

Forest annual carbon cost: a global-scale analysis of autotrophic respiration

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Abstract. Forest autotrophic respiration (R_a) plays an important role in the carbon balance of forest ecosystems. However, its drivers at the global scale are not well known. Based on a global forest database, we explore the relationships of annual R_a with mean annual temperature (MAT) and biotic factors including net primary productivity (NPP), total biomass, stand age, mean tree height, and maximum leaf area index (LAI). The results show that the spatial patterns of forest annual R_a at the global scale are largely controlled by temperature. R_a is composed of growth (R_g) and maintenance respiration (R_m). We used a modified Arrhenius equation to express the relationship between R_a and MAT. This relationship was calibrated with our data and shows that a 10°C increase in MAT will result in an increase of annual R_m by a factor of 1.9–2.5 (Q_{10}). We also found that the fraction of total assimilation (gross primary production, GPP) used in R_a is lowest in the temperate regions characterized by a MAT of ~11°C. Although we could not confirm a relationship between the ratio of R_a to GPP and age across all forest sites, the R_a to GPP ratio tends to significantly increase in response to increasing age for sites with MAT between 8° and 12°C. At the plant scale, direct up-scaled R_a estimates were found to increase as a power function with forest total biomass; however, the coefficient of the power function (0.2) was much smaller than that expected from previous studies (0.75 or 1). At the ecosystem scale, R_a estimates based on both GPP – NPP and TER – R_h (total ecosystem respiration – heterotrophic respiration) were not significantly correlated with forest total biomass ($P > 0.05$) with either a linear or a power function, implying that the previous individual-based metabolic theory may be not suitable for the application at ecosystem scale.

Key words: acclimation; autotrophic respiration (R_a); carbon cycle; carbon-use efficiency; forest ecosystems; growth respiration; maintenance respiration; metabolic theory; temperature sensitivity.

INTRODUCTION

Forest autotrophic respiration (R_a) is a major component of the terrestrial carbon cycle (King et al. 2006). Only 30–50% of photosynthesis (gross primary production, GPP) is used for making leaves, wood, and root tissues, while the remainder returns to the atmosphere in the form of R_a (DeLucia et al. 2007, Litton et al. 2007, Luyssaert et al. 2007). Globally, forest R_a produces 45–55 Pg C/yr of CO₂ annually (Luyssaert et al. 2007). This is six to seven times the current annual carbon release from fossil fuel combustion, and roughly one fifteenth of the total amount of CO₂ in the atmosphere. Therefore, future changes of forest R_a could have a strong potential to affect forest growth and the current trend of increasing atmospheric CO₂ concentration. However, little is known about R_a and

its response to environmental change. Accordingly, plant R_a is not well parameterized in current biogeochemical models (Atkin et al. 2008). Such an incomplete understanding of plant R_a further limits the capacity to more accurately assess the behavior of terrestrial ecosystems in response to climate change (Wythers et al. 2005).

A number of studies have revealed that plant R_a is directly or indirectly influenced by biotic and abiotic factors, such as plant biomass, age, N content, and temperature (Ryan 1991, Reich et al. 2006), but most of these studies have primarily focused on forest R_a at particular locations (Lavigne et al. 1997) or for specific forest types (Ryan et al. 1997). Therefore, a comprehensive understanding of the relative importance of these abiotic and biotic factors to the global controls over forest respiration is yet to be achieved.

Typically, R_a is partitioned into two components: growth or construction respiration (R_g) and maintenance respiration (R_m) (Amthor 1989, 2000, Ryan 1991). Climate change directly alters plant respiration through

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changing R_m , and thus it is necessary to quantify the relationship between forest R_a and biotic and abiotic factors through distinguishing R_g and R_m . It is a big challenge, however, to separate growth and maintenance respiration components of total R_a because growing organs also contain mature tissues whose respiration is limited to the maintenance component (Lavigne et al. 1997). In most process-based biogeochemical models, plant R_m is generally calculated first, and then R_g is obtained as a constant fraction of the difference between GPP and R_m . Accurate model parameters for plant R_m are thus a crucial first step in reliably predicting how plant R_a may change with global warming (Wythers et al. 2005).

Previous theoretical studies have also suggested that whole organism metabolic rate scales with the three-quarter power of their body mass (Gillooly et al. 2001, Brown et al. 2004). Although this relationship has been demonstrated widely in animals, direct evidence from plants is limited (Li et al. 2006). Recently, Reich et al. (2006) pointed out that, in contrast to animals, the relationships between whole-plant R_a and plant biomass is approximately linear. It should be noted, however, that the data used in the study of Reich et al. (2006) were based on instantaneous measurements of specific respiration rates from various parts of herbaceous plants and tree saplings. Thus, it is unclear if the respiration of large trees or the spatially integrated respiration at ecosystem scale still follows the relationship with biomass predicted by previous studies for individuals (DeLucia et al. 2007).

In this study, we use a recently compiled global forest C-flux database (Luyssaert et al. 2007) to investigate the dependency of forest annual R_a to temperature and biotic factors (stand biomass, age, and height). After analyzing the separate relationships between forest R_a , temperature, and biotic factors, we establish a statistical approach using forest annual R_a as the dependent variable and temperature and biotic factors as independent variables to provide information (e.g., temperature sensitivity of forest R_m) for improved parameterization of forest R_a in carbon cycle models. Finally, we discuss the temperature sensitivity of forest R_a and the application of individual organism metabolic rate in forest ecosystems.

