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Biogeosciences Discussions

Thermal adaptation of net ecosystem exchange

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Abstract

Thermal adaptation of gross primary production and ecosystem respiration has been well documented over broad thermal gradients. However, no study has examined their interaction as a function of temperature, i.e. the thermal responses of net ecosystem exchange of carbon (NEE). In this study, we constructed temperature response curves of NEE against temperature using 380 site-years of eddy covariance data at 72 forest, grassland and shrubland ecosystems located at latitudes ranging from ~29° N to 64° N. The response curves were used to define two critical temperatures: transition temperature (T_b) at which ecosystem transferring from carbon source to sink and optimal temperature (T_o) at which carbon uptake is maximized. T_b was strongly correlated with annual mean air temperature. T_o was strongly correlated with mean temperature during the net carbon uptake period across the study ecosystems. Our results suggested that ecosystem CO_2 flux switched from source to sink when air temperature reached annual mean temperature in spring and reached maximum uptake at mean temperature of the net carbon uptake period. Our results imply that the net ecosystem exchange of carbon adapt to the temperature across the geographical range due to intrinsic connections between vegetation primary production and ecosystem respiration.

1 Introduction

Temperature is considered the most important extrinsic factor influencing biological systems across the scales from the kinetics of biochemical reactions to ecosystem biogeochemical processes including carbon cycling (Johnson et al., 1974). Both photosynthetic carbon assimilation (i.e. gross primary production, GPP) and ecosystem respiration (R_e), the two largest fluxes determining the net ecosystem exchange (NEE) of CO_2 in terrestrial ecosystem, are temperature sensitive. A number of studies have shown significant thermal adaptations of GPP and R_e in ecosystems (Luo et al., 2001;

Melillo et al., 2002; Galmés et al., 2005; Eliasson et al., 2005; Wright et al., 2006; Angiletta, 2009; Bradford et al., 2009). For example, Baldocchi et al. (2001) examined a variety of ecosystem types and suggested that the temperature optimum for ecosystem GPP is a function of mean summer temperature. Plant autotrophic respiration also represents the adaptation to the prevailing ambient temperature by adjustment of enzyme activity and substrate availability (Atkin and Tjoelker, 2003).

Thermal adaptation of GPP and R_e, however, has mostly been studied individually, with relatively little known about their interaction as a function of temperature, i.e. the thermal responses of NEE. When considering the combined thermal responses of GPP and R_e, some studies conducted within individual sites demonstrated thermal adaptation of the net ecosystem exchange of CO_2 (Luyssaert et al., 2007; Way and Sage, 2008). For example, a high-elevation forest ecosystem was found to adapt to low temperatures; while high temperatures in the midsummer constrained photosynthesis and stimulated respiration, causing a greater reduction in carbon sequestration strength (Huxman et al., 2003).

Different functions are used to describe the responses of GPP and R_e to temperature among the models for predicting ecosystem responses to global change at global or regional scales (Running and Coughlan, 1988; Running and Gower, 1991; Potter et al., 1993; Woodward et al., 1995; Foley et al., 1996; Wang et al., 2011). These models tend to represent GPP and R_e as separate functions despite recent findings that these opposing carbon fluxes are strongly coupled (Ekblad and Hogberg, 2001; Högberg et al., 2001; Bhupinderpal-Singh et al., 2003). Thermal properties of NEE, if consistent across a broad geographic range, may result in a simple whole-ecosystem understanding of ecosystem carbon metabolism (Baldocchi et al., 2005) that will both be useful for modeling studies while stimulating research on how ecosystems respond to and adjust to shifting thermal constraints.

From the standpoint of ecosystem carbon balance regulation and prediction, one can define temperature threshold points. We study T_b, the temperature at which NEE changes from carbon source to sink and T_o the optimal temperature for carbon uptake.

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T_b is related to the length of carbon uptake period, which is the primary determinant of annual NEE (Baldocchi et al., 2001; Churkina et al., 2003; Jia et al., 2010), and T_o corresponds with the maximum NEE, which is a signature for the potential carbon sequestration capacity of ecosystem (Falge et al., 2002). Our overarching goal of this study is to investigate the thermal adaptation of ecosystems on NEE by examining the value of T_b and T_o of ecosystems across a broad geographic range.

2 Data and methods

We used eddy covariance (EC) data from the AmeriFlux (http://public.ornl.gov/ameriflux) and EuroFlux (http://www.fluxnet.ornl.gov/fluxnet/index.cfm) consortia. Direct flux measurements of CO_2 based on eddy covariance technology from 72 sites consisting of 380 site-years of data were included in this study to explore the changes of T_b and T_o, including five major terrestrial biomes: deciduous broadleaf forests (DBF), evergreen needleleaf forests (ENF), mixed forests of deciduous broadleaf and evergreen needleleaf species (MIX), shrublands (SHR) and grasslands (GRS) (Table 1). Supplementary information on the vegetation, climate, and soil of each site are available on-line.

