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This is an article published by European Geosciences Union in Biogeosciences in 2011, available online:

https://dx.doi.org/10.5194/bg-8-1453-2011

Recommended Citation

Yuan, W., Y. Luo, S. Liang, G. Yu, S. Niu, P. Stoy, J. Chen, A.R. Desai, A. Lindroth, C.M. Gough, R. Ceulemans, A. Arain, C. Bernhofer, B. Cook, D.R. Cook, D. Dragoni, B. Gielen, I.A. Janssens, G. Longdoz, H. Liu, M. Lund, G. Matteucci, E. Moors, R. L. Scott, G. Seufert, and R.K. Varner, (2011) Thermal adaptation of net ecosystem exchange, Biogeosciences, 8, 6,pp.1453-1463, DOI: 10.5194/bg-8-1453-2011.

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Biogeosciences, 8, 1453–1463, 2011
www.biogeosciences.net/8/1453/2011/
doi:10.5194/bg-8-1453-2011
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Biogeosciences

Thermal adaptation of net ecosystem exchange

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Received: 21 December 2010 – Published in Biogeosciences Discuss.: 7 February 2011
Revised: 11 April 2011 – Accepted: 15 April 2011 – Published: 6 June 2011

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:



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Published by Copernicus Publications on behalf of the European Geosciences Union.

transition temperature (T_b) at which ecosystem transfer 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 imply that the net ecosystem exchange of carbon adapts 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 ecosystems, 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. T_b is related to the length of carbon uptake period, which is a primary determinant of annual NEE (Baldocchi et al., 2001; Churkina et al., 2003), 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 CarbonEuropeIP (http://gaia.agraria.unitus.it/database/carboeuropeip/) consortia. We selected the non-crop sites which include at least two years of measurements. Eventually, 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 is available online.

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., 2002), nighttime data with non-turbulent conditions were removed based on a u^*-threshold criterion (site-specific 99 % threshold criterion following Papale et al., 2006, and Reichstein et al., 2005).

Nonlinear regression methods were used to fill F_c data gaps (Falge et al., 2002), and the correlation between measured fluxes and controlling environmental variables were fit using a 15-day moving window. The van't Hoff (see Lloyd

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

Site name	Type[1]	Lat[2]	Lon[3]	PPT[4]	MAT[5]	Period[6]	Ratio (%)[7]	Reference
CA-Oas	DBF	53.63	–106.20	428.53	0.34	1997–2006	45	Griffis et al. (2003)
DE-Hai	DBF	51.08	10.45	780.29	7.15	2000–2007	36	Reichstein et al. (2005)
DK-Sor	DBF	55.49	11.65	573.44	8.03	1996–1999	32	Pilegaard et al. (2001)
FR-Hes	DBF	48.67	7.06	793.3	9.24	1997–1999	39	Reichstein et al. (2005)
IT-Co1	DBF	41.85	13.59	970.88	7.32	1996–2003	42	Scartazza et al. (2004)
IT-Non	DBF	44.69	11.09	741.77	13.56	2001–2003	48	Reichstein et al. (2005)
IT-Ro1	DBF	42.41	11.93	763.66	15.35	2000–2006	39	Tedeschi et al. (2006)
IT-Ro2	DBF	42.39	11.92	760.27	15.40	2002–2006	48	Tedeschi et al. (2006)
Toledo	DBF	41.55	–83.84	357.14	15.40	2004–2005	59	DeForest et al. (2006)
UK-Ham	DBF	51.12	–0.86	829.39	9.38	2004–2005	31[8]	
US-Bar	DBF	44.06	–71.288	1245.77	5.61	2004–2006	69	Richardson et al. (2007)
US-Dk2	DBF	35.97	–79.10	1168.69	14.36	2001–2005	56	Pataki and Oren (2003)
US-Ha1	DBF	43.54	–72.17	1071.00	6.62	1992–2006	47[8]	Urbanski et al. (2007)
US-MMS	DBF	39.32	–86.41	1031.57	10.85	1999–2006	63	Schmid et al. (2000)
US-Moz	DBF	38.74	–92.20	985.50	12.11	2004–2007	52	Gu et al. (2006)
US-Oho	DBF	41.55	–83.84	842.84	9.43	2004–2005	51	DeForest et al. (2006)
US-Wbw	DBF	35.96	–84.29	1372.05	13.71	1995–2007	35[8]	Wilson and Baldocchi (2000)
US-WCr	DBF	45.81	–90.08	787.19	4.02	2000–2005	48	Klazura et al. (2006)
CA-Ca1	ENF	49.87	–125.33	1369.24	9.93	1998–2006	63	Humphreys et al. (2006)
CA-Man	ENF	55.88	–98.48	227.14	–1.17	1994–2006	60[8]	Dunn et al. (2007)
CA-NS1	ENF	55.88	–98.48	500.29	–2.89	2001–2005	58	Goulden et al. (2006)
CA-NS2	ENF	55.91	–98.52	499.82	–2.88	2001–2005	53	Goulden et al. (2006)
CA-NS3	ENF	55.91	–98.38	502.22	–2.87	2001–2005	51	Goulden et al. (2006)
CA-NS4	ENF	55.91	–98.38	152.68	–0.82	2002–2004	47	Goulden et al. (2006)
CA-NS5	ENF	55.86	–98.49	500.34	–2.86	2001–2005	56	Goulden et al. (2006)
CA-NS6	ENF	55.92	–98.96	495.37	–3.08	2001–2005	53	Goulden et al. (2006)
CA-NS7	ENF	56.63	–99.95	319.08	1.25	2002–2005	67	Goulden et al. (2006)
CA-Obs	ENF	53.99	–105.12	405.60	0.79	1994–2006	63	Griffis et al. (2003)
CA-Ojp	ENF	53.92	–104.69	430.50	0.12	2000–2006	62	Griffis et al. (2003)
CA-SF1	ENF	54.49	–10.82	423.69	–0.15	2003–2005	63	Mkhaberla et al. (2009)
CA-SF2	ENF	54.25	–105.88	435.12	–0.08	2003–2005	72	Mkhaberla et al. (2009)
CA-SF3	ENF	54.09	–106.01	441.78	0.08	2003–2005	59	Mkhaberla et al. (2009)
CA-TP1	ENF	42.66	–80.56	907.98	8.57	2003–2007	54	Peichl et al. (2007)
CA-TP2	ENF	42.77	–80.46	935.85	8.74	2003–2007	56	Peichl et al. (2007)
CA-TP3	ENF	42.71	–80.35	935.855	8.74	2003–2007	68	Peichl et al. (2007)
CA-TP4	ENF	42.71	–80.36	935.85	8.74	2002–2007	63	Peichl et al. (2007)
US-AKCon	ENF	63.88	145.73	317.25	–0.25	2002–2004	61	Liu et al. (2005)
DE-Bay	ENF	50.14	11.87	1159.35	5.15	1997–1999	56[8]	Valentini et al. (2000)
DE-Tha	ENF	50.96	13.57	643.09	8.12	1997–2006	52	Grünwald and Berhofer (2007)
FI-Hyy	ENF	61.85	24.29	620.20	2.18	1997–2000	49	Suni et al. (2003)
FR-Lbr	ENF	44.72	–0.77	923.54	12.49	1996–2003	58	Berbigier et al. (2001)
IT-Sro	ENF	43.73	10.28	897.61	14.77	1999–2003	54	Chiesi et al. (2005)
NL-Loo	ENF	52.17	5.74	786.16	9.36	1997–2003	56	Dolman et al. (2002)
SE-Faj	ENF	56.26	13.55	761.00	7.58	2005–2006	52	Lund et al. (2007)
SE-Fla	ENF	64.11	19.46	615.98	0.27	1996–1998/2000–2002	53	Lindroth et al. (1998)
SE-Nor	ENF	60.08	17.47	512.36	6.46	1996–1997	54	Valentini et al. (2000)
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	Falge et al. (2002)
US-Dk3	ENF	35.98	–79.09	1169.69	14.36	1998–2005	61	Hui et al. (2003)
US-Ho1	ENF	45.20	–68.74	1070.29	5.27	1996–2004	63[8]	Hollinger et al. (2004)
US-Ho2	ENF	45.21	–68.75	787.75	6.51	1999–2001	60[8]	Hollinger et al. (2004)
US-Me1	ENF	44.58	–121.50	704.61	7.88	1999–2002	52	Sun et al. (2004)
US-Me2	ENF	44.45	–121.55	522.88	6.28	2002–2007	51	Sun et al. (2004)

