



Biochar increased soil respiration in temperate forests but had no effects in subtropical forests



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ABSTRACT

As a climate change mitigation strategy, biochar application to soil has been demonstrated to increase soil carbon (C) sequestration and reduce greenhouse gas (GHG) emission. Although numerous manipulative studies have been conducted, it is still not fully understood how biochar application affects soil respiration (R_s) and its components (i.e., autotrophic [R_a] and heterotrophic respiration [R_h]) in forest ecosystems, especially in subtropical forests. In this study, we performed a meta-analysis of forest ecosystems and a field experiment with biochar amendments of 0, 10, and 30 t ha⁻¹ in a subtropical forest in Zhejiang, China to examine the effects of biochar application on R_s and its components. Our results showed that biochar application significantly increased R_s by 20.92% at the global scale with an increase of 20.25% in temperate forests and a nonsignificant effect in subtropical forests. Responses of R_s to biochar application varied with experimental methods and soil textures. Similarly, our field experiment showed that biochar amendment did not significantly affect R_a , R_h , and R_s in a subtropical forest in Eastern China. Specifically, the average R_s under biochar amendments of 0, 10, and 30 t ha⁻¹ were 2.37, 2.06 and 2.15 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively ($P > 0.05$). Both R_s and R_h were positively correlated with microbial biomass C (MBC) and negatively with dissolved organic C (DOC). Both apparent temperature sensitivity (Q_{10}) of R_h and R_s were significantly higher under biochar treatments than in the control. Our findings indicate the importance of the differential effects of biochar application on R_s in different forest types for C sequestration, which may inform ecosystem and regional models to improve prediction of biochar effects on forest C dynamics and climate-biosphere feedbacks.

1. Introduction

Biochar, a C-rich charcoal-like substance, is made by pyrolyzing waste biomass at high temperature under oxygen limited conditions, and has been promoted as soil amendment to enhance soil C sequestration, improve soil fertility, and increase crop yield (Van Zwieten et al., 2010; Wang et al., 2014). Over the past 50 years, lots of studies have examined responses of C cycling to biochar application in agriculture, grassland, and forest ecosystems by laboratory incubation or field experiments. These results have considerably improved our understanding of the mechanisms underlying effects of biochar application (Wardle et al., 2008; Wang et al., 2014). For example, biochar

application had no effect on soil respiration (R_s) but significantly enhanced soil organic carbon (SOC) and microbial biomass carbon (MBC) by 40% and 18%, respectively (Liu et al., 2016). In addition, below-ground net primary productivity (BNPP) often increased with biochar application owing to a more favorable environment for plant growth in the biochar-amended soil (Baker et al., 2007; Zimmerman et al., 2011).

R_s represents CO₂ release through soil surface from root/autotrophic respiration (R_a) by live roots and their symbionts (Zhou et al., 2007; Chen et al., 2016) and through microbial/heterotrophic respiration (R_h) during litter and soil organic matter (SOM) decomposition (Luo and Zhou, 2006). As the second-largest C flux (68–80 Pg C yr⁻¹) between terrestrial ecosystems and atmosphere, R_s

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plays a vital role in regulating climate change (Raich et al., 2002). During the past decades, a large number of studies have found that R_s components (R_a and R_h) responded differently to changes in external environments, such as climate warming, nitrogen (N) deposition, and altered precipitation regimes (Luo and Zhou, 2006; Zhou et al. 2007; Liu et al., 2016). However, responses of R_s components to biochar application are still poorly understood in terrestrial ecosystems (Wardle et al., 2008; Sackett et al., 2015). In addition, existing studies usually used relatively small plot sizes ($\leq 100 \text{ m}^2$) to investigate responses of R_s and its components to biochar application (Wang et al., 2014; Sackett et al., 2015). To date, very few studies have been conducted in the field to adequately represent the large spatial heterogeneity of natural forest ecosystems under biochar application (Högberg et al., 2001; Sackett et al., 2015). This shortcoming may pose a challenge to a thorough understanding of the biochar effects on feedbacks between climate change and C cycle (Pan et al., 2004; Bamminger et al., 2014). It is thus necessary to conduct field experiments with larger plot size ($\geq 400 \text{ m}^2$) to better examine the potential effects of biochar application on R_s and its components.

As the most widespread terrestrial ecosystem, forest ecosystems play a dominant role in the global C cycle because of their huge C storage and high productivity (Pan et al., 2011; IPCC, 2013). R_s in forests is a key C process that regulate regional climate change and even determines net C balance in terrestrial ecosystems (Zimmerman et al., 2011; Sackett et al., 2015). Current research on biochar effects mainly focus on the restoration of degraded forest soil and C sequestration of residues after harvesting and fire (Pan et al., 2011; Jefferey et al., 2013). However, in spite of important benefits of biochar application in forests ecosystems, little attention has been paid to their effects on R_s and its components. Although a few studies had been conducted, effects of biochar addition on R_s in forest ecosystems remain controversial due to the methodological difficulties, spatial heterogeneity, and complexity of potential mechanisms (Fig. 1, Van Zwieten et al., 2010; Sackett et al., 2015). Among some individual studies, R_s significantly increased (Bamminger et al., 2014), but R_s largely decreased or remained unchanged for others under biochar application (Wang et al.,

2014; Sackett et al., 2015).

Contradictory responses of R_s to biochar application may be associated with the complicated biotic and abiotic processes underlying their combined effects on the R_s components (R_a and R_h) in forest ecosystems (Fig. 1, Zimmerman et al., 2011; Sackett et al., 2015). Recently, two meta-analyses have been conducted to examine biochar effects on GHGs (including R_s , He et al., 2016; Wang et al., 2016). However, we still do not know the specific effects of biochar application on R_s in forest ecosystems. These uncertainties arise because current studies do not distinguish effects on forests from those of other terrestrial ecosystems, and most of them mainly emphasized the central tendency of associated C pools (i.e., SOC, MBC) under biochar application (He et al., 2016; Liu et al., 2016). Therefore, it is necessary to compile all the available data and to carry out field experiments to reveal novel patterns and mechanisms of R_s and its components in response to biochar application.

In this study, a meta-analysis synthesizing 42 experimental studies was conducted to quantify the responses of R_s to biochar application in forest ecosystems. We also carried out a field experiment with larger plot size in a subtropical forest to examine the potential effects of biochar application on R_s and its components. Specifically, this study was aimed to: (1) investigate the magnitude of biochar application on R_s of global forest ecosystems by a meta-analysis, and (2) determine how R_s and its components (R_a and R_h) respond to biochar application in a subtropical forest ecosystem using a field study.