Half-hourly or hourly averaged global radiation (R_g), photosynthetically active radiation (PAR), air temperature (T_a), and friction velocity (u^*) were used in conjunction with eddy covariance fluxes of CO_2 (F_c). When available, datasets gap-filled by site investigators were used for this study. For other sites, data filtering and gap-filling were conducted according to the following procedures. 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 eddy covariance measurements under stable conditions (Falge et al., 2001), nighttime data with nonturbulent conditions were removed based on a u^*-threshold criterion (site-specific 99% threshold criterion following Papale et al., 2006; Reichstein et al., 2005).

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Nonlinear regression methods were used to fill F_c data gaps (Falge et al., 2001). Nonlinear regression relationships between measured fluxes and controlling environmental variables were fit using a 15-day moving window. The van't Hoff (see Lloyd and Taylor, 1994) equation was used to fill the missing nighttime fluxes ($F_{c,\mathrm{night}}$):

$$F_{\mathrm{c,night}} = Ae^{(BT_\mathrm{a})} \tag{1}$$

where, A and B are estimated model coefficients, and T_a is air temperature. A Michaelis-Menten light response equation was used to fill the missing daytime fluxes ($F_{\mathrm{c,day}}$) (Falge et al., 2001):

$$F_{\mathrm{c,day}} = \frac{\alpha \times PAR \times F_{\mathrm{GPP,sat}}}{F_{\mathrm{GPP,sat}} + \alpha \times \mathrm{PAR}} - F_{\mathrm{RE,day}} \tag{2}$$

where $F_{\mathrm{GPP,sat}}$ (GPP at saturating light) and α (initial slope of the light response function) are empirically-estimated coefficients, and $F_{\mathrm{RE,day}}$ (daytime R_e) was estimated by extrapolation of Eq. (1) using the daytime air temperature. Daily meteorological and flux variables values were synthesized based on half-hourly or hourly values, and the daily values were indicated as missing when missing hourly values exceeded 20% of potential observations during each day.

The decreased solar radiation during cloudy days significantly restricts GPP more than R_e, resulting in a reduced NEE. To exclude the influence of clouds on NEE and thus isolate the temperature response, the cloudy days were excluded from our analysis (Fig. 1a). Cloudiness was defined by using a clearness index (CI), defined as periods when the ratio of the global solar radiation received on the surface to the extraterrestrial solar radiation exceeded 0.5. On average, 35% of days were removed which were defined as the cloudy days. The amount of cloudy days excluded varied among sites and ranged from 45% (US-MMS) to 23% (SE-Nor). Moreover, the effects of drought on NEE during the growing season were accounted for in a simplified way.

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A water stress index (WSI) was calculated as:

$$\mathrm{WSI} = \frac{\mathrm{SW} - \mathrm{SW_W}}{\mathrm{SW_F} - \mathrm{SW_W}} \tag{3}$$

where SW is the observed soil moisture content ($m^3\,m^{-3}$). SW_W is wilting point of soil ($m^3\,m^{-3}$), and SW_F is water field capacity of soil ($m^3\,m^{-3}$). They were set to the maximum and minimum soil moisture content during the growing season. Measurements when the WSI during the growing season (April to September) were less than 15% were excluded from this analysis. The excluding measurements made under water-stressed conditions resulted in the exclusion of 16% of measurements ranging from 13% at US-Bar to 28% at US-Wkg. In total, 53% of available measurements were used in this analysis ranging from 31% at UK-Ham to 72% at CA-SF2.

From −30° to its maximum, temperature categories were set every 1° increments. Air temperature and NEE for each site were averaged within each increment over the study years in order to examine the changes of NEE with temperature to determine T_b and T_o (Fig. 2). The start and end dates of NEE were identified as the day when daily NEE shifted signs (Falge et al., 2002). To deduce these dates objectively, an 11-day running mean was calculated and the onset date of carbon uptake was determined when consecutive foregoing days acted as a net carbon source to the atmosphere, and subsequent days represented a net carbon sink.

3 Results

Our analysis shows that T_b and T_o decreased significantly with latitude, which co-varies strongly with temperature (Fig. 3). T_b was strongly correlated with annual mean air temperature across a broad geographic range (Fig. 4a). Specifically, T_b under the same thermal conditions was higher in deciduous broadleaf forests than in other ecosystem types, though the regression curve of T_b to mean annual temperature in the deciduous broadleaf forests did not show a significant difference among all sites. In contrast, we

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observed a significant difference of regression curve in evergreen needleleaf forests from the overall mean of all sites, with a lower T_b in evergreen needleleaf forests (Fig. 4a). T_o for carbon uptake was strongly correlated with mean air temperatures during the carbon uptake period across the broad spatial scale examined (Fig. 4b).

