Effects of biochar application on root traits: a meta-analysis

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Abstract

Roots are the interfaces between biochar particles and growing plants. Biochar application may alter root growth and traits and thereby affect plant performance. However, a comprehensive understanding of the effects of biochar on root traits is lacking. We conducted a meta-analysis with 2108 paired observations from 136 articles to evaluate the responses of root traits associated with 13 variables under biochar application. Overall, biochar application increased root biomass (+32%), root volume (+29%) and surface area (39%). The biochar-induced increases in root length (+52%) and number of root tips (+17%) were much larger than the increase in root diameter (+9.9%); this result suggests that biochar application benefits root morphological development to alleviate plant nutrient and water deficiency rather than to maximize biomass accumulation. Biochar application did not change root N concentration but significantly increased root P concentration (+22%), particularly when combined with N fertilization. Biochar application also affected root-associated microbes and significantly increased the number of root nodules (+25%). The responses of root traits to biochar application were generally greater in annual plants than in perennial plants and were affected by soil texture and pH values. Moreover, it appears that biochar production process (pyrolysis temperature and time) plays a more important role in regulating root growth than does biochar source. Together, findings obtained from this meta-analysis may have significant implications for the future sustainable development of biochar management to improve plant growth and functioning.

Keywords: biochar, fertilization, meta-analysis, plant growth, root functioning, root morphology

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Introduction

Biochar is a predominantly stable, recalcitrant organic carbon (C) compound that is produced from biomass via pyrolysis (Lehmann, 2007; Laird et al., 2009). Due to the potential to sequester C in the soil, biochar application is currently considered as a means to help mitigate greenhouse gas (GHG) emissions and climate change (Marris, 2006; Woolf et al., 2010). Recent reviews have highlighted that biochar application can also stimulate plant growth and yield (Jeffery et al., 2011; Biederman & Harpole, 2013; Liu et al., 2013) and thereby enhance the sequestration of carbon dioxide (CO₂) from the atmosphere (Lehmann et al., 2006). Plant root systems play an important role in plant growth and soil C sequestration (Matamala et al., 2003; Nie et al., 2013) because they not only take up soil nutrients and water to support plant production but also transport photosynthetically fixed C to soil organic matter pools (Jackson et al., 1997; Li et al., 2015; Peng et al., 2017). Biochar application may have significant effects on plant root morphology and functioning because biochar particles contact plant roots directly (Prendergast-Miller et al., 2014). Therefore, it is critical to determine how root traits respond to biochar application for sustainable biochar management (Laird, 2008; Jeffery et al., 2015).

Numerous case studies have been conducted to examine how plant roots respond to biochar application (Rillig et al., 2010; Prendergast-Miller et al., 2011; Brennan et al., 2014; Vanek & Lehmann, 2015). Some root traits, including root biomass, morphology (Prendergast-Miller et al., 2011; Brennan et al., 2014; Keith et al., 2015), nutrient concentration, and root-associated microbes (Rondon et al., 2007; Rillig et al., 2010; Vanek & Lehmann, 2015), can be significantly influenced by biochar application. However, due to differential

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research objectives, root traits in these case studies are often studied independently (Prendergast-Miller et al., 2014; Jeffer y et al., 2015). In addition, root traits are usually specific and play different roles in plant growth (Jackson et al., 1997; Matamala et al., 2003; Nie et al., 2013). For example, root length is usually assumed to be proportional to water or nutrient acquisition, while root diameter is thought to be beneficial for biomass accumulation (Eissenstat & Yanai, 1997). Thus, it remains unclear how these root traits respond differently to biochar application. To better understand the underlying mechanism of root growth in response to biochar application, quantitative synthesis across these root traits is required (Lehmann et al., 2011; Jeffery et al., 2015).

