BIOLOGICAL REVIEWS

Cambridge Philosophical Society

Biol. Rev. (2023), **98**, pp. 1184–1199. 1184
doi: 10.1111/brv.12949

Trade-offs in carbon-degrading enzyme activities limit long-term soil carbon sequestration with biochar addition

Jiao Feng[1], Dailin Yu[1], Robert L. Sinsabaugh[2], Daryl L. Moorhead[3], Mathias Neumann Andersen[4,5,6], Pete Smith[7], Yanting Song[1], Xinqi Li[1], Qiaoyun Huang[1,8], Yu-Rong Liu[1,8,9,*] and Ji Chen[4,5,10,*]

[1]*College of Resources and Environment, Huazhong Agricultural University, Wuhan, 430070, China*
[2]*Department of Biology, University of New Mexico, Albuquerque, NM, 87102, USA*
[3]*Department of Environmental Sciences, University of Toledo, Toledo, OH, 43537, USA*
[4]*Department of Agroecology, Aarhus University, Blichers Allé 20, Tjele, 8830, Denmark*
[5]*iCLIMATE Interdisciplinary Centre for Climate Change, Aarhus University, Roskilde, 4000, Denmark*
[6]*Sino-Danish Center for Education and Research, Eastern Yanqihu Campus, University of Chinese Academy of Sciences, 380 Huaibeizhuang, Beijing, 101400, China*
[7]*Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, AB24 3UU, UK*
[8]*State Key Laboratory of Agricultural Microbiology, Huazhong Agricultural University, Wuhan, 430070, China*
[9]*State Environmental Protection Key Laboratory of Soil Health and Green Remediation, Wuhan, 430070, China*
[10]*State Key Laboratory of Loess and Quaternary Geology, Institute of Earth Environment, Chinese Academy of Sciences, Xi'an, 710061, China*

ABSTRACT

Biochar amendment is one of the most promising agricultural approaches to tackle climate change by enhancing soil carbon (C) sequestration. Microbial-mediated decomposition processes are fundamental for the fate and persistence of sequestered C in soil, but the underlying mechanisms are uncertain. Here, we synthesise 923 observations regarding the effects of biochar addition (over periods ranging from several weeks to several years) on soil C-degrading enzyme activities from 130 articles across five continents worldwide. Our results showed that biochar addition increased soil ligninase activity targeting complex phenolic macromolecules by 7.1%, but suppressed cellulase activity degrading simpler polysaccharides by 8.3%. These shifts in enzyme activities explained the most variation of changes in soil C sequestration across a wide range of climatic, edaphic and experimental conditions, with biochar-induced shift in ligninase:cellulase ratio correlating negatively with soil C sequestration. Specifically, short-term (<1 year) biochar addition significantly reduced cellulase activity by 4.6% and enhanced soil organic C sequestration by 87.5%, whereas no significant responses were observed for ligninase activity and ligninase:cellulase ratio. However, long-term (≥1 year) biochar addition significantly enhanced ligninase activity by 5.2% and ligninase:cellulase ratio by 36.1%, leading to a smaller increase in soil organic C sequestration (25.1%). These results suggest that shifts in enzyme activities increased ligninase:cellulase ratio with time after biochar addition, limiting long-term soil C sequestration with biochar addition. Our work provides novel evidence to explain the diminished soil C sequestration with long-term biochar addition and suggests that earlier studies may have overestimated soil C sequestration with biochar addition by failing to consider the physiological acclimation of soil microorganisms over time.

Key words: biochar addition, enzyme activity, soil carbon sequestration, experimental duration, soil microorganism, meta-analysis.

* Authors for correspondence: J. Chen (Tel.: +45 71374531; E-mail: ji.chen@agro.au.dk) and Y.-R. Liu (Tel.: +86 27 87676165); E-mail: yrliu@mail.hzau.edu.cn.

Biological Reviews **98** (2023) 1184–1199 © 2023 The Authors. *Biological Reviews* published by John Wiley & Sons Ltd on behalf of Cambridge Philosophical Society.
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by University Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

CONTENTS

I. INTRODUCTION

Biochar amendment of carbon (C)-rich products from biomass pyrolysis has increasingly been regarded as a cost-effective and environmentally friendly method of increasing soil C sequestration (Lehmann *et al.*, 2021; Molina *et al.*, 2009; Moore, Jevrejeva & Grinsted, 2010; Yang *et al.*, 2021). The amount of biochar amendment has increased substantially in recent decades, with predicted sequestration of 0.3–2.0 Pg CO_2 annually by 2050 (Fawzy *et al.*, 2021; Sohi *et al.*, 2010; Woolf *et al.*, 2010). Despite increasing evidence demonstrating the advantages of biochar in enhancing soil C sequestration (Han *et al.*, 2022; Hernandez-Soriano *et al.*, 2016; Zhang, Voroney & Price, 2015*a*), whether and how biochar addition affects soil C dynamics over time remains unclear. Indeed, several recent studies have shown that effects of biochar addition on soil C sequestration can be positive (Ameloot *et al.*, 2014; Azlan Halmi *et al.*, 2018), negative (Peng *et al.*, 2019; Tian *et al.*, 2016) or neutral (Elzobair *et al.*, 2016; Rafael *et al.*, 2019). Such large discrepancies illustrate a poor understanding of the underlying mechanisms. Positive effects of biochar addition on soil C sequestration can be explained by the stimulation of plant growth (Lehmann *et al.*, 2021; Liu *et al.*, 2016*a*) with a subsequent increase in inputs of plant (e.g. litter and root) residues into soil (Hagemann *et al.*, 2017). On the other hand, biochar addition can accelerate decomposition of pre-existing soil organic C (SOC) by changing microbial community composition and activities, leading to negative effects on SOC (Pei *et al.*, 2021; Tian *et al.*, 2016). However, a mechanistic understanding of the composite effects of biochar addition on SOC decomposition process is lacking, hampering the prediction of the long-term effects of biochar addition on soil C dynamics.

Soil extracellular enzymes catalyse the degradation of soil organic matter, deconstructing plant and microbial residues by breaking down large macromolecules into simpler molecules (Margida, Lashermes & Moorhead, 2020; Sinsabaugh, 2010). Various extracellular enzymes target different pools of SOC, for example, ligninases target structurally complex polyphenolic macromolecules, and cellulases degrade ordered polysaccharides with a simpler structure (Chen *et al.*, 2018*a*; Margida *et al.*, 2020; Ren *et al.*, 2017; Yang *et al.*, 2022*b*). Biochar addition may have different impacts on ligninase and cellulase activity, partly due to changes in the chemical composition of soil organic matter and also due to shifts in microbial community composition (Gul *et al.*, 2015; Jing *et al.*, 2022; Singh & Cowie, 2014). For instance, the condensation of cellulose and hemicellulose into humic-like macromolecules on the surface of biochar (Lehmann *et al.*, 2021; Quilliam *et al.*, 2013) could lead to induction of microbial secretion of ligninase relative to cellulase, as enzyme production is commonly induced by the presence of suitable substrates (German *et al.*, 2012; Sinsabaugh *et al.*, 2008). The observed increases in the proportion of structurally complex macromolecules and fungal abundance with time after biochar addition may also lead to increased induction of ligninase relative to cellulase activity over time (Pei *et al.*, 2021; Yi *et al.*, 2020). Although some recent studies indicated that soil C sequestration varied significantly with time after biochar addition, biochar production technologies (e.g. feedstock type and thermal pyrolysis temperature of biochar), and site-specific conditions (e.g. climate and soil properties) (Gronwald *et al.*, 2015; Mitchell *et al.*, 2016), a comprehensive understanding of the underlying mechanisms remains unexplored. In particular, there is no direct evidence for how biochar addition affects key enzyme activities (e.g. cellulase and ligninase) that are likely to influence long-term impacts on soil C sequestration across various environmental conditions.

To address these knowledge gaps, we conducted a global meta-analysis to evaluate the responses of soil cellulase and ligninase activities to biochar addition, and how these responses may affect long-term soil C sequestration. We compiled a database of 923 soil C-degrading enzyme activity observations from 130 biochar addition studies (with biochar addition periods ranging from several weeks to several years) across five continents worldwide (see online Supporting Information, Fig. S1, Table S1). We combined the advantages of classic meta-analysis with advanced model selection analysis to quantify the relative importance of potential predictors in explaining the effects of biochar addition on enzyme activities and soil C sequestration. This approach allows us to assess the role of enzyme activities in determining changes in soil C sequestration with biochar addition across a wide range of climatic, edaphic and experimental factors. Specifically, we test the following hypotheses: (*i*) biochar addition induces shifts in C-degrading enzyme activity, enhancing ligninase activity while suppressing cellulase activity; and (*ii*) ligninase:cellulase ratio may increase with time after biochar addition, leading to weakened soil C sequestration by stimulating the decomposition of structurally complex macromolecules with long-term biochar addition.

II. MATERIALS AND METHODS

(1) Enzymes included in this study

Seven kinds of extracellular enzymes involved in SOC decomposition were included in this meta-analysis (Table S2) following previous studies (Chen *et al.*, 2018*a*; Margida *et al.*, 2020; Ren *et al.*, 2017; Yang *et al.*, 2022*b*): four cellulases [β-1,4-glucosidase (BG), α-1,4-glucosidase (AG), β-1,4-xylosidase (BX) and β-D-cellobiosidase (CBH)] and three ligninases [phenol oxidase (PO), polyphenol oxidase (PPO) and peroxidase (PER)].

(2) Data collection

We searched for articles on the effects of biochar addition on cellulase and ligninase activities using *Web of Science* (http://apps.webofknowledge.com/), *Google Scholar* (http://scholar.google.com/), and *China National Knowledge Infrastructure* (http://www.cnki.net/). Specifically, we searched for peer-reviewed articles, academic theses, and book chapters published in English or Chinese before May 2022. We used the following search string [('biochar addition' OR 'biochar amendment') AND ('cellulase' OR 'ligninase' OR 'glucosidase' OR 'xylosidase' OR 'cellobiosidase' OR 'peroxidase' OR 'phenol oxidase') AND ('soil' OR 'terrestrial' OR 'land')] and their equivalents in Chinese. Additionally, we searched for articles through other sources, including manual searches of reference cited by or citing the articles identified by our search string.

Articles included in this study had to meet the following criteria: (*i*) climatic, vegetation and soil attributes were similar for the control and biochar addition treatments; (*ii*) biochar properties (biochar materials, biochar pH, biochar temperature, biochar C% and biochar N%) and application protocols (biochar application method, biochar application rate and duration) were clearly described; (*iii*) ecosystem types were reported; and (*iv*) standard deviation (SD) and sample size were reported or could be calculated from the data presented in the publication. Measurements with different durations of biochar addition at the same site were considered as independent observations because one of our primary purposes was to explore the impacts of duration on enzyme activities and soil C dynamics. Measurements with insufficient information on study sites and from contaminated soil were excluded to eliminate any confounding effects of pollutants on soil enzyme activities (Campos *et al.*, 2020; Li *et al.*, 2020*c*). The PRISMA flowchart illustrating the processes for selection of the included articles is shown in Fig. S1. All data were selected and collected following PRISMA-EcoEvo guidelines (PRISMA-EcoEvo_WordChecklist) (O'Dea *et al.*, 2021). Based on these criteria, we obtained 923 observations of soil C-degrading enzyme activities from 130 independent publications worldwide (Fig. S2, Table S1; references included in the meta-analysis are identified with asterisks in the reference list). Data were extracted directly from the tables, main text, or appendices of the articles and theses, or digitised from figures using Getdata Graph Digitizer (version 2.26) (http://www.getdata-graph-digitizer.com/download.php).

We first extracted information on cellulase and ligninase activities. If one paper reported two or more kinds of cellulase or ligninase, the sum of these enzyme activities was calculated as the overall responses of cellulase and ligninase activities, respectively (Chen *et al.*, 2018*a*; Wu *et al.*, 2022). If multiple measurements over time were conducted, values from the last time were selected. Multiple methods have been used to measure enzyme activities based on assessments of substrate concentrations or products over time at certain temperatures (Deforest, 2009; Marx, Wood & Jarvis, 2001). Most studies measured soil cellulase activity using fluorimetric methods with fluorescent 4-methylumbelliferone substrates, and assessed soil ligninase activity by colorimetric methods using L-3,4-dihydroxy-phenylalanine as the substrate (Elzobair *et al.*, 2016; Li *et al.*, 2020*c*). Methods and incubation conditions often varied among studies. Moreover, soil enzyme activities may also vary significantly depending on sampling season and soil water content (i.e. dry or moist periods). However, in our analyses we only consider the logarithmic response ratio of enzymes in each individual study, in which experimental conditions such as the type and concentration of substrates, buffer pH, incubation temperature and sampling season, etc., were the same for each paired observation. Comparisons between different sites were carried out using the logarithmic response ratio rather than absolute values of soil enzymes. Therefore, differences in measurement methods and sampling seasons should only have a minor influence on our assessment of the effects of biochar addition on enzyme activities in this meta-analysis (Chen *et al.*, 2020, 2018*a*; Hedges, Gurevitch & Curtis, 1999).

To quantify drivers of biochar effects on enzyme activities and SOC sequestration, we further collected information on a wide range of environmental variables, including elevation (0–1746 m), latitude (−42.95° S to 55.37° N), longitude (−119.74° W to 147.10° E), mean annual precipitation (MAP, 27–2500 mm), mean annual temperature (MAT, −1.0–32.3 °C), and vegetation type (cropland, grassland,

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by University Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by University Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

forest, open area or wetland) for each site. Edaphic properties, including SOC, soil total nitrogen (N), soil C:N ratio, soil pH and soil texture (classified as sandy, loamy or clay following USDA Textural Soil Classification) were also recorded. Table S1 and our Supplementary Data set (available at https://doi.org/10.6084/m9.figshare.21769979) provides detailed values or ranges for these variables obtained from the 130 publications. For missing environmental and edaphic variables, we searched for relevant publications by the same research group at the same study sites or contacted the corresponding authors. Alternatively, missing data for climatic (MAT, MAP) and soil attributes (SOC, total N and soil texture) were obtained from the WorldClimate Database (http://www.worldclim.org/) and Soil grids database (https://www.isric.org/explore/soilgrids), respectively.

