The Use of Biochar for Plant Pathogen Control

Jorge Poveda,¹ Ángela Martínez-Gómez,² Carmen Fenoll,² and Carolina Escobar^{2,3,†}

¹ Biological Mission of Galicia (MBG-CSIC), Pontevedra, Spain

² Facultad de Ciencias Ambientales y Bioquímica, Área de Fisiología Vegetal, Universidad de Castilla-La Mancha, Avda. Carlos III, s/n, 45071 Toledo, Spain

³ International Research Organization for Advanced Science and Technology (IROAST), Kumamoto University, Kumamoto 860-8555, Japan
Accepted for publication 29 January 2021.

ABSTRACT

To support the search for alternative, nonchemical plant disease control strategies, we present a review of the pathogen-suppressive effects of biochar, a product derived from agricultural and other organic wastes, used as a soil amendment. A wide range of biochar effects contribute to the control of root or foliar fungal pathogens through modification of root exudates, soil properties, and nutrient availability, which influence the growth of antagonist microorganisms. The induction of systemic plant defenses by biochar in the roots to reduce foliar pathogenic fungi, the activation of stress-hormone responses, as well as changes in active oxygen species are indicative of a coordinated hormonal signaling within the plant. Although scarce data are available for oomycetes and bacterial pathogens, reports indicate that biochar promotes changes in the soil microbiota influencing pathogen motility and colonization, and the induction of plant systemic defenses, both contributing to disease suppression. Biochar also suppresses nematode and insect pests. For plant-parasitic nematodes, the primary modes of action are changes in soil microbial community diversity, the release of nematicidal compounds, and the induction of plant defenses. Use of biochar-based soil amendments is a promising strategy compatible with a circular economy, based on zero waste, as part of integrated pathogen and pest management. Since biochars exert complex and distinct modes of action for the control of plant pathogens, its nature and application regimes should be designed for particular pathogens and its effects studied locally.

Keywords: bacterial pathogens, biochar, disease control and pest management, disease resistance, fungal pathogens, induced resistance, microbial ecology, nematodes, oomycetes, soil amendment

The term biochar (Lehmann et al. 2006) refers to a biomass-derived carbon-rich material subjected to pyrolysis, which produces a thermal decomposition of organic material in an oxygen-deficient environment at high temperature (Lehmann and Joseph 2009). This process takes place in a reactor and transforms the organic material into different amounts of solid, liquid, and volatile products. The

solid fraction contains fixed carbon and other inorganic materials and is referred to as biochar (Gheorghe et al. 2009; Yaman 2004).

The positive effects of soil amendments with carbon-rich materials were first described in the 1870s in Brazilian soils (Brown 1876; Brown and Lidstone 1878; Hart 1872; Orton 1875; reviewed in Glaser 2014). In the Brazilian Amazon region, *Terra Preta* or *Terra Preta do Índio* refers to a soil with a thick black or dark gray top characterized by a high percentage of organic matter and enhanced fertility. Additionally, these soils contain higher concentrations of nutrients such as calcium (Ca), nitrogen (N), phosphorus (P), and potassium (K), when compared with the surrounding less fertile soils, and have a higher pH and water holding capacity (Glaser et al. 2001b; Zech et al. 1990). Incorporation of biochar as a soil amendment has several positive environmental effects, e.g., carbon sequestration (Glaser et al. 2001a; Kuzakov et al. 2009; Rogovska et al. 2011), reduction of greenhouse gas emissions (Case et al. 2015; Taghizadeh-Toosi et al. 2011; Zhang et al. 2012), energy production (Dong et al. 2018; Foong et al. 2020), soil improvement (Alling et al. 2014; Basso et al. 2013; Nigussie et al. 2012), immobilization of organic and inorganic pollutants (Li et al.

[†]Corresponding author: C. Escobar; carolina.escobar@uclm.es

First and second authors contributed equally to this work.

Funding: This work was supported by the Spanish Government (AGL2016-75287-R, PID2019-105924RB-I00, and RED2018-102407-T) and by the Junta de Castilla La Mancha (SBPLY/17/180501/000287), to C. Escobar. The laboratory received support from UCLM intramural funds, and A. Martínez-Gómez was recipient of a Ph.D. grant from Fundación Tatiana Pérez de Guzmán el Bueno. EU FEDER funds complemented all the grants.

The author(s) declare no conflict of interest.

2018; Shu et al. 2016; Yang et al. 2017), and contribution to waste management (Harel et al. 2012; Jaiswal et al. 2014; Rahman et al. 2014; reviewed in Kavitha et al. 2018; Lehmann and Joseph 2009).

Some of the most common sources of biomass for biochar production are agricultural and forestry residues, algae, sewage sludge, and livestock and poultry wastes (Duku et al. 2011). The nature of the feedstock and the pyrolysis conditions have a significant impact on the physical and chemical properties of biochar that in turn may influence soil fertility. Among these biochar properties are pH, particle surface area, pore size, density, electrical conductivity, cation exchange capacity, hydrophobicity, aromaticity, recalcitrance, ash content, volatile matter content, carbon (C), hydrogen (H), N, and oxygen (O) content, and availability of K, sodium (Na), and P (Angin 2013; Chandra and Bhattacharya 2019; Cheng et al. 2017; Enders et al. 2012; Gai et al. 2014; Gheorghe et al. 2009; Jassal et al. 2015; Jindo et al. 2014; Kameyama et al. 2016; Kloss et al. 2012; McBeath et al. 2014; Rajapaksha et al. 2014; Ronsse et al. 2013; Wang et al. 2015; Yakout 2017). Carbon content ranges from 172 to 905 g kg⁻¹, total P from 3 to 480 g kg⁻¹, total N from 2 to 56 g kg⁻¹, and total K from 1 to 58 g kg⁻¹ (Chan and Xu 2009). The range of bulk density for biochars made from different types of woods is 0.25 to 0.75 g cm⁻³ (Downie et al. 2009). This variability can be attributed to the use of different feedstocks and pyrolysis conditions.

Depending on the intrinsic characteristics of each biochar type, its application has the potential to change a wide variety of soil properties, such as soil pH, water holding capacity, nutrient availability, bulk density, and soil aggregation (Lehmann et al. 2015). The optimal application rate of biochar is not yet established, as it will vary between biochar types, soil types, and target species. However, application rates between 0.5 to 135 t ha⁻¹ have produced positive plant growth responses (Glaser et al. 2002). Biochar generally increases the cation exchange capacity and electrical conductivity of the soils (Cao et al. 2018; Jiang et al. 2012; Liang et al. 2006; Nigussie et al. 2012). In addition, due to its basic nature, it can reduce soil acidity (Biederman and Harpole 2013), which can in turn positively affect crop yield (Shetty and Prakash 2020). Biochar has a porous structure and can hold air and water in its pore spaces, decreasing soil bulk density and tensile strength, increasing porosity, and improving soil aggregation (Blanco-Canqui 2017). Biochar amendment influences soil water retention (Basso et al. 2013), soil biota composition (some examples in Table 1 and in the next section) and the plant rooting pattern, as a reduced tensile strength favors the movement of roots through soils and therefore root proliferation and elongation (Bengough and Mullins 1990) and facilitates root predation by making it easier for invertebrates to move through the soil (Lehmann et al. 2011). Improving water holding capacity is particularly relevant in sandy soils where water drains at a fast rate (Basso et al. 2013; Sohi et al. 2010). Biochar macro-pores can also serve as habitats for a wide variety of microbes (Thies and Rilling 2009), protecting them from desiccation and from predation by larger soil organisms (Pietikäinen et al. 2000; Warnock et al. 2007).

Biochar amendments can increase total soil N, K, and P, all essential nutrients for plant growth (Alling et al. 2014; Biederman and Harpole 2013; Cao et al. 2018; Kamau et al. 2019; Nigussie et al. 2012; Song et al. 2019; Xu et al. 2019). A meta-analysis consisting of 401 paired comparisons from 43 published studies using biochar from varied sources (herbs, wood, lignocellulose, manure, and sludge) found that addition of biochar to soils increased overall soil enzyme activities related to N and P cycling and decreased those related to C cycling (Zhang et al. 2019). Hence, biochar amendment is beneficial to improving soil N and P cycling and C sequestration. Due to its excellent adsorption capacity, biochar can reduce nutrient leaching by retaining nutrients from the soil, both native and added as fertilizers (Rawat et al. 2019). As an example, combining biochar with N fertilizers increased N availability in

soils and dry matter yield of radish crops (Chan et al. 2008). This adsorption capacity can also affect the toxicity and transport of heavy metals. For example, dairy manure-derived biochar was effective in immobilizing atrazine and lead (Pb) in the soil (Cao et al. 2011) and from aqueous solutions (Cao and Harris 2010). Biochar application reduced Pb, chromium (Cr), copper (Cu), and zinc (Zn) availability in contaminated soils, thus decreasing the risk of groundwater contamination by heavy metals (Cao et al. 2018; Dume et al. 2016; Jiang et al. 2012; Nigussie et al. 2012). Biochar can also capture toxic compounds such as pesticides and herbicides, reducing its bioavailability and therefore their accumulation into crops (Ali et al. 2019).

