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Biochar amendment boosts photosynthesis and biomass in C_3 but not C_4 plants: A global synthesis

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Abstract

Biochar is a carbon (C)-rich solid produced from the thermochemical pyrolysis of biomass. Its amendment to soils has been proposed as a promising mean to mitigate greenhouse gas emissions and simultaneously benefit agricultural crops. However, how biochar amendment affects plant photosynthesis and growth remains unclear, especially on a global scale. In this study, we conducted a global synthesis of 74 publications with 347 paired comparisons to acquire an overall tendency of plant photosynthesis and growth following biochar amendment. Overall, we found that biochar amendment significantly increased photosynthetic rate by 27.1%, and improved stomatal conductance, transpiration rate, water use efficiency, and chlorophyll concentration by 19.6%, 26.9%, 26.8%, and 16.1%, respectively. Meanwhile, plant total biomass, shoot biomass, and root biomass increased by 25.4%, 22.1%, and 34.4%, respectively. Interestingly, plant types (C_3 and C_4 plants) showed greater control over plant photosynthesis and biomass than a broad suite of soil and biochar factors. Biochar amendment largely boosted photosynthesis and biomass on C_3 plants, but had a limited effect on C_4 plants. Our results highlight the importance of the differential response of plant types to biochar amendment with respect to plant growth and photosynthesis, providing a scientific foundation for making reasonable strategies towards an extensive application of biochar for agricultural production management.

KEYWORDS

biochar, biomass, C_3 and C_4 plants, ecosystem services, photosynthesis, plant growth

1 | INTRODUCTION

On average, global surface temperature has risen about 0.85°C relative to the preindustrial era, which is mainly attributed to the increased greenhouse gas (GHG) emissions by human activities (IPCC, 2013; Solomon, Plattner, Knutti, & Friedlingstein, 2009). To mitigate global climate change, withdrawing carbon dioxide (CO_2) from the atmosphere has

been suggested as a more feasible mitigation strategy since some emissions are inevitable (Lehmann, 2007; Meinshausen et al., 2009; Smith et al., 2008). Soil carbon (C) sequestration through biochar, which contains a large portion of recalcitrant chemical oxidants and is resistant to biological degradation for hundreds and even thousands of years, has been proposed as one of the technologies to negate GHG emissions (Kuzyakov, Subbotina, Chen, Bogomolova, & Xu, 2009; Lehmann, Czimczik, Laird, & Sohi, 2015; Smith, 2016; Woolf, Amonette, Street-Perrott, Lehmann, & Joseph, 2010).

Biochar is a C-rich solid produced by the pyrolysis of organic materials under oxygen-limited conditions (Laird, 2008; Lehmann, 2007). Biochar is widely advocated as a promising soil amendment to mitigate soil GHG emissions and enhance C sequestration (He et al., 2017; Liu et al., 2016; Zhou et al., 2017). Furthermore, biochar amendment also brings several potential co-benefits, such as reducing nutrient runoff, boosting soil fertility, enhancing soil water-holding capacity, and alleviating soil heavy metal contamination thereby boosting plant productivity and crop yield (CY; Bai et al., 2015; Gao, DeLuca, & Cleveland, 2019; Mukherjee, Lal, & Zimmerman, 2014; Rees, Simonnot, & Morel, 2014; Zhang et al., 2020). However, contradictory reports regarding the effects of biochar amendment on plant photosynthesis and growth exist (Abbas et al., 2018; Farrar et al., 2019; Kumar et al., 2018; Rehman et al., 2017). For example, the net photosynthetic rate (P_n) of *Poncirus trifoliata* (L.) Raf. increased by 47%–58% following biochar application (Guo, Pan, & Peng, 2016), but decreased or had no effect in other studies (Nguyen, Wallace, et al., 2017; Speratti, Johnson, Sousa, Dalmagro, & Couto, 2018; Xu, Hosseini-Bai, et al., 2015).

Several mechanisms underlying the effects of biochar amendment on plant photosynthetic rates have been proposed. In general, biochar amendment increases soil nitrogen (N) availability and retention, improves soil water-holding capacity, increases soil pH and cation exchange capacity, decreases soil bulk density, facilitates beneficial microorganisms, and limits bioavailability of heavy metals, which are associated with increases in plant photosynthesis (Chen, Meng, Han, Lan, & Zhang, 2019; Glaser, Lehmann, & Zech, 2002; Graber et al., 2010; Kolb, Fermanich, & Dornbush, 2009; Liu et al., 2018; Nguyen, Xu, et al., 2017). In addition, biochar amendment and the induced changes in soil properties can also affect plant performance by altering root growth and traits. Accumulating evidence suggest that biochar stimulates root growth and benefits root morphological development, including increased root biomass (RB), root volume, surface area, root density, and root length, to acquire more nutrients and water for stimulating plant photosynthesis and growth (Bruun, Petersen, Hansen, Holm, & Hauggaard-Nielsen, 2014; Joseph et al., 2010; Lehmann et al., 2011; Makoto, Tamai, Kim, & Koike, 2010; Xiang, Deng, Duan, & Guo, 2017). In contrast, increased soil salinity, soil alkalinity, and nutrient immobilization observed after biochar application particularly at high rates can be linked to decreased photosynthetic rates (Nguyen, Xu, et al., 2017; Speratti et al., 2018).

Contradictory reports on changes in magnitude of plant photosynthetic rate following biochar amendment have been explained through multiple mechanisms. Effects of Biochar amendment on plant photosynthesis are also linked to soil properties, farming practices, experimental methods, biochar application rates, biochar physicochemical characteristics, and plant types (Jeffery, Verheijen, van der Velde, & Bastos, 2011; Rehman et al., 2016; Sarma, Borkotoki, Narzari, Kataki, & Gogoi, 2017). These factors could influence soil nutrient and water availability after biochar addition, consequently changing plant physiological characteristics. However, how the above-mentioned factors influence the response of photosynthesis processes to biochar amendment at the global scale is still largely unclear.

