

## Forest annual carbon cost: comment

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Understanding the relative influence of abiotic and biotic forces on ecosystem-level processes across broad scale remains a central question in global ecology (Schimel et al. 1996, Chapin et al. 1997, Kerkhoff et al. 2005). In their report, Piao et al. (2010) addressed how global-scale variation in annual terrestrial autotrophic respiration,  $R_a$ , varies across broad-scale gradients including temperature, biomass, and successional age. In addition, they purported to test several predictions and observations from metabolic scaling theory, MST (West et al. 1997) on how temperature and autotrophic biomass influence rates of ecosystem metabolism and production (Enquist et al. 2007b).

While I agree with Piao et al.'s emphasis on the need to assess variation in ecosystem processes across broad gradients, I question their methodology for comparing and standardizing rates of ecosystem production and disagree with their reading of MST. Issues of how to standardize flux measures in order to compare annual and instantaneous rates across sites are not just specific to Piao et al.'s study. These issues also apply to other studies assessing spatial variation in ecosystem metabolism across broad spatial gradients (for example, see Beer et al. 2010) and are central to how we understand and quantify the relative influence of abiotic and biotic forces on the ecosystem-level processes across broad-scale gradients as well as how to use cross-site analyses to inform predictions for a warming world.

There are four specific issues that can influence Piao et al.'s central conclusions:

1. *Piao et al.'s methodology for comparing fluxes between sites is likely biased, because they did not correct for differences in growing season length or properly control for the scaling effects of biomass on ecosystem metabolism.*—Piao et al. observed that the annual respiration of forests increased with temperature. Piao et al. also claimed that this finding is in contrast to the

findings of Enquist et al. (2007b). However, one cannot compare these two studies because Piao et al.'s methodology does not follow that of Enquist et al. Specifically, Kerkhoff et al. (2005) and Enquist et al. (2007a) argued that in order to mechanistically assess the role of temperature on more instantaneous rates of ecosystem metabolism it is important to also correct for tree biomass *and* growing season length. Enquist et al. showed that these corrected rates of tree growth showed little to no signal with *growing* season temperature.

There are several reasons why studies that use annual measures to compare differing sites in order to infer how climate influences ecosystem performance will be biased. By using annual temperature, the actual temperature under which most of the flux occurs will increasingly be underestimated for colder sites because biological activity is greatly reduced so that the flux is effectively “off” during the dormant season (see also Savage 2004). Next, any relationship between a rate, like autotrophic respiration, and some environmental attribute such as temperature depends on the timescale of measurement (see also discussion in Mahecha et al. 2010). Annual ecosystem fluxes, such as net productivity or respiration, are measured by summing more instantaneous measures throughout the year. Rates of ecosystem respiration are tightly coupled to rates of gross primary production (see Vargas et al. 2010). Similarly, the annual carbon balance of a site is constrained by the length of time autotrophs have to assimilate carbon during the year (Cannell and Thornley 2000, Vargas et al. 2010, Berdanier and Klein, *in press*). As a result, annual respiration measures will be limited by the gross production that occurs during the length of the growing season. The use of annual fluxes can underestimate instantaneous rate measures, especially when one does not account for the (sometimes appreciable) dormant season length (Chapin 2003, Allen et al. 2005, Kikuzawa and Lechowicz 2006). From these points, both the fluxes and temperatures of the colder sites used by Piao et al. will be underestimated by using annual values. Thus, the use of annual measures to assess physiologically based models, even one as simple as MST, will not be applicable. As a result, the methodology used by Piao et al. does not provide a strong assessment of physiologically based models such as MST, which focus on the controls on more instantaneous rates, and its application to the carbon balance of forests.

To highlight the above issues I assessed growing season length and compiled ecosystem data across a similar temperature gradient presented by Piao et al. Across a broad latitudinal and temperature gradient, the length of the growing season changes (Fig. 1). Growing seasons vary from 12 months to as little as 4 months or

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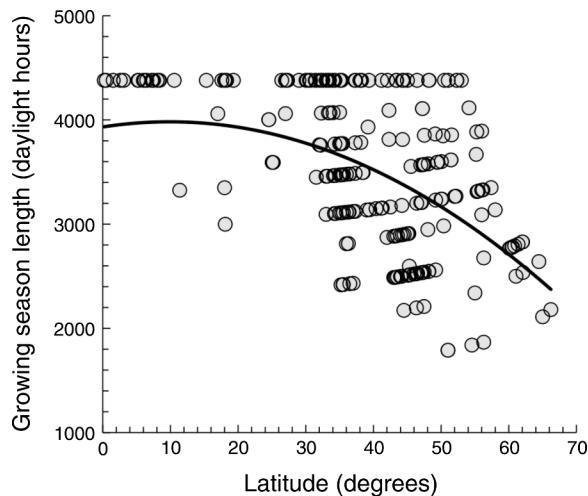


