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Thermal adaptation of net ecosystem exchange

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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:

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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 ($R_o$), 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 $R_o$ in ecosystems (Luo et al., 2001; Melillo et al., 2002; Galmés et al., 2005; Eliasson et al., 2005; Wright et al., 2006; Angelotta, 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 $R_o$, 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 $R_o$, 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 $R_o$ 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 $R_o$ as separate functions despite recent findings that these opposing carbon fluxes are strongly coupled (Ekblad and Högberg, 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$_2$ ($F_{co}$). 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 $F_{co}$ 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
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<th>Site name</th>
<th>Type</th>
<th>Lat</th>
<th>Lon</th>
<th>PPT</th>
<th>MAT</th>
<th>Period</th>
<th>Ratio (%)</th>
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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 (°C).
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 ($F_{c,\text{night}}$):

$$F_{c,\text{night}} = A e^{B T_a}$$ (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 ($F_{c,\text{day}}$) (Falge et al., 2001):

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

where $F_{\text{GPP, sat}}$ (GPP at saturating light) and $\alpha$ (initial slope of the light response function) are empirically-estimated coefficients, and $F_{\text{RE, day}}$ 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 $R_c$, 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:

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

where SW is the observed soil moisture content (m³ m⁻³), $SW_W$ is wilting point of soil (m³ m⁻³), and $SW_F$ is water field capacity of soil (m³ 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 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 extraterrrestrial 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 fitting criterion. For example, at the demonstrated site, there are the differences of $5^\circ$ 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; Formara 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).

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

<table>
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<tr>
<th>Site</th>
<th>Lat</th>
<th>Period$^1$</th>
<th>Avg.$^2$</th>
<th>Std.$^3$</th>
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<td>CA-Oas</td>
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<td>2000–2006</td>
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$^1$ Available years.
$^2$ Averaged delayed days when soil temperature equals to the mean annual temperature compared with air temperature.
$^3$ Standard deviation.

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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, $T_h$ 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 $T_h$ 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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