DATA SETS AND METHODS

Data sets

This work is based on a global forest C-flux database developed by Luyssaert et al. (2007), which included forest carbon-flux data of gross primary productivity (GPP), net primary production (NPP), autotrophic respiration (R_a), heterotrophic respiration (R_h), total ecosystem respiration (TER), and net ecosystem production (NEP). All flux estimates are collected from peer-reviewed literature, established databases, and personal communication with research groups involved in the regional networks of Fluxnet. In this database,

GPP, TER, and NEP estimates are derived from eddy covariance measurements, while NPP and R_a estimates are based on direct field measurements of foliage, wood, and roots. In addition to C-flux data, other forest characteristics, such as stand biomass, age, mean tree height, and basal area, are documented in the database as well. More details concerning the database can be found in Luyssaert et al. (2007).

It is very difficult to directly measure whole-plant R_a in the field. A number of previous studies have estimated plant annual R_a through scaling chamber measurements of foliage, stem, and root respiration in different seasonal periods (e.g., Lavigne et al. 1997, Cavaleri et al. 2008). Since respiration rates vary within the canopy, among types of woody tissue and among individual leaves and roots (Ryan et al. 1994), the up-scaling approach comes with several sources of uncertainty, and it is difficult to quantify them. As an alternative to up-scaling direct R_a estimates, R_a can be indirectly estimated as the difference between GPP and NPP ($GPP - NPP$) or the difference between TER and R_h ($TER - R_h$). However, in this approach, uncertainties in GPP, NPP, TER, and R_h are propagated to the estimate of R_a . For example, since observation-based NPP measurements usually do not account for carbon allocated to reproductive organs (flowers, seeds, fruits), nor for carbon lost through herbivory grazing, volatile organic compounds (VOC), and methane (CH_4) emission, and exuded from roots or transferred to mycorrhizae (Clark et al. 2001), the indirect method based on the difference between GPP and NPP overestimates plant R_a by most likely a small but nevertheless unknown amount. R_h is also an inherently difficult process to separate from root autotrophic respiration as components of total soil respiration (Högberg and Read 2006), and the results may differ substantially depending on the method used (Hanson et al. 2000, Kuzyakov 2006). Furthermore, a simple empirical model is generally used to derive GPP and TER estimates from the eddy covariance based NEP measurements which in turn are surrounded by uncertainty (Barford et al. 2001).

Of the sites reported in the database of Luyssaert et al. (2007), we are able to include 47 directly up-scaled R_a estimates from nine field measurement sites, 36 R_a estimations calculated by the difference between GPP and NPP ($GPP - NPP$) from 26 field measurement sites, and 27 R_a estimations by the difference between TER and R_h ($TER - R_h$) from 25 field measurement sites. At present, none of these three methods is known to be more accurate and precise than the remaining two, and no better method to estimate forest annual R_a and its uncertainty is available. Therefore, forest annual R_a estimated from all three approaches is used in our study. The estimations span a range from 177 to 3323 g C·m⁻²·yr⁻¹. Forest sites included in our final analysis encompass mean annual precipitation (MAP) ranging from 350 to 3700 mm, and mean annual temperature (MAT) between -5° and 27°C. The sites cover almost all

major forest types of the world (except deciduous needle-leaf forests such as larch forest) including evergreen needle-leaf forests, evergreen broadleaf forests, deciduous broadleaf forests, and broadleaf and needle-leaf mixed forests.

Analysis

We developed a statistical approach for predicting forest annual R_a using annual mean temperature and total biomass or maximum leaf area index (LAI) as independent variables. As mentioned, plant autotrophic respiration can be partitioned into two components (Eq. 1a): growth or construction respiration (R_g) and maintenance respiration (R_m). The former is a fraction (α) of NPP, while the latter is expressed as a function of biotic and abiotic factors, such as LAI, sapwood biomass, and temperature (T) (Eq. 1b):

$$R_a = R_g + R_m \quad (1a)$$

$$R_a = [\alpha \times \text{NPP}] + [\beta \times f(T) \times f(B)] \quad (1b)$$

where B is total biomass (g C/m^2) or maximum LAI, T is temperature in K, and α and β are regression parameters. In general, the coefficient of growth respiration (α) varies between 20% and 40% (Schulze and Caldwell 1994, Gower et al. 1997, Middleton et al. 1997). Thus, we constrain α to a range of 0.2–0.4.

Analogous to the temperature sensitivity of heterotrophic respiration, the response of forest R_m to temperature was fitted using a modified Arrhenius equation (Eq. 2), where temperature sensitivity of R_m (Q_{10} , the fractional change in rate with a 10°C increase in temperature) declines with rising temperature (Lloyd and Taylor 1994, Turnbull et al. 2001, Maseyk et al. 2008). Given the spatial and temporal resolution of our data set, we investigated the response of annual forest R_m to temperature based on the spatial gradient of R_m and MAT across different forest sites. Thus, temperature sensitivity of R_m derived in this study is different from that generated by temporal models which are parameterized for single sites and relate seasonal time series of R_m to temperature. Previous studies suggested that the differences between the spatial and temporal models can be interpreted as the difference between long- and short-term effects of climate on R_m (Lauenroth and Sala 1992, Jobbagy et al. 2002):

$$f(T) = e^{\{(E_0/\text{gc}) \times [(1/293) - (1/T)]\}} \quad (2)$$

where E_0 is a parameter related to the activation energy ($\text{J}\cdot\text{mol}^{-1}\cdot\text{K}^{-1}$), and gc is the gas constant ($8.314 \text{ J}\cdot\text{mol}^{-1}\cdot\text{K}^{-1}$).