FIG. 1. Change in growing season length (number of daylight hours) as a function of absolute latitude. Sites are from Cannell (1982), and methodology for calculating growing season length for each site is reported in Kerkhoff et al. (2005). There is a significant negative and curvilinear relationship showing that higher-latitude sites have a lower number of daylight hours by which to photosynthesize and produce biomass. Because respiration is closely tied to rates of carbon assimilation (Cannell and Thornley 2000, Vargas et al. 2010), variation in growing season length will influence their annual measures. The fitted function is a second-order polynomial ( $y = -0.2508x^2 - 14.791x + 4538.8$ ;  $r^2 = 0.30604$ ;  $P < 0.0001$ ).

less (Table 1, Fig. 1). Further, the mean annual temperature is tightly correlated with growing season length (Fig. 2a). Thus, Piao et al.'s central finding, a correlation between mean annual temperature and annual respiration, may be spurious and instead driven by changes in growing season length. Importantly, the relationship between growing season temperature, a

more biologically meaningful measure of temperature, and growing season length shows a weaker correlation (Fig. 2B). As expected, Fig. 2B shows that the actual temperature under which the uptake of carbon during the year occurs is underestimated in colder sites. The problem presented by these data is that when sites are characterized by similar instantaneous rates of respiration (or other physiological rates; see Table 1) but differ in terms of the growing season length, then comparison of these sites will yield differences in annual rates (see also Mahecha et al. 2010, Berdanier and Klein, *in press*). Similarly, comparing two sites that are alike in terms of physiological responses to the environment but who differ in their biomass will also yield differences in ecosystem performance because ecosystem flux and standing stocks of carbon and nutrients will scale with total leaf mass (or area) and biomass (Kerkhoff and Enquist 2006, West et al. 2009). Because Piao et al. are looking over vast gradients, not correcting for growing season length and differences in the total amount of biomass (i.e., leaf area) will inject a bias because of changes in the timescale and differences in photosynthesizing and respiring biomass (Table 1).

2. *Piao et al.'s reading of metabolic scaling theory (MST) is not correct.*—Piao et al. also secondarily assess the influence of autotrophic biomass on ecosystem annual respiration,  $R_a$ , by testing the scaling of biomass and  $R_a$ . They purported to test the prediction from MST for this power function relationship. Specifically, they concluded that “the coefficient of the power function (0.21) was much smaller than that expected from previous studies (0.75 or 1).” In other words, Piao et al. claimed that MST predicts that rates of ecosystem production will scale with total ecosystem biomass,  $M_{Tot}$ , to the 0.75 power (see West et al. 1997, Enquist et al. 1998, Savage et al. 2010) or the 1.0 power as

TABLE 1. Data from Chapin (2003) showing that ecosystem measures are sensitive to the time and size scales of measurement.

Biome	Annual NPP ( $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ )	Growing season length (d)	Daily NPP per ground area ( $\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ )†	Total LAI ( $\text{m}^2/\text{m}^2$ )	Daily NPP per leaf area ( $\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ )‡
Tropical forests	2500	365	6.8	6.0	1.14
Temperate forests	1550	250	6.2	6.0	1.03
Boreal forests	380	150	2.5	3.5	0.72
Mediterranean shrublands	1000	200	5.0	2.0	2.50
Tropical savannas and grasslands	1080	200	5.4	5.0	1.08
Temperate grasslands	750	150	5.0	3.5	1.43
Deserts	250	100	2.5	1.0	2.50
Arctic tundra	180	100	1.8	1.0	1.80
Crops	610	200	3.1	4.0	0.76
Range of values	14-fold	3–7-fold	3–8-fold	6-fold	3.3-fold

Notes: Here ecosystem flux (net primary production, NPP) varies 14-fold across biomes on an annual time scale. However, these differences are largely driven by differences in growing season length and plant size (larger plants will correspond with increases in the leaf area index, LAI). Thus, more instantaneous rates obtained from correcting for growing season length and LAI collapses most of the differences in annual rates between high latitude and low latitude sites (in both forests and grasslands). Of note, tropical and temperate biomes, which have significant differences in annual rates of production, are remarkably similar when production is measured on a mass-corrected and more instantaneous time scale.

† Correcting for growing season length.

‡ Correcting for biomass differences.