All the changes in soil properties described in this section can lead to improved plant growth and yield as demonstrated for crops such as wheat, maize, or tomato (Agbna et al. 2017; Baronti et al. 2010; Kamau et al. 2019). One recent example is the increase in tomato plant growth and quality of fruit, which showed a darker red color and higher sugar, acid, and vitamin C content after soil amendment with bamboo biochar produced at different temperatures (Suthar et al. 2018). Furthermore, biochar amendments increase growth, quality, and crop yield under stress conditions such as salt and drought (Akhtar et al. 2014; Ali et al. 2017; She et al. 2018).

BIOCHAR IN PLANT-BIOTIC INTERACTIONS

Biochar effect on the soil microbial community. Soils contain the most diverse terrestrial communities on the planet and the vast majority of this diversity is attributed to soil microbes (Bardgett and Wardle 2010). Hence, it is also important to examine the effects of biochar on the soil microbiota (Ng and Cavagnaro 2016). Biochar has a porous structure which provides microsites where soil microbes can reside, providing them with a new habitat. While it seems that biochar can function as a microbial habitat, it is unclear how it is selective for different organisms, or if other factors, such as predation and food resources, influence how microbes adapt to biochar (Ng and Cavagnaro 2016).

In most studies, microbial biomass increased as a result of biochar addition, causing significant changes in the microbial community composition and enzyme activities. These changes may explain biogeochemical effects of biochar in nutrient cycling, suppression of plant pathogens and enhanced crop growth (Lehmann et al. 2011; Wiedner and Glaser 2013). Biochar can stimulate microbial activity not only due to the presence of pores as microhabitats, but also as a consequence of changes in abiotic factors which may give a competitive advantage to some populations over others (e.g., modulating pH or changing the presence and availability of toxic compounds). Additionally, biochar can be used as a source of energy or mineral nutrients by microbes (Thies et al. 2015).

Specific examples of biochar–soil–microbiota interactions, with both benefits and harmful effects have been described. In temperate soils, the addition of wheat husk biochar increased microbial diversity but only as a result of the derived physicochemical factors, since the metabolic activity did not vary and the use of organic C present in the biochar was not significant (Watzinger et al. 2014). The addition of 1% (wt/wt) biochar from eucalyptus wood chips increased bacterial diversity and changed the metabolic potential in the rhizosphere microbiome of tomato plants (Kolton et al. 2017). Similar results were obtained with biochar from citrus wood with pepper plants (Kolton et al. 2011). Biochar from red spruce pellets and grapevine residues also promoted growth and enzyme activity of soil-resident ligninolytic fungi (Taskin et al. 2019). The application of biochar from peanut shell and wheat straw increased the diversity of soil bacterial communities in a newly established landfill cover topsoil (Wong et al. 2019). In contrast, the high P content of some types of biochar, like those from poultry, significantly reduced root

TABLE 1
Verified positive effects of biochars against different groups of plant pathogens and pests according to the literature, including biochar origin, production process, and putative mechanisms of action

Group	Pathosystem				Biochar				
	Species	Crop	Type of experiment	Mechanism of action	Origin (feedstock)	Application rate	Production method	Combined with	Reference
Pathogens									
Bacteria	<i>Ralstonia solanacearum</i>	Tomato	Pots	Increased density of soil bacteria and actinomycetes	Peanut shell Wheat straw	2% (wt/wt)	Pyrolysis (2 h, 500°C)	–	Lu et al. (2016)
	<i>Ralstonia solanacearum</i>	Tomato	Greenhouse	Reduced pathogen swarming motility and rhizosphere colonization	Pinewood	3% (wt/wt)	Pyrolysis (700°C)	–	Gu et al. (2017)
	<i>Ralstonia solanacearum</i>	Tobacco	Field	Improved soil physicochemical properties and increased rhizosphere bacteria abundance	Rice straw	3 ton ha ⁻¹	Not indicated	–	Zhang et al. (2017)
Fungi	<i>Leveillula taurica</i> <i>Botrytis cinerea</i>	Pepper and tomato	Pots	Systemic induced resistance	Citrus wood	1 and 3% (wt/wt)	Traditional charcoal kiln	–	Elad et al. (2010)
	<i>Fusarium oxysporum</i> f. sp. <i>asparagi</i> <i>Fusarium proliferatum</i>	Asparagus	Greenhouse	Increased populations of antagonists such as <i>Pseudomonas</i> or AMFs	Hardwood dust	1.5 and 3% (wt/wt)	Pyrolysis (400–700°C)	–	Elmer and Pignatello (2011)
	<i>Botrytis cinerea</i> <i>Podosphaera aphanis</i> <i>Colletotrichum acutatum</i>	Strawberry	Pots	Systemic resistance activation	Pepper plant wastes	1 and 3% (wt/wt)	Pyrolysis (450°C)	–	Harel et al. (2012)
	<i>Rhizoctonia solani</i>	Cucumber	Pots	Not indicated	Eucalyptus wood Greenhouse waste	1% (wt/wt) 0.5% (wt/wt)	Pyrolysis (350 and 600°C)	–	Jaiswal et al. (2014)
	<i>Botrytis cinerea</i>	Tomato	Greenhouse	Induced systemic resistance (ISR)	Greenhouse waste	1 and 3% (wt/wt)	Pyrolysis (450°C)	–	Mehari et al. (2015)
	<i>Rhizoctonia solani</i>	Bean	Pots	It is not through direct toxicity	Eucalyptus wood Greenhouse waste	1% (wt/wt)	Pyrolysis (350 and 600°C)	–	Jaiswal et al. (2015)
	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	Tomato	Greenhouse	Altered root exudates	Beech wood chips Garden waste residues	3% (vol/vol)	Pyrolysis (500°C)	AMFs	Akhter et al. (2015, 2016)
	<i>Botrytis cinerea</i>	Strawberry	Greenhouse	Increased bacterial diversity in rhizosphere	Holm oak	3% (wt/wt)	12–18 h, 650°C	–	De Tender et al. (2016)
	<i>Fusarium oxysporum</i> f. sp. <i>asparagi</i> <i>Fusarium proliferatum</i>	Asparagus	Greenhouse	Increased root colonization by AMFs: competition with the pathogen for colonization sites	Hardwood biomass	3% (wt/vol)	Not indicated	AMFs	Elmer (2016)
	<i>Fusarium</i> spp.	Not indicated	Field	Fungicidal activity of dimethyl disulfide	Hardwood <i>Eupatorium adenophorum</i>	0.5 (wt/wt)	Pyrolysis (500°C) Pyrolysis (700–800°C)	Dimethyl disulfide	Wang et al. (2016)
	<i>Botrytis cinerea</i>	Tomato	Greenhouse	Increased diversity and changes in the metabolic potential of the rhizosphere microbiome	Eucalyptus wood chips	1% (wt/wt)	Charcoal pit (350°C)	–	Kolton et al. (2017)
	<i>Fusarium solani</i> <i>Ilyonectria destructans</i>	<i>Panax ginseng</i>	Field	Changes in the microbial community	Rice husk	5.2 Mg ha ⁻¹	Not indicated	–	Eo et al. (2018)
Oomycetes	<i>Phytophthora cinnamomi</i> <i>Phytophthora cactorum</i>	<i>Quercus rubra</i> <i>Acer rubrum</i>	Greenhouse	Induction of plant defenses through low-level stress	Pine parent material (<i>Pinus taeda</i> , <i>P. palustris</i> , <i>P. echinata</i> , <i>P. elliotti</i>)	5% (vol/vol)	Pyrolysis (1 h, 550–600°C)	–	Zwart and Kim (2012)

(Continued on next page)

TABLE 1
(Continued from previous page)