In this study, we compiled 347 independent experimental observations culled from 74 published manuscripts and synthesized the responses of plant photosynthesis, biomass, and other growth variables to biochar amendment using a meta-analysis. Our study was aimed at (a) obtaining a central tendency of plant photosynthesis and growth in response to biochar amendment and (b) investigating the key driving factors that affect the response of plant photosynthesis and growth following biochar amendment.

2 | MATERIALS AND METHODS

2.1 | Data sources

Research literatures were searched in *Web of Science*, *Google Scholar* and *China National Knowledge Infrastructure* (1900–2019) with the keywords "biochar OR char OR charcoal AND photosynthesis OR photosynthetic activity OR photosynthetic rate". Appropriate publications were selected by the following criteria: (a) observations had one pair of data at lowest (comparing a control and biochar-amended treatment) and measured photosynthesis in plants; (b) the plots for all treatments had the same environmental conditions and dominant vegetation composition as the control at the beginning of the experiments; (c) the methods for biochar amendment were explicitly described, including biochar application rate and experimental duration; and (d) the mean and its standard deviation or error of variables in each treatment could be extracted from contexts or supplemental materials directly. Totally, 74 peer-reviewed literatures published from 2011 to October 2019 with 347 paired comparisons were selected from more than 800 publications (Appendices S1 and S2), and the study sites are distributed globally (Figure S1). Multiple biochar types (Akhter, Hage-Ahmed,

Soja, & Steinkellner, 2016; Kumar et al., 2018), biochar amendment rates (Baronti et al., 2014; Speratti et al., 2018), soil types (Xu, Hosseini-Bai, et al., 2015), or N fertilization levels (Sarma et al., 2017; Xu, Bai, et al., 2015) were considered as different individual studies.

We collected four classifications of data from these selected publications of biochar amendment studies: (a) plant photosynthesis and relative physiological properties (e.g., stomatal conductance [g_s], chlorophyll [Chl] content, and water use efficiency [WUE]), and plant biomass and morphological attributes (e.g., plant high and leaf area); (b) biochar properties, mainly including feedstock sources, pyrolysis temperature, pH and biochar application rate; (c) soil properties, including soil organic C, soil total N, C/N ratio, soil texture, and soil pH; and (d) other auxiliary variables, such as plant types (i.e., C_3 vs. C_4 species; C_3 plants use the carboxylase enzyme of ribulose-1,5-bisphosphate carboxylase/oxygenase to directly fix CO_2 from the air and obtain 3-carbon intermediate molecules in photosynthesis, while C_4 plants use the phosphoenolpyruvate carboxylase (PEPc) enzyme to incorporate CO_2 into a 4-carbon compound, which is then shuttled to specialized bundle sheath cells to participate in photosynthesis), site location, experimental method, N fertilization, and experimental duration. These variables presented in (b)–(d) were treated as explanatory variables of the changes in photosynthesis and biomass responses to biochar amendment.

2.2 | Analysis

The method employed by Hedges, Gurevitch, and Curtis (1999) was adopted to assess the effects of plant photosynthesis and other variables to biochar application. The natural log-transformed response ratio (RR) was used to calculate the effect size as the following equation:

$$\mathrm{RR} = \ln\frac{X_t}{X_c} = \ln(X_t) - \ln(X_c), \tag{1}$$

where X_t and X_c refer to the means of P_n with and without biochar application, respectively. The variance (v) of RR is calculated as:

$$v = \frac{S_t^2}{n_t X_t^2} + \frac{S_c^2}{n_c X_c^2}, \tag{2}$$

where n_c and n_t refer to number of replicates in the control and biochar treatments, respectively. Meanwhile, S_c and S_t refer to the standard deviations (SD) in the control and biochar treatments, respectively.

To summarize the central trends of selected variables to biochar amendment, the mean effect size was quantified by the weighted response ratio (RR_{++}) using the random effects model (Borenstein, Hedges, Higgins, & Rothstein, 20092009; Rosenberg et al., 2000):

$$\mathrm{RR}_{++} = \frac{\sum_{i=1}^{k} W_i^* \mathrm{RR}}{\sum_{i=1}^{k} W_i^*}, \tag{3}$$

where k is the number of RR and W_i^* is the weight of each RR. We converted the effect size to percentage change [%(RR_{++})] based on the following equation:

$$\%(\mathrm{RR}_{++}) = [\exp(\mathrm{RR}_{++}) - 1] \times 100\%. \tag{4}$$

The 95% bootstrap confidence intervals (CIs) were calculated by using a bootstrapping (999 iterations) method (Adams, Gurevitch, & Rosenberg, 1997; He et al., 2017). If the 95% CIs did not overlap with zero, biochar amendment would induce significant effect (Luo, Hui, & Zhang, 2006; Zhou et al., 2014).

The frequency distribution of RR was examined using a Normal-test and fitted using the following Gaussian function:

$$y = \alpha \exp\left[-\frac{(x-\mu)^2}{2\sigma^2}\right], \tag{5}$$

where x represents the mean of RR, y represents the frequency of RR values, μ and σ^2 represent the mean and variance across all RR values, respectively, and α represents a coefficient indicating the expected number of RR at $x = \mu$.

To examine the heterogeneity among subgrouping categories, the between-group heterogeneity (Q_b) was calculated by using the MetaWin 2.1 software. We also used a random effect model to identify these biochar, soil physicochemical characteristics, and other explanatory factors which influence the response of photosynthesis to biochar amendment. Meta-regression was performed to explore the relationships between *RR* (photosynthesis and biomass) and continuous variables (e.g., g_s, transpiration [E], and WUE). Correlation analysis was conducted to examine the correlations of RR between photosynthesis and biomass using R (R Core Team, 2015). The effects of plant type (C_3 and C_4) on physiological variables–photosynthesis and photosynthesis–biomass relationships were examined using analysis of covariance (ANCOVA).