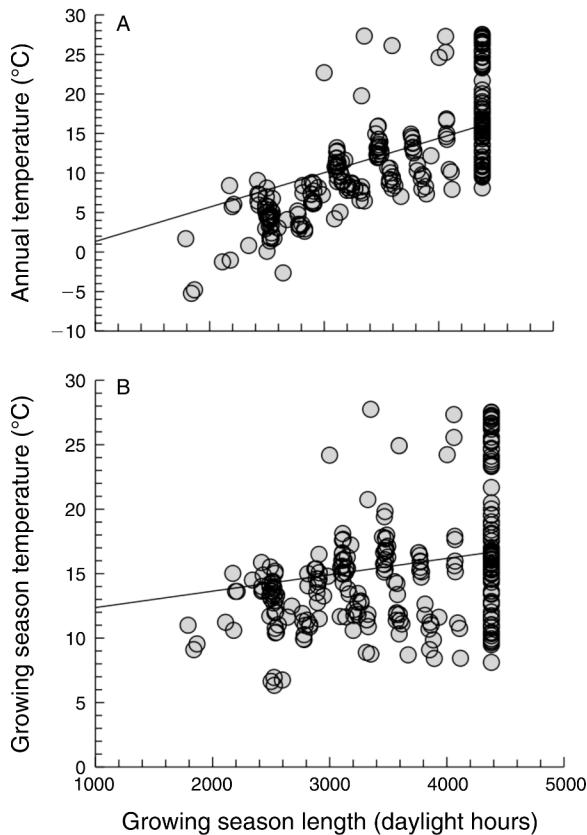


FIG. 2. Change in mean annual temperature ( $^{\circ}\text{C}$ ) with growing season length (number of daylight hours). There is a significant positive relationship between growing season length and mean annual temperature ( $r^2 = 0.608$ ,  $P < 0.0001$ ). Thus, for increasingly colder sites, the use of mean annual temperature will increasingly underestimate the temperature during biologically active periods. Indeed, in panel B, we see that the correlation with growing season temperature is much weaker ( $r^2 = 0.182$ ,  $P < 0.001$ ). Together, these results indicate that the use of annual mean temperature can poorly reflect temperatures during times when carbon is assimilated (see also Savage 2004).

empirically claimed by Reich et al. (2006). However, the scaling exponent that they use, 0.75, is for the idealized scaling of rates of *individual-level* tree growth,  $dM/dt$  with individual tree size,  $M$  (Enquist 2002). Piao et al. incorrectly apply these individual-level scaling predictions (0.75 or 1.0) with an *ecosystem-level* scaling relationship. They investigate the scaling of total stand production,  $dM_{\text{Tot}}/dt$ , and total stand biomass,  $M_{\text{Tot}}$ , where  $M_{\text{Tot}} = \Sigma M$ . Now, MST does makes predictions for the scaling of  $dM_{\text{Tot}}/dt$  with  $M_{\text{Tot}}$  (Enquist et al. 2009, West et al. 2009) but this stand-level prediction for forests at resource steady state was not cited by Piao et al. Further, the predicted stand exponent from MST is different from the scaling exponent for the scaling of individual-tree production. For entire stands, MST predicts (Enquist et al. 2009) that instantaneous rates

of autotrophic respiration across all individual plants,  $R_{\text{Tot}}$ , and their total net production,  $dM_{\text{Tot}}/dt$ , are proportional to each other and will scale isometrically with the total ecosystem leaf mass,  $M_{\text{Tot}}^L$ , but to the 3/5 power of autotrophic biomass,  $M_{\text{Tot}}$  as

$$R_{\text{Tot}} \propto \frac{dM_{\text{Tot}}}{dt} \propto M_{\text{Tot}}^L \propto M_{\text{Tot}}^{3/5}.$$

If heterotrophic respiration is proportional to autotrophic respiration, then this equation should also hold for entire ecosystems. In sum, the expected ecosystem autotrophic allometry from MST,  $R_{\text{Tot}} \propto M_{\text{Tot}}^{3/5}$  is indeed closer to Piao et al.'s observation.

Piao et al.'s reported scaling exponent is sensitive to the type of regression model used. They used Model I ordinary least squares (OLS) regression to estimate their fitted exponent, which was 0.21 ( $r^2 = 0.28$ ). However, because of the likely error structure in their data, Model II regression is likely a more appropriate scaling model (Warton et al. 2006). Piao et al.'s OLS slope corresponds to a model II (reduced major axis regression, RMA) slope of 0.40. This RMA exponent is indeed close to the predicted 3/5 exponent from MST (Enquist et al. 2009). While Piao et al. did not report confidence intervals for their analysis, they would likely be quite large (due to the  $r^2$  value). So, without analysis of confidence intervals for the RMA regression as well as not properly correcting annual  $R_a$  values for growing season length (see 1. Piao et al.'s methodology for comparing fluxes... above) one cannot fully assess their scaling findings and assess predictions from MST. Interestingly, Piao et al. also cite a scaling exponent of 1.0 as one of the expected scaling relationships. However, again, this is an individual-level scaling exponent and an exponent of 1.0 is only expected for very small plants (seedlings) (Enquist et al. 2007a) but will change from 1.0 to approximately 0.75 for trees larger than seedlings (Mori et al. 2010).