For biochar properties and application protocols, we recorded feedstock, pH, pyrolysis temperature, C and N content (%) as well as method (Field, Pot or Laboratory incubation), rate (%) and duration (year) of biochar application. The feedstock types for biochar production were classified into five groups: herb, manure, residue, wood and urban waste. The pyrolysis temperatures used to produce biochar were classified into three groups: low (≤350 °C), medium (350–550 °C) and high temperature (>550 °C). We recorded microbial biomass, the abundance of fungi, bacteria, the fungi:bacteria ratio, and plant biomass for both ambient and biochar addition treatments, when these variables were reported.

In total, this data set included 12,194 records of the above environmental, edaphic, and experimental factors, or the responses of soil organic C, soil nutrient contents, microbial or plant attributes to biochar addition.

(3) Data analysis

We used meta-analysis to investigate the effects of biochar addition on soil cellulase and ligninase activities, ligninase:cellulase ratio and other edaphic and microbial variables. Specifically, we calculated the logarithmic response ratio (LnR) of each variable using the following equation (Chen *et al*., 2017*b*; Hedges *et al*., 1999):

$$\mathrm{LnR} = \mathrm{Ln}\left(\frac{\overline{X^B}}{\overline{X^C}}\right) = \mathrm{Ln}\left(\overline{X^B}\right) - \mathrm{Ln}\left(\overline{X^C}\right) \qquad (1)$$

where $\overline{X^B}$ and $\overline{X^C}$ are the arithmetic average values in the biochar addition and control treatments, respectively. The variance (Vi) of LnR was calculated as:

$$V\mathrm{i} = \frac{\mathrm{SD}_\mathrm{B}^2}{n\mathrm{B}\overline{X}_\mathrm{B}^2} + \frac{\mathrm{SD}_\mathrm{C}^2}{n\mathrm{C}\overline{X}_\mathrm{C}^2} \cdots \qquad (2)$$

where $\mathrm{SD_B}$ and $\mathrm{SD_C}$ are the standard deviations, and n_B and n_C are the number of replicates, respectively.

The overall effects of biochar addition on different variables and 95% confidence intervals (CI) were evaluated using *rma.mv* function in the *metafor* package of R project (version 4.0.2) (Viechtbauer, 2010). We included 'Publication' and 'Observation' as random factors in the mixed-effect models, because some studies contributed more than one paired observation (Chen *et al*., 2018*a*; van Groenigen *et al*., 2017). To facilitate the interpretation of data, the effect size was back-transformed to percentage change using the equation (LnR–1) × 100 (Chen *et al*., 2018*a*). The effect of biochar addition on each variable was considered significant if the 95% CI did not overlap with zero. The normality of data for each kind of enzyme activity was tested using the Kolmogorov–Smirnov and Shapiro–Wilk tests, except for PPO due to its small sample size. A funnel plot and Egger's test were used to detect potential publication bias on soil enzyme activities, ligninase:cellulase ratio and soil organic C using the *metafor* package of R project (version 4.0.2). A sensitivity analysis was conducted to investigate the stability of the results by excluding one study a time using the *leave1out* function in *metafor* (Copas & Shi, 2000).

We conducted a meta-analysis to analyse the combined effects of environmental, edaphic and experimental factors on the responses of soil cellulase activities, ligninase activities, ligninase:cellulase ratio and soil C sequestration to biochar addition. In brief, we used a mixed-effects meta-regression model using the *glmulti* package in R (Calcagno & de Mazancourt, 2010; Chen *et al*., 2020, 2018*b*). The importance of different factors was evaluated using the sum of Akaike weights. The weight was considered as the overall support for each variable in all potential models. A cutoff of 0.8 was set to identify the significant predictors for each model (Chen *et al*., 2018*a*, 2017*b*; Terrer *et al*., 2016). We used Spearman's rank correlation analysis to evaluate the relationships of cellulase activities, ligninase activities, and ligninase:cellulase ratio with environmental, edaphic and experimental factors. To explore further the effect of experiment duration on soil C sequestration, we conducted both linear regression and piece-wise regression models to fit the relationship between the LnR of SOC and time after biochar addition. Specifically, a piece-wise regression model was carried out using the *segmented* R package (Muggeo, 2003). The optimal regression model was selected by comparing regression coefficients (R) and the model was statistically significant if $P < 0.05$. Furthermore, studies were separated into short-term and long-term according to the slope of the curves for the relationship between LnR-SOC and time after biochar addition. Spearman's rank correlation analysis was conducted to investigate factors associated with enzyme activities and soil C sequestration in short-term and long-term studies, respectively.

III. RESULTS

(1) Responses of cellulase and ligninase activity to biochar addition

Averaged across all studies, biochar addition significantly suppressed cellulase activity by 8.3% ($P < 0.001$; Fig. 1A).

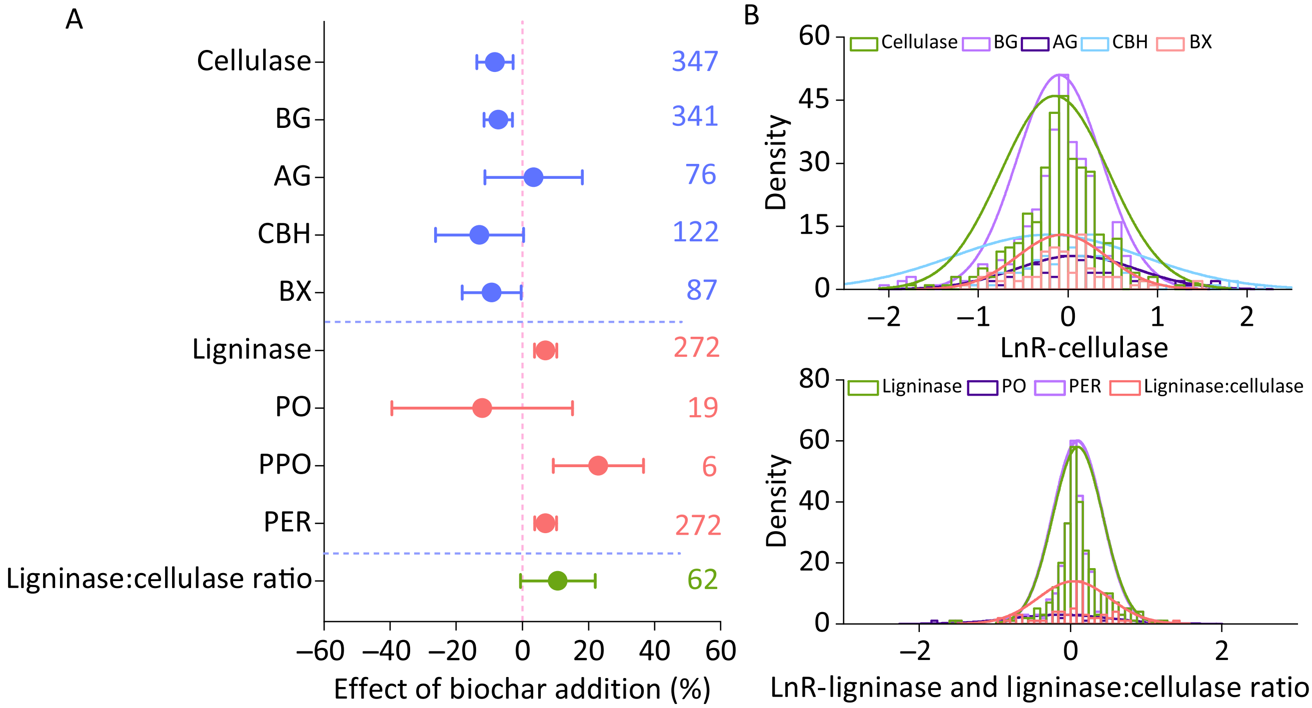

Fig. 1. Carbon-degrading enzyme activities. (A) Effects of biochar addition on activity of cellulases, ligninases, and on the ligninase:cellulase ratio. Values represent the mean percentage change in each variable with biochar addition *versus* control; error bars indicate 95% confidence intervals. Sample sizes for each variable are shown on the right. (B) Distribution of the log response ratios (LnR) of cellulase activity (top), and ligninase activity and the ligninase:cellulase ratio (bottom) to biochar addition. BG, β-1,4-glucosidase; AG, α-1,4-glucosidase; CBH, β-D-cellobiohydrolase; BX, β-1,4-xylosidase; PO, phenol oxidase; PPO, polyphenol oxidase; PER, peroxidase.

Specifically, biochar addition decreased the activities of BG and BX by 7.3% and 9.3% ($P < 0.05$), respectively. By contrast, biochar addition increased ligninase activity by 7.1% on average ($P < 0.001$), with an increase of PER activity by 7.0% ($P < 0.001$) and of PPO by 23%. The differential responses of cellulase and ligninase activities to biochar addition led to a marginally increased ratio of ligninase:cellulase activities by 10.7% ($P = 0.052$). In addition, the responses of cellulase, ligninase and ligninase:cellulase ratio were normally distributed according to both Kolmogorov–Smirnov and Shapiro–Wilk tests ($P > 0.05$; Fig. 1B). Moreover, Egger's funnel plots appeared symmetrical ($P > 0.05$), and the results showed no significant publication bias in this meta-analysis (Fig. S3).

The effects of biochar addition on soil enzyme activities depended on the feedstock type and pyrolysis temperature for biochar production and variation in soil texture (Fig. S4). Herb, wood and urban waste biochar significantly reduced cellulase activity by 4.4–22.0% ($P < 0.05$), while manure and residue biochar enhanced ligninase activity by 2.5–12.7% ($P < 0.05$). Biochar produced at medium (350–550 °C) and high (>550 °C) temperatures significantly decreased the activity of cellulase by 10.0% and 6.7%, respectively ($P < 0.05$). By contrast, biochar produced at low (<350 °C) and medium temperature increased ligninase activity by 16.0% and 4.6%, respectively. There were significant reductions in cellulase activity in sandy (by 16.6%, $P < 0.05$) and clay (by 7.0%, $P < 0.05$) soils, and significant increases in ligninase activity in sandy (by 13.2%, $P < 0.05$) and loamy (by 15.3%, $P < 0.05$) soils. These differential responses of cellulase and ligninase activities resulted in significant increases in ligninase:cellulase ratio by 7.8–14.5% ($P < 0.05$) with biochar produced using feedstock from manure or wood materials, at medium temperature and in sandy and loamy soils (Fig. S4).

Model selection analysis showed that the main factors influencing the response of cellulase and ligninase activities to biochar addition were different (Fig. 2). The effects of biochar addition on cellulase activity were best explained by biochar application rate, MAP, longitude and soil clay content (Fig. 2A). By contrast, the responses of ligninase activity to biochar addition were best explained by soil N content, biochar temperature, site location (i.e. longitude) and biochar pH. Linear regression analysis confirmed that LnR of cellulase activity was negatively correlated with biochar application rate, whereas a positive correlation was found with MAP ($P < 0.05$). Moreover, LnR of ligninase had negative relationships with soil N content and biochar pyrolysis temperature, but a positive correlation with biochar pH ($P < 0.05$; Fig. 2B). For the ligninase:cellulase ratio, the most important predictors were the time after biochar addition, soil C:N ratio, biochar C content, and biochar C:N ratio. Specifically, the LnR-ligninase:cellulase ratio was positively correlated with time after biochar addition but negatively correlated with soil C:N ratio, biochar C content and biochar C:N ratio ($P < 0.05$).