Group	Pathosystem				Biochar				
	Species	Crop	Type of experiment	Mechanism of action	Origin (feedstock)	Application rate	Production method	Combined with	Reference
	<i>Pythium ultimum</i>	Sweet pepper, lettuce, basil, geranium and coriander	Greenhouse	Negative effect: increased root colonization by the pathogen, although not the symptoms	Softwood (<i>Abies balsamea</i> , <i>Picea glauca</i> and <i>Picea mariana</i>)	50% (vol/vol)	Pyrolysis (475°C)	–	Gravel et al. (2013)
Nematodes	<i>Coslenchus</i> , <i>Hirschmanniella</i> , <i>Rotylenchus</i> , and <i>Tylenchus</i>	Not indicated	Field	Increased diversity and quantity of other nonplant parasitic nematodes	Wheat straw	2.4, 12 and 48 ton ha ⁻¹	Pyrolysis (5 h, 400°C)	–	Zhang et al. (2013)
	<i>Meloidogyne javanica</i> , <i>Tylenchulus semipenetrans</i> , <i>Pratylenchus</i> spp., <i>Helicotylenchus</i> spp., and <i>Criconeoid</i> spp.	Grapevine	Field	Increased beneficial microorganisms	Poultry litter	6.9 ton ha ⁻¹	Pyrolysis (550°C)	–	Rahman et al. (2014)
	<i>Meloidogyne graminicola</i>	Rice	Greenhouse	H ₂ O ₂ accumulation and transcriptional enhancement of ethylene genes	Oak wood	1.2% (wt/vol)	Pyrolysis (12–18 h, 650°C)	–	Huang et al. (2015)
	<i>Pratylenchus penetrans</i>	Carrot	Pots	Induced resistance, direct toxicity or altered pH	Coniferous wood and spelt husks	5% (vol/vol)	Pyrolysis (5 h, 500°C)	–	George et al. (2016)
	Root-knot nematodes	Not indicated	Field	Nematicidal activity of dimethyl disulfide	Hardwood <i>Eupatorium adenophorum</i>	2% (wt/wt)	Pyrolysis (500°C) Pyrolysis (700–800°C)	Dimethyl disulfide	Wang et al. (2016)
	<i>Pratylenchus coffeae</i>	Not indicated	Greenhouse	Nematicidal compounds derived from biochar	Burned log of wood	4% (wt/wt)	Not indicated	–	Rahayu and Sari (2017)
	<i>Pratylenchus</i> , <i>Meloidogyne</i> , <i>Tylenchorhynchus</i> , <i>Tylenchidae</i> , <i>Trichodorus</i> , and <i>Mesocriconema</i>	Not indicated	Field	Keeps nematicidal activity while reducing pollutant emissions to the atmosphere from the ground	Coconut shell	40 ton ha ⁻¹	Pyrolysis (550°C)	A mixture of 1,3-dichloro-propene and chloropicrin	Gao et al. (2018)
Complex of several pathogens	Replant disease or sick soil syndrome	Peach	Greenhouse	Not indicated	Pinewood	10 and 20% (vol/vol)	Pyrolysis (700°C)	–	Atucha and Litus (2015)
Arthropod pests and weeds									
Insects	<i>Sogatella furcifera</i>	Rice	Greenhouse	Priming through foliar accumulation of jasmonic acid	Deciduous trees (70%), dolomite (20%), and molasses (10%)	10% (wt/wt)	Not indicated	–	Waqas et al. (2018)
Mites	<i>Polyphagotarsonemus latus</i>	Pepper	Greenhouse	Systemic induced resistance	Citrus wood	1 and 3% (wt/wt)	Traditional charcoal kiln	–	Elad et al. (2010)
Weeds	<i>Setaria viridis</i>	<i>Setaria viridis</i>	Greenhouse	Negative effect: reduction of the effect of herbicides by bioabsorption	Eucalyptus wood	1 and 2% (wt/wt)	Pyrolysis (800°C)	S-metolachlor and sulfentrazone	Graber et al. (2012)

colonization by mycorrhizal fungi, although crop productivity was not affected (Solaiman et al. 2019). Similarly, biochar from rice straw showed a damaging effect to the model organism *Caenorhabditis elegans*, as it had a neurotoxic effect. This effect is probably due to the induction of oxidative stress responses in the nervous system as free radicals were detected in the biochar (Lieke et al. 2018).

Another beneficial effect of biochar includes the reduction of the environmental impact of contaminant metal(loid)s involving microorganisms. In cadmium (Cd)-contaminated soils, biochar from bamboo (*Phyllostachys heterocycla*) significantly reduced Cd uptake and accumulation by altering the rhizosphere bacterial community

in rice (Wang et al. 2019). Similarly, in herbicide-contaminated soils, biochar from wheat straw also increased microbial diversity and wheat plant performance (Meng et al. 2019).

The use of biochar against plant pathogens. Concerning plant pathogens, some studies have revealed that while low concentrations ($\leq 1\%$) of biochar suppress several diseases, higher concentrations ($> 3\%$) are mostly ineffective, resulting in an inverted U-shaped dose-response curve (Frenkel et al. 2017). It is therefore recommended to biochar producers to standardize feedstocks and concentrations for their use in agriculture as well as to consider potential effects of biochar on plant diseases (Graber et al. 2014).

In this way, farmers could rely on consistent and reproducible biochars to obtain the desired outcomes. This is a relevant issue, as the origin and processing of the raw material to produce biochar is so diverse that the reproducibility of the effect to suppress plant disease in agricultural systems is poor.

The mechanisms by which biochar may protect plants against diseases are varied (Fig. 1; Table 1). They include enhancing plant growth by providing nutrients, increasing soil-microbial diversity, adsorbing toxins produced by pathogens (such as extracellular enzymes and organic acids), stimulating antibiotic or fungitoxic compounds, changing the chemistry of root exudates, or inducing systemic plant defense mechanisms through chemical compounds that act as elicitors, or through microorganisms present in microhabitats (Bonanomi et al. 2015; Graber and Elad 2013). Biochar has been used effectively against a wide variety of plant pathogens including airborne and soilborne pathogens and pests (Table 1). In addition, the growth-promoting properties of biochar water-wash extracts have also been confirmed, as they are rich in organic and inorganic compounds (Lou et al. 2016), and this is a promising strategy that merits future studies.

Replant disease often occurs when certain crops are “replanted” in a soil that had previously supported the same or similar plant species. This disease complex typically leads to a reduction in plant growth and crop yield, and its etiology remains ill-defined for most perennial crops (Yang et al. 2012). Although the precise mechanisms by which it happens are still unknown, it has been proven that the use of biochar from pinewood at high concentrations (10 and 20%, vol/vol) significantly reduces the incidence of replant disease in peach (Atucha and Litus 2015).

It is important to point out that beneficial effects of biochar are sometimes more related to their growth-promoting effect than to the induction of plant defenses. One clear example is the application of poplar woodchip biochar in the model plant *Arabidopsis thaliana* and the crop plant lettuce (Viger et al. 2015). This poplar biochar led to a significant increase in plant growth (for both *Arabidopsis* and lettuce) and the induction of genes involved in the metabolism of growth-promoting hormones such as auxins and brassinosteroids that may mediate the observed growth effects. However, the results of global gene expression arrays and metabolomics indicated the downregulation of a large suite of plant defense genes, including those from the jasmonic acid biosynthetic pathway, genes encoding defensins, as well as most categories of secondary metabolites, all of them critical for plant protection against insect and pathogen attack (Viger et al. 2015).

In the next sections, we will comment on the available studies about the use of biochar for the control of specific groups of pathogens and pests.

Biochar for the control of plant-pathogenic bacteria. The use of biochar against plant diseases caused by bacteria has centered on combating bacterial wilt disease caused by *Ralstonia solanacearum*, one of the most important constraints in vegetable production worldwide (Choudhary et al. 2018). Although the information available is still scarce, biochars used against bacteria were generated from diverse origins (Table 1), but these biochars had in common an application rate between 2 to 3% (wt/wt), showing effectiveness in reducing bacterial wilt in tomato and tobacco plants. The mechanisms involved in this protective effect of biochar include the improvement of soil physicochemical properties and

FIGURE 1

Proposed mechanisms contributing to decreasing plant diseases and pests in soils amended with biochar. Different pathosystems have been examined for specific biochar-dependent effects that may explain the beneficial impacts of the soil amendment in the disease outcome. Only those effects documented in the literature for a particular type of pathogen or pest are included in each box (Table 1). Extension of such mechanisms to other plant–pathogen or plant–pest interactions awaits experimental support.

the increase in bacteria and actinomycetes in the rhizosphere, reducing *Ralstonia solanacearum* swarming motility and root colonization capacity (Gu et al. 2017; Lu et al. 2016; Zhang et al. 2017) (Fig. 1).

Biochar for the control of plant-pathogenic fungi. Fungi are among the most common and most destructive plant pathogens (Möller and Stukenbrock 2017), and are a major threat in agriculture. Soilborne diseases caused by species in the genus *Fusarium* (one of the most important groups of plant-pathogenic fungi) affect a vast diversity of crops in a wide range of climatic zones (Summerell 2019). *Fusarium* also produces mycotoxins in stored products of plant origin (Summerell 2019). Crown and root rot disease of asparagus is caused by *F. oxysporum* f. sp. *asparagi* and *F. proliferatum* and it is exacerbated by allelopathic toxins released in the soil. The use of hardwood biochar resulted in an increase in populations of antagonists such as *Pseudomonas* or arbuscular mycorrhizal fungi (AMFs) (Elmer 2016); the latter have also been described as inducers of systemic resistance (Poveda et al. 2020). Although more research is needed to elucidate the mechanisms of action, the results strongly suggested that biochars exert their beneficial effects through the alteration of nutrient availability or soil properties and stimulation of soil microbial populations (Elmer 2016; Elmer and Pignatello 2011) (Table 1). Similar results were observed against *F. solani* and *Ilyonectria destructans* in *Panax ginseng* plants in soil combined with rice husk biochar, also due to changes in the rhizosphere-microbial community (Eo et al. 2018). Likewise, the positive effects of green waste biochar in combination with compost (at concentrations of 0 to 3%, wt/wt) in reducing *F. oxysporum* f. sp. *lycopersici* wilt-inducing chlamydospores in tomato led to an enrichment of beneficial microorganisms, which may function either through direct antagonism or indirectly via induction of systemic resistance in the plant (Akhter et al. 2016) (Table 1). However, the beneficial effect of biochar from beech wood chips or garden waste residues against *F. oxysporum* f. sp. *lycopersici* in tomato plants is probably due to the alteration of plant root exudates that may exert an essential role in determining the plant response to disease stress (Akhter et al. 2015) (Table 1). Furthermore, the application of biochar in combination with gaseous pesticides (fumigants) can potentially reduce fumigant emissions in agriculture. One example is the use of two types of biochar (from a feedstock of mixed hardwoods and from *Eupatorium adenophorum*) combined with dimethyl disulfide. These showed no negative effects for *Fusarium* spp. control at application rates of less than 0.5% (on a weight basis) but significantly reduced the emission of dimethyl disulfide to the atmosphere (Wang et al. 2016) (Table 1).