The relationship between forest annual R_a and total biomass (or maximum LAI) is assumed to be a power function:

$$f(B) = B^{\text{cc}} \quad (3)$$

where cc is the exponent of a power function, and B is

total biomass (g C/m^2) or maximum LAI. The range of cc was defined >0 . All curve fitting was performed using least-squares regression by the curve-fitting module of SPSS (SPSS, Chicago, Illinois, USA).

In order to test if there are differences among the three different methods for estimating forest R_a in the database, we performed an F test on the parameters (a , b , E_0 , cc) derived from the regression analysis (Eq. 1–3) for each approach separately. In the basic structure of the F test, a small model (null hypothesis) is compared to a larger model (alternative hypothesis), and the smaller model can be obtained from the larger by setting some parameters in the larger model equal to 0 or equal to each other. The null hypothesis is rejected if the calculated F is greater than the F given by the critical value of F (Weisberg 1985):

$$F = \frac{(\text{RSS}_{\text{NH}} - \text{RSS}_{\text{AH}})/(\text{df}_{\text{NH}} - \text{df}_{\text{AH}})}{\text{RSS}_{\text{AH}}/\text{df}_{\text{AH}}} \quad (4)$$

where RSS_{NH} and RSS_{AH} are the residual sum of squares under the null model (NH) and the alternative model (AH), respectively, while df_{NH} and df_{AH} are degrees of freedom.

RESULTS

Correlation between R_a and temperature and biotic factors

Fig. 1 illustrates the linear and exponential relationships of forest annual R_a with MAT and biotic factors including NPP, total biomass, height, maximum LAI, and forest-stand age. As shown in Fig. 1, for each factor, the linear and exponential regression analysis explains a similar amount of variation (i.e., the coefficients of determination or R^2) of the spatial gradient of forest annual R_a . Statistically significant and positive linear correlations were observed for forest annual R_a with forest height ($R = 0.274$, $P = 0.012$), maximum LAI ($R = 0.329$, $P < 0.001$), total biomass ($R = 0.393$, $P < 0.001$), and NPP ($R = 0.448$, $P < 0.001$). Such significant correlations between forest annual R_a and biotic factors are, however, most likely caused by the fact that biomass or basal area are used for up-scaling tree-level R_a estimates to the stand level. For the R_a estimates based on both gross primary production – net primary production (GPP – NPP) and total ecosystem respiration – heterotrophic respiration ($\text{TER} - R_h$), we found that R_a is not significantly linearly correlated with maximum LAI ($R = 0.118$, $P = 0.499$ for GPP – NPP; $R = 0.244$, $P = 0.239$ for $\text{TER} - R_h$), total biomass ($R = -0.049$, $P = 0.823$ for GPP – NPP; $R = -0.137$, $P = 0.575$ for $\text{TER} - R_h$), and NPP ($R = 0.274$, $P = 0.106$ for GPP – NPP; $R = 0.310$, $P = 0.184$ for $\text{TER} - R_h$), respectively. In addition, forest height is significantly correlated with R_a estimates derived by GPP – NPP ($R = 0.524$, $P = 0.010$), but not with that estimated by $\text{TER} - R_h$ ($R = 0.077$, $P = 0.761$). Although there is a statistically significant linear positive relationship be-