Table 1. Continued.

Site name	Type[1]	Lat[2]	Lon[3]	PPT[4]	MAT[5]	Period[6]	Ratio (%)[7]	
US-Me3	ENF	44.32	–121.61	719.25	7.07	2004–2005	48	Sun et al. (2004)
US-Me4	ENF	44.50	–121.62	1038.82	7.61	1999–2000	53	Sun et al. (2004)
US-NR1	ENF	40.03	–105.55	632.32	2.46	1998–2004	51	Monson et al. (2005)
US-SP1	ENF	29.74	–82.22	1309.77	20.06	2003/2005/2006	46	Kim et al. (2006)
US-SP2	ENF	29.76	–82.24	1314.41	20.07	1999–2004	45	Kim et al. (2006)
US-SP3	ENF	29.75	–82.16	1312.35	20.25	1999–2003	47	Kim et al. (2006)
US-Wrc	ENF	45.82	–121.95	2451.96	9.45	1999–2004	52	Cook et al. (2004)
NL-Cal	GRS	51.97	4.93	776.67	9.59	2003–2006	45[8]	
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[8]	
NL-Mol	GRS	51.65	4.64	218.48	3.73	2005–2006	54[8]	
CA-Let	GRS	49.71	–112.94	398.40	5.36	2001–2004	61	Flanagan and Johnson (2005)
US-Wlr	GRS	51.52	–96.86	209.31	18.36	2002–2004	63	Song et al. (2005)
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	Desai et al. (2005)
US-UMB	MIX	45.56	–84.71	615.64	7.35	1999–2003	51[8]	Curtis et al. (2005)
BE-Vie	MIX	50.30	6.00	821.02	8.31	1996–1998	45[8]	Aubinet et al. (2001)
BE-Bra	MIX	51.30	4.52	822.39	11.34	1996–1999	42[8]	Gielen et al. (2010)
US-Los	SHR	46.08	–89.98	690.12	4.72	2001–2005	64[8]	Sulman et al. (2009)

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

and Taylor, 1994) equation was used to fill the missing nighttime fluxes ($F_{c,night}$):

$$F_{c,night} = Ae^{(BT_a)} \quad (1)$$

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 ($F_{c,day}$) (Falge et al., 2001):

$$F_{c,day} = \frac{\alpha \cdot PAR \cdot F_{GPP,sat}}{F_{GPP,sat} + \alpha \cdot PAR} - F_{RE,day} \quad (2)$$

where $F_{GPP,sat}$ (GPP at saturating light) and α (initial slope of the light response function) are empirically-estimated coefficients, and $F_{RE,day}$ (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. A water stress index (WSI) was calculated as:

$$WSI = \frac{SW - SW_W}{SW_F - SW_W} \quad (3)$$

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.