3. Piao et al.'s methodology for calculating mass-corrected fluxes is also likely biased, due to an apparent incorrect understanding of how to correct for biomass differences between sites.—Correcting rates of production for differences in organismal size or biomass is important because the mass-specific rate of production depends upon the amount of biomass present (e.g., biological rates scale allometrically [Gillooly et al. 2001]). Piao et al. incorrectly mass corrected their  $R_a$  fluxes. They divided the annual  $R_a$  flux by the whole-stand biomass,  $M_{\text{Tot}}$  raised to the 0.75 power or  $R_a/(M_{\text{Tot}}^{0.75})$ . The issue is that they mass corrected their *stand-level* mass correction by using an *individual tree-level* scaling allometry. Because metabolism and production will scale differently at the stand and individual level ( $\sim 3/4$  vs.  $3/5$ ), one cannot compare results from Piao et al. and Enquist et al. (2007b). If the goal is to assess if measures *stand biomass* corrected rates of respiration are influenced by temperature then they should have divided stand respiration by stand biomass

raised to the 0.40 power (the empirically determined RMA scaling exponent for stands) instead of the 0.75 power (the scaling exponent for individual trees). So, I anticipate that, if Piao et al. would correct for the growing season length *and* properly mass correct their rates of respiration or production, then they will likely find that growing season temperature has little influence on more instantaneous rates of ecosystem physiology and production.

4. *There are several additional methodological issues that question the values of the estimated flux values reported by Piao et al.*—In particular, their methods for estimating  $R_a$  may not be comparable. Piao et al. use a fixed temperature function to correct for temperature differences across sites. In doing so, they assume that the Arrhenius-type temperature function governing how respiration changes with temperature is the same for all sites. This effectively assumes that temperature acclimation and adaptation of metabolism has negligible effects on ecosystem metabolism: a questionable assumption (as discussed in Kerkhoff et al. 2005, Enquist et al. 2007b). Further, the  $R_a$  estimates from eddy flux may likely be larger than chamber-based measurements. This is because the eddy flux estimate is derived assuming that foliar respiration during the day is the same as it would be at night, corrected for temperature. Chamber-based estimates may not include an estimate of dark respiration in the light for foliage in either foliage respiration or GPP because of problems with measurement and interpretation.

Comparative measures of ecosystem fluxes across broad-scale gradients are desperately needed in order to develop a more quantitative understanding to how biology responds to climate change and for understanding the role of biology within the integrated earth system. Piao et al.'s study is important as they attempt to assess large-scale variation in ecosystem performance across geographic gradients. However, in order to compare fluxes in biology, one must put measurements on the same dimensional scale. The central issues are (1) how to best compare fluxes between sites when sites that differ in growing season length and biomass and (2) how to assess predictions of scaling models based upon instantaneous rates by using annual rate measures. Piao et al. conclude that their "results show that the spatial patterns of forest annual  $R_a$  at the global scale are largely controlled by temperature." Enquist et al. (2007b) concluded that temperature had little to no effect on *instantaneous* plant growth once annual measures controlled for growing season length (see also Kerkhoff et al. 2005). I suggest that Piao et al.'s central findings stem from an incorrect methodology for standardizing for biomass (allometric) and growing season effects on ecosystem flux. In short, their reported correlations between temperature and annual flux are likely spurious. In contrast to Piao et al. (see also Beer et

al. 2010), across broad geographic gradients, differences in annual ecosystem metabolism appear to be primarily driven by differences in growing season length and differences in autotrophic biomass (Chapin 2003, Kerkhoff et al. 2005, Enquist et al. 2007b).

Careful assessment of theory that attempts to scale from leaf to ecosystem is needed. This is especially true in the case of metabolic scaling theory where careful empirical assessment of its assumptions simultaneous with assessments of core and secondary predictions has remained relatively rare (Niklas 2004, Savage et al. 2010). Analyses of global-scale variation in rates of terrestrial respiration and production (Kerkhoff et al. 2005, Enquist et al. 2007b) that correct for biomass *and* growing season length are at odds with the conclusions of Piao et al. and largely support the conclusions of Chapin (2003) who stated that when ecosystem rates are "normalized by growing season length and the quantity of leaf area to fix carbon (i.e., biomass), there is no consistent relationship between (instantaneous measures of ecosystem production) and climate."