Furthermore, we selected the meta-analytic models by using Akaike information criterion (AICc; Chen et al., 2018; Terrer, Viccam, Hungate, Phillips, & Prentice, 2016; van Groenigen et al., 2017). Briefly, we analyzed all possible models containing potential combinations of the experimental factors in a mixed-effects meta-regression model using maximum likelihood estimation, using the "metafor" and "glmulti" package in R. The relative importance value for a factor was computed as the sum of Akaike weights for all

models in which the predictor appears. These values could be treated as the total support for each factor across all models.

Publication bias in this study was examined using funnel plot and Kendall's Tau methods (Møller & Jennions, 2001; Rosenberg et al., 2000). When the funnel plot statistics were significant ($p < .05$), Rosenthal's fail-safe number was computed to figure out whether the effect size tended to be influenced by unpublished researches (Rosenberg, 2005). Our result against publication bias when the fail-safe number is greater than $5n + 10$ (n is the number of cases).

3 | RESULTS

3.1 | Biochar effects on plant photosynthetic properties

On average, biochar amendment to soils significantly increased P_n ($RR_{++} = 0.24$), g_s ($RR_{++} = 0.18$), E ($RR_{++} = 0.24$), WUE ($RR_{++} = 0.24$), Chl ($RR_{++} = 0.15$), chlorophyll *a* (Chl *a*, $RR_{++} = 0.22$), chlorophyll *b* (Chl *b*, $RR_{++} = 0.27$) when compared with the corresponding controls. The responses of P_n to biochar amendment were positively correlated with those in g_s, E, WUE, and Chl (Figure S5). Total biomass (TB), shoot biomass (SB), RB, CY, plant height (PH), and leaf area (LA) were also increased by 25.4%, 22.1%, 34.4%, 17.7%, 12.9%, and 11.1%, respectively after biochar amendment, but no significant change in root/shoot ratio was observed (R/S, Figure 1). Publication bias for this analysis was not found among all the investigated variables except for LA (Table S1).

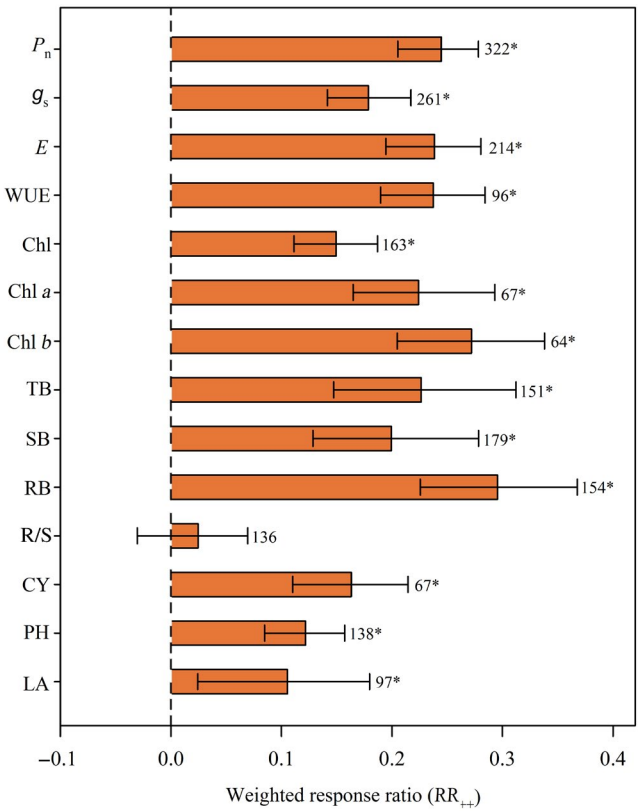

FIGURE 1 Effects of biochar amendment on plant growth (including photosynthetic rate [P_n], stomatal conductance [g_s], transpiration rate [E], water use efficiency [WUE], chlorophyll [Chl], chlorophyll *a* [Chl *a*], chlorophyll *b* [Chl *b*], total biomass [TB], shoot biomass [SB], root biomass [RB], root/shoot ratio [R/S], crop yield [CY], plant height [PH], leaf area [LA]) are shown as mean weighted response ratio (RR_{++}). Mean effect and 95% confidence interval (CI) are shown. If the CI did not overlap with zero, the response was considered significant ('*'). Numerals indicate the number of observations

The response of physiological variables (P_n, g_s, E, WUE, Chl, Chl *a*, and Chl *b*) to biochar amendment significantly depended upon biochar characteristics, plant types, experimental factors (methods and duration), and soil properties (Table 1). A model selection analysis confirmed that responses of P_n, g_s, E, WUE, and Chl were best predicted by plant type and experimental duration, plant type and pyrolysis temperature, plant type and N fertilization, plant type and biochar C/N, soil texture and experimental duration, respectively (Figure 2). Also, plant type and soil texture were the major factors mediating the response of plant morphological attributes (TB, SB, RB, R/S, CY, PH, and LA) to biochar amendment (Table 2).

3.2 | Influence of plant type and other factors on photosynthetic properties

Plant type had a significant effect on the physiological and morphological variables after biochar application (Table 2; Figure 2). The average effect size of photosynthetic properties to biochar amendment for C_3 plants was significantly greater than that of C_4 plants (Figure 3a). Specifically, biochar amendment significantly increased P_n and E by 32.2% and 29.9%, respectively in the C_3 plants, which were significantly higher than those of C_4 plants (7.3% and 10.1%, respectively; Figure 3a). Similar patterns were observed in Chl *a* and Chl *b*. Meanwhile, biochar amendment led to increases of 26.1%, 30.6%, and 18.5% in g_s, WUE, and Chl for C_3 plants respectively, while no significant effects were found for C_4 plants (Figure 3a).

