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RESEARCH ARTICLE

Direct and indirect interactions between biochar properties, plant belowground traits, and plant performance

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Abstract

Biochar is more and more widely recognized as a promising agricultural amendment improving yield and ecosystem services in a range of different contexts. However, underlying mechanisms contributing to biochar's benefits, notably biochar–root interactions, and their mediation by biochar's diverse properties remain unclear and poorly quantified. This study aimed to examine and quantify the interactions between biochar properties and plant traits and their effect on plant performance. To gain a better understanding of biochar–plant interactions and their role in biochar overall effects, biochars with contrasted physical and chemical properties were applied to soils during a 3-month greenhouse experiment with barley (*Hordeum vulgare* L.). Barley biomass as well as several belowground morphological and physiological traits and aboveground traits related to nutrient acquisition were measured. A multivariate structural modeling approach was employed to quantify interactions between biochar properties and plant traits, and their feedback effect on plant biomass. Interactions between biochar chemical and physical properties and barley carboxylate release rate and their contribution to biochar effects were underlined. Among the plant traits examined the release of carboxylate appears as the best proxy to plant biomass following biochar addition, highlighting sparsely reported interactions between total carboxylate release rates and biochar ash content. Multivariate structural modeling offered elements of understanding for the complex interconnected mechanisms involved in biochar influence and their relative contribution. Adopting this approach across a wide range of species and contexts could contribute to ensure more reliable biochar benefits.

KEYWORDS

belowground traits, biochar, biochar properties, biochar–root interaction, root exudation

1 | INTRODUCTION

Biochar, a carbon-rich material issued from biomass pyrolysis, offers many potential benefits for climate change mitigation and agriculture such as improving plant growth and yield (Dai et al., 2020; Jiang et al., 2020), improving plant nutrient use efficiency (Glaser et al., 2015; Prapagdee & Tawinteung, 2017; Yu et al., 2017), increasing plant resistance to drought (Ali, Rizwan, et al., 2017; Kammann et al., 2011; Mulcahy et al., 2013), sequestering carbon in soils (Aubertin et al., 2021; Jien et al., 2015; Qi et al., 2020) or contributing to soil remediation (Houben et al., 2013a, 2013b; Yuan et al., 2019). Biochar application however tends to have inconsistent effects. Indeed, a recent review by Dai et al. (2020) reports large variations between studies with effects on plant productivity ranging from −32% to +974% due to the multiplicity of biochars and heterogeneity of their properties (Dai et al., 2020; Wang & Wang, 2019; Xiang et al., 2017). Biochar can be produced from a wide range of feedstocks, including straw, woody materials or organic wastes (Zhao et al., 2013), under varied pyrolysis conditions (Sun et al., 2014; Zhao et al., 2013), and can be altered to achieve specific environmental services (Wang & Wang, 2019), thus resulting in vastly different properties and potential benefits. A vast array of underlying mechanisms, mediated by biochar properties, have been proposed to be responsible for biochar effects. The role of biochar properties in these multiple interconnected mechanisms however remains unclear and rarely quantified, prompting further investigation (Dai et al., 2020; Liu, Wang, et al., 2021; Prendergast-Miller et al., 2014; Xiang et al., 2017). Gaining a deeper understanding of the role of biochar properties in achieving specific functions could in turn offer to optimize biochar application, ensuring efficient use and reliable results (Dai et al., 2020; Liu, Wang, et al., 2021).

Biochar characteristics such as its high surface area (SA), cation exchange capacity (CEC), organic carbon, ash and total carbon content, pH, density and porosity are responsible for its influence on ecosystem functioning and plant performance via multiple direct and indirect interconnected processes (Sun et al., 2014). Biochar can improve several soil chemical properties (pH, carbon content, nitrogen, phosphorus and micronutrient availability, cation exchange capacity, ...) (Aegnehu et al., 2017) improving soil fertility and thus directly contributing to plant nutrition (Ding et al., 2016; Gascó et al., 2016). Biochar impacts on soil chemical properties but also on soil physical properties (density, porosity, water-holding capacity, soil aggregation, ...) (Yu et al., 2019) and biological properties (microbial community composition, diversity and activity, ...) (Yu et al., 2019) in turn can significantly affect root morphology and functioning (Liu, Li, et al., 2021;