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by University Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

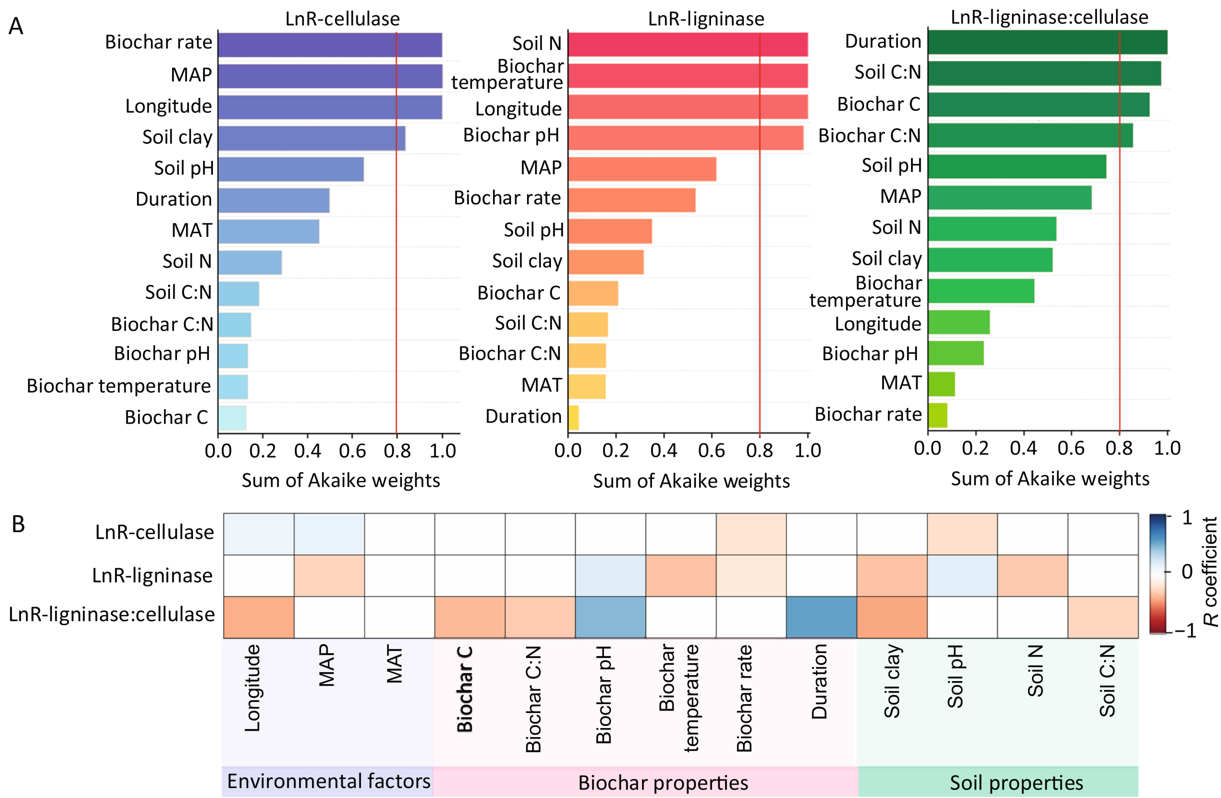

Fig. 2. Factors influencing the responses of soil enzymes. (A) Relative importance of different variables regulating the effects of biochar addition on cellulase activity, ligninase activity, and ligninase:cellulase ratio. Relative importance is shown according to the sum of Akaike weights of model selection. A cutoff of 0.8 was set to differentiate the important *versus* non-essential predictors. (B) Correlations between studied variables and the responses (log response ratio, LnR) of cellulase activity, ligninase activity, and ligninase:cellulase ratio to biochar addition. Biochar temperature, temperature of biochar production; Biochar rate, application rate of biochar addition; Duration, time after biochar addition; MAP, mean annual precipitation, MAT, mean annual temperature.

(2) Linking shifts in soil enzyme activities to changes in SOC with biochar addition

For studies that have reported SOC, biochar addition enhanced SOC by an average of 52.8% ($P < 0.001$) (Fig. 3A). Biochar-induced increases in SOC were found regardless of differences in feedstock, pyrolysis temperature of biochar addition and soil types (Fig. S4). Specifically, wood- and herb-derived biochar significantly increased SOC by over 60% ($P < 0.001$), and biochar produced from manure and residue enhanced SOC by 24.9 and 43.5%, respectively. Biochar produced at high pyrolysis temperature had a more positive effect on SOC (with SOC increased by 119.7%) compared with those produced at low and medium temperature (enhanced SOC by 47.6 and 54.8%, respectively). Moreover, SOC in loamy and clay soils (increased by 68.7 and 62.6%, respectively) showed a more positive response to biochar addition than in sandy soils (increased by 24.5%) (Fig. S4). Our piece-wise regression analysis showed that biochar-induced increases in SOC overall diminished with time after biochar addition (Fig. 3B; $P < 0.001$). The relationship between LnR-SOC and time of biochar addition could be divided into two periods (i.e. <1 year and ≥1 year) according to the slope of the curves identified using piece-wise regression. The model selection analysis showed that the response of SOC to biochar addition was best explained by LnR-ligninase:cellulase ratio (Fig. 3C). Specifically, changes in SOC with biochar application were negatively related to the ligninase:cellulase ratio (Fig. 3D, $P < 0.001$).

(3) The effect of time after biochar addition on soil enzyme activities and SOC sequestration

Studies were separated into short term (<1 year) and long term (≥1 year) according to the results of piece-wise regression between LnR-SOC and time after biochar addition (Fig. 3B). Short-term and long-term biochar addition reduced the activity of cellulase by 4.6 and 12.7%, respectively ($P < 0.05$; Fig. 4A). By contrast, there were no significant effects of biochar addition on ligninase activity and ligninase:cellulase ratio in short-term studies ($P > 0.05$), while long-term biochar addition significantly enhanced soil ligninase activity by 5.2% ($P < 0.05$) and ligninase:cellulase ratio by 36.1% ($P < 0.001$). Short-term biochar addition had more positive effects on SOC compared with long-term studies, with significant increase in SOC by 87.5 and

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by University Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

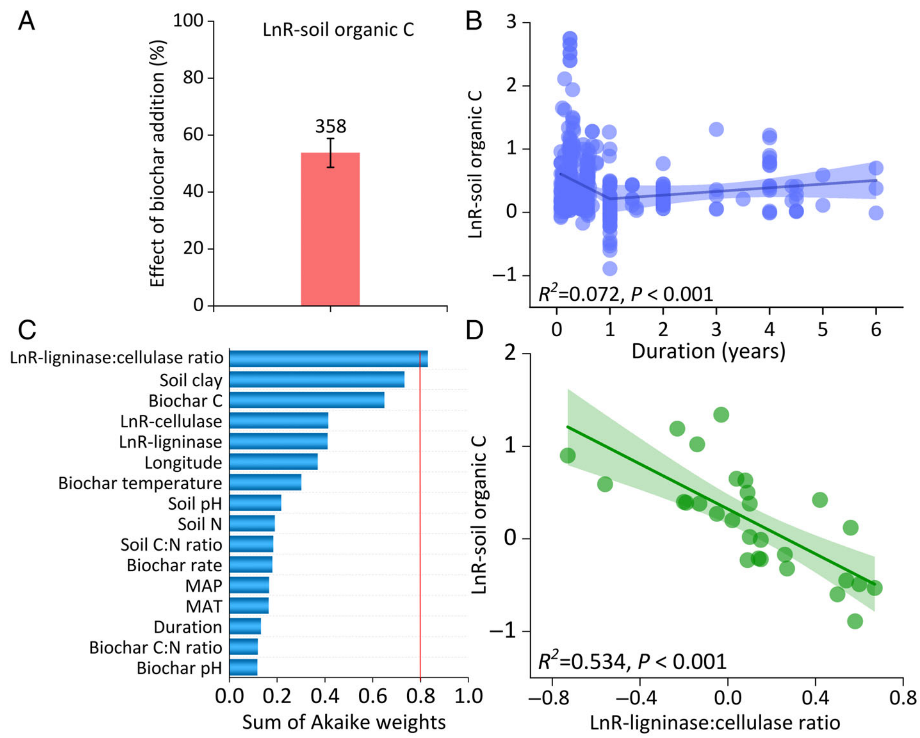

Fig. 3. The response of soil organic C to biochar addition and associated driving factors. (A) Effects of biochar addition on soil organic C sequestration. Value represents the mean percentage change with biochar addition *versus* control; error bar indicates 95% confidence intervals. Sample size is shown above the column. (B) Relationship between duration of biochar addition and the log response ratio (LnR) of soil organic C to biochar addition. The relationship between duration of biochar addition and LnR-soil organic C was analysed using a piece-wise regression model. (C) Relative importance of different variables regulating the effects of biochar addition on soil organic C sequestration. A cutoff of 0.8 is set to differentiate the important *versus* non-essential predictors. (D) Relationship between the response of ligninase:cellulase ratio and the response of soil organic C to biochar addition. Biochar temperature, temperature of biochar production; Biochar rate, application rate of biochar addition; Duration, time after biochar addition; MAP, mean annual precipitation; MAT, mean annual temperature.

25.1%, respectively. In short-term studies, the response of soil enzyme activities was significantly associated with changes in soil properties. Specifically, LnR-cellulase activity had negative relationship with soil clay content, but positive associations with soil pH and soil N content, whereas LnR-ligninase activity showed opposite relationships with these soil properties (Fig. 4B). LnR-SOC correlated negatively with soil pH and positively with biochar pyrolysis temperature. In long-term studies, the response of both soil enzyme activities and SOC were significantly related to soil clay content. LnR-cellulase activity and LnR-SOC showed positive relationships with soil clay content, whereas LnR-ligninase and LnR-ligninase:cellulase ratio correlated negatively with soil clay content.

IV. DISCUSSION

Our results indicate that shifts in C-degrading enzyme activities are key drivers of soil C sequestration with time (ranging from several weeks to several years) after biochar addition. Most importantly, our model selection analysis underscores that changes in ligninase:cellulase ratio explains the most variation in the response of SOC to biochar addition, with biochar-induced shift in ligninase:cellulase ratio correlating negatively with SOC content (Fig. 3D). Specifically, the significantly increased ligninase:cellulase ratio under long-term (≥1 year) biochar addition leads to progressively diminished soil C sequestration. These results provide strong support for our hypothesis that the increasing ligninase:cellulase ratio with time contributes to a declining capacity for soil C sequestration with long-term biochar addition. To the best of our knowledge, this is the first comprehensive study linking enzyme activity and soil C with biochar addition, providing novel evidence to unravel the mechanisms controlling soil C sequestration with prolonged biochar exposure.

We propose several possible underlying mechanisms to explain differential responses of cellulase and ligninase activity with biochar addition (Fig. 5). First, biochar-induced reductions in soil N availability could stimulate ligninase rather than cellulase activity. Several lines of evidence have demonstrated reductions in soil N availability after biochar addition, which might be driven by (*i*) higher plant biomass

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by University Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

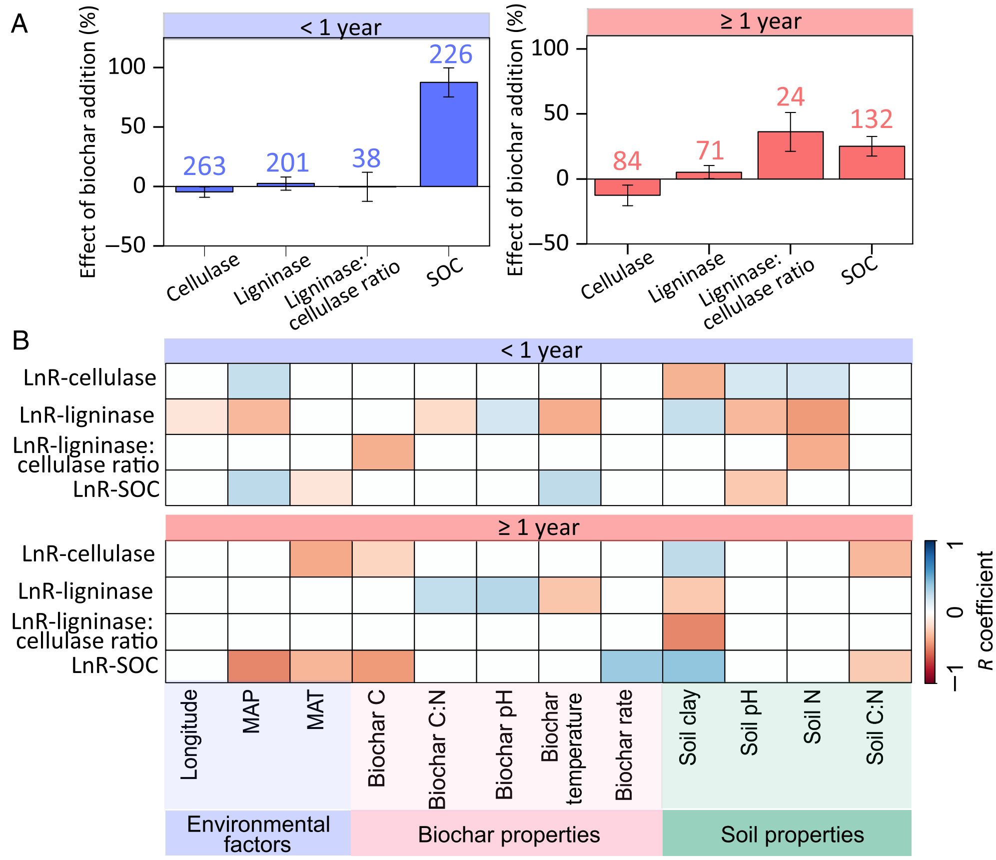

Fig. 4. Responses of soil enzymes and soil organic C to short-term and long-term biochar additions. (A) Effects of biochar addition on soil enzyme activities, ligninase:cellulase ratio, and soil organic C (SOC) sequestration in short-term (<1 year) and long-term (≥1 year) studies. Values represent the mean percentage change in each variable with biochar addition *versus* control; error bars indicate 95% confidence intervals. Sample sizes for each variable are shown above the column. (B) Relationships between different variables and the log response ratio (LnR) of enzyme activities, ligninase:cellulase ratio, and SOC sequestration. Biochar temperature, temperature of biochar production; Biochar rate, application rate of biochar addition; MAP, mean annual precipitation; MAT, mean annual temperature.

production (Fig. S5) and associated translocation of N from soil to vegetation, (*ii*) the additional C inputs increasing bulk soil stoichiometric C:N ratio (Fig. S6A), and (*iii*) occlusion of soil NH_4^+ by phenolic- and lignin-like compounds through complex organo-mineral interactions on biochar surfaces (Fig. S6B). In response, soil microorganisms may increase ligninase production to stimulate the breakdown of complex phenolic- and lignin-like compounds to acquire bound N. In support of this explanation, we found that soil N content was the most important predictor (negative relationship) of the effects of biochar addition on soil ligninase activity (Fig. 4). This explanation supports the 'microbial N mining theory', which assumes that soil microorganisms will likely invest resources to decompose complex structural macromolecules to acquire N under N limitation (Craine, Morrow & Fierer, 2007; Meyer *et al*., 2017; Moorhead & Sinsabaugh, 2006).