To date, the effects of biochar application on root traits remain controversial and highly variable. For example, root biomass may increase (Prendergast-Miller et al., 2011; Varela Milla et al., 2013), decrease (Aguilar-Chávez et al., 2012; Van De Voorde et al., 2014) or remain relatively stable (Macdonald et al., 2014; Keith et al., 2015) under biochar application. These highly diverse results are not surprising because multiple factors and processes are involved in root responses (Prendergast-Miller et al., 2014). For instance, root establishment in the soils can be enhanced by biochar addition (Brennan et al., 2014). The choice of biochar type is also important as biochar generated from different materials or pyrolysis conditions varies significantly in structure, nutrient content, pH, and phenolic content (Novak et al., 2009; Lehmann et al., 2011). The characteristics of biochar, as well as its application rate and cumulative amount, may affect the soil environment and thereby alter root traits (Taghizadeh-Toosi et al., 2012; Reverchon et al., 2014; Reibe et al., 2015). Biochar application promotes plant growth mainly by improving characteristics of the soil environment, such as nutrient status, pH and cation-exchange capacity (CEC) (Lehmann et al., 2011; Noguera et al., 2012; Vanek & Lehmann, 2015). Consequently, the responses of root traits to biochar application may depend on soil conditions (Macdonald et al., 2014; Olmo et al., 2016). In addition, biochar is often applied with fertilizer to the soil; this combined application may interactively regulate root growth (Alburquerque et al., 2015). However, to our knowledge, no synthesis has revealed any general patterns of responses of root traits to biochar application. The lack of a comprehensive synthesis significantly prevents biochar from being widely popularized as a highly efficient, sustainable soil management practice for food security under climate change (Jeffery et al., 2015).

The objective of this study was to quantitatively evaluate biochar-induced changes in root traits and their potentially determining factors. We compiled a large global dataset of root traits including 13 variables totaling 2108 paired observations from 136 articles and conducted a comprehensive meta-analysis. The two major questions we aimed to answer here were as follows: (i) how do root traits change with biochar application and (ii) how do fertilization, experimental method and duration, plant species, soil conditions, biochar materials, and application rate affect the response of root traits? More specifically, we hypothesized that (i) biochar application would improve root growth and morphology with an overall greater increase in root length than root diameter in response to biochar-induced rapid plant growth and an increased demand for nutrients and water; (ii) the responses of root traits to biochar application would vary with fertilizer inputs; and (iii) experimental method and duration, plant species, soil conditions, biochar materials, and application rate would contribute significantly to variation in root trait responses to biochar application.

Materials and methods

Dataset assembly

We searched journal articles that reported root trait responses to biochar application using ISI Web of Science (Thomson Reuters, New York, NY, USA) and Google and Google Scholar (Google Inc., Mountain View, CA, USA). Searches included combinations of the terms ‘root’, ‘belowground’, ‘biochar’, ‘char’, ‘black carbon’, ‘charcoal’, ‘pyrogenic organic matter’, and ‘agchar’. We also screened previous reviews and meta-analyses that investigated the impact of biochar application on plant growth (Atkinson et al., 2010; Jeffer y et al., 2011; Biederman & Harpole, 2013; Liu et al., 2013) for additional sources.

To avoid bias in reference selection, the following four criteria were applied: (i) studies were selected in which at least one of the target variables (root traits) was measured under both biochar treatment and control; (ii) the initial environmental conditions, plant species, and soil properties of each experiment were the same, and experiments were performed at the same temporal and spatial scales in the control and treatment plots; (iii) to avoid possible interactive effects, studies that included soil contaminants, tested allelopathic interference, or contained other treatments (except for fertilization in both control and treatment plots because combined application of biochar plus fertilizer was common) were excluded; and (iv) studies containing multiple levels of biochar application, biochar types, soil conditions, plant species, or fertilization statuses were treated as multiple independent studies. Finally, our searches yielded a total of 2108 paired observations from 136 useful articles (Table S1, Appendix S1). The compiled dataset of root traits included 13 variables [root biomass, root : shoot ratio, root volume, root surface area, root diameter, root length, specific root length, number
of root tips, number of nodules, fungal colonization, root length colonized, and root nitrogen (N) and phosphorus (P) concentrations) (Table S2).

Most of the data were either obtained from tables or extracted from figures using the GETDATA GRAPH DIGITIZER (version 2.24, http://www.getdata-graph-digitizer.com/). Additionally, we calculated some indices such as root : shoot ratio (root biomass/shoot biomass) and specific root length (root length/root biomass) when data were available. All of the data represented the entire root level, as only one study reported fine root data (George et al., 2016).