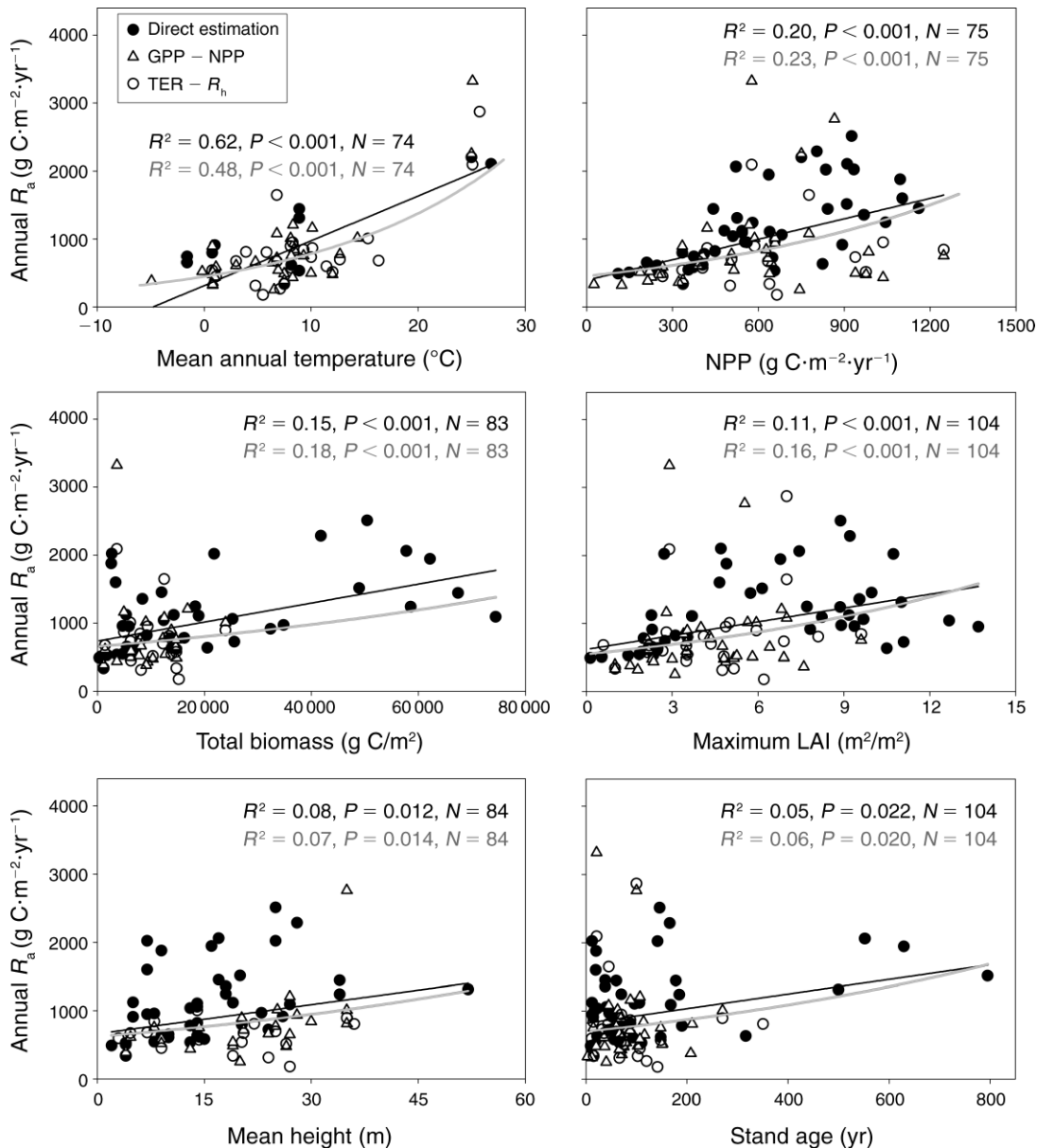


FIG. 1. Spatial relationship of forest autotrophic respiration (R_a) against mean annual temperature (MAT), net primary productivity (NPP), total biomass, maximum leaf area index (LAI), height, and stand age. Black circles indicate direct up-scaled R_a estimates; triangles indicate R_a estimation based on the difference between gross primary productivity (GPP) and NPP, and open circles indicate R_a estimation based on the difference between total ecosystem respiration (TER) and heterotrophic respiration (R_h). The black line shows the linear fit, and the gray line, the exponential fit.

tween forest-stand age and annual R_a across all the data ($R = 0.225, P = 0.022$), the ratio of R_a to biomass decreases with increasing forest-stand age (Fig. 2).

There are significant linear relationships between R_a and MAT for the pooled data ($R = 0.787, P < 0.001$) and for data separated by method ($R = 0.824, P < 0.001$ for direct up-scaled method; $R = 0.784, P < 0.001$ for the method based on GPP - NPP; $R = 0.814, P < 0.001$ for the method based on TER - R_h). These correlations are much stronger than those of R_a with biotic factors. This result not only suggests that temperature is the dominant

factor controlling spatial patterns of R_a at global scale, but also implies that temperature-variation-caused R_m may be the key factor driving spatial patterns of forest annual R_a at global scale. Thus, an accurate parameterization of the temperature sensitivity of R_m is particularly important for realistic prediction of forest R_a .

Statistical approach for predicting R_a

Table 1 presents the values of different parameters estimated by least-squares regression analysis. Due to the limited number of sites where R_a , NPP, total

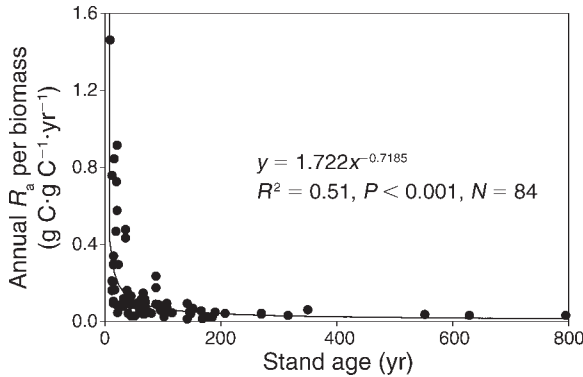


FIG. 2. The relationship between forest annual autotrophic respiration (R_a) per biomass and stand age.

biomass, LAI, and MAT are all available ($n = 6$), we did not perform regression analysis for R_a measured by the direct up-scaled method. The results of F tests show that there is a significant difference in the regression obtained for the indirect methods based on the GPP – NPP and TER – R_h when maximum LAI is an independent variable ($P = 0.031$). In contrast, when total biomass is an independent variable, we did not find a statistically significant difference of R_a estimates between GPP – NPP and TER – R_h methods ($P = 0.275$).

As shown in Table 1, the estimated value of cc is ~ 0 for both GPP – NPP and TER – R_h method estimated R_a , while the values of E_0 and β estimated by GPP – NPP method ($E_0 = 66840$, $\beta = 1900$ for the regression with total biomass as an independent variable; $E_0 = 65496$, $\beta = 1904$ for the regression with maximum LAI as an independent variable) are higher than those by TER – R_h method ($E_0 = 54274$, $\beta = 1262$ for the regression with total biomass as an independent variable; $E_0 = 48048$, $\beta = 1202$ for the regression with maximum LAI as an independent variable). This result implies that R_m estimated by the GPP – NPP method has a higher sensitivity to MAT than when estimated by the TER – R_h method (Table 1). Overall, across all sites, a 10°C increase in MAT results in an increase in annual R_m by a factor of 2.09–2.52 and 1.86–2.17 when total