We compared the temperature curves of NEE among adjacent ecosystems to investigate the impacts of stand age on temperature thresholds of NEE. Comparison of seven adjacent boreal forest sites showed a constant T_b and T_o among ecosystems comprising stand ages between 30 and 160 years (Fig. 5). Significantly higher T_b and T_o were found at 20- and 12-years stands (i.e. CA-NS6 and CA-NS7).

4 Discussion

A set of data selection criterion was used to remove the effects from other environmental factors when characterizing the temperature curves of NEE. Two critical environmental limitation of low radiation at cloudy days and drought, which can significantly reduce NEE, were considered in this analysis. We used clearness index (CI), defined as the ratio of the global solar radiation received on the surface to the extraterrestrial solar radiation, to exclude the cloudy days (Gu et al., 1999, 2003). Numerous of field observations have shown that the highest rate of forest net ecosystem exchanges (NEE) of CO_2 often occurs on cloudy rather than on sunny days (Price and Black, 1990; Hollinger et al., 1994). Several mechanisms have been postulated to explain such observations. They include increases in diffuse radiation (Price and Black, 1990; Hollinger et al., 1994; Fan et al., 1998), decreases in the respiration of sunlit leaves (Baldocchi, 1997), and stomatal dynamics associated with light fluctuations (Sakai et al., 1996). Gu et al. (1999) examined the influences of clouds on forest carbon uptake at a boreal aspen forest and a temperate mixed deciduous forest in Canada, and found that both forests can tolerate exceedingly large reductions of solar radiation (CI of 0.53 for the aspen forest and 0.46 for the mixed forest) caused by increases in cloudiness without lowering their capacities of carbon uptake. We examined the threshold of CI when NEE significantly decreased over other study sites, and found the threshold values were close to 0.5 (data not shown). So, in this study, we excluded the cloudy days when the ratio was less than 0.5. Figure 1a showed the significant decreases of NEE due to lower solar radiation of cloudy days at demonstrated site (i.e. DE-Tha).

It has been well known that NEE is strongly influenced by water availability in terrestrial ecosystems (Meyers, 2001; Granier et al., 2000, 2007). For example, Europe experienced a particularly extreme climate anomaly during 2003, with July temperatures up to 6.8° above long-term means, and annual precipitation deficits up to 300 mm yr^{-1}, 50% below the average (Ciais et al., 2005). The net ecosystem production decreased with increasing water stress at almost all of studied 12 forest flux sites (Granier et al., 2007). Therefore, it is necessary to characterize temperature curve of NEE using the potential NEE measurements given no water or radiation limitation. In this analysis, a simply water stress index was used to quantify the impacts of drought on NEE. The results showed that WSI can effectively ascertain the drought effects (Fig. 1b). At the DE-Tha site, decreased measurements of NEE resulted from water stress were excluded, and especially at 2003, more than half of measurements were excluded due to severe drought.

Temperature curves of NEE under the different data selection criterion showed the considerable differences (Fig. 2) at the demonstrated DE-Tha site. In generally, ecosystem carbon uptake after excluding drought and cloudy days were higher than those at the other three conditions (Fig. 2). Especially, low radiation at cloudy days substantially decreased the carbon uptake, and drought influenced NEE at the high temperature periods. The transition temperature points (i.e. T_b and T_o) showed the prominent differences among the temperature curves under the different data filting criterion. For example, at the demonstrated site, there are the differences of 5° between the curves derived from original measurements and measurements excluding cloudy and drought days. Therefore, it is necessary to characterize temperature curve of NEE using the potential NEE measurements given no water or radiation limitation.

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It would not otherwise be expected that ecosystem thermal optima track so closely with average temperatures by chance; significant correlations between ecosystem T_b and annual mean air temperature, as well as T_o and mean temperature during the carbon uptake period, suggests that ecosystem-level thermal adaptation of NEE took place. Previous studies have demonstrated strong thermal adaptation of photosynthesis and respiration independently at the ecosystem level (Baldocchi et al., 2008), while the scientific investigations on thermal properties of NEE are examined in this study. NEE is the balance between the carbon uptake by photosynthetic carbon uptake and plant and microbial respiratory losses, suggesting that the coupling of two thermally-dependent processes should be further examined to evaluate the mechanisms driving thermal adaptation of ecosystems. The variation of soil respiration and its temperature sensitivity are both strongly correlated with GPP at diurnal, seasonal and annual (Janssens et al., 2001; Tang et al., 2005; Sampson et al., 2007; Ma et al., 2007). An increasing number of evidences further show that this complex influence on plant growth rate also determines the microbial processing of carbon in the soil. Chemical properties that promote high physiological activity and growth in plants and low lignin content also promote rapid decomposition (Hobbie, 1992). The quality of leaf litter, as often measured by litter C:N ratio and carbon quality, correlates strongly with corresponding plant production parameters in living leaves (Aerts and Chapin, 2000). Furthermore, the quantity of litter input provides a second critical link between CO_2 uptake and decomposition because plant growth governs the quantity of organic matter inputs to decomposers (Deforest et al., 2009).