We also collected background information from the selected studies, including data source, location (country), experimental type (field and pot), experimental duration, fertilization status (fertilized or unfertilized), plant functional group (life form, life cycle duration, or legumes), soil conditions (soil type, pH, total C, total N, and C/N ratio), and biochar characteristics (biochar feedstock types, rate of biochar application, temperature and time of pyrolysis, pH, and C/N ratio) (Table S1). The plant life forms included crop, grass, and woody plants. The examined plants were also assigned as annual or perennial based on their life cycle duration. The biochar feedstock types included crop, grass, woody plants, manure, and waste. The rate of biochar application was transformed to mass per area (expressed as t ha⁻¹) according to the soil layer reported in each study and the soil bulk density (BD). If the BD was not directly provided in the studies, we assumed a soil BD of 1.5 g cm⁻³ (Biederman & Harpole, 2013). Similarly, we assumed a soil layer of 20 cm when the soil depth was not provided (Liu et al., 2016). Soil texture was divided into sand, loam, and clay. The variables listed as background information were used as factors (either categorical or continuous) explaining the variation in root traits in response to biochar application.

**Statistical analysis**

We quantified the effects of biochar on root traits by calculating the natural log of the response ratio (RR), which is a metric commonly used in meta-analyses (Hedges & Olkin, 1985; Luo et al., 2016; Deng et al., 2015):

\[
RR = \ln \left( \frac{X_t}{X_c} \right) = \ln(X_t) - \ln(X_c)
\]

(1)

where RR is the ratio of the mean value of the chosen variable in the biochar treatment group \(X_t\) to that in the control group \(X_c\) and is an index of the effect of the experimental treatment on the target variable. The variance (\(v\)) of each individual RR is then estimated as:

\[
v = \frac{S_t^2}{n_t \times X_t^2} + \frac{S_c^2}{n_c \times X_c^2}
\]

(2)

where \(n_t\) and \(n_c\) are the sample sizes of the variable in the treatment and control groups, and \(S_t\) and \(S_c\) are the standard deviations for the treatment and control groups, respectively. When standard error, standard deviation, or confidence interval (CI) was not provided, we assumed a standard deviation of one-tenth of the mean value (Luo et al., 2006; Deng et al., 2015). A weighted RR (RR++) and a 95% CI were calculated from the individual RR by giving greater weight (\(W\)) to study estimates of which have greater precision (lower \(v\)) (Hedges & Olkin, 1985; Luo et al., 2006; Deng et al., 2015).

\[
W = \frac{1}{v}
\]

(3)

\[
RR_{++} = \frac{\sum_{i=1}^{w} \sum_{j=1}^{v} W_{ij}RR_{ij}}{\sum_{i=1}^{w} \sum_{j=1}^{v} W_{ij}}
\]

(4)

\[
S(RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^{w} \sum_{j=1}^{v} W_{ij}}} \left( \sum_{i=1}^{w} \sum_{j=1}^{v} W_{ij}Q_{total} \right)
\]

(5)

95% CI = RR_{++} ± 1.96S(RR_{++})

(6)

where \(m\) is the number of groups and \(k\) is the number of comparisons in the \(i\)th group. The treatment effect of biochar was considered significant if the 95% CI of the mean RR did not overlap with zero (Luo et al., 2006; Deng et al., 2015). The mean RR++ and 95% CIs were then transformed back (i.e., exponentially transformed) and presented as percentage change.

To test the reliability of the data used in the meta-analysis, the frequency distribution of the individual RR was tested by a Normal test and fitted by a Gaussian function (Fig. S1) using Eqn (7).

\[
y = x \exp \left( - \frac{(x - \mu)^2}{2\sigma^2} \right)
\]

(7)

where \(x\) is the RR of a variable; \(y\) is the frequency (i.e., number of RR values); \(x\) is a coefficient showing the expected number of RR values at \(x = \mu\); and \(\mu\) and \(\sigma\) are the mean and variance of the frequency distributions of RR, respectively.