My colleagues and I (Kerkhoff et al. 2005, Enquist 2007, Enquist et al. 2007b) have hypothesized that the approximate independence of instantaneous ecosystem- and individual plant-level rates across temperature gradients (see the daily NPP values in Table 1) originate from how biology responds to broad-scale differences in temperature and growing season length. In particular, physiological temperature *acclimation* and *adaptation*, as well as how species *assemble* within and across communities (what we have called the three A's of biotic feedback [Enquist 2007, Enquist et al. 2007b]) has resulted in the approximate constancy of instantaneous mass-corrected rates with temperature. This approximate constancy reflects the powerful role of compensatory adaptive and ecological responses to changes in temperature.

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## Forest annual carbon cost: reply

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In our report (Piao et al. 2010), we found that forest annual autotrophic respiration ( $R_a$ ) varies largely over the global scale; the difference in MAT (mean annual temperature) can explain about 60% of the cross-site  $R_a$  spatial gradients. Enquist (2011) challenged our finding by suggesting that  $R_a$  could be invariant with temperature after being standardized against growing season length (GSL) and a power function of mass. While Enquist (2011) is right in outlining the complexity of data harmonization for forest autotrophic respiration across a broad geography range, he may have over-

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looked some complexity of autotrophic respiration processes in forest ecosystems. A normalization of annual  $R_a$  against GSL is too simple because (1)  $R_a$  and temperature both fluctuate during the growing season and the relationship between them is nonlinear (Paembonan et al. 1992, Ryan et al. 1997) and (2) maintenance  $R_a$  exists during the non-growing season (Paembonan et al. 1992, Ryan et al. 1997, Zha et al. 2004). On the other hand, across sites at the global scale, the impact of temperature on forest annual  $R_a$  occurs not only directly through changes in instantaneous metabolism rates of respiratory biomass, but also could be indirectly regulated by many other biotic and abiotic processes, such as seasonal dynamics of photosynthesis and nutrient availability, which are strongly coupled with forest annual  $R_a$  as well. Hence, the fundamental role of temperature in determining forest ecosystem annual  $R_a$  as revealed by our data analysis (Piao et al. 2010) can not be dismissed. Below we provide detailed analysis and arguments why temperature is a critical factor controlling the variation of forest  $R_a$  over a larger scale, while addressing the specific issues raised by Enquist (2011).

1. *Spatial variation of forest annual  $R_a$  at the global scale is more responsive to temperature rather than to growing season length.*—Enquist (2011) first questioned our methodology of data harmonization for inter-site comparison and he suggested to normalize forest annual  $R_a$  against GSL and to control the scaling effect of biomass. He further conjectured that if  $R_a$  is normalized by GSL and biomass scaling effects are properly accounted for, then forest ecosystem  $R_a$  could be invariant across temperature gradient. We will first discuss the impact of GSL in this section, and the scaling effect of biomass in the next section.

There are many more factors besides those mentioned in our original paper that affect forest ecosystem  $R_a$ , and analyzing  $R_a$  in relationship to GSL is a welcome suggestion. In order to test if the spatial variance of forest  $R_a$  is dependent on GSL more than on than temperature, we perform a partial correlation analyses between mean annual temperature (MAT), GSL, and forest annual  $R_a$ . Instead of temperature-defined GSL used in Enquist (2011), here GSL information for each forest site is extracted from remote-sensing phenology observations produced by the MODIS Global Vegetation Phenology (*available online*).<sup>7</sup> The GSL of tropical evergreen forest is assumed to be 365 days. Fig. 1 illustrates the relationship between annual  $R_a$  and GSL or MAT across the 59 forests where both GSL and MAT data are available. Partial correlation analyses suggest that, when the effect of MAT is controlled for,  $R_a$  is not significantly correlated with GSL (partial correlation coefficient  $r' = 0.03$ ,  $P = 0.799$ ). In contrast,

<sup>7</sup> [https://lpdaac.usgs.gov/lpdaac/products/modis\\_products\\_table/land\\_cover/dynamics\\_yearly\\_l3\\_global\\_1km/mod12q2](https://lpdaac.usgs.gov/lpdaac/products/modis_products_table/land_cover/dynamics_yearly_l3_global_1km/mod12q2)