2. Materials and methods

2.1. Meta-analysis

Published journal articles that studied effects of biochar on R_s in forest ecosystems before June 2016 were searched out from the Web of Science and China Knowledge Resource Integrated Database (CNKI) with the combinations: (biochar or black carbon or charcoal) and (carbon or CO_2) and (Forest). The following criteria were set: (1) treatment with biochar application and control were simultaneously

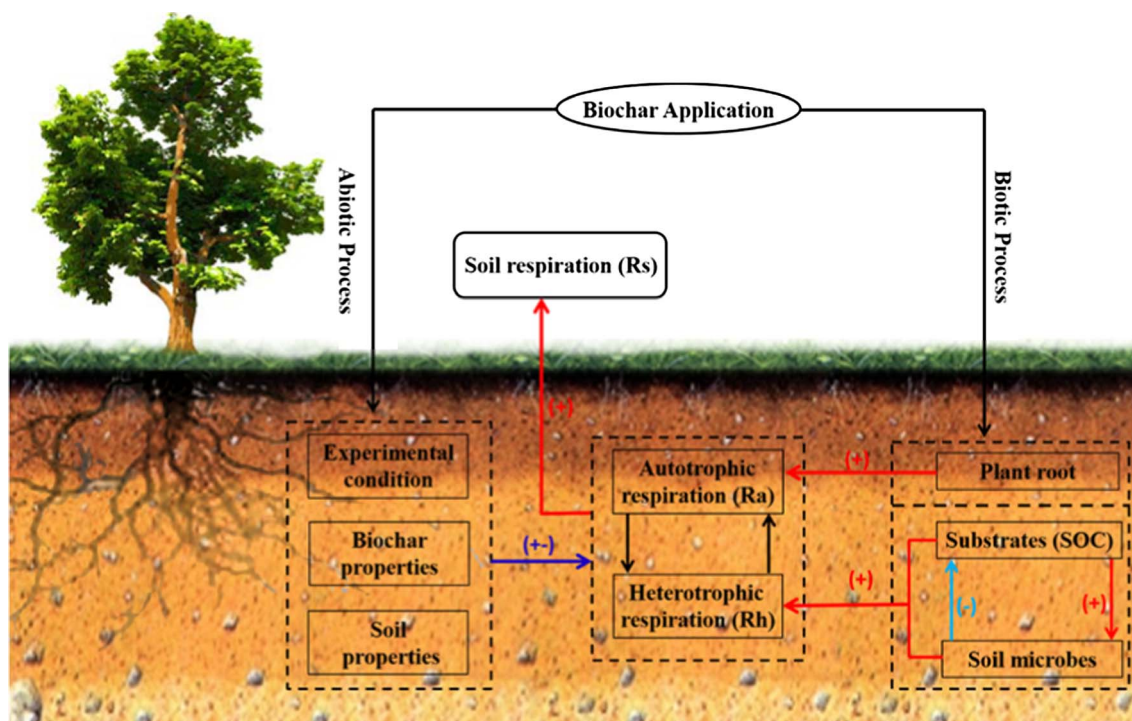


Fig. 1. The potential mechanisms underlying effects of biochar on soil respiration and its components. The red, azure and navy blue lines represent the positive, negative and both effects, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

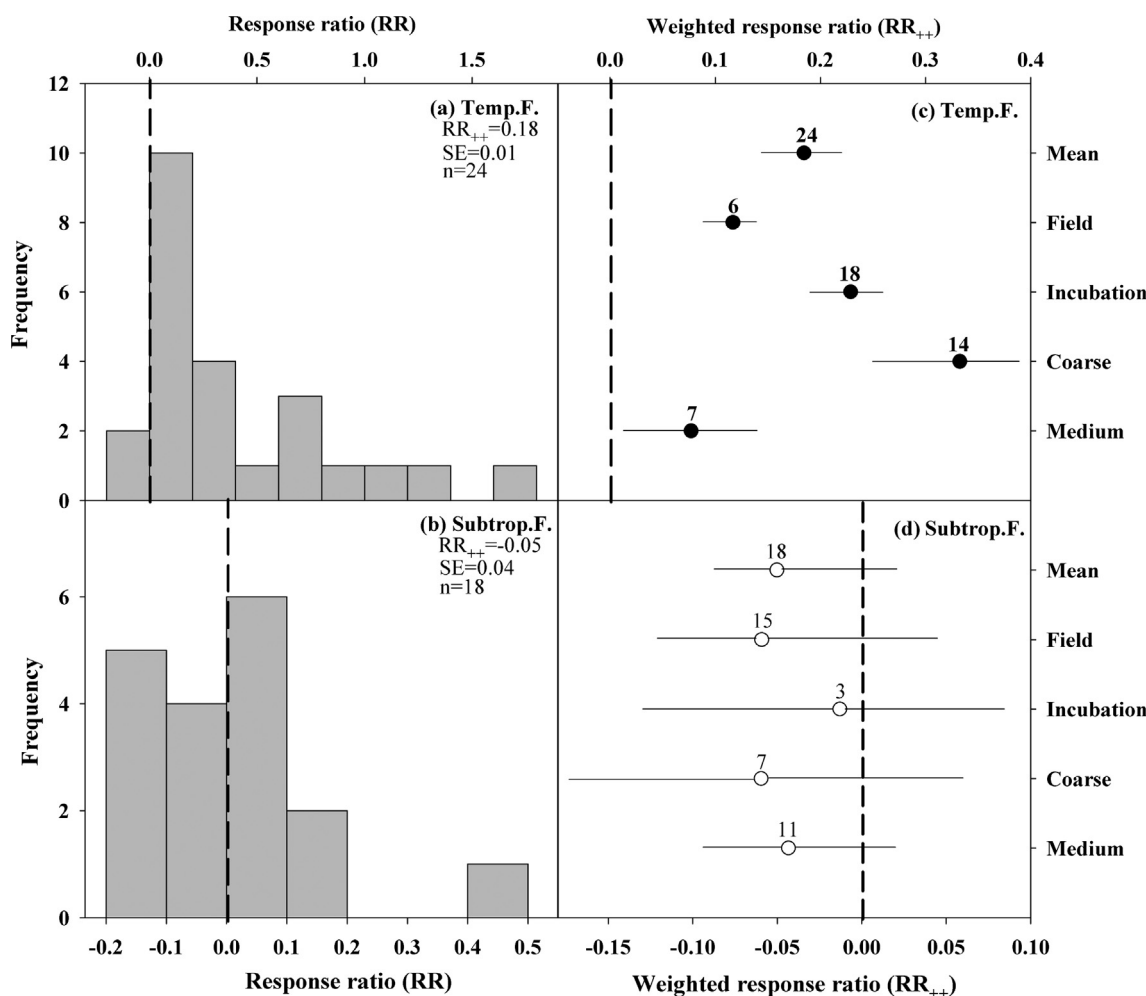


Fig. 2. Frequency distributions of response ratio (RR) of soil respiration (Rs) to biochar application in temperate forest (a) and subtropical forest (b). The effect of biochar application on Rs differed with experimental method and soil texture in temperate (c) and subtropical forest (d). Bars represent $RR_{++} \pm 95\%$ confidence intervals. The vertical line was drawn at $RR_{++} = 0$. Number values for each bar indicate the sample size. Solid circle indicates significant difference at $P < 0.05$. Hollow circle indicates nonsignificant. Notes that no data were available for boreal and tropical forests as well as in pot experiments.

Table 1
Percentage change of soil respiration in response to biochar application.