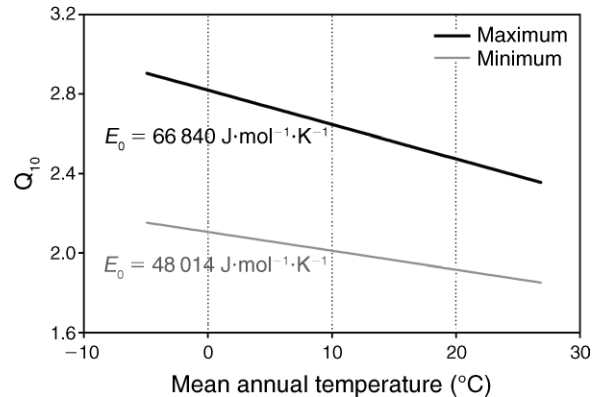


FIG. 3. Change in the sensitivity of forest annual autotrophic respiration to temperature (Q_{10}) in response to rising mean annual temperature estimated by a modified Arrhenius equation (Table 1). The sensitivity of respiration to temperature is higher for low than for high mean annual temperatures.

biomass and maximum LAI is an independent variable, respectively (Table 1). The modified Arrhenius equation also shows that across a MAT gradient going from -5°C to 27°C , the sensitivity of R_m to MAT decreases by ~ 17 – 20% (Fig. 3).

Spatial patterns of the ratio of R_a to GPP

Fig. 4 describes the change in the ratio of R_a to GPP as a function of MAT. Our results suggest that the R_a to GPP ratio decreases with increasing MAT when MAT is below a threshold of $\sim 11^\circ\text{C}$, but then increases when MAT reaches above this value. This result implies that the fraction of total assimilation lost into R_a is the lowest in temperate regions with MAT close to 11°C . The threshold temperatures derived from three different R_a estimation methods are also very close (11.8°C for directly up-scaled; 10.3°C for the estimation based on GPP–NPP; and 10.8°C when based on TER – R_h).

In order to investigate the effect of forest age on the ratio of forest R_a to GPP, we performed correlation analysis between the forest R_a to GPP ratio and age. As shown in Fig. 5A, the ratio of R_a to GPP is not significantly correlated with age across all forest sites

TABLE 1. Parameters of a statistical approach for predicting forest annual autotrophic respiration, R_a , using annual mean temperature and total biomass or maximum leaf area index (LAI) as independent variables.

Methods	B	α	β	E_0	Q_{10}	cc	R^2	n
All	biomass	0.2	1574.6	57 234	2.1–2.5	0.01	0.57	49
	LAI	0.2	1433.2	48 015	1.9–2.2	0.00	0.63	59
GPP – NPP	biomass	0.2	1900.7	66 840	2.4–2.9	0.00	0.74	23
	LAI	0.2	1904.4	65 496	2.3–2.9	0.00	0.74	34
TER – R_h	biomass	0.3	1261.6	54 274	2.0–2.4	0.00	0.53	17
	LAI	0.2	1202.4	48 048	1.9–2.2	0.06	0.68	19

Notes: Autotrophic respiration is calculated as $R_a = \alpha \times \text{NPP} + \beta \times e^{\{(E_0/\text{gc}) \times [(1/293) - (1/T)]\}} \times B^{cc}$, where NPP is forest annual net primary productivity, B is total biomass (g C/m^2) or maximum LAI, T is annual mean temperature in K, gc is the gas constant ($8.314 \text{ J}\cdot\text{mol}^{-1}\cdot\text{K}^{-1}$), and α , β , E_0 (parameter related to the activation energy, $\text{J}\cdot\text{mol}^{-1}\cdot\text{K}^{-1}$) and cc are regression parameters, Q_{10} is the multiplier by which respiration rates increase for a 10°C increase in temperature, and n is the number of samples. GPP – NPP is gross primary production – net primary production. TER – R_h is total ecosystem respiration – heterotrophic respiration.