To examine whether the mean RR++ of root traits differed among treatments, the total heterogeneity among groups (\(Q_{total}\)) was partitioned into within-group heterogeneity (\(Q_w\)) and between-group heterogeneity (\(Q_B\)). A significant \(Q_B\) suggested that the mean RR++ differed among these categorical factors (Hedges et al., 1999). When \(Q_B\) was not significant, there was no statistical justification for the further subdivision of the data. If the 95% CI of one group did not overlap with another group within a categorical factor, there was a significant difference between these two groups (Luo et al., 2006; Deng et al., 2015; He et al., 2016). A random-effect model was used to explore the continuous factors that may explain the response of root traits to biochar application. We also conducted a meta-regression analysis to examine the relationships between the RRs and the continuous factors (Luo et al., 2006; Deng et al., 2015; He et al., 2016).

To test the publication bias, funnel plots were presented as scatter plots of the RRs against their standard errors (Egger regression analysis to examine the relationships between the RRs and the continuous factors (Luo et al., 2006; Deng et al., 2015; He et al., 2016).

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affected by the nonpublished data (Rosenberg, 2005). If the fail-safe number was over 5n + 10 (where n is the number of cases in the analysis), we concluded that our result strongly suggested against publication bias. Otherwise, significant publication bias for the analysis existed.

All data were analyzed using SAS software (SAS Institute Inc., Cary, NC, USA), and the results were considered significant at \( \alpha = 0.05 \). The graphs were drawn with SIGMAPLOT software (SigmaPlot 12.5 for windows; Systat Software Inc., San Jose, CA, USA).

**Results**

The results obtained when considering the entire data set suggested that biochar application significantly increased root biomass, root volume, and surface area by an average of 32% (95% CI: +26%, +37%), 29% (95% CI: +13%, +48%), and 39% (95% CI: +25%, +54%), respectively (Fig. 1a). Biochar application also increased the root diameter, root length, and number of root tips by an average of +9.9% (95% CI: +1.8%, +19%), 52% (95% CI: +42%, +63%), and 17% (95% CI: +9.1%, +26%), respectively (Fig. 1a). However, significant publication bias on root diameter was suggested by Egger’s regression and Rosenthal’s fail-safe number (Table S3). The root : shoot ratio was not significantly altered by biochar application, while the specific root length was significantly enhanced by 17% (95% CI: +7.7%, +27%) (Fig. 1a). Biochar application did not significantly change the root N concentration (+5.5%; 95% CI: −5.1%, +17%) but significantly increased the root P concentration (+22%; 95% CI: +14%, +30%) (Fig. 1b). Additionally, biochar application significantly increased the number of root nodules and root length colonized by 25% (95% CI: +15%, +36%) and 35% (95% CI: +31%, +61%), respectively, but had no significant effects on fungal colonization (−4.0%; 95% CI: −11%, +4.0%) (Fig. 1c).

Biochar-induced changes in root biomass, morphology, and root N concentration were not significantly different between unfertilized and fertilized soil (Fig. 2a, Table S4), while responses of root P concentration varied (Table S4). Plant P concentration increased by 33% (95% CI: +26%, +40%) in fertilized soil; this increase was greater than that in unfertilized soil (18%, 95% CI: +13%, +24%) (Fig. 2b). Nonetheless, due to insufficient sample sizes (n < 5), it remained unclear whether fertilization could affect the responses of root-associated microbes to biochar application. By contrast, experimental duration and type appear to have little effect on the responses of root traits to biochar application (Table S4).

The effects of biochar application on root biomass and length varied remarkably among plant functional groups (Table S4). For instance, the RRs of root biomass (41%; 95% CI: +34%, +49%), root length (24%; 95% CI: +17%, +32%), and specific root length (60%; 95% CI: +53%, +67%) in annual plants were higher than those in perennial plants (Fig. 3a–c). The biochar-induced increase in root biomass was significantly higher for legumes (45%, 95% CI: +36%, +56%) than for non-legumes (25%, 95% CI: +18%, +32%) (Fig. 3d). In addition, the root length of crops (62%; 95% CI: +55%, +71%) under biochar treatment increased more than did the root length of trees (Fig. 3e).
The soil pH value significantly affected the responses of root P concentration, number of root nodules, and root length to biochar application (Table S4). As the soil pH value at the control sites increased, the log RR of the number of root nodules decreased (Fig. 4a). A negative linear relationship between the log RRs of root length and the soil pH value at the control sites was also observed (Fig. 4b). Only soil type had significant effects on the response of root biomass to biochar application (Table S4); root biomass increased more in sandy soils (42%, 95% CI: +34%, +51%) than in loamy soils (20%, 95% CI: +14%, +27%) (Fig. 4c).