		Temperate forest	n	Subtropical forest	n
	Total	20.25 ± 0.92	24	-4.89 ± 3.68	18
Experimental method	Field	12.39 ± 1.47	6	-5.75 ± 4.12	15
	Incubation	25.71 ± 1.20	18	-1.29 ± 8.52	3
Soil texture	Coarse	26.18 ± 2.23	14	-5.78 ± 5.72	7
	Medium	19.38 ± 1.38	7	-4.24 ± 4.88	11

Percent change is represented as the mean ± 95% confidence intervals; the bold number indicates significant difference at $P < 0.05$.

conducted in field or laboratory incubation or pot experiments; (2) The biochar and control treatment were established to have the same initial environmental and climate conditions, species compositions and soil texture; (3) The means, standard deviations/errors, and sample sizes (n) of the chosen variables could be directly calculated from the studies with digitized graphs, contexts or tables. In total, 42 studies were selected from the database out of 1500 publications. Among these, 24 addressed temperate forests, and 18 addressed subtropical forests. No data on boreal and tropical forests were found.

We used a meta-analysis approach as described by Hedges et al. (1999) and Zhou et al. (2014) to evaluate the response of Rs to biochar application. The effect size of the concerned Rs was calculated by the

response ratio (RR, natural log of the ratio of the mean value of concerned Rs in biochar application treatment to that in control) as $RR = Ln(\bar{X}t/\bar{X}c)$, where $\bar{X}t$ and $\bar{X}c$ were the means of the biochar application and control pairs, respectively. Variance (v) of RR is estimated by $v = \frac{s_t^2}{n_t \bar{x}_t^2} + \frac{s_c^2}{n_c \bar{x}_c^2}$, where n_t and n_c represent the sample sizes, and s_t and s_c were the standard deviations of the chosen variables in biochar application and control pairs, respectively. Reciprocal of variance ($w = \frac{1}{v}$) was represent as the weight (W) of each RR. The weighted response ratio (RR_{++}) was calculated from RR of individual pairwise comparison between the biochar application and control, RR_{ij} ($i = 1, 2, \dots, m; j = 1, 2, \dots, k$). Here, m is the number of groups (e.g., forest type, experimental method or soil texture type), and k is the number of comparisons in the i th group.

The mean response ratios were calculated using the following equation:

$$RR_{++} = \frac{\sum_{i=1}^m \sum_{j=1}^k W_{ij} RR_{ij}}{\sum_{i=1}^m \sum_{j=1}^k W_{ij}} \tag{1}$$

The standard error of weighted response ratio (RR_{++}) was estimated by:

$$S(RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^m \sum_{j=1}^k W_{ij}}} \tag{2}$$

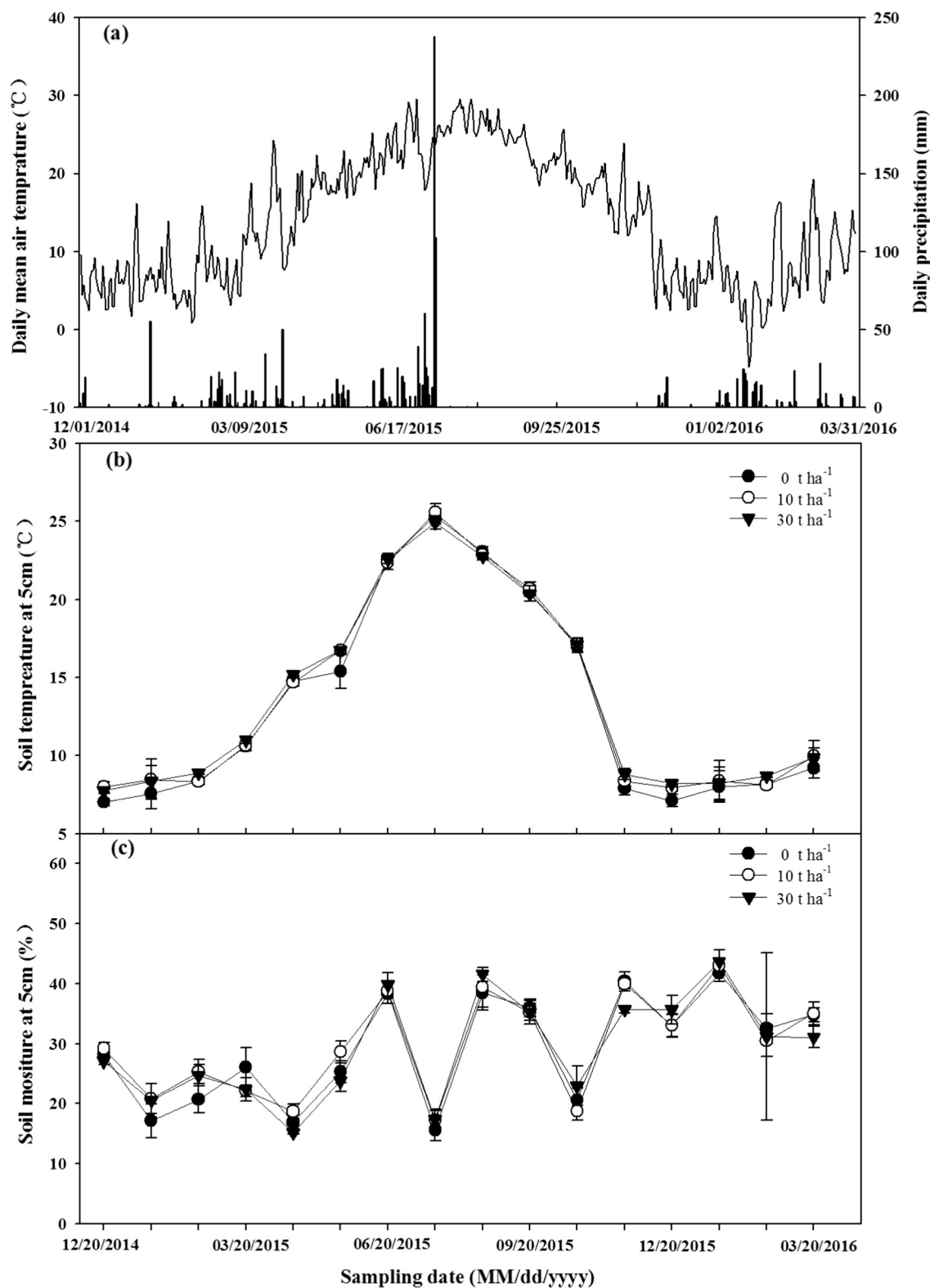


Fig. 3. Temporal variation of climate factors from December 2014 to March 2016. (a) Daily mean air temperature (gray line) and daily precipitation (black bar), (b) soil temperature at 5 cm, and (c) volumetric soil moisture to a depth of 5 cm (v/v%). Data of air temperature and precipitation were collected from a nearby weather station of Tiantong.

We calculated the 95% confidence interval (95% CI) as $RR_{++} \pm 1.96 S(RR_{++})$ when the data point number that used for estimating RR_{++} of chosen variable was larger than 20. If not, a bootstrapping method by a resampling simulation was used to obtain the lowest and highest 2.5% values as our CI based on 5000 iterations (Janssens et al., 2010). The effect of biochar on R_s was considered as

significance if the 95% CI did not overlap with zero. The percentage changes of concerned variables induced by biochar application were measured by $[\exp(RR_{++}) - 1] \times 100\%$. Frequency distribution of RR_s ($n > 20$) of R_s were plotted to validate the results by a Gaussian function using the equation $y = \alpha \exp\left[-\frac{(x-\mu)^2}{2\sigma^2}\right]$ in SigmaPlot 10.0 software (Systat Software Inc., CA, USA). Where y is the frequency in an

Table 2

Results (*F* and *P* values) of repeated measurements analysis of variance: effects of biochar application (*B*), sampling time (*S*) and their interactive effects (*B* × *S*) on *Ra*, *Rh*, *Rs*, *SM*, *ST*, *DOC* and *MBC*.