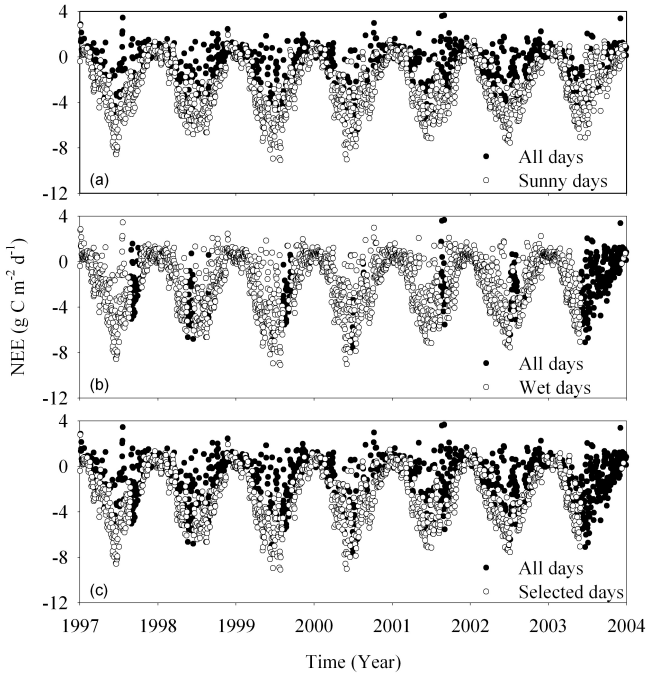


Fig. 1. Comparison on net ecosystem exchange (NEE) between all days and sunny days **(a)** and wet days **(b)** and selected days excluding both cloudy and drought days **(c)** at DE-Tha site. Negative values on y-axes indicate that carbon is absorbed by the ecosystem, while positive values indicate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

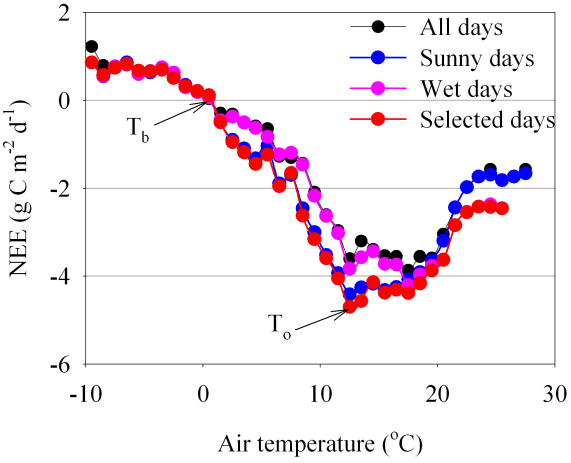


Fig. 2. Typical example of response curve of net ecosystem exchange (NEE) with temperature at DE-Tha site. Negative values at y-axes indicate that carbon is absorbed by the ecosystem, while positive values indicate that carbon is released by the ecosystem to the atmosphere. The curve of "all days" was 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).

From −30° to its maximum, temperature categories were set at 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 carbon uptake 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 (data not shown). T_b was strongly correlated with annual mean air temperature across a broad geographic range (Fig. 3a). 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 observed a significant difference in the regression curves in evergreen needleleaf forests from the overall mean of all sites, with a lower T_b in evergreen needleleaf forests (Fig. 3a). T_o for carbon uptake was strongly correlated with mean air temperatures during the carbon uptake period across the broad spatial scale examined (Fig. 3b).

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 yr (Fig. 4). Significantly higher T_b and T_o were found at 20- and 12-yr 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. Low radiation on cloudy days and drought, which can significantly reduce NEE, were considered in this analysis. We used a 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 NEE per unit radiation often occurs on cloudy rather than on

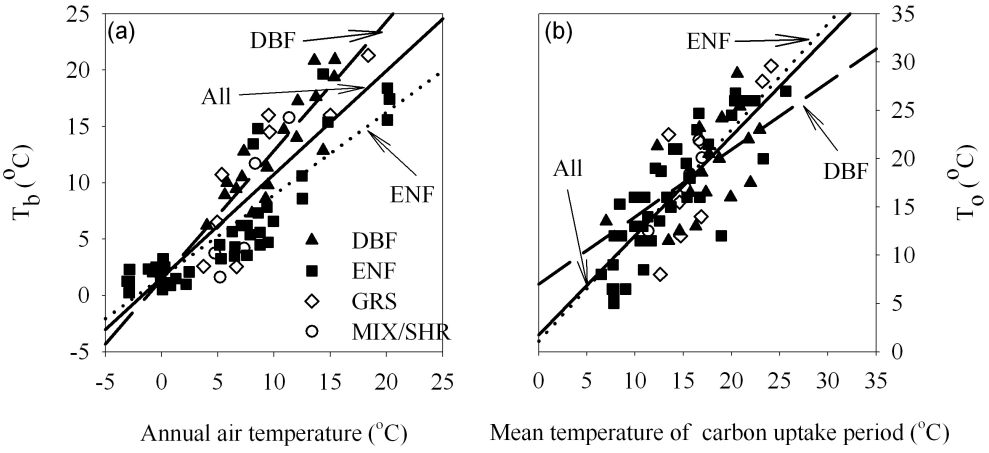


Fig. 3. The relationship between annual mean air temperature vs. T_b **(a)** and mean temperature of carbon uptake period vs. T_o **(b)** in deciduous broadleaf forests (DBF), evergreen needleleaf forests (ENF), grasslands (GRS), mixed forests (MIX) and Shurblands (SHR) as well as all ecosystems. T_b: the transition temperature from ecosystem carbon source to sink; T_o: the optimal temperature for net carbon uptake. In panel **(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).