At a given mean annual temperature, T_b of evergreen needleleaf forests is lower than that in deciduous broadleaf forests (Fig. 4). Rapid induction of spring photosynthesis and the low soil respiration compared to assimilation due to low spring temperature, and the evergreen habit of these forests, likely resulted in earlier transition from ecosystem carbon source to uptake in evergreen needleleaf forests (Black et al., 2000; Falge et al., 2002; Welp et al., 2007). Our observation of delayed T_b in deciduous broadleaf forests was consistent with a previous study by Baldocchi et al. (2005), which showed that net carbon uptake occurs at the period when the mean daily soil temperature equals the mean annual air temperature. We found that T_b was often delayed past the day when soil temperature equaled mean annual air temperature, with 18 deciduous broadleaf forests showing an average delays of 4.67 days (Table 2).

We investigated the impacts of stand age on the thermal response of NEE within seven adjacent forest stands comprising a fire chronosequence to ascertain whether climate or stand characteristics were responsible for the timing of T_b and T_o (Fig. 5). Our results did not show differences of T_b and T_o among 30 to 160 year-old stands, suggesting that the thermal environment may be more important than successional stage in determining thermal optima. The two youngest sites showed higher T_b and T_o partly because the vegetation was dominated by deciduous broadleaf seedlings and grasses, which have slightly different temperature/thermal optima relationships than evergreen needleleaf forests (Fig. 4). Previous studies have shown that forest development following stand-replacing disturbance influences a variety of ecosystem processes including carbon exchange with the atmosphere (Law et al., 2003). The magnitude of NEE differed dramatically among stands of different ages (Fig. 5a–c), suggesting, along with the spatially-distributed results (Fig. 4), that thermal adaptation is independent of flux magnitude.

All Global Dynamic Vegetation Models (GDVM) for predicting NEE at global or regional scales use separate functions to describe the temperature relationship of GPP and R_e with substantial variations among these functions (Running and Coughlan, 1988; Running and Gower, 1991; Potter et al., 1993; Woodward, 1995; Foley et al., 1996). However, no study has been conducted to evaluate the accuracy of these independent temperature functions across models. Temperature functions of GPP and R_e in these models are often poorly constrained because the thermal adaptation of GPP and R_e, and its aggregate flux, NEE, are poorly understood, posing limitations in simulation certainty. In this study, the thermal adaptation of ecosystem on NEE across latitudes suggests the intrinsic physiological connections between thermal responses of GPP and R_e, which will be very useful to constrain ecosystem models. For example,

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our another study showed that the inversion method, using only GPP observations from eddy covariance towers, constrained 5 of 16 parameters in the model, and the improved method using both GPP observations and the interior coupling relationship between GPP and R_e constrained 12 of 16 parameters (Yuan et al., 2011). Especially, the improved method constrained the parameters on R_e without additional R_e observations, accordingly improved substantially the model performance of simulating R_e.

5 Conclusions

Investigating the thermal adaptation of ecosystems on NEE will improve our ability to model regional and global carbon balance both in the present and in the future. This study adds to an existing empirical basis of thermal adaptation of NEE that we anticipate will form a foundation for mechanistic, process-based studies on the response of GPP and R_e to temperature. In this study, T_b and T_o showed significantly decreasing trends with latitude and adapted to the mean temperature during the whole year and growing season separately across 72 study sites with a wide geographic distribution. Thermal response of T_b and T_o provides a promising physiological rule that can be implemented in regional carbon balance models constraining presently separated temperature functions of GPP and R_e.

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Table 1. The FLUXNET sites used in this study arranged according to ecosystem type.