	<i>B</i>		<i>S</i>		<i>B</i> × <i>S</i>	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Ra</i>	0.822	0.484	81.205	< 0.001	0.599	0.869
<i>Rh</i>	0.194	0.829	59.763	< 0.001	0.569	0.906
<i>Rs</i>	1.042	0.409	63.825	< 0.001	0.354	0.991
<i>SM</i>	0.300	0.751	91.114	< 0.001	0.461	0.977
<i>ST</i>	0.193	0.829	759.742	< 0.001	1.073	0.400
<i>DOC</i>	6.567	0.012	52.417	< 0.001	5.397	< 0.001
<i>MBC</i>	3.586	0.060	24.696	< 0.001	1.568	0.185

Ra, autotrophic respiration; *Rh*, heterotrophic breathing; *Rs*, soil respiration; *SM*, soil moisture; *ST*, soil temperature; *DOC*, dissolved organic carbon; *MBC*, microbial biomass carbon.

interval; x is the RR of *Rs*; α is the expected number of RR values at $x = \mu$; and μ and σ^2 are the mean and variance of the normal distribution of RR, respectively.

The between-group heterogeneity (Q_b) across all data for a given response variable was calculated to further analyze the biochar effect among different subgrouping categories (i.e., forest type, experimental method, and soil texture). The forest type was divided into temperate and subtropical forests, because no data were available from boreal and tropical forests. Experimental method was classified as field experiments and soil incubation, and soil texture as coarse and medium soils. Before analysis, we used Kendall's Tau method to test and assess the publication bias (Møller and Jennions, 2001). If the mean effect was significantly different from zero (i.e., indicating the existence of publication bias), Rosenthal's fail-safe number, which was applicable to both fixed-and random effects models, was calculated by MetaWin 2.1 Software to estimate whether our conclusion was likely to be affected by the unpublished studies (Rosenberg et al., 1997; Rosenberg, 2005).

2.2. Field biochar study

2.2.1. Site description

A field study was conducted in Tiantong National Forest Ecosystem Observation and Research Station (29°48' N, 121°47' E) in Zhejiang Province, China. The study region has a typical subtropical monsoon climate with humid hot summers and dry cold winters. Mean annual temperature (MAT) is 16.2 °C with mean monthly air temperature ranging from 4.2 °C in January to 28.1 °C in July; and mean annual precipitation is 1374.7 mm, which mainly occurs from May to August (Wang et al., 2007, data from Tiantong weather station). Soils are mainly red and yellow, with pH ranging from 4.4 to 5.1, and texture is mainly sandy to silty clay loam (Yan et al., 2006). The soil was developed on deeply weathered deposits of mesozoic sediments and acidic intrusive rocks, mainly granite and quartzite (Yan et al., 2006). The dominant tree species in the study region include *Pseudolarix amabilis*, *Cinnamomum subavenium*, and *Phoebe chekiangensis*.

2.2.2. Experimental design

The study region was divided into five blocks based on location, topography (slope and aspect), and site properties (the amount of vegetation and rock). In each block, there were three 20 × 20 m plots, each randomly allocated to one of three treatments (0, 10 and 30 t biochar ha⁻¹). Each plot was enclosed with PVC board buried into soil at 50 cm depths and separated by at least 5 m from each other.

Biochar used in this experiment was produced from bamboo using an industry-scale vertical kiln slow with 800 °C pyrolysis temperature, which is considered to be more stable than low-temperature biochar and more appropriate for soil C sequestration (He et al., 2016). Physicochemical properties of the experimental biochar are described in

Table S1 and Fig. S1. The biochar was ground to pass through a 5 mm sieve and homogenized before being applied to soil. Experimental treatments started in March 2013. Biochar was spread over the ground as even as possible and then manually hoed to mix with surface soil to ~15 cm depth. The control plots were hoed without applying any biochar. The dominant species in the plots were *Pseudolarix amabilis* and *Phoebe chekiangensis*.

2.2.3. Measurement protocols

To measure *Rs*, three PVC collars (20 cm in diameter and 5 cm in height) were installed 2–3 cm into the ground in each plot with triangular distribution. Trenched subplots with no trees or tree shading were established for *Rh* measurement adjacent to each PVC collar. Subplots were 0.2 × 0.2 m and trenched to 0.8 m depth (with little root distribution below this depth). After lining the trenched subplots with PVC plates (2.5 mm), we refilled the trench according to its original soil profiles to minimize the disturbance of trenching. The same PVC collar was installed in the trenched subplots for the measurements of *Rh*. In total, three PVC collars in each plot were used for the measurements of *Rh* and *Rs*, respectively.

The *Rs* and *Rh* were measured for all PVC collars three months after installation. Autotrophic respiration (*Ra*) was calculated as the difference between *Rs* and *Rh*. To eliminate aboveground plant respiration, we clipped all small living plant inside the collars at the soil surface one day ahead of the measurements. *Rh* and *Rs* were measured once or twice a month from December 2014 to March 2016, between 9:00 and 14:00 (local time), using a LI-COR 8100 portable soil CO₂ flux system (LI-COR, Inc., Lincoln, NE, USA). When measuring *Rs* and *Rh*, soil temperature at the 5 cm depth was monitored adjacent to each PVC collar using a thermocouple probe connected to the LI-COR 8100, and volumetric soil water content (%V) between 0 and 15 cm depth was directly measured with manual time domain reflectometry (TDR) equipment (Soil moisture Equipment Corp., Santa Barbara, CA, USA).

From July 2015 to November 2015, three soil cores of the top soil (0–10 cm) in each plot were randomly sampled and then pooled together and treated as one sample, to determine the concentration of *MBC* and soil dissolved organic carbon (*DOC*). Within 24 h of sampling, after removing roots and rocks, 10 g soil from each sample was split into two parts. 5 g soils subsamples one was treated as fumigated and the other as nonfumigated soils. *DOC* was extracted with a 1:5 soil-water ratio, shaking end-over-end for 1 h, centrifuged at 4000 rpm for 10 min and passed through a 0.45 μm filter under vacuum (Mavi et al., 2012). The *DOC* concentration of the extracts was analyzed with a soluble total carbon analyzer (Multi N/C; Analytik, Jena, Germany). *MBC* was determined by subtracting the total *DOC* of nonfumigated subsamples from that of the fumigated subsamples with a conversion factor of 0.45 (Brookes et al., 1985).

2.2.4. Modeling soil CO₂ efflux and its components

Soil moisture and temperature are two main abiotic variables affecting *Rs*, but they vary with sampling conditions and season of samplings (Luo and Zhou, 2006; Zhou et al., 2007). Thus, we employed two modified exponential functions (van't Hoff, 1884; Gullidge and Schimel, 2000) to evaluate the influence of temperature and moisture.

$$Rs = R_0 Q_{10}^{\frac{T-T_0}{10}} \frac{M}{M + \varepsilon} \quad (3)$$

$$Q_{10} = e^{10b} \quad (4)$$

where R_0 is the respiration rate at temperature T_0 ; Q_{10} , respiration quotient, is the relative increase (R/R_0) as temperature increases by 10 °C (Högberg et al., 2001; Luo and Zhou, 2006); b was the temperature sensitivity of CO₂ flux (*Ra*, *Rh* and *Rs*); T is the temperature at sampling time, M is the moisture content (%) at sampling time; and ε is a moisture response constant.