Prendergast-Miller et al., 2014; Xiang et al., 2017). A 39% increase in root surface area and a 52% increase in root length on average was for instance reported in a recent meta-analysis as a result of biochar application (Xiang et al., 2017). A vast array of biochar–root interactions, ranging from direct influence of biochars on roots via the release of hormone-like substances (Lou et al., 2015) to indirect influence via altered soil biogeochemistry and structure (Olmo et al., 2014; Xiang et al., 2017) are responsible for biochar influence on root system development. These biochar–root interactions are mediated by multiple biochar properties such as biochar labile carbon and nutrient content (Olmo et al., 2014; Sandhu et al., 2019), density, SA and porosity (Aslam et al., 2014) as well as pH (Chen et al., 2021) among others but are poorly predictable and have scarcely been explored (Olmo & Villar, 2019). The influence of biochar properties on root morphology and physiology indeed remains unclear and highly variable (Jabborova, Annapurna, et al., 2021; Jabborova, Ma, et al., 2021; Prendergast-Miller et al., 2014; Xiang et al., 2017). Biochar–root interactions in turn influence plant nutrient and water acquisition strategies, for instance increases in plant specific root length (SRL) result in more efficient increases in root absorptive area per root weight (Ryser, 2006) leading to increased nutrient use efficiency (Backer et al., 2017). Biochar–root interactions may also impact plant nutrient acquisition efficiency via altered root physiology and exudation, for instance increased carboxylate release (Oladele, 2019) or increased enzyme release and activity (Jabborova, Annapurna, et al., 2021; Jabborova, Ma, et al., 2021). Altered root traits due to biochar application may thus importantly influence plant performance (Abiven et al., 2015; Bruun et al., 2014), but little is known about the influence and contribution of biochar–root trait interactions on plant performance (Olmo & Villar, 2019). As key factors in biochar–root interaction, biochar properties likely impact the influence of biochar–root trait interactions on plant performance. However while sources of uncertainty pertaining to the combined effects of biochar properties and soil conditions are increasingly being understood (Al-Wabel et al., 2018; Dai et al., 2020), the influence of biochar on root traits remains highly variable and its contribution to the overall services ensured by biochar, as conditioned by biochar properties, remains largely unquantified (Liu, Wang, et al., 2021; Xiang et al., 2017). Understanding and managing biochar application, notably for increased productivity, thus requires approaches able to decipher and quantify the role and contribution of biochar properties interaction with plant traits and especially traits involved in nutrient acquisition and its effects on plant performance.

To examine covariations between biochar properties and plant traits involved in or indicator of nutrient

acquisition and their relationship with plant performance, we performed a 3-month greenhouse experiment with barley and biochars with contrasted physical and chemical properties and employed a partial least square path modeling approach (PLS-PM). The PLS-PM approach is a promising method for deciphering relations between multiple interconnected factors interacting directly and indirectly in the plant soil system (Ali, Reineking, & Münkemüller, 2017; Kim et al., 2021). Its structural approach allowed us to separate and examine the effects of biochar properties in direct effects on plant biomass and nutrient acquisition and indirect effects via their influence on plant traits involved in or indicator of nutrient acquisition and their feedback effects on plant biomass and examine their relative contribution to the overall effects of biochar. Common traits involved in nutrient foraging (SRL) and mobilization (carboxylate exudation rate, change in rhizosphere pH) and indicators of plant nutrition (SLA, leaf nutrient concentration) were selected to reflect biochar effects on plant nutrient acquisition strategy. Mechanistic understanding of the effects of biochars as influenced by their properties is needed to ensure reliable biochar benefits and could offer to further optimize biochar use for specific functions and systems (Gezahegn et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Organic amendments

Six commercial grade biochars (VTGreen, Allier, France) produced from different feedstocks available in large quantities in France were used: coffee residues (hereafter referred as coffee biochar) resulting from coffee liqueur extraction and provided by Compomar (Essone, France); wood granules (<8 mm) (hereafter referred as wood biochar) from resinous trees provided by a wood storage center (LCE, Maine-et-Loire, France); maize cobs (hereafter referred as maize biochar) cultivated, dried and crushed by Agrivalor (Alsace, France); miscanthus and rapeseed straws (hereafter referred as miscanthus biochar and rapeseed biochar, respectively) cultivated, dried, and crushed by Agriopale (Pas-de-Calais, France); and green wastes compost rejects (hereafter referred as compost biochar) composed of poplar and conifers branches and provided by FertiVert (Seine-Maritime, France). Biochars were produced using an industrial pyrolysis reactor (Biogreen® Technology, ETIA, Oise, France) and employing continuous thermal treatment without oxygen with a set residence time of 10 min. Different pyrolysis temperatures were selected to obtain biochars with contrasting chemical and physical properties: 550°C for wood biochar

and miscanthus biochar, 450°C for maize biochar and compost biochar, and 650°C for rapeseed biochar and coffee biochar.

Biochars were analyzed for conductivity (AFNOR, 2012a), CEC (AFNOR, 1999), density, porosity (AFNOR, 2012b), air-holding capacity (AHC), pH (AFNOR, 2012c), C content (AFNOR, 2011), total nitrogen (N) content (AFNOR, 2002a), C:N ratio, ash content at 550°C (ISO, 2016), total phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) contents (AFNOR, 2002b) (Table 1).

2.2 | Greenhouse pot experiment

The soil used for the experiment was a Luvisol (IUSS Working Group WRB, 2015) sampled from the topsoil of a cultivated field in Beauvais, North of France (49°28'N; 2°4' W). The soil texture was a silt loam with 18% clay, 67% silt and 15% sand. The soil pH_{H2O} was 7.8 (1:5 ratio NF ISO 10390), the cation exchange capacity was 12.5 cmolc kg⁻¹ (CEC Metson NFX 31-130), and the organic carbon content was 15.4 g kg⁻¹ (dry combustion on decarbonated soil NF ISO 14235). Available P was 71 mg kg⁻¹ (Joret Hebert NFX 31-161), exchangeable K and Mg were 292 and 101 mg kg⁻¹ (Exchangeable cations, NFX 31-108), respectively, and total N 1.8 g kg⁻¹ (Dumas method). The soil was used as a model soil and mixed with sand at a dry weight (DW) ratio of 1:5 (w:w -sand: soil) to facilitate root trait measurements.