Second, shifts in microbial community composition could contribute to the opposite effects of biochar addition on cellulase and ligninase activity. Our results show positive associations between ligninase activity and microbial biomass with biochar addition, but not for cellulase activity (Fig. S7A,B). These results suggest that soil microbial community composition or enzyme production efficiency may change under biochar addition. Indeed, previous studies have reported that biochar addition stimulates fungal growth including the two most commonly occurring types of mycorrhizal (arbuscular mycorrhizal and ectomycorrhizal) fungi (Lehmann *et al*., 2011; Yang *et al*., 2022*a*). This increase in fungal abundance with biochar addition could arise because fungal hyphae can grow into biochar pores and thereby access complex macromolecules adsorbed on biochar (Gul *et al*., 2015; Lehmann *et al*., 2011). Moreover, the protection of soil fungi from grazers or competitors on biochar pores may also contribute to increased soil fungal abundance (Li *et al*., 2020*b*). Consistently, we found that increased fungal abundance associated with biochar addition was positively correlated with changes in ligninase activity (Figs S7 and S8). These results indicate that biochar-induced shifts towards a fungi-dominant microbial community could

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by University Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

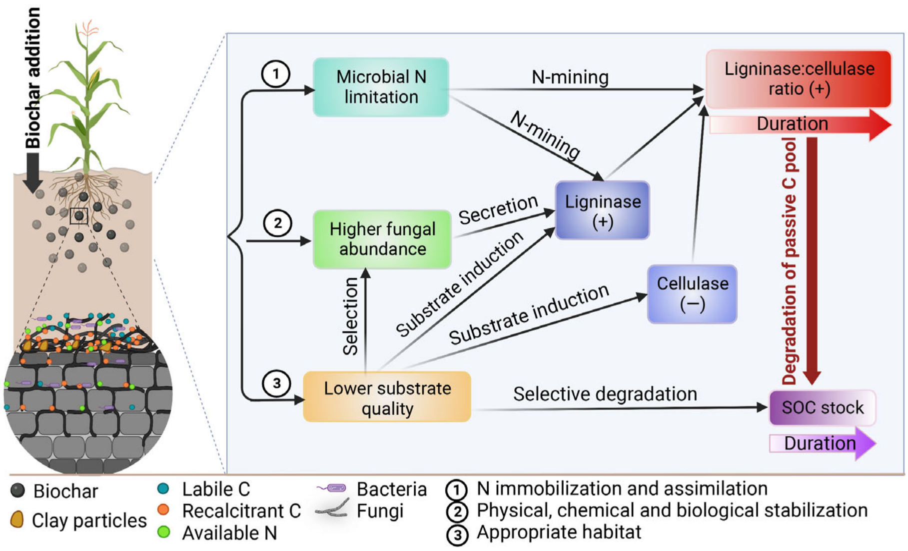

Fig. 5. Schematic of enzyme-mediated soil organic C sequestration. A conceptual paradigm illustrating the mechanisms of biochar addition on soil carbon-degrading enzyme activities and their impacts on soil organic C (SOC) dynamics. Biochar addition has differential effects on soil cellulase and ligninase activities *via* direct and indirect effects on substrate quality, microbial community composition and soil N availability. The differential responses of cellulase and ligninase activities to biochar addition results in an increasing ligninase:cellulase ratio with duration of biochar addition, which may reduce SOC sequestration over time.

promote ligninase activity, possibly because fungi are more efficient at mineralizing structural complex macromolecules than bacteria and are the primary producers of phenol oxidase (Burke & Cairney, 2002). In addition, we observed a positive relationship between LnR-ligninase:cellulase ratio and LnR-fungi:bacteria ratio (Fig. S7D), further suggesting that the observed shifts in extracellular enzyme activities were related to changes in microbial community composition.

Third, biochar addition significantly altered the chemical composition of soil organic matter (Mitchell *et al.*, 2016; Tian *et al.*, 2016), which likely contributed to the differential responses of cellulase and ligninase activities. By introducing additional phenolic- and lignin-like compounds, biochar could reduce the availability of readily decomposable C compounds because they could be occluded within macromolecule assemblages through complex organo-mineral interactions (e.g. H-bonding, cation bridging, and hydrophobic interactions) on biochar surfaces (Jing *et al.*, 2022; Kleber, Sollins & Sutton, 2007; Singh & Cowie, 2014). In particular, the resulting non-polar and hydrophobic compounds are composed predominantly of alkyl and aromatic functional groups (Hernandez-Soriano *et al.*, 2016; Kleber *et al.*, 2007). Microbial utilisation of readily decomposable C compounds thus could be suppressed due to limitation in substrate availability (Jing *et al.*, 2022; Singh & Cowie, 2014). By contrast, the increase in lignin-like soil organic C would possibly induce expressional and/or translational upregulation of ligninase activity. Therefore, our findings indicate that after the initial depletion and stabilisation of readily decomposable C by biochar, soil microbes likely stimulate ligninase production to access more chemically recalcitrant soil C pools (Li *et al.*, 2020*b*).

Biochar production technologies (e.g. feedstock type and thermal pyrolysis temperature of biochar) and soil properties (e.g. soil texture) may also be potential reasons underlying shifts in enzyme activities with biochar addition. For instance, biochar made from wood fibres commonly had higher degree of aromaticity and recalcitrance (Liu *et al.*, 2016*a*; Wang, Xiong & Kuzyakov, 2016), which could reduce cellulase activity and enhance ligninase:cellulase ratio by affecting the chemical composition of soil substrates (Fig. S4). By contrast, the addition of carbohydrate-rich biochar (e.g. biochar derived from crop residues) may alleviate substrate restriction on cellulase activity and contribute to a reduced ligninase:cellulase ratio (Fig. S4). Additionally, our model selection and correlation analysis indicates that the pyrolysis temperature of biochar had differential effects on the response of cellulase and ligninase activity to biochar addition. Biochar produced at high (>550°C) pyrolysis temperatures commonly has more C present as aromatic compounds (Mukherjee, Zimmerman & Harris, 2011; Wang *et al.*, 2015), which may explain its reduced cellulase activity, but lack of a significant effect on ligninase activity (Fig. S4). Moreover, the response of soil ligninase activities to biochar addition correlated negatively with soil clay content, because humics and complex aromatic compounds could be preferentially or competitively adsorbed by soil clay particles (Balcke *et al.*, 2002). Therefore, loamy and clay soils with higher soil clay content had higher retention capacity for SOC compared with sandy soils (Fig. S4).

Shifts in responses of cellulase and ligninase activity to biochar addition could exert inverse effects on soil C sequestration. Specifically, suppressed cellulase activity may promote soil C sequestration with biochar by reducing the

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by University Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by University Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

decomposition of ordered polysaccharides with simpler structure (Margida *et al*., 2020). By contrast, enhanced ligninase activity may cause increased decomposition of complex phenolic macromolecules, which is commonly considered to be a rate-limiting step of SOC decomposition (Fontaine *et al*., 2007; Schmidt *et al*., 2011). For instance, the decomposition of phenolics such as tannins may result in reduced stabilisation of fungal necromass (Adamczyk *et al*., 2019) and alleviate the toxicity and binding effects of phenols on hydrolase activities (Freeman *et al*., 2004; Sinsabaugh, 2010), consequently limiting the effect of biochar addition on soil C sequestration. Therefore, biochar-induced sequestration of SOC could reflect the differential responses of these key extracellular enzymes. In support of this idea, our model selection analysis results indicate that shifts in soil enzyme activity from cellulase to ligninase explained the most variation in soil C sequestration with biochar addition (Fig. 3). Our regression analysis further showed a significant negative relationship between ligninase:cellulase ratio and SOC with biochar addition (Fig. 3D), suggesting that the increased decomposition of lignin-like substrates relative to cellulose-like substrates may limit soil C sequestration with biochar addition.

Moreover, the response of ligninase activity and ligninase:cellulase ratio to biochar addition varied between short-term (<1 year) and long-term (≥1 year) studies, contributing to the observed changes in the soil C sequestration capacity with time after biochar addition. In short-term studies, biochar addition significantly reduced cellulase activity, but had no significant effect on ligninase activity and ligninase:cellulase ratio, contributing to a significant 87.5% increase in SOC. However, the increased ligninase activity and ligninase:cellulase ratio observed in long-term studies may counteract the effects of cellulase activity on SOC sequestration and lead to weakened soil C sequestration (increased by only 25.1%) under biochar addition. These results indicate that some studies may have overestimated the long-term effects of biochar addition on soil C sequestration by failing to consider dynamics in activities of different enzymes with time after biochar addition (Woolf & Lehmann, 2012). Furthermore, the ligninase:cellulase ratio increases with time after biochar addition, which could exacerbate the decline in soil C over time. Previous studies have reported that complex-macromolecular C adsorbed on the surface of biochar could be used by the microbial community when polysaccharides with simple ordered structure are depleted over time (Gul *et al*., 2015; Yi *et al*., 2020). Therefore, this gradual increase in ligninase:cellulase ratio over time may also reflect changes in the chemical composition of soil organic matter and associated shifts in microbial community composition with time after biochar addition (Acosta-Martínez & Harmel, 2006; Pei *et al*., 2021). Similar declines in soil C sequestration with time after biochar addition have also been observed in long-term case studies, and are mainly considered the result of declining adsorption capacity of biochar over time (Lefebvre *et al*., 2020; Quilliam *et al*., 2013). These results provide new evidence from enzyme activities that a functional acclimation of soil microorganisms to the chemical composition of organic substrates affects the response of soil C sequestration to biochar addition over time.

However, the moderate correlations between soil C sequestration and ligninase:cellulase ratio suggest that shifts in soil enzyme activity alone cannot fully explain the variations in soil C sequestration with biochar addition (Fig. 3D). Indeed, overall soil C sequestration is determined by interactions among at least three C pools, namely biochar, the pre-existing SOC and plant litter/root exudates (Lehmann *et al*., 2021). Therefore, other soil processes, such as the decomposition of labile components of biochar and priming of pre-existing C in soil could also affect soil C sequestration with biochar addition (Singh *et al*., 2014; Zhang *et al*., 2022). For example, a previous meta-analysis indicated that a small part of biochar (~3%) is bioavailable with a mean residue time of 108 days (Wang *et al*., 2016), which may partly contribute to the initial decline in the response of soil C sequestration during the first year of biochar addition in this study. Further studies deciphering these processes (e.g. using isotopic tracers) are needed to predict accurately the long-term consequences of biochar addition to soil C sequestration. In addition, heterogeneity in experimental design (e.g. sampling season, properties of the original soil, type and concentration of substrate used for enzyme analysis, etc.) may affect our results and inferences. To investigate the sensitivity of our results to these heterogeneities, the influences of individual studies on the overall results were estimated by excluding one study a time. Our results showed that the response ratio of enzyme activities and SOC to biochar addition were relatively constant and without marked fluctuations (Table S3). This stability of results suggests that our findings do not merely reflect biases in the data set and provides support for our conclusions.

Models used to predict soil C sequestration with biochar addition vary significantly, with annual increases in SOC ranging from 0.07 to 10% per unit of biochar C added (Lehmann *et al*., 2021; Woolf & Lehmann, 2012). These large uncertainties may stem from the timescales and soil C mineralisation processes simulated in different models. Existing biochar models commonly consider soil C mineralisation as simple first-order reactions (Woolf & Lehmann, 2012). However, C mineralisation is a complex process that combines enzyme-mediated catalysis of both fast- and slow-mineralised organic fractions (Chen *et al*., 2020; Wu *et al*., 2022). Our results suggest that retaining inflexible microbial functional traits over the duration of biochar addition may lead to inaccurate predictions of soil C sequestration. Therefore, it is necessary to include the temporal shifts in microbial C-degrading enzyme activity to improve model predictions of soil C sequestration over time with added biochar.

Our study provides evidence for the contribution of biochar addition to enzyme-catalysed microbial decomposition processes and soil C sequestration over wide temporal and environmental scales. Our results show that shifts in cellulase and ligninase activities drive long-term impacts of biochar addition on soil C sequestration. This physiological acclimation in microbial metabolic activity has been overlooked to date (Hernandez-Soriano *et al*., 2016; Jing *et al*., 2022). In addition, our analyses offer insights to options for regulating soil C sequestration with biochar addition across a broad range of environmental and experimental conditions. Specifically, the responses of cellulase and ligninase depend on different environmental, edaphic and experimental factors (Fig. 2). Therefore, it should be possible to promote soil C accrual with biochar addition by regulating factors controlling different soil enzyme activities. For instance, biochar can be applied with N fertiliser to promote C sequestration by reducing N-mining and associated ligninase activity. Moreover, reduced response of soil ligninase activity and associated increase in soil C sequestration could also be achieved by selecting the appropriate pyrolysis temperature of biochar production. Therefore, there are promising potentials for innovative biochar management techniques for long-lasting climate mitigation, which will require the collective actions of policy makers, farmers and industry at both local and regional scales.

V. CONCLUSIONS

(1) Our synthesis identifies differential responses of cellulase and ligninase to biochar addition, with important implications for long-term soil C sequestration.
(2) Biochar addition increased ligninase activity but reduced cellulase activity, with an increasing ligninase:cellulase ratio with time after biochar addition.
(3) Biochar-induced changes in ligninase:cellulase ratio were negatively related to SOC pool size, suggesting a progressive reduction in soil C sequestration with long-term biochar addition.
(4) Various factors influenced the responses of cellulase and ligninase activities to biochar addition, providing insights into options for increasing soil C sequestration under prolonged biochar exposure.
(5) We provide new evidence to explain the diminished soil C sequestration with long-term biochar addition, and highlight that the C sequestration potential of biochar may be overestimated without considering temporal changes in the physiological acclimation of soil microorganisms.

