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Global patterns and predictors of stem CO_2 efflux in forest ecosystems

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Abstract

Stem CO_2 efflux (E_S) plays an important role in the carbon balance of forest ecosystems. However, its primary controls at the global scale are poorly understood and observation-based global estimates are lacking. We synthesized data from 121 published studies across global forest ecosystems and examined the relationships between annual E_S and biotic and abiotic factors at individual, biome, and global scales, and developed a global gridded estimate of annual E_S. We tested the following hypotheses: (1) Leaf area index (LAI) will be highly correlated with annual E_S at biome and global scales; (2) there will be parallel patterns in stem and root CO_2 effluxes (R_A) in all forests; (3) annual E_S will decline with forest age; and (4) LAI coupled with mean annual temperature (MAT) and mean annual precipitation (MAP) will be sufficient to predict annual E_S across forests in different regions. Positive linear relationships were found between E_S and LAI, as well as gross primary production (GPP), net primary production (NPP), wood NPP, soil CO_2 efflux (R_S), and R_A. Annual E_S was correlated with R_A in temperate forests after controlling for GPP and MAT, suggesting other additional factors contributed to the relationship. Annual E_S tended to decrease with stand age. Leaf area index, MAT and MAP, predicted 74% of variation in E_S at global scales. Our statistical model estimated a global annual E_S of 6.7 ± 1.1 Pg C yr^{-1} over the period of 2000–2012 with little interannual variability. Modeled mean annual E_S was 71 ± 43, 270 ± 103, and 420 ± 134 g C m^2 yr^{-1} for boreal, temperate, and tropical forests, respectively. We recommend that future studies report E_S at a standardized constant temperature, incorporate more manipulative treatments, such as fertilization and drought, and whenever possible, simultaneously measure both aboveground and belowground CO_2 fluxes.

Keywords: gross primary production, leaf area index, respiration, root CO_2 efflux, stem CO_2 efflux

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Introduction

Stem CO_2 efflux (E_S), the diffusion of CO_2 from plant stems to the atmosphere, is an important component in regional and global carbon cycles (Bowman *et al.*, 2008). Historically, E_S was considered a direct measure of stem respiration as it was assumed that E_S represented the respiratory activity of local phloem, cambium, and ray cells (MacDougal & Working, 1933; Eklund, 1990; Cernusak & Marshall, 2000); however, it is now accepted that it also incorporates some of the respiratory activity of cells located below the point of measurement, including those of roots (Teskey *et al.*, 2008; Aubrey & Teskey, 2009; Powers & Marshall, 2011; Angert *et al.*, 2012). It has been suggested that E_S accounts for 11–23% and 40–57% of the carbon assimilated in temperate and tropical forests, respectively (Ryan *et al.*, 1995; Chambers *et al.*, 2004). Unlike other components of ecosystem respiration, such as soil CO_2 efflux (R_S) (Bond-Lamberty & Thomson, 2010), we are not aware of any observation-based analysis of global patterns and estimates of E_S. Moreover, E_S remains poorly represented in current ecosystem models, where the contribution of E_S was either not explicitly considered (e.g., Terrestrial Ecosystem Model, Raich *et al.*, 1991; Zhuang *et al.*, 2003; He *et al.*, 2013) or was simply described as a temperature modulated ratio of base maintenance respiration (e.g., Community Land Model, Bonan *et al.*, 2013). Despite its substantial contribution to ecosystem respiration and the global carbon cycle, we lack a comprehensive understanding of the fundamental biotic and abiotic factors controlling E_S across scales.

Plant respiration is often considered to be proportional to, or even a relatively constant fraction of, gross primary production (GPP) (Ryan *et al.*, 1997, 2004; Waring *et al.*, 1998; Gifford, 2003); therefore, the individual

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components of plant respiration, such as E_S and root CO_2 efflux (R_A), should also be closely correlated to GPP and should be controlled by similar biotic and abiotic factors (Litton *et al.*, 2007; Chen *et al.*, 2014). The amount of leaf area and the duration of that leaf area are the strongest biotic controls on GPP (Gower *et al.*, 2001; Duursma *et al.*, 2009). The amount of leaf area is, in turn, controlled by soil resource availability (soil moisture and nutrients), whereas leaf area duration is largely controlled by temperature and soil moisture availability. Thus, biotic and abiotic factors interact to determine GPP, and based on the relationship between GPP and plant respiration, we might expect these factors to control E_S as well. Indeed, E_S was well-correlated with GPP in a Scots pine (*Pinus sylvestris*) plantation (Zha *et al.*, 2004) and across a variety of forest ecosystems (Litton *et al.*, 2007). It would follow that other ecosystem characteristics that are well-correlated with production would also be well-correlated with ecosystem respiration and its components. For example, leaf area index (LAI) is well-correlated with GPP and net primary production (NPP) (Kassnacht & Gower, 1997; Gower *et al.*, 2001; Asner *et al.*, 2003; Bond-Lamberty & Thomson, 2010; Drake *et al.*, 2011) and can be measured or estimated relatively easily through indirect methods. Thus, LAI may serve as a useful predictor of E_S at various spatial scales. Evidence of this was provided by Meir & Grace (2002) and Meir *et al.* (2008) who reported an exponential relationship between LAI and E_S across a small number (<10) of boreal, temperate, and tropical forest stands.

That autotrophic respiration changes with stand age have been explored in many studies (Kira & Shidei, 1967; Odum,1969; Ryan & Waring,1992; Ryan *et al.*, 1997, 2004; DeLucia *et al.*, 2007; Tang *et al.*, 2008, 2014; Piao *et al.*, 2010; Drake *et al.*, 2011). Some studies have reported that respiration increases relative to GPP as stands age (Kira & Shidei, 1967; DeLucia *et al.*, 2007). Other studies have found that autotrophic respiration does not increase substantially with stand age (Tang *et al.*, 2008), or that it decreases with age in stands after canopy closure (Ryan & Waring, 1992; Ryan *et al.*, 1997, 2004; Piao *et al.*, 2010; Drake *et al.*, 2011; Tang *et al.*, 2014). Therefore, we may expect that E_S will also decrease with forest age.

Here, we examine the relationships between annual E_S and biotic and abiotic factors at multiple scales – stands, biomes, and globally and provide an observation-based global gridded estimate of annual E_S to test the following hypotheses: (1) LAI will be highly correlated with annual E_S at biome and global scales; (2) there will be parallel patterns in stem and root CO_2 effluxes in all forests; and (3) annual E_S will decline with forest age; and (4) LAI coupled with mean annual temperature (MAT) and mean annual precipitation (MAP) will be sufficient to predict annual E_S across forests in different regions.