The necrotrophic fungus *Rhizoctonia solani* is an economically important soilborne pathogen of crop plants causing primarily seedling diseases (Verwaaijen et al. 2017). Although the mechanisms involved in biochar-mediated suppression of *R. solani* are still unknown, direct toxicity has been ruled out. An application of 1% (wt/wt) biochar from eucalyptus wood and greenhouse wastes significantly reduced disease in cucumber and bean plants (Jaiswal et al. 2014, 2015) (Table 1). In contrast, biochar from maple bark increased *R. solani* damping-off disease of several plant species, probably due to the presence of different organic compounds that enhance the pathogen's primary metabolism (Copley et al. 2015). Therefore, not all sources of biochar have a desirable pathogen control effect.

Biochar also improves plant resistance to foliar plant pathogenic fungi. The main mechanism observed for the induced resistance is the systemic activation of defenses (Poveda et al. 2020). *Botrytis cinerea* is a polyphagous fungal pathogen that causes necrotic disease on more than a thousand known hosts widely spread across the plant kingdom (Caseys et al. 2020). In strawberry, *B. cinerea* causes gray mold, a commercially damaging disease (Petrasch et al. 2019). The use of biochar from holm oak in strawberry fields

increased the bacterial diversity in the rhizosphere (De Tender et al. 2016) (Table 1), which may result in the activation of systemic resistance against the pathogen, reducing the disease. Similar results against *B. cinerea* have been observed after the application of biochar from eucalyptus wood chips in tomato, which increased microbial diversity and metabolism in the rhizosphere and enhanced defense responses of tomato (Kolton et al. 2017). Accordingly, the use of biochar from greenhouse waste in tomato against *B. cinerea* induced priming of early- and late-acting defense responses (Mehari et al. 2015). Among others, these included an induction of the expression of genes related to jasmonic acid and ethylene responses, and a high accumulation of active oxygen species such as H₂O₂, both crucial in the resistance against *B. cinerea* (Mehari et al. 2015). Similarly, the use of biochar from citrus wood (1 to 5%) in tomato and pepper against *B. cinerea* and *Leveillula taurica* (which causes powdery mildew) reduced both diseases significantly, probably through the induction of systemic induced resistance elicitors (Elad et al. 2010). In line with this, biochar from pepper plant wastes was also effective against other fungal pathogens such as *Colletotrichum acutatum* and *Podosphaera aphanis* (Harel et al. 2012) (Table 1; Fig. 1), the causative agents in strawberry of anthracnose (Dinler and Benlioglu 2019) and powdery mildew (Carisse et al. 2013), respectively.

Biochar for the control of plant-pathogenic oomycetes. Oomycetes are adapted to infect and kill countless plant species, many of which are economically important food and cash crops (Hargreaves and van West 2019). As is the case with plant-pathogenic bacteria, there are few studies related to the use of biochar in the control of oomycetes (Table 1; Fig. 1). As far as *Phytophthora* is concerned, the use of biochar to reduce plant disease has only been applied against tree-infecting species (Table 1). For example, it has been shown that the application of 5% (vol/vol) biochar from pine plant tissues causes the activation of plant defenses through the induction of systemic resistance, both in *Quercus rubra* against *Phytophthora cinnamomi* and in *Acer rubrum* against *Phytophthora cactorum*, alleviating disease progression and physiological stress (Zwart and Kim 2012). In contrast, the treatment with softwood biochar caused an increase in root colonization by *Pythium ultimum* in sweet pepper, lettuce, basil, and geranium, but no clear damage to the root system or to plant development was observed (Gravel et al. 2013) (Table 1).

Biochar for the control of plant-parasitic nematodes. Plant-parasitic nematodes (PPNs) can cause average yield losses in crops of about 12.3% (Singh et al. 2015). Biochar represents a sustainable strategy to combat PPNS through various mechanisms (Table 1; Fig. 1). For instance, changes in the biodiversity of nematode populations in the soil can be effective against PPNS. In this respect, the application of biochar from wheat straw influenced the diversity of nematodes in the soil in a microcosm trial by increasing the abundance of fungivores and decreasing PPNS such as those from the genus *Coslenchus*, *Hirschmanniella*, *Rotylenchus*, and *Tylenchus*, among others (Zhang et al. 2013).

Biochar from burned log wood was effective in reducing the populations of *Pratylenchus coffeae*, a migratory endoparasitic and major destructive root lesion nematode of banana (Muthusamy et al. 2019; Vieira et al. 2019), at a concentration of 4% (wt/wt) (Rahayu and Sari 2017). In grapevine, the use of biochar from poultry litter significantly reduced the PPN populations present in soils, such as *Meloidogyne javanica*, *Tylenchulus semipenetrans*, *Pratylenchus* spp., *Helicotylenchus* spp., and *Criconeimoid* spp., due to an increase in the diversity of plant-beneficial organisms (Rahman et al. 2014). Induction of plant defenses constitutes another effective mechanism against *Pratylenchus* spp. for example, the application of biochar from coniferous wood and spelt husks at a concentration of 5% (vol/vol) enhanced resistance against *Pratylenchus penetrans* in carrot plants, due to the induction of plant defenses. Yet, direct toxicity or alteration of soil pH cannot be ruled out as a mechanism

(George et al. 2016). Furthermore, the endoparasitic root-knot nematode *Meloidogyne graminicola*, one of the most prevalent PPNs in rice agrosystems (Mantelin et al. 2017), was successfully controlled by the addition of biochar from oak wood at an application rate of 1.2% (wt/vol). This effect was linked to a local H₂O₂ accumulation and a transcriptional enhancement of ethylene-related genes, which influenced plant defense genes (Huang et al. 2015).

An interesting application of biochar is that it can be effective in reducing fumigant emissions without reducing nematode control. For example, the use of 1,3-dichloropropene and chloropicrin in combination with biochar from coconut shell sustained nematicidal activity against PPNs from the genus *Pratylenchus*, *Meloidogyne*, *Tylenchorhynchus*, *Tylenchidae*, *Trichodorus*, and *Mesocriconema*, while reducing atmospheric pollutant emissions (Gao et al. 2018). Another example, previously mentioned for the control of *Fusarium* spp. is the use of biochar from hardwood and *Eupatorium adenophorum*, that was also effective for root-knot nematode control at an application rate of 0.5% on a soil weight basis, causing a significant reduction of fumigant emissions (Wang et al. 2016).

Biochar for the control of arthropod pests and weeds.

There are only a few studies analyzing the effects of biochar application for arthropod pest control (Table 1; Fig. 1). In most cases, the mode of action is thought to involve priming of plant insect-defense responses. One example is the control of *Sogatella furcifera* (white-backed planthopper; Hemiptera: Delphacidae), an important herbivore pest of rice in Asia (Dang et al. 2019). The use of biochar from deciduous trees, dolomite, and molasses at a concentration of 10% (wt/wt) increased the resistance of rice plants against *S. furcifera* due to the activation of a priming response through foliar accumulation of jasmonic acid (Waqas et al. 2018). Similarly, biochar from citrus wood induced systemic resistance in pepper against *Polypogon tarsonemus latus* (Acari: Tarsonemidae) (Elad et al. 2010), commonly known as the broad mite, a pest of economic importance on many agricultural and horticultural crops (Akyazi et al. 2019).

Biochar has also been used in combination with herbicides against weeds. However, the effect has not always been as desired. One example is the combination of biochar from eucalyptus wood with the herbicides S-metolachlor and sulfentrazone on the weed *Serattia viridis*. Known as green foxtail, it is one of the most abundant and troublesome annual grass weeds in cereal crops (Satchivi et al. 2017). In this case, the treatment caused a significant reduction in the effectiveness of the herbicides due to their bioabsorption (Graber et al. 2012),

CONCLUSIONS AND FUTURE PERSPECTIVES

Biochar application has been shown to have beneficial antipathogen effects, although these effects varied in effectiveness and mode of action. Biochar characteristics, and the associated effects on soil properties and pathogen control, depend mostly on the raw material, the pyrolysis conditions, and the application rate used in soils. This seems a disadvantage, as biochar production and application would have to be specifically designed in each case. However, this optimization could also serve to customize the treatment to the type of pathogen and the severity of the disease, representing one of the potential advantages of biochar use. Since the beneficial effects of biochar are also soil-specific, its use must be studied, tested, and designed for each agricultural system and place. Yet, most of the studies described herein indicate that biochar from very different origins can be effective against a range of plant pathogens and pests, after adjusting several variables such as the application rate or the production method (Table 1). Furthermore, biochar contributes positively to the agricultural system by increasing nutrient availability, improving soil structure, immobilizing heavy metals and organic contaminants, reducing greenhouse gas emissions and biotic stresses, and generally, increasing crop yields. In addition, its application also provides socio-economic benefits, as it involves the

use of locally produced resources that do not require long-distance transport and that promote the circular economy of the area.