The six biochars were applied separately on 3 kg DW equivalent of soil, homogenized, and transferred into plastic pots. The dose of biochar applied was 1.6 g DM kg soil⁻¹ (equivalent to 4 t ha⁻¹, a low but realistic and more economically viable application rate). A control without biochar addition was also included. The experiment was carried out in four replicates. Distilled water was applied to reach 80% of water-holding capacity of the soil, as determined following the procedure by Yu et al. (2013).

Barley (*Hordeum vulgare* L.) (Barley "Pewter" provided by Semences de France, La Chapelle d'Armentières, France) was sown and grown for 3 months in a greenhouse with the following climatic conditions: 16 h of light day⁻¹, 24/16°C (day/night). Eight seeds per pot were sown, and after 1 week, the plants were thinned to two plants per pot. Distilled water was applied every 2 days during the growth period. After 3 months, aboveground parts and roots of plants were harvested separately after carboxylate emission rate measurements. Aboveground parts were mostly past flowering, with multiple tillers per individual. Aerial part of one plant was dried at 60°C for 48 h and weighed.

Rhizosphere, that is, the soil adhering to the root surface within 2 mm after shaking (Pang et al., 2017),

TABLE 1 Chemical and physical properties of the six biochars used

	Unit (dry mass)	Coffee BC	Wood BC	Maize BC	Miscanthus BC	Rapeseed BC	Compost BC
Porosity ^a	%	92.6	87.3	88.5	92.5	95.9	86.3
Density ^a	g/L	108	280	171	112	78	291
Conductivity ^b	dS/m	0.56	2.40	1.14	1.30	1.22	3.54
AHC ^a	% v/v	50.6	15.06	19.5	30.0	34.9	38.3
CEC ^c	cmol _c /kg	32.4	12.3	27.3	31.0	2.9	8.5
pH ^d		10.5	7.9	9.6	10.4	11.2	11.4
Ash 550°C ^e	%	10.1	1.4	5.4	18.6	26.4	33.7
C ^f	%	74.1	77.2	63.9	74.0	62.3	55.5
Total N ^g	%	3.60	0.41	1.06	0.53	0.81	0.88
C/N		21	191	61	141	77	63
P ^h	g/kg	0.24	0.06	0.14	0.31	0.38	0.37
K ^h	g/kg	1.89	0.27	1.65	2.52	1.82	1.78
Ca ^h	g/kg	0.11	0.18	0.23	0.21	6.57	3.38
Mg ^h	g/kg	0.13	0.05	0.10	0.06	0.41	0.50

^aAFNOR (2012b).^bAFNOR (2012a).^cAFNOR (1999).^dAFNOR (2012c).^eISO (2016).^fAFNOR (2011).^gAFNOR (2002a).^hTotal extracted with aqua regia (AFNOR 2002b).

was separated from bulk soil and any remaining root fragments. Rhizosheath and bulk soils were air dried and analyzed for pH_{H2O} (AFNOR, 2012c). Difference of pH between rhizosheath soil and bulk soil (Δ pH) was calculated.

2.3 | Specific leaf area and leaves nutrients concentrations

At harvest three mature leaves per plant were collected, dried at 60°C for 48 h, separately weighed and area of each leaf was determined using a scanner (Calibrated Color Optical scanner STD4800 with special lighting system. S/N URUW009925-6714112, Optical Resolution 4800 dpi, max scan area: 22 × 30 cm) and ImageJ software (Schneider et al., 2012). The specific leaf area (SLA) was calculated as the ratio between leaf area and leaf dry biomass.

The three leaves were then ground together. A subsample was analyzed for N by elemental analysis by combustion (LECO FP628 Series, LECO Corporation), while another subsample was digested in 8 ml 65% nitric acid and 2 ml 37% hydrochloric acid in a microwave system (Mars 5, CEM Corporation). Leaves P and K

concentrations were determined by Inductively Coupled Plasma Mass Spectrometry (ICP-MS, Thermo Scientific XSERIES 2).

2.4 | Roots carboxylate exudation

The day of harvest, after intact plants were removed from the soil and roots were cleaned with distilled water, the whole root system was dunked in 50 ml of 0.2 mM CaCl₂ solution for 30 min. The solution was centrifuged (2 min, 10,000 g) and supernatant solution was filtered through a sterile 0.22 µm millipore filter. Fifty microliters of filtrate were injected into the HPLC system (Thermo Fisher) equipped with an auto-injector, a degasser, and a diode array detector. Malate, malonate, maleate, citrate, and fumarate were separated according the method of Cawthray (Cawthray, 2003; Yacoumas et al., 2020) on a reverse phase Luna 5 µm C18 column (250 mm 4 mm [phenomenex]) at 25°C by using an isocratic mobile phase: 25 mM KH₂PO₄: methanol (99:1; v-v) buffered at pH 2.40. The sum of the exudation rates of these carboxylates was calculated to obtain the total carboxylate exudation rate (TCR). The flow rate was set at 1 ml min⁻¹. The UV signal was recorded at 210 nm.