Materials and methods

Data sources

We searched Google Scholar (Google Inc., Mountain View, CA, USA) and Web of Science (Thomson Reuters, formerly Web of Knowledge) to identify relevant journal articles published before September 20, 2015. Our search terms included 'stem CO_2 efflux', 'stem respiration', 'woody tissue respiration', 'wood CO_2 efflux', and 'woody tissue efflux'. We also included 'ecosystem respiration', 'carbon balance', 'net ecosystem productivity', and 'net ecosystem exchange' to identify journal articles reporting annual E_S. Those journal articles reporting E_S measurements at individual tree, stand, or ecosystem level were then screened to insure they included at least three of the following: (1) E_S measurements made by infrared gas analyzer; (2) annual E_S based on ground surface area; (3) mean seasonal E_S; (4) mean E_S normalized to a standard temperature; (5) Q_{10}; and (6) stand arithmetic mean tree stem diameter (DBH) or individual tree DBH. In addition, the following variables were extracted from the literature when reported: mean annual temperature (MAT), mean annual precipitation (MAP), gross primary production (GPP), net primary production (NPP), aboveground wood NPP, ecosystem respiration (R_{eco}), annual soil CO_2 efflux (R_S), annual root CO_2 efflux (R_A), annual foliar CO_2 efflux, annual ecosystem respiration, elevation, stand age, leaf area index (LAI), basal area (BA, i.e., the cross-sectional area of all stems per unit land area), stand arithmetic mean DBH, individual tree DBH, Q_{10}, species, sapwood nitrogen content, normalized E_S at different temperatures, and sapwood density. If MAT and MAP were not provided, we obtained similar data from the Climatic Research Unit (CRU TS v. 3.21) (Harris *et al.*, 2014).

We constructed a database consisting of 121 papers representing 104 study sites across the globe that were published from 1992 to 2015 and reported data from 1986 to 2014. Many of the articles reported data from multiple years, multiple sites, or different experimental treatments, and we treated each of these as a discrete record in the database. In total, there were 372 data entries mainly from North America, Europe, East Asia, and South America, but there were also a few sites in Africa, Australia, and New Zealand (Fig. 1). Datasets were classified into boreal, temperate, and tropical forest biomes based on the literature descriptions (see Table S2 for detailed site information). Reported estimates of GPP, NPP, and R_{eco} used different methods and included different components (Table S2). We limited our analysis to studies that reported information that could be used to reconstruct consistent and comparable measures of GPP, NPP, and R_{eco}. Specifically, our GPP calculation included the biomass increment of leaf, branch, stem, coarse roots, and fine roots, and autotrophic respiration of leaf, woody tissue, and root or rhizospheric respiration. We included both the aboveground increment components and belowground components (i.e., fine roots

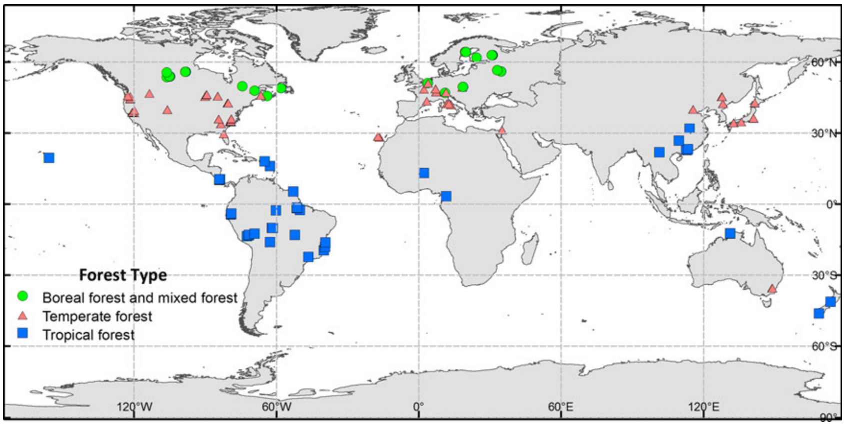

Fig. 1 Locations of the study sites used in this synthesis.

and coarse roots) to calculate NPP. Although various methods were used to estimate fine root NPP, we limited our analysis to studies that employed the ingrowth core approach. Coarse root NPP relied on allometric equations. Most of the data used in the analysis came from natural or un-manipulated forests or plantations; however, managed forests and plantations, including stands that had been fertilized, irrigated, thinned, or had competing vegetation controlled, were also included. Data from manipulative experimental studies were also included (e.g., increased atmospheric O_3, elevated atmospheric CO_2, soil and air warming, pruning, girdling, and throughfall reduction). When no treatment effects were detected between the control and the manipulated groups, we used the mean across groups to represent the entire forest. When treatment effects were detected between the control and manipulated groups, we used only the mean of the control group to represent the forest.

Statistical data analysis

In several studies, annual E_S was not derived from direct measurement, but from calculations based on biomass, temperature, and the fixed ratio of the construction cost of NPP. We included the calculated annual E_S and their proportion of GPP, NPP, and ecosystem respiration in Table S1 to broaden the information about E_S research, but did not include these values in our regression analyses. The values derived from calculations were similar to direct measurements with the exception of those from tropical forests. All measured data were tested for normality and homoscedasticity. If either assumption was violated, data were log-transformed before analysis. Although each year in a study was considered a separate record, mean values were used for studies that reported annual E_S from one site over multiple years.

Ideally, it would be preferable to use stepwise backward selection to quantitatively examine the effects of individual biotic and abiotic variables on E_S. However, there was a limited subset of data ($n < 18$) that included all variables of interest. Therefore, we used linear regression to examine the effect of individual biotic and abiotic factors on E_S and multiple linear regression to estimate global E_S. Initial data analysis for the global E_S estimate indicated that all variables passed the χ^2 goodness-of-fit test ($P > 0.05$) for normality except for GPP, R_S, and MAP. In particular, MAP was severely left skewed. A $\log_{10}$ transformation enabled all three variables to pass the normality test ($P > 0.05$); thus, we applied that transformation in all subsequent analyses. To eliminate the effects of GPP and temperature on the relationship between E_S and R_S and R_A, we calculated partial correlations between E_S and R_S, and E_S and R_A.