The results described in the literature strongly suggest that the effects of biochar are the result of soil microsite changes influencing a combination of tripartite or higher degree interactions among the pathogens, the plant, and soil microorganisms (Fig. 1) where coordinated hormonal signaling responses within the plant seem to play an important role. Interestingly, several studies show that biochar contributes to reduce fumigant emissions from currently used chemicals that are economically viable and effective against nematodes, thus decreasing the environmental impact of their application. The available information indicates that a gradual implementation of biochar amendments could be included in integrated pest management strategies, compatible with actual practices based mainly on agrichemicals, but with the advantage of reducing potential negative impacts in the agricultural systems.

In conclusion, biochar as a derived product of feedstock, particularly of agricultural waste, is a promising strategy that should be locally studied and optimized and that exerts complex modes of action for plant pathogen control. Moreover, a still unexploited aspect of biochar that has been barely studied is the potential to apply aqueous extracts from biochar washes for pathogen control. In this respect, the need for basic research to understand the modes of action of biochar either directly on the pathogen or indirectly through the plant is essential in the near future.

LITERATURE CITED

- Agbna, G. H. D., Ali, A. A. S., Elbasher, M. M. A., Bakir, M., Osman, A., and Elshaikh, A. E. A. 2017. Effect of biochar on some soil properties and tomato growth under saline water conditions. *Int. J. Engine Res.* 8:24-28.
- Akhtar, S. S., Li, G., Andersen, M. N., and Liu, F. 2014. Biochar enhances yield and quality of tomato under reduced irrigation. *Agric. Water Manage.* 138:37-44.
- Akhter, A., Hage-Ahmed, K., Soja, G., and Steinkellner, S. 2015. Compost and biochar alter mycorrhisation, tomato root exudation, and development of *Fusarium oxysporum* f. sp. *lycopersici*. *Front. Plant Sci.* 6:529.
- Akhter, A., Hage-Ahmed, K., Soja, G., and Steinkellner, S. 2016. Potential of *Fusarium* wilt-inducing chlamydospores, in vitro behaviour in root exudates and physiology of tomato in biochar and compost amended soil. *Plant Soil* 406:425-440.
- Akyazi, R., Sekban, R., Soysal, M., Akyol, D., Colee, J., and Bostan, S. Z. 2019. Ecofriendly control approaches for *Polypogon tarsonemus latus* (Acari: Tarsonemidae) on tea (*Camellia sinensis* L.). *Int. J. Acarol.* 45:79-89.
- Ali, N., Khan, S., Yao, H., and Wang, J. 2019. Biochars reduced the bioaccessibility and (bio)uptake of organochlorine pesticides and changed the microbial community dynamics in agricultural soils. *Chemosphere* 224:805-815.
- Ali, S., Rizwan, M., Qayyum, M. F., Ok, Y. S., Ibrahim, M., Riaz, M., Arif, M. S., Hafeez, F., Al-Wabel, M. I., and Shahzad, A. N. 2017. Biochar soil amendment on alleviation of drought and salt stress in plants: A critical review. *Environ. Sci. Pollut. R.* 24:12700-12712.
- Ailling, V., Hale, S. E., Martinsen, V., Mulder, J., Smebye, A., Breedveld, G. D., and Cornelissen, G. 2014. The role of biochar in retaining nutrients in amended tropical soils. *J. Soil Sci. Plant Nutr.* 177:671-680.
- Angin, D. 2013. Effect of pyrolysis temperature and heating rate on biochar obtained from pyrolysis of safflower seed press cake. *Bioresour. Technol.* 128:593-597.
- Atucha, A., and Litus, G. 2015. Effect of biochar amendments on peach replant disease. *HortScience* 50:863-868.
- Bardgett, R. D., and Wardle, D. A. 2010. Aboveground-belowground linkages: Biotic interactions, ecosystem processes, and global change. Oxford University Press, Oxford, U.K.
- Baronti, S., Alberti, G., Vedove, G. D., di Gennaro, F., Fellet, G., Genesio, L., Miglietta, F., Peressotti, A., and Vaccari, F. P. 2010. The biochar option to improve plant yields: First results from some field and pot experiments in Italy. *Ital. J. Agron.* 5:3-11.
- Basso, A. S., Miguez, F. E., Laird, D. A., Horton, R., and Westgate, M. 2013. Assessing potential of biochar for increasing water-holding capacity of sandy soils. *GCB Bioenergy* 5:132-143.
- Bengough, A. G., and Mullins, C. E. 1990. Mechanical impedance to root growth: A review of experimental techniques and root growth responses. *J. Soil Sci.* 41:341-358.