Site name	Type[a]	Lat[b]	Lon[c]	PPT[d]	MAT[e]	Period[f]	Ratio(%)[g]
CA-Oas	DBF	53.63	−106.20	428.53	0.34	1997–2006	45
DE-Hai	DBF	51.08	10.45	780.29	7.15	2000–2007	36
DK-Sor	DBF	55.49	11.65	573.44	8.03	1996–1999	32
FR-Hes	DBF	48.67	7.06	793.3	9.24	1997–1999	39
IT-Co1	DBF	41.85	13.59	970.88	7.32	1996–2003	42
IT-Non	DBF	44.69	11.09	741.77	13.56	2001–2003	48
IT-Ro1	DBF	42.41	11.93	763.66	15.35	2000–2006	39
IT-Ro2	DBF	42.39	11.92	760.27	15.40	2002–2006	48
Toledo	DBF	41.55	−83.84	357.14	15.40	2004–2005	59
UK-Ham	DBF	51.12	−0.86	829.39	9.38	2004–2005	31*
US-Bar	DBF	44.06	−71.288	1245.77	5.61	2004–2006	69
US-Dk2	DBF	35.97	−79.10	1168.69	14.36	2001–2005	56
US-Ha1	DBF	43.54	−72.17	1071.00	6.62	1992–2006	47*
US-MMS	DBF	39.32	−86.41	1031.57	10.85	1999–2006	63
US-Moz	DBF	38.74	−92.20	985.50	12.11	2004–2007	52
US-Oho	DBF	41.55	−83.84	842.84	9.43	2004–2005	51
US-Wbw	DBF	35.96	−84.29	1372.05	13.71	1995–2007	35*
US-WCr	DBF	45.81	−90.08	787.19	4.02	2000–2005	48
CA-Ca1	ENF	49.87	−125.33	1369.24	9.93	1998–2006	63
CA-Man	ENF	55.88	−98.48	227.14	−1.17	1994–2006	60*
CA-NS1	ENF	55.88	−98.48	500.29	−2.89	2001–2005	58
CA-NS2	ENF	55.91	−98.52	499.82	−2.88	2001–2005	53
CA-NS3	ENF	55.91	−98.38	502.22	−2.87	2001–2005	51
CA-NS4	ENF	55.91	−98.38	152.68	−0.82	2002–2004	47
CA-NS5	ENF	55.86	−98.49	500.34	−2.86	2001–2005	56
CA-NS6	ENF	55.92	−98.96	495.37	−3.08	2001–2005	53
CA-NS7	ENF	56.63	−99.95	319.08	1.25	2002–2005	67
CA-Obs	ENF	53.99	−105.12	405.60	0.79	1994–2006	63
CA-Ojp	ENF	53.92	−104.69	430.50	0.12	2000–2006	62
CA-SF1	ENF	54.49	−10.82	423.69	−0.15	2003–2005	63
CA-SF2	ENF	54.25	−105.88	435.12	−0.08	2003–2005	72
CA-SF3	ENF	54.09	−106.01	441.78	0.08	2003–2005	59
CA-TP1	ENF	42.66	−80.56	907.98	8.57	2003–2007	54
CA-TP2	ENF	42.77	−80.46	935.85	8.74	2003–2007	56
CA-TP3	ENF	42.71	−80.35	935.855	8.74	2003–2007	68
CA-TP4	ENF	42.71	−80.36	935.85	8.74	2002–2007	63
US-AKCon	ENF	63.88	145.73	317.25	−0.25	2002–2004	61
DE-Bay	ENF	50.14	11.87	1159.35	5.15	1997–1999	56*
DE-Tha	ENF	50.96	13.57	643.09	8.12	1997–2006	52
FI-Hyy	ENF	61.85	24.29	620.20	2.18	1997–2000	49
FR-Lbr	ENF	44.72	−0.77	923.54	12.49	1996–2003	58
IT-Sro	ENF	43.73	10.28	897.61	14.77	1999–2003	54
NL-Loo	ENF	52.17	5.74	786.16	9.36	1997–2003	56
SE-Faj	ENF	56.26	13.55	761.00	7.58	2005–2006	52
SE-Fla	ENF	64.11	19.46	615.98	0.27	1996–98/00–02	53
SE-Nor	ENF	60.08	17.47	512.36	6.46	1996–1997	54
SE-Sk2	ENF	60.12	17.84	573.45	5.25	2004–2005	45
US-Blo	ENF	38.90	−120.63	1630.00	12.50	1997–2006	53
US-Dk3	ENF	35.98	−79.09	1169.69	14.36	1998–2005	61
US-Ho1	ENF	45.20	−68.74	1070.29	5.27	1996–2004	63*
US-Ho2	ENF	45.21	−68.75	787.75	6.51	1999–2001	60*
US-Me1	ENF	44.58	−121.50	704.61	7.88	1999–2002	52
US-Me2	ENF	44.45	−121.55	522.88	6.28	2002–2007	51
US-Me3	ENF	44.32	−121.61	719.25	7.07	2004–2005	48
US-Me4	ENF	44.50	−121.62	1038.82	7.61	1999–2000	53
US-NR1	ENF	40.03	−105.55	632.32	2.46	1998–2004	51
US-SP1	ENF	29.74	−82.22	1309.77	20.06	2003/2005/2006	46
US-SP2	ENF	29.76	−82.24	1314.41	20.07	1999–2004	45
US-SP3	ENF	29.75	−82.16	1312.35	20.25	1999–2003	47
US-Wrc	ENF	45.82	−121.95	2451.96	9.45	1999–2004	52
NL-Cal	GRS	51.97	4.93	776.67	9.59	2003–2006	45*
NL-Haa	GRS	52.00	4.81	534.72	4.94	2003–2004	52
NL-Hor	GRS	52.03	5.07	779.70	9.50	2004–2006	53*
NL-Mol	GRS	51.65	4.64	218.48	3.73	2005–2006	54*
CA-Let	GRS	49.71	−112.94	398.40	5.36	2001–2004	61
US-Wkg	GRS	51.52	−96.86	209.31	18.36	2002–2004	63
US-Wlr	GRS	37.52	−96.85	995.70	13.10	2002–2004	52
US-Syv	MIX	46.24	−89.35	391.93	5.20	2002–2006	71
US-UMB	MIX	45.56	−84.71	615.64	7.35	1999–2003	51*
BE-Vie	MIX	50.30	6.00	821.02	8.31	1996–1998	45*
BE-Bra	MIX	51.30	4.52	822.39	11.34	1996–1999	42*
US-Los	SHR	46.08	−89.98	690.12	4.72	2001–2005	64*