2.5 | Specific root length

After collecting carboxylate exudates, roots were separated from the aboveground part and total root length was determined using a scanner (Calibrated Color Optical scanner STD4800 with special lighting system. S/N URUW009925-6714112, Optical Resolution 4800 dpi, max scan area: 22×30cm) and WinRHIZO (Regent Instruments Inc.) software. The entire root was then dried at 60°C for 48 h and weighed. The SRL was calculated as the ratio between total root length and root dry biomass.

2.6 | Data processing and analysis

Differences among plant functional traits and biomass among treatments were first examined with ANOVA followed by Tukey post hoc tests. Because the aim of this study was not to describe the effect of each biochar but rather to decipher how biochar properties drive the plant response, the relationships between key biochar physical and chemical properties selected during model building (see below) and plant traits and biomass were tested via either Pearson or Spearman correlation test according to data distribution.

A Partial Least Square Path Modeling (PLS-PM) approach was then employed to understand the direct and indirect effects of biochar properties on plant traits and plant biomass. Briefly, all biochars properties measured were grouped in two clusters of variables or “latent variables”: porosity, density, WHC, and AHC were grouped in “Biochar physical properties”, while pH, ash content, conductivity, C content, total N content, C:N, and total P, K, Ca, and Mg contents were grouped in “Biochar chemical properties”. Leaf N, P and K concentrations were grouped in a third latent variable, called “Leaf [NPK]”. The most relevant properties and variables for each latent variable were selected based on their individual loading (superior to 0.7) and their crossloading scores as in Sanchez (2013). Only biochar AHC was retained in the “Biochar physical properties” as well as leaf N, P and K concentrations in

the “Leaf [NPK]” latent variable. In the “biochar chemical properties” latent variable only biochar pH, ash content, P, Mg and carbon content were retained. To ensure positive correlations within a latent variable as required for model building in Sanchez (2013), the sign of some variables was modified. Unidimensionality of latent variables was evaluated based on their Dillon-Golstein coefficients. The latent variables “Biochar physical properties”, “Biochar chemical properties” and “Leaf [NPK]” were then used alongside individual traits, namely SLA, SRL, delta pH, and TCR to predict plant biomass. To account for the influence of biochar properties on plant traits interactions between “Biochar physical properties” as well as “Biochar chemical properties” and plant traits were specified in the model structure. Interactions between plant traits and “NPK leaves concentrations” were also specified in the model structure to investigate the influence of changes in plant traits on plant nutrition via leaf nutrient concentrations. The model structure allowed us to gain a better understanding of the underlying mechanisms contributing to biochar effects via specifying and quantifying direct relationships between biochar properties and plant biomass but also indirect relationships, defined here as relationships between biochar properties and plant trait and their feedback effect on plant biomass. Models were evaluated based on their goodness of fit (GOF). All tests were performed with R v 3.6.0 and the packages Rcmdr 2.5–3 and plsmpm 0.4.9 with a significance level of 0.05.

3 | RESULTS

3.1 | Correlations between biochar properties

Correlations were observed between biochar chemical properties, with biochar P content and pH being positively correlated with biochar ash content, and biochar pH being positively correlated with biochar P and Mg contents (Table 2). Biochar carbon content was not correlated with the other chemical properties, while negative tendencies

TABLE 2 Correlation coefficient between biochar properties

	AHC	Ash	C	P	Mg	pH
AHC	1	—	—	—	—	—
Ash	0.66	1	—	—	—	—
C	−0.37	−0.83	1	—	—	—
P	0.60	0.94*	−0.77	1	—	—
Mg	0.77	0.83	−0.83	0.77	1	—
pH	0.83	0.94*	−0.77	0.89*	0.94*	1

Note: Significant correlations presented in bold.

* $p < 0.05$.

($p = 0.058$) were observed between biochar carbon content and biochar ash and Mg contents. Biochar AHC was not correlated with any biochar chemical property.

3.2 | Plant traits and biomass and relationships with biochar properties

The impact of biochar on plant traits and biomass was variable and significant differences between plant biomass and leaf P concentration, were observed between treatments while no significant differences were observed for leaf K and N concentration (Figure 1). Positive delta pH values as well as carboxylate exudation rates significantly differed between treatments whereas SRL and SLA did not (Figure 2).

Few significant correlations were observed between biochar properties and plant biomass. Two biochar chemical properties, biochar ash and K contents, were moderately correlated with plant biomass ($R_s = 0.48$ and 0.56 , $p = 0.02$ and $p = 0.01$, respectively), while no significant correlations were observed between plant biomass and biochar AHC.

Barley leaf N, P, and K concentrations, as well as SLA and SRL were not correlated with any biochar property (Table 3). The Δ pH between rhizosheath and bulk soil was positively correlated with several biochar chemical properties, namely biochar ash, P and Mg content and biochar

pH. TCR was positively correlated with the same biochar chemical properties and negatively with biochar carbon content. Both Δ pH and TCR were also correlated with biochar AHC. TCR was moderately positively correlated with plant biomass ($R_s = 0.46$, $p = 0.03$), while Δ pH was not correlated with plant biomass.