We compared 9 multiple linear regression models for predicting global E_S (Table 2). Outliers were excluded based on residual analysis, and residuals were checked for normality and homoscedasticity. We selected the best model for predicting global total Es from the nine candidate models based on model performance (adj-R^2 and RMSE; AICc was not discriminating adequately due to different sample sizes), spatial data availability, and the number of observations. The model we selected included MAT, MAP, and LAI as predictors and had a reasonable performance with adj-R^2 of 0.74 and RMSE of 62.1 g C m^2 yr^{-1}. The variance inflation factor did not detect multicollinearity for independent variables at a tolerance level of 0.2 (Table 2).

Spatial extrapolation

For global E_S estimation, we extracted forest land cover information from the Moderate Resolution Imaging Spectroradiometer (MODIS) land cover product (MCD12C1) for the period of 2000–2012. The original 0.05°×0.05° (longitude × latitude) resolution grid was aggregated to 0.5°×0.5° by majority vote method. The percentage cover of each forest type was aggregated by mean for each grid cell to calculate the percent area of total forest cover. Climate data (MAT, MAP) during the same period were extracted from CRU TS 3.21 (Harris *et al.*, 2014) at 0.5°×0.5° resolution. LAI data were extracted from reprocessed MODIS collection 5 data (MOD15A2) with 30″ resolution used in Yuan *et al.* (2011) for 2000–2009. LAI for 2010–2012 was based on MCD15A2 (LAI/FPAR 8-day L3 Global 1 km SIN grid V005) downloaded from LDAAC database (https://lpdaac.usgs.gov/). All LAI data were aggregated to 0.5° × 0.5° by calculating the mean. To be consistent with the field reported LAI which is normally measured during the growing season, and to avoid the interference of understory vegetation (Serbin *et al.*, 2013), we used the peak monthly LAI to represent the LAI for the growing season of each grid cell.

The 95% confidence interval of the mean predicted E_S at each grid cell was calculated based on the least-squares method where the response variable follows Student's t-distribution with confidence level at $(1-\alpha)$ being $y_0 \pm t_{n-p,\frac{\alpha}{2}}\sqrt{\sigma^2(x_0^T(X^TX)^{-1}x_0)}$, where y_0 is the mean predicted E_S, $t_{n-p,\frac{\alpha}{2}}$ is the upper $\alpha/2$ critical value of Student's t-distribution with n-p degrees of freedom, σ^2 is the estimate of error variance, x_0 is the predictor, and X is the design matrix.

Results

Mean annual E_S in different forest biomes and effects of abiotic factors

Annual E_S was lowest in boreal forests and highest in tropical forests (Table 1). The contribution of E_S to ecosystem respiration was ≤ 15% in boreal and temperate forests and approximately 27% in tropical forests. The proportion of GPP accounted for by E_S was larger in tropical and temperate forests than in boreal forests. A similar pattern was observed in the ratio of E_S to NPP. Annual E_S was positively related to both MAT and MAP in all three biomes (Fig. 2). Mean annual temperature explained slightly more variation of annual E_S than MAP ($R^2 = 0.30$ vs. 0.25). For every 1 °C increase in MAT, annual E_S increased by 14 g C m^2 yr^{-1}, and for every 100 mm increase in MAP, annual E_S increased by 11 g C m^2 yr^{-1}. There was a large amount of variation in annual E_S, MAT and MAP among tropical forests. In tropical forests annual E_S ranged from 103 g C m^2 yr^{-1} to 970 g C m^2 yr^{-1}. While these data include both wet and dry seasonal forests, there was no clear pattern of annual E_S between those forest types. Similar annual E_S was observed in temperate and tropical forests when they were compared at similar levels of MAT or MAP. The annual or growing season apparent Q_{10} (change in E_S per 10°C increase in temperature) of E_S varied from 1.0 to 4.7 across different forests (Fig. S1). The modal Q_{10} of E_S ranged from 1.5 to 2.0 with overall arithmetic mean of 2.23. The mean Q_{10} of E_S derived from boreal, temperate, and tropical forests were (mean ± SD) 1.93 ± 0.33, 2.36 ± 0.84, and 2.17 ± 0.45, respectively. The Q_{10} of E_S in boreal forests was significantly lower than in temperate forests ($P < 0.05$). The apparent Q_{10} in boreal forests was positively related to both MAT and stand mean DBH, whereas no such relationship was observed in temperate or tropical forests (Fig. S2).

Effects of biotic factors on annual E_S

Positive linear relationships were observed between annual E_S and LAI, as well as the E_S/GPP ratio and LAI, at the global scale (Fig. 3). The relationship between E_S and LAI held at the biome scale for temperate and boreal forests, but not for tropical forests. At the biome scale, the relationship between E_S and LAI was stronger in boreal than temperate forests ($R^2 = 0.55$ vs. 0.26). Of the three biomes, the relationship between the E_S/GPP ratio and LAI held only for the temperate forest. Annual E_S was positively related to basal area, across all forests (Fig. S3). Annual E_S was positively related to both GPP and NPP globally, and the relationship was stronger with GPP than NPP (Fig. 4, $R^2 = 0.53$ vs. 0. 34). The slope of the linear relationship between annual E_S and GPP was not significantly different among biomes ($P > 0.1$). The amount of variation in annual E_S explained by GPP was highest in temperate forests (60%), intermediate in boreal forests (41%), and lowest in tropical forests (15%). A positive linear relationship was also observed between annual E_S and wood NPP. The slope of the relationship between annual E_S and wood NPP was much lower for tropical than temperate forests (0.22 vs. 0.69), indicating that annual E_S in tropical forests increased less per unit increase in wood NPP than in temperate forests.

Positive linear relationships were observed between annual E_S and belowground carbon fluxes, R_S and R_A, at the global scale (Fig. 5). Similar positive relationships between annual E_S and R_A were observed at the biome scale for tropical and temperate forests, but not for boreal forests. We examined whether the relationship between annual E_S and R_A, and annual E_S and R_S, could be fully explained by GPP or MAT, or both, by performing partial correlation analyses (Fig. 6a–c). The

Table 1 Mean ± SD and ranges (in parentheses) of annual stem CO_2 efflux (E_S) in boreal, temperate, and tropical forest ecosystems. R_{eco} is ecosystem respiration, GPP is gross primary production, and NPP is net primary production. Annual E_S values were derived from infrared gas analyzer measurements and scaled to the stand level using the calculation provided in the original paper

Ecosystem type	Sample size	Annual E_S (g C m^{-2} yr^{-1})	Sample size	E_S/R_{eco} (%)	Sample size	E_S/GPP (%)	Sample size	E_S/NPP (%)
Boreal	24	89 ± 53 (0.8–204)	13	8 ± 4 (1–17)	11	7 ± 2 (2–10)	9	21 ± 10 (9–41)
Temperate	71	248 ± 127 (3.0–620)	28	15 ± 9 (4–38)	31	17 ± 11 (4–45)	27	38 ± 31 (8–57)
Tropical	45	506 ± 262 (103–970)	17	27 ± 9 (8–42)	26	18 ± 7 (7–30)	12	37 ± 15 (25–58)