[a] Ecosystem type, DBF: deciduous broadleaf forest; ENF: evergreen needleleaf forest; GRS: grassland; SHR: shrub wetland; MIX: mixed deciduous and evergreen needleleaf forest.
[b] Positive value indicates north latitude.
[c] Negative value indicates west longitude, positive value indicates east longitude.
[d] PPT: mean annual precipitation (mm y^{-1}).
[e] MAT: mean annual temperature (°).
[f] Available years.
[g] The percent of measurements that were used in this analysis.
* These sites do not measure the soil moisture, so all measurements are used in these sites.

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Table 2. Delayed days of soil temperature equals to mean annual temperature compared with air temperature in the deciduous broadleaf ecosystems (Table 1).

Site	Lat	Period[a]	Avg.[b]	Std.[c]
CA-Oas	53.63	1997–2006	5.56	3.35
DE-Hai	51.08	2000–2007	3.64	2.31
IT-Co1	41.85	1996–2003	5.78	1.57
IT-Non	44.69	2001–2003	3.89	2.01
IT-Ro1	42.41	2000–2006	2.65	1.68
IT-Ro2	42.39	2002–2006	3.89	2.36
Toledo	41.55	2004–2005	6.21	3.56
UK-Ham	51.12	2004–2005	5.87	2.37
US-Ha1	43.54	1992–2006	4.61	1.68
US-Moz	38.74	2004–2007	5.26	2.75
US-Oho	41.55	2004–2007	3.10	1.80
US-Bar	44.06	2004–2006	7.33	2.08
US-Wbw	35.96	1995–2004	5.75	3.65
US-WCr	45.81	2000–2005	2.57	2.07
FR-Hes	48.67	1997–1999	4.00	2.65
DK-Sor	55.48	1996–1999	4.67	0.58
US-DK2	35.97	2001–2005	2.20	1.90
US-MMS	39.32	1999–2006	7.20	4.80

[a] Available years.
[b] Averaged delayed days when soil temperature equals to the mean annual temperature compared with air temperature.
[c] Standard deviation.

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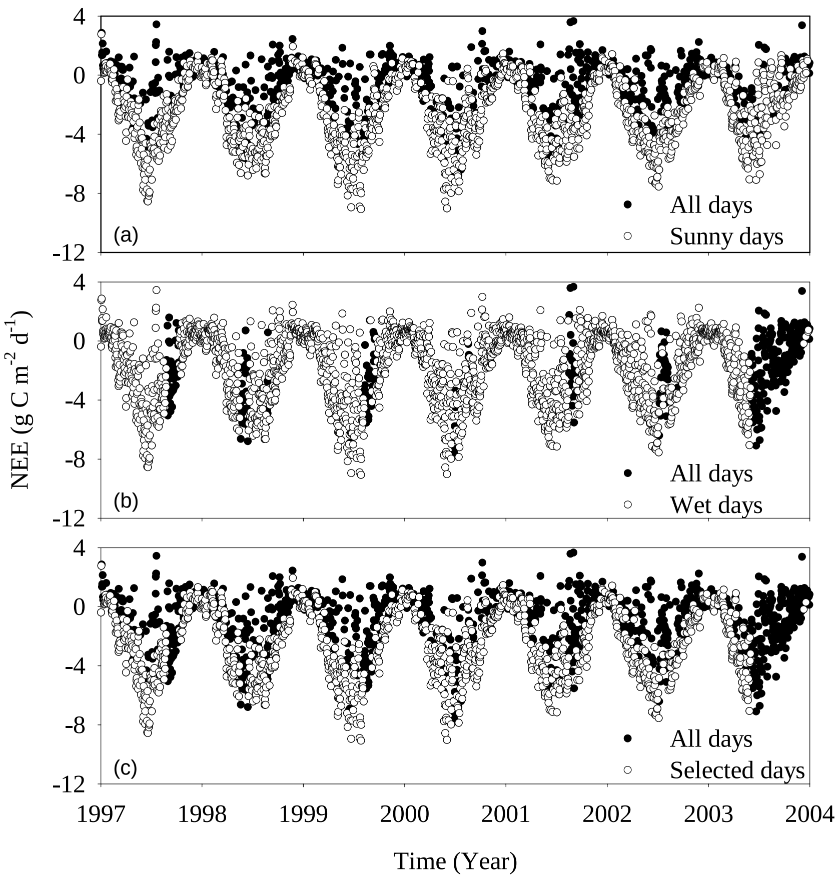