On average, biochar amendment significantly increased TB, SB, RB, and CY by 39.2%, 36.4%, 48.1%, and 21%, respectively in the C_3 plants, which were significantly higher than those of the C_4 plants. Also, the amendment of biochar to soils resulted in increased PH (13.8%) and LA (13.8%) for C_3 plants, but no significant effects were observed in the C_4 plants. Biochar amendment did not significantly affect R/S ratio for both for C_3 and C_4 plants (Figure 3b).

Pyrolysis temperature of biochar, biochar C/N, experimental duration, N fertilization, and soil texture showed significant effects on physiological and morphological variables (Table 2).

TABLE 1 Between-group variability (Q_b) among observations (n) suggesting their potential as predictive variables influencing plant physiological variables to biochar amendment

	P_n		g_s		E		WUE		Chl		Chl *a*		Chl *b*	
Variables	n	Q_b	n	Q_b	n	Q_b	n	Q_b	n	Q_b	n	Q_b	n	Q_b
Plant type	322	17.19***	261	27.69***	214	6.92**	96	15.33**	163	8.58**	67	1.64	64	1.56
N fertilization	322	1.93	261	2.96	214	7.63**	96	0.58	163	0.00	67	11.21***	64	5.01*
Exp. method	322	12.57***	261	0.23	214	0.04	96	3.50	163	0.002	67	0.64	—	—
Exp. duration	311	8.45**	254	0.31	207	4.96*	93	1.76	156	6.09*	67	8.16**	64	4.78*
Addition rate (t/ha)	208	1.40	161	0.006	122	2.31	81	1.84	94	0.29	30	1.67	27	4.76*
Feedstock source	279	4.44	228	5.11	199	2.19	93	18.68***	140	28.56***	67	3.30	64	8.28*
Pyrolysis temp. (°C)	250	3.41	210	13.78***	185	0.009	92	1.31	112	1.54	67	0.13	64	1.14
Biochar C/N	199	9.91**	160	5.23*	139	8.43**	55	13.14***	104	16.47***	61	17.22***	58	14.02***
Biochar pH	267	10.07**	214	7.55**	181	1.72	92	7.51**	136	17.39***	67	15.99***	64	20.92***
Soil pH	235	21.77***	186	28.82***	165	25.41***	73	2.52	127	22.31***	61	18.82***	58	15.22***
Soil texture	300	4.39	244	12.44**	197	19.73***	88	5.69	155	19.47***	67	3.82	64	4.67

Note: A larger Q_b is a better predictor of variation than a variable with smaller Q_b. Statistical significance of Q_b: *$p < .05$; **$p < .01$; ***$p < .001$.

Abbreviations: Chl, chlorophyll; E, transpiration rate; g_s, stomatal conductance; P_n, photosynthetic rate.

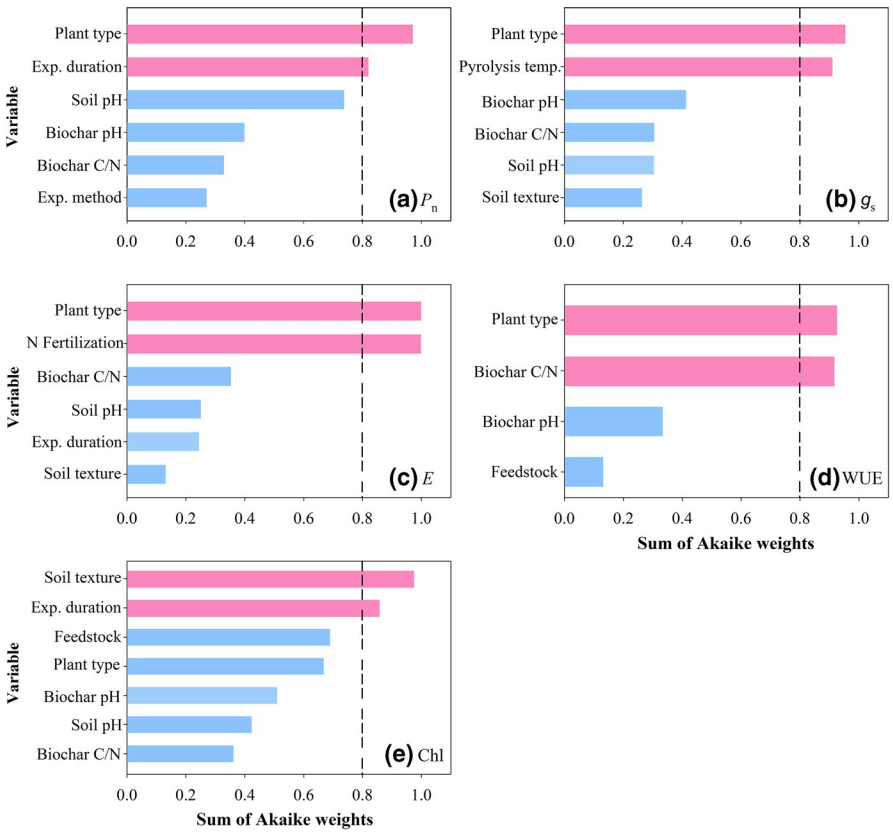

FIGURE 2 Model-averaged importance of the predictors of biochar amendment on photosynthetic variables, including photosynthetic rate (P_n, a), stomatal conductance (g_s, b), transpiration rate (E, c), water use efficiency (WUE, d), chlorophyll (Chl, e). The importance value is based on the sum of Akaike weights, which was derived from model selection using corrected Akaike's information criteria. Cutoff is set at 0.8 to differentiate between essential and nonessential predictors