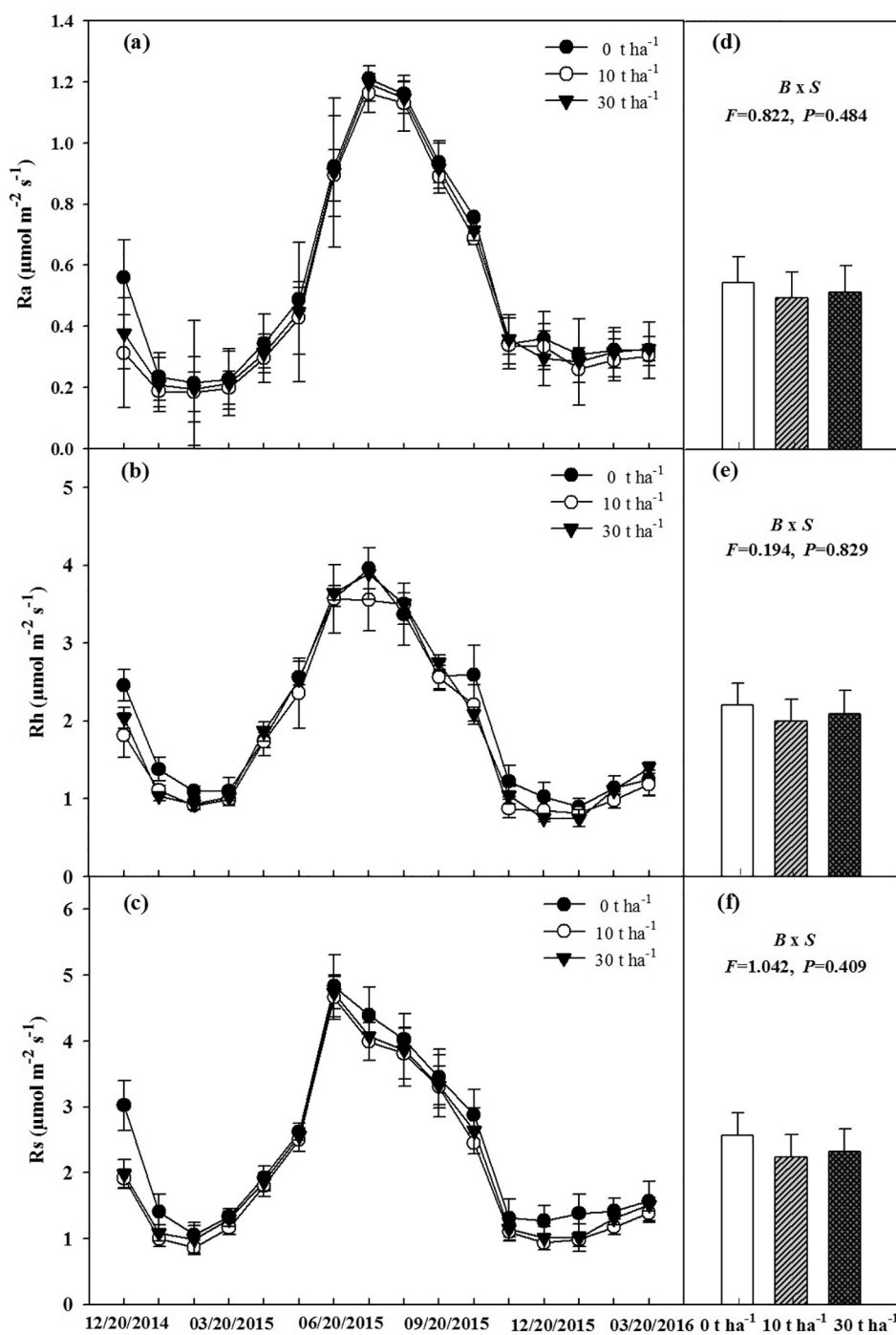


Fig. 4. Seasonal variability of autotrophic respiration (*R_a*, a), heterotrophic respiration (*R_h*, b) and soil respiration (*R_s*, c) under three biochar application treatments. Average and standard error values of autotrophic respiration (*R_a*, d), heterotrophic respiration (*R_h*, e) and soil respiration (*R_s*, f) over the whole studies time under three biochar application are shown as histogram in the right part of each figure. Symbols a represents the significant differences among three application levels for the responses of selected variables to biochar.

2.3. Data analysis

In this study, *t*-test was used to examine the significance of the variation of concerned variable between biochar application and control, as well as the difference of *RR₊₊* for effects of experimental method and soil textures in meta-analysis. The same procedure was used to determine the effect of biochar application on annual average *R_a*, *R_h*, *R_s*, and the related parameters *T₀* and *Q₁₀*. The sensitivity of CO₂ efflux (*R_a*, *R_h* and *R_s*) to soil temperature was assessed through the following equation to fit an exponential function to the individual treatments data.

$$R = ae^{bT} \tag{5}$$

where *R* is the mean value of *R_a*, *R_h* and *R_s* (μmol m⁻² s⁻¹); *a* is the

intercept of *R_s* when temperature is zero (basal respiration rate); and *T* is the soil temperature (°C) at the 5 cm depth.

Daily *R_h* or *R_s* was estimated based on hourly emissions calculated by the following equation:

$$R_T = \sum_{i=1}^{48} R_0 Q_{10}^{\frac{T_i - T_0}{10}} * 1800 * \left(\frac{12}{1000000} \right) \tag{6}$$

where *R_T* was the daily emissions; *T_i* was the average soil temperature per half hour. Monthly and annual *R_h* and *R_s* were calculated by adding up daily emissions.

Repeated measures ANOVAs was used to examine biochar application (*B*), Sampling time (*S*) and their interactive effects (*B* × *S*) on monthly *R_a*, *R_h*, *R_s*, SM, ST, DOC and MBC. Differences were evaluated at the level *P* < 0.05. One-way ANOVA was used to determine the