Fig. 1. Comparison on net ecosystem exchange (NEE) between all days and sunny days **(a)** and wet days **(b)** and selected days excluding both cloudy and drought days **(c)** at DE-Tha site. Negative values on *y*-axes indicate that carbon is absorbed by the ecosystem, while positive values indicate that that carbon is released by the ecosystem to the atmosphere.

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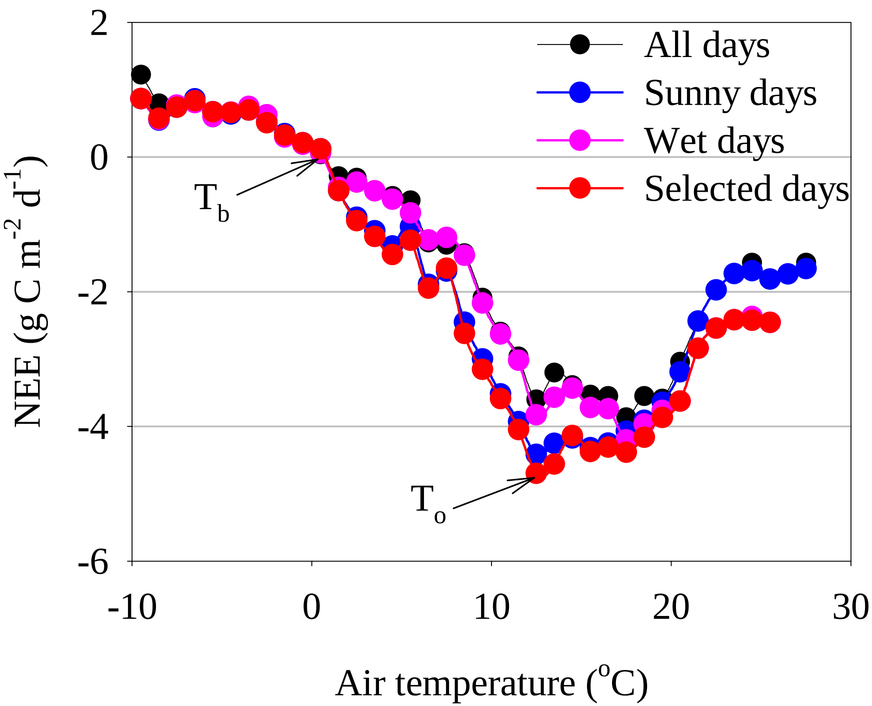

Fig. 2. Typical example of response curve of net ecosystem exchange (NEE) with temperature at DE-Tha site. Negative values at *y*-axes indicate that carbon is absorbed by the ecosystem, while positive values indicate that carbon is released by the ecosystem to the atmosphere. The curve of "all days" was derived from all measurements without any data filting; the curve of "sunny days" was derived after excluding the cloudy days; the curve of "wet days" was generated based on the measurements excluding the drought days; and the curve of "selected days" was derived from the measurements excluding the cloudy and drought days, and which was used to determine the T_b (the transition temperature from ecosystem carbon source to sink) and T_o (the optimal temperature for net carbon uptake).

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Thermal adaptation of net ecosystem exchange

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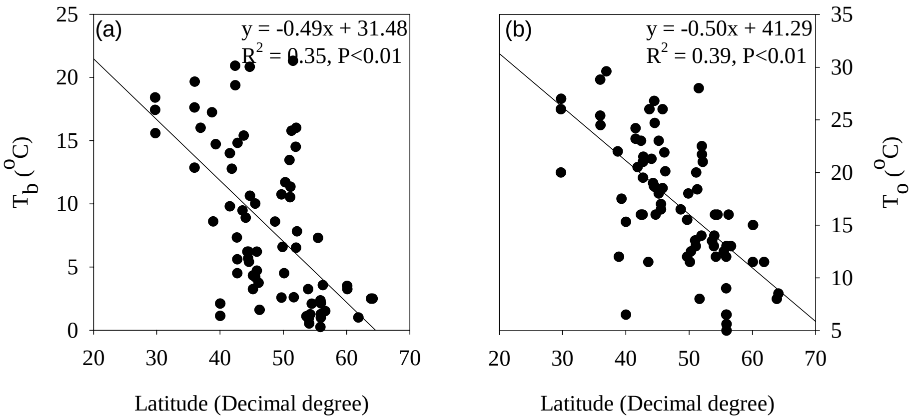

Fig. 3. Latitudinal patterns of transition temperature from ecosystem carbon source to sink T_b **(a)** and the optimal temperature for net carbon uptake **(b)**.