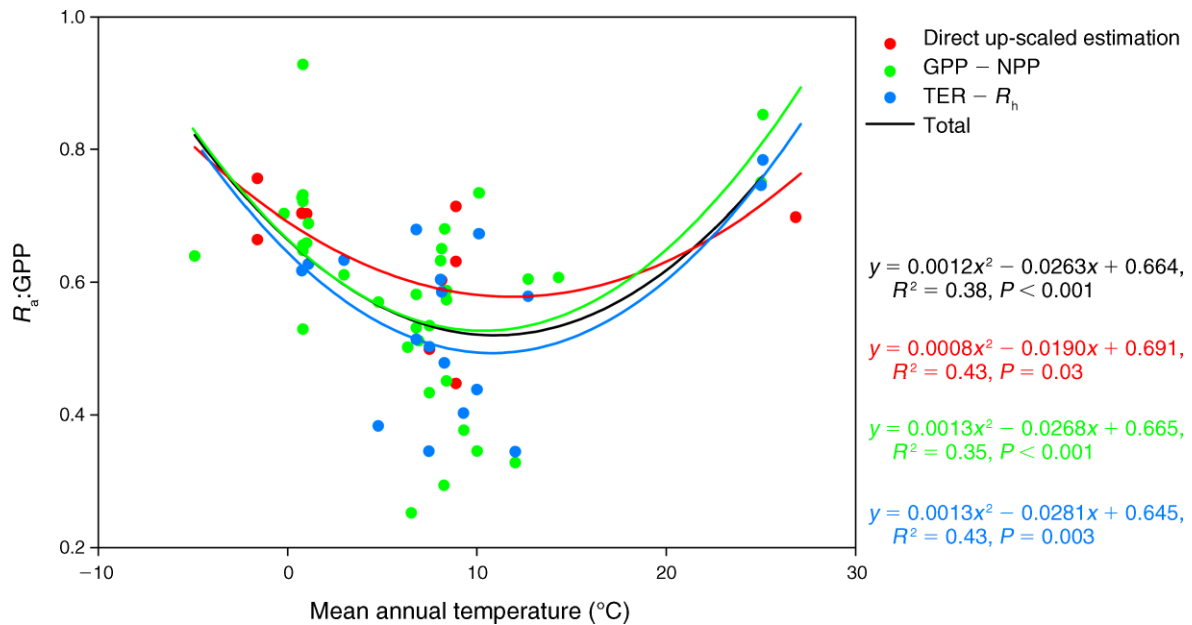


FIG. 4. Change in the ratio of forest annual autotrophic respiration (R_a) to gross primary productivity (GPP) with temperature change. Red circles indicate direct up-scaled R_a estimates, green circles indicate R_a estimation based on the difference between GPP and net primary productivity (NPP), and blue circles indicate R_a estimation based on the difference between total ecosystem respiration (TER) and heterotrophic respiration (R_h).

($R^2 = 0.01$, $P = 0.422$), suggesting that the effects of forest age on the ratio of R_a to GPP is not strong enough to be observable at the global scale. Further analysis, however, suggests that the R_a to GPP ratio tends to significantly increase in response to increase in forest age when only considering the sites with MAT between 8° and 12°C ($R_a/\text{GPP} = 0.0006 \times \text{age} + 0.4484$; $R^2 = 0.25$, $P = 0.017$; or $R_a/\text{GPP} = 0.208 \times \log(\text{age}) + 0.1215$; $R^2 = 0.33$, $P = 0.005$) (Fig. 5B). This result implies that the substantial variation in the ratio of R_a to GPP at moderate MAT between 8° and 12°C shown in Fig. 4 may be related to forest age, supporting the conclusion of DeLucia et al. (2008) who found that forest carbon-use efficiency (CUE, or $1 - R_a/\text{GPP}$) strongly decreases with stand age.

DISCUSSION

Effects of temperature

Temperature is one of the key environmental factors that regulate biological processes (Davidson and Janssens 2006, Piao et al. 2008). The sensitivity of R_a to temperature changes is often described as a Q_{10} function (van't Hoff 1898). Our analysis of a forest carbon-flux database compiled by Luyssaert et al. (2007) suggests that at the global scale, the overall Q_{10} value of forest annual R_a varies from 1.8 to 2.9 (Table 1), which falls into the range reported in the previous studies (Ryan et al. 1997, Tjoelker et al. 2001) and was expected based on first principles (Davidson and Janssens 2006). It has also been suggested that plant respiration sensitivity to temperature often declines with rising

temperature because of so-called acclimation (King et al. 2006), although the magnitude of reduction in Q_{10} value in response to rising temperature remains unclear. Based on analyzing Q_{10} values for 238 records of foliar respiration data, Tjoelker et al. (2001) reported that a 1°C increase in mean ambient (instantaneous or daily) temperature may reduce the Q_{10} value by 0.04, which is about two to four times the slope of the regression line between forest annual R_a and MAT estimated from our analysis using a modified Arrhenius equation (reduction of 0.01–0.02°C) (Fig. 3). The difference in the slope of Q_{10} vs. temperature between our study and Tjoelker et al. (2001) may be due to the different approaches used in these two studies. Tjoelker et al. (2001) investigated the change of Q_{10} in response to temperature where the Q_{10} values were derived from seasonal variation in ambient daily temperatures and corresponding respiration for each site. Therefore, the temperature sensitivity of R_a in the study of Tjoelker et al. (2001) is related to the short-term (i.e., instantaneous) temporal response of respiration to temperature. Our analysis, however, is based on the spatial relationship between forest annual R_a and temperature (Table 1), and thus rather may be interpreted as a reflection of the long-term responses of respiration to temperature (Lauenroth and Sala 1992, Jobbagy et al. 2002). Due to the temperature acclimation of respiration, the sensitivity of respiration to temperature changes at long-term scale may be lower than that at short-term scale (Tjoelker et al. 2008).

Forest growth and its response to climate change are dependent on the balance between photosynthesis and

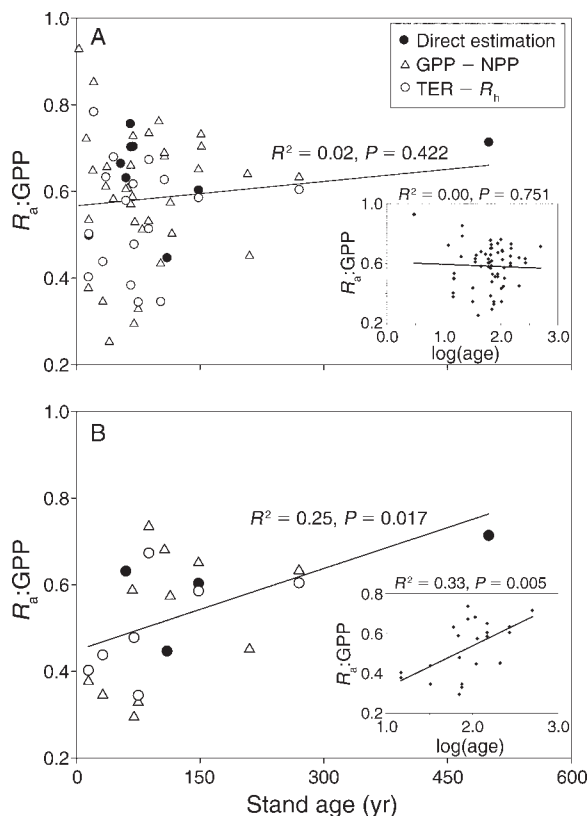


FIG. 5. The relationship between ratio of forest annual autotrophic respiration (R_a) to gross primary productivity (GPP) and stand age across (A) all forest sites and (B) the sites with mean annual temperature (MAT) between 8° and 12°C.