- Biederman, L. A., and Harpole, W. S. 2013. Biochar and its effects on plant productivity and nutrient cycling: A meta-analysis. *GCB Bioenergy*. 5:202-214.
- Blanco-Canqui, H. 2017. Biochar and soil physical properties. *Soil Sci. Soc. Am. J.* 81:687-711.
- Bonanomi, G., Ippolito, F., and Scala, F. 2015. A "black" future for plant pathology? Biochar as a new soil amendment for controlling plant diseases. *J. Plant Pathol.* 97:223-234.
- Brown, C. B. 1876. *Canoe and Camp Life in British Guiana*. Edward Stanford, London.
- Brown, C. B., and Lidstone, W. 1878. *Fifteen Thousand Miles on the Amazon and Its Tributaries*. Edward Stanford, London.
- Cao, X., and Harris, W. 2010. Properties of dairy-manure-derived biochar pertinent to its potential use in remediation. *Bioresour. Technol.* 101:5222-5228.
- Cao, X., Yuan, L., Gao, B., and Harris, W. 2011. Simultaneous immobilization of lead and atrazine in contaminated soils using dairy-manure biochar. *Environ. Sci. Technol.* 45:4884-4889.
- Cao, Y., Gao, Y., Qi, Y., and Li, J. 2018. Biochar-enhanced composts reduce the potential leaching of nutrients and heavy metals and suppress plant-parasitic nematodes in excessively fertilized cucumber soils. *Environ. Sci. Pollut. Res.* 25:7589-7599.
- Carisse, O., Morissette-Thomas, V., and Van der Heyden, H. 2013. Lagged association between powdery mildew leaf severity, airborne inoculum, weather, and crop losses in strawberry. *Phytopathology* 103:811-821.
- Case, S. D. C., McNamara, N. P., Reay, D. S., Stott, A. W., Grant, H. K., and Whitaker, J. 2015. Biochar suppresses N₂O emissions while maintaining N availability in a sandy loam soil. *Soil Biol. Biochem.* 81:178-185.
- Caseys, C., Shi, G., Soltis, N., Gwinner, R., Corwin, J., Atwell, S., and Kliebenstein, D. 2020. Quantitative interactions drive *Botrytis cinerea* disease outcome across the plant kingdom. *BioRxiv* 507491.
- Chan, K. Y., Van Zwieten, L., Meszaros, I., Downie, A., and Joseph, S. 2008. Using poultry litter biochars as soil amendments. *Aust. J. Soil Res.* 46:437-444.
- Chan, K. Y., and Xu, Z. H. 2009. Biochar: Nutrient properties and their enhancement. Pages 67-84 in: *Biochar for Environmental Management: Science and Technology*. J. Lehmann and S. Joseph, eds. Earthscan, London, U.K.
- Chandra, S., and Bhattacharya, J. 2019. Influence of temperature and duration of pyrolysis on the property heterogeneity of rice straw biochar and optimization of pyrolysis conditions for its application in soils. *J. Clean. Prod.* 215:1123-1139.
- Cheng, H., Jones, D. L., Hill, P., Bastami, M. S., and Tu, C. 2017. Influence of biochar produced from different pyrolysis temperature on nutrient retention and leaching. *Arch. Agron. Soil Sci.* 64:850-859.
- Choudhary, D. K., Nabi, S. U., Dar, M. S., and Khan, K. A. 2018. *Ralstonia solanacearum*: A wide spread and global bacterial plant wilt pathogen. *Int. J. Pharmacogn. Phytochem.* 7:85-90.
- Copley, T. R., Aliferis, K. A., and Jabaji, S. 2015. Maple bark biochar affects *Rhizoctonia solani* metabolism and increases damping-off severity. *Phytopathology* 105:1334-1346.
- Dang, C., Sun, C., Lu, Z., Zhong, F., Wang, F., Wang, Q., Sun, R., Peng, Y., and Ye, G. 2019. Cry2A rice did not affect the interspecific interactions between two rice planthoppers, *Nilaparvata lugens*, and *Sogatella furcifera*. *GM Crops Food* 10:170-180.
- De Tender, C. A., Debode, J., Vandecasteele, B., D'Hose, T., Cremelie, P., Haegeman, A., Ruttink, T., Dawyndt, P., and Maes, M. 2016. Biological, physicochemical and plant health responses in lettuce and strawberry in soil or peat amended with biochar. *Appl. Soil Ecol.* 107:1-12.
- Dinler, H., and Benlioglu, S. 2019. The possibility to control diseases caused by *Colletotrichum* species in strawberries. *Int. J. Agric. For. Life Sci.* 3:362-370.
- Dong, Q., Li, H., Niu, M., Luo, C., Zhang, J., Qi, B., Li, X., and Zhong, W. 2018. Microwave pyrolysis of moso bamboo for syngas production and bio-oil upgrading over bamboo-based biochar catalyst. *Bioresour. Technol.* 266:284-290.
- Downie, A., Crosky, A., and Munroe, P. 2009. Physical properties of biochar. Pages 13-33 in: *Biochar for Environmental Management: Science and Technology*. J. Lehmann and S. Joseph, eds. Earthscan, London, U.K.
- Duku, M. H., Gu, S., and Ben Hagan, E. 2011. Biochar production potential in Ghana—A review. *Renew. Sustain. Energy Rev.* 15:3539-3551.
- Dume, B., Mosissa, T., and Nebiyu, A. 2016. Effect of biochar on soil properties and lead (Pb) availability in a military camp in South West Ethiopia. *Afr. J. Environ. Sci. Technol.* 10:77-85.
- Elad, Y., David, D. R., Harel, Y. M., Borenstein, M., Kalifa, H. B., Silber, A., and Graber, E. R. 2010. Induction of systemic resistance in plants by biochar, a soil-applied carbon sequestering agent. *Phytopathology* 100:913-921.
- Elmer, W. H. 2016. Effect of leaf mold mulch, biochar, and earthworms on mycorrhizal colonization and yield of asparagus affected by *Fusarium crown and root rot*. *Plant Dis.* 100:2507-2512.
- Elmer, W. H., and Pignatello, J. J. 2011. Effect of biochar amendments on mycorrhizal associations and *Fusarium crown and root rot* of asparagus in replant soils. *Plant Dis.* 95:960-966.
- Enders, A., Hanley, K., Whitman, T., Joseph, S., and Lehmann, J. 2012. Characterization of biochars to evaluate recalcitrance and agronomic performance. *Bioresour. Technol.* 114:644-653.
- EO, J., Park, K. C., Kim, M. H., Kwon, S. I., and Song, Y. J. 2018. Effects of rice husk and rice husk biochar on root rot disease of ginseng (*Panax ginseng*) and on soil organisms. *Biol. Agric. Hortic.* 34:27-39.
- Foong, S. Y., Latiff, N. S. A., Liew, R. K., Yek, P. N. Y., and Lam, S. S. 2020. Production of biochar for potential catalytic and energy applications via microwave vacuum pyrolysis conversion of cassava stem. *Mater. Sci. Energy Technol.* 3:728-733.
- Frenkel, O., Jaiswal, A. K., Elad, Y., Lew, B., Kammann, C., and Graber, E. R. 2017. The effect of biochar on plant diseases: What should we learn while designing biochar substrates? *J. Environ. Eng. Landsc. Manag.* 25:105-113.
- Gai, X., Wang, H., Liu, J., Zhai, L., Liu, S., Ren, T., and Liu, H. 2014. Effects of feedstock and pyrolysis temperature on biochar adsorption of ammonium and nitrate. *PLoS One* 9:e113888.
- Gao, S., Doll, D. A., Stanghellini, M. S., Westerdahl, B. B., Wang, D., and Hanson, B. D. 2018. Deep injection and the potential of biochar to reduce fumigant emissions and effects on nematode control. *J. Environ. Manage.* 223:469-477.
- George, C., Kohler, J., and Rillig, M. C. 2016. Biochars reduce infection rates of the root-lesion nematode *Pratylenchus penetrans* and associated biomass loss in carrot. *Soil Biol. Biochem.* 95:11-18.
- Gheorghe, C., Marculescu, C., Badea, A., Dinca, C., and Apostol, T. 2009. Effect of pyrolysis conditions on bio-char production from biomass. Pages 239-241 in: *Energy Problems and Environmental Engineering*. L. Perlovsky, D. D. Dionysiou, L. A. Zadeh, M. M. Kostic, C. Gonzalez-Concepcion, H. Jaberg, N. E. Mastorakis, A. Zaharim, and K. Sopian, eds. World Scientific and Engineering Academy and Society, Tenerife, Spain.
- Glaser, B. 2014. *Soil Biogeochemistry. From Molecular to Ecosystem Level Using Terra Preta and Biochar as Examples*. Pages 1-40 in: *Agroecology, Ecosystems, and Sustainability*. N. Benkeblia, ed. CRC Press, Boca Raton, FL.
- Glaser, B., Bol, R., Preedy, N., McTiernan, K. B., Clark, M., and Amelung, W. 2001a. Short term sequestration of slurry-derived carbon and nitrogen in temperate grassland soil as assessed by ¹³C and ¹⁵N natural abundance measurements. *J. Plant Nutr. Soil Sci.* 164:467-474.
- Glaser, B., Haumaier, L., Guggenberger, G., and Zech, W. 2001b. The "Terra Preta" phenomenon: A model for sustainable agriculture in the humid tropics. *Naturwissenschaften* 88:37-41.
- Glaser, B., Lehmann, J., and Zech, W. 2002. Ameliorating physical and chemical properties of highly weathered soils in the tropics with charcoal—A review. *Biol. Fertil. Soils* 35:219-230.
- Graber, E. R., and Elad, Y. 2013. Biochar impact on plant resistance to disease. Pages 41-68 in: *Biochar and Soil Biota*. N. Ladygina and F. Rineau, eds. CRC Press, Boca Raton, FL.
- Graber, E. R., Frenkel, O., Jaiswal, A. K., and Elad, Y. 2014. How may biochar influence severity of diseases caused by soilborne pathogens? *Carbon Manag.* 5:169-183.
- Graber, E. R., Tsechansky, L., Gerstl, Z., and Lew, B. 2012. High surface area biochar negatively impacts herbicide efficacy. *Plant Soil* 353: 95-106.
- Gravel, V., Dorais, M., and Ménard, C. 2013. Organic potted plants amended with biochar: Its effect on growth and *Pythium* colonization. *Can. J. Plant Sci.* 93:1217-1227.
- Gu, Y., Hou, Y., Huang, D., Hao, Z., Wang, X., Wei, Z., Jousset, A., Tan, S., Xu, D., Shen, O., Xu, Y., and Fridman, V. P. 2017. Application of biochar reduces *Ralstonia solanacearum* infection via effects on pathogen chemotaxis, swarming motility, and root exudate adsorption. *Plant Soil* 415:269-281.
- Harel, Y. M., Elad, Y., Rav-David, D., Borenstein, M., Shulchani, R., Lew, B., and Graber, E. R. 2012. Biochar mediates systemic response of strawberry to foliar fungal pathogens. *Plant Soil* 357:245-257.
- Hargreaves, J., and van West, P. 2019. Oomycete-root interactions. Pages 83-103 in: *Methods in Rhizosphere Biology Research*. D. Reinhardt and A. K. Sharma, eds. Springer, Singapore.
- Hartt, C. F. 1872. Recent explorations in the valley of the Amazonas, with map. *Ann. Rep. Am. Geogr. Soc. NY.* 3:231-252.