3.3 | PLS-path model

The PLS-path model explained 28% of the variance in plant biomass and 70% of the variance in leaf N, P, K concentrations ($R^2 = 0.28$ and 0.70) with an overall GOF of 0.52 . Figure 3 shows correlation among latent variables (ovals) and variables (rectangles). Values on dotted arrows between latent variables and variables represent the effect of the variables.

Biochar AHC alone was selected to represent the variability in biochar physical properties (loading = 1). Biochar ash and P content strongly contributed to the chemical properties latent variable (loadings of 0.98 , 0.95). Finally, leaf K concentration contributed the most to the latent variable "leaf NPK" followed by leaf N concentration (loadings of 0.95 and 0.92).

TCR presented the highest correlation with plant biomass (corr = 0.40), followed by the biochar physical properties latent variable (corr = 0.23). TCR and the biochar physical properties latent variable had positive effects on

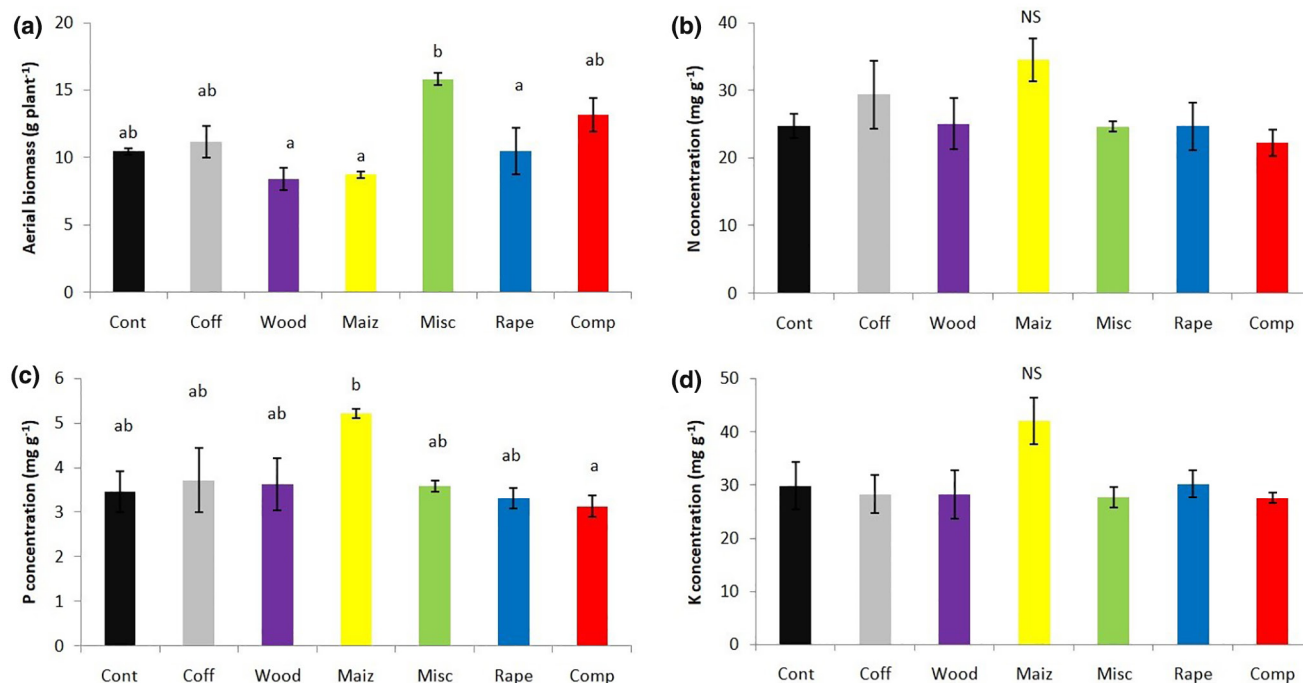


FIGURE 1 Mean barley biomass and nutrient concentration per treatment. Aerial biomass (a) and leaves concentrations in N (b), P (c), and K (d) of barley grown in soil without biochar addition (Cont), or amended with six biochar: Coff: Coffee biochar; Wood: Wood biochar; Maiz: Maize biochar; Misc: Miscanthus biochar; Rape: Rapeseed biochar; Comp: Compost refusal biochar ($n = 4$)