Specifically, the responses of physiological variables (P_n, g_s, E, WUE, and Chl) significantly decreased with biochar C/N, and g_s decreased with biochar pyrolysis temperature. Meanwhile, P_n and E decreased with experimental duration, while Chl increased (Figure S2). The combined effect of biochar amendment with N fertilization was not pronounced for physiological

TABLE 2 Between-group variability (Q_b) among observations (n) suggesting their potential as predictive variables influencing plant morphological variables to biochar amendment

	TB		SB		RB		R/S		CY		PH		LA	
Variables	n	Q_b	n	Q_b	n	Q_b	n	Q_b	n	Q_b	n	Q_b	n	Q_b
Plant type	151	15.79***	179	18.37***	154	21.16***	136	0.03	67	4.57*	138	1.38	97	1.72
N Fertilization	151	2.68	179	3.82	154	2.36	136	0.29	67	0.69	138	8.79**	97	0.03
Exp. method	151	0.71	179	1.03	154	1.07	136	0.31	67	0.38	138	0.67	97	9.57**
Exp. duration	151	0.07	179	0.12	150	0.003	136	0.54	67	0.21	134	1.38	97	0.44
Addition rate (t/ha)	91	14.16***	121	7.59**	98	0.60	84	1.36	48	0.03	89	1.23	96	1.13
Feedstock source	135	0.17	161	0.84	138	1.99	120	8.75*	63	10.65**	131	7.14*	75	1.20
Pyrolysis temp. (°C)	126	0.52	152	0.18	125	1.01	111	0.00	49	6.74**	111	2.23	69	3.52
Biochar C/N	96	2.86	121	6.32*	100	3.83	86	2.09	48	1.21	82	0.47	45	0.008
Biochar pH	134	0.03	154	0.51	133	0.29	119	0.04	49	0.06	113	1.43	79	0.39
Soil pH	128	0.01	149	0.16	124	0.01	122	8.34**	67	7.23**	95	0.56	65	8.48**
Soil texture	136	18.08***	167	27.81***	142	18.37***	124	1.58	67	3.49	125	1.41	87	1.31

Note: A larger Q_b is a better predictor of variation than a variable with smaller Q_b. Statistical significance of Q_b: *$p < .05$; **$p < .01$; ***$p < .001$.
Abbreviations: PH, plant height; R/S, root/shoot ratio; RB, root biomass; SB, shoot biomass; TB, total biomass.

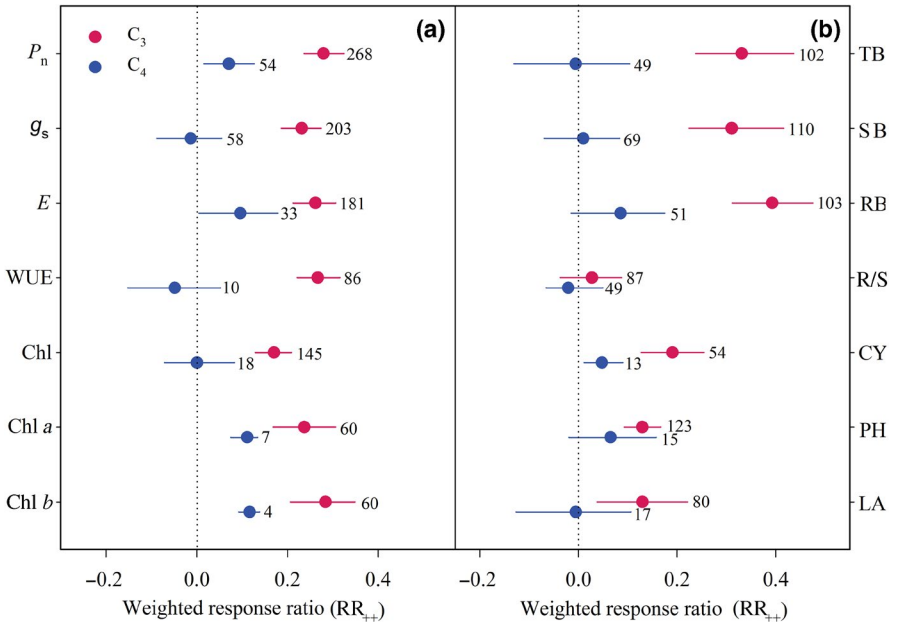

FIGURE 3 The effect of biochar amendment on plant photosynthesis (a) and growth (b) in C_3 and C_4 plants. Mean effect and 95% CIs are shown. If the CI did not overlap with zero, the response was considered significant. Numerals indicate the number of observations. Chl, chlorophyll; Chl *a*, chlorophyll *a*; Chl *b*, chlorophyll *b*; CI, confidence interval; CY, crop yield; *E*, transpiration rate; g_s, stomatal conductance; LA, leaf area; P_n, photosynthetic rate; PH, plant height; R/S, root/shoot ratio; RB, root biomass; RR_{++}, weighted response ratio; SB, shoot biomass; TB, total biomass; WUE, water use efficiency

variables except for *E* and Chl *a* (Figure S3). Biochar amendment significantly increased plant biomass in soils with medium and fine texture, but no changes were observed in soils with coarse texture (Figure S4).

3.3 | Relationships between physiological properties and plant biomass differed between C_3 and C_4 plants

Changes in P_n following biochar amendment were positively correlated with those in g_s ($R^2 = .54$, $p < .01$), *E* ($R^2 = .39$, $p < .01$), WUE ($R^2 = .37$, $p < .01$), and Chl ($R^2 = .29$, $p < .01$) for C_3 plants, respectively. Similar patterns were observed for C_4 plants, but biochar-induced changes in P_n and WUE were not significantly correlated ($p = .19$; Figure 4). Meanwhile, the relationships between responses of P_n with those in g_s ($F = 1.65$, $p = .20$), *E* ($F = 2.98$, $p = .09$), WUE ($F = 0.37$, $p = .54$), and Chl ($F = 0.60$, $p = .44$) were not significant regardless of plant types (either C_3 or C_4 plants) using analysis of covariance (ANCOVA; Figure 4).