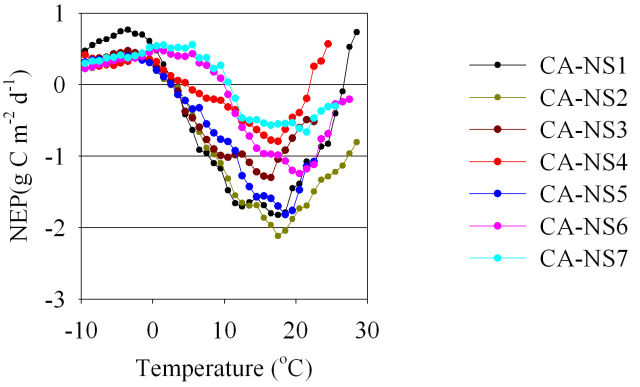


Fig. 4. Temperature response curves of NEE at seven adjacent evergreen needleleaf forests in Canada shown at Table 1. Negative values at y-axes indicate that carbon is absorbed by the ecosystem, while positive values indicate that carbon is released by the ecosystem to the atmosphere.

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 investigated 12 forest 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 simple 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 during 2003, more than half of measurements were excluded due to severe drought.

Temperature curves of NEE under the different data selection criteria 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). 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) differed 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.

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, 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 scales (Janssens et al., 2001; Tang et al., 2005; Sampson et al., 2007; Ma et al., 2007). An increasing number of studies show that this complex influence on plant growth rate also determines the microbial processing of carbon in the soil (Christopher and Lal, 2007; Fornara and Tilman, 2008; Cable et al., 2009). 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 III., 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).

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[1]	Avg.[2]	Std.[3]
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

[1] Available years.
[2] Averaged delayed days when soil temperature equals to the mean annual temperature compared with air temperature.
[3] Standard deviation.

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. 4). Our results did not show differences of T_b and T_o among 30 to 160 yr-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. 3). 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. 4a, b, c), suggesting, along with the spatially-distributed results (Fig. 3), 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 et al., 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.

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.

Acknowledgements. This research was financially supported by National Key Basic Research and Development Plan of China (2010CB833504), the Fundamental Research Funds for the Central Universities, US National Science Foundation (NSF) under DEB 0444518, and the Terrestrial Carbon Program at the Office of Science, US Department of Energy, Grants No.: DE-FG02-006ER64317. Research at the University of Antwerp was financially supported by the Research Center of Excellence ECO. We acknowledge the work of principal investigators and collaborators in EC sites, who provided the eddy covariance flux measurements.

Edited by: J. Kesselmeier

References

Aerts, R. and Chapin III., F. S. : The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns, Adv. Ecol. Res., 30, 1–67, 2000.

Angiletta, M. J.: Thermal Adaptation: a Theoretical and Empirical Analysis, Oxford University Press, New York, 2009.

Atkin, O. K. and Tjoelker, M. G.: Thermal acclimation and the dynamic response of plant respiration to temperature, Trends Plant Sci., 8, 343–351, 2003.

Aubinet, M., Chermanne, B., Vandenhaute, M., Longdoz, B., Yernaux, M., and Laitat, E.: Long term carbon dioxide exchange above a mixed forest in the Belgian Ardennes, Agr. Forest Meteorol., 108, 293–315, 2001.

Baldocchi, D. D: Measuring and modelling carbon dioxide and water vapour exchange over a temperate broad-leaved forest during the 1995 summer drought, Plant Cell Environ., 20, 1108–1122, 1997.

Baldocchi, D. D.: "Breathing" of the Terrestrial Biosphere: Lessons Learned from a Global Network of Carbon Dioxide Flux Measurement Systems, Aust. J. Bot., 56, 1–26, 2008.

Baldocchi, D. D., Falge, Eva., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw, K. T., Pilegaard, K., Schmid, H. P., Valentini, R., Verma, S., Vesala, T., Wilson, K., and Wofsy, S.: FLUXNET: a new tool to study the temporal and spatial variability of ecosystem scale carbon dioxide, water vapor, and energy flux densities, B. Am. Meteorol. Soc., 82, 2415–2434, 2001.

Baldocchi, D. D., Black, T. A., Curtis, P. S., Falge, E., Fuentes, J. D., Granier, A., Gu, L., Knohl, A., Pilegaard, K., Schmid, H. P., Valentini, R., Wilson, K., Wofsy, S., Xu, L., and Yamanoto, S.: Predicting the onset of net carbon uptake by deciduous forests with soil temperature and climate data: a synthesis of FLUXNET data, Int. J. Biometeorol., 49, 377–387, 2005.

Berbigier, P., Bonnefond, J. M., and Mellmann, P.: CO_2 and water vapour fluxes for 2 years above Euroflux forest site, Agr. Forest Meteorol., 108, 183–197, 2001.