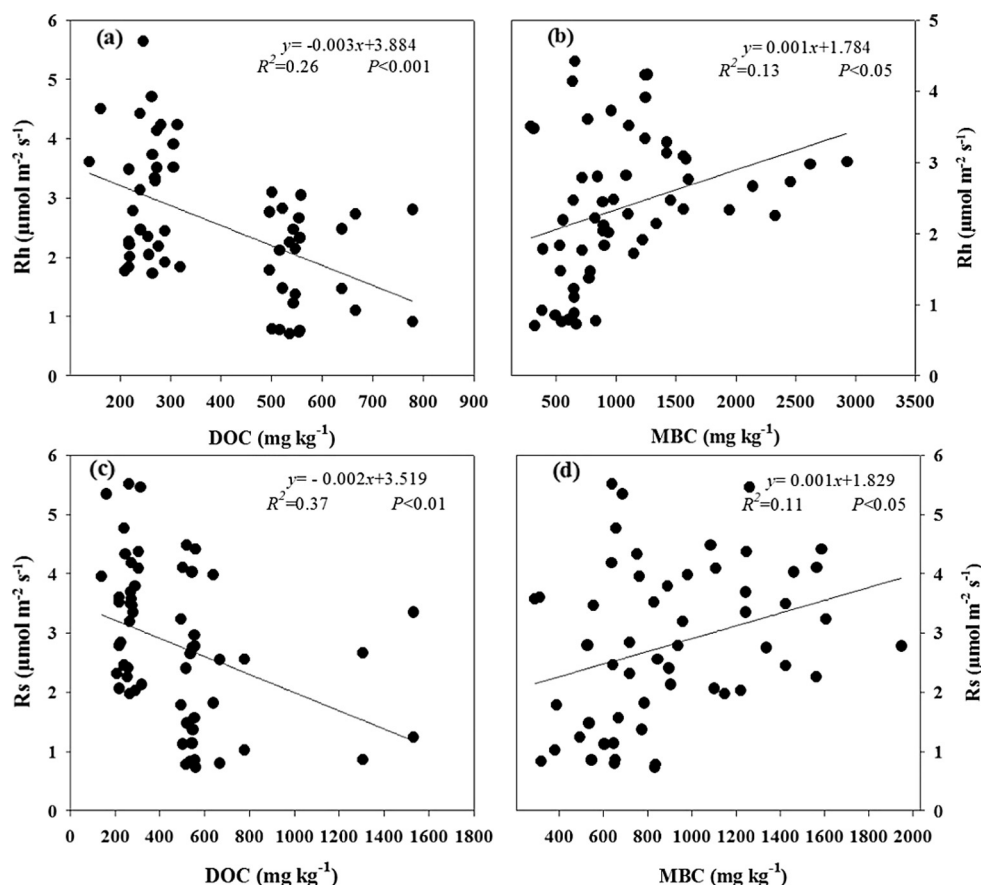


Fig. 5. Relationship of dissolve organic matter (a) and microbial biomass carbon (b) with heterotrophic respiration (R_h , a, b) and soil respiration (R_s , c, d) under biochar application treatments.

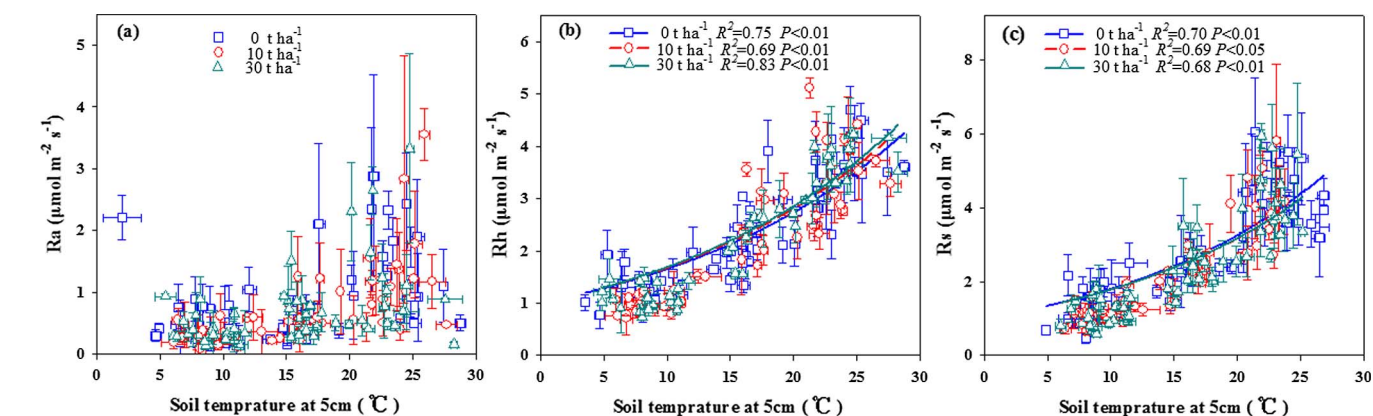


Fig. 6. Exponential relationships between soil temperature at 5 cm and autotrophic respiration (R_a , a), heterotrophic respiration (R_h , b) and soil respiration (R_s , c) under different biochar application treatments.

impacts of biochar on R_o , Q_{10} , seasonal accumulative R_h and R_s and the relative contribution of R_h to R_s . All statistical analyses were conducted with SPSS 16.0 for Windows (SPSS, Inc., Chicago, IL, USA), and figures were drawn with Sigmaplot 10.0 (Systat Software Inc., CA, USA).

3. Results

3.1. Effects of biochar application on soil respiration (R_s) in global forest ecosystems

The mean response ratios (RR_{++}) of R_s to biochar applications showed diverse patterns of different forest types (Figs. 2a, b and S2). On average, biochar application significantly increased R_s by 20.92% at a global scale ($P < 0.001$, Table 1). However, different forest types (e.g.,

temperate vs. subtropical forests) showed different magnitudes and direction of changes for R_s (Fig. 2a, b, Table S2). Biochar induced a significant increase in R_s in temperate forests, but there was no significant effect on R_s in subtropical forests. There was no publication bias as suggested by Rosenthal's method (Table S2).

The responses of R_s to biochar application significantly changed with experimental method and soil texture (Fig. 2, Table S2). On average, R_s in temperate forests showed a large increase by 25.71% under incubation conditions vs. 12.39% under field conditions. Biochar increased R_s in coarse soil (26.18%) more than in medium soil (19.38%) in temperate forests ($P < 0.05$; Fig. 2c). In subtropical forests, experimental method (i.e., incubation and field condition) and soil texture (i.e., coarse and medium soils) did not significantly affect responses of R_s to biochar application ($P > 0.05$, Fig. 2d).

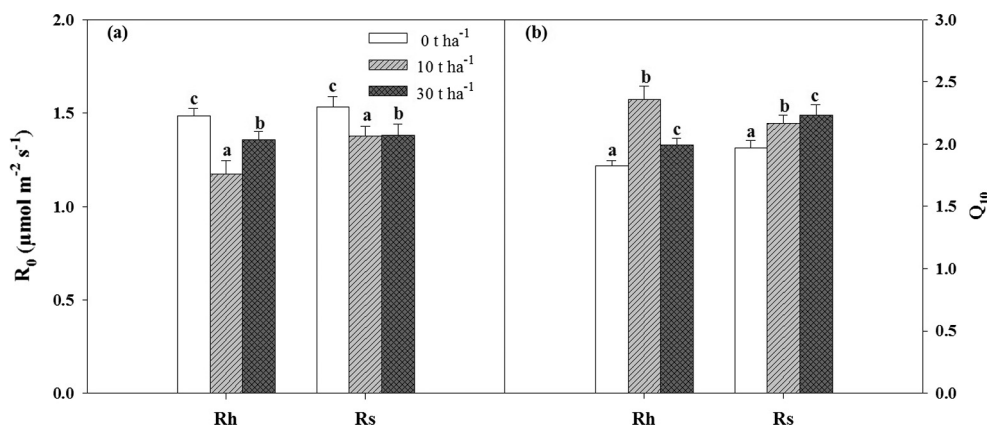


Fig. 7. Maximum likelihood estimators (MLEs) for R_0 (a) and Q_{10} (b) in heterotrophic respiration (R_h) and soil respiration (R_s) under three biochar application treatments. Error bars represent standard deviations (SDs) of parameters calculated from 5000 samples of Metropolis-Hastings (M-H) simulation. Symbols a, b and c represents the significant differences among three application levels for the responses of selected variables to biochar.