There was no significant effect of biochar feedstock type, pH, or C : N ratio on the responses of root traits to biochar application (Table S4). Conversely, significantly positive linear correlations between pyrolysis temperature and the log RR of root length or specific root length were observed (Fig. 5a, b). Biochar application with faster pyrolysis generally increased root length and specific root length more strongly than did biochar application with slower pyrolysis (Fig. 5c, d).

**Discussion**

As hypothesized, our meta-analysis demonstrated that biochar application significantly enhanced root growth, which included greater root biomass, root volume, and surface area (Fig. 1a). The increased root biomass contradicts a recent meta-analysis reported by Biederman & Harpole (2013) that found that biochar application had no significant effect on root biomass. This inconsistency may be due to the different sample sizes between our study and their study (627 vs. 28, respectively). Our larger dataset may be more representative. The unchanged root : shoot ratio suggests that biomass allocation was not altered and thus that root growth is coordinated with shoot growth (Jeffery et al., 2011; Biederman & Harpole, 2013; Liu et al., 2013).

Despite the increased root biomass, our results suggested that plants under biochar application tended to invest their root biomass more efficiently to absorb soil water and nutrients rather than accumulate root biomass. This result is not surprising because biochar application stimulates plant growth and increases the demand for nutrients and water (Jeffery et al., 2011; Biederman & Harpole, 2013; Liu et al., 2013). In addition, biochar tends to absorb nutrient ions, particularly inorganic N, which may result in greater nutrient deficiency (Steiner et al., 2008; Clough et al., 2013). As a result, root length (+52%) under biochar application increased more than did the root diameter (+9.9%), which resulted in an overall enhancement in specific root length (Fig. 1a). The increased root length and specific root length suggest that biochar application is beneficial because it enlarges the plant rhizosphere to absorb water and nutrients that otherwise could not be reached by the roots (Eissenstat, 1992; Prendergast-Miller et al., 2014). Moreover, the increased number of root tips under biochar application could further extend root surface area and thus accelerate the exchange rates of resources at the plant–soil interface (Eissenstat & Yanai, 1997). The improvement in root morphological development would benefit plants grown under biochar application by alleviating nutrient and water deficiency.

Although biochar application improved root morphological development by alleviating nutrient deficiency, its effects on different nutrient elements appear to differ. Biochar application significantly enhanced root P concentration but had little effect on root N concentration (Fig. 1b). One possible reason is that biochar may contain an imbalance of nutrient elements and may release more available P than N via weathering (Yamato et al., 2006; Rajkovich et al., 2012). This effect, however, depends on the biochar feedstock type and pyrolysis processes (Hass et al., 2012). Another possible reason is that biochar-induced increases in soil alkalinity may

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Fig. 2 Percentage change (%) in (a) root N concentration and (b) root P concentration in unfertilized and fertilized soils in response to biochar application. Error bars represent 95% confidence intervals. The sample size for each variable is shown next to the error bar. The statistical significance of the effects of fertilization is evaluated in Table S4.

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increase the soil pH value and thereby enhance soil available P (Cui et al., 2011). Additionally, soil P is less mobile than N (Walker & Syers, 1976; Vitousek et al., 2010). The increased root length under biochar application may benefit the plant absorption of relatively immobile nutrients such as P and K (Eissenstat, 1992). Biochar application also inconsistently affected root-associated microbes. Our meta-analysis showed that root nodulation by rhizobia generally increased under biochar application (Fig. 1c). Root nodules are sensitive to P availability (Graham, 1981; Rondon et al., 2007; Lehmann et al., 2011). Biochar application often enhances P availability (Cui et al., 2011) and thus promotes root nodulation. Nevertheless, biochar did not significantly alter root colonization by mycorrhizal fungi but increased the root length colonized (Fig. 1c). The higher root length colonized under biochar application can help plants to explore more soil nutrients and thus may reduce plant dependence on mycorrhizae (Eissenstat, 1992; Raznikiewicz et al., 1994).