Black, T. A., Chen, W. J., Barr, A. G., Arain, M. A., Chen, Z., Nesic, Z., Hogg, E. H., Neumann, H. H., and Yang, P. C.: Increased carbon sequestration by a boreal deciduous forest in years with a warm spring, Geophys. Res. Lett., 27, 1271–1274, 2000.

Bradford, M. A., Watts, B. W., and Davies, C. A.: Thermal adaptation of heterotrophic soil respiration in laboratory microcosms, Glob. Change Biol., 16, 1576–1588, 2009.

Cable, J. M., Ogle, K., Tyler, A. P., Pavao-Zuckerman, M. A., and Huxman, T. E.: Woody plant encroachment impacts on soil carbon and microbial processes: results from a hierarchical Bayesian analysis of soil incubation data, Plant Soil, 320, 153–167, 2009.

Chiesi, M., Maselli, F., Bindi, M., Fibb, L., Cherubini, P., Arlotta E., Tirone, G., Matteucci, G., and Seufert, G.: Modelling carbon budget of Mediterranean forests using ground and remote sensing measurements, Agr. Forest Meteorol., 135, 22–34, 2005

Christopher, S. F. and Lal, R.: Nitrogen management affects carbon sequestration in North American cropland soils, CRC Cr. Rev. Plant Sci., 26, 45–64, 2007.

Churkina, G., Tenhunen, J., Thornton, P. E., Falge, E. M., Elbers, J. A., Erhard, M., Grünwald, T., Kowalski, A. S., Rannik, ü, and Sprinz, D.: Analyzing the ecosystem carbon dynamics of four European coniferous forest using a biogeochemistry model, Ecosystems, 6, 168–184, 2003.

Ciais, P. H., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, Chr., Carrara, A., Chvallier, F., Noblet, N. D., Friend, A. D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J. M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J. F., Sanz, M. J., Schulze, E. D., Vesala, T., and Valentini, R.: Europe-wide reduction in primary productivity caused by the

heat and drought in 2003, Nature, 437, 529–533, 2005.

Cook, B. D., Davis, K. J., Wang, W., Desai, A. R., Berger, B. W., Teclaw, R. M., Martin, J. G., Bolstad, P. V., Bakwin, P. S., Yi, C., and Heilman, W.: Carbon exchange and venting anomalies in an upland deciduous forest in northern Wisconsin, USA, Agr. Forest Meteorol., 126, 271–295, 2004.

Curtis, P. S., Vogel, C. S., Gough, C. M., Schmid, H. P., Su, H. B., and Bovard, B. D.: Respiratory carbon losses and the carbon use efficiency of a northern hardwood forest, 1999–2003, New Phytol., 167, 437–456, 2005.

DeForest, J. L., Noormets, A., McNulty, S. G., Sun, G., Teeney, G., and Chen, J.: Phenophases alter the soil respiration-temperature relationship in an oak-dominated forest, Int. J. Biometeorol., 51, 135–144, 2006.

DeForest, J. L., Chen, J., and McNulty, S. G.: Leaf litter is an important mediator of soil respiration in an oak-dominated forest, Int. J. Biometeorol., 53, 127–134, 2009.

Desai, A. R., Bolstad, P. V., Cook, B. D., Davis, K. J., and Carey, E. V.: Comparing net ecosystem exchange of carbon dioxide between an old-growth and mature forest in the upper Midwest, USA, Ecol. Appl., 14, S22–S32, 2005.

Dolman, A. J., Moors, E. J., and Elbers, J. A.: The carbon uptake of a mid latitude pine forest growing on sandy soil, Agr. Forest Meteorol., 111, 157–170, 2002.

Dunn, A. L., Barford, C. C., Wofsy, S. C., Goulden, M. L., and Daube, B. C.: A long-term record of carbon exchange in a boreal black spruce forest: means, responses to interannual variability and decadal trends, Glob. Change Biol., 13, 577–590, 2007.

Ekblad, A. and Hogberg, P.: Natural abundance of ^{13}C reveals speed of link between tree photosynthesis and root respiration, Oecologia, 127, 305–308, 2001.

Eliasson, P. E., McMurtrie, R. E., Pepper, D. A., Strömgren, M., Linder, S., and Ågren, G. I.: The response of heterotrophic CO_2-flux to soil warming, Glob. Change Biol., 11, 167–181, 2005.

Falge, E., Tenhunen, J., Baldocchi, D., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, C., Bonnefound, J. M., Clement, R., Davis, K. J., Elbers, J. A., Falk, M., Goldstein, A. H., Grelle, A., Granier, A., Grünwald, T., Guðmundsson, J., Hollinger, D., Janssens, I. A., Keronen, P., Kowalskim, A. S., Katul, G., Lawo, B. E., Malhi, Y., Meyers, T., Monson, R. K., Moors, E., Mungert, J. W., Oechel, W., Paw, K. T. U., Pilegaard, K., Rannikw, Ü., Rebmannx, C., Suyker, A., Thorgeirsson, H., Tirone, G., Turnipseed, A., Wilson, K., and Wofsy, S.: Phase and amplitude of ecosystem carbon release and uptake potentials as derived from FLUXNET measurements, Agr. Forest Meteorol., 113, 75–95, 2002.

Fan, S., Gloor, M., Mahlman, J., Pacala, S., Sarminento, J., Takahashi, T., and Tans, P.: A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models, Science, 282, 442–446, 1998.