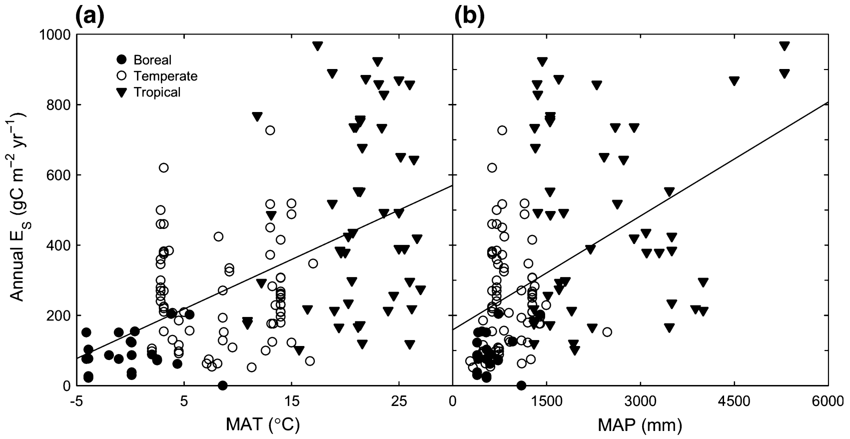

Fig. 2 Relationships between annual stem CO_2 efflux (annual E_S) and (a) mean annual temperature (MAT) and (b) mean annual precipitation (MAP) globally for tropical, temperate, and boreal forests. Annual E_S = 13.90MAT + 144 (n = 140, R^2 = 0.30, $P < 0.001$) and annual E_S = 0.11MAP + 145 (n = 140, R^2 = 0.25, $P < 0.001$).

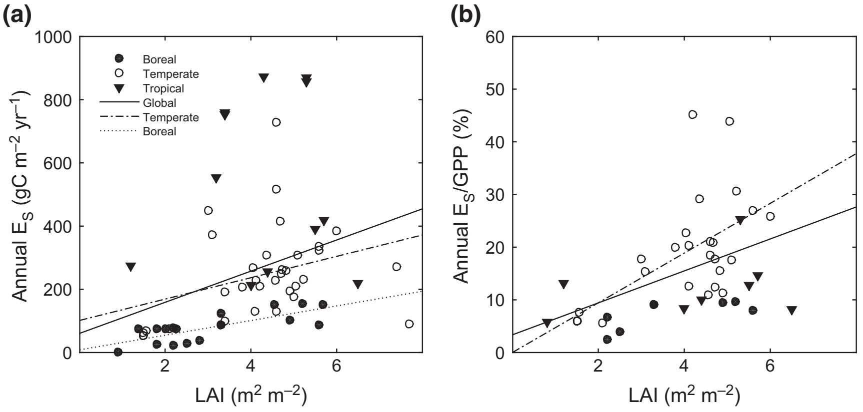

Fig. 3 Relationships between (a) annual stem CO_2 efflux (annual E_S) and leaf area index (LAI) and (b) annual E_S/GPP ratio and LAI. (a) In global forests (boreal, temperate, and tropical combined), annual E_S = 45LAI+ 58 (n = 64, R^2 = 0.36, $P < 0.001$); in boreal forests, annual E_S = 8.41LAI + 23.2 (n = 18, R^2 = 0.55, $P < 0.001$); and in temperate forests, annual E_S = 39.6 LAI + 46.6 (n = 31, R^2 = 0.26, $P < 0.01$). (b) In global forests (boreal, temperate, and tropical combined), annual E_S/GPP = 3.04LAI+ 3.85 (n = 42, R^2 = 0.22, $P < 0.001$), and in temperate forests, annual E_S/GPP = 8.05LAI + 6.35 (n = 26, R^2 = 0.41, $P < 0.001$).

positive relationships between annual E_S and R_A were maintained for temperate and tropical forests after controlling for GPP and MAT, suggesting that additional factors were contributing to the E_S and R_A fluxes. We also examined the relationship between annual E_S and R_S using residuals of GPP and MAT (Fig. S4). For the combined global dataset, and for temperate forests separately, there was a positive relationship after controlling for MAT (but not after controlling for GPP). For the boreal and tropical biomes, GPP and/or MAT explained most of the variation in annual E_S and R_S.

Annual E_S was related to stand age for the combined global dataset, as well as for temperate forests, but not for tropical or boreal forests (Fig. 7a). Annual E_S was highest at young stand ages and appeared to stabilize in stands more than 200 years old, although limited data were available for stands of that age. A pattern was also observed between the normalized E_S at 15°C and individual tree DBH in the temperate forest, but not in tropical or boreal forests (Fig. 7b). In temperate forests, normalized E_S increased with DBH and then decreased at DBH > 20 cm.

Global estimate of annual E_S

Different linear combinations of MAT, MAP, LAI, NPP, R_S, and R_A explained 30% to 84% of the observed variability in annual E_S (Table 2). These variables showed mostly positive correlations with annual E_S across the different models. Models that