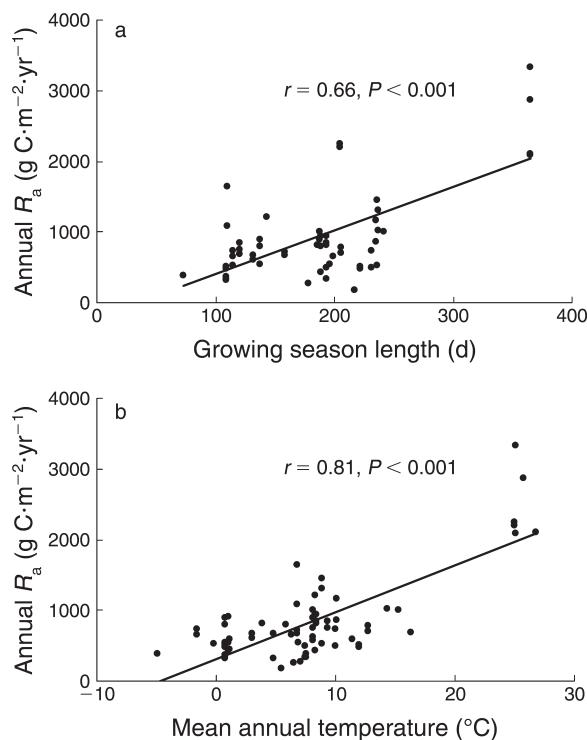


FIG. 1. Relationships between forest annual autotrophic respiration ( $R_a$ ) and (a) growing season length (GSL) and (b) mean annual temperature (MAT) across 59 sites where both GSL and MAT are available. While significant correlations are found between  $R_a$  and GSL and between  $R_a$  and MAT with ordinal corrections, partial correlation analyses show that  $R_a$  is not significantly correlated with GSL ( $r = 0.03$ ,  $P = 0.799$ ) when MAT is controlled. In contrast, the significant and positive correlation between annual  $R_a$  and MAT is not affected by the covariation with GSL ( $r = 0.61$ ,  $P < 0.001$ ).

covariation with GSL has little impact on the significant and positive correlation between annual  $R_a$  and MAT ( $r' = 0.61$ ,  $P < 0.001$ ). Therefore, the claim by Enquist (2011) that “Piao et al.’s central finding, a correlation between mean annual temperature and annual respiration, may be spurious and instead driven by changes in growing season length” is unwarranted. Instead, this additional study suggests that GSL is not a dominant factor controlling spatial patterns of  $R_a$  across the sites. Furthermore, one must keep in mind that GSL, defined either by temperature thresholds or by phenology observations, is itself highly temperature controlled. For example, Zhang et al. (2004) found that GSL for forest is strongly correlated with variation in MAT across northern mid and high latitudes. In fact, Enquist (2011) admit that “the mean annual temperature is tightly correlated with growing season length.” Yet it is MAT that controls the GSL, and not the reverse. Hence, we confirm that forest annual  $R_a$  across a broad geographic range is controlled by MAT rather than GSL, the significant positive covariance between forest

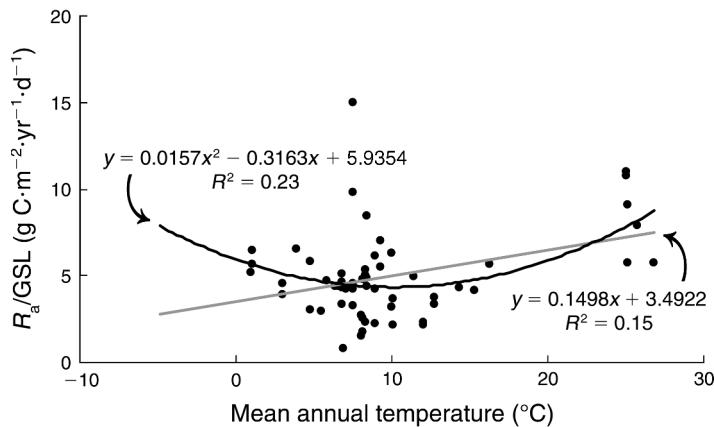


FIG. 2. The relationship between the ratio of forest annual  $R_a$  to growing season length (GSL) and mean annual temperature. GSL-normalized annual  $R_a$  is significantly correlated with temperature ( $P < 0.05$ ).

annual  $R_a$  and GSL being mainly an indirect result from the covariance between MAT and GSL.

Enquist (2011) further hypothesized that annual  $R_a$  corrected by GSL may be not related to temperature, and provided as an example a NPP comparison at biome scale in their Table 1. But our data oppositely give evidence for a clear dependency of GSL-standardized annual  $R_a$  to temperature ( $P < 0.05$ ; Fig. 2). Nevertheless, one can not simply normalize annual NPP or  $R_a$  by evenly dividing it by GSL, since even during the duration of growing season, both carbon flux and temperature are still variable and the relationship between carbon flux and temperature is nonlinear (Paembonan et al. 1992, Ryan et al. 1997, Zha et al. 2004). For example, Zha et al. (2004) found that seasonal change in stem  $R_a$  responds exponentially, rather than linearly, to corresponding temperature change. This is a good illustration of the fact that local-scale instantaneous forest  $R_a$  changes with temperature, which is in contrast to Enquist's claim that "growing season temperature has little influence on more instantaneous rates of ecosystem physiology and production." The nonlinearity between  $R_a$  and temperature were ignored by Enquist in his comment.