Flanagan, L. B. and Johnson, B. G.: Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland, Agr. Forest Meteorol., 130, 237–253, 2005.

Foley, J. A., Prentice, I. C., Ramankutty, N., Levis, S., Pollard, D., Sitch, S., and Haxeltine, A.: An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics, Global Biogeochem. Cy., 10, 603–628, 1996.

Fornara, D. A. and Tilman, D.: Plant functional composition influences rates of soil carbon and nitrogen accumulation, J. Ecol., 96, 314–322, 2008.

Galmés, J., Flexas, J., Keys, A. J., Cifre, J., Mitchell, R. A. C., Madgwick, P. J., Haslam, R. P., Medrano, H., and Parry, M. A. J.: Rubisco specificity factor tends to be larger in plant species from drier habitats and in species with persistent leaves, Plant Cell environ., 28, 571–579, 2005.

Gielen, B., Verbeeck, H., Neirynck, J., Sampson, D. A., Vermeiren, F., and Janssens, I. A.: Decadal water balance of a temperate Scots pine forest (*Pinus sylvestris* L.) based on measurements and modelling, Biogeosciences, 7, 1247–1261, doi:10.5194/bg-7-1247-2010, 2010.

Goulden, M. L., Winston, G. C., McMillan, A. M. S., Litvak, M. E., Read, E. L., Rocha, A. V., and Elliot, J. R.: An eddy covariance mesonet to measure the effect of forest age on land-atmosphere exchange, Glob. Change Biol., 12, 2146–2162, 2006.

Granier, A., Bréda, N., and Loustau, D.: A generic model of forest canopy conductance dependent on climate, soil water availability and leaf area index, Ann. For. Sci., 57, 755–765, 2000.

Granier, A., Reichstein, M., and Breda, N.: Evidence for soil water control on carbon and water dynamics in european forests during the extremely dry year: 2003, Agr. Forest Meteorol., 143, 123–145, 2007.

Griffis, T. J., Black, T. A., Morgenstern, K., Barr, A. G., Nesic, Z., Drewitt, G. B., Gaumont-Guay, G., and McCaughey, J. H.: Ecophysiological controls on the carbon balances of three southern boreal forests, Agr. Forest Meteorol., 117, 53–71, 2003.

Grünwald, T. and Berhofer, C.: A decade of carbon, water and energy flux measurements of an old spruce forest at the Anchor Station Tharandt, Tellus, 59B, 387–396, 2007.

Gu, L. H., Fuentes, J. D., Shugart, H. H., Staebler, R. M., and Black, T. A.: Responses of net ecosystem exchanges of carbon dioxide to changes in cloudiness: Results from two North American deciduous forests, J. Geophys. Res., 104, 31421–31434, 1999.

Gu, L. H., Baldocchi, D. D., Wofsy, S. C., Munger, J. W., Michalsky, J. J., Urbanski, S. P., and Boden, T. A.: Response of a deciduous forest to the Mount Pinatubo eruption: Enhanced photosynthesis, Science, 299, 2035–2038, 2003.

Gu, L. H., Meyers, T., Pallardy, S. G., Hanson, P. J., Yang, B., Heuer, M., Hosman, K. P., Riggs, J. S., Sluss, D., and Wullschleger, S. D.: Direct and indirect effects of atmospheric conditions and soil moisture on surface energy partitioning revealed by a prolonged drought at a temperate forest site, J. Geophys. Res., 111, D16102, doi:10.1029/2006JD007161, 2006.

Hobbie, S. E.: Effects of plant species on nutrient cycling, Trends Ecol. Evol., 7, 336–339, 1992.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., Nyberg, G., Ottosson-Löfvenius, M., and Read, D. J.: Large-scale forest girdling shows that current photosynthesis drives soil respiration, Nature, 411, 789–792, 2001.

Hollinger, D. Y., Kelliher, F. M., Byers, J. N., Hunt, J. E., McSeveny, T. M., and Weir, P. L.: Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere, Ecology, 75, 134–150, 1994.

Hollinger, D. Y., Aber, J., Dail, B., Davidson, E. A., Goltz, S. M., Hughes, H., Leclerc, M. Y., Lee, J. T., Richardson, A. D., Rodrigues, C., Scott, N. A., Achuatavarier, D., and Walsh, J.: Spatial and temporal variability in forest-atmosphere CO_2 exchange, Glob. Change Biol., 10, 1689–1706, 2004.

Hui, D. F., Luo, Y. Q., and Katul, G.: Partitioning interannual variability in net ecosystem exchange into climatic variability and functional change, Tree Physiol., 23, 433–442, 2003.

Humphreys, E. R., Black, T. A., Morgenstern, K., Cai, T., Drewitt, G. B., Nesic, Z., and Trofymow, J. A.: Carbon dioxide fluxes in coastal Douglas-fir stands at different stages of development after clearcut harvesting, Agr. Forest Meteorol. 140, 6–22, 2006.

Huxman, T. E., Turnipseed, A. A., Sparks, J. P., Harley, P. C., and Monson, R. K.: Temperature as a control over ecosystem CO_2 fluxes in a high-elevation, subalpine forest, Oecologia, 134, 537–546, 2003.

Janssens, I. A., Lankreijer, H., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E. J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Guðmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N. O., Vesala, T., Granier, A., Schulze, E. D, Lindroth, A., Dolman, A. J., Jarvis, P. G., Ceulemans, R., and Valentini, R.: Productivity overshadows temperature in determining soil and ecosystem respiration across European forests, Glob. Change Biol., 7, 269–278, 2001.