- Huang, W. K., Ji, H. L., Gheysen, G., Debode, J., and Kyndt, T. 2015. Biochar-amended potting medium reduces the susceptibility of rice to root-knot nematode infections. *BMC Plant Biol.* 15:267.
- Jaiswal, A. K., Elad, Y., Graber, E. R., and Frenkel, O. 2014. *Rhizoctonia solani* suppression and plant growth promotion in cucumber as affected by biochar pyrolysis temperature, feedstock and concentration. *Soil Biol. Biochem.* 69:110-118.
- Jaiswal, A. K., Frenkel, O., Elad, Y., Lew, B., and Graber, E. R. 2015. Non-monotonic influence of biochar dose on bean seedling growth and susceptibility to *Rhizoctonia solani*: The "Shifted R max-Effect". *Plant Soil* 395:125-140.
- Jassal, R. S., Johnson, M. S., Molodovskaya, M., Black, T. A., Jollymore, A., and Sveinson, K. 2015. Nitrogen enrichment potential of biochar in relation to pyrolysis temperature and feedstock quality. *J. Environ. Manage.* 152:140-144.
- Jiang, T. Y., Jiang, J., Xu, R. K., and Li, Z. 2012. Adsorption of Pb(II) on variable charge soils amended with rice-straw derived biochar. *Chemosphere* 89:249-256.
- Jindo, K., Mizumoto, H., Sawada, Y., Sanchez-Monedero, M. A., and Sonoki, T. 2014. Physical and chemical characterization of biochars derived from different agricultural residues. *Biogeosciences* 11:6613-6621.
- Kamau, S., Karanja, N. K., Ayuke, F. O., and Lehmann, J. 2019. Short-term influence of biochar and fertilizer-biochar blends on soil nutrients, fauna and maize growth. *Biol. Fertil. Soils* 55:661-673.
- Kameyama, K., Miyamoto, T., Iwata, Y., and Shiono, T. 2016. Influences of feedstock and pyrolysis temperature on the nitrate adsorption of biochar. *J. Soil Sci. Plant Nutr.* 62:180-184.
- Kavitha, B., Reddy, P. V. L., Kim, B., Lee, S. S., Pandey, S. K., and Kim, K. H. 2018. Benefits and limitations of biochar amendment in agricultural soils: A review. *J. Environ. Manage.* 227:146-154.
- Kloss, S., Zehetner, F., Dellantonio, A., Hamid, R., Ottner, F., Liedtke, V., Schwanninger, M., Gerzabek, M. H., and Soja, G. 2012. Characterization of slow pyrolysis biochars: Effects of feedstocks and pyrolysis temperature on biochar properties. *J. Environ. Qual.* 41:990-1000.
- Kolton, M., Graber, E. R., Tshansky, L., Elad, Y., and Cytryn, E. 2017. Biochar-stimulated plant performance is strongly linked to microbial diversity and metabolic potential in the rhizosphere. *New Phytol.* 213:1393-1404.
- Kolton, M., Harel, Y. M., Pasternak, Z., Graber, E. R., Elad, Y., and Cytryn, E. 2011. Impact of biochar application to soil on the root-associated bacterial community structure of fully developed greenhouse pepper plants. *Appl. Environ. Microbiol.* 77:4924-4930.
- Kuzyakov, Y., Subbotina, I., Chen, H. Q., Bogomolova, I., and Xu, X. L. 2009. Black carbon decomposition and incorporation into soil microbial biomass estimated by C-14 labeling. *Soil Biol. Biochem.* 41:210-219.
- Lehmann, J., Gaunt, J., and Rondon, M. 2006. Bio-char sequestration in terrestrial ecosystems—A review. *Mitig. Adapt. Strategies Glob. Change* 11:403-427.
- Lehmann, J., and Joseph, S. 2009. Biochar for environmental management: An introduction. Pages 1-12 in: *Biochar for Environmental Management: Science and Technology*. Lehmann, J., and Joseph, S., eds. Earthscan, London, U.K.
- Lehmann, J., Kuzyakov, Y., Pan, G., and Ok, Y. S. 2015. Biochars and the plant-soil interface. *Plant Soil* 395:1-5.
- Lehmann, J., Rillig, M. C., Thies, J., Masiello, C. A., Hockaday, W. C., and Crowley, D. 2011. Biochar effects on soil biota—A review. *Soil Biol. Biochem.* 43:1812-1836.
- Li, G., Khan, S., Ibrahim, M., Sun, T., Tang, J., Cotner, J. B., and Xu, Y. 2018. Biochars induced modification of dissolved organic matter (DOM) in soil and its impact on mobility and bioaccumulation of arsenic and cadmium. *J. Hazard. Mater.* 348:100-108.
- Liang, B., Lehmann, J., Solomon, D., Kinyangi, J., Grossman, J., O'Neill, B., Skjemstad, J. O., Thies, J., Luizão, F. J., Petersen, J., and Neves, E. G. 2006. Black carbon increases cation exchange capacity in soils. *Soil Sci. Soc. Am. J.* 70:1719-1730.
- Lieke, T., Zhang, X., Steinberg, C. E., and Pan, B. 2018. Overlooked risks of biochars: Persistent free radicals trigger neurotoxicity in *Caenorhabditis elegans*. *Environ. Sci. Technol.* 52:7981-7987.
- Lou, Y., Joseph, S., Li, L., Graber, E. R., Liu, X., and Pan, G. 2016. Water extract from straw biochar used for plant growth promotion: An initial test. *BioResources* 11:249-266.
- Lu, Y., Rao, S., Huang, F., Cai, Y., Wang, G., and Cai, K. 2016. Effects of biochar amendment on tomato bacterial wilt resistance and soil microbial amount and activity. *Int. J. Agron.* 2016:10.
- Mantelin, S., Bellafiore, S., and Kyndt, T. 2017. *Meloidogyne graminicola*: A major threat to rice agriculture. *Mol. Plant Pathol.* 18:3-15.
- McBeath, A. V., Smernik, R. J., Krull, E. S., and Lehmann, J. 2014. The influence of feedstock and production temperature on biochar carbon chemistry: A solid-state ¹³C NMR study. *Biomass Bioenergy* 60:121-129.
- Mehari, Z. H., Elad, Y., Rav-David, D., Graber, E. R., and Harel, Y. M. 2015. Induced systemic resistance in tomato (*Solanum lycopersicum*) against *Botrytis cinerea* by biochar amendment involves jasmonic acid signaling. *Plant Soil* 395:31-44.
- Meng, L., Sun, T., Li, M., Saleem, M., Zhang, Q., and Wang, C. 2019. Soil-applied biochar increases microbial diversity and wheat plant performance under herbicide fomesafen stress. *Ecotoxicol. Environ. Saf.* 171:75-83.
- Möller, M., and Stukenbrock, E. H. 2017. Evolution and genome architecture in fungal plant pathogens. *Nat. Rev. Microbiol.* 15:756-771.
- Muthusamy, M., Uma, S., Suthanthirani, B., Saraswathi, M. S., and Chandrasekar, A. 2019. Genome-wide identification of novel, long non-coding RNAs responsive to *Mycosphaerella eumusae* and *Pratylenchus coffeae* infections and their differential expression patterns in disease-resistant and sensitive banana cultivars. *Plant Biotechnol. Rep.* 13:73-83.
- Ng, E. L., and Cavagnaro, T. R. 2016. Biochar effects on ecosystems: Insights from lipid-based analysis. Pages 55-77 in: *Biochar Application*. T. K. Ralebitso-Senior and C. H. Orr, eds. Elsevier, Amsterdam, Netherlands.
- Nigussie, A., Kissi, E., Misganaw, M., and Ambaw, G. 2012. Effect of biochar application on soil properties and nutrient uptake of lettuce (*Lactuca sativa*) grown in chromium polluted soils. *Am.-Eurasian J. Agric. Environ. Sci.* 12:369-376.
- Orton, J. 1875. The Andes and the Amazon. Harper and Brothers, New York.
- Petrusch, S., Knapp, S. J., Van Kan, J. A., and Blanco-Ulate, B. 2019. Grey mould of strawberry, a devastating disease caused by the ubiquitous necrotrophic fungal pathogen *Botrytis cinerea*. *Mol. Plant Pathol.* 20:877-892.
- Pietikäinen, J., Kiikkilä, O., and Fritze, H. 2000. Charcoal as a habitat for microbes and its effect on the microbial community of the underlying humus. *Oikos* 89:231-242.
- Poveda, J., Abril-Urias, P., and Escobar, C. 2020. Biological control of plant-parasitic nematodes by filamentous fungi inducers of resistance: Trichoderma, mycorrhizal and endophytic fungi. *Front. Microbiol.* 11:992.
- Rahayu, D. S., and Sari, N. P. 2017. Development of *Pratylenchus coffeae* in biochar applied soil, coffee roots and its effect on plant growth. *Pelita Perkebunan*. 33:24-32.
- Rahman, L., Whitelaw-Weckert, M. A., and Orchard, B. 2014. Impact of organic soil amendments, including poultry-litter biochar, on nematodes in a Riverina, New South Wales, vineyard. *Soil Res.* 52:604-619.
- Rajakapsha, A. U., Vithanage, M., Zhang, M., Ahmad, M., Mohan, D., Chang, S. X., and Ok, Y. S. 2014. Pyrolysis condition affected sulfamethiazole sorption by tea waste biochars. *Bioresour. Technol.* 166:303-308.
- Rawat, J., Saxena, J., and Sanwal, P. 2019. Biochar: A sustainable approach for improving plant growth and soil properties. Pages 1-17 in: *Biochar—An Imperative Amendment for Soil and the Environment*. V. Abrol and P. Sharma, eds. IntechOpen, London, U.K.
- Rogovska, N., Laird, D., Cruse, R., Fleming, P., Parkin, T., and Meek, D. 2011. Impact of biochar on manure carbon stabilization and greenhouse gas emissions. *Soil Sci. Soc. Am. J.* 75:871-879.
- Ronsse, F., van Hecke, S., Dickinson, D., and Prins, W. 2013. Production and characterization of slow pyrolysis biochar: Influence of feedstock type and pyrolysis conditions. *GCB Bioenergy*. 5:104-115.
- Satchivi, N. M., deBoer, G. J., and Bell, J. L. 2017. Understanding the differential response of *Setaria viridis* L. (green foxtail) and *Setaria pumila* Poir. (yellow foxtail) to pyroxsulam. *J. Agric. Food Chem.* 65:7328-7336.
- She, D., Sun, X., Gamareldawla, A. H. D., Nazar, E. A., Hu, W., Edith, K., and Yu, S. 2018. Benefits of soil biochar amendments to tomato growth under saline water irrigation. *Sci. Rep.* 8:14743.
- Shetty, R., and Prakash, N. B. 2020. Effect of different biochars on acid soil and growth parameters of rice plants under aluminum toxicity. *Sci. Rep.* 10:12249.
- Shu, R., Wang, Y., and Zhong, H. 2016. Biochar amendment reduced methylmercury accumulation in rice plants. *J. Hazard. Mater.* 313:1-8.
- Singh, S., Singh, B., and Singh, A. P. 2015. Nematodes: A threat to sustainability of agriculture. *Procedia Environ. Sci.* 29:215-216.
- Sohi, S. P., Krull, E., Lopez-Capel, E., and Bol, R. 2010. A review of biochar and its use and function in soil. *Adv. Agron.* 105:47-82.
- Solaiman, Z. M., Abbott, L. K., and Murphy, D. V. 2019. Biochar phosphorus concentration dictates mycorrhizal colonization, plant growth and soil phosphorus cycling. *Sci. Rep.* 9:5062.
- Song, D., Xi, X., Zheng, Q., Liang, G., Zhou, W., and Wang, X. 2019. Soil nutrient and microbial activity responses to two years after maize straw biochar application in a calcareous soil. *Ecotoxicol. Environ. Saf.* 180:348-356.
- Summerell, B. A. 2019. Resolving *Fusarium*: Current status of the genus. *Annu. Rev. Phytopathol.* 57:323-339.
- Suthar, R. G., Wang, C., Nunes, M. C. N., Chen, J., Sargent, S. A., Bucklin, R. A., and Gao, B. 2018. Bamboo biochar pyrolyzed at low temperature improves tomato plant growth and fruit quality. *Agriculture* 8:153.
- Taghizadeh-Toosi, A., Clough, T. J., Condron, L. M., Sherlock, R. R., Anderson, C. R., and Craigie, R. A. 2011. Biochar incorporation into