It should also be noted that annual  $R_a$  is not just a fraction of plant photosynthesis during the GSL. As mentioned in Piao et al. (2010),  $R_a$  is made up by two components: growth or construction respiration ( $R_g$ ) and maintenance respiration ( $R_m$ ). During the non-growing season, although  $R_g$  equals to 0,  $R_m$  is maintained (Paembonan et al. 1992, Ryan et al. 1997, Zha et al. 2004), since it still requires some maintenance respiration to keep a tree alive. Hence, there is no "dormant" season from the perspective of autotrophic respiration, and normalizing annual  $R_a$  by GSL may overestimate normalized  $R_a$  in high latitudes. Furthermore, the magnitude of  $R_m$  during the non-growing season is still temperature dependent (Ryan et al. 1995), and thus one can not ignore the role of temperature over the non-growing season when studying forest annual  $R_a$ .

The comment of Enquist (2011) also shows the change in daylight hours with latitude. Again, here, daily  $R_a$  is not equal to daytime  $R_a$ , since  $R_a$  occurs not only in the day, but also in the night.

2. *Biomass as a predictor of forest ecosystem annual  $R_a$ : the explanatory power and the metabolism scaling.*—Enquist (2011) also hypothesized that annual  $R_a$  should be "properly corrected" against the scaling effect of biomass, the so-called metabolism scaling theory (MST). He makes two predictions here. First, the power coefficient of forest total biomass against  $R_a$  estimation from our database should lie close to a value of 3/5 predicted by their recent study (Enquist et al. 2009) published after the submission of Piao et al. (2010). Second, forest  $R_a$  corrected "properly" using a 3/5 (or 0.4 derived from the RMA regression from our data set) power function of biomass should be invariant with temperature. Here we test and discuss these two predictions.

First, while we did discuss the application of individual-plant-derived MST to ecosystem metabolism in Piao et al. (2010), the main purpose of our study was to test if stand biomass, as well as other biotic and abiotic factors, is a good predictor of forest annual  $R_a$  on a broad scale. We found that stand biomass is a weak predictor of forest annual  $R_a$  (Piao et al. 2010). At the ecosystem scale, we found that  $R_a$  estimates based on both  $GPP - NPP$  and  $TER - R_h$  (total ecosystem respiration - heterotrophic respiration) are not significantly correlated with forest total biomass ( $P > 0.05$ ) with either a linear or a power function (Piao et al. 2010).

Second, Enquist claims that "Piao et al.'s reading of metabolic scaling theory (MST) is not correct" by speculating that "Piao et al. claimed that MST predicts that rates of ecosystem production will scale with total ecosystem biomass,  $M_{Tot}$ , to the 0.75 power or the 1.0 power." However, this speculation is not correct. While we did mention in the abstract of our original paper that "at the plant level, the coefficient of the power function

(0.21) was much smaller than that expected from previous studies (0.75 or 1),” we did not make any claim of MST prediction at the ecosystem level. Rather, by fitting a power function between forest annual  $R_a$  and stand biomass, we sought to test “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” (Piao et al. 2010:653). And our results indeed confirmed that previous individual-based MST was not suitable for forest-ecosystem-level metabolism. As discussed in Piao et al. (2010), unlike animals or tree saplings, bigger trees contain larger amounts of heartwood, which does not respire. Therefore, one can not simply use total biomass as a proxy for living biomass to predict metabolic rates, even of individual trees, especially when the ratio of heartwood biomass to total biomass varies largely among different forest types and environmental conditions. Moreover, the sum of power law relationships at the individual tree level does not necessary to keep the same shape at the ecosystem level.