Fertilization appeared to not alter the response magnitude of root biomass and morphology to biochar application (Table S4), which means that biochar-stimulated root growth was more profound under fertilizer input, as we previously expected. Moreover, the response magnitude of root P concentration to biochar application was significantly enhanced by fertilization (Fig. 2b). According to our dataset, N fertilizer was the

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Fig. 3  Responses of root traits to biochar application for different plant functioning groups. (a–c) Percentage change (%) in root biomass (a), root length (b), and specific root length (c) in response to biochar application for annual and perennial plants. (d) Percentage change (%) in root biomass in response to biochar application for nonlegume and legume plants. (e) Percentage change (%) in root length in response to biochar application for crop, grass, and tree plants. Error bars represent 95% confidence intervals. The sample size for each variable is shown next to the error bar. The statistical significance of the effects of fertilization is evaluated in Table S4.

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most applied fertilizer (Table S1). More available inorganic N sources under N fertilization could limit the root uptake of P due to nutrient imbalance and soil acidification (Vitousek et al., 2010; Tian & Niu, 2015). Biochar tended to absorb NH$_4^+$ and NO$_3^-$/C$_2$O$_4$ after fertilizers were applied and hence could decrease the available N and soil N : P ratio (Steiner et al., 2008; Clough et al., 2013). Biochar’s liming effect may also improve fertilization-induced soil acidification (Cui et al., 2011). Therefore, the contrasting effects of fertilization and biochar application on soil P cycling might be the main cause for the higher biochar-induced increase in root P concentration in the fertilized soils. Accordingly, the biochar immobilization of N might be responsive to the slight suppression of root N concentration in the fertilized soils (Steiner et al., 2008; Clough et al., 2013). These findings indicate that the combined applications of biochar and fertilizer may improve soil nutrient balances compared to biochar application or fertilization alone.

The duration of biochar application had no significant impact on root traits (Table S4); this result suggests that the root traits are altered quickly after biochar application. However, it remains unclear how long the biochar effects will last due to the lack of long-term experiments in our dataset (Table S1). Compared with the pot experiment, plants grown in a field plot may have more space for root extension in response to biochar application. However, such a short-term experimental dataset makes it difficult to detect a significant difference in root response between pot and field experiments. Thus, more long-term biochar field experiments are needed to generate a clear temporal trend of root responses.

The responses of root traits to biochar application differed among plant functional groups (Table S4). Our meta-analysis showed that biochar application generally induced a higher increase in root biomass, root length, and specific root length in annual plants than in perennial plants (Fig. 3a–c). These results may be associated with the different root strategies between the two plant life forms. In comparison with perennial plants that often develop root systems to maximize nutrient conservation, annual plants generally promote root growth to support greater nutrient acquisition (Chapin, 1980). Therefore, annual plants are likely to show more efficient root growth than perennial plants due to the improved soil nutrient environment under biochar application. The responses of root length to biochar application also varied with plant life form; the root length increased more in crops than in trees (Table S4). Nevertheless, because of the limited number of studies and sample size (201 for crops vs. 13 for trees; Fig. 3e), we were unable to draw a solid conclusion regarding how biochar will affect root traits among plant life forms. The greater root biomass responses of legumes than of nonlegumes (Fig. 3c) likely resulted from the increased root nodulation and more efficient N fixation for legumes treated by biochar application (Graham, 1981; Rondon et al., 2007; Lehmann et al., 2011).