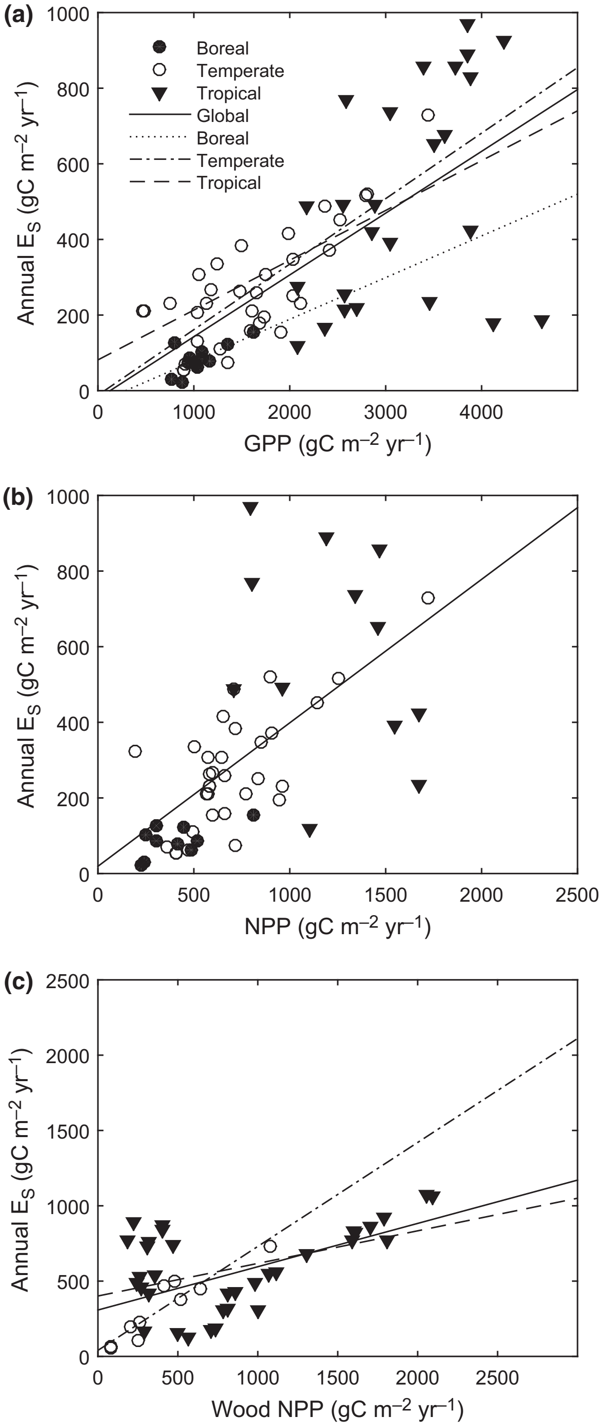

Fig. 4 Relationships between annual stem CO_2 efflux (annual E_S) and (a) gross primary productivity (GPP), (b) net primary productivity (NPP), and (c) wood NPP. For plot (a) in boreal, temperate, and tropical combined, annual $E_S = 0.16GPP - 21$ ($n = 68$, $R^2 = 0.53$, $P < 0.001$). In boreal forest ecosystems, annual $E_S = 0.11GPP - 32$ ($n = 11$, $R^2 = 0.41$, $P < 0.05$); in temperate forests, annual $E_S = 0.17GPP - 12$ ($n = 31$, $R^2 = 0.60$, $P < 0.01$); and in tropical forests, annual $E_S = 0.13GPP + 81$ ($n = 26$, $R^2 = 0.15$, $P < 0.05$). For plot (b), annual $E_S = 0.37NPP + 18$ ($n = 48$, $R^2 = 0.34$, $P < 0.01$). For plot (c) in temperate and tropical forests combined, annual $E_S = 0.29$ wood NPP + 308 ($n = 44$, $R^2 = 0.34$, $P < 0.001$). In temperate forests, annual $E_S = 0.69$ wood NPP + 40 ($n = 10$, $R^2 = 0.86$, $P < 0.001$); and in tropical forests, annual $E_S = 0.22$ wood NPP + 401 ($n = 34$, $R^2 = 0.21$, $P < 0.05$).

included both aboveground (i.e., LAI and NPP) and belowground biotic factors (i.e., R_S and R_A) predicted more than 75% of annual E_S. We selected the model that included MAT, MAP, and LAI to estimate global E_S. Models that included LAI and R_S or R_A were not selected because of a lack of gridded product for R_S and R_A. Our model estimated the highest annual E_S in tropical forests (420 ± 134 g C m^2 yr^{-1}), an intermediate annual E_S in subtropical-warm temperate forests that fall between 20°N and 45°N (270 ± 103 g C m^2 yr^{-1}), and the lowest annual E_S in cool temperate-boreal forests above 45°N (< 210 g C m^2 yr^{-1}) (Fig. 8). The total annual E_S from forest ecosystems across the globe during 2000–2012 was estimated to be 6.7 ± 1.1 Pg C yr^{-1} (95% confidence interval) and exhibited very little interannual variability.

Discussion

Annual E_S and LAI

Supporting our first hypothesis, we found a linear relationship between LAI and annual E_S, and between LAI and E_S/GPP in the global dataset that combined boreal, temperate, and tropical forests. Leaf area index is a critical determinant of forest NPP and GPP. It plays an important role in energy, carbon and water exchanges between forests and the atmosphere, affecting solar radiation interception, photosynthesis, and evapotranspiration (Gower *et al.*, 2001; Asner *et al.*, 2003; Bond-Lamberty & Thomson, 2010; Drake *et al.*, 2011). The linear relationship between E_S/GPP and LAI indicates that the amount of GPP allocated to E_S is proportional to LAI and suggests an underlying relationship between E_S and LAI caused by the quantity of carbohydrates available for growth and respiration. Although we used linear regression to model the relationship between LAI and GPP and LAI and NPP, it is possible that both relationships could become asymptotic after LAI surpasses 5 or 6 (Drake *et al.*, 2011; He *et al.*, 2012); however, there was little data available at LAI >6 in our dataset to confirm it. Among both temperate and tropical forests, there was high degree of variability in the relationship between LAI and annual E_S. We speculate that this may have been due to differences in species,

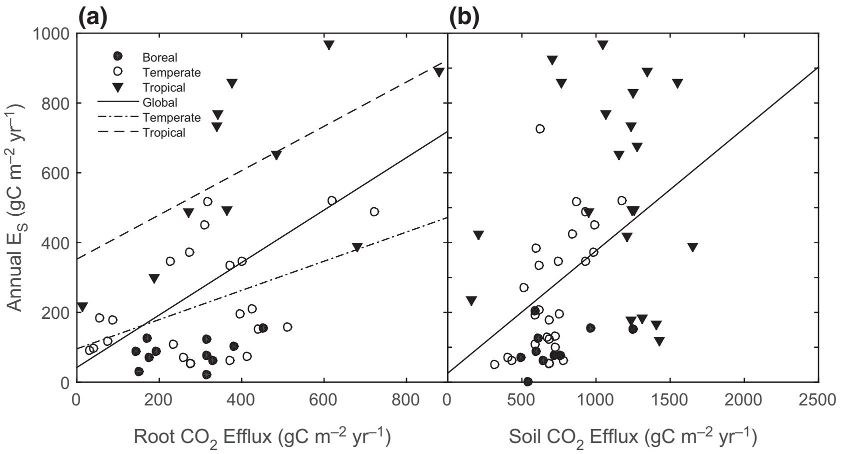

Fig. 5 Relationships between annual E_S and (a) root CO$_2$ efflux (R_A) and (b) soil CO$_2$ efflux (R_S). (a) In forests globally (boreal, temperate, and tropical combined): annual $E_S = 0.75R_A + 42$ ($n = 44$, $R^2 = 0.39$, $P < 0.001$); in temperate forests, annual $E_S = 0.42R_A + 96$ ($n = 22$, $R^2 = 0.42$, $P < 0.001$); and in tropical forests, annual $E_S = 0.63R_A + 352$ ($n = 11$, $R^2 = 0.38$, $P < 0.05$). (b) Annual $E_S = 0.35R_S$ -25 ($n = 60$, $R^2 = 0.21$, $P < 0.001$).