VI. ACKNOWLEDGEMENTS

We would like to thank all the authors whose data and work are included in this meta-analysis. This study was supported by the National Natural Science Foundation of China (32071595, 41830756 and 42177022). We also thank the Fundamental Research Funds for the Central Universities (Program no. 2662019QD055). We acknowledge Cunbin Gao, Qianqian Zhao and Qin Liu for their assistance in data collection. J.C. received funding from Aarhus Universitets Forskningsfond (AUFF-E-2019-7-1), EU H2020 Marie Skłodowska-Curie Actions (839806), Danish Independent Research Foundation (1127-00015B), and Nordic Committee of Agriculture and Food Research (https://nordicagriresearch.org/2020-5/). The authors declare no competing interests.

VII. AUTHOR CONTRIBUTIONS

J. C. designed the meta-analysis. D. Y., J. F., Y. S. and X. L. conducted independent parallel screening of studies and collected data, J. F. analysed the data with help from J. C. and Y.-R. L. The manuscript was written by J. F., edited by J. C., Y.-R. L., R. L. S., D. L. M., M. N. A., P. S., and Q. H. All authors reviewed the paper and approved the final version.

VIII. DATA AVAILABILITY STATEMENT

The raw data used in the meta-analysis are available in the online digital repository figshare at https://doi.org/10.6084/m9.figshare.21769979.

IX. REFERENCES

References identified with an asterisk (*) are the primary studies included in the meta-analysis. Additional references cited only within the supporting information are identified with a dagger symbol (†).

*Abujabhah, I. S., Bound, S. A., Doyle, R. & Bowman, J. P. (2016). Effects of biochar and compost amendments on soil physico-chemical properties and the total community within a temperate agricultural soil. *Applied Soil Ecology* **98**, 243–253.

Acosta-Martínez, V. & Harmel, R. D. (2006). Soil microbial communities and enzyme activities under various poultry litter application rates. *Journal of Environmental Quality* **35**, 1309–1318.

Adamczyk, B., Sietiö, O.-M., Biasi, C. & Heinonsalo, J. (2019). Interaction between tannins and fungal necromass stabilizes fungal residues in boreal forest soils. *New Phytologist* **223**, 16–21.

*Al Marzooqi, F. & Yousef, L. F. (2017). Biological response of a sandy soil treated with biochar derived from a halophyte (*Salicornia bigelovii*). *Applied Soil Ecology* **114**, 9–15.

*Ameloot, N., Sleutel, S., Case, S. D. C., Alberti, G., McNamara, N. P., Zavalloni, C., Vervisch, B., Vedove, G. d. & De Neve, S. (2014). C mineralization and microbial activity in four biochar field experiments several years after incorporation. *Soil Biology and Biochemistry* **78**, 195–203.

*Awad, Y. M., Blagodatskaya, E., Ok, Y. S. & Kuzyakov, Y. (2013). Effects of polyacrylamide, biopolymer and biochar on the decomposition of 14C-labelled maize residues and on their stabilization in soil aggregates. *European Journal of Soil Science* **64**, 488–499.

*Awad, Y. M., Lee, S. S., Kim, K.-H., Ok, Y. S. & Kuzyakov, Y. (2018). Carbon and nitrogen mineralization and enzyme activities in soil aggregate-size classes: effects of biochar, oyster shells, and polymers. *Chemosphere* **198**, 40–48.

*Azeem, M., Hale, L., Montgomery, J., Crowley, D. & McGiffen, M. E. Jr. (2020). Biochar and compost effects on soil microbial communities and nitrogen induced respiration in turfgrass soils. *PLoS One* **15**, e0242209.

*Azlan Halmi, M. F., Hasenan, S. N., Simarani, K. & Abdullah, R. (2018). Linking soil microbial properties with plant performance in acidic tropical soil amended with biochar. *Agronomy* **8**, 255.

*Bailey, V. L., Fansler, S. J., Smith, J. L. & Bolton, H. (2011). Reconciling apparent variability in effects of biochar amendment on soil enzyme activities by assay optimization. *Soil Biology and Biochemistry* **43**, 296–301.

Balcke, G. U., Kulikova, N. A., Hesse, S., Kopinke, F.-D., Perminova, I. V. & Frimmel, F. H. (2002). Adsorption of humic substances onto kaolin clay related to their structural features. *Soil Science Society of America Journal* **66**, 1805–1812.

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by University Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

*Bamminger, C., Marschner, B. & Jüschke, E. (2014). An incubation study on the stability and biological effects of pyrogenic and hydrothermal biochar in two soils. *European Journal of Soil Science* **65**, 72–82.
*Bandara, T., Herath, I., Kumarathilaka, P., Seneviratne, M., Seneviratne, G., Rajakaruna, N., Vithanage, M. & Ok, Y. S. (2017). Role of woody biochar and fungal-bacterial co-inoculation on enzyme activity and metal immobilization in serpentine soil. *Journal of Soils and Sediments* **17**, 665–673.
*Benavente, I., Gascó, G., Plaza, C., Paz-Ferreiro, J. & Méndez, A. (2018). Choice of pyrolysis parameters for urban wastes affects soil enzymes and plant germination in a Mediterranean soil. *Science of the Total Environment* **634**, 1308–1314.
*Bera, T., Collins, H. P., Alva, A. K., Purakayastha, T. J. & Patra, A. K. (2016). Biochar and manure effluent effects on soil biochemical properties under corn production. *Applied Soil Ecology* **107**, 360–367.
*Bera, T., Vardanyan, L., Inglett, K. S., Reddy, K. R., O'Connor, G. A., Erickson, J. E. & Wilkie, A. C. (2019). Influence of select bioenergy by-products on soil carbon and microbial activity: a laboratory study. *Science of the Total Environment* **653**, 1354–1363.
*Bian, R., Joseph, S., Shi, W., Li, L., Taherymoosavi, S. & Pan, G. (2019). Biochar DOM for plant promotion but not residual biochar for metal immobilization depended on pyrolysis temperature. *Science of the Total Environment* **662**, 571–580.
Burke, R. & Cairney, J. (2002). Laccases and other polyphenol oxidases in ecto- and ericoid mycorrhizal fungi. *Mycorrhiza* **12**, 105–116.
Calcagno, V. & de Mazancourt, C. (2010). glmulti: An R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software* **34**, 1–29.
Campos, P., Miller, A. Z., Prats, S. A., Knicker, H., Hagemann, N. & De la Rosa, J. M. (2020). Biochar amendment increases bacterial diversity and vegetation cover in trace element-polluted soils: a long-term field experiment. *Soil Biology and Biochemistry* **150**, 108014.
*Chang, J., Luo, X., Li, M., Wang, Z. & Zheng, H. (2016). Short-term influences of peanut-biochar addition on abandoned orchard soil organic N mineralization in North China. *Polish Journal of Environmental Studies* **25**, 67–72.
*Chang, P. & Han, S. (2016). Effects of biochar on soil microorganism and enzyme activity in lou soil. *Agricultural Sciences* **4**, 39–40.
*Chen, J., Chen, D., Xu, Q., Fuhrmann, J. J., Li, L., Pan, G., Li, Y., Qin, H., Liang, C. & Sun, X. (2019). Organic carbon quality, composition of main microbial groups, enzyme activities, and temperature sensitivity of soil respiration of an acid paddy soil treated with biochar. *Biology and Fertility of Soils* **55**, 185–197.
Chen, J., Elsgaard, L., van Groenigen, K. J., Olesen, J. E., Liang, Z., Jiang, Y., Lærke, P. E., Zhang, Y., Luo, Y., Hungate, B. A., Sinsabaugh, R. L. & Jørgensen, U. (2020). Soil carbon loss with warming: new evidence from carbon-degrading enzymes. *Global Change Biology* **26**, 1944–1952.
*Chen, J., Li, S., Liang, C., Xu, Q., Li, Y., Qin, H. & Fuhrmann, J. J. (2017*a*). Response of microbial community structure and function to short-term biochar amendment in an intensively managed bamboo (*Phyllostachys praecox*) plantation soil: effect of particle size and addition rate. *Science of the Total Environment* **574**, 24–33.
*Chen, J., Liu, X., Zheng, J., Zhang, B., Lu, H., Chi, Z., Pan, G., Li, L., Zheng, J., Zhang, X., Wang, J. & Yu, X. (2013). Biochar soil amendment increased bacterial but decreased fungal gene abundance with shifts in community structure in a slightly acid rice paddy from Southwest China. *Applied Soil Ecology* **71**, 33–44.
Chen, J., Luo, Y., García-Palacios, P., Cao, J., Dacal, M., Zhou, X., Li, J., Xia, J., Niu, S., Yang, H., Shelton, S., Guo, W. & van Groenigen, K. J. (2018*a*). Differential responses of carbon-degrading enzyme activities to warming: implications for soil respiration. *Global Change Biology* **24**, 4816–4826.
Chen, J., Luo, Y., Li, J., Zhou, X., Cao, J., Wang, R.-W., Wang, Y., Shelton, S., Jin, Z., Walker, L. M., Feng, Z., Niu, S., Feng, W., Jian, S. & Zhou, L. (2017*b*). Costimulation of soil glycosidase activity and soil respiration by nitrogen addition. *Global Change Biology* **23**, 1328–1337.
Chen, J., Luo, Y., van Groenigen, K. J., Hungate, B. A., Cao, J., Zhou, X. & Wang, R. W. (2018*b*). A keystone microbial enzyme for nitrogen control of soil carbon storage. *Science Advances* **4**, eaaq1689.
*Chen, J., Sun, X., Li, L., Liu, X., Zhang, B., Zheng, J. & Pan, G. (2016). Change in active microbial community structure, abundance and carbon cycling in an acid rice paddy soil with the addition of biochar. *European Journal of Soil Science* **67**, 857–867.
*Chen, P., Liu, Y., Mo, C., Jiang, Z., Yang, J. & Lin, J. (2021). Microbial mechanism of biochar addition on nitrogen leaching and retention in tea soils from different plantation ages. *Science of The Total Environment* **757**, 143817.
*Chen, X. X., Xu-Sheng, H. E., Geng, Z. C., Shang, J., Zhao, J., Liu, C. Y., Wang, Y. P. & Yin, X. H. (2015). Relationship between soil biological activities and soil fertility after biochar application. *Agricultural Research in the Arid Areas* **33**, 47–54.
*Chen, Y. (2019). *Effects of Biochar and Water Retaining Agent on Water Characteristics and Enzyme Activities of Gangue Soil Matrix*. Beijing Forestry University, Beijing.
*Chintala, R., Schumacher, T. E., Kumar, S., Malo, D. D., Rice, J. A., Bleakley, B., Chilom, G., Clay, D. E., Julson, J. L., Papiernik, S. K. & Gu, Z. R. (2014). Molecular characterization of biochars and their influence on microbiological properties of soil. *Journal of Hazardous Materials* **279**, 244–256.
Copas, J. B. & Shi, J. Q. (2000). Meta-analysis, funnel plots and sensitivity analysis. *Biostatistics* **1**, 247–262.
*Cordovil, C. M. d. S., Pinto, R., Silva, B., Sas-Paszt, L., Sakrabani, R. & Skiba, U. M. (2019). The impact of woody biochar on microbial processes in conventionally and organically managed arable soils. *Communications in Soil Science and Plant Analysis* **50**, 1387–1402.
Craine, J. M., Morrow, C. & Fierer, N. (2007). Microbial nitrogen limitation increases decomposition. *Ecology* **88**, 2105–2113.
Deforest, J. L. (2009). The influence of time, storage temperature, and substrate age on potential soil enzyme activity in acidic forest soils using MUB-linked substrates and L-DOPA. *Soil Biology and Biochemistry* **41**, 1180–1186.
*Demisie, W., Liu, Z. & Zhang, M. (2014). Effect of biochar on carbon fractions and enzyme activity of red soil. *Catena* **121**, 214–221.
*Du, Z., Wang, Y.-D., Huang, J.-X., Lu, N., Liu, X., Lou, Y. & Zhang, Q.-z. (2014). Consecutive biochar application alters soil enzyme activities in the winter wheat growing season. *Soil Science* **179**, 75–83.
*Duan, C. (2020). *Effects of Eucalptus Branches Biochar Application on Soil Nitrogen Components and Microbiological Characteristics of Eucalyptus Plantation in Nitrogen Guangxi*. Guangxi Normal University, Guilin.
*Elzobair, K. A., Stromberger, M. E., Ippolito, J. A. & Lentz, R. D. (2016). Contrasting effects of biochar versus manure on soil microbial communities and enzyme activities in an Aridisol. *Chemosphere* **142**, 145–152.
*Espinosa, N. J., Moore, D. J. P., Rasmussen, C., Fehmi, J. S. & Gallery, R. E. (2020). Woodchip and biochar amendments differentially influence microbial responses, but do not enhance plant recovery in disturbed semiarid soils. *Restoration Ecology* **28**, S381–S392.
Fawzy, S., Osman, A. I., Yang, H., Doran, J. & Rooney, D. W. (2021). Industrial biochar systems for atmospheric carbon removal: a review. *Environmental Chemistry Letters* **19**, 3023–3055.
Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B. & Rumpel, C. (2007). Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature* **450**, 277–280.
Freeman, C., Ostle, N. J., Fenner, N. & Kang, H. (2004). A regulatory role for phenol oxidase during decomposition in peatlands. *Soil Biology and Biochemistry* **36**, 1663–1667.
*Gao, W., Guo, Z., XUe, C., Yin, H., Chang, M., Zhou, Q., Wang, G., Li, F. & Liu, Y. (2020). Effect of biochar and biochar compound fertilizer on soil enzyme activity of soybean on soil enzyme activity of soybean. *Journal of Huaibei Normal University (Natural Sciences)* **41**, 48–52.
*Gascó, G., Paz-Ferreiro, J., Cely, P., Plaza, C. & Méndez, A. (2016). Influence of pig manure and its biochar on soil CO_2 emissions and soil enzymes. *Ecological Engineering* **95**, 19–24.
*Gebhardt, M., Fehmi, J. S., Rasmussen, C. & Gallery, R. E. (2017). Soil amendments alter plant biomass and soil microbial activity in a semi-desert grassland. *Plant and Soil* **419**, 53–70.
German, D. P., Marcelo, K. R. B., Stone, M. M. & Allison, S. D. (2012). The Michaelis–Menten kinetics of soil extracellular enzymes in response to temperature: a cross-latitudinal study. *Global Change Biology* **18**, 1468–1479.
*Ghosh, D. & Maiti, S. K. (2021). Effect of invasive weed biochar amendment on soil enzymatic activity and respiration of coal mine spoil: a laboratory experiment study. *Biochar* **3**, 519–533.
Gronwald, M., Don, A., Tiemeyer, B. & Helfrich, M. (2015). Effects of fresh and aged chars from pyrolysis and hydrothermal carbonization on nutrient sorption in agricultural soils. *Soil* **1**, 475–489.
Gul, S., Whalen, J. K., Thomas, B. W., Sachdeva, V. & Deng, H. (2015). Physico-chemical properties and microbial responses in biochar-amended soils: mechanisms and future directions. *Agriculture, Ecosystems & Environment* **206**, 46–59.
*Guo, K., Zhao, Y., Liu, Y., Chen, J., Wu, Q., Ruan, Y., Li, S., Shi, J., Zhao, L., Sun, X., Liang, C., Xu, Q. & Qin, H. (2020). Pyrolysis temperature of biochar affects ecoenzymatic stoichiometry and microbial nutrient-use efficiency in a bamboo forest soil. *Geoderma* **363**, 114162.
*Guo, T. (2018). *Effects of Short-Term Tillage and Fertilization on Enzyme Activities and Bacterial Diversity of Meadow Black Soil*. Northeast Agricultural University, Harbin.
Hagemann, N., Joseph, S., Schmidt, H.-P., Kammann, C. I., Harter, J., Borch, T., Young, R. B., Varga, K., Taherymoosavi, S., Elliott, K. W., McKenna, A., Albu, M., Mayrhofer, C., Obst, M., Conte, P., *et al.* (2017). Organic coating on biochar explains its nutrient retention and stimulation of soil fertility. *Nature Communications* **8**, 1089.
*Halmi, M. F. A. & Simarani, K. (2021). Responses of soil microbial population and lignocellulolytic enzyme activities to palm kernel shell biochar amendment. *Eurasian Soil Science* **54**, 1903–1911.
Han, M., Zhao, Q., Li, W., Ciais, P., Wang, Y.-P., Goll, D. S., Zhu, L., Zhao, Z., Wang, J., Wei, Y. & Wu, F. (2022). Global soil organic carbon changes and economic revenues with biochar application. *GCB Bioenergy* **14**, 364–377.