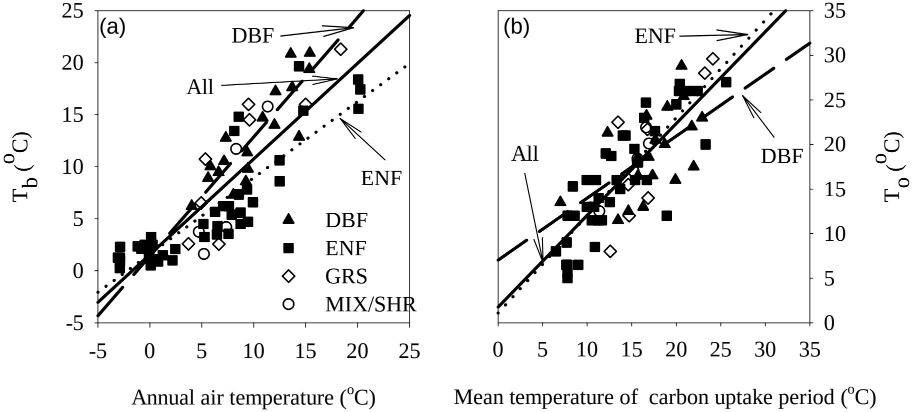

Fig. 4. The relationship between annual mean air temperature vs. T_b **(a)** and mean temperature of carbon uptake period vs. T_o **(b)** in deciduous broadleaf forests (DBF), evergreen needleleaf forests (ENF), grasslands (GRS), mixed forests (MIX) and Shurblands (SHR) as well as all ecosystems. T_b: the transition temperature from ecosystem carbon source to sink; T_o: the optimal temperature for net carbon uptake. In **(a)**, the regression lines are: $y = 1.15x + 1.41$, $R^2 = 0.81$, $P < 0.01$ (DBF); $y = 0.92x + 1.57$, $R^2 = 0.73$, $P < 0.01$ (All); $y = 0.73x + 1.59$, $R^2 = 0.77$, $P < 0.01$ (ENF). At **(b)**, $y = 0.69x + 7.02$, $R^2 = 0.32$, $P < 0.05$ (DBF); $y = 1.02x + 1.76$, $R^2 = 0.64$, $P < 0.01$ (All); $y = 1.09x + 1.09$, $R^2 = 0.71$, $P < 0.01$ (ENF).

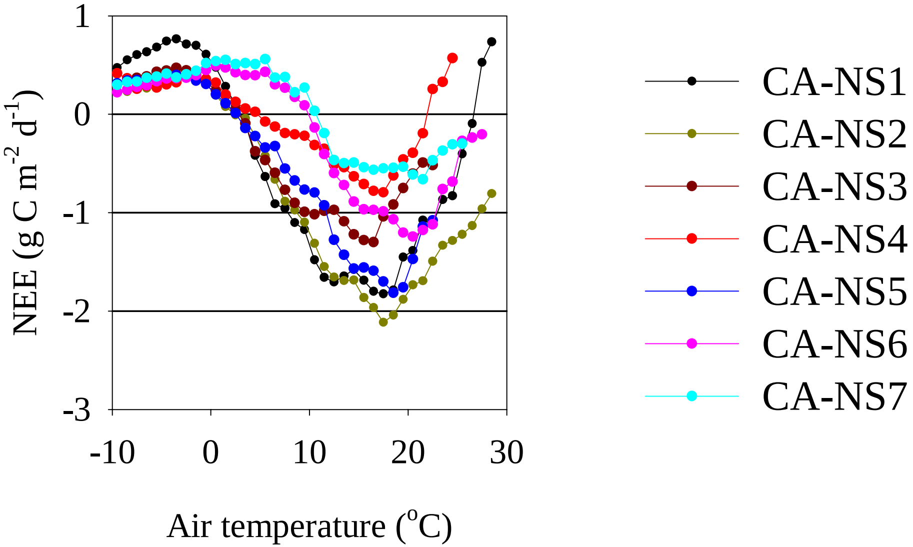

Fig. 5. Temperature response curves of NEE at seven adjacent evergreen needleleaf forests in Canada shown at Table 1. Negative values at *y*-axes indicate that carbon is absorbed by the ecosystem, while positive values indicate that carbon is released by the ecosystem to the atmosphere.

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