plant respiration. Previous studies suggested that R_a is generally more sensitive to rising temperature than GPP (Ryan 1991), implying that rising temperature may cause an increase in fraction of R_a vs. GPP (Woodwell 1990). However, little direct evidence on this phenomenon has been reported. We found that the R_a to GPP ratio decreases with MAT when MAT is below ~11°C, suggesting that the fraction of forest annual respiration cost in total assimilation is higher in cold regions than in warm regions when MAT is lower than ~11°C. In cold areas (i.e., MAT < 10°C), forest growth is limited by a short growing-season length, and rising MAT usually is accompanied by extension of growing season, which may cause a significant increase in vegetation GPP (Piao et al. 2007) but a limited cost of increasing autotrophic respiration because of respiration acclimation (Atkin 2008, Maseyk et al. 2008). Due to the lack of phenology information for each site, it is difficult to quantify the effect of phenology on the R_a to GPP ratio, hence, this issue requires more attention in future research. When MAT is higher than ~11°C, the R_a to GPP ratio increases with increasing MAT, indicating that R_a is more sensitive to temperature than GPP despite the presence of acclimation of plant respiration to temperature (Dewar et al. 1999). This may be related to the fact

that the soil moisture deficit due to higher evapotranspiration demand at warmer MAT may partially cancel out the positive effect of temperature on vegetation growth through increased photosynthesis and extended growing season length (Piao et al. 2006). The nonlinear response of the R_a to GPP ratio to temperature also implies that forest carbon-use efficiency (CUE, $1 - R_a/GPP$) is nonlinear, with the highest CUE at ~11°C. It should be noted that there are very limited observation data from subtropical and tropical regions, which may cause uncertainty in the estimation of the temperature threshold. In order to check to what extent the four tropical sites at the highest mean annual temperatures drive the relationship, we performed regression analysis by removing these four sites. The results show that, after removal of these tropical sites, the R_a to GPP ratio still responds nonlinearly to temperature change ($R^2 = 0.27$, $P < 0.001$). However, the MAT corresponding to the minimum value of the R_a to GPP ratio shifted from 11° to 16°C; this temperature range may be interpreted as an uncertainty surrounding the threshold of MAT. To reduce uncertainty, more observation data across land surface, particularly from subtropical and tropical regions are needed.

Our knowledge of the processes that govern the terrestrial carbon fluxes is materialized in numerical models of the biosphere. Numerous models of the carbon-climate coupled system have suggested that changes of terrestrial carbon cycle associated with global warming will have a positive feedback to atmospheric CO₂ concentration and global climate; but model results differ in magnitude and sometimes even in direction (Cox et al. 2000, Friedlingstein et al. 2006). Thus, it has been a challenge to accurately predict potential vegetation growth and terrestrial carbon balance in response to future changing climate regimes using current global carbon cycle models. One of the central questions of carbon-climate interactions is how plant R_a responds to climate changes (Luo 2007). Most models share a common structure that the effect of temperature on plant R_a is often reflected by a Q_{10} function or a modified Arrhenius equation, and thus different models have different R_a sensitivity to temperature (Ruimy et al. 1996). For example, Q_{10} was set at 2.0 in TEM (Terrestrial Ecosystem Model) from Melillo et al. (1993), while it was described by a modified Arrhenius equation in LPJ model (Lund-Potsdam-Jena) from Sitch et al. (2003). Since the projection of future terrestrial carbon cycle and its feedback to climate change largely depends on the simulation results from these models, it is very critical to evaluate model performance in terms of temperature sensitivity of forest R_a against observation data. Until recently, however, forest R_a has not generally received much attention in these modeling studies or in the publications describing the studies. For example, recently published comparisons of forest biogeochemistry models (Morales et al. 2005) did not specify how forest R_a was treated in the models. Fig. 6 shows how

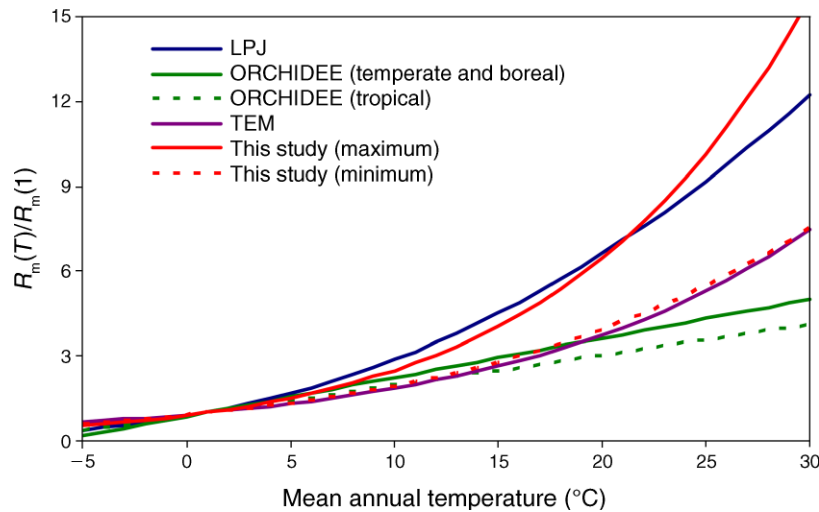


FIG. 6. Change in the ratio of maintenance respiration (R_m) at temperature T to that at 1°C with rising temperature derived from data used in different ecosystem models (TEM [Melillo et al. 1993], ORCHIDEE [Krinner et al. 2005], LPJ [Sitch et al. 2003]). Max and Min indicate the maximum and minimum value of $R_m(T):R_m(1)$ ratios derived from Table 1.