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by University Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

*Han, S. (2017). *Effects of Exogenous Carbon and Nitroge Addition on Soil Biological Activity and the Role of Ectomycorrhizal Fungi in Nitrogen Transformation*. Jinan University, Jinan.
Hedges, L. V., Gurevitch, J. & Curtis, P. S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology* **80**, 1150–1156.
Hernandez-Soriano, M. C., Kerré, B., Kopittke, P. M., Horemans, B. & Smolders, E. (2016). Biochar affects carbon composition and stability in soil: a combined spectroscopy-microscopy study. *Scientific Reports* **6**, 25127.
*Hou, J.-X., Zhang, S.-M., Yuan, J.-C., Cheng, S., Liu, J.-Z., Liu, S.-T., Liang, Y., Ren, J. & Cai, H.-G. (2021). Effects of maize straw-derived organic materials on improving soil nutrient availability and enzyme activities in a Mollisol. *Journal of Plant Nutrition and Fertilizers* **27**, 610–618.
*Hu, H., Yin, D., Cao, S., Zhang, H., Zhou, C. & He, Z. (2019). Effects of biochar on soil nutrient, enzyme activity, and bacterial properties of Chinese fir plantation. *Acta Ecologica Sinica* **39**, 4138–4148.
*Imparato, V., Hansen, V., Santos, S. S., Nielsen, T. K., Giagnoni, L., Hauggaard-Nielsen, H., Johansen, A., Renella, G. & Winding, A. (2016). Gasification biochar has limited effects on functional and structural diversity of soil microbial communities in a temperate agroecosystem. *Soil Biology and Biochemistry* **99**, 128–136.
*Jegajeevagan, K., Mabilde, L., Gebremikael, M. T., Ameloot, N., De Neve, S., Leinweber, P. & Sleutel, S. (2016). Artisanal and controlled pyrolysis-based biochars differ in biochemical composition, thermal recalcitrance, and biodegradability in soil. *Biomass and Bioenergy* **84**, 1–11.
*Jenkins, J. R., Viger, M., Arnold, E. C., Harris, Z. M., Ventura, M., Miglietta, F., Girardin, C., Edwards, R. J., Rumpel, C., Fornasier, F., Zavalloni, C., Tonon, G., Alberti, G. & Taylor, G. (2017). Biochar alters the soil microbiome and soil function: results of next-generation amplicon sequencing across Europe. *GCB Bioenergy* **9**, 591–612.
*Jia, J. & Xie, Y. (2016). Effects of biochar on soil nutrient and enzyme activity from coal mining subsidence reclamation area. *Journal of Irrigation and Drainage* **35**, 88–91.
*Jin, Z., Chen, C., Chen, X., Hopkins, I., Zhang, X., Han, Z., Jiang, F. & Billy, G. (2019). The crucial factors of soil fertility and rapeseed yield – a five year field trial with biochar addition in upland red soil, China. *Science of the Total Environment* **649**, 1467–1480.
Jing, F., Sun, Y., Liu, Y., Wan, Z., Chen, J. & Tsang, D. C. W. (2022). Interactions between biochar and clay minerals in changing biochar carbon stability. *Science of the Total Environment* **809**, 151124.
*Kaewpradit, W. & Toomsan, B. (2019). Impact of eucalyptus biochar application to upland rice-sugarcane cropping systems on enzyme activities and nitrous oxide emissions of soil at sugarcane harvest under incubation experiment. *Journal of Plant Nutrition* **42**, 362–373.
*Karimi, A., Moezzi, A., Chorom, M. & Enayatizamir, N. (2020). Application of biochar changed the status of nutrients and biological activity in a calcareous soil. *Journal of Soil Science and Plant Nutrition* **20**, 450–459.
Kleber, M., Sollins, P. & Sutton, R. (2007). A conceptual model of organo-mineral interactions in soils: self-assembly of organic molecular fragments into zonal structures on mineral surfaces. *Biogeochemistry* **85**, 9–24.
*Kumar, S., Masto, R. E., Ram, L. C., Sarkar, P., George, J. & Selvi, V. A. (2013). Biochar preparation from *Parthenium hysterophorus* and its potential use in soil application. *Ecological Engineering* **55**, 67–72.
Lefebvre, D., Williams, A., Meersmans, J., Kirk, G. J. D., Sohi, S., Goglio, P. & Smith, P. (2020). Modelling the potential for soil carbon sequestration using biochar from sugarcane residues in Brazil. *Scientific Reports* **10**, 19479.
Lehmann, J., Cowie, A., Masiello, C. A., Kammann, C., Woolf, D., Amonette, J. E., Cayuela, M. L., Camps-Arbestain, M. & Whitman, T. (2021). Biochar in climate change mitigation. *Nature Geoscience* **14**, 883–892.
Lehmann, J., Rillig, M. C., Thies, J., Masiello, C. A., Hockaday, W. C. & Crowley, D. (2011). Biochar effects on soil biota – a review. *Soil Biology and Biochemistry* **43**, 1812–1836.
*Lei, H. (2016). *Effects of Chinese Fir Litter and its Biochar on Soil CO_2 Emission, Microbe and Enzyme Activity*. Fujian Normal University, Fujian.
*Li, J. (2016). *Effects of Combined Application of Biochar and Nitrogen Fertilizers Opn Soil Peoperties, Growth and Quality of Flue-Cured Tabacoo*. Henan Agricultural University, Zhengzhou.
*Li, J., Ding, S.-S., Li, Y.-P., Yun, F., Yan, H., Wang, Z. & Liu, G. (2016). Effects of biochar and nitrogen fertilizers on dry matter accumulation of flue-cured tobacco and soil biological characteristics. *Acta Agriculturae Zhejiangensis* **28**, 96–103.
*Li, Q., Song, X., Yrjälä, K., Lv, J., Li, Y., Wu, J. & Qin, H. (2020*a*). Biochar mitigates the effect of nitrogen deposition on soil bacterial community composition and enzyme activities in a *Torreya grandis* orchard. *Forest Ecology and Management* **457**, 117717.
*Li, S., Liang, C. & Shangguan, Z. (2017). Effects of apple branch biochar on soil C mineralization and nutrient cycling under two levels of N. *Science of the Total Environment* **607–608**, 109–119.
Li, X., Wang, T., Chang, S. X., Jiang, X. & Song, Y. (2020*b*). Biochar increases soil microbial biomass but has variable effects on microbial diversity: a meta-analysis. *Science of the Total Environment* **749**, 141593.
Li, X., Yao, S., Bian, Y., Jiang, X. & Song, Y. (2020*c*). The combination of biochar and plant roots improves soil bacterial adaptation to PAH stress: insights from soil enzymes, microbiome, and metabolome. *Journal of Hazardous Materials* **400**, 123227.
*Li, Y., Li, Y., Chang, S. X., Yang, Y., Fu, S., Jiang, P., Luo, Y., Yang, M., Chen, Z., Hu, S., Zhao, M., Liang, X., Xu, Q., Zhou, G. & Zhou, J. (2018). Biochar reduces soil heterotrophic respiration in a subtropical plantation through increasing soil organic carbon recalcitrancy and decreasing carbon-degrading microbial activity. *Soil Biology and Biochemistry* **122**, 173–185.
*Liang, C., Gascó, G., Fu, S., Méndez, A. & Paz-Ferreiro, J. (2016). Biochar from pruning residues as a soil amendment: effects of pyrolysis temperature and particle size. *Soil and Tillage Research* **164**, 3–10.
*Liang, C., Zhu, X., Fu, S., Méndez, A., Gascó, G. & Paz-Ferreiro, J. (2014*a*). Biochar alters the resistance and resilience to drought in a tropical soil. *Environmental Research Letters* **9**, 064013.
*Liang, F., Li, G.-T., Lin, Q.-M. & Zhao, X.-R. (2014*b*). Crop yield and soil properties in the first 3 years after biochar application to a calcareous soil. *Journal of Integrative Agriculture* **13**, 525–532.
*Liao, N., Li, Q., Zhang, W., Zhou, G., Ma, L., Min, W., Ye, J. & Hou, Z. (2016). Effects of biochar on soil microbial community composition and activity in drip-irrigated desert soil. *European Journal of Soil Biology* **72**, 27–34.
*Liu, S., Meng, J., Jiang, L., Yang, X., Lan, Y., Cheng, X. & Chen, W. (2017). Rice husk biochar impacts soil phosphorous availability, phosphatase activities and bacterial community characteristics in three different soil types. *Applied Soil Ecology* **116**, 12–22.
Liu, S., Zhang, Y., Zong, Y., Hu, Z., Wu, S., Zhou, J., Jin, Y. & Zou, J. (2016*a*). Response of soil carbon dioxide fluxes, soil organic carbon and microbial biomass carbon to biochar amendment: a meta-analysis. *GCB Bioenergy* **8**, 392–406.
*Liu, X., Wang, Q., Qi, Z., Han, J. & Li, L. (2016*b*). Response of N_2O emissions to biochar amendment in a cultivated sandy loam soil during freeze–thaw cycles. *Scientific Reports* **6**, 35411.
*Liu, Y., Guo, K., Zhao, Y., Li, S., Wu, Q., Liang, C., Sun, X., Xu, Q., Chen, J. & Qin, H. (2020). Change in composition and function of microbial communities in an acid bamboo (*Phyllostachys praecox*) plantation soil with the addition of three different biochars. *Forest Ecology and Management* **473**, 118336.
*Lu, H., Bian, R., Xia, X., Cheng, K., Liu, X., Liu, Y., Wang, P., Li, Z., Zheng, J., Zhang, X., Li, L., Joseph, S., Drosos, M. & Pan, G. (2020). Legacy of soil health improvement with carbon increase following one time amendment of biochar in a paddy soil – a rice farm trial. *Geoderma* **376**, 114567.
*Luo, L. & Gu, J.-D. (2016). Alteration of extracellular enzyme activity and microbial abundance by biochar addition: implication for carbon sequestration in subtropical mangrove sediment. *Journal of Environmental Management* **182**, 29–36.
*Ma, H., Egamberdieva, D., Wirth, S. & Bellingrath-Kimura, S. D. (2019). Effect of biochar and irrigation on soybean-rhizobium symbiotic performance and soil enzymatic activity in field rhizosphere. *Agronomy* **9**, 626.
*Manna, S., Singh, N. & Singh, S. B. (2018). Evaluation of rice and wheat straw biochars' effect on pyrazosulfuron-ethyl degradation and microbial activity in rice-planted soil. *Soil Research* **56**, 579–587.
Margida, M. G., Lashermes, G. & Moorhead, D. L. (2020). Estimating relative cellulolytic and ligninolytic enzyme activities as functions of lignin and cellulose content in decomposing plant litter. *Soil Biology and Biochemistry* **141**, 107689.
Marx, M.-C., Wood, M. & Jarvis, S. (2001). A microplate fluorimetric assay for the study of enzyme diversity in soils. *Soil Biology & Biochemistry* **33**, 1633–1640.
*Masto, R. E., Ansari, M. A., George, J., Selvi, V. A. & Ram, L. C. (2013). Co-application of biochar and lignite fly ash on soil nutrients and biological parameters at different crop growth stages of *Zea mays*. *Ecological Engineering* **58**, 314–322.
*Meng, F. H., Gao, J. L., Xiao-Fang, Y. U., Wang, Z. G., Shu-Ping, H. U., Ge-Er, Q., Sun, J. Y. & Jia-Wei, Q. U. (2018). Inprovent of biochemical property of surface soil by combined application of biochar with nitrogen fertilizer. *Journal of Plant Nutrition and Fertilizers* **24**, 1214–1226.
*Meng, K. (2016). *Effects of Biochar on Four Kinds of Soil Physicall and Chemical Properties of Flued-Cured Tobacco in Xiangxi Area*. Hunan Agricultural University, Zhengzhou.
Meyer, N., Welp, G., Bornemann, L. & Amelung, W. (2017). Microbial nitrogen mining affects spatio-temporal patterns of substrate-induced respiration during seven years of bare fallow. *Soil Biology & Biochemistry* **104**, 175–184.
Mitchell, P. J., Simpson, A. J., Soong, R. & Simpson, M. J. (2016). Biochar amendment altered the molecular-level composition of native soil organic matter in a temperate forest soil. *Environmental Chemistry* **13**, 854–866.
Molina, M., Zaelke, D., Sarma, K. M., Andersen, S. O., Ramanathan, V. & Kaniaru, D. (2009). Reducing abrupt climate change risk using the Montreal protocol and other regulatory actions to complement cuts in CO_2 emissions. *Proceedings of the National Academy of Sciences* **106**, 20616–20621.
Moore, J. C., Jevrejeva, S. & Grinsted, A. (2010). Efficacy of geoengineering to limit 21st century sea-level rise. *Proceedings of the National Academy of Sciences* **107**, 15699–15703.