The responses of root traits to biochar application also varied with soil pH value. For example, biochar application increases the root P concentration in acidic soils because increased soil alkalinity (liming effect) by biochar can directly increase available P by unbinding phosphate ions with Al and Fe (Busman et al., 2002; Devau et al., 2009). No significant...
relationship was observed between the log RR of root nodulation and the soil pH values at the control sites probably due to insufficient data (n = 35 with only six studies). However, biochar-induced changes in soil P availability significantly affected root nodules (Fig. 4a); the log RR of the number of root nodules was positively correlated with the soil pH values (Graham, 1981; Rondon et al., 2007; Lehmann et al., 2011). Acidic, high-Al soils may also serve as a barrier to the growth of roots toward deeper soil horizons (Soethe et al., 2006). Biochar application likely broke down these barriers by elevating soil alkalinity and soil porosity and hence causing a greater increase in root length (Fig. 4b). Several studies have suggested that biochar application could improve the soil nutrient and water environment in response to faster plant growth (Graber et al., 2010; Major et al., 2010). We did not detect any significant effect of soil nutrients, such as SOC, total N, and C : N ratio, on root traits in response to biochar application. However, biochar application increased root biomass more strongly in sandy soils than in the other soils (Fig. 4c) presumably because sandy soil is generally more acidic, dry, and nutrient-poor than are loam or clay soils.

The response of root traits to biochar application may be affected by the physicochemical properties and nutrient contents of biochar depending on the feedstock type and application rate. For instance, manure biochar generally contains large amounts of available nutrients, while municipal waste biochar may produce toxic effects on plant growth (Sohi et al., 2010). However, the nutrient or toxic contents of biochar and its application rate appeared to have little effect on root growth in our meta-analysis (Table S4). The effects of biochar pH on root traits were not significant (Table S4); this result suggests that the liming effect of biochar may not be directly induced by biochar pH. Alternatively, biochar produced at higher temperatures or under faster pyrolysis was generally more effective at promoting root length (Fig. 5). This result is not surprising because biochar characteristics partly depend on pyrolysis temperature (Sohi et al., 2010). For example, high-temperature biochar tends to be alkaline (Bagreev et al., 2001; Novak et al., 2009). Processing temperature is also the main factor governing surface area; the surface area is greater under high temperature than under low temperature (Sohi et al., 2010). In addition, biochar produced at low temperatures usually contains more nutrients and water and may limit root growth. It is noteworthy that pyrolysis temperature and rate are often negatively correlated with each other (Sohi et al., 2010).

This study, to the best of our knowledge, is the first comprehensive synthesis to quantitatively evaluate the responses of root traits to biochar application. The findings in this meta-analysis may provide some insights into how biochar application would improve root traits for faster plant growth and may offer suggestions for the future sustainable development of biochar.
management. Plant growth is generally subjected to water and nutrient limitations. To address these deficiencies, plants often extend root length and other traits (Eissenstat & Yanai, 1997; Prendergast-Miller et al., 2014). However, the responses of root traits to nutrient and water deficiencies are also limited by soil physical and chemical conditions (Soethe et al., 2006). Biochar application likely improved soil environments and, in turn, significantly promoted root growth mainly by increasing root length, and hence eventually alleviating the deficiency of water and nutrients, particularly soil P. We also recommended that biochar can be applied with fertilizer to maximize plant growth because the combined application of biochar and fertilizer stimulated root growth and improved soil nutrient balance more effectively than did the application of biochar or fertilizer alone. Biochar application improved root growth and morphology more efficiently in annual plants than in perennial plants, particularly in acidic and sandy soils. Moreover, it appears that biochar production plays a more important role in regulating root growth than does biochar source. Thus, future biochar management should fully consider the factors associated with plant species, soil conditions, and biochar type to develop higher plant productivity.

Our results from this meta-analysis may also have significant implications for soil C cycling under biochar application. Biochar is characterized by stable and recalcitrant organic C with an extremely low decomposition rate and hence has been selected to increase soil C sequestration and climate change mitigation (Marris, 2006; Lehmann, 2007; Laird et al., 2009; Woolf et al., 2010). In this meta-analysis, we found that biochar application did not change the root : shoot ratio but significantly increased root length and the number of root tips more strongly than on root diameter. An increased number of thin roots may stimulate soil microbial activity due to the greater input of root exudates and may have priming effects on soil organic matter decomposition (Wang et al., 2016). Indeed, several studies have reported that biochar application significantly altered soil microbial community composition and increased soil respiration (Lehmann et al., 2011; He et al., 2016; Liu et al., 2016). Thus, the potential soil C sequestration of biochar may be re-estimated depending on the trade-off between biomass C inputs and soil C losses. Future land surface models must account for the shift in root morphology due to biochar application and its effects on soil C cycling.

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Conflict of interest

The authors declare that there is no conflict of interest.

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