We now test if the power coefficient of forest total biomass against  $R_a$  estimation from our database is close to a value of 3/5 predicted by their recent study (Enquist et al. 2009). Because of the uncertainties of the power coefficient of forest total biomass against respiration, we perform both type I regression and type II regression (RMA regression) between total biomass and  $R_m$  based on the direct up-scaled  $R_a$  estimation and a 0.2 coefficient of growth respiration (Piao et al. 2010). We estimate the confidence limits of the power coefficient by bootstrapping with 1000 samples (Manly 2007). We find that, although type II regression estimates exhibit higher power coefficients ( $0.395 \pm 0.048$  [mean  $\pm$  SD]) than estimates by type I regression ( $0.209 \pm 0.058$ ), the power coefficients of both methods are significantly smaller than 0.6 ( $P < 0.001$  and  $P < 0.001$ , respectively), the value predicted by Enquist et al. (2009). In fact, not a single bootstrap sample yields a power coefficient larger than or equal to 0.6, which does not support Enquist (2011)’s claim that “the expected ecosystem autotrophic allometry from MST,  $R_{Tot} \propto M_{Tot}^{3/5}$  is indeed closer to Piao et al.’s observation.”

Finally, we test here Enquist’s null hypothesis that  $R_a$  “properly corrected” using a 3/5 (or 0.4 derived from the RMA regression from our data set) power function of biomass could be invariant with temperature. We find a statistically significant positive relationship remaining between annual  $R_a$  and MAT across the sites ( $r = 0.59$ ,  $P < 0.001$  for 3/5, and  $r = 0.62$ ,  $P < 0.001$  for 0.4, respectively). And hence this null hypothesis is not verified by our data.

3. *Other issues.*—Enquist (2011) also raised several other minor issues in his comment, and here we will address the concern of temperature acclimation and adaptation effect. Enquist claimed that we have assumed

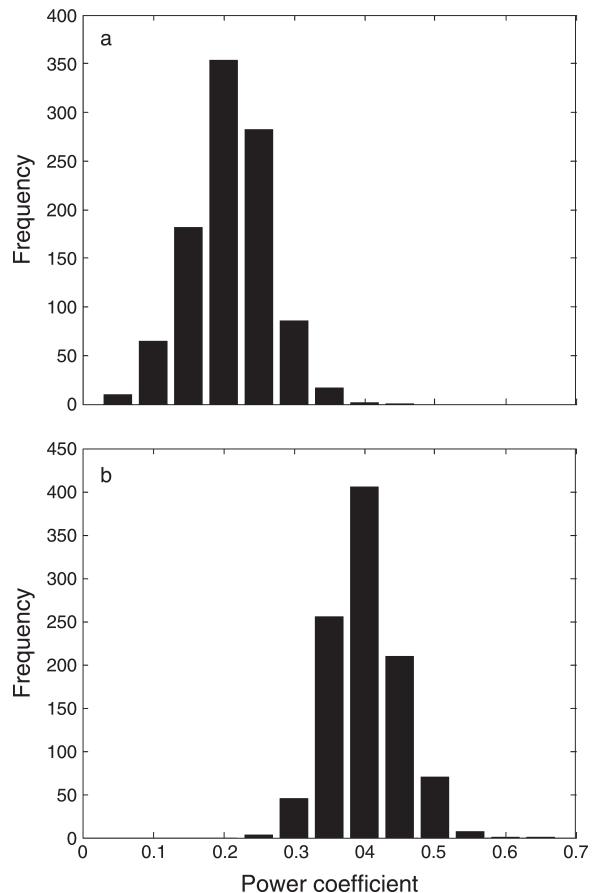


FIG. 3. Frequency distribution of the power coefficient of forest autotrophic respiration ( $R_a$ ) against total stand biomass estimated by (a) Type I and (b) Type II regressions of 1000 bootstrap samples. Maintenance respiration (metabolic cost of maintaining a plant in a living state; one component of  $R_a$ ) is calculated using the direct up-scaled  $R_a$  estimation and a 0.2 coefficient of growth respiration.

“temperature acclimation and adaptation of metabolism has negligible effects on ecosystem metabolism.” We agree with Enquist (2011) that temperature acclimation and adaptation is important in evaluating the effect of temperature on forest  $R_a$ , and we did not assume it negligible as claimed by Enquist (2011). In fact, in Piao et al. (2010), we clearly stated that “temperature sensitivity of  $R_m$ ...declines with rising temperature,” and mentioned that “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.” In Fig. 3 of Piao et al. (2010), we also clearly demonstrated that how the sensitivity of forest annual  $R_a$  to temperature ( $Q_{10}$ ) changes in response to rising MAT.

In summary, Enquist (2011) suggests using GSL and a specific power function of mass for normalization of  $R_a$ . However, autotrophic respiration is not restricted to the

growing season and is temperature dependent both within and beyond the growing season. Using GSL as a normalizer therefore lacks a sound ecological basis. Nevertheless, we applied his two suggestions to our data set but find that they do not provide explanative power for spatial variations of  $R_a$ . Hence, the conclusion of Piao et al. (2010), that the spatial distribution of forest annual  $R_a$  is closely linked with temperature at the global scale, is again confirmed with the additional analyses.

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