.

Richardson AD, Black TA, Ciais P *et al.* (2010) Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **365**, 3227–3246.

Richardson AD, Hollinger DY, Dail DB, Lee JT, Munger JW, O'Keefe J (2009) Influence of spring phenology on seasonal and annual carbon balance in two contrasting New England forests. *Tree Physiology*, **29**, 321–331.

Sampson DA, Janssens IA, Yuste JC, Ceulemans R (2007) Basal rates of soil respiration are correlated with photosynthesis in a mixed temperate forest. *Global Change Biology*, **13**, 2008–2017.

Schmid HP, Grimmond CSB, Cropley F, Offerle B, Su HB (2000) Measurements of CO_2 and energy fluxes over a mixed hardwood forest in the mid-western United States. *Agricultural and Forest Meteorology*, **103**, 357–374.

Skinner RH, Adler PR (2010) Carbon dioxide and water fluxes from switchgrass managed for bioenergy production. *Agriculture Ecosystems & Environment*, **138**, 257–264.

Suni T, Berninger F, Markkanen T, Keronen P, Rannik U, Vesala T (2003a) Interannual variability and timing of growing-season CO_2 exchange in a boreal forest. *Journal of Geophysical Research-Atmospheres*, **108**, 4265, doi:10.1029/2002JD002381.

Suni T, Berninger F, Vesala T *et al.* (2003b) Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring. *Global Change Biology*, **9**, 1410–1426.

Suni T, Rinne J, Reissell A *et al.* (2003c) Long-term measurements of surface fluxes above a Scots pine forest in Hyytiala, southern Finland, 1996–2001. *Boreal Environment Research*, **8**, 287–301.

Tang JW, Baldocchi DD, Xu L (2005) Tree photosynthesis modulates soil respiration on a diurnal time scale. *Global Change Biology*, **11**, 1298–1304.

Urban O, Janous D, Acosta M *et al.* (2007) Ecophysiological controls over the net ecosystem exchange of mountain spruce stand. Comparison of the response in direct vs. diffuse solar radiation. *Global Change Biology*, **13**, 157–168.

Urbanski S, Barford C, Wofsy S *et al.* (2007) Factors controlling CO_2 exchange on timescales from hourly to decadal at Harvard Forest. *Journal of Geophysical Research-Biogeosciences*, **112**.

Valentini R, DeAngelis P, Matteucci G, Monaco R, Dore S, Mugnozza GES (1996) Seasonal net carbon dioxide exchange of a beech forest with the atmosphere. *Global Change Biology*, **2**, 199–207.

Vargas R, Allen MF (2008) Diel patterns of soil respiration in a tropical forest after Hurricane Wilma. *Journal of Geophysical Research-Biogeosciences*, **113**, G03021, doi:10.1029/2007JG000620.

Vesala T, Launiainen S, Kolari P *et al.* (2010) Autumn temperature and carbon balance of a boreal Scots pine forest in Southern Finland. *Biogeosciences*, **7**, 163–176.

Vourlitis GL, Nogueira JDS, Priante N *et al.* (2005) The sensitivity of Diel CO_2 and H_2O vapor exchange of a tropical transitional forest to seasonal variation in meteorology and water availability. *Earth Interactions*, **9**, 1–23.

Zeppel MJB, Murray BR, Barton C, Eamus D (2004) Seasonal responses of xylem sap velocity to VPD and solar radiation during drought in a stand of native trees in temperate Australia. *Functional Plant Biology*, **31**, 461–470.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Temperature response curves of global radiation during the increasing (solid) and decreasing (open) temperature seasons.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.