the ratio of R_a at temperature T ($^\circ\text{C}$) to that at 1°C changes with rising temperature in different models. The $R_a(T):R_a(1)$ ratios in LPJ model are close to the maximum estimate of this study, while those in TEM model and ORCHIDEE model (ORganizing Carbon and Hydrology In Dynamic Ecosystems; Krinner et al. 2005) are similar to the minimum value derived by this study. When temperature is larger than $\sim 15^\circ\text{C}$, ORCHIDEE from Krinner et al. (2005) underestimated the $R_a(T):R_a(1)$ ratios. This may be one of the reasons why in the recent DGVMII intercomparison of Sitch et al. (2008), the LPJ model shows a higher positive feedback of terrestrial carbon cycle to warming than does ORCHIDEE model, although the subroutine of vegetation dynamics of these two models is similar. This result highlights the importance of precise description of the R_a sensitivity to temperature change.

Metabolic theory and its application in forest ecosystem

Diverse fundamental characteristics of animals and plants, such as physiological, morphological, and allometric attributes, are expected to scale with body mass, as described with power functions (Brown et al. 2004, Hedin 2006, Reich et al. 2006, Enquist et al. 2007). Our results show that the relationship of forest annual R_a against total biomass is not constant across different methods used to derive R_a . For example, the direct up-scaled R_a significantly correlated with a power function of forest total biomass ($R^2 = 0.30$, $P < 0.001$), while R_a estimated from either gross primary productivity – net primary productivity (GPP – NPP) or total ecosystem respiration – heterotrophic respiration (TER – R_h) is not significantly correlated with forest total biomass with either linear or power functions ($P > 0.05$). This result implies that the previous metabolic theory formulated at the individual level may not hold at the

at the ecosystem level. Most direct up-scaled R_a estimations were based on measurements of individual organisms, while R_a estimation using both GPP – NPP and TER – R_h is from ecosystems composed of many individuals. Thus it is possible that the sum of nonlinear relationships at the individual level becomes linear or nonlinear with a different shape at the ecosystem level, or even that there are no significant correlations between these two variables at the ecosystem level as observed from R_a estimation based on GPP – NPP and TER – R_h in this study.

In addition, for mature trees, some parts of total biomass are occupied by heartwood, which does not perform metabolism. In other words, not whole biomass, but only living biomass consumes carbon through autotrophic respiration. The ratio of heartwood biomass to total biomass may vary among different forest types and environmental conditions. This theoretical consideration leads us to speculate that the amount of living biomass but not total biomass should be the best predictor of tree metabolic rate. Although a significant correlation between forest total biomass and R_m based on the direct up-scaled R_a estimation and 0.2 of α (coefficient of growth respiration) is observed ($R_m = 124.35 \times \text{Biomass}^{0.2093}$; $R^2 = 0.28$, $P < 0.001$), the coefficient of the power function (0.21) is much smaller than that expected by previous studies (0.75 or 1; Gillooly et al. 2001, Brown et al. 2004, Reich et al. 2006). Furthermore, there is a significant positive relationship between total mass-corrected annual R_a (the ratio of R_a to the three-quarter power of total biomass) and MAT across all the sites ($R = 0.55$, $P < 0.001$), which does not support the hypothesis of Enquist et al. (2007). The latter suggested that mass-corrected autotrophic biomass production is invariant with respect to latitude or growing season temperature.

CONCLUSIONS

Our study showed that forest annual R_a increases with an increase in MAT across large spatial scales. However, it is difficult to speculate whether future global warming will lead to enhanced carbon loss from forest ecosystems, because the response of R_a :GPP ratio varies with changes in temperature. In response to increasing mean annual temperature, the R_a :GPP ratio decreases when MAT is below $\sim 11^\circ\text{C}$, and then increases for higher MAT. Therefore, our analysis does not support the notion that R_a is generally more sensitive to rising temperature than GPP (Woodwell et al. 1990, Ryan 1991) or that the respiration : photosynthesis ratio would be insensitive to temperature (Arnone and Körner 1997, Enquist et al. 2007).

While our global quantification of temperature effects on forest R_a will help predict future changes in carbon cycle processes and vegetation growth, there are a few points that deserve further study. First, our analysis did not consider the effects of nitrogen (N) on forest annual R_a . There is substantial evidence for universal relations between respiration and N in higher plants (Reich et al. 2006). Thus, future studies are needed to quantify the effects of N on the global patterns of forest annual carbon cost of R_a . Second, analysis on forest R_a should be extended to different tree organs including leaf, stem, and root (Ryan et al. 1997). What fractions of the total R_a are the respiration of leaf, stem, and root? Does R_a for each tree organ show similar temperature sensitivity? Third, the acclimation of forest R_a to rising temperature should be explored in greater detail. For example, do different forest tissues or forests with different ages show a similar decreasing trend in sensitivity of forest R_a to temperature in response to global warming? What is the mechanism of this phenomenon? Finally, although the simple empirical statistical approach developed in this work should benefit our understanding and projection of forest annual R_a , future modeling tests against new long-term ecosystem experimental data sets are necessary.

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