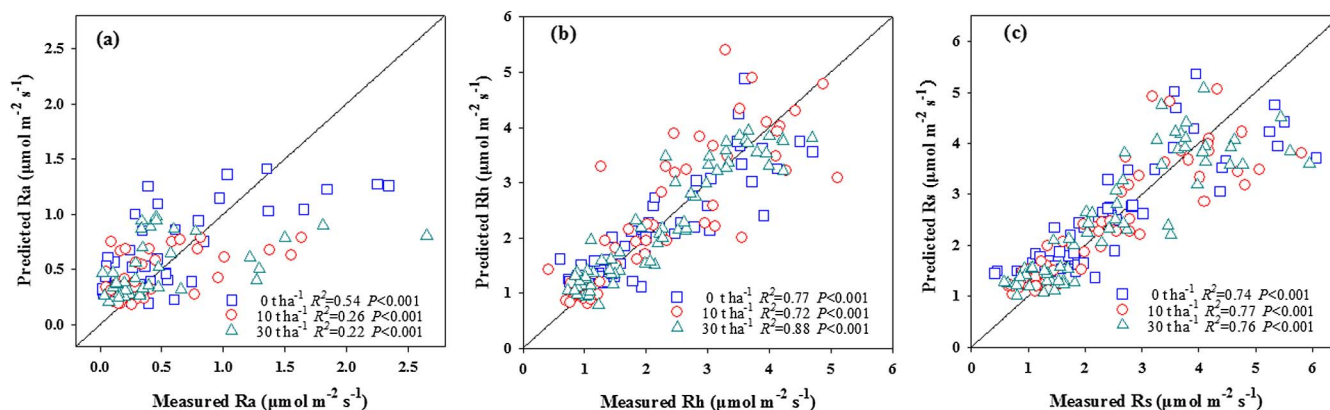


Fig. 8. Measured vs. modeled autotrophic respiration (R_a , a), heterotrophic respiration (R_h , b) and soil respiration (R_s , c) under three biochar application treatments.

3.2. Effects of biochar application on microclimate and R_s in a Tiantong subtropical forest

Both air temperature and soil temperature at 5 cm depth showed a significant seasonal pattern over the experimental period, but there was no clear seasonal pattern for soil moisture. Biochar application had no effect on soil temperature or soil moisture in this study ($P > 0.05$, Fig. 3b, c; Table 2).

Similar to soil temperature, the temporal dynamics of R_a , R_h and R_s also showed distinct seasonal pattern during the experimental period, with the highest value in summer and lowest in winter (Fig. 4; Table 2). However, consistent with the results from our meta-analysis (Fig. 2b), biochar application had no significant effect on R_s and its components in Tiantong forest across the experimental period. Specifically, the average R_a were 0.54, 0.49 and 0.51 $\mu\text{mol m}^{-2} \text{s}^{-1}$ under 0, 10 and 30 t ha^{-1} treatments, respectively, and the average R_s were 2.37, 2.06 and 2.15 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively ($P > 0.05$, Fig. 4c). Similarly, there were no significant differences under the three biochar application rates for either annual or seasonal cumulative R_h and R_s (Figs. S3 and S4). Our results show that R_h and R_s were positively correlated with MBC but negatively with DOC ($P < 0.05$, Fig. 5).

On the basis of the temperature relationship with R_s and its components in Eqn (5), soil temperature at 5 cm depth accounted for 69–83% of the variation of R_h and nearly 70% of the variation of R_s (Fig. 6b and c). However, no clear relationship between R_a and soil temperature under both control and biochar treatments was observed in this study (Fig. 6a). The apparent Q_{10} values of R_h and R_s under biochar treatments were significantly higher than those in the control, and Q_{10} values of R_h were similar to those of R_s under both control and treatments (Fig. 7b, $P < 0.05$). The R_0 values of R_h and R_s under biochar application were significantly lower than those in the control (Fig. 7a, $P < 0.05$). In addition, R_h contributed to approximately 84% of R_s

across the study period, which was relatively consistent among treatments (Fig. S5).

3.3. Modeled soil respiration and its components

The empirical model containing both soil temperature and moisture largely improved the fitting of observed R_a for the three biochar application treatments than exponential model only using temperature (Figs. 6a and 8a). Despite the fact that soil temperature and moisture usually covary, the fitting results from the two models indicated that R_a was more sensitive to soil moisture than to soil temperature. However, the model performance for R_h and R_s were very close to those from that only considering soil temperature (Figs. 6 and 8), suggesting that soil temperature mainly regulated the dynamic changes in R_h and R_s in the subtropical forest in Zhejiang, China (Fig. 8).

4. Discussion

4.1. Biochar effects on soil respiration in forest ecosystems

Through meta-analysis, we found that biochar application significantly stimulated R_s in forest ecosystems at the global scale (Fig. S2). The biochar-induced increase in R_s may be largely ascribed to the higher labile C mineralization and/or its priming effect on native soil C decomposition through biotic or abiotic means (Fig. 1; Jones et al., 2011; Zimmerman et al., 2011; He et al., 2016). Specifically, the higher DOC induced by biochar inputs would increase labile C mineralization and stimulate the turnover of SOM (Fig. 1; Jones et al., 2011; Zimmerman et al., 2011). Biochar with high nutrient level was also linked to increases in belowground NPP and soil C accumulation, which stimulated R_s , especially root respiration (R_a), during the long term experiments (Van Zwieten et al., 2010; Zhou et al., 2014).

Different ecosystems may show different responses of R_s to biochar application. Our analysis found that biochar application significantly increased R_s in temperate forests ($P < 0.01$), but did not significantly affect R_s in subtropical forests (Fig. 2, Table S2). The stimulation of R_s in temperate forests may arise from increased soil temperature, which is an important limiting factor for soil microbial activity in middle and high latitude forests (Mikan et al., 2002). On the other hand, the more closed canopy in forest ecosystems may reduce the effects of biochar application on soil temperature and moisture (Mikan et al., 2002).

Subtropical and tropical regions have a higher amount of N deposition than temperate regions (Galloway et al., 2004). The higher N deposition in subtropical forests usually caused soil acidification and increased toxic metal ions (i.e., aluminum ions), which decreased microbial biomass and mycorrhizal abundance, thereby limiting root and microbial activities and respiration (Fig. 1; Thomas et al., 2010; Zhou et al., 2017). In subtropical forests, therefore, effects of N deposition and human activity on R_s were likely to be greater than that of biochar application. Our experimental region experienced a serious long-term soil acidification with an average total N input rate of $291 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, which has inhibited the growth of tree species as well as soil bacterial community abundance and diversity, and then decreased R_a and R_h (Fig. 1, Deng et al., 2007; Thomas et al., 2010).

Our field experiment in a subtropical forest in Tiantong, Zhejiang Province, China also showed that biochar application had no statistically significant effect on R_s or its components (Fig. 4; Table 2), which was consistent with our results from the meta-analysis and another field study in a subtropical chestnut forest (Wang et al., 2014). For example, neither the relative growth rate (RGR) of the dominant species nor the microbial biomass were significantly affected by biochar treatments at the experimental site (Raich et al., 2002; Zhao, 2015), causing non-significant effect on R_s (Fig. 1). Biochar with relative higher pyrolysed temperature was generally recalcitrant and usually had little available C and nutrients for microbial growth, resulting in little effect on SOM decomposition (or R_h , Fig. 1, (He et al., 2016). We also found that biochar application did not significantly affect soil temperature or moisture to change R_s and its components in Tiantong, Zhejiang (Fig. 3; Mikan et al., 2002).