The responses of TB, SB, and RB to biochar amendment were positively correlated with those in P_n for C_3 ($R^2 = .55$,

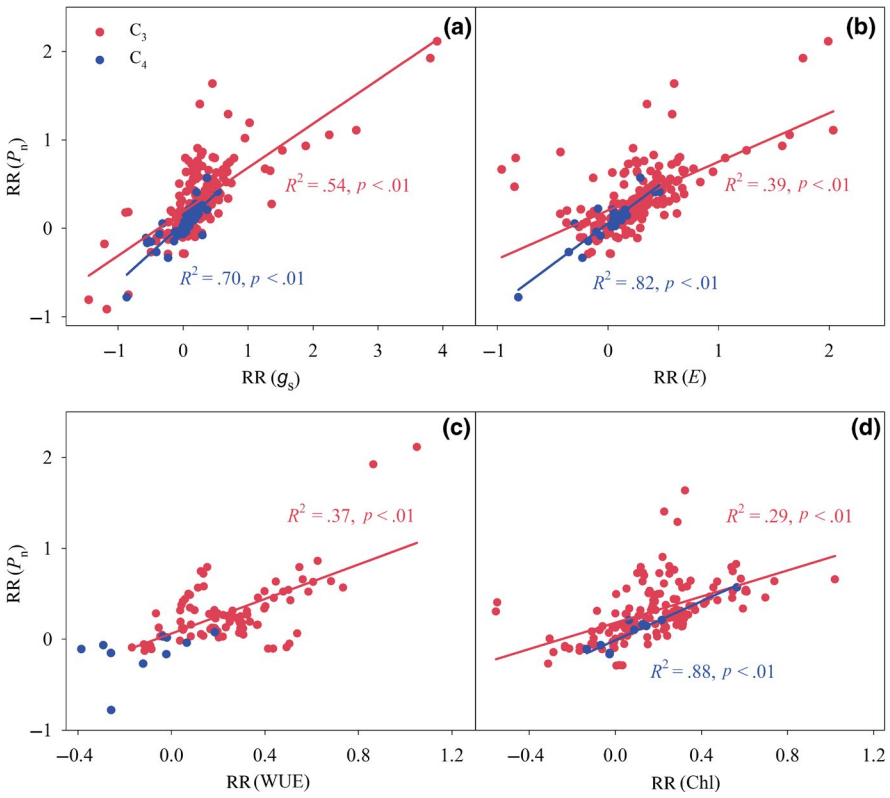

FIGURE 4 The relationships between the response ratio of photosynthetic rate (P_n) and stomatal conductance (g_s, a), transpiration rate (E, b), water use efficiency (WUE, c), and chlorophyll (Chl, d) in C_3 and C_4 plants. RR_{++}, weighted response ratio

$p < .01$; $R^2 = .50$, $p < .01$; $R^2 = .66$, $p < .01$, respectively) and C_4 plants ($R^2 = .54$, $p < .01$; $R^2 = .40$, $p < .01$; $R^2 = .44$, $p < .01$, respectively), but the slopes of linear regressions in C_3 plants were significantly greater than those in C_4 plants (ANCOVA, $F = 6.39$, $p = .01$; $F = 9.63$, $p < .01$; $F = 7.17$, $p < .01$; Figure 5a–c).

4 | DISCUSSION

4.1 | Biochar effects on plant photosynthesis and biomass

The positive effect of biochar on plant growth depends largely on alleviating soil constrains and reducing the absorption of heavy metals and pesticides by plants (Kavitha et al., 2018; Moradi, Pourghasemian, & Naghizadeh, 2019). Our results showed that biochar amendment significantly increased P_n by 29.7%, which is basically in accordance with previously published studies (Sarma et al., 2017; Speratti et al., 2018; Sun, Chen, Cao, Li, & Zhang, 2017). The increase in P_n could be explained by increased leaf g_s, E, and Chl following biochar amendment (Figure 1; Figure S5). The improving g_s and E may be associated with the increased soil water holding capacity, which might resulted from the porous physical structure of biochar (Kammann & Graber, 2015; Laghari et al., 2015; Novak et al., 2012). Meanwhile, the increased leaf Chl content may be due to the increased soil N availability followed by a subsequent increase of foliar N concentrations (Agegnehu et al., 2015; Bai et al., 2015; Liu et al., 2018). A recent study has also shown that N levels in maize aboveground biomass have been significantly enhanced by biochar amendment in a 2 year field experiment (Xiao et al., 2016).

Biochar amendment increased above- and below-ground biomass significantly, which is consistent with prior studies reporting the beneficial aspects of biochar applications (Biederman & Harpole, 2013; Dai, Zheng, Jiang, & Xing, 2020; Lehmann, Gaunt, & Rondon, 2006; Sun et al., 2017). The positive relationship between increased photosynthesis and plant biomass accumulation has been wildly established (Allen et al., 1987; Malhi et al., 2015). Therefore, in our experiment, the biomass improvements could be explained by the increased P_n following biochar amendment. The biochar-induced improvement in soil water-holding capacity and soil N or P availability have been proposed to explain the enhanced plant productivity (Gao et al., 2019; Jeffery et al., 2017; Van Zwieten et al., 2010). Meanwhile, the increase in soil alkalinity following biochar amendment could also be beneficial to plant growth (Speratti et al., 2018), which was further supported by our finding indicating an increased P_n with biochar pH in C_3 plants (Figure S6). Biochar, acting as a liming agent, generally reduces the concentration of iron (Fe) and aluminum (Al) in the soil solution, liberates P from associations with