climate, and soils across the geographic range covered by the temperate and tropical forest biomes (Goulden *et al.*, 2011; Gower *et al.*, 1997). An exponential relationship between annual E_S and LAI, and a linear relationship between E_S/GPP and LAI were reported in two studies that combined data from several sites (Meir & Grace, 2002; Meir *et al.*, 2008). However, with our larger dataset, both relationships were linear at the global scale. The difference between our study and the Meir & Grace (2002) and Meir *et al.* (2008) studies may be related to sample size ($n = 64$ vs. $n = 10$).

Annual E_S and R_A

We observed a linear relationship between E_S and R_A which supports our second hypothesis. We propose three possible explanations for this: (1) functional relationships between GPP, E_S and R_A; (2) proportional changes in air and soil temperature; and (3) the upward transport of CO$_2$ derived from root respiration. Regarding the first explanation, if plant respiration is a linearly related to GPP, then the different components of respiration, both aboveground and belowground, should also be proportional to GPP. Litton *et al.* (2007) reported that the E_S as well as total belowground carbon flux (the sum of metabolic fluxes to support root production, root respiration, root exudates, herbivory, and symbionts) increased linearly with GPP. Similarly, E_S was also related to stem wood NPP, and R_A to root NPP, which covary with GPP as well (Litton *et al.*, 2007). Likewise, Chen *et al.* (2014) synthesized data on component fluxes, including R_A, from global forest ecosystems and found that directly measured GPP explained 48% of the variation in R_A across different forest types. Therefore, it would be logical to attribute the relationship between E_S and R_S or R_A to forest productivity.

As to the second explanation, relationships between E_S and stem temperature and between R_A and soil temperature have been observed in many studies. Total autotrophic respiration and R_A were closely related to MAT in forest ecosystems (Piao *et al.*, 2010; Wang *et al.*, 2010). The partial correlation analysis we did indicated that significant correlations between E_S and R_A remained in temperate and tropical forests after controlling for temperature (Fig. 6), which suggested that other factors may play a role, in addition to MAT, in regulating E_S. Also, after we controlled for both GPP and MAT, a weak correlation remained between E_S and R_A in temperate and tropical forests, again suggesting other factors influenced the relationship.

Regarding the third explanation, there has been mounting evidence from different measurement approaches that the CO$_2$ derived from roots can be transported aboveground via the xylem stream, leading to an underestimation of R_A (Teskey & McGuire, 2007; Aubrey & Teskey, 2009; Grossiord *et al.*, 2012; Bloemen *et al.*, 2013, 2014). As our partial correlation analysis based on GPP and MAT could not fully explain the relationship of annual E_S and R_A, we suggest that CO$_2$ transport in the xylem should be considered as an additional source of CO$_2$ contributing to E_S. Although such a mechanism has been mostly described in studies with short-term measurement periods and in forests of a relatively young stand age, it was also implicated in one study of mature temperate forest stands (from 39 to 56 years old) (Yang *et al.*, 2012) and could be an additional factor contributing to the variation in E_S and R_A observed in our study.

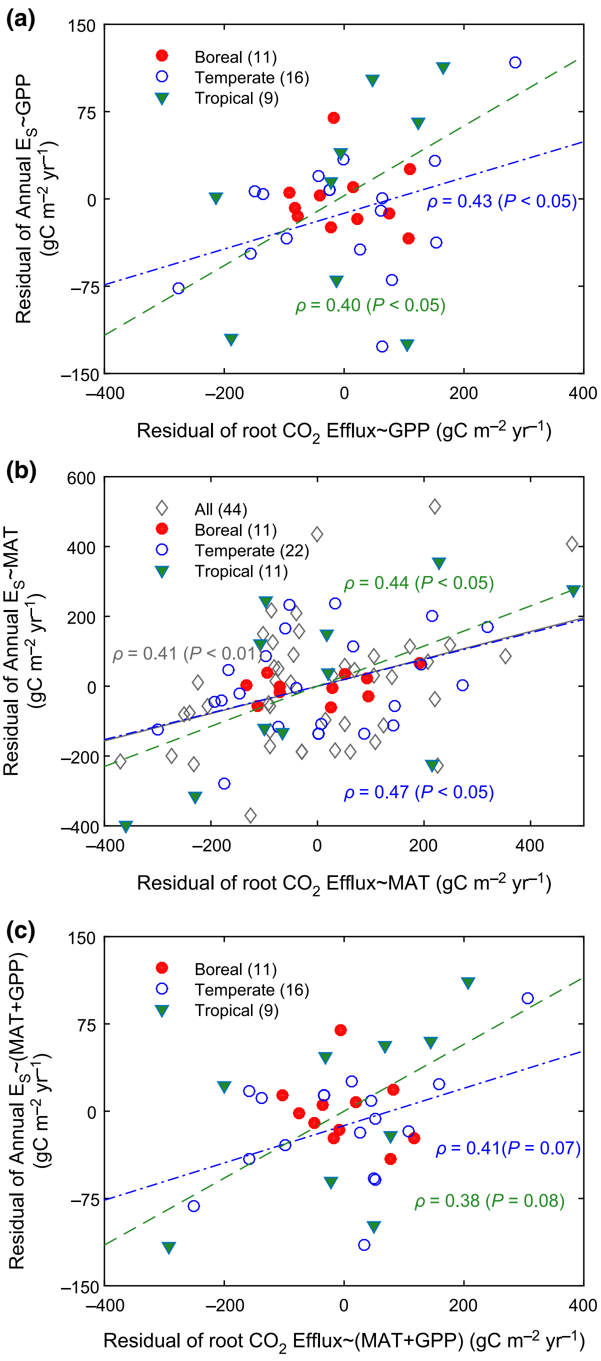

Fig. 6 Partial correlation between annual E_S and root CO_2 efflux after controlling for (a) GPP, (b) MAT, and (c) MAT and GPP combined.

While the relationship between E_S and R_A could be caused by many factors, including some we did not examine, its existence indicates that in the future we might be able to predict E_S from R_A, or vice versa. But before we can adequately address this issue, many more studies that simultaneously measure respiratory CO_2 fluxes aboveground and belowground are needed.