- pasture soil suppresses in situ nitrous oxide emissions from ruminant urine patches. *J. Environ. Qual.* 40:468-476.
- Taskin, E., Branà, M. T., Altomare, C., and Loffredo, E. 2019. Biochar and hydrochar from waste biomass promote the growth and enzyme activity of soil-resident ligninolytic fungi. *Heliyon* 5:e02051.
- Thies, J. E., Rillig, M. C., and Graber, E. R. 2015. Biochar effects on the abundance, activity and diversity of the soil biota. Pages 327-389 in: *Biochar for Environmental Management: Science and Technology*. J. Lehmann and J. Joseph, eds. Earthscan, London, U.K.
- Thies, J. E., and Rillig, M. C. 2009. Characteristics of biochar: Biological properties. Pages 85-105 in: *Biochar for Environmental Management: Science and Technology*. J. Lehmann and J. Joseph, eds. Earthscan, London, U.K.
- Verwaaijen, B., Wibberg, D., Kröber, M., Winkler, A., Zrenner, R., Bednarz, H., Niehaus, K., Grosch, R., Pühler, A., and Schlüter, A. 2017. The *Rhizoctonia solani* AG1-IB (isolate 7/3/14) transcriptome during interaction with the host plant lettuce (*Lactuca sativa* L.). *PLoS One* 12:e0177278.
- Vieira, P., Mowery, J., Shao, J., Eisenback, J. D., and Nemchinov, L. G. 2019. Cellular and transcriptional responses of resistant and susceptible cultivars of alfalfa to the root lesion nematode, *Pratylenchus penetrans*. *Front. Plant Sci.* 10:971.
- Viger, M., Hancock, R. D., Miglietta, F., and Taylor, G. 2015. More plant growth but less plant defense? First global gene expression data for plants grown in soil amended with biochar. *GCB Bioenergy* 7:658-672.
- Wang, Q., Fang, W., Yan, D., Han, D., Li, Y., Ouyang, C., Gou, M., and Cao, A. 2016. The effects of biochar amendment on dimethyl disulfide emission and efficacy against soil-borne pests. *Water Air Soil Pollut.* 227:98.
- Wang, R., Wei, S., Jia, P., Liu, T., Hou, D., Xie, R., Lin, Z., Ge, J., Qiao, Y., Chang, X., Lu, L., and Tian, S. 2019. Biochar significantly alters rhizobacterial communities and reduces Cd concentration in rice grains grown on Cd-contaminated soils. *Sci. Total Environ.* 676:627-638.
- Wang, X., Zhou, W., Liang, G., Song, D., and 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. *Sci. Total Environ.* 538:137-144.
- Waqas, M., Shahzad, R., Hamayun, M., Asaf, S., Khan, A. L., Kang, S. M., and Yun, S., Kim, K.-M., and Lee, I.-J. 2018. Biochar amendment changes jasmonic acid levels in two rice varieties and alters their resistance to herbivory. *PLoS One* 13:e0191296.
- Warnock, D. D., Lehmann, J., Kuypers, T. W., and Rillig, M. C. 2007. Mycorrhizal responses to biochar in soil—Concepts and mechanisms. *Plant Soil* 300:9-20.
- Watzinger, A., Feichtmair, S., Kitzler, B., Zehetner, F., Kloss, S., Wimmer, B., Zechmeister-Boltenstern, S., and Soja, G. 2014. Soil microbial communities responded to biochar application in temperate soils and slowly metabolized ¹³C-labelled biochar as revealed by ¹³C PLFA analyses: Results from a short-term incubation and pot experiment. *Eur. J. Soil Sci.* 65:40-51.
- Wiednera, K., and Glaser, B. 2013. Biochar–fungi interactions in soils. Pages 69-99 in: *Biochar and Soil Biota*. N. Ladygina and F. Rineau, eds. CRC Press, Boca Raton, FL.
- Wong, J. T. F., Chen, X., Deng, W., Chai, Y., Ng, C. W. W., and Wong, M. H. 2019. Effects of biochar on bacterial communities in a newly established landfill cover topsoil. *J. Environ. Manage.* 236:667-673.
- Xu, M., Gao, P., Yang, Z., Su, L., Wu, J., Yang, G., Zhang, X., Ma, J., Peng, H., and Xiao, Y. 2019. Biochar impacts on phosphorus cycling in rice ecosystem. *Chemosphere* 225:311-319.
- Yakout, S. M. 2017. Physicochemical characteristics of biochar produced from rice straw at different pyrolysis temperature for soil amendment and removal of organics. *P. Natl. A. Sci. India A.* 87:207-214.
- Yaman, S. 2004. Pyrolysis of biomass to produce fuels and chemical feedstocks. *Energy Convers. Manage.* 45:651-671.
- Yang, J. I., Ruegger, P. M., McKenry, M. V., Becker, J. O., and Borneman, J. 2012. Correlations between root-associated microorganisms and peach replant disease symptoms in a California soil. *PLoS One* 7:e46420.
- Yang, X., Lu, K., McGrouther, K., Che, L., Hu, G., Wang, Q., Liu, X., Shen, L., Huang, H., and Ye, Z. 2017. Bioavailability of Cd and Zn in soils treated with biochars derived from tobacco stalk and dead pigs. *J. Soils Sediments* 17:751-762.
- Zech, W., Haumaier, L., and Hempfling, R. 1990. Ecological aspects of soil organic matter in tropical land use. Pages 187-202 in: *Humic Substances in Soil and Crop Sciences: Selected Readings*. P. MacCarthy, C. E. Clapp, R. L. Malcolm, and P. R. Bloom, eds. American Society of Agronomy, Wisconsin.
- Zhang, A., Bian, R., Pan, G., Cui, L., Hussain, Q., Li, L., Zheng, J., Zheng, J., Zhang, X., Han, X., and Yu, X. 2012. Effects of biochar amendment on soil quality, crop yield and greenhouse gas emission in a Chinese rice paddy: A field study of 2 consecutive rice growing cycles. *Field Crops Res.* 127:153-160.
- Zhang, C., Lin, Y., Tian, X., Xu, Q., Chen, Z., and Lin, W. 2017. Tobacco bacterial wilt suppression with biochar soil addition associates to improved soil physiochemical properties and increased rhizosphere bacteria abundance. *Appl. Soil Ecol.* 112:90-96.
- Zhang, L., Xiang, Y., Jing, Y., and Zhang, R. 2019. Biochar amendment effects on the activities of soil carbon, nitrogen, and phosphorus hydrolytic enzymes: A meta-analysis. *Environ. Sci. Pollut. R.* 26:22990-23001.
- Zhang, X. K., Qi, L. I., Liang, W. J., Zhang, M., Xue-Lian, B. A. O., and Zu-Bin, X. I. E. 2013. Soil nematode response to biochar addition in a Chinese wheat field. *Pedosphere* 23:98-103.
- Zwart, D. C., and Kim, S. H. 2012. Biochar amendment increases resistance to stem lesions caused by *Phytophthora* spp. in tree seedlings. *HortScience* 47:1736-1740.