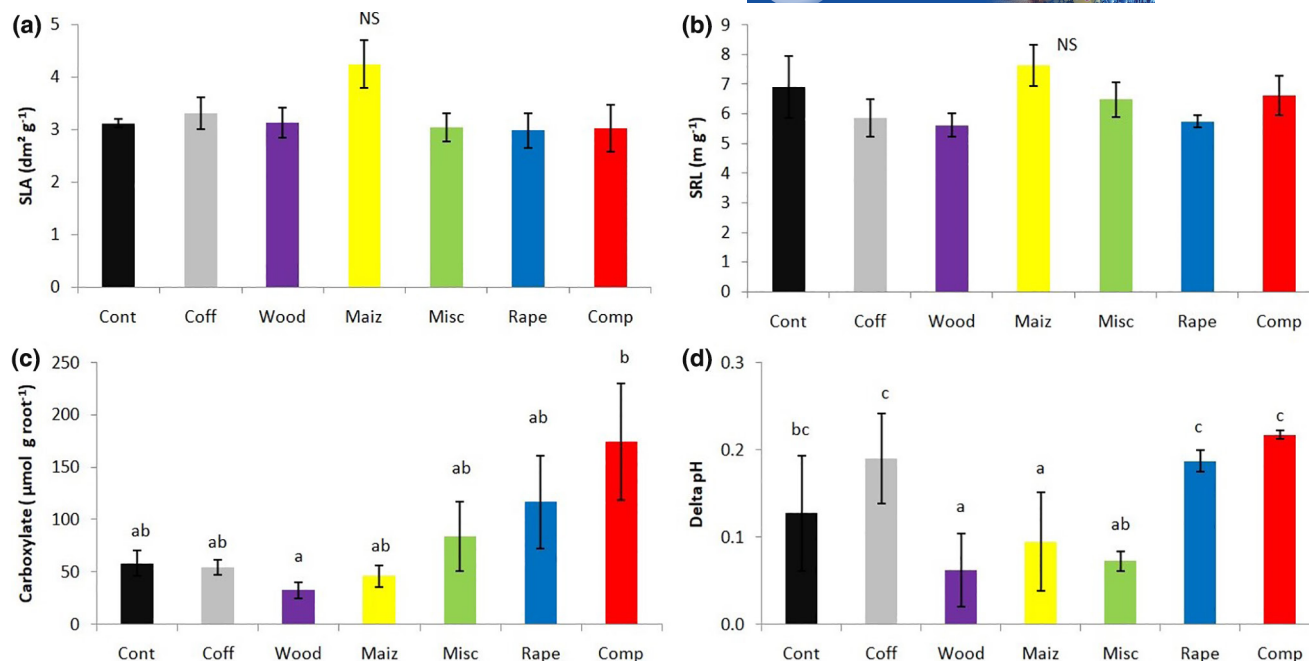


FIGURE 2 Mean traits per treatment. Traits in soil without biochar addition (Cont), or amended with six biochar: Coff: Coffee biochar; Wood: Wood biochar; Maiz: Maize biochar; Misc: Miscanthus biochar; Rape: Rapeseed biochar; Comp: Compost refusal biochar ($n = 4$). SLA: specific leaf area; SRL: specific root length, Carboxylate: total amount of roots carboxylate exudates; Delta pH: difference of pH between rhizosphere soil and bulk soil.

TABLE 3 Correlation coefficient between plant traits and biochar properties

Biochar properties		Plant traits						
		Δ pH	SLA	SRL	TCR	Leaf N	Leaf P	Leaf K
Chemical	Ash	0.58**	-0.29	-0.02	0.55**	-0.36	-0.36	-0.30
	C	-0.38	0.05	-0.23	-0.47*	0.14	0.11	-0.05
	P	0.52*	-0.30	-0.09	0.50*	-0.32	-0.33	-0.26
	Mg	0.71***	-0.10	0.02	0.51*	-0.16	-0.26	-0.10
	pH	0.75***	-0.24	-0.08	0.55*	-0.30	-0.38	-0.29
Physical	AHC	0.81***	-0.14	-0.14	0.43*	-0.17	-0.29	-0.30

Notes: Significant correlation presented in bold.

Δ pH, pH difference between rhizosphere soil and bulk soil; SLA, specific leaf area (dm²/g); SRL, specific root length (m/g); TCR, total carboxylate emission rate (μmol g⁻¹ root h⁻¹); Leaf N: leaf nitrogen concentration (mg g⁻¹); Leaf P: leaf phosphorus concentration (mg g⁻¹); Leaf K: leaf potassium concentration (mg g⁻¹). Ash: biochar ash content (%); C: biochar carbon content (%); P: biochar total phosphorus concentration (g kg⁻¹); Mg: biochar total magnesium concentration (g kg⁻¹); pH: biochar pH; AHC: biochar air-holding capacity (% v v⁻¹).

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

plant biomass. Biochar chemical properties also had a very low positive correlation with plant biomass. SRL had little effects on plant biomass (corr = -0.04). SLA had low negative effects on plant biomass (corr = -0.20).

The total effect of biochar chemical properties latent variable on plant biomass was moderate and positive (corr = 0.27) due to positive indirect effects (corr = 0.26) (Figure 4). Correlations between the biochar chemical properties latent variable and total root carboxylate exudation rate (corr = 0.69) contributed to this indirect positive

effect of the chemical properties latent variable on plant biomass. The total effect of the biochar physical properties latent variable (corr = 0.17) was lower than its direct effect due to indirect negative effects (corr = -0.05). Due to strong correlation between SLA and the leaf [NPK] latent variable (corr = 0.70), SLA had higher total effects (corr = -0.12) than its direct effect on biomass (corr = -0.20). The total effects of TCR and SRL were similar to their direct effects, while Δ pH had very low total effects.