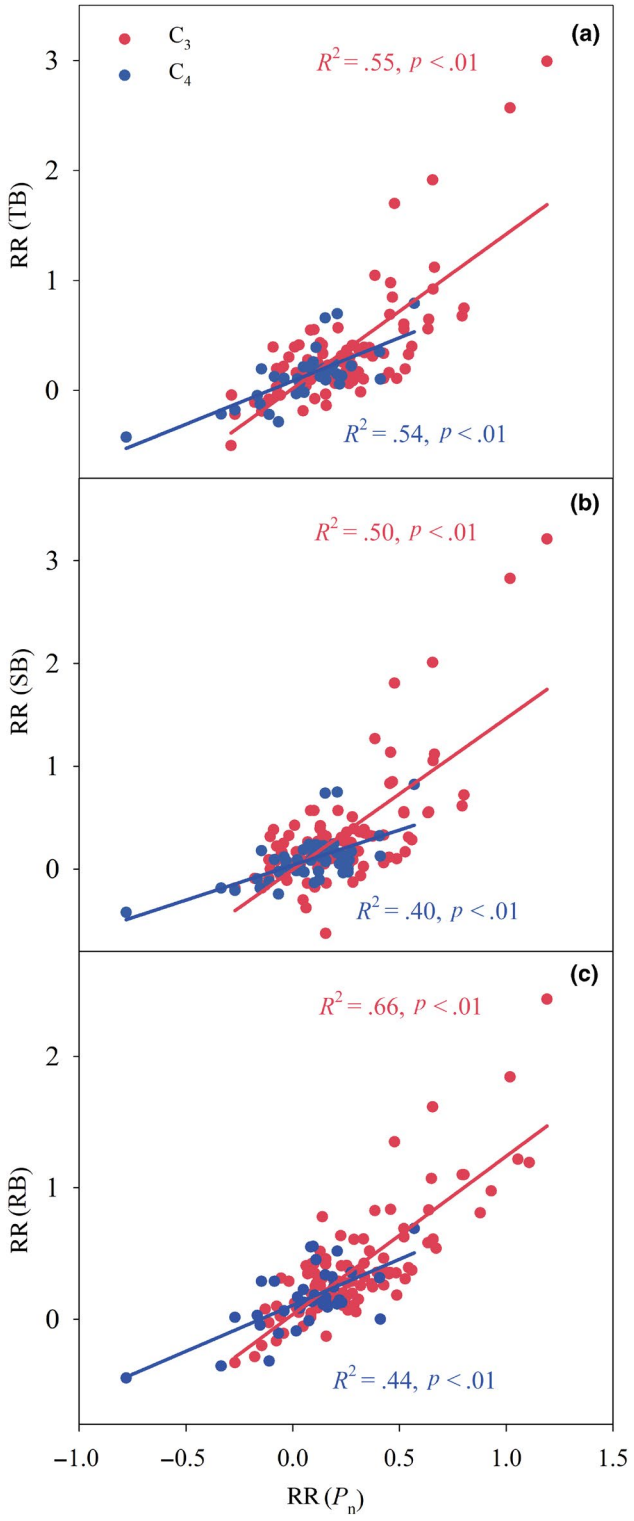

FIGURE 5 The relationships between the response ratio of biomass (including total biomass [TB, a], shoot biomass [SB, b], root biomass [RB, c]) and photosynthetic rate (P_n) differed from plant types (C_3 and C_4). RR_{++}, weighted response ratio

Fe and Al oxides, and makes P available to plants (Cui, Wang, Fu, & Ci, 2011; Lustosa Filho, Barbosa, Carneiro, & Melo, 2019). In addition, the stimulated production of growth-promoting hormones (brassinosteroid, auxin, and their signaling molecules) after biochar amendment could contribute to the growth stimulation of biochar-treated plants (Viger, Hancock, Miglietta, & Taylor, 2015). Therefore, our study provided evidence to show that biochar holds promise in being a win–win solution to ecosystem function and C sequestration.

4.2 | Biochar effects on photosynthesis and biomass between C_3 and C_4 plants

Numerous studies have suggested that the effects of biochar amendment on crop productivity vary with experimental conditions, site regions, soil characteristics, and biochar properties (Dai et al., 2020; Jeffery et al., 2017; Liu et al., 2013). However, our study found that plant type (C_3 and C_4 plants) showed more pronounced effects on photosynthesis than edaphic characteristics, biochar physicochemical properties, soil characteristics, and artificial cultivation management practices, which may be explained by several mechanisms. Firstly, previous works have demonstrated that C_4 species tend to have lower water potential deficits and g_s than C_3 species (Osmond, Winter, & Ziegler, 1982; Taylor et al., 2010). Thus, there is less room for additional benefits from biochar in C_4 species than that in C_3 species, which is largely in accordance with our findings of biochar-induced increases in g_s for C_3 plants but with no significant changes for C_4 plants (Figure 3). The different effects of biochar amendment on g_s in C_3 and C_4 species could be partly explained by the different responses of P_n and productivity to biochar amendment between C_3 and C_4 plants.

Secondly, the photosynthetic pathway of C_4 species is catalyzed by a coupled set of carbonic anhydrase and PEPc. Hence, C_4 species have higher affinity for CO_2 and possess greater maximum velocity than C_3 species which fix CO_2 through ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO) at the carboxylation site (Ehleringer & Monson, 1993). C_4 species also have higher WUE relative to C_3 species (Long, 1999; Taylor, Ripley, Woodward, & Osborne, 2011; Wolf & Ziska, 2018). Despite variation among species, C_4 plants tend to occupy a drier niche than C_3 plants (Edwards & Smith, 2010; Osborne & Freckleton, 2009), implying that C_3 plants are more susceptible to water limitation than C_4 plants. Therefore, the improved soil water retention following biochar amendment would exert more significant positive effects on P_n and productivity for C_3 over C_4 species. Our findings of biochar-induced increases in WUE for C_3 plants but with no effects for C_4 plants (Figure 3), are consistent with this theoretical expectation.