Stand age, tree size and E_S

Due to the close relationship between E_S and GPP, our third hypothesis was that annual E_S will decline with forest age. Our analysis supported this hypothesis (Fig. 7). The cause of the declined E_S with age is unclear. Some studies have reported that there was an increase in respiration relative to GPP as stand age increased (Kira & Shidei, 1967; DeLucia *et al.*, 2007). However, other studies in boreal, temperate, and tropical forests have found that autotrophic respiration did not increase substantially with stand age and therefore cannot explain the decline in NPP (Ryan & Waring,1992; Ryan *et al.*, 1997, 2004; Tang *et al.*, 2008, 2014; Piao *et al.*, 2010; Drake *et al.*, 2011). Stem respiration has also been reported to decrease with age in stands long after canopy closure (Ryan & Waring, 1992; Ryan *et al.*, 2004; Drake *et al.*, 2011). The reduction in annual E_S with age was likely due to age-related decline in GPP caused by progressive nutrient limitations, tree size-related hydraulic limitations, and genetically controlled reductions in metabolic activity with age (Odum,1969; Yoda *et al.*, 1965; DeLucia *et al.*, 2007; Ryan *et al.*, 2004; Drake *et al.*, 2011; Tang *et al.*, 2014).

Tree size has been reported to be correlated with E_S in tropical and temperate forests, but the direction of the correlation varied across studies (Levy *et al.*, 1999; Chambers *et al.*, 2004; Kim *et al.*, 2007; Bowman *et al.*, 2008; Yang *et al.*, 2012). For example, Cavaleri *et al.* (2006) found that E_S per unit stem surface area at 25 °C increased with diameter in a primary tropical rain forest. Levy *et al.* (1999) reported a negative linear relationship between stem diameter and E_S per unit of volume in a temperate forest. A similar negative relationship between E_S per unit of fresh weight and stem diameter was observed in other temperate forests (Yoda, 1967; Hagihara & Hozumi, 1981). This relationship may be related to the metabolic activity of the cells in the tree stem, xylem cell number and development, cambial activity, ray parenchyma percentage and distribution, and carbohydrate synthesis (Pruyn *et al.*, 2002; Lavigne *et al.*, 2004; Gruber *et al.*, 2009; Carbone *et al.*, 2013; Muhr *et al.*, 2013). In our study, E_{15} initially increased with increasing DBH, and then decreased. However, due to the limited range of individual tree sizes used in our analysis (DBH < 40 cm), we should be cautious about how the relationship between E_{15} and tree size scales to larger trees.

Global E_S estimates

Although global estimates and related uncertainties for GPP, NPP, R_S, and total autotrophic respiration

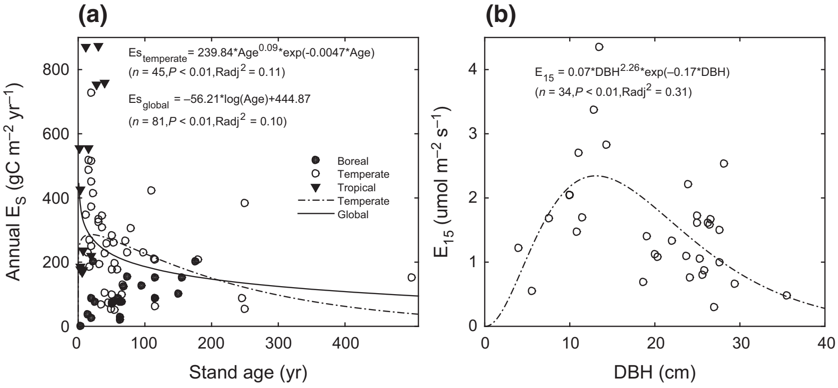

Fig. 7 Relationships between (a) annual stem CO$_2$ efflux (annual E$_S$) and stand age and (b) E$_S$ normalized at 15 °C (E$_{15}$) and individual tree diameter at breast height (DBH).

Table 2 Summary of diagnostics of statistical models examined to predict annual stem CO$_2$ efflux. n is the number of observations; Adj-R^2 is the adjusted coefficient of determination (R^2); RMSE is the root-mean-square error (g C m^2 yr^{-1}); P-value is the significance level associated with the F-statistic; AICc is the Akaike information criterion corrected for finite sample size to account for overfitting with a small sample size. The model in bold was used in global extrapolation of stem CO$_2$ efflux

#	Independent variable	Multiple linear regression model	n	Adj-R^2	RMSE	P-value (F-stat)	AICc
1	MAT**, MAP**	8.4MAT + 143.4log(MAP)278	140	0.30	174	<0.001	2003
2	**MAT**, MAP**, LAI****	**5.52MAT + 157.2log(MAP) + 12.1LAI360**	**64**	**0.74**	**62.1**	**<0.001**	**793**
3	MAT*, MAP**, GPP	2.32MAT + 162log(MAP) + 93log(GPP) − 683.34	68	0.54	164	<0.05	944
4	MAT*, MAP**, NPP	8.35MAT + 151log(MAP) + 0.03NPP − 870.7	48	0.45	179	<0.01	746
5	MAT**, MAP*, R$_S$**	8.5MAT + 148log(MAP) + 124log(R$_S$) − 1336	60	0.45	170	<0.01	858
6	MAT**, MAP, LAI**, R$_S$	9.72MAT + 0.98log(MAP) + 23.2LAI + 98log(R$_S$) − 347	31	0.78	68.9	<0.05	360
7	MAT, MAP*, R$_A$**	5.44MAT + 148log(MAP) + 0.21 R$_A$ − 821	44	0.52	151	<0.001	675
8	MAT**, MAP, LAI*, R$_A$**	10.32 MAT − 86.6log(MAP) + 19.7LAI + 0.25 R$_A$ + 243	24	0.82	45.8	<0.005	261
9	MAT**, MAP*, NPP**, R$_A$**	12.1MAT − 246log(MAP) − 0.14NPP + 0.65 R$_A$ + 974	40	0.84	74.3	<0.001	467

t-stat significance level for variables: *significant at P < 0.1; **significant at P < 0.05; no superscript, not significant.