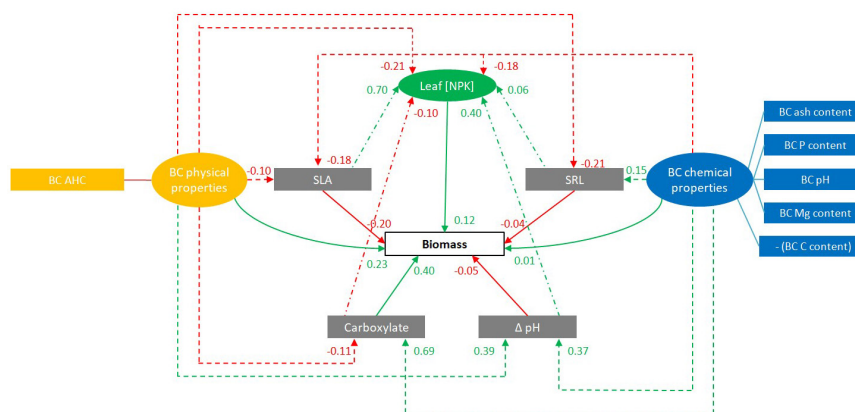


FIGURE 3 PLS-path model describing the relationships between biochar properties, plant traits and N, P, and K leaves concentrations and biomass. Based on latent variables: “BC physical properties” grouping biochar AHC; “BC chemical properties” grouping biochar pH, ash, C, P and Mg content; “Leaf NPK” grouping Leaf N, P and K concentrations. Variables negatively transformed indicated by -(variable). Δ pH: Difference between rhizosphere pH and bulk soil pH; SLA: Specific leaf area ($\text{dm}^2 \text{g}^{-1}$); SRL: Specific root length (m g^{-1}); TCR: Total carboxylate emission rate ($\mu \text{mol g}^{-1} \text{root h}^{-1}$); BC ash content: Biochar ash content (%); BC C content: Biochar carbon content (%); BC P content: Biochar phosphorus concentration (g kg^{-1}); BC Mg content: Biochar magnesium concentration (g kg^{-1}); BC pH: Biochar pH; Conductivity: Biochar conductivity (dS m^{-1}); BC AHC: Biochar air-holding capacity ($\% \text{v v}^{-1}$).

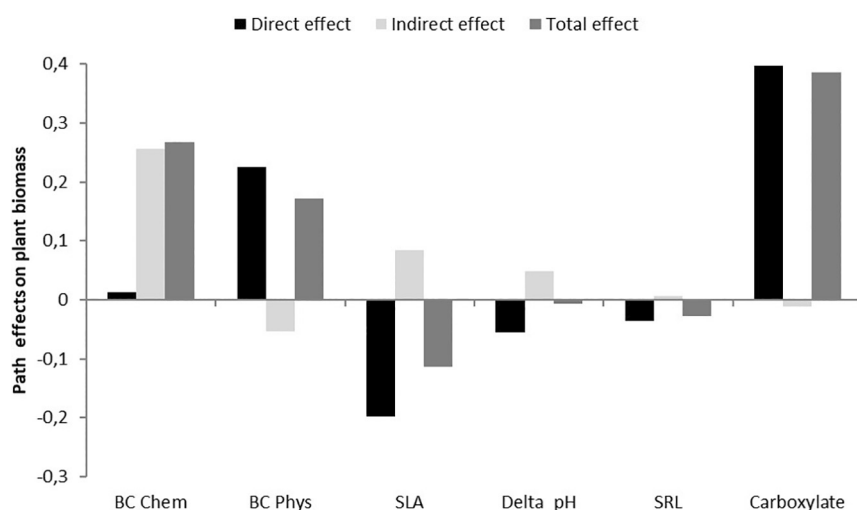


FIGURE 4 Direct and indirect path effects of the variables on plant biomass. BC Phys: latent variable grouping biochar AHC; BC Chem: latent variable grouping biochar pH, ash content, C, P and Mg content; Delta_pH: Δ pH, difference between rhizosphere soil and bulk soil pH; SLA: Specific leaf area ($\text{dm}^2 \text{g}^{-1}$); SRL: Specific root length (m g^{-1}); Carboxylate: Total carboxylate emission rate ($\mu \text{mol g}^{-1} \text{root h}^{-1}$).

4 | DISCUSSION

The variable effects of biochars on plant performance, as observed in our study, underline the need to further understand how biochar properties mediate its benefits via the multiple underlying mechanisms involved (Gezahegn et al., 2019; Jabbarova, Ma, et al., 2021). Biochar impacts on root morphology and physiology and their feedback effects on plant performance especially remain unclear and poorly quantified (Liu, Wang, et al., 2021; Prendergast-Miller et al., 2014; Xiang et al., 2017). Therefore, the purpose of this study was not to describe the effects of biochar on plant performance but rather to gain insight into how these effects are directly and indirectly driven by biochar properties. Our approach underlined relationships between biochar chemical properties and barley