Our results from this meta-analysis showed that experimental method (both laboratory incubation and field experiment) and soil texture (both coarse and medium) substantially affected R_s in response to biochar application (Wardle et al., 2008; Zimmerman et al., 2011; He et al., 2016). Biochar-induced increases in R_s were more significant in laboratory incubations than field experiments in temperate forests, which could be attributed to the mineralization of labile C fraction and the enhanced microbial activity under incubation condition (Fig. 2b, Zimmerman et al., 2011). Similar to the results observed by Stewart et al. (2013) and He et al. (2016), biochar application in coarse soil exerted more significant positive effects on R_s than those in medium soil in temperate forests (Fig. 2c). Biochar application to coarse soil was likely to improve soil aeration and increase MBC, and thus accelerated SOM decomposition and then increased R_s (Fig. 5, Wardle et al., 2008; Stewart et al., 2013; Liu et al., 2016).

4.2. Temporal variability of on soil respiration and its source components

Substrate availability, temperature and soil moisture have been recognized as the major factors in controlling R_s and its temporal variability (Luo and Zhou, 2006). Both soil temperature and water availability can alter activities of plant roots and soil microbes, which directly affect R_s (Wan et al., 2007; Li et al., 2013). In our field study, temporal variability of R_h and R_s exhibited a strong positive correlation with soil temperature under control and biochar treatments (Figs. 6 and 8). These results suggest that soil temperature is a good predictor for temporal variability of R_h and R_s in the Tiantong forest ecosystem. Such a strong temperature dominance of R_s and R_h has been supported in many studies in subtropical forest ecosystems (Tan et al., 2013; Wang

et al., 2014). There were no clear relationship between R_a and soil temperature fitted from the exponential model (Fig. 6a). The uncertainty of the modeled R_a might be attributed to the fact that R_a only contributed to a small proportion to R_s (16%), and the activities of roots and associated rhizosphere organisms might be strongly affected by other factors (e.g., soil moisture) (Trumbore et al., 1996; Sheng et al., 2010). On the other hand, trenching methods to distinguish R_s components may cause some biases in precisely estimating R_a , although the method is simple, cost effective and easily comparable to other methods in terrestrial ecosystems (Zhou et al., 2007). Specifically, the severed roots by trenching may remain undecomposed for a long time and soil moisture may be different between in and outside the trenched plots, resulting in underestimating or overestimating R_a , thus contributing to larger uncertainties (Luo and Zhou, 2006).

Compared with the results from the exponential model only using temperature, the fit between observed and modeled R_h and R_s was not improved with the inclusion of both soil temperature and moisture (Fig. 8). Although soil temperature and moisture often covary in forest ecosystems, the comparisons between the two models suggest that R_h and R_s were more sensitive to soil temperature than to soil moisture at our experimental site. This is because, generally, soil water is not a limiting factor for R_s in the subtropical forest (Sheng et al., 2010). R_a exhibited a better fit in the model including both soil temperature and moisture (Fig. 8a). It has been known that soil moisture has strong effect on plant photosynthesis, which would influence photosynthetically fixed C inputs to belowground roots, and then root biomass and activities (Luo and Zhou, 2006). Therefore, it is necessary to address both biotic and abiotic factors (e.g., biomass, NPP, soil moisture) to better understand their impacts on R_a .

Different forest management practices can markedly influence the temperature sensitivity of R_s and its components (Q_{10} , Boone et al., 1998; Zhou et al., 2007). We found that the apparent Q_{10} value of R_h and R_s increased after biochar application to the forest soil, indicating that biochar application enhanced their temperature sensitivity (Fig. 7b), which has been supported by Wang et al. (2014) in another subtropical forest. The biochar-induced increase in Q_{10} values may result from the enhanced substrate availability, which promoted the decomposition of SOM and then R_s (Woolf et al., 2010). On the other hand, biochar application may contribute to the accumulation of resistant C pools in SOM, leading to the increase of temperature sensitivities (Thiessen et al., 2013). In addition, our results found that the Q_{10} value for R_h was close to those for R_s , indicating that the sensitivity of R_s mainly depend on the contribution of microbial respiration (Fig. S5).

4.3. Implications for soil C balance in forest management and model development

Understanding effects of biochar application on R_s and its components and revealing their key mechanisms in forest ecosystems is very important to mitigate C emissions. Biochar has often been used as a management strategy to promote soil C sequestration in forest ecosystems (Cox et al., 2000; Zimmerman et al., 2011). However, our understanding of effects of single environmental factors (e.g., soil temperature and moisture) or their interactive effects on soil C dynamics under biochar application is still limited (Zimmerman et al., 2011; Liu et al., 2016). Meanwhile, forests ecosystems are simultaneously suffering multiple environmental factors such as N deposition, rising temperature, and changes in precipitation patterns, which would cause different responses of R_s components (R_a and R_h) to biochar application at the global scale (Zhou et al., 2014). In addition, only 42 studies related to the R_s in forest ecosystems under biochar application were integrated into our database. Therefore, it is necessary to conduct more long term manipulative experiments, especially in tropical and boreal forests, to further evaluate the effects of biochar application on R_s and its components under the rapid changing environments.

Our results from the meta-analysis found that biochar application significantly increased R_s in temperate forest but had no statistically significant effect in a subtropical forest. However, current land surface models usually do not take into explicit consideration the differential effects of biochar application on R_s in different forest types, which often create a vital constraining factor to precisely quantify and predict C fluxes from forest to the whole Earth scales (Lal, 2004; He et al., 2016). Therefore, diverse responses of R_s to biochar application in different forest type should be adequately considered in future modelling prediction. In addition, a large number of forests are facing the potential high risk of large-scale wildfire, which would stimulate the emission of GHGs and thus pose great threats for global climate change in the future. Utilizing the biomass from forest-origin residues in wildfire risk regions to produce biochar has now been widely recognized as a viable economical and environmentally sustainable strategy for C sequestration (Jefferey et al., 2013). Meanwhile, biochar was usually produced by wildfire in natural forest ecosystems, which may have a vital role in affecting terrestrial ecosystem processes and then R_s . Therefore, future Earth system models may need to incorporate the effects of biochar originated from nature wildfire on R_s in regional and global forest.

5. Conclusions

Using a meta-analysis technique, we found that biochar application significantly increased R_s by 20.25% in temperate forest ecosystems, while had no effects in subtropical forest (−4.89%). Meanwhile, a field experiment further confirmed that biochar amendment had no significant effects on R_s and its components (R_a and R_h) during the whole period in a subtropical forest in Eastern China. However, biochar application significantly increased apparent temperature sensitivity (Q_{10}) of both R_h and R_s . The differential effects of biochar application on R_s in different forest types may improve our understanding of how biochar stimulates C sequestration. Therefore, it is necessary to develop different strategies towards widespread adoption of biochar as a soil amendment in diverse forests ecosystems to mitigate climate change.

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Appendix A. Supplementary materials

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.09.038>.

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