Johnson, F. H., Eyring, H., and Stover, B. J.: The Theory of Rate Processes in Biology and Medicine, John Wiley and Sons, New York, NY, 1974.

Kim, J., Guo, Q., Baldocchi, D. D., Leclerc, M. Y., Xu, L., and Schmid, H. P.: Upscaling fluxes from tower to landscape: overlaying flux footprints on high-resolution (IKONOS) images of vegetation cover, Agr. Forest Meteorol., 136, 132–146, 2006.

Klazura, G. E., Cook, D. R., Coulter, R. L., Hart, R. L., Holdridge, D. J., Lesht, B. M., Lucas, J. D., Martin, T. J., Pekour, M. S., and Wesely, M. L.: Atmospheric Boundary Layer Measurements in South-Central Kansas 1997–2004, B. Am. Meteorol. Soc., 87, 1319–1324, 2006.

Law, B. E., Sun, O., Campbell, J., Van, T. J., and Thornton, P.: Changes in carbon storage and fluxes in a chronosequence of ponderosa pine, Glob. Change Biol., 9, 510–524, 2003.

Lindroth, A., Grelle, A., and Morén, A. S.: Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity, Glob. Change Biol., 4, 443–450, 1998.

Liu, H. P., Randerson, J. T., Lindfors, J., and Chapin III., F. S.: Changes in the surface energy budget after fire in boreal ecosystems of interior Alaska: an annual perspective, J. Geophys. Res., 110, D13101, doi:10.1029/2004JD005158, 2005.

Lloyd, J. and Taylor, J. A.: On the temperature dependence of soil respiration, Funct. Ecol., 8, 315–323, 1994.

Lund, M., Lindroth, A., Christensen, T. R., and Ström, L.: Annual CO_2 balance of a temperate bog, Tellus, 59B, 812–825, 2007.

Ma, S. Y., Baldocchi, D. D., Xu, L. K., and Hehn, T.: Interannual variability in carbon exchange of an oak/grass savanna and an annual grassland in California, Agr. Forest Meteorol., 147, 157–171, 2007.

Melillo, J. M., Steudler, P. A., Aber, J. D., Newkirk, K., Lux, H., Bowles, F. P., Catricala, C., Maglill, A., Ahrens, T., and Morrisseau, S.: Soil warming and carbon-cycle feedbacks to the climate system, Science, 298, 2173–2175, 2002.

Meyers, T. P.: A comparison of summertime water and CO_2 fluxes over rangeland for well watered and drought conditions, Agr. Forest Meteorol., 106, 205–214, 2001.

Mkhabela, M. S., Amiro, B. D., Barr, A. G., Black, T. A., Hawthorne, I., Kidston, J., McCaughey, J. H., Orchansky, A. L., Nesic, Z., Sass, A., Shashkov A., and Zha, T.: Comparison of carbon dynamics and water use efficiency following fire and harvesting in Canadian boreal forests, Agr. Forest Meteorol., 149, 783–794, 2009.

Monson, R. K., Sparks, J. P., Rosenstiel, T. N., Scott-Denton, L. E., Huxman, T. E., Harley, P. C., Turnipseed, A. A., Burns, S. P., Backlund, B., and Hu, J.: Climatic influences on net ecosystem CO_2 exchange during the transition from wintertime carbon source to springtime carbon sink in a high-elevation, subalpine forest, Oecologia, 146, 130–147, 2005.

Papale, D., Reichstein, M., Aubinet, M., Canfora, E., Bernhofer, C., Kutsch, W., Longdoz, B., Rambal, S., Valentini, R., Vesala, T., and Yakir, D.: Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation, Biogeosciences, 3, 571–583, doi:10.5194/bg-3-571-2006, 2006.

Pataki, D. E. and Oren, R.: Species differences in stomatal control of water loss at the canopy scale in a mature bottomland deciduous forest, Adv. Water Resour., 26, 1267–1278, 2003.

Peichl, M. and Arain, M. A.: Allometry and partitioning of above- and below-ground tree biomass in an age sequence of white pine forests, Forest Ecol. Manag., 253, 68–80, 2007.

Pilegaard, K., Hummelshoj, P., Jensen, N. O., and Chen, Z.: Two years of continuous CO_2 eddy-flux measurements over a Danish beech forest, Agr. Forest Meteorol., 107, 29–41, 2001.

Potter, C. B., Randerson, J. T., Field, C. B., Matson, P. A., Vitousek, P. M., Mooney, H. A., and Klooster, S. A.: Terrestrial ecosystem production: a process model based on global satellite and surface data, Global Biogeochem. Cy., 7, 811–841, 1993.

Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grünwald, T., Havránková, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J. M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., and Valentini, R.: On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm, Glob. Change Biol., 11, 1424–1439, 2005.

Richardson, A. D., Hollinger, D. Y., Aber, J. D., Ollinger, S. V., and Braswell, B. H.: Environmental variation is directly responsible for short- but not long-term variation in forest-atmosphere carbon exchange, Glob. Change Biol., 13, 1–16, 2007.

Running, S. W. and Coughlan, J. C.: A general model of forest ecosystem processes for regional applications, I. Hydrologic balance, canopy gas exchange and primary production processes. Ecol. Model., 42, 125–154, 1988.