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by University Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Moorhead, D. L. & Sinsabaugh, R. L. (2006). A theoretical model of litter decay and microbial interaction. *Ecological Monographs* **76**, 151–174.

Muggeo, V. M. R. (2003). Estimating regression models with unknown break-points. *Statistics in Medicine* **22**, 3055–3071.

Mukherjee, A., Zimmerman, A. R. & Harris, W. (2011). Surface chemistry variations among a series of laboratory-produced biochars. *Geoderma* **163**, 247–255.

O'Dea, R. E., Lagisz, M., Jennions, M. D., Koricheva, J., Noble, D. W., Parker, T. H., Gurevitch, J., Page, M. J., Stewart, G. & Moher, D. (2021). Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a PRISMA extension. *Biological Reviews of the Cambridge Philosophical Society* **96**, 1695–1722.

*Ouyang, L., Tang, Q., Yu, L. & Zhang, R. (2014). Effects of amendment of different biochars on soil enzyme activities related to carbon mineralisation. *Soil Research* **52**, 706–716.

*Pandey, V., Patel, A. & Patra, D. D. (2016). Biochar ameliorates crop productivity, soil fertility, essential oil yield and aroma profiling in basil (*Ocimum basilicum* L.). *Ecological Engineering* **90**, 361–366.

*Paz-Ferreiro, J., Fu, S., Méndez, A. & Gascó, G. (2014). Interactive effects of biochar and the earthworm *Pontoscolex corethrurus* on plant productivity and soil enzyme activities. *Journal of Soils and Sediments* **14**, 483–494.

*Paz-Ferreiro, J., Gascó, G., Gutiérrez, B. & Méndez, A. (2012). Soil biochemical activities and the geometric mean of enzyme activities after application of sewage sludge and sewage sludge biochar to soil. *Biology and Fertility of Soils* **48**, 511–517.

*Pei, J., Dijkstra, F. A., Li, J., Fang, C., Su, J., Zhao, J., Nie, M. & Wu, J. (2020). Biochar-induced reductions in the rhizosphere priming effect are weaker under elevated CO_2. *Soil Biology and Biochemistry* **142**, 107700.

Pei, J., Li, J., Mia, S., Singh, B., Wu, J. & Dijkstra, F. A. (2021). Biochar aging increased microbial carbon use efficiency but decreased biomass turnover time. *Geoderma* **382**, 114710.

Peng, C., Li, Q., Zhang, Z., Wu, Z., Song, X., Zhou, G. & Song, X. (2019). Biochar amendment changes the effects of nitrogen deposition on soil enzyme activities in a Moso bamboo plantation. *Journal of Forest Research* **24**, 275–284.

*Pokharel, P., Kwak, J.-H., Ok, Y. S. & Chang, S. X. (2018). Pine sawdust biochar reduces GHG emission by decreasing microbial and enzyme activities in forest and grassland soils in a laboratory experiment. *Science of the Total Environment* **625**, 1247–1256.

Quilliam, R. S., Glanville, H. C., Wade, S. C. & Jones, D. L. (2013). Life in the 'charosphere' – does biochar in agricultural soil provide a significant habitat for microorganisms? *Soil Biology & Biochemistry* **65**, 287–293.

*Rafael, R. B. A., FernÁNdez-Marcos, M. L., Cocco, S., Ruello, M. L., Fornasier, F. & Corti, G. (2019). Benefits of biochars and NPK fertilizers for soil quality and growth of cowpea (*Vigna unguiculata* L. Walp.) in an acid arenosol. *Pedosphere* **29**, 311–333.

*Rafael, R. B. A., FernÁNdez-Marcos, M. L., Cocco, S., Ruello, M. L., Fornasier, F. & Corti, G. (2020). Increased phosphorus availability to corn resulting from the simultaneous applications of phosphate rock, calcareous rock, and biochar to an acid sandy soil. *Pedosphere* **30**, 719–733.

Ren, C., Zhao, F., Shi, Z., Chen, J., Han, X., Yang, G., Feng, Y. & Ren, G. (2017). Differential responses of soil microbial biomass and carbon-degrading enzyme activities to altered precipitation. *Soil Biology and Biochemistry* **115**, 1–10.

*Ren, H., Lv, C., Fernández-García, V., Huang, B., Yao, J. & Ding, W. (2021). Biochar and PGPR amendments influence soil enzyme activities and nutrient concentrations in a eucalyptus seedling plantation. *Biomass Conversion and Biorefinery* **11**, 1865–1874.

*Sanchez-Hernandez, J. C., Ríos, J. M., Attademo, A. M., Malcevschi, A. & Andrade Cares, X. (2019). Assessing biochar impact on earthworms: implications for soil quality promotion. *Journal of Hazardous Materials* **366**, 582–591.

†Sayre, R., Karagulle, D., Frye, C., Boucher, T., Wolff, N. H., Breyer, S., Wright, D., Martin, M., Butler, K., Van Graafeiland, K., Touval, J., Sotomayor, L., McGowan, J., Game, E. T. & Possingham, H. (2020). An assessment of the representation of ecosystems in global protected areas using new maps of world climate regions and world ecosystems. *Global Ecology and Conservation* **21**, e00860.

Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D. A. C., Nannipieri, P., Rasse, D. P., Weiner, S. & Trumbore, S. E. (2011). Persistence of soil organic matter as an ecosystem property. *Nature* **478**, 49–56.

*Sekaran, U., Sandhu, S. S., Qiu, Y., Kumar, S. & Gonzalez Hernandez, J. L. (2020). Biochar and manure addition influenced soil microbial community structure and enzymatic activities at eroded and depositional landscape positions. *Land Degradation & Development* **31**, 894–908.

*Sial, T. A., Khan, M. N., Lan, Z., Kumbhar, F., Ying, Z., Zhang, J., Sun, D. & Li, X. (2019*a*). Contrasting effects of banana peels waste and its biochar on greenhouse gas emissions and soil biochemical properties. *Process Safety and Environmental Protection* **122**, 366–377.

*Sial, T. A., Lan, Z., Khan, M. N., Zhao, Y., Kumbhar, F., Liu, J., Zhang, A., Hill, R. L., Lahori, A. H. & Memon, M. (2019*b*). Evaluation of orange peel waste and its biochar on greenhouse gas emissions and soil biochemical properties within a loess soil. *Waste Management* **87**, 125–134.

*Sial, T. A., Lan, Z., Wang, L., Zhao, Y., Zhang, J., Kumbhar, F., Memon, M., Lashari, M. S. & Shah, A. N. (2019*c*). Effects of different biochars on wheat growth parameters, yield and soil fertility status in a silty clay loam soil. *Molecules* **24**, 1798.

*Sial, T. A., Shaheen, S. M., Lan, Z., Korai, P. K., Ghani, M. I., Khan, M. N., Syed, A.-u.-A., Hussain Asghar Ali, M. N., Rajpar, I., Memon, M., Bhatti, S. M., Abdelrahman, H., Ali, E. F., Rinklebe, J. & Zhang, J. (2022). Addition of walnut shells biochar to alkaline arable soil caused contradictory effects on CO_2 and N_2O emissions, nutrients availability, and enzymes activity. *Chemosphere* **293**, 133476.

Singh, B. P. & Cowie, A. L. (2014). Long-term influence of biochar on native organic carbon mineralisation in a low-carbon clayey soil. *Scientific Reports* **4**, 3687.

Singh, N., Abiven, S., Maestrini, B., Bird, J. A., Torn, M. S. & Schmidt, M. W. I. (2014). Transformation and stabilization of pyrogenic organic matter in a temperate forest field experiment. *Global Change Biology* **20**, 1629–1642.

Sinsabaugh, R. L. (2010). Phenol oxidase, peroxidase and organic matter dynamics of soil. *Soil Biology & Biochemistry* **42**, 391–404.

Sinsabaugh, R. L., Lauber, C. L., Weintraub, M. N., Ahmed, B., Allison, S. D., Crenshaw, C., Contosta, A. R., Cusack, D., Frey, S., Gallo, M. E., Gartner, T. B., Hobbie, S. E., Holland, K., Keeler, B. L., Powers, J. S., *et al.* (2008). Stoichiometry of soil enzyme activity at global scale. *Ecology Letters* **11**, 1252–1264.

Sohi, S. P., Krull, E., Lopez-Capel, E. & Bol, R. (2010). Chapter 2 - A review of biochar and its use and function in soil. In *Advances in Agronomy* (Volume **105**), pp. 47–82. Academic Press, Kidlington.

*Song, D., Chen, L., Zhang, S., Zheng, Q., Ullah, S., Zhou, W. & Wang, X. (2020*a*). Combined biochar and nitrogen fertilizer change soil enzyme and microbial activities in a 2-year field trial. *European Journal of Soil Biology* **99**, 103212.

*Song, D., Tang, J., Xi, X., Zhang, S., Liang, G., Zhou, W. & Wang, X. (2018). Responses of soil nutrients and microbial activities to additions of maize straw biochar and chemical fertilization in a calcareous soil. *European Journal of Soil Biology* **84**, 1–10.

*Song, D., Xi, X., Huang, S., Liang, G., Sun, J., Zhou, W. & Wang, X. (2016). Short-term responses of soil respiration and C-cycle enzyme activities to additions of biochar and urea in a calcareous soil. *PloS one* **11**, e0161694.

*Song, D., Xi, X., Zheng, Q., Liang, G., Zhou, W. & Wang, X. (2019*a*). Soil nutrient and microbial activity responses to two years after maize straw biochar application in a calcareous soil. *Ecotoxicology and Environmental Safety* **180**, 348–356.

*Song, J. (2014). *The Research of Biorchar Input on Soil Conservation and Quality Enchancement of Tobacco in Western Henan*. Henan University of Science and Technology, Luoyang.

*Song, Q., He, Y., Wu, Y., Chen, S., Zhang, T. & Chen, H. (2020*b*). Biochar impacts on acidic soil from *Camellia oleifera* plantation: a short-term soil incubation study. *Agronomy* **10**, 1446.

*Song, X., Razavi, B. S., Ludwig, B., Zamanian, K., Zang, H., Kuzyakov, Y., Dippold, M. A. & Gunina, A. (2020*c*). Combined biochar and nitrogen application stimulates enzyme activity and root plasticity. *Science of the Total Environment* **735**, 139393.

*Song, X., Yang, J., Hussain, Q., Liu, X., Zhang, J. & Cui, D. (2020*d*). Stable isotopes reveal the formation diversity of humic substances derived from different cotton straw-based materials. *Science of the Total Environment* **740**, 140202.

*Song, Y., Li, Y., Cai, Y., Fu, S., Luo, Y., Wang, H., Liang, C., Lin, Z., Hu, S., Li, Y. & Chang, S. X. (2019*b*). Biochar decreases soil N_2O emissions in Moso bamboo plantations through decreasing labile N concentrations, N-cycling enzyme activities and nitrification/denitrification rates. *Geoderma* **348**, 135–145.

*Sudeshna, B., Ramesh, C., Navneet, P. & Kiran, P. R. (2016). Biochar and crop residue application to soil: effect on soil biochemical properties, nutrient availability and yield of rice (*Oryza sativa* L.) and wheat (*Triticum aestivum* L.). *Archives of Agronomy and Soil Science* **62**, 1095–1108.

*Sun, J. (2015). *Effect of Nitrogen Fertilizer and Biochar on Microbial Activity and Ammonia Oxidation in Soils*. University of Science and Technology Beijing, Beijing.

Terrer, C., Vicca, S., Hungate, B. A., Phillips, R. P. & Prentice, I. C. (2016). Mycorrhizal association as a primary control of the CO_2 fertilization effect. *Science* **353**, 72–74.

*Teutscherova, N., Lojka, B., Houska, J., Masaguer, A., Benito, M. & Vazquez, E. (2018). Application of holm oak biochar alters dynamics of enzymatic and microbial activity in two contrasting Mediterranean soils. *European Journal of Soil Biology* **88**, 15–26.