Thirdly, a more efficient photosynthetic carboxylation enzyme system leads to higher N use efficiencies in C_4

species than C_3 species (Anten, Schieving, Medina, Werger, & Schuffelen, 1995; Pinto, Powell, Sharwood, Tissue, & Ghannoum, 2016). The leaf RuBisCO and N content in C_4 plants are usually lower than that in C_3 plants (Ehleringer & Monson, 1993; Taylor et al., 2010), indicating a smaller investment of N in photosynthetic enzymes and a lower N requirement for C_4 than C_3 plants. Accordingly, the increases in plant N uptake and decreases in soil N leaching following biochar amendment (Clough, Condron, Kammann, & Müller, 2013; Liu et al., 2019; Reverchon et al., 2014), are more likely to stimulate the P_n and productivity for C_3 species compared with C_4 species.

Although the responses of P_n to biochar amendment differed within C_3 and C_4 species, the relationships of changes in P_n with those in g_s, E, WUE, and Chl showed no significant difference between C_3 and C_4 species (Figure 4). These results indicated that biochar amendment did not shift the interrelationships between physiological processes at the leaf level. The photosynthesis rate was mainly determined by photosynthesis-related physiological properties. Future researches should focus on a mechanistic understanding of the interactions of biochar application on plant physiological properties. Furthermore, the slopes of linear regressions between response of plant biomass and P_n to biochar amendment in C_3 plants were significantly greater than those in C_4 plants (Figure 5), indicating that biochar seems to be a good strategy to stimulate plant growth and moderate global warming in C_3 plants dominated agroecosystems.

4.3 | Implications for future studies

This study showed that biochar amendment could promote P_n and TB by 32.2% and 39.2%, respectively, for C_3 species, while it induced a minor positive effect (7.3%) on P_n and had no significant effect on TB for C_4 species (Figure 6). Further, P_n increased with biochar pH, but decreased with biochar C content in C_3 species (Figure S6). Thus, we recommend that biochar with higher pH and lower C content would be a better option for C_3 plant-dominated systems than those of C_4 species to maximize plant biomass accumulation. In the study, the compiled database was mainly obtained from short-term experiments in the Northern Hemisphere, and most studies lasting less than one successive season (e.g., Azhar et al., 2019; Haider et al., 2015; Rizwan et al., 2018). Therefore, a lack of long-term field experiments, especially those conducted in the Southern Hemisphere, may hamper our evaluation of ecosystem structure and functioning, including photosynthesis and plant productivity, in response to biochar amendment over a larger timescale.

To establish achievable C sequestration meeting global climate targets, "4 per thousand" initiative was launched by the French government at the 21st session of the Conference of the Paris to the United Nations Framework Convention on Climate Change, aspiring to enhance global soil organic C storages by 0.4% per year (Chabbi et al., 2017; Lal, 2016; Minasny et al., 2017). This goal would trigger a tendency of large quantities of biochar application to a great portion of the earth's cultivated land (Chen et al., 2019; Hansen

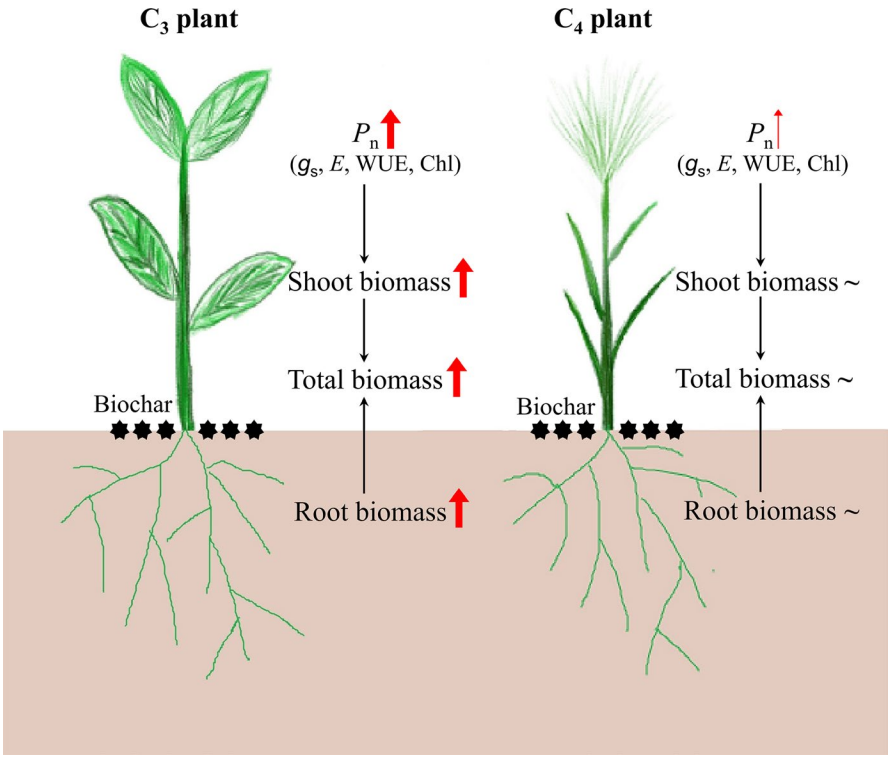

FIGURE 6 Effects of biochar amendment on plant photosynthesis rate (P_n) and biomass varied with C_3 and C_4 plants. The red upward arrows represent positive responses, the thickness of red arrows represent the increase range, and the black wavy line represents non-significance. Chl, chlorophyll; E, transpiration rate; g_s, stomatal conductance; WUE, water use efficiency

et al., 2015). Therefore, it is imperative to study the effects of biochar amendment on soil C sequestration, GHG emission, and water regulation and its interactions with multiple environmental and management factors across various temporal and spatial scales prior to its widespread application.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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