Running, S. W. and Gower, S. T.: FOREST-BGC, a general model of forest ecosystem processes for regional applications, II. Dynamic carbon allocation and nitrogen budgets, Tree Physiol., 9, 147–160, 1991.

Sakai, R. K., Fitzjarrald, D. R., Moore, K. E., and Freedman, J. M.: How do forest surface fluxes depend on fluctuating light level?, in: Preprints of 22nd Conference on Agricultural and Forest Meteorology, Atlanta, Georgia, USA, 28 January–2 February, 90–93, 1996.

Sampson, D. A., Janssens, I. A., Curiel-Yuste, J., and Ceulemans,

R.: Basal rates of soil respiration are correlated with photosynthesis in a mixed temperate forest, Glob. Change Biol., 13, 2008–2017, 2007.

Scartazza, A., Mata, C., Matteucci, G., Yakir, D., Moscatello, S., and Brugnoli, E.: Comparisons of d13C of photosynthetic products and ecosystem respiratory CO_2 and their responses to seasonal climate variability, Oecologia, 140, 340–351, 2004.

Schmid, H. P., Grimmond, C. S. B., Cropley, F., Offerle, B., and Su, H. B.: Measurements of CO_2 and energy fluxes over a mixed hardwood forest in the mid-western United States, Agr. Forest Meteorol., 103, 357–374, 2000.

Singh, B., Nordgren, A., Löfvenius, M. O., Högberg, M. N., Mellander, P. E., and Högberg, P.: Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year, Plant Cell Environ., 26, 1287–1296, 2003.

Song, J., Liao, K., Coulter, R. L., and Lesht, B. M.: Climatology of the low-level jet at the southern Great Plains atmospheric Boundary Layer Experiments site, J. Appl. Meteorol., 44, 1593–1606, 2005.

Sulman, B. N., Desai, A. R., Cook, B. D., Saliendra, N., and Mackay, D. S.: Contrasting carbon dioxide fluxes between a drying shrub wetland in Northern Wisconsin, USA, and nearby forests, Biogeosciences, 6, 1115–1126, doi:10.5194/bg-6-1115-2009, 2009.

Sun, O. J., Campbell, J., Law, B. E., and Wolf, V.: Dynamics of carbon stocks in soils and detritus across chronosequences of different forest types in the Pacific Northwest, USA, Glob. Change Biol., 10, 1470–1481, 2004.

Suni, T., Rinne, J., Reissel, A., Altimir, N., Keronen, P., Rannik, Ü., Dal Maso, M., Kulmala, M., and Vesala, T.: Long-term measurements of surface fluxes above a Scots pine forest in Hyytiälä, southern Finland, 1996–2001, Boreal Environ. Res., 4, 287–301, 2003.

Tang, J., Baldocchi, D. D., and Xu, L.: Tree photosynthesis modulates soil respiration on a diurnal time scale, Glob. Change Biol., 11, 1298–1304, 2005.

Tedeschi, V., Rey, A., Manca, G., Valentini, R., Jarvis, P. G., and Borghetti, M.: Soil respiration in a Mediterranean oak forest at different developmental stages after coppicing, Glob. Change Biol., 12, 110–121, 2006.

Urbanski, S., Barford, C., Wofsy, S., Kucharik, C., Pyle, E., Budney, J., McKain, K., Fitzjarrald, D., Czikowsky, M., and Munger, J. W.: Factors controlling CO_2 exchange on timescales from hourly to decadal at Harvard Forest, J. Geophys. Res.-Biogeo., 112, G02020, doi:10.1029/2006JG000293, 2007.

Valentini, R., Matteucci, G., Dolman, A. J., Schulze, E. D., Rebmann, C., Moors, E. J., Granier, A., Gross, P., Jensen, N. O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, T. M., Ceulemans, R., Kowalski, A. S., Vesala, T., Rannik, ü., Berbigier, P., Loustau, D., Guðmundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., and Jarvis, P. G.: Respiration as the main determinant of carbon balance in European forests, Nature, 404, 861–865, 2000.

Wang, W. L., Dungan, J., Hashimoto, H., Michaelis, A. R., Milesi, C. A., Ichii, K., and Nemani, R. R: Diagnosing and assessing uncertainties of terrestrial ecosystem models in a multi-model ensemble experiment: 1. Primary production, Glob. Change Biol., 17, 1350–1366, 2011.

Way, D. A. and Sage, R. F.: Elevated growth temperatures reduce the carbon gain of black spruce [Picea mariana (Mill.) B.S.P], Glob. Change Biol., 14, 624–636, 2008.

Welp, L. R., Randerson, J. T., and Liu, H. P.: The sensitivity of carbon fluxes to spring warming and summer drought depends on plant functional type in boreal forest ecosystems, Agr. Forest Meteorol., 147, 172–185, 2007.

Wilson, K. B. and Baldocchi, D. D.: Seasonal and interannual variability of energy fluxes over a broadleaved temperate deciduous forest in North American, Agr. Forest Meteorol., 100, 1–18, 2000.

Woodward, F. I., Smith, T. M., and Emanuel, W. R.: A global land primary productivity and phytogeography model, Global Biogeochem. Cy., 9, 471–490, 1995.

Wright, I. J., Riech, P. B., Atkin, O. K., Lusk, C. H., Tjoelker, M. G., and Westoby, M.: Irradiance, temperature and rainfall influence leaf dark respiration in woody plants: evidence from comparisons across 20 sites, Plant Cell Environ., 169, 309–319, 2006.