*Tian, J., Wang, J., Dippold, M., Gao, Y., Blagodatskaya, E. & Kuzyakov, Y. (2016). Biochar affects soil organic matter cycling and microbial functions but does not alter microbial community structure in a paddy soil. *Science of the Total Environment* **556**, 89–97.

van Groenigen, K. J., Osenberg, C. W., Terrer, C., Carrillo, Y., Dijkstra, F. A., Heath, J., Nie, M., Pendall, E., Phillips, R. P. &

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by University Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Hungate, B. A. (2017). Faster turnover of new soil carbon inputs under increased atmospheric CO_2. *Global Change Biology* **23**, 4420–4429.

*Ventura, M., Zhang, C., Baldi, E., Fornasier, F., Sorrenti, G., Panzacchi, P. & Tonon, G. (2014). Effect of biochar addition on soil respiration partitioning and root dynamics in an apple orchard. *European Journal of Soil Science* **65**, 186–195.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software* **36**, 1–48.

*Walelign, D. & Mingkui, Z. (2015). Effect of biochar application on microbial biomass and enzymatic activities in degraded red soil. *African Journal of Agricultural Research* **10**, 755–766.

*Wang, C., Chen, S., Wu, L., Zhang, F. & Cui, J. (2018*a*). Wheat straw-derived biochar enhanced nitrification in a calcareous clay soil. *Polish Journal of Environmental Studies* **27**, 1297–1305.

*Wang, H. (2018). *Effects of Rape Straw Biochars on Sulfur Conversion and Microbial Community Strcuture under Anaerobic Conditions in Light Sierozem*. Lanzhou Jiaotong University, Lanzhou.

Wang, J., Xiong, Z. & Kuzyakov, Y. (2016). Biochar stability in soil: meta-analysis of decomposition and priming effects. *GCB Bioenergy* **8**, 512–523.

*Wang, X., Liu, J., Hu, Y., Li, F., Wang, R., Wang, X. & Li, M. (2018*b*). Effect of biochar on microorganism, nutrient content and enzyme activity of cucumber rhizosphere soil. *Journal of Nuclear Agricultural Sciences* **32**, 370–376.

*Wang, X., Zhou, W., Liang, G., Song, D. & Zhang, X. (2015). Characteristics of maize biochar with different pyrolysis temperatures and its effects on organic carbon, nitrogen and enzymatic activities after addition to fluvo-aquic soil. *Science of the Total Environment* **538**, 137–144.

*Wei, F. (2019). *Effects of Straw and Biochar on Soil Organic Carbon Mineralization and Soil Enzyme Activity of Red Soil in South China*. Jiangxi Agricultural University, Nanchang.

*Wei, J. & Hong, J. (2019). Effect of inorganic organic fertilizer combined with biochar on enzyme activity and phosphorus forms in reclaimed soil. *Acta Agriculturae Boreali-Sinica* **34**, 170–176.

Woolf, D., Amonette, J. E., Street-Perrott, F. A., Lehmann, J. & Joseph, S. (2010). Sustainable biochar to mitigate global climate change. *Nature Communications* **1**, 56.

Woolf, D. & Lehmann, J. (2012). Modelling the long-term response to positive and negative priming of soil organic carbon by black carbon. *Biogeochemistry* **111**, 83–95.

*Wu, C., Hou, Y., Bie, Y., Chen, X., Dong, Y. & Lin, L. (2020*a*). Effects of biochar on soil water-soluble sodium, calcium, magnesium and soil enzyme activity of peach seedlings. *IOP Conference Series: Earth and Environmental Science* **446**, 032007.

*Wu, D., Senbayram, M., Zang, H., Ugurlar, F., Aydemir, S., Brüggemann, N., Kuzyakov, Y., Bol, R. & Blagodatskaya, E. (2018*a*). Effect of biochar origin and soil pH on greenhouse gas emissions from sandy and clay soils. *Applied Soil Ecology* **129**, 121–127.

*Wu, F., Jia, Z., Wang, S., Chang, S. X. & Startsev, A. (2013). Contrasting effects of wheat straw and its biochar on greenhouse gas emissions and enzyme activities in a chernozemic soil. *Biology and Fertility of Soils* **49**, 555–565.

Wu, J., Cheng, X., Luo, Y., Liu, W. & Liu, G. (2022). Identifying carbon-degrading enzyme activities in association with soil organic carbon accumulation under land-use changes. *Ecosystems* **25**, 1219–1233.

*Wu, J., Peng, G., Yang, Y., Ren, T., Zhang, L. & Liu, G. (2018*b*). Effects of mined biochar and nitrogen fertilizer on biological characteristics of soil and nitrogen absorption of flue-cured tobacco. *Acta Tabacaria Sinica* **24**, 53–61.

*Wu, S., Zhang, Y., Tan, Q., Sun, X., Wei, W. & Hu, C. (2020*b*). Biochar is superior to lime in improving acidic soil properties and fruit quality of Satsuma mandarin. *Science of the Total Environment* **714**, 136722.

*Xu, Y., He, L., Liu, Y., LV, H., Wang, Y., Chen, J. & Yang, S. (2019). Effects of biochar addition on enzyme activity and fertility in paddy soil after six years. *Chinese Journal of Applied Ecology* **30**, 1110–1118.

*Yadav, V., Jain, S., Mishra, P., Khare, P., Shukla, A. K., Karak, T. & Singh, A. K. (2019). Amelioration in nutrient mineralization and microbial activities of sandy loam soil by short term field aged biochar. *Applied Soil Ecology* **138**, 144–155.

*Yang, L., Bian, X., Yang, R., Zhou, C. & Tang, B. (2018). Assessment of organic amendments for improving coastal saline soil. *Land Degradation & Development* **29**, 3204–3211.

Yang, Q., Ravnskov, S., Pullens, J. W. M. & Andersen, M. N. (2022*a*). Interactions between biochar, arbuscular mycorrhizal fungi and photosynthetic processes in potato (*Solanum tuberosum* L.). *Science of the Total Environment* **816**, 151649.

Yang, Q., Zhou, H., Bartocci, P., Fantozzi, F., Masek, O., Agblevor, F. A., Wei, Z., Yang, H., Chen, H., Lu, X., Chen, G., Zheng, C., Nielsen, C. P. & McElroy, M. B. (2021). Prospective contributions of biomass pyrolysis to China's 2050 carbon reduction and renewable energy goals. *Nature Communications* **12**, 1698.

*Yang, S., Chen, X., Jiang, Z., Ding, J., Sun, X. & Xu, J. (2020*a*). Effects of biochar application on soil organic carbon composition and enzyme activity in paddy soil under water-saving irrigation. *International Journal of Environmental Research and Public Health* **17**, 333.

*Yang, S., Sun, X., Ding, J., Jiang, Z., Liu, X. & Xu, J. (2020*b*). Effect of biochar addition on CO_2 exchange in paddy fields under water-saving irrigation in Southeast China. *Journal of Environmental Management* **271**, 111029.

Yang, Y., Moorhead, D. L., Craig, H., Luo, M., Chen, X., Huang, J., Olesen, J. E. & Chen, J. (2022*b*). Differential responses of soil extracellular enzyme activities to salinization: implications for soil carbon cycling in tidal wetlands. *Global Biogeochemical Cycles* **36**, e2021GB007285.

*Yi, Q., Fan, X., Tang, S., Huang, Q., Moustafa-Farag, M., Zhang, M. & Pang, Y. (2019). Short-term changes in chemical and microbial characteristics of paddy soil in response to consecutive addition of organic ameliorants in a rice–rice–vegetable rotation system. *Soil Science and Plant Nutrition* **65**, 393–400.

Yi, Q., Liang, B., Nan, Q., Wang, H., Zhang, W. & Wu, W. (2020). Temporal physicochemical changes and transformation of biochar in a rice paddy: insights from a 9-year field experiment. *Science of the Total Environment* **721**, 137670.

*Yoo, G. & Kang, H. (2012). Effects of biochar addition on greenhouse gas emissions and microbial responses in a short-term laboratory experiment. *Journal of Environmental Quality* **41**, 1193–1202.

*Yoo, G., Kim, Y. J., Lee, Y. O. & Ding, W. (2016). Investigation of greenhouse gas emissions from the soil amended with rice straw biochar. *KSCE Journal of Civil Engineering* **20**, 2197–2207.

*Zhai, L., CaiJi, Z., Liu, J., Wang, H., Ren, T., Gai, X., Xi, B. & Liu, H. (2015). Short-term effects of maize residue biochar on phosphorus availability in two soils with different phosphorus sorption capacities. *Biology and Fertility of Soils* **51**, 113–122.

Zhang, H., Voroney, R. P. & Price, G. W. (2015*a*). Effects of temperature and processing conditions on biochar chemical properties and their influence on soil C and N transformations. *Soil Biology and Biochemistry* **83**, 19–28.

*Zhang, Q. F. (2013). *The Properties of Biochar Derived from Crop Residues and its Using Effects in Albic and Black Soil*. Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun.

*Zhang, R., Cheng, H., Wu, M., Tian, Y. & Dong, Q. (2017). Effects of different mushroom residue on growth of rape and soil physicochemical properties *experimental. Science* **4**, 76–79.

*Zhang, S., Fang, Y., Luo, Y., Li, Y., Ge, T., Wang, Y., Wang, H., Yu, B., Song, X., Chen, J., Zhou, J., Li, Y. & Chang, S. X. (2021). Linking soil carbon availability, microbial community composition and enzyme activities to organic carbon mineralization of a bamboo forest soil amended with pyrogenic and fresh organic matter. *Science of the Total Environment* **801**, 149717.

*Zhang, Y., Tan, Q., Hu, C., Zheng, C., Gui, H., Zeng, W., Sun, X. & Zhao, X. (2015*b*). Differences in responses of soil microbial properties and trifoliate orange seedling to biochar derived from three feedstocks. *Journal of Soils and Sediments* **15**, 541–551.

Zhang, Y., Xie, H., Wang, F., Sun, C. & Zhang, X. (2022). Effects of biochar incorporation on soil viable and necromass carbon in the luvisol soil. *Soil Use and Management* **38**, 318–330.

*Zhao, J. (2016). *Effects of Biochar and Biochar-Based Slow-Released Nitrogenous Fertilizer on Soil Microbial Biomass and Soil Enzymes and Crop Yield*. Northwest Agriculture & Forestry University, Yangling.

*Zhao, J., Geng, Z., Shang, J., Geng, R., Wang, Y., Wang, S. & Zhao, H. (2016). Effects of biochar and biochar-based ammonium nitrate fertilizers on soil microbial biomass carbon and nitrogen and enzyme activities. *Acta Ecologica Sinica* **36**, 2355–2362.

*Zhao, X., Li, B., Kang, H. & Zhang, N. (2015). Straw biochar influence on soil properties quality for subtropical vineyards. *Chinese Agricultural Science Bulletin* **31**, 104–108.

*Zhao, Y. (2018). *Effect of Different Rice Straw Addition Methods on Nitrogen Supplying Capacity and Activity of Enzyme in Coastal Saline Paddy Soil*. Shenyang Agricultural University, Shenyang.

*Zheng, H., Xu, H., Wang, X. & Deng, W. (2018). Effect of sugarcane bagasse biochars on enzyme activities of latosol. *Chinese Journal of Soil Science* **49**, 1109–1114.

*Zheng, J., Chen, J., Pan, G., Liu, X., Zhang, X., Li, L., Bian, R., Cheng, K. & Jinwei, Z. (2016). Biochar decreased microbial metabolic quotient and shifted community composition four years after a single incorporation in a slightly acid rice paddy from Southwest China. *Science of the Total Environment* **571**, 206–217.

*Zheng, Y., Han, X., Li, Y., Yang, J., Li, N. & An, N. (2019). Effects of biochar and straw application on the physicochemical and biological properties of paddy soils in Northeast China. *Scientific Reports* **9**, 16531.

*Zhou, Z., Zhang, H., Yuan, Z. & Gong, R. (2020). The nutrient release rate accounts for the effect of organic matter type on soil microbial carbon use efficiency of a *Pinus tabulaeformis* forest in northern China. *Journal of Soils and Sediments* **20**, 352–364.

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by University Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. PRISMA flowchart illustrating the processes for the selection of articles included in the meta-analysis.
Fig. S2. Global distribution of the biochar addition experiments selected for this meta-analysis.
Fig. S3. Funnel plots for soil enzyme activities, ligninase:cellulase ratio and soil organic carbon in this meta-analysis.
Fig. S4. Effects of biochar addition on soil enzyme activities, ligninase:cellulase ratio and soil organic carbon sequestration as categorised by feedstock type, pyrolysis temperature of biochar and soil type.
Fig. S5. Effects of biochar addition on plant biomass and relationship between the responses of soil organic carbon and plant biomass to biochar addition.
Fig. S6. Effects of biochar addition on soil carbon:nitrogen ratio and NH_4^+ availability, and relationship between biochar-induced changes in carbon:nitrogen ratio and the application rate of biochar addition.
Fig. S7. Relationships between the responses of cellulase, ligninase and ligninase:cellulase ratio with various microbial attributes after biochar addition.
Fig. S8. Effects of biochar addition on fungal abundance, and relationship between the log response ratio of fungal abundance and biochar carbon:nitrogen ratio after biochar addition.
Table S1. Overview of studies included in our meta-analysis.
Table S2. Overview of cellulases and ligninases included in this meta-analysis.
Table S3. Results of sensitivity analysis for soil enzyme activities and soil organic carbon with biochar addition.

(*Received 18 August 2022; revised 27 February 2023; accepted 1 March 2023; published online 13 March 2023*)

1469185x, 2023, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12949 by Universiy Of Aberdeen, Wiley Online Library on [04/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License