belowground traits, namely carboxylate release rates, and their contribution to the overall effects of biochar on plant performance. Release rates of the sum of all carboxylates, and especially malonate and malate, increased with biochar ash content. Although relatively little is known on how biochar properties influence specific exudates such as carboxylates, higher exudation of citrate, malate, acetate, oxalate and malonate have been reported (Akhter et al., 2015; Cheng et al., 2018; Oladele, 2019) and was attributed to the stimulation of root functioning by labile carbon and ash added by biochar (Oladele, 2019). Our results confirm the role of biochar-derived ash on carboxylate release by plants. Indeed, they showed a positive correlation between carboxylate release and ash content in biochar. Since ash content was found to be tightly correlated to P and Mg contents in biochar, higher release of

carboxylate by plants in the presence of ash-rich biochars might be due to the beneficial effects of biochar-derived P and Mg on plant growth. Plant exudation patterns indeed tend to be very plastic and heavily influenced by several factors including plant growth itself in a complex three-way interaction between soil, plant and root architecture and exudations (Cheng et al., 2018; Zhu et al., 2016), prompting further investigations of this sparsely reported interaction. Unlike to biochar influence on carboxylate exudation, biochar influence on soil pH has received extensive attention (Dai et al., 2017; Gezahegn et al., 2019; Singh et al., 2017). Studies have shown that biochar liming effect may importantly contribute to its overall impact on plant productivity (Hale et al., 2020; Masud et al., 2020; Raboin et al., 2016). However, we observed no correlation between bulk soil pH and plant biomass in this study, suggesting that liming effect of biochar did not provide a good proxy for assessing biochar effect on plant biomass. By contrast, rhizosheath pH was correlated with plant biomass. Because it is known that rhizosheath pH value is driven by both the initial bulk soil pH value and by root activity (Hinsinger et al., 2003), the correlation between rhizosheath pH and plant biomass suggests that biomass was affected by the coupled effect of biochar on bulk soil pH and root activity. As reported by Houben and Sonnet (2015), root-induced changes on rhizosheath pH in the presence of biochar may be related to biochar impact on nutrient availability, which in turn leads rhizosheath alkalisation/acidification due to unbalanced cation/anion uptake by plant (Hinsinger et al., 2003). Root-induced pH changes had a moderate correlation factor with the leaf NPK latent variable, reinforcing that their relationship with plant biomass was probably related to plant nutrient acquisition strategy. Other changes in plant nutrient acquisition strategy such as the positive influence of the biochar chemical properties latent variable on plant SRL may also have contributed to improved plant nutrition (Olmo & Villar, 2019). Increased SRL following biochar application is indeed often reported (Liu, Li, et al., 2021; Xiang et al., 2017; Xiao et al., 2016) and was proposed to be due to alleviated nutrient limitation and contribute to improved plant nutrition (Olmo & Villar, 2019). However, the calcareous, nutrient-rich soil used likely largely attenuated this interaction in our study (Dai et al., 2020). The multivariate structural modelling approach we employed thus reinforced and further expanded our knowledge of biochar–root interactions as observed via root carboxylate exudation rate, change in rhizosheath pH (Houben & Sonnet, 2015; Oladele, 2019; Olmo & Villar, 2019). Interactions between biochar properties and root exudation pattern were especially underlined via estimating their contribution to biochar overall effects. Belowground traits were highlighted to offer a good proxy to predict

plant biomass following biochar addition. Biochar–root interactions contribution to biochar impacts were influenced by biochar chemical properties and especially ash content. Biochar chemical properties showed higher effects through these interactions than their direct effect in our model. The PLS-PM approach by simultaneously evaluating the multiple interactions between biochar, belowground trait, plant nutrition and biomass offered element of understanding for complex interacting systems, highlighting the sparsely quantified and still unclear effect of biochar on plant performance via its impact on root traits and its mediation by biochar properties. Employing a similar approach to a range of species with diverse nutrient acquisition strategies and root traits could help provide key elements towards gaining a more mechanistic understanding of biochar effects, which is needed to ensure reliable benefits and implement large-scale biochar use.

5 | CONCLUSION

Optimizing the use of biochar requires approaches able to decipher the multiple direct and indirect interactions between biochar properties and plants and their effect on plant performance. Our multivariate structural modelling approach allowed us to highlight direct interactions between biochar properties and plant performance as well as indirect interactions between biochar properties and plant traits and their feedback effects on plant performance as well as their contribution to the overall effects. Interactions between biochar chemical properties and belowground traits, that is, carboxylates release rate, and their contribution were underlined. Total carboxylate release rate was related to biochar ash content and offered a good proxy for plant performance whereas other belowground traits offered poor proxies. Highlighting direct and indirect interactions between biochar properties and plant performance via similar structural modelling approaches in a range of diverse species could improve our mechanistic understanding of biochar effects and contribute to optimize the use of biochar to improve plant performance.

AUTHOR CONTRIBUTIONS

Michel-Pierre Faucon (MPF), David Houben (DH) and Cécile Nobile (CN) helped define the experimental design. CN and Stéphane Firmin (SF) carried out the experiment. Nicolas Honvault (NH), MPF and DH helped process and interpret the data and write the manuscript. All authors contributed to the final version of the manuscript.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings are openly available on Dryad. The DOI of the dataset is <https://doi.org/10.5061/dryad.qfttdz0kz>.

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