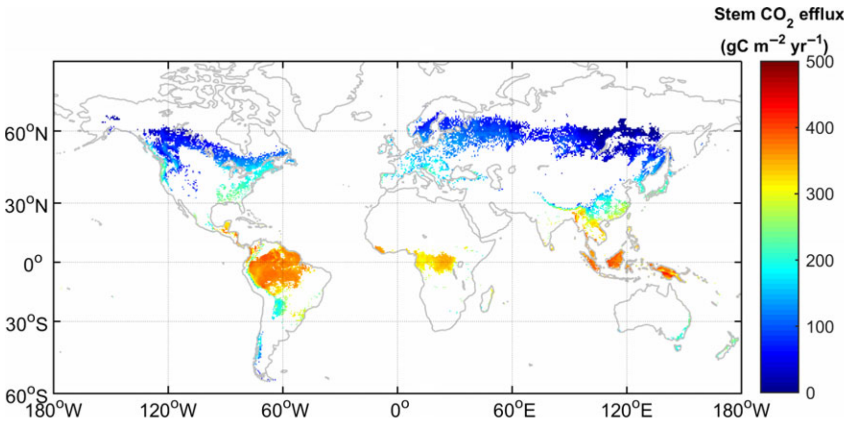

Fig. 8 Global annual mean forest stem CO$_2$ efflux over the period 2000–2012 based on statistical models of annual E$_S$ derived using mean annual temperature, mean annual precipitation, and leaf area index.

have been quantified in several studies (Litton *et al.*, 2007; Luyssaert *et al.*, 2007; Beer *et al.*, 2010; Bond-Lamberty & Thomson, 2010; Piao *et al.*, 2010), to the best of our knowledge, this study is the first to provide an observation-based annual estimate of E$_S$ (6.7 ± 1.1 Pg C yr^{-1}) for global forest ecosystems.

Supporting our fourth hypothesis, we were able to use LAI, MAT, and MAP to predict annual E_S in boreal, temperate, and tropical forest biomes. Our estimation of E_S for temperate and boreal forests fell well within the range of observations; however, our estimate for tropical forests was lower than previous observations and may be related to the limited sample size of original data. Additional observations from tropical forests may help reduce the uncertainty of global estimates of E_S. Beer *et al.* (2010) estimated that GPP of global forest ecosystems was 59 Pg C yr^{-1} (40.8 Pg C yr^{-1}, 9.9 Pg C yr^{-1} and 8.3 Pg C yr^{-1} for tropical, temperate and boreal forests, respectively). The global NPP of forest ecosystems was reported to range from 33 to 50.5 Pg C yr^{-1} (Beer *et al.*, 2010; Ise & Moorcroft, 2010). Our estimated global E_S thus accounts for 11% and 20% of global forest ecosystem GPP and NPP, respectively. The E_S estimate was also 14% of total forest autotrophic respiration and about 7% of global R_S (Raich *et al.*, 2002; Bond-Lamberty & Thomson, 2010; Piao *et al.*, 2010). The global estimates of annual E_S from forest ecosystems from 2000 to 2012 were about 84% of annual anthropogenic CO_2 emissions, which were about 8 Pg C yr^{-1} (Quéré *et al.*, 2013). Our estimated E_S remained relatively stable over the past decade and may be related to the low variability observed in annual LAI during the 13-year period. However, an averaging effect across a large footprint also contributed to stable estimates. In the future, the global annual E_S we calculate may differ because of land use changes, including an increase of 2% yr^{-1} of the area of managed forests and plantations (FAO, 2009). In addition, E_S should be expected to change as MAT and MAP change in response to climate change.

Directions for future E_S studies

Unlike other ecosystem processes such as R_S, which has been extensively reviewed and synthesized in the past decade (e.g., Raich & Potter, 1995; Raich & Tufekciogul, 2000; Bond-Lamberty & Thomson, 2010; Zhou *et al.*, 2014), studies, reviews, and syntheses focused on E_S have received much less attention. We identified several issues that, if resolved, could improve our understanding of E_S at the biome and global scales. First, there has been a lack of standardization for reporting E_S across studies. Specifically, there have been at least four approaches for expressing E_S: surface area based (μmol CO_2 surface area m^2 s^1), sapwood area based (μmol CO_2 sapwood area m^2 s^1), sapwood volume based (μmol m^3 sapwood volume s^1), and sapwood mass based (μmol Kg^1 s^1). There were also several normalized temperatures used for E_S in different studies (25 °C, 20 °C, 15 °C, 10 °C, 5 °C, and 0 °C). Usually, there was not enough information reported in papers to interchange among these normalized temperatures, which made it difficult to compare results across studies. We recommend that all studies reporting E_S include at least one common unit (e.g., surface area based) and one common normalized temperature (e.g., 15 °C). Authors can certainly use other units and normalized temperatures based on their objectives, but a standard unit and temperature would greatly improve our ability to synthesize E_S across studies. Secondly, our compilation of data revealed a need for more annual E_S observations at the stand level. The lack of annual E_S estimates has hampered representation of E_S in ecosystem, regional, and global models. These drawbacks may impede the understanding of carbon balance in forest ecosystems. Thirdly, more emphasis is needed on integrating aboveground and belowground processes for a holistic understanding forest carbon dynamics. Considering the close relationship between roots and stems, belowground CO_2 efflux research should not omit the aboveground physiological process and vice versa. In the 121 papers we compiled, less than 38% of studies reported measurements of both aboveground and belowground CO_2 efflux. Similarly, most studies estimating R_A did not consider its relationship with E_S. Finally, there has been a lack of observations regarding the effects of experimental treatments on E_S, such as E_S responses to altered temperature or precipitation patterns. This knowledge gap may impede our understanding of the mechanisms controlling E_S and presents difficulty in predicting the response of E_S to future environmental changes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Mean ± SD and ranges (in parentheses) of annual stem CO_2 efflux (E_S) in boreal, temperate and tropical forest ecosystems.
Table S2. Information about the study sites used in our analysis.
Fig. S1. (a) Q_{10} of E_S (change in E_S per 10 °C change in temperature) and (b) its distribution among forest biomes (total $n = 208$; boreal $n = 52$, temperate $n = 125$, tropical $n = 31$).
Fig. S2. (a) Relationship between Q_{10} and mean annual temperature for boreal forests; and (b) relationship between Q_{10} and stand mean diameter at breast height (DBH) in boreal forests.
Fig. S3. Relationships between annual stem CO_2 efflux (E_S) and basal area (BA): in global forests (tropical, temperate and boreal, solid line), annual $E_S = 2.43BA + 119$ ($n = 60$, $R^2 = 0.12$, $P < 0.005$); and) in boreal forests alone (dotted line), annual $E_S = 1.2BA + 63$ ($n = 19$, $R^2 = 0.13$, $P < 0.05$).
Fig. S4. Correlations between soil CO_2 efflux and stem CO_2 efflux after controlling for MAT. The solid line is the relationship for tropical, temperature and boreal forests combined.